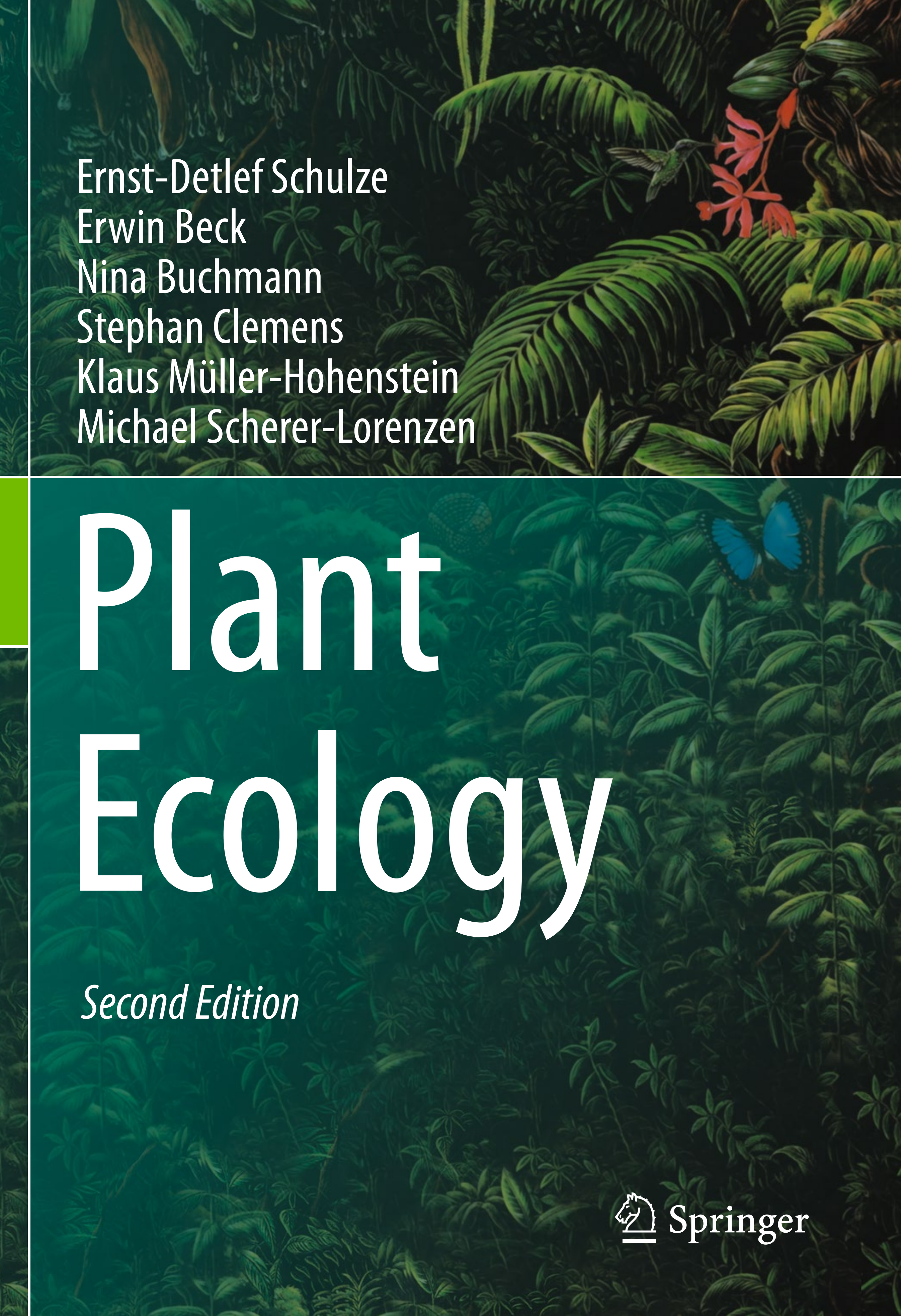

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With Contributions by Almuth Arneth,
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Ernst Detlef Schulze (born 1941) is a plant ecologist and was Full Professor of Plant Ecology at the University of Bayreuth (1975–1997). From 1997 until 2009, he served as Director of the Max-Planck Institute of Biogeochemistry in Jena. His scientific interests focused initially on the ecophysiology of plants, with an emphasis on gas exchange and water and nutrient relations, which included applied research for acid rain studies. Later on, his research addressed global biogeochemistry, for example the European carbon balance and trace gas exchange in agriculture and forestry. He established the Jena Experiment, the Biotree experiment and the Deadwood experiment. Since 2004, he has managed his own forest land, and his research interests now include the understanding of interactions between plant biodiversity and land management. He was a member of the IPCC team that received the 2007 Nobel Peace Prize. He received the German Environmental Award (*Deutsche Umweltpreis*), the Bavarian State Medal in Silver, the Max Planck Research Award (*Max-Planck Forschungspreis*), the Vernadzky Medal of the European Geosciences Union, the Ernst Haeckel Medal of the European Ecological Federation, and the Order of Merit, First Class, Federal Republic of Germany (*Bundesverdienstkreuz Erster Klasse*).

Introduction

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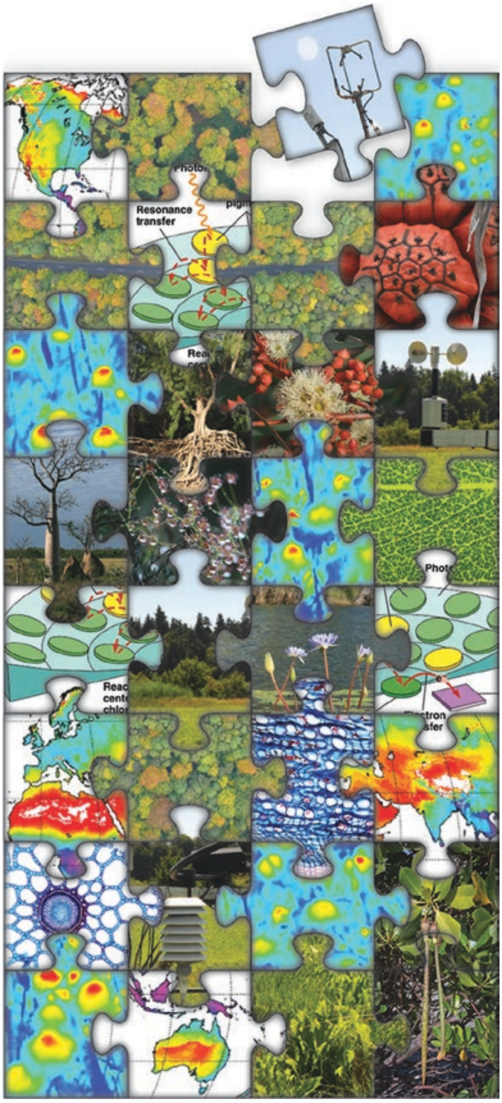

The puzzle illustrates the characteristics of modern Plant Ecology which aims to relate genetic information and molecular physiology with the biological and environmental constraints of plant life across the globe. Many parts of this puzzle are still not well known nor understood. This new edition of “Plant Ecology” aims to bridge these gaps, linking molecular stress physiology with plant performance, identifying processes which drive plant coexistence in plant communities, and assessing interactions of terrestrial ecosystems with their environment under past, current and future conditions.

E.-D. Schulze et al., *Plant Ecology*, https://doi.org/10.1007/978-3-662-56233-8_1

The term "**ecology**" was defined by Ernst Haeckel in 1866 in his book *Generelle Morphologie der Organismen* [*General Morphology of Organisms*], as follows: "Ecology is the science of relations of the organism to the surrounding environment which includes, in its broadest sense, all 'conditions for existence'. These conditions may be organic or inorganic; both are of the greatest importance for the form of organisms, because they force the organism to adjust."

Haeckel included in the science of ecology the research fields of physiology, morphology, phylogeny and chorology (the science of the distribution of organisms) to understand the "conditions for existence" and the "adjustment of organisms". Today we define the conditions for existence in a very broad sense, taking abiotic and also biotic interactions into account, even among different organism groups such as plants, animals and microorganisms. Haeckel's term "adjustment" is today differentiated into "acclimation" and "adaptation". While **acclimation** describes reversible and rather short-term adjustments of the physiology or morphology of plant individuals to the environment or biotic interactions, **adaptation** describes genetic adjustments mainly of populations over longer time scales.

Plants are sessile. Thus, they cannot physically escape predators and spreading pathogens, search for pollinators or hide from approaching extreme climatic situations. For example, forest understorey herbs rest in the deep shade of the tree canopy but are suddenly hit by an intense beam of direct sunlight as sunflecks move across the forest floor. To avoid damage to the shade-adapted light-harvesting machinery from high light intensity, leaves can change their orientation in space. Chloroplasts can move to the edges of a cell, and the antennae of light-harvesting complex II can be redistributed between photosystems II and I. Obviously, plants, as sessile organisms, must continuously cope with changing environmental conditions—from minute-by-minute to daily, seasonal and decadal fluctuations in temperature and light; changes in nutrient and water availability; and herbivore pressure, pathogen load and loss of mutualistic partners. Plants have therefore evolved a variety of mechanisms that enables them to tolerate and withstand environmental change, and to re-achieve internal homeostasis: plants are highly plastic and resilient to cope with a highly dynamic environment. Moreover, plants shape their own environment when growing together in a plant community, creating a three-dimensional canopy that affects microclimatic variables impacting on plant traits and plant performance. This microclimate, together with litter chemistry and litter production, controls water and biogeochemical fluxes on the ecosystem scale, adding to landscape heterogeneity and connectivity.

All of these aspects are addressed in this revision of the book *Plant Ecology*, expanding the very original views of ecology put forward by Haeckel (1866), Tansley (1935) and many others since then. Starting with molecular stress physiology and then focusing on physiological and biophysical plant ecology and ecosystem ecology, we place plant communities and terrestrial ecosystems in a global context. Thus, this book integrates different perspectives on plant ecology and presents these perspectives in five major parts, each divided into several chapters. In Part I, we start with **Molecular Stress Physiology**, which builds the basis for plant existence in a varying environment. We continue in Part II with the **Physiological and Biophysical Plant Ecology**. In Part III we focus on **Ecosystem Ecology**, in Part IV on **Community Ecology** and in Part V on **Global Ecology**. Many links across these five parts facilitate reading and, hopefully, the understanding of plant ecological concepts and mechanisms on different organisational scales.

The molecular mechanisms of stress responses as the basis for "adjustments" are outlined in Chap. 2. On the basis of this molecular foundation, the responses to the main environmental stresses are discussed. The model plant is often *Arabidopsis thaliana*, for which the total genome is known—an excellent prerequisite for linking genetic information to ecology. Thus, **Part I** of this book focuses on the effects of light (Chap. 3), temperature (Chap. 4), oxygen (Chap. 5), water (Chap. 6) and salt and soil factors (Chap. 7). The molecular level of biological interactions (Chap. 8) is explained in terms of signalling and stress responses.

At the level of the plant organism, we consider the responses of plant individuals to their environment, including **plant structure**, **ecophysiological change** in gas exchange and nutrient relations to the **life cycles** of various plant life forms (phenology, lifespan and strategies for reproduction and distribution). Although the active life of plants is typically limited to favourable conditions, there are mechanisms in long-lived plants that enable survival in unfavourable periods such as drought, heatwaves or frost. The scope for "adjustments" of plant organisms is very broad, like the responses of cells to stress. Plant responses range from changes in leaf structure to the differentiation of roots, and they include acclimation of biophysical processes during the exchange of substances with the environment. Thus, in **Part II** of this book the focus is on the use of resources by plant organisms. This includes their thermal balance (Chap. 9), water relations (Chap. 10), nutrient relations (Chap. 11) and carbon relations (Chap. 12).

Plants live in a neighbourhood with others and have to share resources with each other. Thus, water, nutrient and carbon relations are embedded in an **ecosystem**, where plants, animals and soil organisms interact with each other and their environment. This leads to questions as to whether ecosystems are more than the sum of their individual components and what **emergent properties** develop at this scale of organisation. Many characteristics of vegetation result in ecosystem-level matter fluxes, which control the performance of individual plants in this system. For example, the spatial structure of an ecosystem determines its coupling to the atmosphere, which may determine the survival of plant individuals or a species in this ecosystem. **Part III** of this book therefore introduces ecosystem characteristics and relevant concepts on the ecosystem scale (Chap. 13), and explains approaches to the study of terrestrial ecosystems (Chap. 14). One powerful approach to analysis of processes in complex systems is modelling (Chap. 15). Furthermore, we provide detailed insights into biogeochemical fluxes in terrestrial ecosystems (Chap. 16), since these processes are both drivers of, but also driven by global change.

Ecosystem processes and the spatial and temporal patterns of plant life are the basis for community ecology. **Competition** results from the limited amounts of resources that all plants rely on, growing adjacent to each other in limited space. If resources become scarce, efficiency means better use of limited resources at the cost of a neighbour. Of course, this does not always imply saving resources or using them most economically. Indeed, it may be more advantageous to use more resources than required, to pre-empt resources that will thus not be anymore available to competing neighbours. In community ecology, we learn that systems are very dynamic in the long-term and not all processes in a system change linearly in one direction. **Community ecology** does not consider the fate of a single individual plant or organ; it considers the dynamic spatial and temporal behaviour of populations, including growth and mortality. Generally, natural vegetation includes a **diversity** of species, which determine—in varying proportions—the composition of the vegetation cover of the Earth. Species differ in their characteristics, life strategies and traits, which may result in complementary use of available resources. Thus, the broad spectrum of responses at the cellular and plant levels is replaced by the enormous diversity of species (350,000 species of vascular plants), which respond to environmental conditions. Therefore, in **Part IV** of this book, the temporal dimensions (Chap. 17), spatial dimensions (Chap. 18) and biological interactions of plants (Chap. 19) are discussed. The numerous factors that determine biodiversity and the effects that biodiversity have on the functioning of ecosystems are summarised in Chap. 20.

Understanding of plant ecology at all levels, from cells to plants to communities and ecosystems, is the fundamental prerequisite for addressing pressing global problems related to plants and ecosystems. With respect to food security, one of the most relevant aspects is **global change**, which is also discussed by the wider public. Knowing answers to the question of how the biosphere reacts to direct and indirect anthropogenic impacts triggered by land use, changes in land use and changes in climate caused by the use of fossil energy will help us to develop strategies to sustainably manage the Earth's terrestrial ecosystems. Thus, plant ecology—including aspects of **agriculture and silviculture**—plays an important and even vital role in providing scientific information for decision makers in policy and society to address questions concerning ecosystem health and human well-being. Therefore **in Part V**, global biogeochemical cycles and **ecosystem services** are introduced (Chap. 21). The complex interactions between global ecosystems and their global environment are presented using dynamic global vegetation models in Chap. 22. The future challenges for terrestrial ecosystems at times of global change and potential solutions in terms of international agreements are discussed in Chap. 23.

Combining the ecology of ecosystems with the field of plant and community ecology enables us to understand the distribution of species. Both the potential and the actual **distribution areas** (Fig. 1.1) are determined by numerous factors. Potentially, a plant species could grow in a much larger area than the region in which it actually reproduces. However, this region is limited by different types of competition with other species, so the area that is eventually occupied is restricted. Agricultural management of arable crops (such as maize, rice, wheat, soybean and potato) is an interesting example for species that evolved in a geographically limited area (the so-called genetic centres of origin) but are now distributed worldwide after breeding (domestication) and agricultural dispersal by humans. Often these external effects are seen as "filters" that determine who and what survives. However, the filter analogy is not fully correct, because the species—as the filtered substances—change the mesh size of the filter through selection, genetic drift and adaptation.

When we are dealing with processes and responses on different scales, ranging from the cell to the Earth's surface, it becomes apparent that over time, scientific disciplines working on these different scales have developed their own sets of definitions and terminology. When we move from the cell to the global biosphere, the

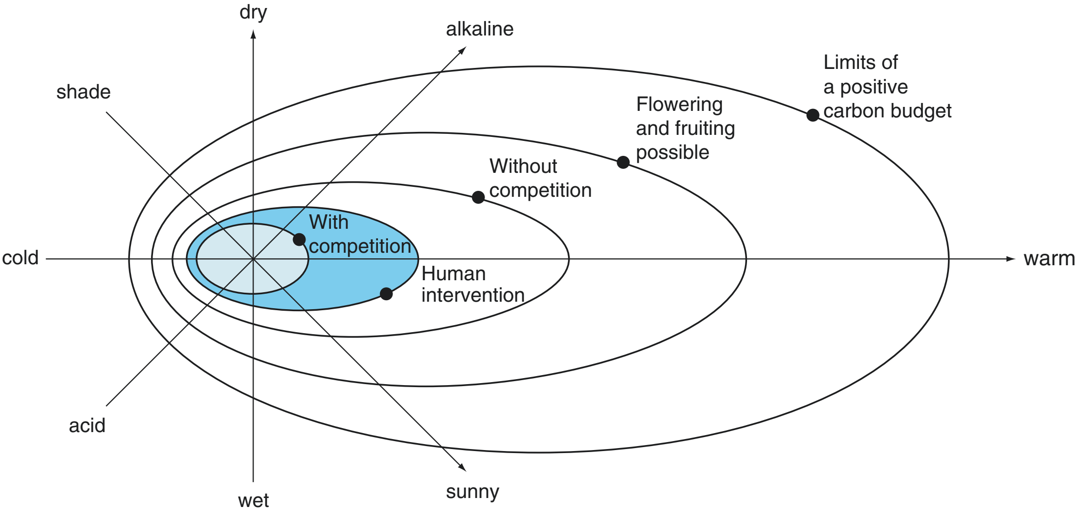

Fig. 1.1 The distribution of a plant species depends on different environmental factors. The actual distribution range (shown in *blue*) is significantly smaller than the potential area of distribution that is reached without competition—for example, at the extreme limits of flowering or at the boundaries of a positive carbon budget. Human interventions, particularly in agriculture, interact with these natural filters and can expand the spatial distribution of a species tremendously. In the example shown, temperature is the dominant factor. The limits of distribution change according to the species. The historical dimension of distribution is encapsulated in the present geographical range

precision of interpretation decreases because the system's complexity increases. With each new scale, the initial processes continue but new interactions are added. This requires simplification of increasing complexity to the level of a few driving variables that we, as human beings, are able to understand. In parallel, a change in terminology happens; thus, the use of words also changes with scale. For example, the level of detail that is known and called a "control factor" or "regulatory factor" at the genetic level is not comparable to a control factor driving processes at the ecosystem level. This is a fact we have to accept and keep in mind when reading this book, which aims to link and span all of these scales of plant ecology.

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References

Haeckel E (1866) Generelle Morphologie der Organismen. Berlin. Vol. 2

Tansley AG (1935) The use and abuse of vegetational concepts and terms. Ecology 42:237–245

Part I

Molecular Stress Physiology

Giant sequoia trees grow in Sequoia National Park in California. Individuals of ***Sequoiadendron giganteum*** are the largest living organisms on Earth, at least by volume. Tree height can exceed 85 m, and trunk diameters of more than 8 m are documented. Giant sequoias are also among the oldest organisms. Some trees have been able to withstand all biotic and abiotic stresses for more than 3000 years, demonstrating an amazing degree of resilience. Surely they survived many extreme weather events such as strong frost, heat, drought, or storms, causing loss of branches and defoliation. Still, ***Sequoiadendron giganteum*** occurs only in scattered groves with humid climate and dry summers along the western Sierra Nevada at elevations between around 1500 and 2000 m. At this altitude winter temperatures are not too low and enough soil moisture remains available during the summer drought. Reproduction of sequoia trees is dependent on fire. Seed germination is stimulated by fire, and seedling development can only proceed in the absence of competing vegetation. Mature trees are protected from fire by a thick bark (note the fire scars on the left and right) and elevated canopy. (Photo: Stephan Clemens)

General Themes of Molecular Stress Physiology

2

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Environmental factors restrict the habitats that can be colonised by any given plant species. This is shown very clearly by the limitations in the distribution of particular types of vegetation—for example, the treelines on mountains. Extremely high light intensities, mechanical stress from wind, frequent periods of frost and a winter period of many months have left their mark on these spruces and pines at an altitude of about 3000 m on Mt. Hood (OR, USA). (Photo: E. Beck)

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The environment affects an organism in multiple ways and at any time. In order to understand the influence of the environment in a given situation, individual external conditions—so-called **environmental factors**—are usually considered. Environmental factors can be of abiotic or biotic nature. Abiotic environmental factors include temperature, humidity, light intensity, and the supply of water, minerals and CO_2. Together these resources determine the growth of a plant. Other abiotic factors are mechanical forces such as wind or the presence of toxins without physiological function. Biotic environmental factors encompass the interactions of a plant with other organisms: competitors, pathogens and herbivores, as well as symbionts, pollinators and seed dispersers.

Plants are sessile organisms and therefore are continuously exposed to ever-changing environmental conditions. Arguably the amplitude of fluctuations is much wider for plants than for animals or humans because plants cannot move to sites with more beneficial conditions. A desert plant has to cope with water scarcity on the spot. There is no way for it to migrate to a watering hole elsewhere.

Interest in the interaction of plants with their environment is motivated by fundamental biological questions and by the need to increase agricultural productivity. Environmental factors, most prominently temperature and precipitation, determine the distribution of species to a large extent. At the same time they limit the growth of crop plants and therefore yields (Boyer 1982).

2.1 Definitions and Concepts

Molecular stress physiology aims to understand the mechanisms enabling a plant to cope with fluctuating environmental conditions at the level of genes, proteins and metabolites. When looking at a vast body of literature, however, there is no generally accepted consensus as to the meaning and appropriate usage of widely distributed terms such as **adaptation** or **tolerance**. Also, different perspectives can be adopted to describe and analyse the wide spectrum of phenomena in plant biology that are associated with stress and the responses to it. Thus, it is important to first outline the concepts and distinctions that can be used to structure the rapidly expanding knowledge about plant molecular stress physiology.

2.1.1 Stress

Plants practically never have the optimal quantities or intensities of all essential abiotic factors available (Fig. 2.1). Thus, the physiological optimum is rather the exception. Suboptimal or even damaging quantities or intensities of an environmental factor—for example, low light, scarcity of minerals or sub-zero temperatures—represent deviations from the physiological optimum. For such situations we use the term **stress**, a concept that is naturally and frequently used in our everyday life. Accordingly, environmental factors deviating from the optimal intensity or quantity for the plant are called **stress factors**. Stress factors that could potentially influence a

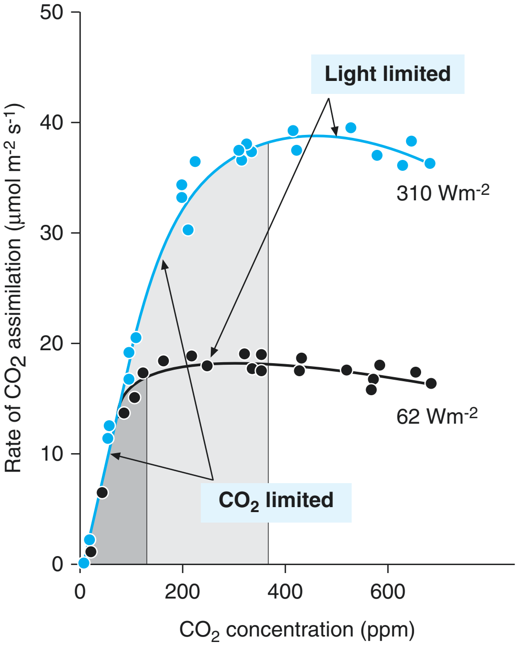


Fig. 2.1 Limitation of photosynthesis by CO_2 and light. The rate of photosynthesis in a *Sorghum sudanense* leaf is shown at different light intensities and CO_2 concentrations in air. (After Fitter and Hay (1987))

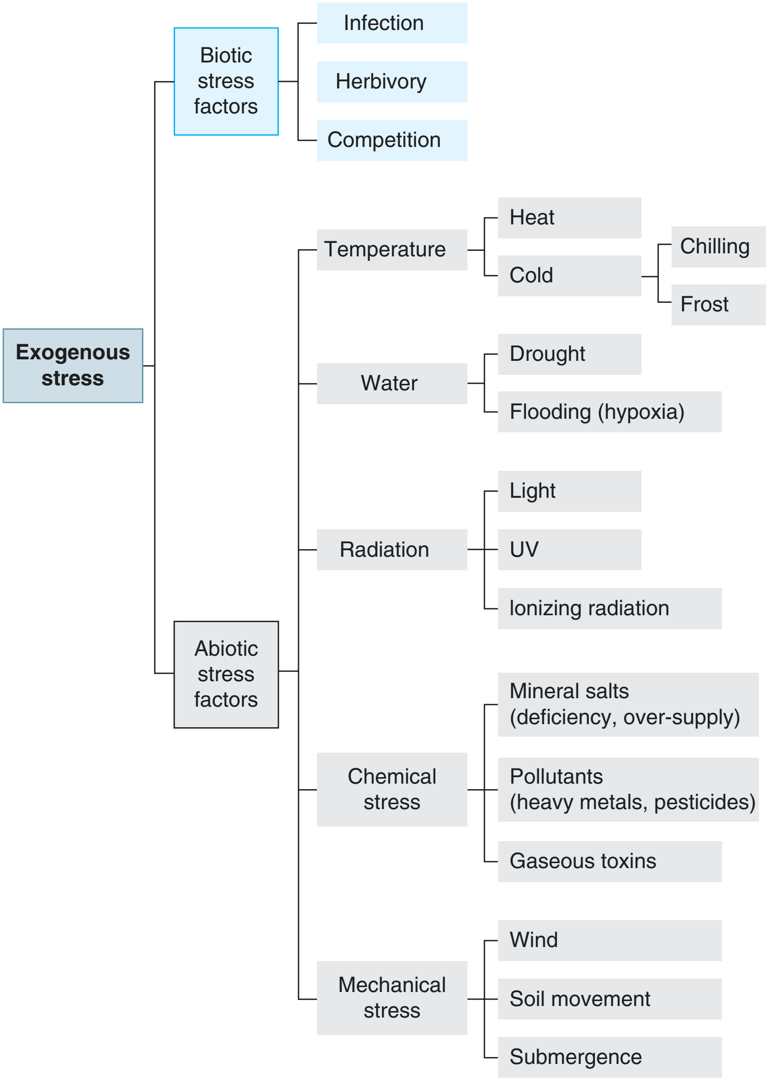


Fig. 2.2 Biotic and abiotic environmental factors creating stress for plants

plant are listed in Fig. 2.2. For many of them the situation away from the physiological optimum is immediately clear: light (weak light, strong light), temperature (cold, frost, heat), water (drought, flooding), nutrients (lack of mineral ions, over-fertilisation, the presence of salt and other toxic minerals), and carbon dioxide and oxygen (CO_2 limitation of photosynthesis, respiration/photorespiration, oxidative stress, anaerobiosis). The optimal quantity can in fact be zero—for example, when considering potentially toxic molecules without a physiological function, such as non-essential metals (e.g. cadmium) or xenobiotics.

Furthermore, it is important to note that optimal intensities and concentrations of environmental factors may differ for individual organisms and for particular organs of the same organism. Plant species naturally occurring in shaded environments such as the understorey of a forest have an optimum at lower light intensities than plants occurring in open habitats (e.g. savannas). Optimal growth temperatures can vary between plant species, as exemplified in Fig. 2.3.

An individual exposed to a stress will develop a **strain**. Jacob Levitt published a theoretical understanding of stress reactions that is applicable to all groups of organisms (Levitt

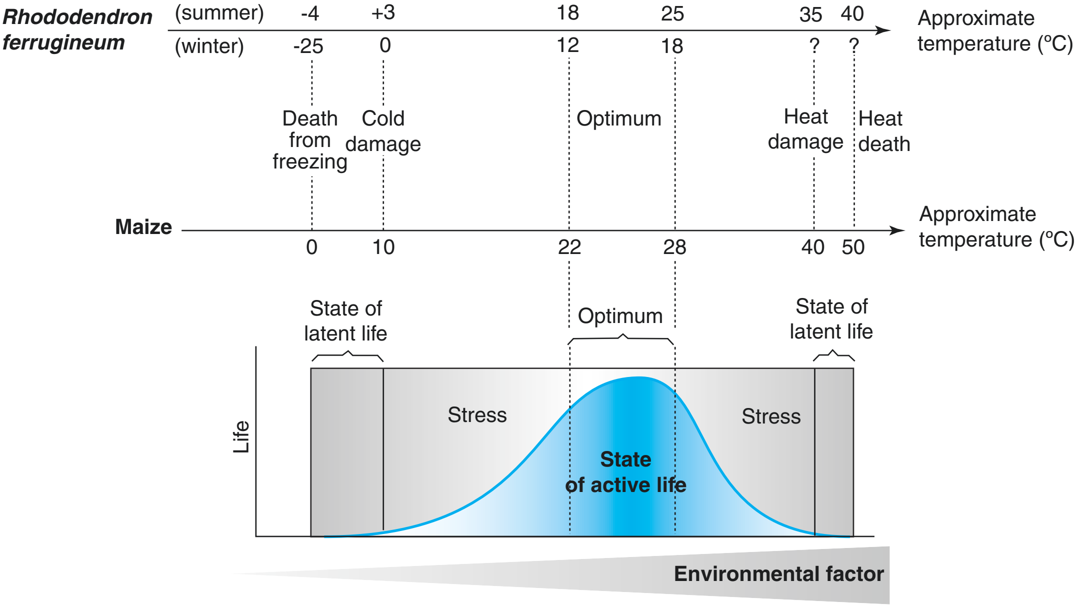


Fig. 2.3 Life processes of an organism described as a function of an (abiotic) environmental factor. The different temperature ranges of two plant species—*Rhododendron ferrugineum* and maize—serve as an example (Fig. 4.1)

1980). It is known as the **physical stress concept** and can be illustrated by an analogy derived from civil engineering. A body such as a steel beam resting on two pillars is deformed (stressed) when a heavy load is placed on it. The weight of the load and its position on the beam determine the magnitude of the strain. The deformation (stress) caused by the load can be measured and provides a quantification of the strain. Depending on the severity of the strain, the deformation can be reversible ("elastic") or irreversible ("plastic"). An elastically deformed beam will return to its initial shape upon removal of the weight, while a plastically deformed beam will remain bent. When the severity of the strain exceeds the tolerance of the beam, the beam will break. Figure 2.4 illustrates this correspondingly with a spring holding a weight.

In the context of physiology, one has to determine the molecular nature of the strain that is caused by a certain stress—for example, the stress "hypoxic conditions" (i.e. inadequate O_2 supply; Chap. 5) restricts respiration. As a consequence, strains develop: the energy load of a cell drops because glycolysis yields much less adenosine triphosphate (ATP) per mole of glucose than respiration (2 moles of ATP as compared with 36 moles of ATP). Furthermore, the fermentation that is essential in order to keep glycolysis running can damage a cell as the accumulation of the fermentation product lactate lowers the cytosolic pH.

The physical stress concept is instructive, but the analogy to infinitely more complex biological systems is of course limited. First, in a physical system, the amount of stress equals the strength of stress. In a biological system, the amount of stress is the product of the intensity of stress and the duration of stress. For example, if one cools the tropical ornamental *Saintpaulia ionantha* (African violet) to 5 °C for a short time (6 h) and then returns it to the original temperature, some of the metabolic reactions will be changed in their rates according to the Q_{10} temperature coefficient, which describes the effect of temperature on rates of biochemical reactions. However, the increase or decrease in metabolite pools is not altered to such an extent that the plant is damaged. In contrast, when the plant is left at 5 °C

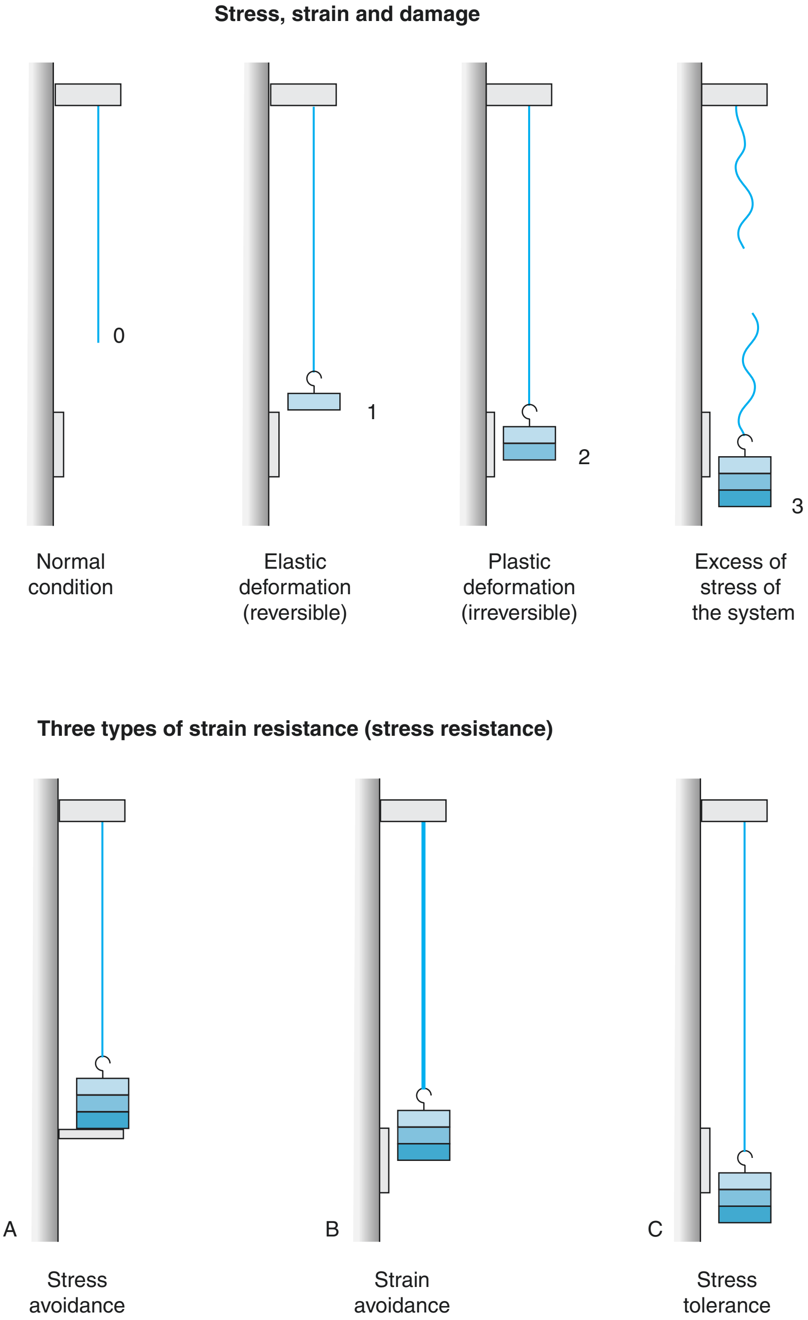


Fig. 2.4 The physical stress concept according to Levitt (1980)

Stress, strain and damage

Three types of strain resistance (stress resistance)

for a longer period (48 h), metabolic chaos arises. Individual metabolite pools empty, while others grow disproportionally. The plant is damaged; in other words, an elastic strain is transformed into a plastic strain (Fig. 2.5).

Second, a biological system responds. Changes occur that reduce the strain exerted by a stress. Such changes represent a large part of stress physiology and are a major topic of this and subsequent chapters.

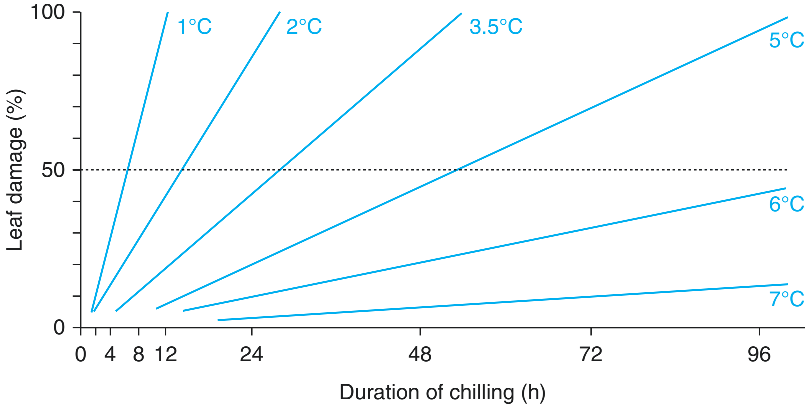


Fig. 2.5 Chilling damage to the African violet (*Saintpaulia ionantha*). Below the threshold temperature of +8 °C, leaves suffer chilling damage, recognisable by the incidence of necroses. The strength of the stress can be estimated as the product of cold stress (above the freezing point) multiplied by the duration of exposure; it is proportional to the extent of the damage. (After Larcher and Bodner (1980); Chap. 4, Sect. 4.1.3)

Third, owing to the existence of repair mechanisms, plastic change or deformation is not completely irreversible. In most cases, the organism is able to repair the damage. One example is DNA repair after damage by ultraviolet (UV) irradiation. Plastic strain can thus be transformed into elastic strain. Furthermore, because of the open life form of plants, "repairs" can also be accomplished by replacement of damaged organs following premature senescence and shedding.

Finally, in biological systems, stress is commonly due not to a single physical force affecting the organism but to a load arising from many individual environmental factors. Plants in a natural habitat are often simultaneously exposed to a multitude of stresses. Water scarcity, for example, is frequently accompanied by heat. While this is immediately clear, physiological research has nonetheless, and for good reasons, followed the **reductionist approach**. Single parameters are varied in controlled experiments. This has been extremely successful in revealing mechanisms that plants use to cope with stressful environments. Enabled by new experimental techniques that allow the parallel monitoring of thousands of molecules in an organism, research is only just beginning to systematically address the overlaps between responses and the question as to how plants integrate multiple environmental signals into adequate modulation of growth and physiology (Suzuki et al. 2014). Accordingly, and for the sake of clarity, the molecular stress physiology part is still structured in a way that considers stress factors separately.

2.1.2 Quantification of Stress

Stress, as such, is difficult to measure, because it manifests itself only in the interaction between environmental factors and organisms. What usually is observed and quantified is the strain, i.e., the effects a particular stress or stress combination has on an organism. The most general indicators of stress are reductions in growth, survival or reproductive success relative to genetically identical or similar plants growing under control conditions free of the stress factor in question. When stress is applied up to a severe level, tolerance can be quantified as the **LD_{50}**—the dosage at which 50% of the treated plants or cells survive, or the dosage that is lethal for 50% of the plants or cells. The LD_{50} can be derived from **dose–response curves** that measure survival or growth parameters over a range of values for a given environmental factor—for example, the exposure to different degrees of cold and frost (Fig. 2.5).

It remains a widely used strategy to quantify biomass, seed production, leaf area or root length to determine the stress a plant is or has been exposed to. In the simplest form of a stress physiology experiment, a growth parameter is measured at the end of the cultivation and the difference relative to control conditions is determined for each exposure level. Imaging techniques allow continuous monitoring of growth—for example, by measuring the leaf area of a rosette plant at regular intervals and thereby determining growth rates. Alternatively, dose–response curves can be derived through a variety of invasive methods used to quantify the damage developing upon stress exposure. The examples depicted in Box 2.1 include the scoring of necrosis, vitality stains, plasmolysis and electrolyte leakage.

Stress can also be visualised by non-invasive techniques not requiring the harvest of material or the exposure of detached organs. A prominent approach is the determination of **chlorophyll fluorescence** (Box 2.1; Chap. 3). This applies especially to types of stress for which the photosynthetic apparatus is the first point of damage, such as heat, cold and UV stress. Chlorophyll fluorescence increases when excitation energy is less efficiently funnelled into photosynthesis. Another widely used technique is thermal imaging. Transpiration through stomata has a cooling effect on leaves. Thus, recording of leaf temperature with infrared thermography provides an indirect measure of stomatal responses—for example, to drought stress (Chap. 6, Fig. 6.19).

A completely different strategy for strain detection is the molecular analysis of stress-induced changes in either gene expression or the abundance of stress response–related proteins and metabolites. Such analyses are invasive, as they require extraction of biological material. An early example of detectable changes at the protein level is the massive up-regulation of **heat shock protein** synthesis when cells are exposed to elevated temperatures threatening to cause protein denaturation (Chap. 4). Because of the prevalence of **oxidative stress** whenever organisms encounter unfavourable conditions (Sect. 2.2.3), increases in the concentrations of reactive oxygen species (ROS) or oxidised metabolites (e.g. the products of lipid peroxidation) are frequently determined as indicators of strain. Especially for model species such as *Arabidopsis thaliana* and rice, thousands of transcriptome data sets are available for myriad abiotic and biotic stress conditions. Initially they were obtained with microarrays (DNA arrays) representing thousands of genes of the organism under study. Today, most studies employ the so-called **RNA-seq** approach, that is, the use of next-generation sequencing to detect and quantify all RNA molecules present in a biological sample at a given time. In contrast to microarrays, this technique can in principle be applied to any organism and even to field samples, thereby providing opportunities for **molecular ecophysiology** studies with unprecedented resolution. The thousands of data sets available for the model species can be queried with bioinformatic tools to identify gene expression changes associated with a distinct physiological situation, thus providing specific and highly sensitive **stress markers** indicative of a particular stress and the strains it causes.

Transgenic approaches enable sensitive in vivo monitoring of strain through the expression of a rapidly increasing number of sophisticated molecular sensors. Two principal approaches can be distinguished. One commonly applied approach is the expression of DNA constructs combining the promoter region of a stress-responsive gene with the sequence encoding a **reporter protein** whose activity can easily be visualised. The prominent reporter protein firefly luciferase makes a stress response visible through the emission of light, provided the gene is expressed under control of the right promoter. Many components of signal transduction processes activated under stress have been identified with luciferase reporter plants. The second approach exploits fluorescent proteins that have been engineered to directly indicate a change within a cell. For example, many derivatives of the **green fluorescent protein** are available, whose properties change depending on the redox state or the pH.

Box 2.1: Methods to Quantify Stress

1. **Counting of necrotic areas after stress application**: Plant tissue (e.g. pieces of a leaf) are exposed to a defined stress and then placed for 2 days on moist filter paper. Damage is shown by the formation of necroses (brown, often soggy areas) (Fig. 2.6).

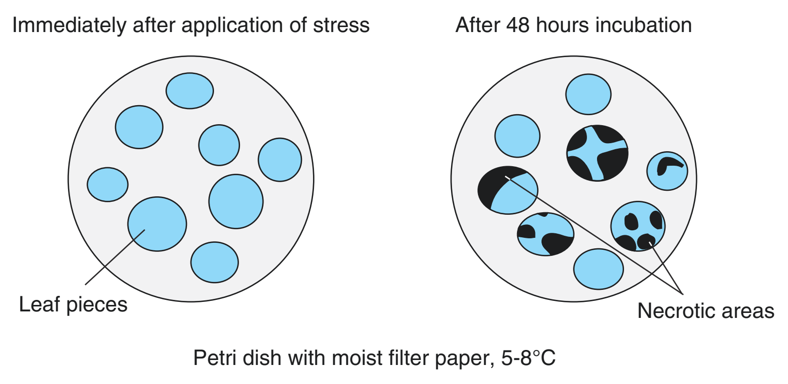


Fig. 2.6 Simple leaf disc assay

2. **Use of indicator dyes to stain living cells**: An example is neutral red, which only living cells can accumulate in the vacuole; this is generally accompanied by a change in the colour of the indicator because the vacuolar pH is slightly acidic (Fig. 2.7).

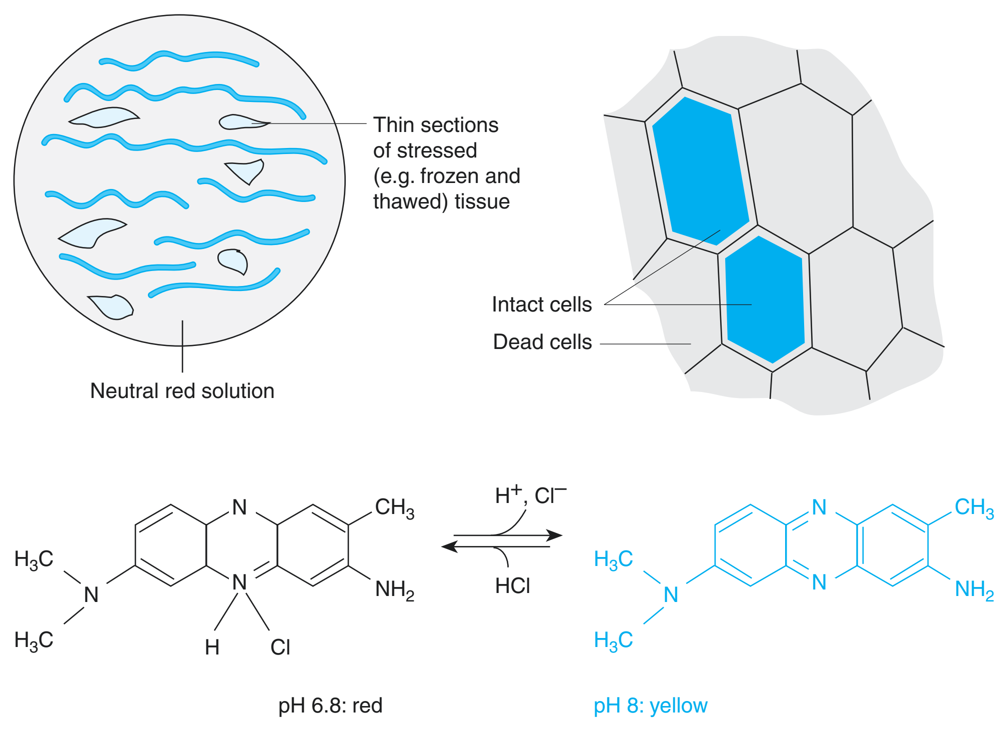


Fig. 2.7 Quantification of living cells with a vital pH indicator dye (neutral red)

3. **Plasmolysis of undamaged cells**: Only intact cells can undergo plasmolysis. This reaction is assayed after stressing of the tissue (Fig. 2.8).

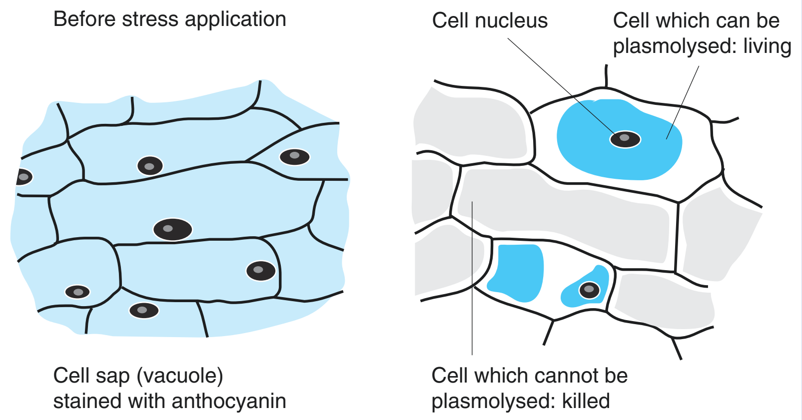


Fig. 2.8 Quantification of living cells by plasmolysis

4. **Measurement of electrical conductivity to determine the loss of ions from damaged cells**: Damage to plant tissues is indicated by a loss of selective permeability of the cell membranes. As a consequence, solutes leak from the cells. When pieces of tissue (e.g. leaf discs) are floated on distilled water, low molecular weight compounds diffuse into the medium. They include many ions, so the conductivity of the water increases. This can be measured conductometrically. Conductivity is expressed in µSiemens (Fig. 2.9; Chap. 4, Fig. 4.12).

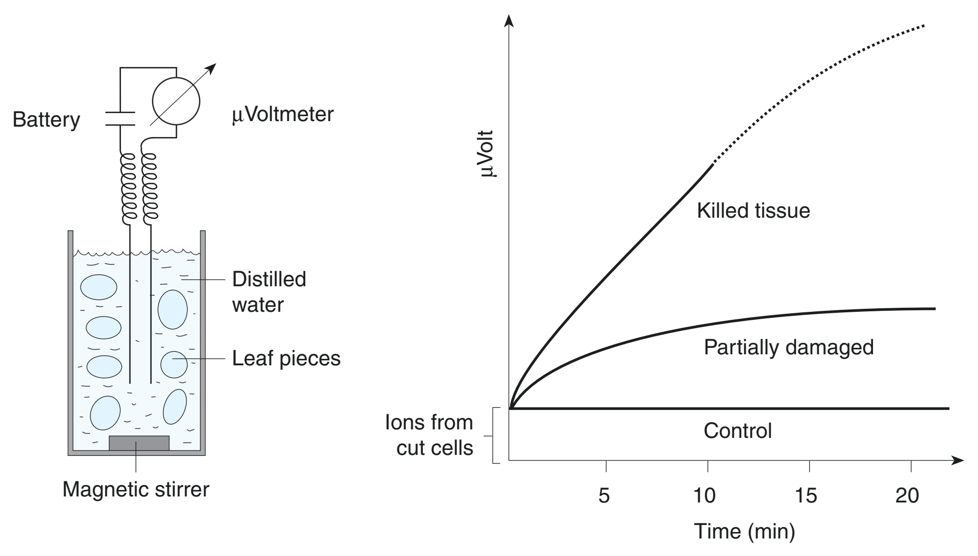


Fig. 2.9 The electrical conductivity test: left: The arrangement; right: A record

5. **Measurement of chlorophyll fluorescence in photosynthesis**: Photosynthetic electron transport may be measured by means of the chlorophyll fluorescence from photosystem II (red colour). With modern imaging systems, the impact of stress on photosynthesis can immediately be visualised as fluorescence quenching. In the example shown, a foxglove (*Digitalis*) plant was treated by applying the herbicide diuron [3-(3,4-dichlorophenyl)-1,1-dimethylurea; DCMU] to the roots. The increase in fluorescence quenching could be seen within 3.5 days (after Lichtenthaler and Miehe (1997)) (Fig. 2.10).

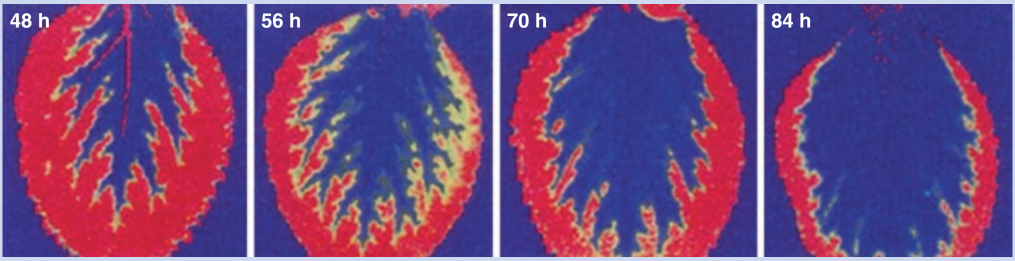


Fig. 2.10 The non-invasive chlorophyll a fluorescence assay

6. **Changes in transcript abundance**: For the model species *Arabidopsis thaliana* and a growing number of crops and other plant species, data are available on the abundance of thousands of transcripts under hundreds of different physiological conditions in particular organs, tissues and even cell types. They allow identification of stress marker genes and definition of patterns of gene activity that are characteristic of a given stress. Fig. 2.11 shows a simple example of changes in transcript abundance for a few stress-responsive genes upon exposure of *A. thaliana* seedlings to different types of stress. *NAC032* and *AKR4C9* are oxidative stress markers; *CYP707A3* and *NCED3* are abscisic acid (ABA) markers; *LEA5*, *RD29B* and *DREB2A* are dehydration markers; and *ERF5*, *WRKY33* and *MYB51* are mild osmotic stress markers. The colours indicate changes relative to non-stressed plants (red indicates up-regulation, green indicates down-regulation). Significant changes are indicated by asterisks. It becomes apparent, for example, that ABA is involved in the response to osmotic and salt stress, but not to H_2O_2, and the mild osmotic stress marker genes are not activated by salt treatment (Claeys et al. 2014).

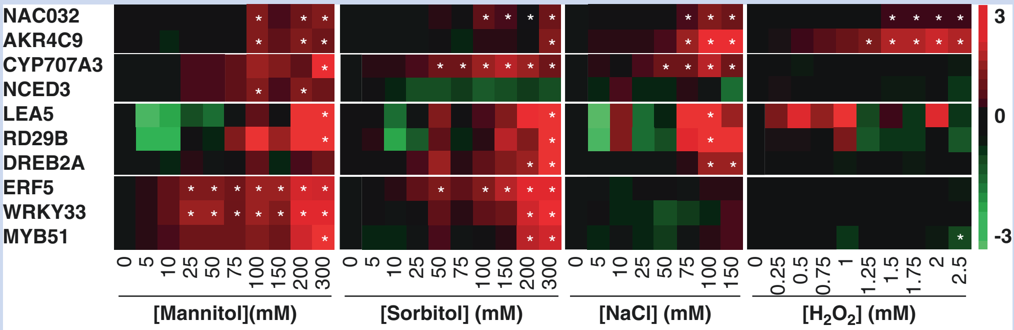


Fig. 2.11 Principle of transcript analysis for visualizing stress effects

2.1.3 Escape–Resistance–Avoidance–Tolerance

Why does a species live in one particular habitat but not in another? To be able to answer this fundamental question of biology, one has to address another question: Which traits and mechanisms enable individuals of this species to survive and reproduce in a particular environment? Several types of strategies can be differentiated. When we analyse the possible fates of a given plant in a particular environment characterised by a certain stress factor—for example, the frequent occurrence of hypoxic conditions due to flooding or the occurrence of sub-zero temperatures at some point during the year—the first distinction is that between a plant able to successfully reproduce in such an environment and a plant unable to successfully reproduce. Among the former group, some plants may be able to evade conditions of frost by restricting growth and reproduction to periods not prone to sub-zero temperatures. This is referred to as the **escape strategy** (Fig. 2.12). It depends on the ability to anticipate seasons with unfavourable conditions (Sect. 2.4.2) and on the competence to form organs that can await the disappearance of the stress factor in question. Many plant species, for example, withstand harsh winter temperatures by retreating into a state of **dormancy**. Annual plants overwinter as seeds, which are much more resilient than vegetative organs, and become active again when the next generation germinates in spring.

The alternative to escape is **resistance**, a term that is often used interchangeably with the term **tolerance**. In the molecular physiology chapters of this book and in other textbooks (Lambers et al. 2008), but not consistently throughout the scientific literature, resistance refers to the general ability of a plant to maintain reasonable growth in the presence of a particular stress factor and the associated strain. This definition is adopted, for example, in the case of aluminium-resistant plants (Kochian et al. 2015). Such plants can colonise acidic soils with a pH below 5, a condition that makes the toxic element aluminium available for plant uptake as Al^{3+} ions (Chap. 7). It does not mean, however, that the resistant organism is unaffected by the stress. With respect to costs, the resistance to an abiotic stress is quantitatively different from resistance to a pathogen. In host–pathogen interactions, resistance often arises from the host's ability to limit colonisation by a pathogen, meaning that a strain practically does not develop (Chap. 8).

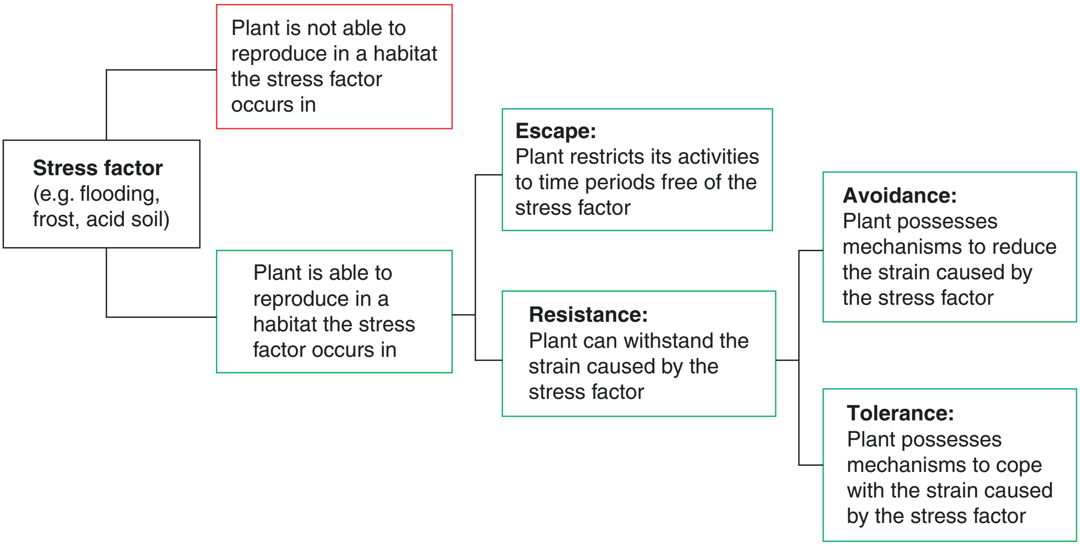


Fig. 2.12 Principal strategies to survive and reproduce in a habitat characterised by the (temporary) presence of a stress factor

Tolerance is the term most commonly used to describe a plant's ability to survive a given stress. It represents one of two principal ways to achieve resistance. Owing to constitutive and inducible mechanisms, a tolerant plant manages to limit the damage caused by a stress. Many flooding-tolerant plants can modulate their metabolism in such a way that they can endure the lack of oxygen for longer periods than flooding-sensitive species. They go into a state of **quiescence**, that is, they reduce their energy needs and increase their fermentative capacity (Chap. 5). Al^{3+} tolerance is conferred by transporter proteins that mediate sequestration of Al^{3+} in root cell vacuoles (Chap. 7). In the context of the physical stress concept, tolerance would arise from use of superior material for the beam or a stronger spring (Fig. 2.4).

The other type of strategy is **avoidance**. A plant is able to restrict the strain caused by a stress factor. Competence to live in flooded areas is conferred by morphological adaptations such as aerenchyma or the pneumatophores of mangroves, root-like organs that protrude from the flooded soil and supply oxygen to the tissues below-ground. The intracellular formation of ice crystals, as the most devastating consequence of temperatures below 0 °C, can be avoided through lowering of the freezing point (Chap. 4). The uptake of toxic Al^{3+} ions can be limited by the secretion of organic acids that form extracellular complexes with Al^{3+}. Avoidance of a strain in the civil engineering analogy (Levitt) would be provided by a structure supporting the beam or the spring (Fig. 2.4).

Most stress physiology research has addressed mechanisms of tolerance and avoidance—the biochemical and morphological traits of plants exposed to a stress. However, the understanding of plant species' distribution and vegetation structure will remain incomplete without the analysis of escape strategies that allow plants to thrive in habitats characterised by the presence of particular stress conditions. Thanks in large part to the research on *A. thaliana* (Chap. 2, Sect. 2.2.5), tremendous molecular knowledge has been obtained in the past two decades on how plants anticipate changes in environmental conditions and find the right time window for key developmental processes such as **germination** and the switch to **reproduction**. This is discussed further in Sect. 2.4 as an integral part of molecular stress physiology.

2.1.4 Stress Responses–Acclimation–Adaptation

Figure 2.13 illustrates typical differences in the survival rate upon exposure to a particular stress (e.g. frost) between plant species and between different genotypes (accessions, ecotypes, cultivars, varieties) within one species. The figure shows the survival rates with and without prior **acclimation**, that is, a few days in the presence

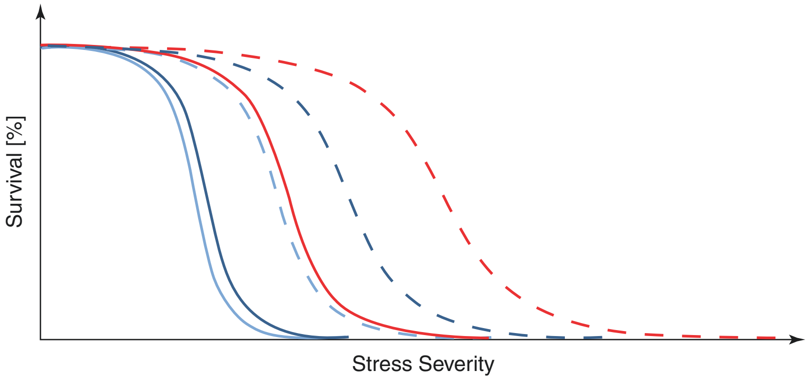


Fig. 2.13 Schematic comparison of survival rates between different species and between ecotypes. *Solid lines* indicate survival without acclimation, *dashed lines* indicate survival with acclimation, *blue lines* indicate genotypes of one species differing in acclimation potential and *red lines* indicate related species with greater tolerance

of milder stress before exposure to severe stress. It becomes clear that when studying molecular stress physiology, one has to address several questions:

1. What are the mechanisms underlying the differences in constitutive stress tolerance between species and between genotypes?
2. What happens during acclimation? Which metabolic, physiological or developmental changes explain the greater tolerance in the acclimated state?
3. What is the mechanistic basis of differences in acclimative capacity between species and between genotypes?
4. What were the evolutionary events that brought about these differences?

When one is addressing these questions, it is important to be aware of the different time scales (Lambers et al. 2008). The **stress responses** of an individual entail the immediate negative effects of a stress on growth or other plant processes.

The term **acclimation** is used to describe the adjustments of an individual plant to limit the negative consequences of a stress. Acclimation is triggered by changes in environmental factors and can be either physiological or morphological. The time scale is usually minutes to weeks. Physiological acclimation occurs through biochemical changes in the activity or abundance of proteins, and is usually reversible. Staying with the example of hypoxia, an acclimative change in response to lactate accumulation and the threat of cellular acidosis is the activation of ethanol fermentation through the increased synthesis of enzymes such as alcohol dehydrogenase. Morphological adjustments, in contrast, are irreversible. In response to hypoxia, certain plant species form aerenchyma in order to improve the access of root cells to atmospheric oxygen. Another well-known example is the development of shade leaves under low-light conditions (Chap. 3). The higher surface to volume ratio of such leaves allows more photosynthetic gain per unit of biomass.

Acclimation improves the ability of an individual to withstand a particular stress. In Fig. 2.13 this is indicated by the difference between the solid line and the dashed line of the same colour. The **LD_{50}** (the dosage at which 50% of the individuals survive) is shifted to more extreme stress levels because the strain caused by any given extent of stress is lesser owing to acclimative adjustments. Acclimation can be demonstrated by growing genetically similar or, ideally, identical individuals under conditions of severe stress either with or without prior exposure to a milder degree of the stress. A classic example is the acclimation to low temperature. Individuals of many plants species will die when they are transferred from temperatures near their physiological optimum directly to sub-zero temperatures. However, when they are allowed to acclimate for a few days at low temperatures above freezing, they will develop **freezing tolerance** (Chap. 4).

In contrast to acclimation being the result of changes displayed by an individual, **adaptation** (in the sense used throughout the molecular physiology chapters of this book) refers to genetic changes occurring in populations over evolutionary time scales, that is, many generations. Such changes explain the greater fitness under the environmental conditions to which the population is adapted relative to non-adapted populations. In Fig. 2.13 the effect of adaptation is indicated by the differences between the lines of different colours. Adaptation in this evolutionary sense can be demonstrated by comparing the fitness of genetically distinct plants of the same or closely related species cultivated under identical conditions. Such studies were pioneered in California in the 1930s and 1940s by Clausen, Keck, Hiesey and their co-workers (Clausen et al. 1947). They compared *Achillea* genotypes or *Potentilla* subspecies originating from different elevations in common garden experiments at various altitudes. A consistent outcome of such experiments was the greater relative fitness of individuals when grown at the altitude of their origin. This was associated with distinct morphologies. The shortened vegetation period at high elevations of around 3000 m in the Sierra Nevada had selected for allele combinations that resulted in dwarf phenotypes, which provide an advantage in these alpine conditions. In contrast, the competition present near the coast had selected for allele combinations favouring tall growth, which is advantageous under these conditions. An alternative approach to show such **local adaptation** is a **reciprocal transplant** experiment. Local and foreign individuals are planted at different sites where a particular species occurs. Greater fitness, commonly quantified as reproductive success (i.e. seed number or seed weight) of local individuals, is indicative of local adaptation.

Molecular physiology aims to elucidate the mechanistic basis of biochemical or morphological differences underlying adaptation. Typical questions would be: What are the physiological and morphological characteristics of **Crassulacean Acid Metabolism** (**CAM**)? What were the events that resulted in the evolution of this adaptation to dry habitats (Chap. 6)?

Very often, adaptation is explained not by constitutively expressed traits but by a greater potential of certain species or populations to acclimate to environmental changes. In Fig. 2.13 this is indicated by the varying distance between the solid lines and the dashed lines. For example, *A. thaliana* ecotypes originating from Scandinavia show a stronger cold acclimation response and as a result can tolerate more extreme freezing temperatures than ecotypes from the Iberian peninsula (Chap. 4, Fig. 4.23). The contribution of acclimation potential to adaptation makes it a bit more difficult to clearly distinguish between acclimation and adaptation. In fact, the term **adaptation** is often used in an ambiguous way in the scientific literature, describing acclimation as well. When this occurs, it is important to distinguish physiological from evolutionary adaptation in order to emphasise the fundamental difference between the responses of an individual and the changes occurring over generations in populations. In the following sections, the terms **acclimation** and **adaptation** are used when addressing the respective levels.

2.1.5 Filters Determining Species Distribution

This chapter began by considering what the factors are that control the distribution of species. Adaptation to the environmental factors characterising a habitat certainly represents one of the main prerequisites. This is sometimes summarised in terms of the **physiological filters** that a plant species has to pass through in order to colonise a habitat (Fig. 2.14). Growth in habitats prone to flooding necessitates adaptation to low-oxygen conditions, and survival in arid environments requires mechanisms that lower the demand for water. Furthermore, a species or population has to pass through **biotic filters**. Individuals need to be able to successfully compete with other plants, defend themselves against co-occurring pathogens and limit the damage caused by herbivores (Chap. 8). The mechanisms underlying such adaptations at the molecular level constitute the topic of molecular stress physiology. It is, however, important to realise that not all traits exhibited by a plant in a particular environment are necessarily adaptive, as was famously outlined by Gould and Lewontin (1979). The first filter a species or population passes through is the **historical filter** (Fig. 2.14; Chap. 20, Sect. 20.3 and Fig. 20.20). Individuals have to arrive in the habitat in question. Establishment in this habitat is then dependent on passing through the physiological and biotic filters. This is not equivalent to being well adapted. Other species may in fact be better adapted but have never arrived in this habitat. Similarly, not all genetic differences between individuals of a species or between closely related species are a product of selection. A considerable fraction of **genetic diversity** is due to chance events, summarised as **genetic drift**.

2.2 Activation of Stress Tolerance and Avoidance Mechanisms

Achieving **stress resistance** is often costly—that is, it consumes energy as well as building materials—and the respective resource allocation may compromise growth and reproduction. In order to limit the costs, mechanisms of tolerance or avoidance are very often inducible, i.e., activated only under conditions in which they are required. Thus, an individual responds to a stress with far-reaching

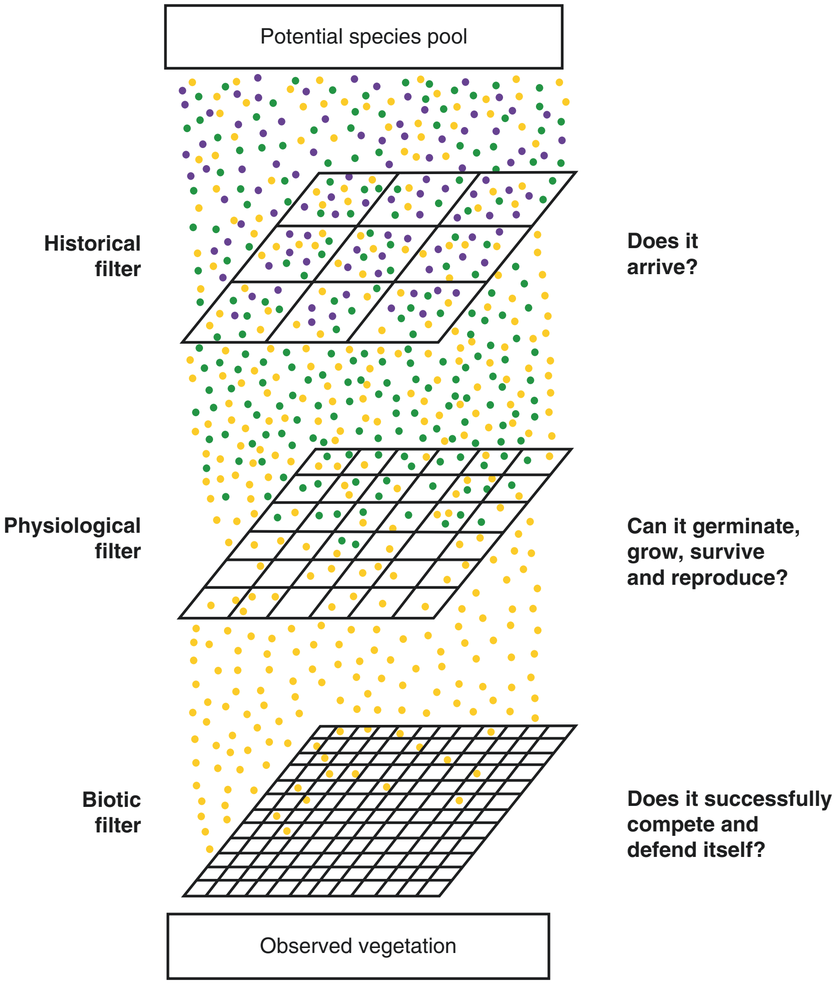


Fig. 2.14 Historical, physiological and biotic filters. (After Lambers et al. (2008))

changes in gene expression that translate into physiological changes. Most studies have found significant alterations in the abundance of several hundred transcripts upon exposure to a single stress factor (Kilian et al. 2007). Such modulation of gene activities results in acclimation and resistance due to greater stress tolerance or more efficient avoidance. Organismal homeostasis is modulated, resulting in a steady-state physiology adjusted to the external environment. The underlying processes, which represent a major part of molecular stress physiology, can be structured into distinct layers (Fig. 2.15). Different **primary stress factors** cause a strain, which has both specific and non-specific elements. The non-specific components of most stress conditions are **oxidative stress** (i.e. the increase in the concentrations of ROS (Sect. 2.2.3)) and **osmotic stress**. Both can be referred to as **secondary stresses**. The environmental factor itself (e.g. temperature), or the strain caused by primary and secondary stress, has to be sensed. The **sensing** triggers **signal transduction** cascades, which modulate the activity of transcription factors. Finally, changes in gene expression confer stress tolerance—for example, through the synthesis of protective proteins, the modulation of metabolic processes, changes in resource allocation, or the repair and replacement of damaged cellular components. The following sections describe general features; these are then discussed in more detail in Chaps. 3–8, which are devoted to particular types of stress (Fig. 2.15).

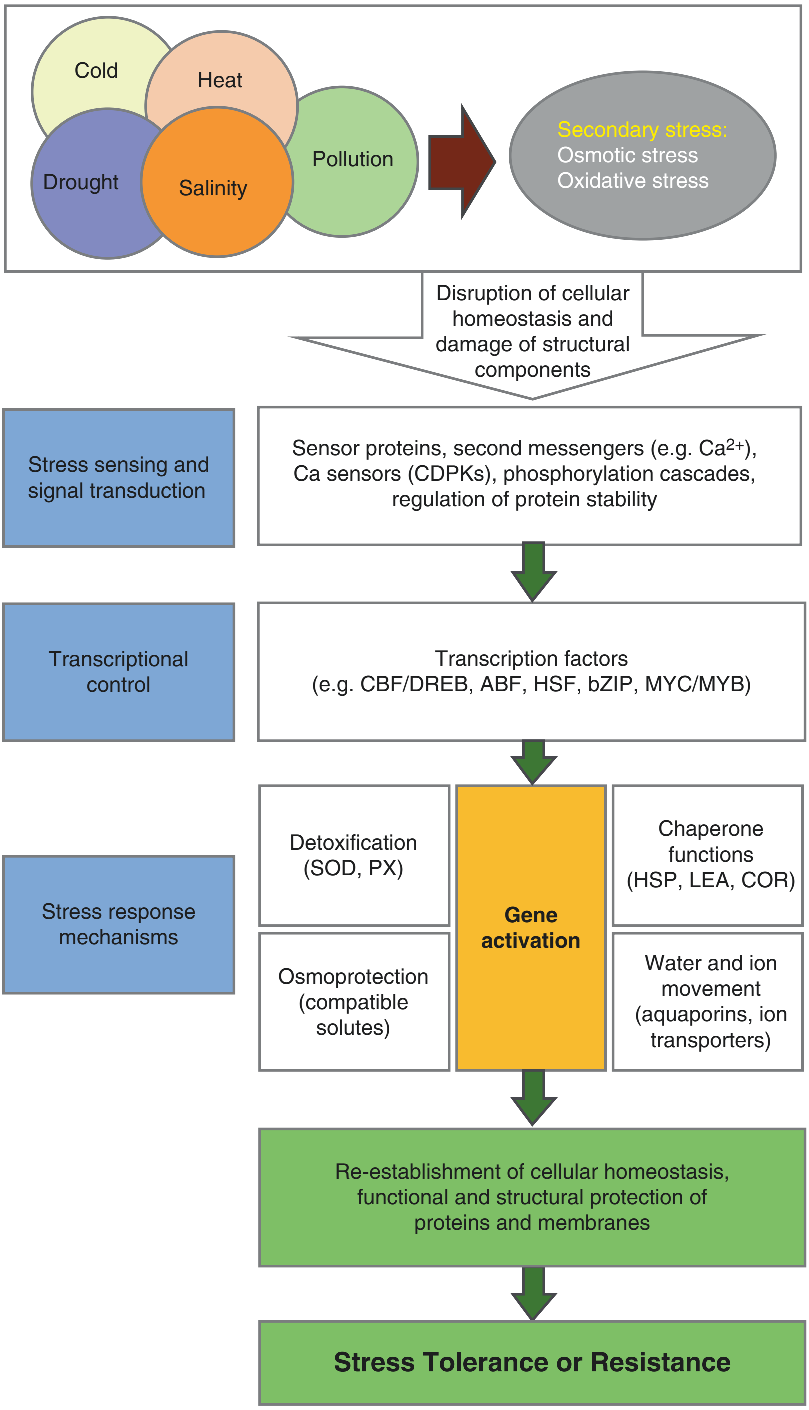


Fig. 2.15 Layers of abiotic stress acclimation through changes in gene expression. *CDPK* calcium-dependent protein kinase, *SOD* superoxide dismutase, *PX* peroxidase, *HSP* heat shock protein, *LEA* late embryogenesis-abundant, *COR* cold-responsive (transcription factor names are explained elsewhere). (Modified from Vinocur and Altman (2005))

2.2.1 Stress Sensing and Signal Transduction

The degree of molecular understanding of the different layers varies tremendously. Since the 1990s a lot of knowledge has been generated on the signal transduction cascades and transcriptional changes, but the stress-sensing mechanisms remain largely obscure. Generally accepted **sensor proteins** for temperature or hyperosmolarity have not been identified yet. Also, it is still difficult to specifically assign a molecular function to many of the putative protective proteins synthesised by cells during the course of a stress response.

A typical component of stress-activated signal transduction cascades is a transient increase in cytosolic Ca^{2+} concentrations. In fact, most interactions of plant cells with the abiotic or biotic environment involve **Ca^{2+} signals** (Dodd et al. 2010). This versatility may have had its origin in early constraints during evolution. Maintenance of cytosolic Ca^{2+} concentrations in the nanomolar range is mandatory to prevent precipitation of calcium phosphate, a salt with low solubility. Inorganic phosphate cannot be kept at such low concentrations, because of its integral role in energy metabolism (ATP). The transporter-mediated export of Ca^{2+} from the cytosol out of the cell or into organelles generates an extremely steep electrochemical gradient, which can be exploited for very rapid signalling through **transient Ca^{2+} influx** into the cytosol. Specificity of the Ca^{2+} signal is achieved by spikes and oscillations, whose periods and amplitudes (the **Ca^{2+} signature**) are stimulus dependent (Fig. 2.16). Additionally, Ca^{2+} signals are perceived by large numbers of **Ca^{2+} sensors** such as calcium-dependent protein kinases (CDPKs), which provide further specificity.

Another recurring scheme of stress signalling is the activation of phosphorylation cascades upon perception of a stimulus. Those most prominent in eukaryotes are mitogen-activated protein (MAP) kinase cascades—conserved modular signalling cassettes that regulate a wide range of stress responses and many other processes. The cassette consists of three principal components:

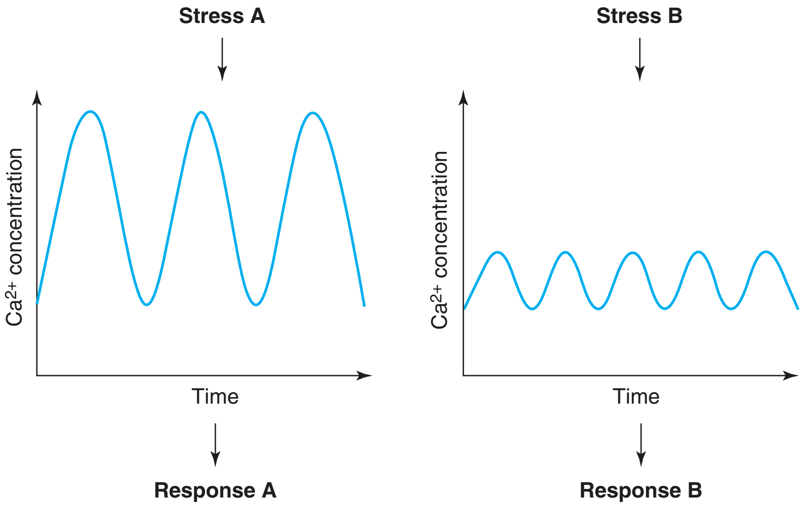


Fig. 2.16 Ca^{2+} signatures encode the specificity of stress responses. One of the earliest detectable events after perception of many different biotic and abiotic stress factors is a transient increase in cytosolic Ca^{2+} concentrations. In fact, the cytosolic Ca^{2+} concentrations oscillate. The specificity of the response is mediated by the amplitude and period of these oscillations, which are shaped by the specific activities and subcellular localisations of Ca^{2+} channels, Ca^{2+} pumps and Ca^{2+} sensor proteins. (Modified from McAinsh and Pittman (2009))

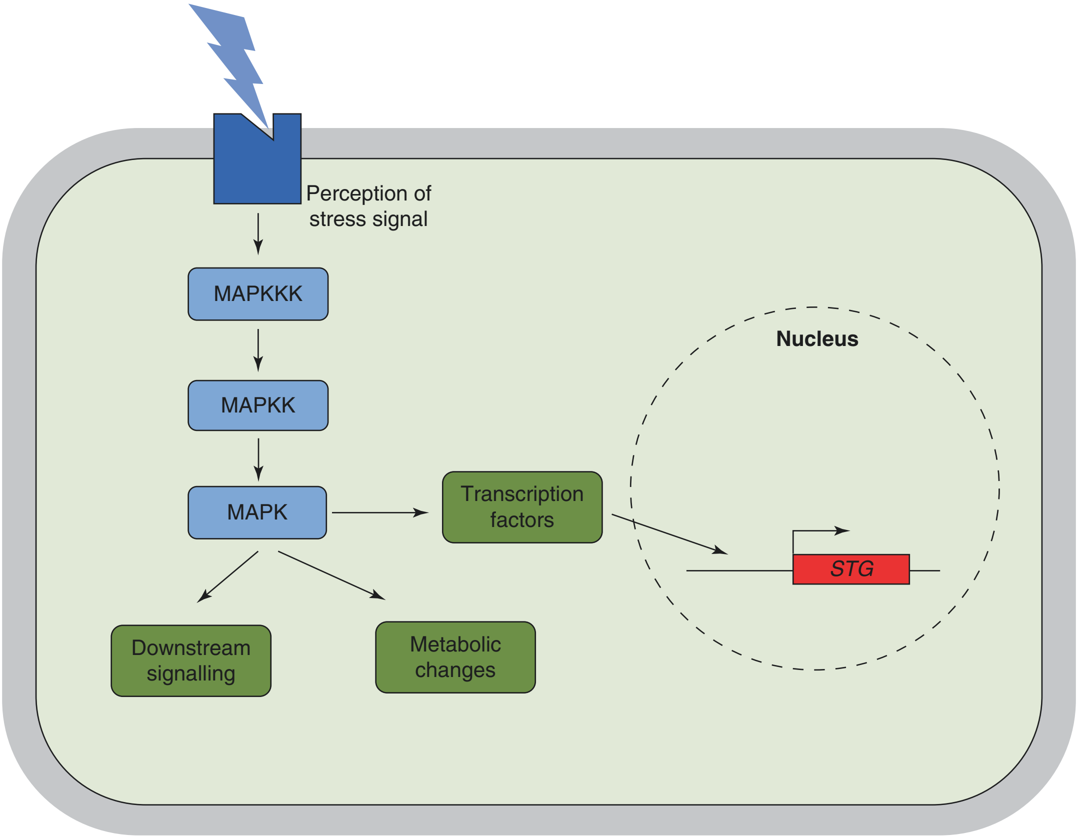


Fig. 2.17 Activation of stress acclimation by mitogen-activated protein (MAP) kinase pathways. Perception of a stress signal by a sensor or receptor protein is converted into the activation of a MAP kinase kinase kinase (MAPKKK). The MAPKKK activates a MAP kinase kinase (MAPKK) by phosphorylation; the MAPKK then activates a MAP kinase (MAPK). MAPKs have a variety of target proteins—for example, other signalling kinases, enzymes or transcription factors. The latter often move to the nucleus after phosphorylation and activate the transcription of stress tolerance genes (STG)

a MAP kinase kinase kinase (MAPKKK), which activates a MAP kinase kinase (MAPKK), which activates a MAP kinase (MAPK). MAPKs then target a wide variety of proteins. Through phosphorylation they can modulate the activity or subcellular localisation of transcription factors, alter the activity of enzymes or trigger additional signalling cascades (Fig. 2.17). Plant genomes encode many different versions of these components. *A. thaliana*, for example, possesses about 60 MAPKKK genes, 10 MAPKK genes and 20 MAPK genes, theoretically enabling thousands of different pathways. The cascade is usually initiated when a signal such as a drop in temperature or the presence of a potential pathogen is perceived and a MAPKKK becomes phosphorylated. Several kinase cascades can be activated by one stimulus, and one kinase cascade can be activated by several stimuli. This provides a framework for the integration of different environmental cues via converging and diverging signalling pathways.

A third widely recruited element of signalling chains involved in stress acclimation (e.g. cold acclimation; Chap. 4), as well as in myriad developmental processes (e.g. the response to phytohormones such as auxin and gibberellic acid (GA)), is the control of **protein stability**. Many regulatory proteins are known that are not controlled, or are only weakly controlled, at the transcriptional level. Instead, their biological half-life is dependent on post-translationally added modifications that either flag the protein for degradation in the proteasome (poly-ubiquitination—the addition of several copies of the small protein ubiquitin) or inhibit such flagging (sumoylation—the addition of an ubiquitin-related protein, which prevents ubiquitination). The flagging is executed by so-called E3 ligase complexes, of which several hundred are encoded in a typical plant genome.

2.2.2 Transcriptional Control

Ultimately, changes in gene expression upon exposure to a stress are mediated by the interaction of transcription factors with *cis* elements in the promoters of stress-responsive genes. Many of the approximately 1500–3000 different **transcription factors** encoded in plant genomes contribute to stress acclimation. The activity of transcription factors can be controlled in several ways. For example, they can themselves be under transcriptional control, their DNA-binding activity can be modulated by post-translational modifications or their subcellular localisation may change and they move from the cytosol to the nucleus.

Transcriptional control in cells exposed to **osmotic stress**—that is, an extremely negative water potential of the external medium (Chap. 6)—or cold stress (Chap. 4) are by far the most widely studied stress conditions. Signal transduction chains are usually divided into ABA-dependent and ABA-independent ones. The phytohormone **abscisic acid** (ABA) plays a key role especially in activating mechanisms that confer abiotic stress tolerance. The perception of ABA is described in more detail in Chap. 6 in the context of stomatal regulation.

Detailed analyses of the molecular events triggered by abiotic stress have revealed convergence and divergence of signalling processes (Fig. 2.18). Different pathways target the same genes and, conversely, a particular stress activates different

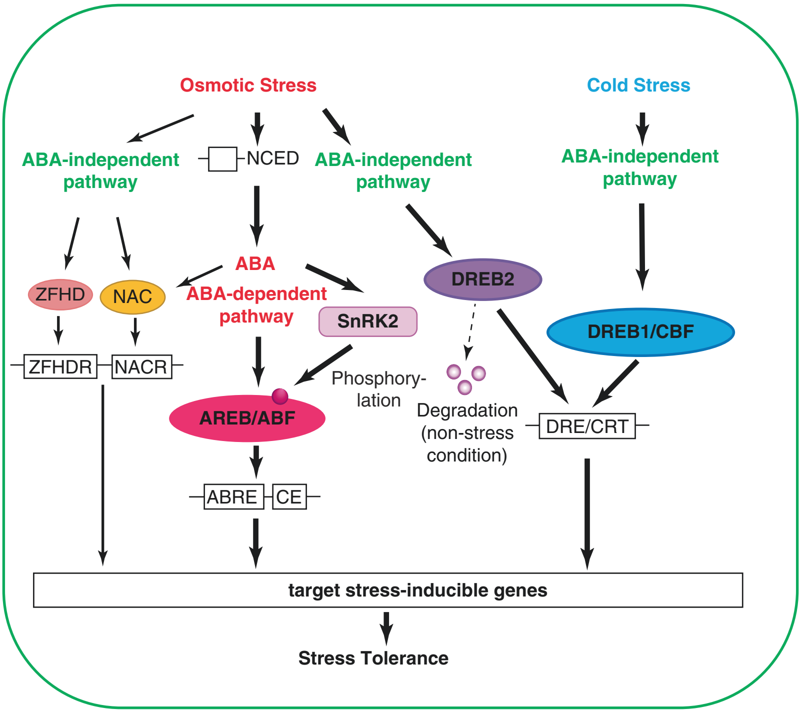


Fig. 2.18 Abscisic acid (ABA)–dependent and –independent signal transduction pathways involved in abiotic stress acclimation. Different pathways converge on stress-inducible genes whose activity confers stress tolerance. Transcription factors are represented by *ovals*, promoters of stress-responsive genes are represented by *white boxes* and kinases are represented by a *pink square*. The *small circle* indicates modifications of transcription factors in response to stress signals. NCED: 9-cis-epoxycarotenoid dioxygenase, a key enzyme in ABA biosynthesis. The *abbreviations* in the *white boxes* describe *cis* elements (e.g. ABA-responsive elements). (Modified from Nakashima et al. (2009))

pathways. This explains a phenomenon termed **cross-protection**. Previous drought stress or salt stress (osmotic stress) is known to acclimate plants to temperature stress—particularly, cold stress. One example of such cross-protection is induction of frost hardening in wild potatoes by salt stress (Fig. 2.19). Potato plants treated with NaCl are able to tolerate lower temperatures than untreated control plants. The osmotic stress activates signalling processes and transcriptional changes that improve cold tolerance as well because the signalling pathways converge on shared stress tolerance genes. A transient increase in the ABA concentration mediates this hardening reaction.

Such seemingly unspecific stress responses are biologically meaningful because the strains caused by different stress factors often are very similar. When we consider the physiological effects of salt and drought stress on cells—and, on the other hand, the effects of frost—all three factors lead to partial dehydration of cells (in an ivy leaf at −7 °C, approximately 90% of the total leaf water is frozen, forming ice, and thus is no longer available as free water). This causes problems with the stability of biomembranes in particular, as the lipid bilayers are stabilised by hydrophobic interactions, which are disturbed when the availability of water or the ion concentration at the surface of membranes is drastically changed (Chap. 4). When too much water is removed from the aqueous environment of the biomembranes (by evaporation or freezing), the concentration of solutes increases. An increase in the ion concentrations in turn alters the charges at the surface of membranes and, as a consequence, the membrane potentials. This usually leads to destabilisation of membrane structures. High charge densities result not only from water deficiency but also from an excessive salt concentration. A general reaction to stress is the synthesis of hydrophilic low molecular weight protectants—so-called **compatible solutes** (sugars, sugar alcohols, cyclitols, amino acids and betaines; Chaps. 4 and 6)—which replace water at the membrane surfaces and dislodge the ionic compounds upon loss of cellular water. Production of compatible solutes of course requires synthesis of the respective enzymes, triggered by stress. Synthesis of these enzymes is often preceded by signal transduction pathways such as those dependent on ABA.

2.2.3 Oxidative Stress

Reactive oxygen species (Fig. 2.20) arise as an inevitable consequence of life in an aerobic world (Halliwell 2006). As the non-polar oxygen

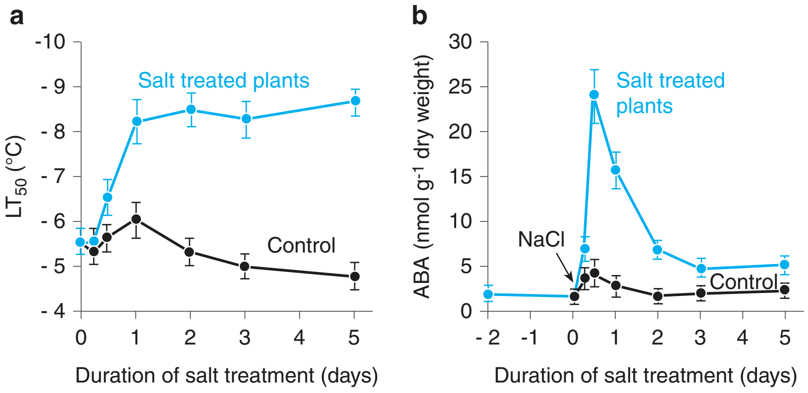


Fig. 2.19 Frost hardening through salt treatment. Cuttings of potato plants (*Solanum commersonii* Dun Pl 458317) were grown in Murashige–Skoog medium to which NaCl was added (100 mM final concentration). **a** Frost hardiness of plants. **b** Abscisic acid (ABA) content of plants. (After Ryu et al. (1995))

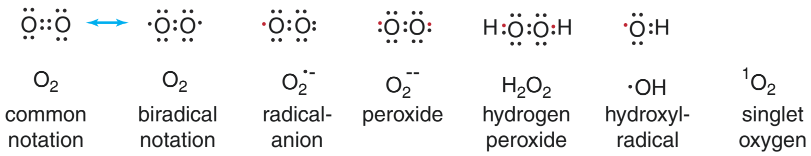


Fig. 2.20 Oxygen and reactive oxygen species (ROS)

molecule can easily cross cellular membranes, the intracellular oxygen concentrations in plant tissues correspond in principle to those of the plant's immediate environment.

2.2.3.1 Generation of Reactive Oxygen Species as a Consequence of Stress

ROS, resulting either from the organelle's own metabolism or from import by diffusion, have been detected in all plant organelles that are surrounded by biomembranes. Organelles with high rates of electron flow, i.e., chloroplasts, peroxisomes/glyoxysomes and mitochondria—are major sites of ROS production. Because of their extreme reactivity, ROS are very toxic, causing peroxidation of lipids, oxidation of proteins and nucleic acids, enzyme inhibition or activation of **programmed cell death** (**PCD**). The damage they cause depends on their concentrations and half-lives, their ability to diffuse through membranes and the activity of ROS scavengers in the various compartments of the cell (Scheibe and Beck 2011). ROS species carrying an unpaired electron, such as the oxygen radical anion ($O_2^{\bullet-}$) or the hydroxyl radical ($OH^{\bullet}$), cannot readily pass through cellular membranes, while singlet oxygen ($^1O_2$) and the relatively stable hydrogen peroxide (H_2O_2) are non-polar molecules and thus can permeate through biomembranes. Still, singlet oxygen has an extremely short lifetime and thus cannot migrate far from its site of origin.

The extreme reactivity of ROS requires high activity of **ROS-scavenging** reactions to maintain ROS and their toxic effects at a low level. Such a balance is impaired under stress. The classic case is the so-called **Mehler reaction** at the acceptor site of photosystem I (Fig. 2.21). When metabolic reoxidation of reduced nicotinamide adenine dinucleotide phosphate (NADPH) is slower than its production and the ferredoxin pool thereby becomes overly reduced, the only amply available electron acceptor is the photo-

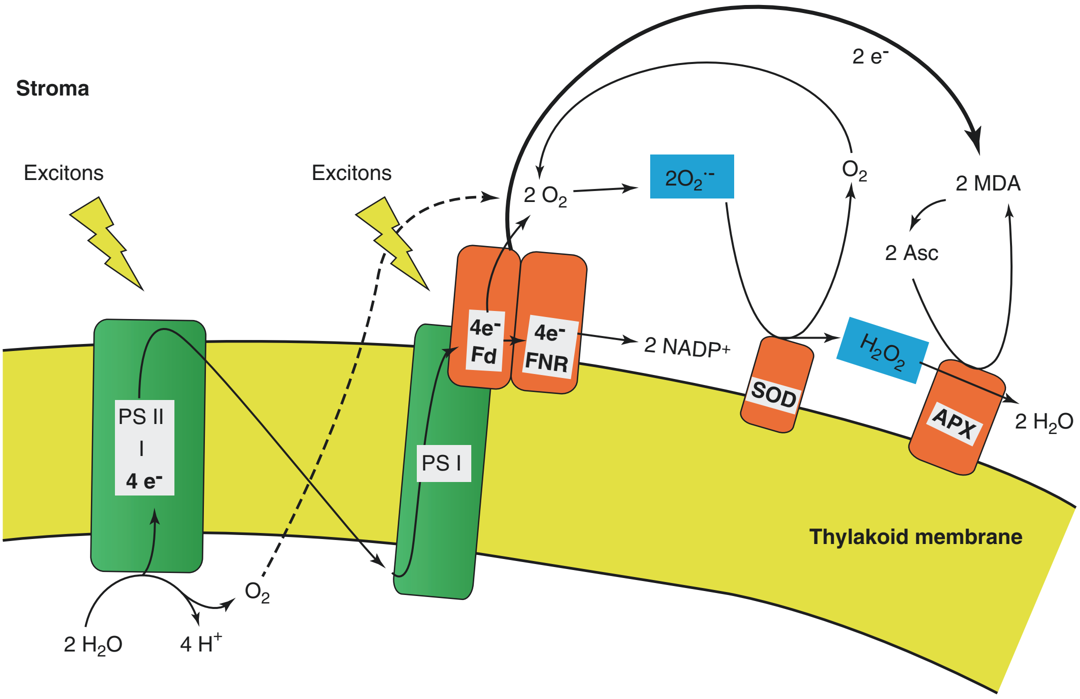


Fig. 2.21 Production and detoxification of $O_2^{\bullet-}$ and H_2O_2 in the photosynthetic electron flow. Transfer of an electron from ferredoxin (Fd) generates $O_2^{\bullet-}$. Superoxide dismutase (SOD) catalyses the disproportionation of $O_2^{\bullet-}$ to O_2 and H_2O_2. H_2O_2 is reduced to H_2O by ascorbate peroxidase (APX), yielding monodehydroascorbate (MDA). *FNR* ferredoxin-NADP⁺ reductase

synthetically produced oxygen, which can take up one electron, forming $O_2^{\bullet-}$. Under normal conditions the rate of the Mehler reaction is low, as there is no enzyme catalysing the electron transfer to oxygen. However, metabolic reoxidation of NADPH can be limited by various abiotic stress conditions. One of them is low temperature. The reactions of the photosynthetic electron flow from water to $NADP^+$ are barely affected by low temperature (with a low Q_{10} value), while the rates of the enzymatic reactions in the Calvin cycle decrease considerably (with a high Q_{10} value). Thus, NADPH accumulates, causing an over-reduction of ferredoxin. A similar situation arises under drought. Stomata are closed and the CO_2 concentration inside the leaves drops. Again, reoxidation of NADPH in the Calvin cycle is slowed down, this time because of a shortage of a reducible substrate.

Besides the Mehler reaction there are many other ways in which cellular homeostasis can be disturbed, inevitably causing an increase in the production of ROS. The resulting **oxidative stress** has been documented in plant cells exposed to heat stress, excessive UV radiation, ozone and other air pollutants, nutrient deficiencies or toxic minerals. Thus, elevated ROS levels are a common theme of stress conditions and can function as cellular indicators of stress (Mittler 2002).

A special form of ROS confined to the chloroplast is singlet oxygen ($^1O_2$). Like the $O_2^{\bullet-}$ radical and H_2O_2 it is continuously produced by the plant's metabolism, albeit at much higher rates during stress. Oxygen in the air possesses two unpaired electrons and thus occurs in the rather unreactive triplet state, $^3O_2$. Energy transfer from excited chlorophyll to oxygen can cause spin reversal and formation of the far more reactive $^1O_2$—the "curse of the illuminated chloroplast" (Halliwell 2006). Because of its very labile paired electrons, $^1O_2$ can easily react with many organic compounds, particularly with unsaturated molecules such as polyunsaturated lipids under formation of hydroperoxides. The rate of $^1O_2$ formation increases strongly whenever excitation energy cannot be efficiently dissipated as photosynthesis, fluorescence or heat. This is the case, for example, under high-light conditions (Chap. 3).

2.2.3.2 Reactive Oxygen Species as Signals

The other side of the connection between ROS and stress is the active production of ROS under abiotic and biotic stress conditions (Mittler 2002; Apel and Hirt 2004). Besides the unavoidable production of ROS as a consequence of aerobic metabolism, plant cells actively synthesise ROS through **NADPH oxidases** and other enzymes. NADPH oxidases in particular have been shown to be important for a wide range of stress responses and developmental processes. NADPH oxidases reside in the plasma membrane of plant cells and transfer electrons from cytosolic NADPH to extracellular O_2, forming $O_2^{\bullet-}$. Initially they were identified as the proteins responsible for the **oxidative burst**, a rapid increase in the concentrations of ROS displayed by plant cells recognising pathogen-derived molecules (Chap. 8). Later their involvement in growth regulation (e.g. the tip growth of root hairs and pollen tubes) and in stress signalling pathways was recognised (Marino et al. 2012). One example is stomatal closure under water-limited conditions. The ABA-dependent signalling involves NADPH oxidases (Chap. 6). Thus, the characterisation of ROS as solely deleterious molecules represents an incomplete picture. Instead, they function not only as stress indicators but also as **second messengers** and as rather unstable signalling molecules acting locally, i.e., between neighbouring cells.

2.2.3.3 Reactive Oxygen Species Scavenging

An extensive network of antioxidant metabolites and enzymes balances the level of ROS by directly inactivating or by converting ROS, respectively. Many components of this network are up-regulated in cells enduring stress conditions, once more reflecting the major role that ROS play in stress physiology. At the physiological pH of 7, $O_2^{\bullet-}$ spontaneously decomposes to oxygen and hydrogen peroxide at a high rate ($\sim 10^5\ M^{-1}\ s^{-1}$), but the enzyme superoxide dismutase catalyses this process at an even 10,000-fold higher rate. This is important, as the reaction of $O_2^{\bullet -}$ with H_2O_2 yields the most toxic ROS, $OH^{\bullet}$, which has the shortest lifetime (~1 μs) of all ROS.

$$2\,O_2^{\bullet -} + 2\,H_2O \rightarrow O_2 + 2\,H_2O_2 \tag{2.1}$$

$$O_2^{\bullet -} + H_2O_2 + Fe^{2+} \rightarrow OH^{\bullet} + OH^{-} + O_2 + Fe^{3+} \\ (\text{Haber – Weiss reaction}) \tag{2.2}$$

Hydrogen peroxide is the least reactive ROS, with a lifetime of about 1 ms and a redox potential still more positive ($\varepsilon_0 = 0.85$ mV) than that of water. Apart from disproportionation of $O_2^{\bullet -}$ it forms also by a two-electron transfer from various donors to oxygen in oxidase reactions. Because of its occurrence in most cell organelles, several H_2O_2-detoxifying enzymes are known—for example, ascorbate peroxidases (Eq. 2.3, Fig. 2.21).

$$H_2O_2 + 2\,\text{ascorbate} \rightarrow \\ 2\,\text{monodehydroascorbate} + 2\,H_2O \tag{2.3}$$

$$2\,\text{monodehydroascorbate} + 2\,e^{-} + \\ 2\,H^{+} \rightarrow 2\,\text{ascorbate} \tag{2.4}$$

Monodehydroascorbate can be reduced by non-enzymatic electron transfer from thylakoid-bound ferredoxin or in the stroma by monodehydroascorbate reductases, which use NADPH as an electron donor. Monodehydroascorbate can be further oxidised to didehydroascorbate, from which ascorbate is regenerated by didehydroascorbate reductase, which takes the reducing equivalents from glutathione (GSH) (Eq. 2.5):

$$\text{Didehydroascorbate} + 2\,\text{GSH} \rightarrow \\ \text{ascorbate} + \text{GSSG} \tag{2.5}$$

$$\text{GSSG} + 2\,(\text{NADPH} + H^{+}) \rightarrow \\ 2\,\text{GSH} + 2\,\text{NADP}^{+} \tag{2.6}$$

Oxidised glutathione (GSSG) is finally re-reduced by glutathione reductase, which uses NADPH as an electron donor (Eq. 2.6). In the chloroplast, photosynthetically produced oxygen is thus again reduced to water, a reaction sequence that has been accordingly termed the "**water–water cycle**". This cycle can keep the linear electron flow running, at least at a low rate, thus avoiding heavy over-reduction of the redox components of the electron transport chain and formation of radicals in other places.

In peroxisomes, hydrogen peroxide is produced in the glycolate oxidase reaction:

$$\text{Glycolate} + O_2 \rightarrow \text{glyoxylate} + H_2O_2 \tag{2.7}$$

and decomposed by catalase, which uses H_2O_2 as an electron donor (producing oxygen), as well as an electron acceptor (producing water) (Eq. 2.8).

$$2\,H_2O_2 \rightarrow O_2 + 2\,H_2O \tag{2.8}$$

Depending on the environmental conditions—for example, under high light, high temperature and a shortage of water (therefore partial closure of stomata)—large amounts of (phospho)glycolate can be formed by the oxygenase reaction of ribulose-1,5-bisphosphate carboxylase/oxygenase (RubisCO). However, catalase is still in abundance, sometimes even in a crystalline form.

2.2.4 Long-Distance Stress Signalling

The activation of stress tolerance mechanisms discussed so far represents predominantly local responses. A cell perceives a stress-related strain or damage and responds possibly in concert with neighbouring cells of the same tissue. While it is a hallmark of plant biology that most cells are competent to acclimate autonomously, there is clearly also **systemic signalling**. A particular cell or tissue is exposed to a stress and conveys this information to distant tissues and organs, enabling them to prepare for the stress before it actually arises. Such a "warning" can increase the stress resistance particularly when stress occurs that is highly localised. Systemic signalling has been very well documented for biotic interactions. Pathogen infection triggers **systemic acquired resistance**. Cells in uninfected tissue activate defence mechanisms upon receiving information about the presence of a pathogen from infected cells. Similarly, the attack of herbivores such as caterpillars on one leaf sparks the up-regulation of **herbivore defences**, which render other leaves on the same plant much less palatable to the herbivore (Chap. 8).

Another physiological situation requiring long-distance signalling is when stress that is experienced by an organ or tissue can be alleviated only through the activity of a different organ or tissue. A drop in water availability is often sensed first by the root system. However, an important aspect of acclimation is the saving of water through a reduction in **stomatal transpiration**. Thus, information about the water status has to travel from the root to the guard cells (Chap. 6). Conversely, leaves suffering from poor nutritional status—for example, iron or phosphate deficiency—depend on mineral nutrient acquisition by the roots. Leaves convey respective information to the roots via the release of systemic signals (Chap. 7). Generally, systemic responses to abiotic stresses are analogous to systemic acquired resistance, sometimes referred to as **systemic acquired acclimation** (Karpinski et al. 1999).

The principal types of long-distance signals are hydraulic, electrical and chemical (Huber and Bauerle 2016). Water moves through a plant under tension along water potential gradients, and it connects the cells, tissues and organs of a plant (Chaps. 6 and 10). Thus, water represents a suitable medium to convey information throughout a plant. The turgor pressure of cells and the (negative) pressure within xylem vessels fluctuate depending, among others, on water status and transpiration rate. Pressure changes in the xylem can travel fast along the xylem elements and could then be perceived as a mechanical signal—meaning a physical force acting on the plasma membrane—by cells surrounding xylem vessels. In this way, a change in the water status of root cells, resulting in a more negative water potential, could be hydraulically signalled to leaf xylem parenchymal cells and translated into a chemical signal, that is, through the biosynthesis of ABA (Chap. 6, Sect. 6.5).

Electrical signals were first recorded in plants that show rapid movement in response to a stimulus: *Dionaea muscipula* (the Venus flytrap) and *Mimosa pudica*. The possibility that plants without such leaf movement could use electrical signalling was for a long time largely neglected. Electrical signals consist of plasma membrane potential changes that trigger ion fluxes, which then cause membrane potential changes in adjacent regions of the membrane. In this way a signal can be propagated. For example, the typical initial stimulus for an **action potential** is a depolarisation caused by a sudden influx of cations such as Ca^{2+}. The depolarisation causes Cl^- channels to open, allowing Cl^- ions to diffuse out of the cell along an electrochemical gradient. When the depolarisation reaches a threshold, voltage-gated K^+ channels are activated and K^+ efflux occurs, leading to repolarisation. The cells best suited to the propagation of an electrical signal in plants are the sieve tubes in the phloem. They form long "cables" with plasma membrane continuity and comparatively low resistance. However, the identities of ion channels mediating long-distance electrical signalling and the exact physiological roles of such signalling are largely unknown.

An obvious mode of chemical signalling is the transmission of information via the release and perception of volatile molecules. Upon attack by a herbivore, such a type of signalling has been demonstrated. Remote organs are warned of an attack through airborne signals (Howe and Jander 2008). Other types of chemical signalling are less well understood. Many early assumptions about the long-distance travelling of signalling molecules within a plant have since been falsified. Good examples are the phytohormones ABA, jasmonic acid (JA) and salicylic acid (SA) (Huber and Bauerle 2016). ABA transport with the transpiration stream in the xylem was thought to convey the information about an ensuing water shortage from the roots to the leaves. However, the movement of ABA is too slow, and grafting experiments have shown that ABA biosynthesis in the roots is not required (Chap. 6, Sect. 6.5). Similarly, SA and JA are not the actual signals moving between the site of pathogen infection or herbivore attack, respectively, to systemic tissue not yet in contact with the enemy.

Recent observations, enabled by the use of reporter proteins under the control of stress-responsive promoters (Fig. 2.22) and plants expressing genetically encoded sensor proteins,

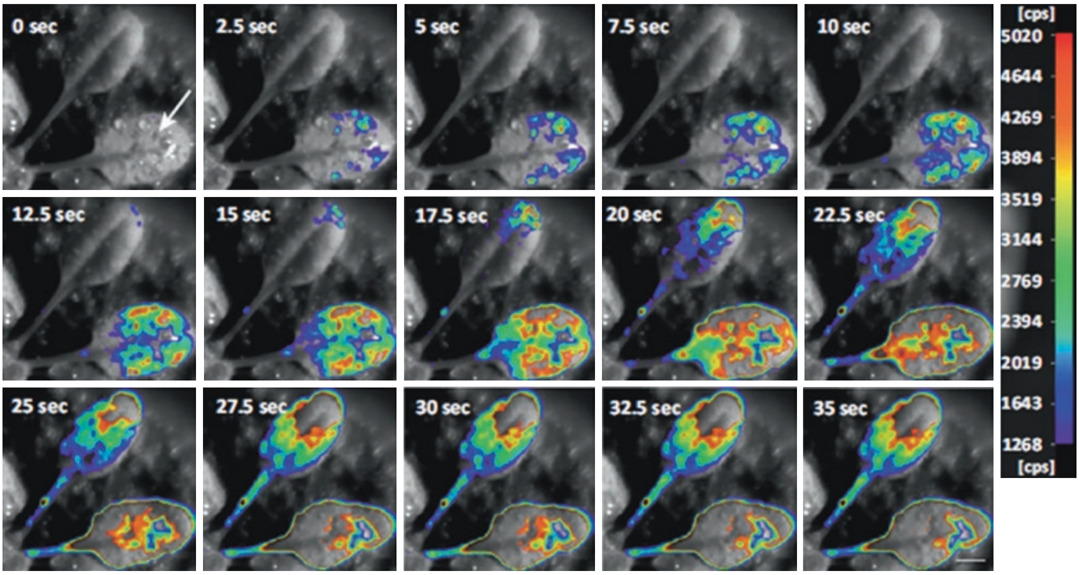


Fig. 2.22 The reactive oxygen species (ROS) wave. Time-lapse video imaging of the ROS wave, using plants expressing the reporter gene firefly luciferase under control of the stress-responsive *ZAT12* promoter. Luciferase emits light when converting the substrate luciferin. More light emission (see counts per second scale on the right) indicates stronger activation of the *ZAT12* promoter by ROS. The ROS wave spreads from an injured *Arabidopsis thaliana* leaf (*arrow*) to an adjacent systemic leaf (Gilroy et al. 2014)

have shown that the two major signalling molecules, ROS and Ca^{2+}, function not only in local signal transduction cascades (see above). A rise in cellular ROS production mediated by **NADPH oxidases** in the plasma membrane can trigger an auto-propagating **systemic ROS wave**, which can travel at a speed of several centimetres per minute (Fig. 2.22). This ROS wave, which depends on the perception and production of ROS by each cell along the path of the signal, is integrated with a Ca^{2+} wave elicited by a local increase in cytosolic Ca^{2+} (Mittler and Blumwald 2015). A particular Ca^{2+} signature (Fig. 2.16) triggers the release of a signalling molecule, which activates Ca^{2+} influx into the adjacent cell, thereby initiating propagation.

2.2.5 The Model System *Arabidopsis thaliana*

The large majority of molecular insights into stress responses and acclimation, as well as into most other aspects of plant biology, have come through studies performed in the past three decades with the model system *A. thaliana* (vernacular names: thale cress or mouse-ear cress) (Fig. 2.23). Thus, throughout the first part of this book (Chaps. 2 through 8), *A. thaliana* is the most frequently mentioned species name. The main reason for this prominence is the status of *A. thaliana* as a model system for molecular and genetic studies. The remarkable progress achieved in elucidating mechanisms underlying a plant's phenomenal ability to develop and survive in fluctuating environments has been possible only by focusing the attention and resources of a large global scientific community on one plant, for which sophisticated experimental tools have been developed.

As initially proposed by Friedrich Laibach in 1943, *A. thaliana* was widely adopted as a model system in the 1980s (Provart et al. 2016). Important features guiding this choice were its short life cycle, ease of cultivation, high fecundity (abundance of offspring), self-compatibility and small genome. Rather fortuitously, it was later found that transformation—that is, the introduction of foreign genes—is particularly easy in *A. thaliana*. Together, these features greatly facilitate genetic analyses. A short life cycle and high

Fig. 2.23 The model species *Arabidopsis thaliana*. (Photo courtesy of Bo Melander, Aarhus University, Aarhus, Denmark)

fecundity enable access to several generations and many different genotypes. Self-compatibility results in widely homozygous genomes, which are much easier to analyse, because in most loci only one allele is present. Ease of cultivation makes it possible to screen thousands of individuals from mutagenised populations for particular phenotypes. Finally, the year 2000 brought the breakthrough of the first completely sequenced **plant genome** (*Arabidopsis* Genome Initiative 2000).

The perception of light; hormone signalling pathways; pathogen resistance; transcriptional regulation mediating stress acclimation; transport of sugars, nitrate and micronutrients; cell cycle control; the biological clock; lignin biosynthesis—these and countless other fundamental aspects of plant biology have been molecularly dissected in *A. thaliana*. Genes involved in these processes were cloned, which then enabled studies on the encoded proteins and the interaction between components of a pathway. The principal approach was the isolation of mutants showing a phenotype of interest—for example, lack of response to a hormone or light stimulus. Such mutants were then analysed physiologically to obtain a more detailed understanding of the process in question. Finally, through tedious, painstaking work, the causal mutation was located in the genome. After the sequencing of the *A. thaliana* genome, the so-called **map-based cloning** of genes became much easier. Numerous genetic screens have been performed with mutagenised transgenic plants. A good example is the identification of genes involved in cold, salt and drought acclimation. A strongly stress-responsive promoter was fused to the reporter gene luciferase and transformed into *A. thaliana*. Following mutagenesis, mutants were selected that showed a perturbed stress response such as a response even in the absence of stress, a stronger or weaker response than wild-type plants or a response to one stress factor but not another (Ishitani et al. 1997).

The isolation and characterisation of mutants, referred to as **forward genetics**, was—essentially after the completion of the genome sequence—complemented by **reverse genetics**. A mutant line for a particular gene is isolated and then physiologically characterised to infer the function of the gene. The prerequisites for this approach are knowledge about the existence of the genes, provided by the genome sequence, and the availability of mutant collections for ideally every gene in an organism. For *A. thaliana* such a resource was developed over many years by generating several hundred thousand transgenic lines with a random insertion of transfer DNA (T-DNA) from *Agrobacterium tumefaciens*, the bacterium widely used for plant transformation (Chap. 8). The site of insertion was determined in these several hundred thousand transgenic lines, the information deposited in a database (Alonso et al. 2003) and the seeds stored at a stock centre, where researchers can obtain them for a small fee. Owing largely to these approaches, information on the functions of the majority of the approximately 28,000 genes in *A. thaliana* is now available. At the same time it is important to note that this is by no means equivalent to a comprehensive understanding of plant biology. Most of the interactions between the hundreds of thousands of molecules within a plant have not been described and analysed yet. Specifically, with respect to stress physiology, most acclimative and adaptive mechanisms are understood only qualitatively, not quantitatively. For example, many of the components of signal transduction cascades are known but the exact dose–response relationships are not understood. Similarly, the integration of multiple environmental cues has only in the past few years become a focus of intensive research activities. How does a plant integrate potentially conflicting stimuli into an appropriate response? This and other questions mark a frontier in molecular stress physiology.

A. thaliana has not just been instrumental in identification of hormone receptors, ion channels, transcription factors and many other key players in basic plant biological processes such as growth regulation, nutrition or stress acclimation. *A. thaliana* is a pioneer species native to Europe, Asia and north-western Africa, and has been introduced into North America. It thrives in diverse habitats throughout the northern hemisphere. Also, unlike crops, which are often studied for stress physiology, species that are naturally occurring in a wide range of habitats, such as *A. thaliana*, have not gone through genetic bottlenecks due to selection by humans. They therefore encompass much greater **genetic diversity**. Thus, *A. thaliana* is also an ideal model system for studying the molecular basis of **local adaptation** (Mitchell-Olds and Schmitt 2006; Assmann 2013). What are the mechanisms underlying differences in cold tolerance between Scandinavian and northern African accessions of *A. thaliana* (Chap. 4, Sect. 4.2)? What were the molecular events selected during the colonisation of such diverse habitats? These and other questions can now be asked, and sometimes answered, with a resolution down to single bases of the DNA.

Still, one might ask why studies on one plant species can be so enlightening with respect to the stress acclimation and adaptation of most other plants species, even though those species may have colonised habitats with sometimes vastly different conditions. The answer lies in the principal conservation of mechanisms. Every higher plant regulates the aperture of its stomata in response to the internal and external water status. Understanding of the processes involved in opening and closing of stomata, and of signals and signal transduction chains employed to integrate diverse information into a physiological response, can then be used to study differences between plants. Likewise, modulation of growth depends on the same basic mechanisms of control over cell cycle activity and cell expansion. Furthermore, most plants possess **basal tolerance** of most environmental stress factors. Differences in the degree of tolerance are due to variations in the fundamental mechanisms. The examples of **halophytes** and **metallophytes**, discussed in Chap. 7, can illustrate this. *A. thaliana* has a considerable ability to tolerate elevated salt or metal concentrations. This becomes apparent as **hypersensitivity** when genes involved in this tolerance are non-functional. Plant species adapted to extreme conditions that are not tolerable for *A. thaliana* often employ the same mechanisms involved in basal tolerance but with some variation.

Nonetheless, there are phenomena relevant to molecular stress physiology that cannot be studied in *A. thaliana*. Perhaps the most obvious ones are the major plant symbioses of mycorrhizae and nitrogen fixation. Most Brassicaceae, including *A. thaliana*, do not engage in these symbioses. Thus, other model systems have been established—namely, the legumes *Lotus japonicus* and *Medicago truncatula* (Chap. 7).

2.3 Stress and Growth Regulation

Growth is an increase in biomass, volume, area or length as a result of highly coordinated cell division, cell expansion and cell differentiation. Stem cell populations are maintained in meristems. They produce new cells, which then expand and acquire a fate, that is, a specific role within a tissue and organ. All of these processes are under hormonal control and are responsive to both internal and external factors. The integration of environmental cues into a growth response is the basis for a hallmark of plant biology: the **plasticity** of developmental steps and organ formation (Pierik and Testerink 2014). In contrast to animals, which are born with a complete set of organs, plants develop their organs only after embryogenesis and germination. The **morphol-**

ogy of a plant individual not only is the realisation of a blueprint but also arises under strong influence from environmental factors. Light conditions govern **leaf morphology** (sun leaves versus shade leaves; Chap. 3), and nutrient availability in the soil determines **root architecture** (Chap. 7). Charles Darwin studied **phototropism**, the growth of a plant towards a light source (Darwin 1880). These and many other examples illustrate that the regulation of growth and development is an integral part of stress physiology (for more details on plant development, see plant physiology and plant molecular biology textbooks).

The strain caused by a stress factor could be regarded as a perturbation of the complex processes that constitute development, necessarily causing stagnation of growth. Indeed, growth reduction is widely seen and interpreted as an indicator of stress (Chap. 2, Sect. 1.2). Such effects can be defined as **passive growth reduction** due to interference of stress factors, such as water scarcity, with metabolic and physiological processes that are important for growth. However, there is also acclimation via **active growth modulation**. A plant must always balance resource allocation between investment in growth and stress acclimation (Fig. 2.24; Chap. 12, Sect. 12.5). In the past decade, molecular insights into the mechanisms of hormonal growth control have provided direct evidence of this fundamental **trade-off**.

Gibberellic acid (**GA**) is one of the classic **plant growth hormones**. Among other effects it promotes the elongation of plant organs such as internodes. The so-called **DELLA proteins**, which are negative regulators of the GA response, are key components of active growth modulation in plants (Santner and Estelle 2009). DELLA proteins repress the transcription of GA-responsive genes. The soluble GA receptor protein GID1 associates more strongly with DELLA proteins when GA is bound. This interaction promotes the tagging of DELLA proteins for degradation by the 26S proteasome and thereby the release of a GA response brake (Fig. 2.25). When *A. thaliana*

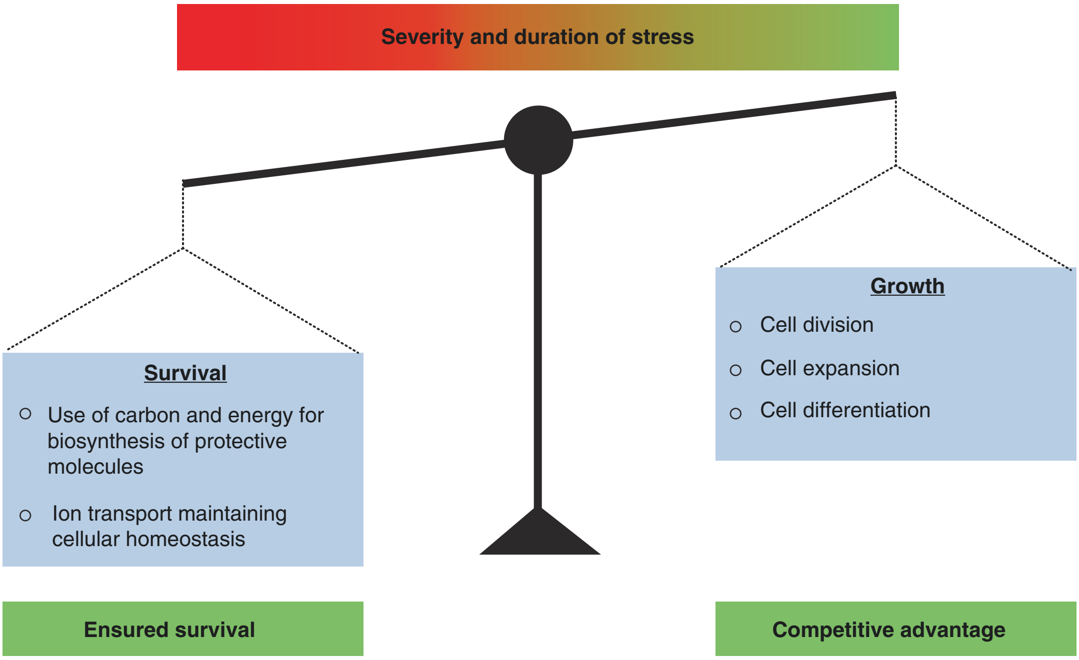


Fig. 2.24 The fundamental trade-off between growth and stress acclimation. Plants need to find the right balance in resource allocation between growth and survival, depending on the severity of stress. (Modified from Claeys and Inzé (2013))

mutants lacking most of the DELLA proteins are exposed to salt stress, they do not show the same reduction of root growth that is displayed by wild-type seedlings (Achard et al. 2006). This simple experiment clearly demonstrates that growth is actively slowed down under stress and in a manner dependent on DELLA proteins. Salt stress does not per se inhibit growth under the tested conditions. The consequence for the mutant seedlings is a lower survival rate. They maintain growth at the expense of an acclimative response, such as osmotic adjustment, and eventually die. Similar outcomes can be observed under drought conditions. Plants with an artificially high GA status (e.g. through overexpression of GA biosynthesis genes) grow and compromise survival, while plants with a low GA status (e.g. DELLA mutants) remain small and survive (Colebrook et al. 2014). Under natural conditions they would of course suffer a disadvantage in competition with neighbouring plants (Fig. 2.24).

Not all stress conditions trigger active growth reduction. Plants often attempt to escape a low-light condition caused by other vegetation through a **shade avoidance** response, that is, an investment in more growth, especially of the stem and the petioles (Chap. 3). Some species adapted to flooding-prone habitats try to reach the water surface when they are submerged (Chap. 5). This strategy is to ensure continuing oxygen supply to tissues under water. As in the case of shade avoidance, the up-regulation of GA biosynthesis is a component of this strategy (Fig. 2.25).

2.4 Molecular Basis of Escape and Anticipation of Stress

The environment on our planet is characterised by regularly occurring changes in abiotic factors. First, the rotation of the Earth causes a day/night cycle with obvious consequences for factors such as light availability, temperature and moisture. Second, as a result of the Earth's orbit around the sun and the tilt in the axis of the Earth's rotational plane relative to the orbital plane, different seasons exist—periods of the year marked by typical changes in light intensity, temperature or precipitation. Day/night cycles and seasonal changes also influence biotic factors. The threat of fungal pathogens, for example, is dependent on temperature and moisture, as spore germination is favoured by high humidity.

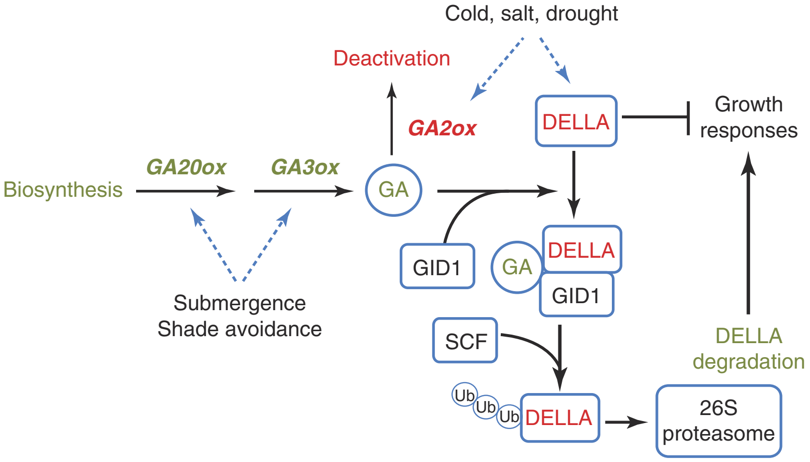


Fig. 2.25 The gibberellic acid (GA) signalling pathway and DELLA proteins are key regulators of growth under stress conditions. Stresses such as cold, salt and drought trigger active growth reduction, while acclimation to shade and submergence often involves growth stimulation. GA20ox (GA20 oxidase) and GA3ox are GA biosynthesis enzymes; GA2ox is an enzyme catalysing a step in GA turnover. GID1 is the soluble GA receptor. Upon GA binding it associates with an SCF E3 ligase, which tags DELLA proteins for degradation by poly-ubiquitination (Colebrook et al. 2014)

Given the amplitude of such regular changes—for example, day/night temperature fluctuations in deserts, warm summers and winters with subzero temperatures in Central Europe or mild winters and dry summers in the Mediterranean—they can potentially represent severe stress. The anticipation of recurring stressful environmental conditions is therefore an extremely useful strategy employed by all kinds of organisms to limit damage and the cost of investment in acclimative processes. The needles of many conifers, for example, begin their cold acclimation, measurable as an increase in cold hardiness, even before the temperatures actually drop in autumn (Fig. 2.26).

More generally, the restriction of physiological activity to seasons with more favourable conditions (the **escape strategy**) can ensure survival and reproductive success. Across the eukaryotic domain, biological clocks generate intrinsic **circadian rhythms** that help organisms coordinate physiological activities with fluctuating environmental conditions in day/night cycles. Furthermore, combined with the perception of light, the circadian clock enables the perception of changes in the day length (**photoperiodism**) and thereby the anticipation of seasons. The latter is also afforded by reliable perception of abiotic conditions typical of a cold winter. This is exemplified by **vernalisation**. Many plants require prolonged exposure to cold temperatures before they develop an inflorescence. This ensures a switch to reproduction only after a typical winter in the subpolar oceanic climate has been endured.

2.4.1 Circadian Rhythms

Myriad biological processes are influenced by circadian rhythms (Hsu and Harmer 2014). The hallmark of circadian control is an oscillation with a rhythm of approximately 24 h even after transfer of an organism into constant darkness or constant light, that is, in the absence of external cues as to the day/night cycle (Fig. 2.27).

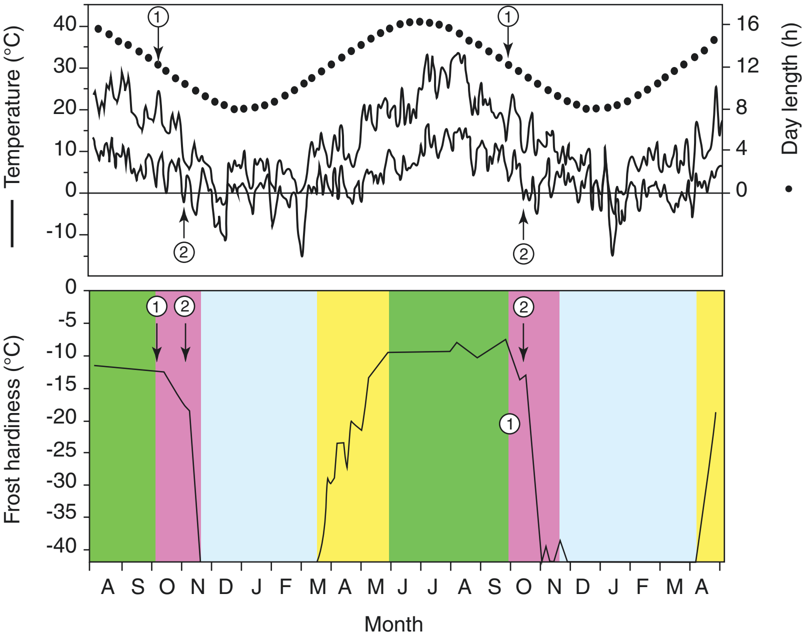


Fig. 2.26 Changes in the frost hardiness of pine needles over the course of a year. The *upper panel* shows temperature data (upper/lower line: 2 m/5 cm, respectively above ground) and day lengths in Bayreuth (330 m above sea level). The frost hardiness of *Pinus sylvestris* needles was determined as the temperature at which tissue damage occurs (*lower panel*). An increase in frost tolerance is already detectable when the day length falls below a threshold (1) and before frost actually occurs for the first time (2). *Green* indicates the phase of relative frost sensitivity, *magenta* indicates the frost-hardening phases, *blue* indicates the phases of extreme frost tolerance, and *yellow* the phases of de-hardening (Modified from Hansen (2000))

Early observations of circadian rhythms in plants included rhythmic movements of leaves (e.g. in *Oxalis acetosella*) and flower petals, or the rhythmic emission of volatile compounds by flowers. Genome-wide molecular analyses of gene expression revealed that control by biological clocks is not just a curiosity; it affects most physiological processes. Genes encoding proteins of the photosystems, for example, become more active before dawn. Conversely, gene activities needed for the mobilisation of transiently stored starch increase before the end of the day (Harmer et al. 2000). Overall about half of all genes in a typical plant show a circadian rhythm in transcript abundance.

Comparatively simple experiments have demonstrated how strongly fitness is improved through the clock-mediated coordination of physiology with the day/night cycle even under controlled laboratory conditions without much stress. When plants are cultivated under the wrong artificial day/night cycle—for example, with a 20- or 28-h period—their biomass production is markedly reduced and they succumb in competition with other plants for which the imposed day/night cycle is the appropriate one (Dodd et al. 2005). Such experiments have been enabled by the availability of *A. thaliana* mutants with altered period length (Fig. 2.28).

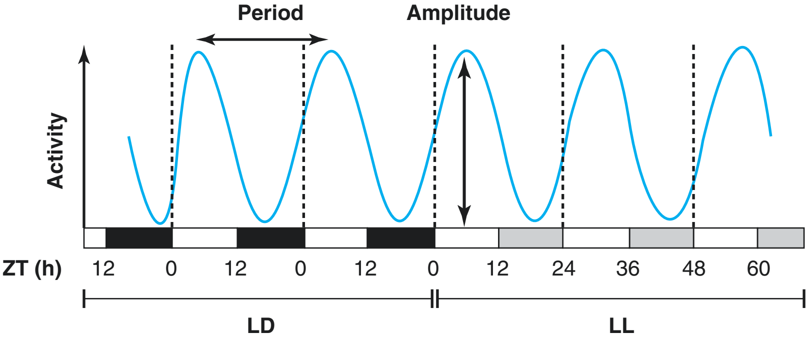


Fig. 2.27 The hallmarks of a circadian rhythm. The *blue line* represents a rhythmic biological process such as a metabolic pathway, the transcription of a gene, a leaf movement etc. It is characterised by a specific amplitude and a period length of about 24 h. ZT stands for the Zeitgeber time, measured from the last onset of light. The rhythmicity of the process is maintained even when the organism is shifted from a light/dark cycle (LD) to constant light (LL). *White bars* indicate light, *black bars* indicate dark and *grey bars* indicate subjective night during LL

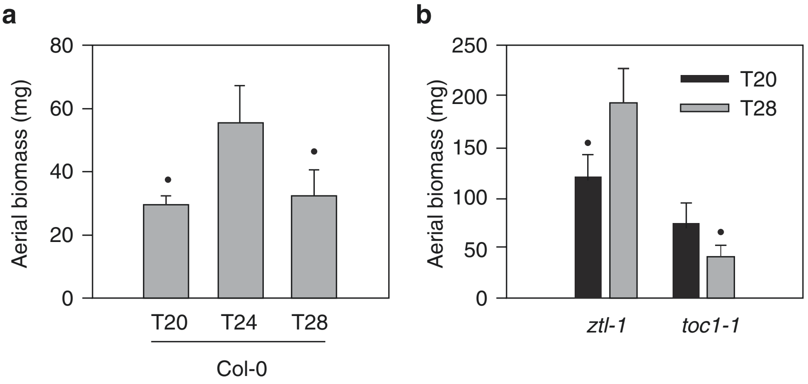


Fig. 2.28 Fitness defects of plants grown in day/night cycles not in sync with their circadian rhythm. **a** *Arabidopsis thaliana* wild-type plants (the main laboratory accession Columbia-0, Col-0) were cultivated either in a normal 24-h day/night cycle (T24) or in artificially shortened or extended day/night cycles (T20 and T28, respectively). Growth was strongly reduced in both artificial day/night cycles. **b** Two *A. thaliana* mutants with altered rhythmicity—*ztl-1* with a defect in the *ZEITLUPE* gene and *toc1–1* with a defect in *TIMING OF CAB*—were grown in different day/night cycles, one appropriate for *ztl-1* (T28) and one appropriate for *toc-1* (T20) (Dodd et al. 2005)

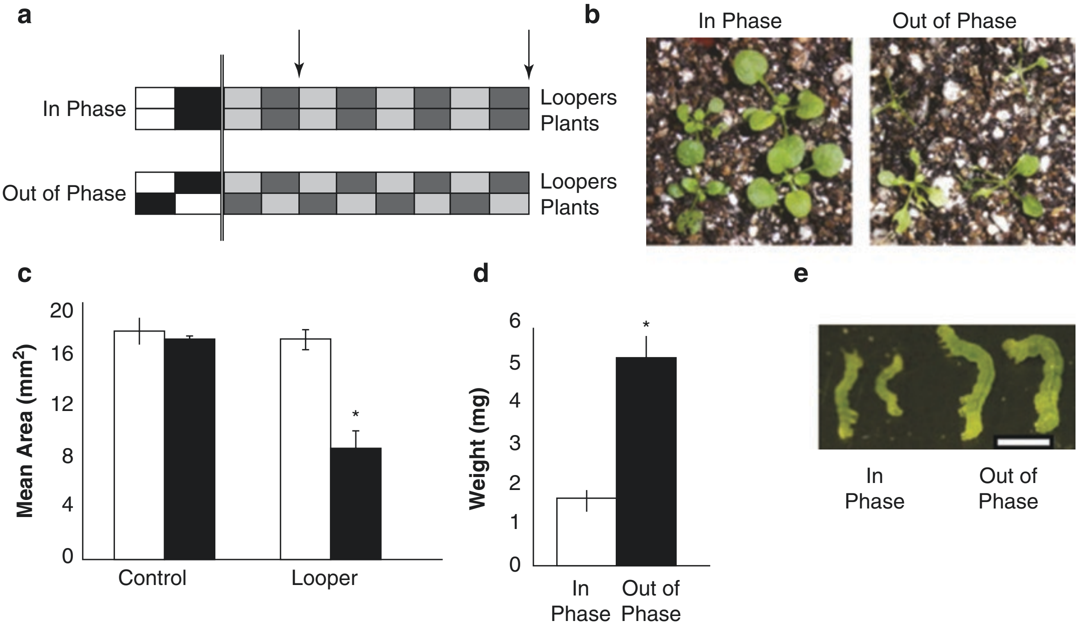


Fig. 2.29 *Arabidopsis thaliana* shows greater herbivory resistance when entrained in phase rather than out of phase with *Trichoplusia ni* looper entrainment. **a** Light/dark cycle entrainment scheme and experimental protocol. The *rectangles* symbolise 12-h periods of light (*open*), dark (*filled*), darkness representing subjective day (*light grey*) and darkness representing subjective night (*dark grey*), according to the entrainment. The *two arrows* represent the timing of the *T. ni* looper addition and looper removal, respectively. The *vertical bars* symbolise the shift from light/dark cycles to constant darkness. **b** Plant tissue remaining from plants entrained in phase and out of phase with looper entrainment after plants and loopers were co-incubated for 72 h. **c** Quantification of leaf area (mean ± standard error (SE); $n = 6$; $*p < 0.0002$) remaining from plants entrained in phase (*white bars*) and out of phase (*filled bars*) with *T. ni* entrainment after 72 h of incubation without (control) or with *T. ni* loopers. **d** Looper biomass (mean ± SE; $n = 15$; $*p < 0.05$). **e** Representative loopers 72 h after co-incubation with *A. thaliana* plants (*scale bar*, 0.5 mm) (Goodspeed et al. 2012)

In addition to a general gain in the effectiveness of growth, there is direct modulation of stress responses (Hsu and Harmer 2014). Lack of clock function renders plants more susceptible to downy mildew infection at dawn when infection is most likely (Wang et al. 2011). When plants are in phase with the rhythmic feeding behaviour of herbivores, they suffer less damage, presumably because the **defence hormone jasmonate**, which activates many **herbivore resistance** mechanisms (Chap. 8), accumulates in a circadian rhythm that allows preparation for the anticipated peak in herbivore feeding activity (Goodspeed et al. 2012) (Fig. 2.29).

2.4.2 Anticipation of Seasonal Changes in Environmental Conditions

A higher plant passes through distinct developmental phases during its life cycle (Fig. 2.30). The formation of a zygote after pollination and fertilisation triggers embryo development within a ripening seed. The seed can enter a state of **dormancy** and germinates when favourable environmental conditions are perceived. **Vegetative growth** is divided into a juvenile phase and an adult phase. Only in the latter is a plant competent to enter the reproductive phase, which is characterised by the formation of

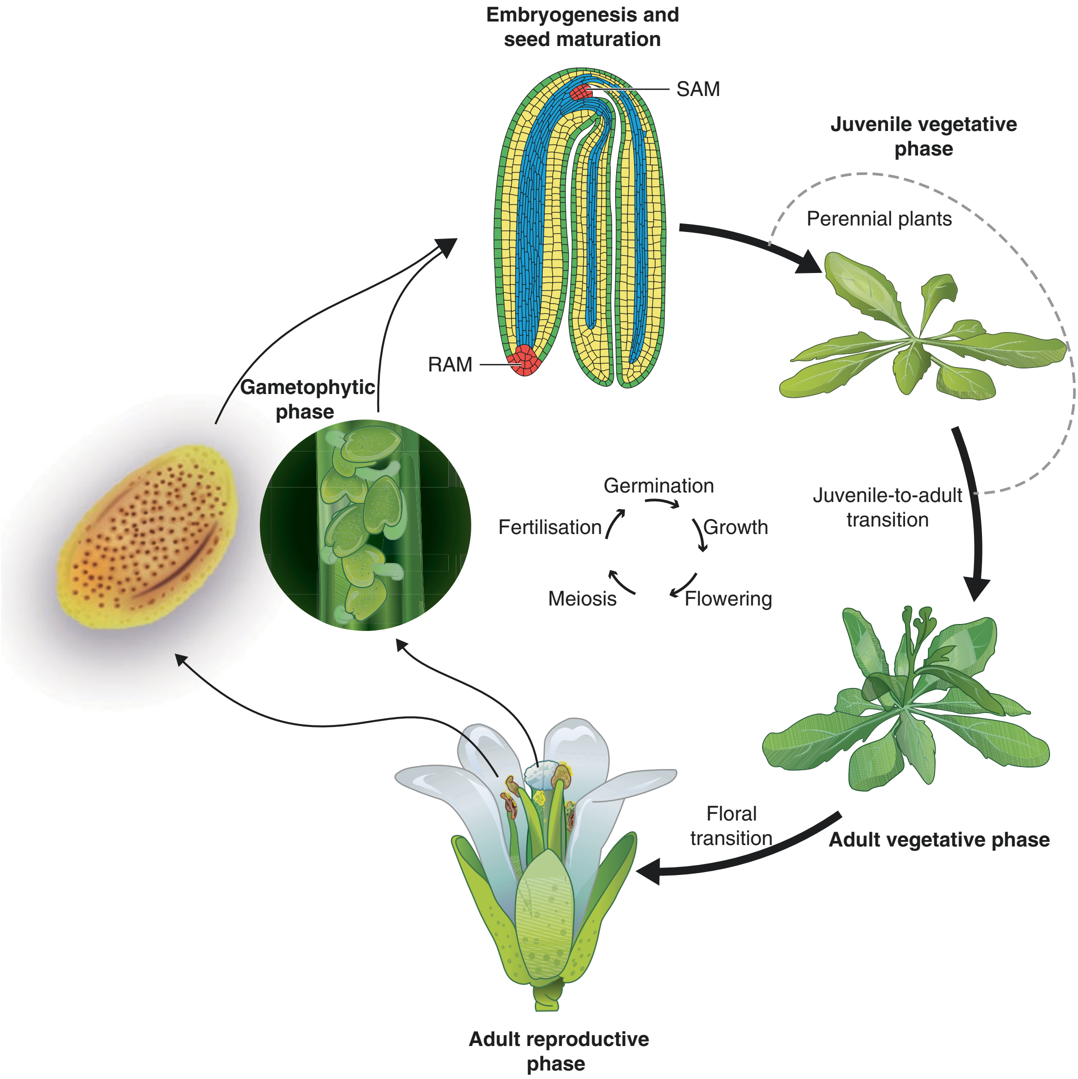


Fig. 2.30 Plant developmental phases (Huijser and Schmid 2011)

flowers. Many plant species, most prominently trees, go through an extended juvenile period. It takes several years of development before they are competent to respond to environmental signals that trigger flowering. Within the flowers, the male and female **gametophytes** arise from spores and produce the male and female gametes.

Obviously, in seasonal environments the timing of major **life history** transitions such as germination and flowering is crucial for establishment, survival and successful reproduction. Thus, most plants in such environments have evolved the ability to escape from stressful conditions such as cold or water scarcity by restricting the major phases of

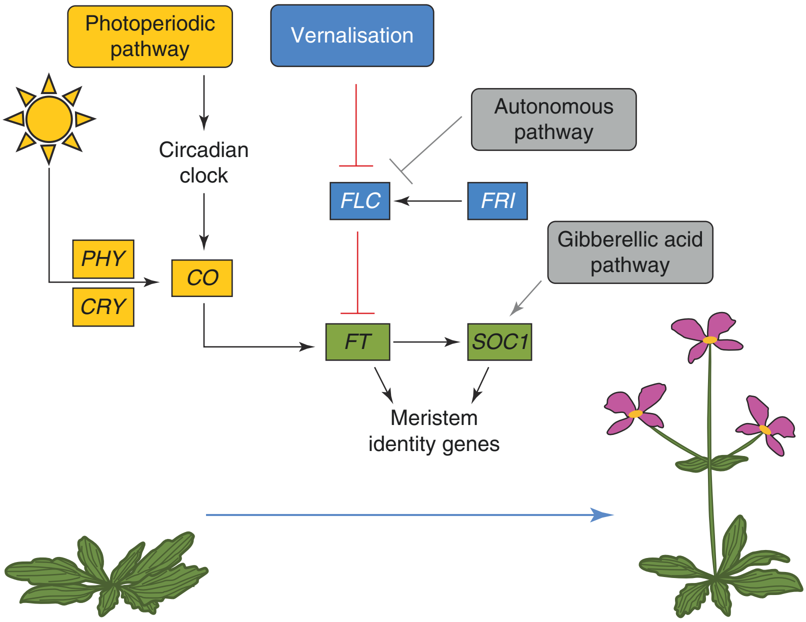


Fig. 2.31 Control of flowering time. In *Arabidopsis thaliana* (note that the flower morphology and petal colour in the figure are not representative of *A. thaliana*), four different pathways are known to control flowering time. Two of them are described in this chapter and are highlighted here as examples of the anticipation of seasonal changes via photoperiodism and stress memory (vernalisation). *SOC1* Suppressor of Overexpression of Constans1, for other abbreviations see text. (for more details Figs. 2.32 and 2.33)

development to windows of rather advantageous conditions.

What is arguably best understood is the control of the flowering time via anticipation of seasonal changes (Fig. 2.31). Thus, flowering under favourable environmental conditions not only is a direct escape mechanism but also can serve as an example for the molecular mechanisms underlying the anticipation of recurring stress. A reliable and therefore important environmental cue is the day length. Processes governed by it are summarised under the term **photoperiodism**. Many plant species have been classified, for example, as short-day plants or long-day plants. A short-day plant flowers strictly only when the day length falls below a specific threshold. Conversely, a long-day plant requires a day length exceeding a specific threshold in order to flower. Plant species not influenced in their flowering behaviour are called day neutral. Variations in day length requirements exist not only between plant species but also within plant species. There are, for example, short-day as well as day-neutral and long-day *Nicotiana tabacum* genotypes.

Instead of—or in addition to—a particular day length, many winter annual and perennial plants require prolonged exposure to cold (i.e. to winter conditions in temperate regions) before they flower (**vernalisation**). This ensures flowering at a time when conditions are likely to be favourable for reproduction. Spring temperatures enable resource allocation to the development of reproductive organs and allow the activity of pollinators, for example.

2.4.2.1 Photoperiodism

How does a plant determine that the right day length for the initiation of flowering in spring or for cessation of growth and bud set in autumn has arrived? Photoreceptor-mediated perception of light is a prerequisite but is not sufficient, because no information on the duration of light exposure is recorded. The mechanisms enabling the measurement of the day length have been elucidated in *A. thaliana* and in the monocot model rice. *A. thaliana* is a facultative long-day plant—that is, long days trigger inflorescence development—but even without this cue, flowering will eventually happen. The same mechanisms, however, also explain the behaviour of short-day plants and even the basis of other photoperiodic processes such as bud set in aspen trees. This illustrates the value of a model system, as discussed in Sect. 2.2.5.

Classic grafting experiments led to the concept of **florigen**, a flowering hormone that remained hypothetical for decades. Florigen refers to the chemical signal that travels from leaves to the shoot apical meristem to deliver the information that the right day length has arrived for the switch from vegetative to reproductive growth. When one leaf of a plant (e.g. *Perilla frutescens* var. *crispa*, common name Shiso, Lamiaceae) is exposed to the right day length for flowering and this leaf is grafted onto a plant not exposed to the right day length, flowering is induced nonetheless. Such a transmission of information via grafting is even possible between related species—for example, the Solanaceae *Petunia* and tobacco (Zeevaart 2006). After many years of futile attempts to identify florigen, the careful analysis of *A. thaliana* flowering mutants (Koornneef et al. 1991) finally revealed the core photoperiodic mechanism (Yanovsky and Kay 2002). It depends on the circadian rhythm in the abundance of *CONSTANS* (*CO*) transcript. *CO* encodes a key regulator of flowering. The transcript level peaks late in the afternoon (Fig. 2.32). However, CO protein accumulates only when light is still present at the time of the highest transcription. Light is perceived by the **photoreceptors** cryptochrome and phytochrome. In the dark the CO protein is very unstable and quickly degraded. Thus, CO is active only upon the **coincidence** of two events: the regularly recurring peak in transcription controlled by the intrinsic biological clock, and exposure to the external factor light (**external coincidence model**; its history was described by Kobayashi and Weigel 2007). For *A. thaliana* this happens only when the day length exceeds a certain threshold, that is, when the sun sets after the time of maximal *CO* transcript abundance. Active CO protein then triggers the synthesis of FLOWERING LOCUS T (FT) in the leaf. The FT protein is florigen. It travels via the phloem to the shoot apical meristem and signals the right day length for flower induction (Fig. 2.33).

The module consisting of *CO* and *FT* is essential for other photoperiodic processes as well, and is likely to explain such phenomena

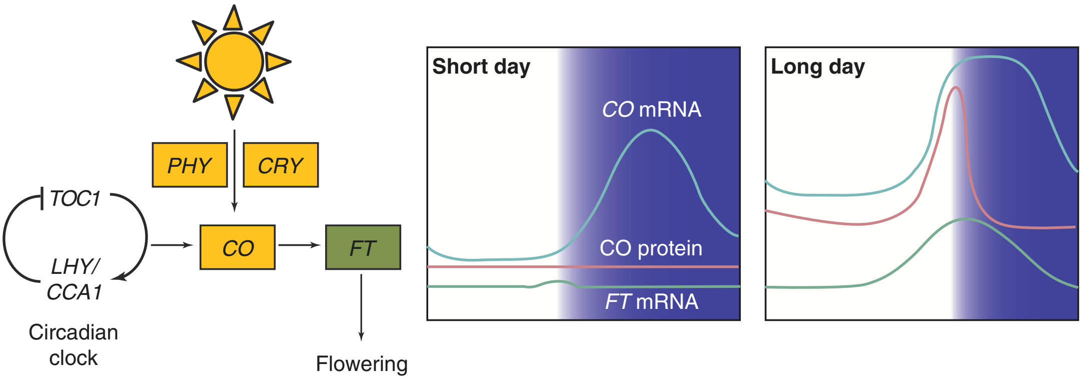


Fig. 2.32 Control of flowering by the photoperiod. The day length is perceived via the coincidence of an internal factor and an external stimulus. The central regulator *CONSTANS* (*CO*) is under control of the circadian clock (TOC1 and LHY/CCA1 are key components of the clock). Under short-day conditions the peak in transcript abundance occurs in the dark and the protein does not accumulate. It is only when light is perceived by the photoreceptors phytochrome (PHY) and cryptochrome (CRY) at the time of high *CO* expression that CO protein accumulates and activates the synthesis of the FT protein, florigen. (Modified from Buchanan et al. (2015))

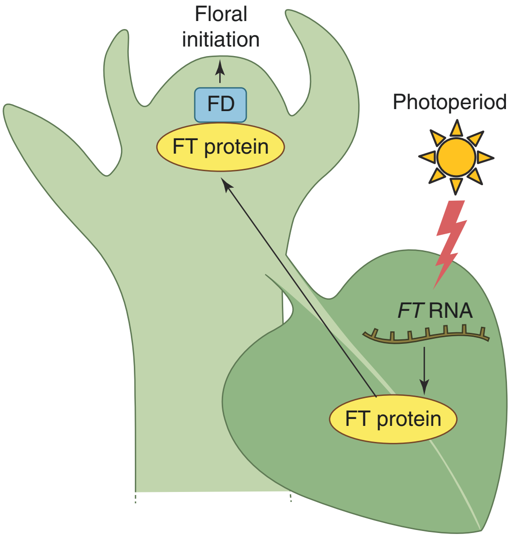
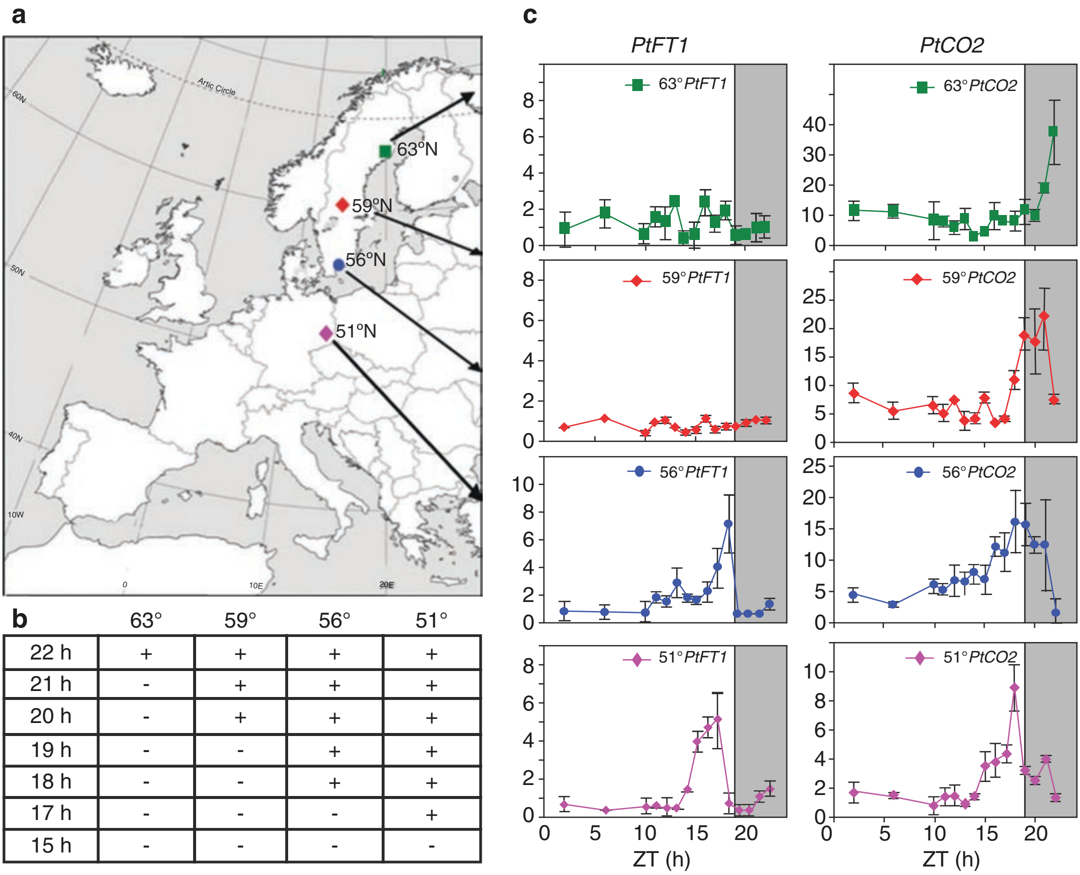


Fig. 2.33 Induction of flowering by the FT protein, florigen. It is synthesised in leaves under control of the photoperiod (Fig. 2.32) and travels via the phloem to the shoot apical meristem, where it heterodimerises with FD, a bZIP transcription factor, and initiates the formation of flowers (Buchanan et al. 2015)

throughout the plant kingdom. An analysis of aspen trees growing at different northern latitudes demonstrated a key role of CO and FT in **local adaptation** (Fig. 2.34). Aspen trees enter a state of **dormancy** at the end of summer. Growth ceases, buds are set and cold tolerance increases (Fig. 2.26). These processes are triggered when the day length falls below a critical threshold. In northern Sweden, winterly conditions arrive earlier than in Germany, for example. Thus, aspen trees need to go through this transition into dormancy at a time of the year when the days are still comparatively long, while in Germany they maintain growth until the day length is already much shorter (Fig. 2.34b). An important aspect of local adaptation to the stress conditions of a cold winter is therefore to respond to the day length change that matches the specific seasonal pattern of the habitat. FT in *Populus tremula* suppresses the short-day-induced cessation of growth and bud set, that is, as long as FT reaches the meristems, they continue to grow (Böhlenius et al. 2006). When the transcript abundance of *CO* and *FT* in *P. tremula* individuals originating from different latitudes was analysed in identical 19-h-light–5-h-dark cycles, it was found that the endogenous rhythm of *CO* transcript accumulation was different. In high-latitude individuals the peak of *CO* is shifted to later in the day and reaches its peak only after the end of the light period in a 19-h-light/5-h-dark cycle. As a consequence, *FT* expression is no longer activated, the signal supporting growth is absent and a state of dormancy is initiated. In contrast, the *CO* peak in individuals from lower latitudes reaches a peak earlier in the day. Hence, *FT* is expressed and growth is maintained in a 19-h day. Such observations demonstrate that local adaptation to the pattern of seasonal changes can occur via the fine-tuning of endogenous oscillations in the expression of central regulators such as *CO*. Moreover, the challenges arising from rapid climate changes, especially for perennial plants such as aspen trees, become obvious. When seasonal changes in temperature or precipitation can no longer be reliably anticipated by measuring the day length, organisms will suffer from a loss of fitness. They might initiate dormancy too early (thereby reducing biomass production) or too late, hence running a greater risk of damage through unfavourable conditions.

2.4.2.2 Vernalisation

Many plant species will not flower unless they have experienced winter cold. Avoidance of unfavourable conditions in this way maximises reproductive success. It implies that an individual plant retains a memory of a stress exposure. Vernalisation shows a time course very different from that of cold acclimation. The latter is triggered by comparatively brief cold exposure of minutes to hours. Vernalisation, in contrast, usually requires several weeks of cold. In fact, early physiological experiments showed that the memory of cold exposure can remain intact for many months. When a plant with a flowering behaviour that is dependent on



	63°	59°	56°	51°
22 h	+	+	+	+
21 h	-	+	+	+
20 h	-	+	+	+
19 h	-	-	+	+
18 h	-	-	+	+
17 h	-	-	-	+
15 h	-	-	-	-

Fig. 2.34 Variation in the photoperiodic control of transition to dormancy in aspen trees from different northern latitudes. **a** Map of Europe indicating the origin of the four different European aspen (*Populus tremula*) clones. The *green squares* indicate Umea (63°N), the *red diamonds* indicate Brunsberg (59°N), the *blue circles* indicate Ronneby (56°N) and the *lilac diamonds* indicate Brauna (51°N). **b** Critical day lengths for growth cessation in the collected *P. tremula* clones; + indicates growth and – indicates bud set. **c** *PtFT1* and *PtCO2* expression in the different *P. tremula* clones in a 19-h-light/5-h-dark cycle. The *shaded boxes* indicate night and the *white boxes* indicate light (Böhlenius et al. 2006)

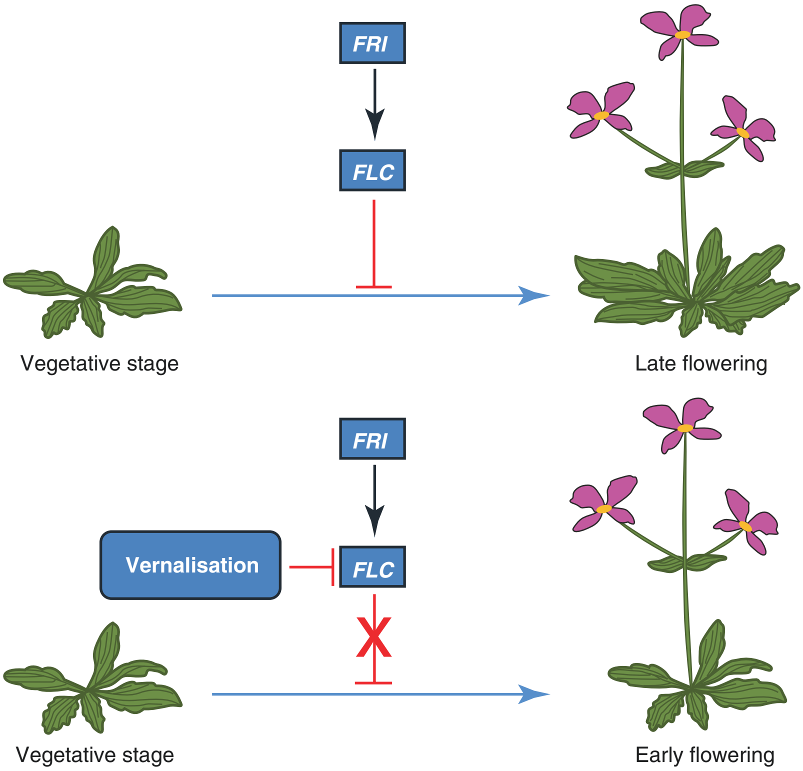
the day length and vernalisation is exposed to cold and then cultivated for a long time under a day/night cycle that represses flowering, it will flower when shifted to the permissive day length. Thus, the memory does not fade during the growth in the "wrong" day/night cycle. The memory of cold survives even when meristematic cells give rise to a new individual in tissue culture, that is, through vegetative propagation. The new individual behaves as if it had experienced the winter itself, not just the mother plant it is derived from.

How does this reliable memory work without a brain? Friedrich Laibach observed that there are winter annual accessions of *A. thaliana* that require vernalisation and there are summer annual accessions that do not. Genetic analyses of this difference led to the identification of **Flowering Locus C** (***FLC***). When the underlying gene was cloned it became clear that in winter annual accessions, the expression of *FLC* is gradually repressed during vernalisation (Fig. 2.35) (Amasino 2010). FLC acts as a repressor of flowering (Fig. 2.31) and has to be inactivated before the transition into the reproductive phase can occur. *FLC* inactivation proceeds through **epigenetic changes**. Chromatin at the *FLC* locus changes from an active state, allowing transcription of the gene to an inactive state. This change is associated with alterations in the post-translational modification of histones. The DNA thread is wrapped around histones and, depending on the molecular appearance of the histones, other proteins are recruited that either promote or suppress gene activity. Histone modifications represent one of the classic epigenetic mechanisms (see molecular biology textbooks). When cells undergo mitosis and divide, the information—that is, the pattern of histone modification—is passed onto the daughter cells. In this way the memory is maintained over long periods of time. After sexual reproduction, however, the vernalisation has to be reset, otherwise the next generation would not be able to adequately respond to its environment; for example, the plants would flower without experiencing a winter first, which could clearly be disastrous. Therefore, the epigenetic mark at the *FLC* locus is erased during the formation of gametes in meiosis.

The summer annual habit of some *A. thaliana* accessions arose through defects in the genes underlying the vernalisation requirement. Loss-of-function mutations in either the *FLC* gene itself or the gene *FRIGIDA* (*FRI*), which activates *FLC* (Johanson et al. 2000), can turn *A. thaliana* into a rapid cycler that no longer needs exposure to winter conditions. These mutations represent an early documented example of how a loss of gene function can lead to a dramatic change in a **life history** trait that may confer a potential competitive advantage in particular habitats.

The key role of FLC is not restricted to annual plants. As is the case for CO and FT, different life history traits and strategies are mediated by variations in the same factors. The

Fig. 2.35 Control of vernalisation through the floral repressor FLC. In winter annual accessions of *Arabidopsis thaliana* (note that the flower morphology and petal colour in the figure are not representative of *A. thaliana*), flowering occurs late unless winter conditions have been experienced. The *FRIGIDA* (*FRI*)–dependent expression of *FLC* suppresses the transition to flowering. Prolonged exposure to cold gradually inactivates *FLC* via histone modifications, that is, through an epigenetic mechanism. Plants acquire a mitotically stable memory of winter and flower earlier



crucifer *Arabis alpina* is perennial, that is, it goes through repeated cycles of vegetative and reproductive growth. The *FLC* orthologue in *A. alpina* (*PEP1*, for *Perpetual flowering1*) controls this behaviour as well. In contrast to the annual plant *A. thaliana*, the inactivation of *FLC* by epigenetic changes during long cold exposure is only transient in *A. alpina* (Wang et al. 2009). The plants "forget" the winter experience after a while and are again ready to respond to the next seasonal cycle.

2.4.3 Developmental Switches Triggered by Favourable Conditions

The preceding subchapters described molecular mechanisms enabling a plant to switch to reproduction at the right time by anticipating favourable conditions. Another developmental transition during a plant's life cycle, which is of at least equal importance for adaptation, is **seed germination** (Donohue et al. 2010). It determines when a new plant individual enters an ecosystem (Bewley 1997). A mature seed in its dormant state is normally well protected from abiotic and biotic stress factors. For example, its low water content practically rules out pathogen infection. Water scarcity is not a problem and the seed coat protects against damaging doses of radiation. When a seed germinates it becomes much more vulnerable to stress factors. Thus, undergoing this dramatic transition under the wrong circumstances entails an acute risk of death. The appropriate timing of germination is therefore an important aspect of an **escape**, possibly illustrated best by desert blooms. Many desert-adapted plant species are actually not able to cope with the typical conditions of a desert: scorching heat and lack of water. Still, they survive in such habitats because their seeds can lie dormant in the soil for many years and germinate only after one of the rare rain events allows a few weeks of vigorous physiological activity (Fig. 2.36).

What is critical for a successful escape is germination under favourable conditions. The ability to germinate is dependent on the **dormancy** of a seed, which imposes a delay between the shedding of a seed by the mother plant and the germination of the seed. A dormant seed is not able to germinate even when conditions such as water and permissive temperatures are present that would physiologically allow germination in the non-dormant state (Finch-Savage and Leubner-Metzger 2006). Thus, dormancy defines the conditions under which germination occurs, and dormancy has usually evolved in

Fig. 2.36 Desert bloom in the Atacama Desert

such a way that a seed of a particular plant germinates under environmental conditions that are expected to favour seedling establishment and survival. Many forms of dormancy are known—for example, **physical dormancy**, caused by a water-impermeable seed coat. Most widespread is **physiological dormancy**, and mechanistic understanding of this is available for only a few species. One of the molecular factors involved in establishing a state of dormancy is ABA. It functions as a positive regulator of dormancy, as shown by the early germination of many ABA biosynthesis and ABA perception mutants. The ABA antagonist is GA. This growth hormone can break the dormant state, and GA biosynthesis mutants of *A. thaliana* are unable to germinate (Finkelstein et al. 2008). A simplified view of dormancy regards it as a state that is controlled by the balance—that is, the ratio of concentrations—between the two hormones.

In accordance with the **hormone balance concept**, release of dormancy is associated with a shift in the ABA to GA ratio towards lower values through GA biosynthesis and ABA breakdown. Mature seeds continuously perceive information on environmental conditions. This information is used to decide on the right time for germination. Several different environmental factors can trigger the release of dormancy, and there is tremendous variation between plant species as to which factors are decisive (Lambers et al. 2008) (Fig. 2.37). A very common factor is a stimulating effect of light on seed germination. Light exposure can indicate the absence of competing vegetation above, which would give the developing seedling the chance to escape low-light stress. Also, the light requirement prevents germination of a seed buried too deeply in the soil to reach the surface. It has been known for a long time that the red light receptor **phytochrome** (Chap. 3) mediates this response. Red light absorption by the chromophore triggers a conformational change in phytochrome to its physiologically active far-red-absorbing form, P_{fr}. A high far-red to red ratio, which is typical for shade caused by vegetation, therefore inhibits the response (Chap. 3). Active phytochrome represses ABA biosynthesis and stimulates GA biosynthesis. Furthermore, it interacts with repressors of germination such as PIL5 (phytochrome interacting factor 3-like5) and causes their degradation (Holdsworth et al. 2008).

Many plants in seasonally changing climates produce seeds that should germinate only after the winter is over. For example, seeds of summer annuals shed in autumn require extended exposure to cold. This process is termed **stratification** and applies to imbibed seeds, that is, seeds that have taken up water and are now waiting for the right conditions to proceed to germination. Stratification activates GA biosynthesis. How the winter memory functions molecularly is not understood but may well be based on processes similar to the ones unravelled for vernalisation.

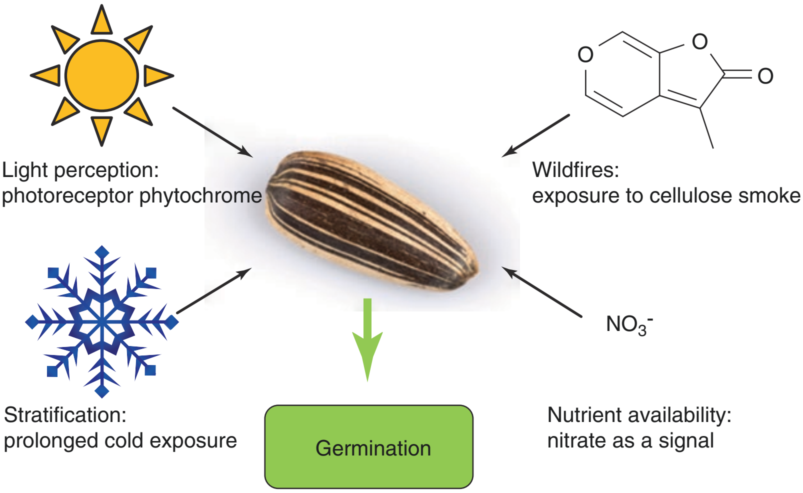


Fig. 2.37 Triggers of seed germination. Diverse environmental stimuli can be used as indicators of favourable conditions

Nitrate and molecules contained in smoke are chemical germination stimulants. Nitrate not only is an important nutrient for plants but also can serve as an indicator of nutrient availability and the absence of competing vegetation. As this is typical for a disturbed site, seeds of ruderal species particularly respond to nitrate. How nitrate sensing is translated into a modulation of the ABA to GA ratio is molecularly unresolved.

Wildfires occur in many habitats around the world and are frequent especially in hot and dry Mediterranean-type climates. After a fire the chances of successful seedling establishment are often strongly improved because shading vegetation cover is removed and nutrient availability may be greater. Several plants are so highly adapted to such conditions that germination of their seeds is strictly dependent on fire. It can proceed only after compounds released by the combustion of plant biomass are perceived. Seeds of many plant species, even those of *A. thaliana* and others that normally do not grow in fire-prone habitats, are stimulated to germinate by smoke exposure (Nelson et al. 2012). Burning cellulose and hemicellulose are very good sources of volatile germination stimulants. The first compound to be isolated was a butenolide (Flematti et al. 2004) (Fig. 2.37). It was found to be active at concentrations below 1 part per billion (ppb). Later, several closely related molecules were isolated and they are now collectively called **karrikins**. Interestingly, these karrikins are very similar to **strigolactones**, which are recently discovered plant hormones and stimulants of seed germination for **parasitic plants** (Chap. 8). At least one molecular factor (called MAX2, for MORE AXILLIARY GROWTH2) is required for the responses to both strigolactones and karrikins (Nelson et al. 2012). Thus, the signalling pathways most likely overlap.

2.4.4 Trans-Generational Stress Memory

Perception of a potential stress factor clearly influences the physiology and development of a plant in various ways. This is apparent from several phenomena discussed in previous paragraphs (Sects. 2.2–2.4). Exposure to cold induces a hardening or **acclimation** process that results in improved cold tolerance. Long-term cold experience inactivates repression of flowering (**vernalisation**). Attack by a pathogen or herbivore triggers systemic changes that result in a state of greater resistance (**systemic acquired resistance**). A fourth type of phenomenon is summarised as "**priming**". The response of a plant individual to a stress factor is shaped by a previous exposure in such a way that the plant is better able to cope with the stress factor because of the conditions it has experienced before. An example is the positive effect that colonisation by beneficial rhizobacteria can have on the pathogen resistance of a plant. This is also referred to as **induced systemic resistance**. All of these phenomena constitute a kind of **memory**. The plant's ability to cope with a stress is improved through the changes elicited by preceding conditions (Hilker et al. 2016).

A fundamental question of plant biology and also of molecular stress physiology is whether the experience of stress is passed on to the offspring as well. If this were the case, it is easy to envision how such **trans-generational stress memory** would improve the ability to thrive in a habitat characterised by certain stress factors. Indeed, it has been observed repeatedly that the offspring of parental plants exposed to a stress show greater stress tolerance than the offspring of genetically identical parental plants not exposed to the stress. This could be interpreted as evidence of a transfer of experience to the filial generation, which is reminiscent of the concept proposed by Jean-Baptiste Lamarck: an individual acquires an adaptive trait and this trait is then inherited by its progeny. The basis for such a transfer would be **epigenetics**. This term refers to heritable changes in gene expression without changes in the DNA sequence. The mechanisms underlying epigenetic phenomena are:

- Covalent modification of DNA by methylation of mostly cytosine; such methylation especially of promoter regions can silence genes
- Covalent modifications of histones (the proteins DNA is wrapped around in nucleosomes); specific modifications (e.g. acetylation, meth-

ylation, phosphorylation) can result either in chromatin that is transcriptionally active (classically called **euchromatin**) or in chromatin that is transcriptionally inactive (**heterochromatin**); the specific modifications and their consequences for the chromatin state are universal and are referred to as the **histone code**

The positions of these modifications, also called **epigenetic marks**, are often influenced by non-coding RNAs in a sequence-specific manner. For example, small RNAs guide DNA methylation (for more details, see molecular biology textbooks).

Gradual inactivation of *FLC* expression during **vernalisation** (Sect. 4.2.2) represents a form of memory conferred by epigenetic marks—in this case, histone modifications. As discussed, the memory is passed on to daughter cells in the meristems and therefore can be stable for several months. The transfer is mediated by an enzyme machinery that recognises histone modifications and introduces corresponding changes during cell division. We have also seen that the memory is erased when gametes are formed, so the memory of winter is not inherited by the offspring. This is essential for the vernalisation to serve its biological function. The key question regarding trans-generational stress memory is whether, in contrast to vernalisation, a change in chromatin that is caused by exposure to stress is passed on to the filial generation—in other words, whether stress-induced epigenetic changes can be meiotically stable. Current knowledge suggests that mitotic stability is widespread (as is the case for *FLC*), but there is very little direct evidence to support meiotic stability (Iwasaki and Paszkowski 2014) (Fig. 2.38). Thus, the existence of true trans-generational stress memory is insufficiently supported to date. Several criteria have to be met before one can truly diagnose trans-generational memory (Pecinka and Mittelsten Scheid 2012). Among them are the following: the stress memory effects should be documented for more than two non-stressed generations to rule out that in fact non-epigenetic changes caused by stress in the egg cell are carried over into the next generation (so-called **maternal effects**); the stress treatment of the parents should occur early in life and well before gamete formation in order to minimise such carry-over; and better stress acclimation of the progeny should be demonstrated under natural conditions. This is important also because one could just as well postulate that stress memory effects could be disadvantageous for the filial generation by restraining their ability to acclimate. Thus, resetting of epigenetic changes during meiosis, as seen in *FLC*, may in fact confer better adaptation than stress memory (Iwasaki and Paszkowski 2014).

What could be alternative explanations for the observed stress memory effects, that is, the greater stress tolerance of individuals originating from parents that were exposed to the stress? The most obvious ones are the aforementioned maternal effects. Acclimative changes occurring during reproduction, especially in the egg cell, influence the individual developing from the fertilised egg. A second explanation could be the well-documented activation of mobile genetic elements—**transposons**—during stress (Fig. 2.38), which was postulated by Barbara McClintock, the discoverer of transposons. Transposon mobility can influence the chromatin state in neighbouring regions of the DNA and thereby influence gene activity. Such changes could improve the stress tolerance of the progeny but would not represent stably inherited epigenetic marks.

Summary

- Plants are sessile organisms and therefore continuously exposed to abiotic and biotic environmental conditions that can fluctuate with large amplitudes. Molecular stress physiology aims to understand the mechanisms enabling a plant to cope with such fluctuations in environmental factors at the level of genes, proteins and metabolites.
- The term stress refers to suboptimal or even damaging quantities or intensities of an environmental factor. Thresholds beyond which the quantities of an environmental factor constitute stress differ widely for individual organisms and even for particular organs in the same organism.

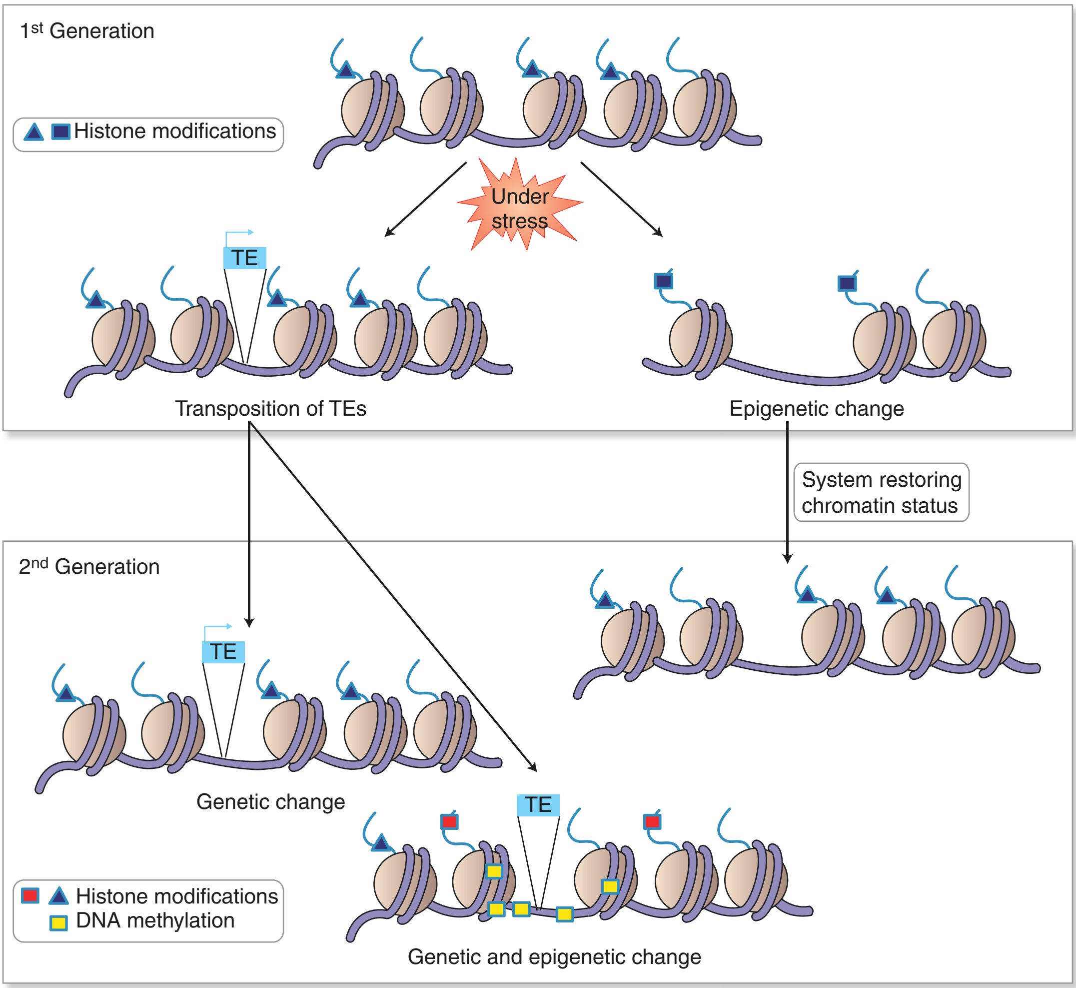


Fig. 2.38 Epigenetic changes under stress. Stress exposure causes epigenetic changes, such as histone modifications, that influence the chromatin state and thereby transcriptional activity. Such changes are mostly transient because they are reset during meiosis and therefore are not passed on to the next generation. Positive stress memory effects could be due to the activation of transposons (TE: transposable elements)—mobile DNA that could, upon transposition, influence the chromatin stage of neighbouring genes and affect transcriptional activity (Iwasaki and Paszkowski 2014)

- Stress can be observed and quantified as the strain, i.e., the effects a particular stress or stress combination has on an organism.
- Several different strategies enable individuals of a species to survive and reproduce in a particular environment. Organisms escape when they are able to evade unfavourable conditions by restricting growth and reproduction to periods free of a particular stress factor. Tolerance is the term most commonly used to describe a plant's ability to survive a given stress. It represents one of two principal ways to achieve resistance. The other is avoidance: a plant is able to limit the strain caused by a stress factor. Stress resistance varies strongly between plant species. Also, there is intraspecific variation in stress resistance between genotypes, accessions and cultivars.
- Changes occurring under stress are generally referred to as stress responses. Acclimation is achieved when the exposure of an individual to stress results in greater stress tolerance. In contrast, adaptation is the consequence of genetic changes occurring in populations over evolutionary time scales, that is, many generations.

- Abiotic environmental factors are summarised as the physiological filters that a plant species has to pass through in order to colonise a habitat. Also, a species or population has to pass through biotic filters such as competition from other plants, pathogens or herbivores. The first filter a species or population passes through is the historical filter, that is, individuals have to arrive in the habitat in question.
- In order to limit the costs, mechanisms of stress tolerance or avoidance are very often inducible. The underlying processes represent a major part of molecular stress physiology and can be structured into distinct layers: primary stress–secondary stress–stress sensing–signal transduction–activation of tolerance mechanisms.
- Stress sensing is not yet understood molecularly. Also, it is still difficult to specifically assign a molecular function to many of the putative protective proteins synthesised by cells during the course of a stress response.
- Ubiquitous elements of signal transduction under stress are Ca^{2+} signals, the activation of phosphorylation cascades and the modulation of protein stability. The phytohormone abscisic acid (ABA) plays a key role particularly in activating mechanisms conferring abiotic stress tolerance. In addition, there is ABA-independent signalling. Pathways converge and diverge, which explains cross-protection.
- The enhanced accumulation of reactive oxygen species (ROS) is a common theme of stress conditions and thus a typical secondary stress. Organelles with high rates of electron flow—that is, chloroplasts, peroxisomes/glyoxysomes and mitochondria—are major sites of ROS generation. Stress disturbs cellular homeostasis, inevitably causing an increase in the production of ROS—for example, in the Mehler reaction in photosystem I.
- ROS are not only stress indicators. Plant cells under stress actively synthesise ROS as second messengers through reduced nicotinamide adenine dinucleotide phosphate (NADPH) oxidases and other enzymes (oxidative bursts).
- An extensive network of antioxidant metabolites and enzymes balances the level of ROS by directly inactivating or by converting ROS, respectively.
- Stress signalling is not only local (i.e. within a cell or between neighbouring cells) but also systemic. Information on the occurrence of a stress is conveyed to distant tissues and organs, enabling them to prepare for the stress before it actually arises. Systemic signalling can act as a warning and is essential when stress that is experienced by one organ or tissue can be alleviated only through the activity of a different organ or tissue. The principal types of long-distance signals are hydraulic, electrical and chemical.
- The large majority of molecular insights into plant stress responses and acclimation have come through studies performed with the model system *Arabidopsis thaliana*. They are applicable to higher plants in general because the mechanisms are principally conserved.
- The plasticity of developmental steps and organ formation—that is, the integration of environmental cues into growth responses—is a hallmark of plant biology. Active growth modulation is an integral element of stress acclimation. The key components are negative regulators of the response to gibberellic acid (GA), one of the classic plant growth hormones.
- Escape and the ability to limit the cost of investment in acclimative processes are enabled by the anticipation of recurring stressful environmental conditions. In seasonal environments the timing of major life history transitions such as germination and flowering is crucial for establishment, survival and successful reproduction. Biological clocks generate intrinsic circadian rhythms that help organisms coordinate physiological activities with fluctuating environmental conditions in day/night cycles. Combined with the perception of light, the circadian clock enables the perception of changes in the day length (photoperiodism). Anticipation of seasons is also afforded by reliable perception of abiotic conditions typical of a cold winter (vernalisation).
- Photoperiodism controls flowering in many plants. It depends on the coincidence of two

events: the recurring peak in transcription controlled by the intrinsic biological clock and exposure to the external factor light. Key players identified in *A. thaliana* are the regulator CONSTANS (CO)—whose expression follows a circadian rhythm—and the photoreceptors phytochrome and cryptochrome. CO activity triggers the synthesis of the flowering signal florigen (FT protein), which is produced in leaves and travels to the shoot apical meristem via the phloem. The module consisting of CO and FT is essential for other photoperiodic processes as well and likely explains such phenomena throughout the plant kingdom.

- Challenges arise from rapid climate changes, especially for perennial plants. When seasonal changes in temperature or precipitation can no longer be reliably anticipated by measurement of the day length, organisms will suffer from a loss of fitness.
- Instead of—or in addition to—a particular day length, many winter annual and perennial plants require prolonged exposure to cold (i.e. to winter conditions in temperate regions) before they flower. Vernalisation is conferred through the gradual inactivation of the floral repressor *FLC* by histone modifications, a typical epigenetic mark.
- Seed germination represents another developmental transition that is important for adaptation. The right timing to ensure germination under favourable conditions is critical for successful establishment. According to the hormone balance concept, release of seed dormancy is associated with a shift in the ABA to GA ratio towards lower values through GA biosynthesis and ABA degradation. Several environmental cues—including light, temperature, smoke and nutrients—can trigger germination in different plant species.
- Acclimation, systemic acquired resistance and vernalisation can be seen as manifestations of stress memory. A plant’s ability to cope with a stress is improved through the changes elicited by preceding conditions. An open question in biology is the existence of trans-generational memory, that is, the possible transfer of stress experience to progeny through epigenetic changes.

References

Achard P, Cheng H, De Grauwe L et al (2006) Integration of plant responses to environmentally activated phytohormonal signals. Science 311:91–94

Alonso JM, Stepanova AN, Leisse TJ et al (2003) Genome-wide insertional mutagenesis of *Arabidopsis thaliana*. Science 301:653–657

Amasino R (2010) Seasonal and developmental timing of flowering. Plant J 61:1001–1013

Apel K, Hirt H (2004) Reactive oxygen species: metabolism, oxidative stress, and signal transduction. Annu Rev Plant Biol 55:373–399

Arabidopsis Genome Initiative (2000) Analysis of the genome sequence of the flowering plant *Arabidopsis thaliana*. Nature 408:796–815

Assmann SM (2013) Natural variation in abiotic stress and climate change responses in Arabidopsis: implications for twenty-first-century agriculture. Int J Plant Sci 174:3–26

Bewley JD (1997) Seed germination and dormancy. Plant Cell 9:1055–1066

Böhlenius H, Huang T, Charbonnel-Campaa L et al (2006) CO/FT regulatory module controls timing of flowering and seasonal growth cessation in trees. Science 312:1040–1043

Boyer JS (1982) Plant productivity and environment. Science 218:443–448

Buchanan B, Gruissem W, Jones R (2015) Biochemistry and molecular biology of plants, 2nd edn. Wiley, Hoboken

Claeys H, Inzé D (2013) The agony of choice: how plants balance growth and survival under water-limiting conditions. Plant Physiol 162:1768–1779

Claeys H, Landeghem SV, Dubois M et al (2014) What is stress? Dose–response effects in commonly used in vitro stress assays. Plant Physiol 165:519–527

Clausen J, Keck D, Hiesey W (1947) Heredity of geographically and ecologically isolated races. Am Nat 81:114–133

Colebrook EH, Thomas SG, Phillips AL, Hedden P (2014) The role of gibberellin signalling in plant responses to abiotic stress. J Exp Biol 217:67–75

Darwin C (1880) The power of movement in plants. John Murray, London

Dodd AN, Kudla J, Sanders D (2010) The language of calcium signaling. Annu Rev Plant Biol 61:593–620

Dodd AN, Salathia N, Hall A et al (2005) Plant circadian clocks increase photosynthesis, growth, survival, and competitive advantage. Science 309:630–633

Donohue K, Rubio de Casas R, Burghardt L et al (2010) Germination, postgermination adaptation, and species ecological ranges. Annu Rev Ecol Evol Syst 41:293–319

Finch-Savage WE, Leubner-Metzger G (2006) Seed dormancy and the control of germination. New Phytol 171:501–523

Finkelstein R, Reeves W, Ariizumi T, Steber C (2008) Molecular aspects of seed dormancy. Annu Rev Plant Biol 59:387–415.

Fitter A, Hay RKM (1987) Environmental physiology of plants, 2nd edn. Academic Press, London

Flematti GR, Ghisalberti EL, Dixon KW, Trengove RD (2004) A compound from smoke that promotes seed germination. Science 305:977

Gilroy S, Suzuki N, Miller G et al (2014) A tidal wave of signals: calcium and ROS at the forefront of rapid systemic signaling. Trends Plant Sci 19:623–630

Goodspeed D, Chehab EW, Min-Venditti A et al (2012) Arabidopsis synchronizes jasmonate-mediated defense with insect circadian behavior. Proceedings of the National Academy of Sciences 109:4674–4677

Gould S, Lewontin R (1979) Spandrels of San Marco and the Panglossian paradigm—a critique of the adaptationist program. Proc R Soc Lond B Biol Sci 205:581–598

Halliwell B (2006) Reactive species and antioxidants. Redox biology is a fundamental theme of aerobic life. Plant Physiol 141:312–322

Hansen J (2000) Überleben in der Kälte—wie Pflanzen sich vor Froststress schützen. Biologie in unserer Zeit 30:24–34

Harmer SL, Hogenesch JB, Straume M et al (2000) Orchestrated transcription of key pathways in Arabidopsis by the circadian clock. Science 290:2110–2113

Hilker M, Schwachtje J, Baier M et al (2016) Priming and memory of stress responses in organisms lacking a nervous system. Biol Rev 91:1118–1133

Holdsworth MJ, Bentsink L, Soppe WJJ (2008) Molecular networks regulating Arabidopsis seed maturation, after-ripening, dormancy and germination. New Phytol 179:33–54

Howe GA, Jander G (2008) Plant immunity to insect herbivores. Annu Rev Plant Biol 59:41–66

Hsu PY, Harmer SL (2014) Wheels within wheels: the plant circadian system. Trends Plant Sci 19:240–249

Huber AE, Bauerle TL (2016) Long-distance plant signaling pathways in response to multiple stressors: the gap in knowledge. J Exp Bot 67:2063–2079

Huijser P, Schmid M (2011) The control of developmental phase transitions in plants. Development 138:4117–4129

Ishitani M, Xiong LM, Stevenson B, Zhu JK (1997) Genetic analysis of osmotic and cold stress signal transduction in Arabidopsis: interactions and convergence of abscisic acid–dependent and abscisic acid–independent pathways. Plant Cell 9:1935–1949

Iwasaki M, Paszkowski J (2014) Epigenetic memory in plants. EMBO J 33:1987–1998

Johanson U, West J, Lister C et al (2000) Molecular analysis of FRIGIDA, a major determinant of natural variation in Arabidopsis flowering time. Science 290:344–347

Karpinski S, Reynolds H, Karpinska B et al (1999) Systemic signaling and acclimation in response to excess excitation energy in Arabidopsis. Science 284:654–657

Kilian J, Whitehead D, Horak J et al (2007) The AtGenExpress global stress expression data set: protocols, evaluation and model data analysis of UV-B light, drought and cold stress responses. Plant J 50:347–363

Kobayashi Y, Weigel D (2007) Move on up, it's time for change—mobile signals controlling photoperiod-dependent flowering. Genes Dev 21:2371–2384

Kochian LV, Piñeros MA, Liu J, Magalhaes JV (2015) Plant adaptation to acid soils: the molecular basis for crop aluminum resistance. Annu Rev Plant Biol 66:571–598

Koornneef M, Hanhart CJ, van der Veen JH (1991) A genetic and physiological analysis of late flowering mutants in *Arabidopsis thaliana*. Mol Gen Genet 229:57–66

Lambers H, Chapin FS III, Pons TL (2008) Plant physiological ecology, 2nd edn. Springer, New York

Larcher W, Bodner M (1980) Dose-lethality nomogram for characterizing of the chilling susceptibility of tropical plants. Angew Bot 54:273–278

Levitt J (1980) Responses of plants to environmental stresses, 2nd edn. Academic Press, New York

Lichtenthaler HK, Miehe JA (1997) Fluorescence imaging as a diagnostic tool for plant stress. Trends Plant Sci 2:316–320

Marino D, Dunand C, Puppo A, Pauly N (2012) A burst of plant NADPH oxidases. Trends Plant Sci 17:9–15

McAinsh MR, Pittman JK (2009) Shaping the calcium signature. New Phytol 181:275–294

Mitchell-Olds T, Schmitt J (2006) Genetic mechanisms and evolutionary significance of natural variation in Arabidopsis. Nature 441:947–952

Mittler R (2002) Oxidative stress, antioxidants and stress tolerance. Trends Plant Sci 7:405–410

Mittler R, Blumwald E (2015) The roles of ROS and ABA in systemic acquired acclimation. Plant Cell 27:64–70

Nakashima K, Ito Y, Yamaguchi-Shinozaki K (2009) Transcriptional regulatory networks in response to abiotic stresses in Arabidopsis and grasses. Plant Physiol 149:88–95

Nelson DC, Flematti GR, Ghisalberti EL et al (2012) Regulation of seed germination and seedling growth by chemical signals from burning vegetation. Annu Rev Plant Biol 63:107–130

Pecinka A, Mittelsten Scheid O (2012) Stress-induced chromatin changes: a critical view on their heritability. Plant Cell Physiol 53:801–808

Pierik R, Testerink C (2014) The art of being flexible: how to escape from shade, salt, and drought. Plant Physiol 166:5–22

Provart NJ, Alonso J, Assmann SM et al (2016) 50 years of Arabidopsis research: highlights and future directions. New Phytol 209:921–944

Ryu S, Costa A, Xin Z, Li P (1995) Induction of cold-hardiness by salt stress involves synthesis of cold-responsive and abscisic acid–responsive proteins in potato (*Solanum commersonii* Dun). Plant Cell Physiol 36:1245–1251

Santner A, Estelle M (2009) Recent advances and emerging trends in plant hormone signalling. Nature 459:1071–1078

Scheibe R, Beck E (2011) Drought, desiccation, and oxidative stress. In: Lüttge U, Beck E, Bartels D (eds) Plant desiccation tolerance, Ecol. Studies, vol 215. Springer, Berlin, Heidelberg, pp 209–231

Suzuki N, Rivero RM, Shulaev V et al (2014) Abiotic and biotic stress combinations. New Phytol 203:32–43

Vinocur B, Altman A (2005) Recent advances in engineering plant tolerance to abiotic stress: achievements and limitations. Curr Opin Biotechnol 16:123–132

Wang RH, Farrona S, Vincent C et al (2009) Pep1 regulates perennial flowering in *Arabis alpina*. Nature 459:423–427

Wang W, Barnaby JY, Tada Y et al (2011) Timing of plant immune responses by a central circadian regulator. Nature 470:110–114

Yanovsky MJ, Kay SA (2002) Molecular basis of seasonal time measurement in Arabidopsis. Nature 419:308–312

Zeevaart JAD (2006) Florigen coming of age after 70 years. Plant Cell 18:1783–1789

3 Light

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Wide spatial and temporal gradients of light intensity characterise the light climate of a tropical mountain forest in the Andes of Ecuador. On average, less than 10% of the incoming radiation reaches the vegetation on the forest floor. However, spatially limited sunflecks can increase the light intensity several hundredfold for a short while, challenging the adaptability of the photosynthetic apparatus of the leaves. Note the dense cover of epiphytes on the branches of the trees. (Photo: M. Richter, Erlangen)

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3.1 The Dual Significance of Light

Sunlight is by far the most dominant energy source for all life on Earth. For plants, as sessile photoautotrophic organisms, it is one of the most important environmental factors. Light varies in intensity and spectral composition from place to place, from season to season, and in the course of the daily photoperiod. In order to optimally harvest the **energy** of light and to minimise stress arising from insufficient or supraoptimal absorption of photons, plants have evolved multiple ways to modulate light exposure and photosynthesis (Scholes et al. 2011; Chaps. 9 and 12).

Furthermore, light quality (colour), intensity (quantum flux) and duration (day length) have a second function as **environmental cues**, which guide the plant through its entire life cycle. Developmental plasticity of plants enables effective **adaptation** and **stress avoidance** strategies and is to a large extent based on the ability to perceive and transduce light signals. Key transitions from seed to germination, through subsequent phases of vegetative growth, to flowering and finally senescence of the entire plant or its organs are regulated in response to a fluctuating light environment (Chap. 2, Sect. 2.1.4).

Plants have evolved photosynthetic pigments such as chlorophylls to harvest the energy of light, and a diverse set of photoreceptors to monitor the intensity, spectral composition and direction of light. Photoreceptors differ from the photosynthetic pigments with respect to absorption spectra, intracellular localisation and the effects of excitation by photons. While the light-harvesting systems are found in the chloroplasts/thylakoids, the sensors regulating developmental processes are localised in the cytosol and the nucleus. Excitation of chlorophyll initiates an electron transfer chain coupled to the production of adenosine triphosphate (ATP) and reduced nicotinamide adenine dinucleotide phosphate (NADPH). Excitation of photoreceptors triggers signal transduction processes and concomitant changes in gene expression. In spite of the fundamental differences in the molecular, biochemical and biophysical processes involved, the two functions of light for plants—as an energy source and as an environmental cue—are tightly interlaced. Many of the responses of a plant to changing light conditions result in an optimisation of utilisation of light for photosynthesis.

Terrestrial plants, as well as the majority of algae, use blue and red light for photosynthesis. The respective accessory pigments are **carotenoids** and **chlorophyll b** (in some algae also other chlorophylls), while the reactive photopigments are dimers of chlorophyll a, termed **P680** and **P700**, respectively. The bulk of **chlorophyll a** serves as a light-harvesting pigment. **Cyanobacteria** and red algae have no chlorophyll b but have additional accessory pigments, which allow them to inhabit aquatic biotopes with an altered composition of the visible spectrum. **Phycobiliproteins**, assembled in the **phycobilisomes**, allow these organisms to effectively use blue-green light for photosynthesis and thus to inhabit deeper water layers or muddy waters where green algae cannot harvest sufficient light for photosynthesis. Red light is absorbed in the top layers of a water body and blue light is scattered, resulting in the dominance of blue green at greater depth. Red algae and cyanobacteria are able to dynamically modify the proportions of the red-absorbing and blue-green-absorbing pigments in the phycobilisomes to acclimate to special light climates (MacIntyre et al. 2002) (Fig. 3.1).

A minor yet highly relevant component of the solar radiation reaching the Earth's surface is ultraviolet (**UV**) **light**. Because of its high energy it can be damaging to the macromolecules of biological systems, including DNA. Therefore, plants—like other organisms colonising the land—have evolved very effective mechanisms for protection against UV radiation and to repair UV-induced damage. Activation of repair is in part dependent on the perception of UV light as a signal.

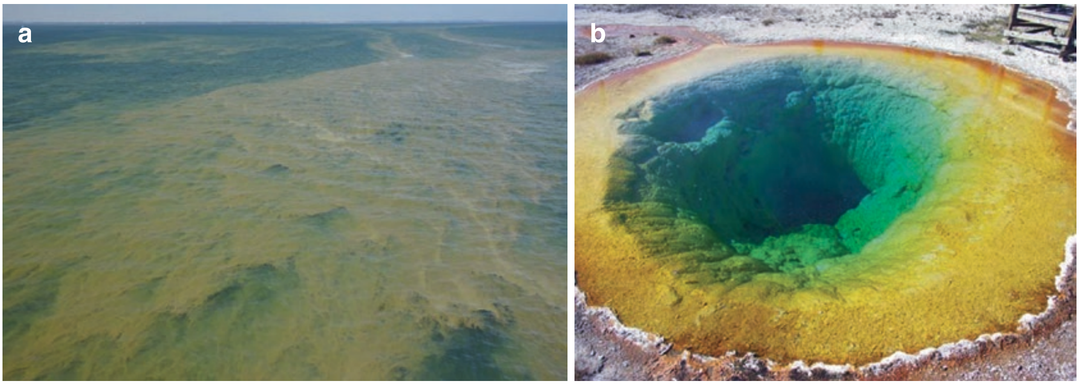

Fig. 3.1 Cyanobacteria are photosynthesising prokaryotes in saline as well as fresh waters. **a** Whips of cyanobacteria accumulating close to the surface in the southern Baltic Sea. The brownish colour of these unicellular organisms does not support their common name, blue-green algae, as the typical phycobilins are often overlaid by carotenoids (Rastogi et al. 2010) (Nordic Microalgae c/o SMHI Oceanographic Unit Sven Källfelts gata 15, SE-426 71 Västra Frölunda Sweden; Copyright by Bengt Karlson). **b** Colourful zonation of cyanobacteria in the Morning Glory Pool at the Yellowstone National Park, Wyoming (from *Encyclopaedia Britannica Online* (2016); license no. SSTK-041E2-CF2B by Shutterstock)

Avoidance of damage by excessive irradiation or of low light, as well as acclimation to different and changing light climates, occur at different levels: morphological, anatomical (Chaps. 9 and 12), cellular, subcellular and molecular. Several of the responses, particularly the morphological and structural ones, are principally irreversible—for instance, the formation of shade and sun leaves. Others are dynamic and reversible, such as hinge movements of entire leaves or the displacement of chloroplasts within the cells. In a few cases (e.g. the **shade avoidance response** and state transitions), mechanisms have been elucidated in molecular detail.

This chapter will focus on avoidance and acclimation responses of plants to fluctuating light climate and to UV exposure, as well as the perception systems underlying light-controlled plasticity of plant development. For the mechanisms of photosynthesis and comprehensive accounts of light signal transduction, the reader is referred to plant physiology and plant biochemistry textbooks (e.g. Buchanan et al. (2015) and Taiz et al. (2015)).

3.2 Visible Light

3.2.1 Avoidance of Light Stress and Permanent or Dynamic Acclimation

Lack of light, interspersed with high light intensity of short-term **sunflecks**, combined with a change in the spectral composition of the radiation (Fig. 3.2), is a major stressor of the vegetation on the forest floor and, less dramatically, in the shade crown of a tree (Chap. 9). As the leaves in the canopy absorb mainly blue and red light, green light is enriched in the spectral composition of the subcanopy space (“**green shade**”). Not visible to the human eye is another change in the spectrum of sunlight by passage through the forest canopy: the dramatic decrease in the **red to far-red ratio**, as the leaves absorb red and blue light but transmit and reflect far-red light (Chap. 9).

Responses to low light are obvious at the forest edges where subcanopy plants (e.g. ferns and other herbaceous species) show a pronounced **phototropic reaction**—that is, they grow

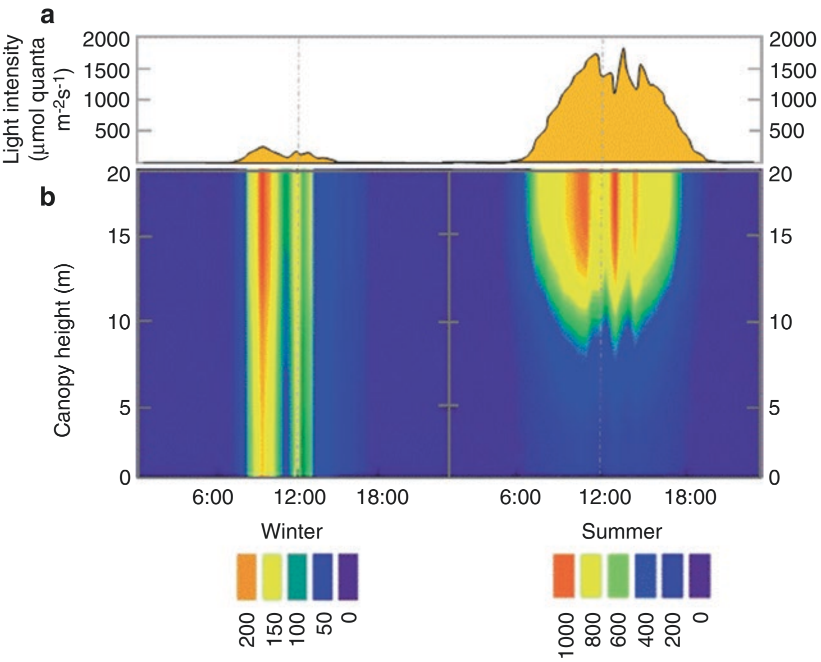

Fig. 3.2 Seasonal change of the light climate in an oak–pine forest. **a** Daily courses of the light intensity above the canopy. **b** Light attenuation in the New Jersey Pine Barrens oak-pine forest in early February (*left side*) and at the end of July (*right side*). Note the *different scales* used for the *colour bars* for winter and summer. All units are in micromoles of photons per square metre per second. (Modified from Schäfer and Dirk (2011))

towards the higher radiation intensity outside the forest. Plant life forms that avoid the attenuated light climate under the canopy of a forest are functional types such as **epiphytes** and **lianas**; both are light parasites that use trees as support to reach more favourable light conditions (Chap. 9).

On the other hand, a surplus of light intensity can also cause problems, as photosynthetic pigments cannot avoid energy absorption, which may overstrain the photosynthetic capacity of the chloroplasts and produce reactive oxygen species (ROS) (Chap. 2, Sect. 2.2.3). Leaves often avoid excessive irradiation by adopting a parallel position to the incident light. The hanging leaves of *Eucalyptus* are well known from the "shadeless forests" in Australia. Likewise, the upright position of the leaves of the characteristic giant rosette plants of the tropical high mountains (Fig. 4.25) has been described as a mechanism for avoiding direct solar radiation.

The position of the leaf lamina of many plants varies during the daily light period, changing the angle and intensity of the incoming radiation. Such leaves often have joints between the petiole and the lamina, known as pulvini (Fabaceae, Oxalidaceae), which enable fast changes in the position of the entire leaves or at least the pinnules (Chap. 9). The reaction of the North American wood sorrel (*Oxalis oregano*) to short-term high-light stress from a **sunfleck** is shown in Fig. 3.3.

Dynamic acclimation to the light intensity can be observed at the cellular level too. In many algae and mosses, but also in vascular plants, chloroplasts can change their position in the cell. They accumulate on the light-exposed surfaces in the case of low light and at the light-parallel cell boundaries when the radiation becomes too strong (Fig. 3.4). Such readily reversible intracellular reactions are mediated through the blue light receptor phototropin (Wada 2013).

Besides such short-term acclimations (with a reaction time in minutes), development of leaves responds to the light environment by the so-called shade avoidance syndrome and the formation of sun and shade leaves. The **shade avoidance syndrome** is part of the morphogenetic reaction of seedlings when they are grown under low light intensities caused, for instance, by competing

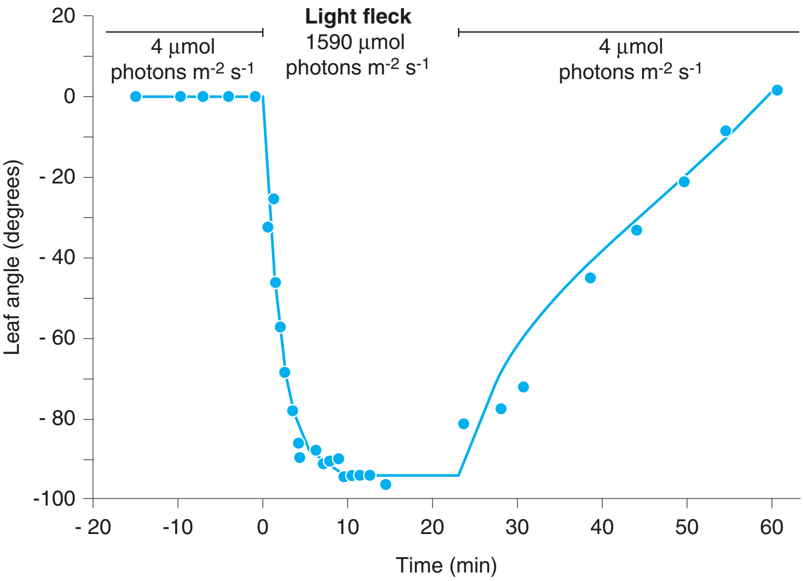

Fig. 3.3 Avoidance of light stress by a change in the leaf angle. *Oxalis oregano*, the wood sorrel, is a particular shade plant whose leaves avoid light stress of bright sunflecks by rapidly changing the angle of their leaflets by virtue of pulvini. When the sunfleck is over they slowly return to their horizontal position, which is optimal for light harvesting. (After Björkman and Powles (1981))

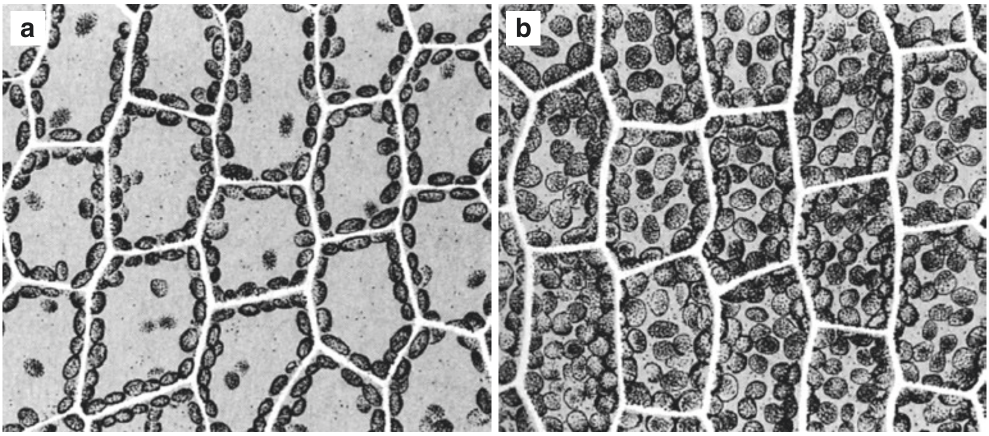

Fig. 3.4 Chloroplast movement is important for avoiding photodamage under high light and for efficient light harvesting under low light. Object: Leaflet of the moss *Funaria hygrometrica*, consisting of a single layer of chloroplast-containing cells. **a** Position on the lateral walls of the cells in high light. **b** Position of the chloroplast on the light-exposed side in low light (Nultsch 2001). A special protein named Chloroplast Unusual Position 1 (CHUP 1) is unique in positioning and moving chloroplasts in the *Arabidopsis thaliana* leaf cell. It is assumed that CHUP 1 connects the chloroplast with the actin cell skeleton and the cell membrane (Oikawa et al. 2003, 2008; Usami et al. 2012)

neighbours. Owing mostly to the identification of the main photoreceptors in the model plant *Arabidopsis thaliana* and the availability of respective mutants, knowledge on the molecular regulation of plant growth and development by light is rapidly accumulating (Casal 2013; Lau and Deng 2012; Liu et al. 2011; Lau and Deng 2012; Kami et al. 2010). Because a separation of acclimation and development is principally difficult here, we focus on the reactions triggered by **light stress**—that is, by either insufficient or supraoptimal light intensities.

The typical **shade avoidance reaction** in *A. thaliana* can serve as an example illustrating the integration of light cues and growth at the molecular level. Seedlings show an inhibition of lamina expansion, while petiole elongation and stem growth are enhanced. **Phytochromes** (PhyB) and **cryptochromes** (Cry1 and Cry2), as photoreceptors, have been demonstrated to play specific roles in these differential growth responses. Phytochromes especially are ideally suited to convey information on shade occurrence because of their switching between red and far-red absorption and the pronounced difference in the ratio of these two light qualities between sunlight and shade light. Low **red to far-red ratios** typical of shade light reduce the levels of active PhyB. Because PhyB inactivates a class of transcription factors named **phytochrome-interacting factors** (**PIFs**), their activity increases under shade light conditions. PIFs have been demonstrated to induce growth responses—for instance, through the activation of genes involved in cell wall biosynthesis. In addition, PIFs influence phytohormone signalling. They enhance **auxin** concentrations through the activation of auxin biosynthesis. Promotion of shade avoidance reactions by the other growth hormones **gibberellic acid** and **brassinosteroids** can be attributed to a positive effect on PIF abundance. The function of cryptochromes in shade avoidance is associated with degradation of the **constitutive photomorphogenesis protein 1** (**COP1**) (Fig. 3.22), which is jointly triggered by cryptochromes and phytochromes, albeit in an unknown fashion different from photomorphogenesis (Casal 2013).

The **shade avoidance reaction** as observed under low red to far-red illumination must be attenuated when exposure to this light climate is prolonged and also when the leaf reaches into a space with sufficient light intensity. Similarly, sunflecks reduce the shade avoidance response. An autoregulatory mechanism involving transcription factors such as **HY5** (Figs. 3.21 and 3.22) has been described that helps to avoid exaggerated shade avoidance responses (Jiao et al. 2007).

Through the shade avoidance reaction the plant strives to escape unfavourable low light intensity, using its resources to grow into a better-illuminated space. A typical example is the ground flora in a forest, consisting of herbs and bushes with elongated internodes and smaller leaves (Chap. 9). The **formation of sun and shade leaves**, on the other hand—which is well known from tree crowns—can be understood as differential acclimation of a plant's foliage to high light intensities in the outer part (the so-called sun crown) and low light intensity in the centre of the crown (termed the shade crown). Such differentiation within the same shoot is possible because of the modularity of the plant structure, which is composed principally of similar units called **phytomers**, whose development can be individually guided by local environmental cues (Chap. 2, Sect. 2.4.3). Sun leaves deliver the major share of the photosynthetic gain owing to an acclimated photosynthetic machinery but also exhibit greater dynamics of cell respiration. In shade leaves, both processes run at lower rates, which shows their autonomy and ensures survival. Export of assimilates from shade leaves to other plant organs, however, may be low or non-existent. Further characteristics of thick sun leaves and thin shade leaves are summarised in Table 3.1.

In contrast to trees, herbs are amenable to experimental approaches aimed at understanding the formation of physiologically and anatomically different types of leaves (Fig. 3.5). The signals indicating a high-light climate are perceived by the mature leaves, which trigger the respective development of the young leaves in the apical shoot meristem via long-distance signalling. Interestingly, the **ambient CO_2 concentration** has effects on the formation of sun and shade leaves similar to those of the light intensity. High CO_2 leads to the formation of sun leaves (Prior et al. 2004; Pritchard et al. 1999).

From experiments such as those shown in Fig. 3.5 it was concluded that, at least in dicots, **systemic signalling** (Chap. 2, Sect. 2.2.4) depending on the light environment influences the development of new foliage and thus triggers acclimation to the actual light quality and intensity. Long-distance signalling from mature to developing leaves is also known from herbivore and pathogen attacks (Chap. 8), and most likely a multitude of signals is involved in mediating

Table 3.1 Comparison of characteristic traits of shade- and sun-acclimated leaves

Characteristic	Sun leaf	Shade leaf
Structural traits		
Dry mass per area	High	Low
Leaf thickness	Thick	Thin
Palisade parenchyma thickness	Thick	Thin
Spongy parenchyma thickness	Similar	Similar
Density of stomata	High	Low
Chloroplasts per area	Many	Few
Thylakoid density in the stroma	Low	High
Thylakoids per granum	Few	Many
Biochemical traits		
Chlorophyll per chloroplast	Low	High
Chlorophyll per area	Similar	Similar
Chlorophyll per dry mass	Low	High
Chlorophyll a to chlorophyll b ratio	High	Low
Light-harvesting complexes per area	Few	Many
Electron transport components per area	High	Low
ATPase per area	High	Low
RubisCO per area	High	Low
Nitrogen per area	High	Low
Xanthophylls per area	High	Low
Gas exchange		
Photosynthetic capacity per area	High	Low
Dark respiration per area	High	Low
Photosynthetic capacity per dry mass	Similar	Similar
Dark respiration per dry mass	Similar	Similar
Carboxylation capacity per area	High	Low
Electron transport capacity per area	High	Low
Quantum yield	Similar	Similar
Light response curve		

RubisCO ribulose-1,5-bisphosphate carboxylase/oxygenase. (Modified from Lambers et al. (2008))

different types of responses. Acclimation of the **photosynthetic apparatus** appears to be under the control of the redox state. Thus, redox signalling may also be part of the long-distance conveyance of biochemical information. Also, the concentrations of **photosynthates** may act as an indirect cue for the light climate of mature leaves. However, since the formation of sun and shade leaves is a highly complex syndrome, involvement of various further signals can be expected.

At the cellular level the epidermal cells, in particular, contribute to the protection of the mesophyll cells against **high-light stress**. A felt-like layer of dense hairs, which reflects incident light, is found on young leaves of many plant species. Although it can be kept for permanent protection, it mostly disappears during maturation of the leaves (Chap. 9). Protective pigments, which absorb predominantly short-wave radiation, are also found in the epidermis of young leaves. A typical example is the so-called **juvenile anthocyanin** (Fig. 3.25), which protects not yet fully green leaves during the development of the photosynthetic apparatus. Later, protection is conferred mostly by carotenoids in the antennae. This is apparent from the disappearance of the pigments in the epidermis.

3.2.1.1 Ultrastructural Acclimation to the Light Environment

Chloroplasts of **sun and shade leaves** differ greatly with respect to their thylakoid systems (Fig. 3.6). Chloroplasts of sun leaves possess only thin grana, while chloroplasts of shade leaves show large grana stacks. The importance of the size of the thylakoid system in a chloroplast becomes obvious when the molecular structure of the thylakoid membranes and the functions of the photosynthetic protein complexes are considered. As photosystem II (PS II) has a larger antenna than photosystem I (PS I), over half of the total **chlorophyll a**, almost all of the **chlorophyll b** and most of the **carotenoids** (β-carotene and xanthophylls) are associated with PS II. The largest part of a cross-section through a photosystem consists of its antennae. PS II and its antennae are located in the so-called appressed regions—the contact zones of the stacked thylakoids. The number of antenna complexes—especially the outer or mobile antennae, which feed excitation energy to the photosynthetic reaction centre—is variable. A shade chloroplast contains a very large number of light-harvesting systems relative to the reaction centres, owing to the large thylakoid stacks and big antennae. This corresponds to a lower **chlorophyll a to chlorophyll b ratio**, indicating

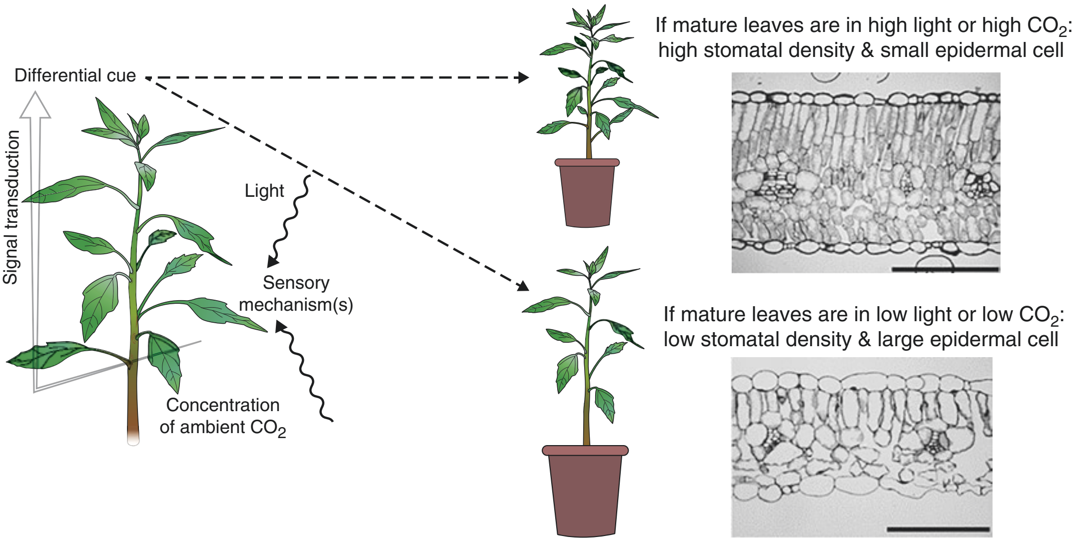

Fig. 3.5 Differential development of sun and shade leaves in *Chenopodium album* in response to light intensity and CO_2 concentration. Sun leaves have a dense mesophyll with at least two layers of palisade parenchyma cells, which originate from a directional change of the cell divisions. The *scale bars* indicate 100 µm (Kim et al. 2005)

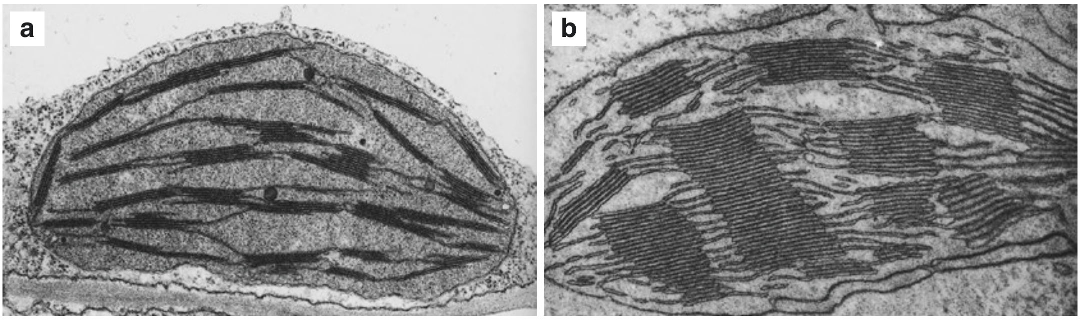

Fig. 3.6 Acclimation of chloroplast ultrastructure to the light environment. **a** Chloroplast from a sun leaf of tobacco. The small grana stacks are typical of chloroplasts from high-light leaves (Hall and Rao 1994). **b** Transverse section of a chloroplast from a shade leaf of snapdragon (*Antirrhinum majus*), showing enhanced thylakoid stacking (Strasburger 1983)

a higher proportion of the light-harvesting chlorophyll b–containing antennae around photosystem II (Table 3.1) (Kitajima and Hogan 2003). Chloroplasts of sun leaves, in contrast, contain smaller antennae and thus the ratio of antennae to reaction centres is smaller. The different organisation of the thylakoid systems of sun leaf and shade leaf chloroplasts can be considered a physiological acclimation to the ambient light environment, as both combinations allow optimal utilisation of the incident light. Such differences are observed not only in sun and shade leaves but also between the upper and lower mesophyll cells of dorsiventral leaves. Chloroplasts of the better-illuminated upper side appear as sun leaf chloroplasts, while those of the lower side (usually the spongy parenchyma) show characteristics of shade leaf chloroplasts. As the thylakoid system of a chloroplast is a dynamic substructure, fixing a leaf upside down accordingly results in a reorganisation of the thylakoid systems of the mesophyll cells.

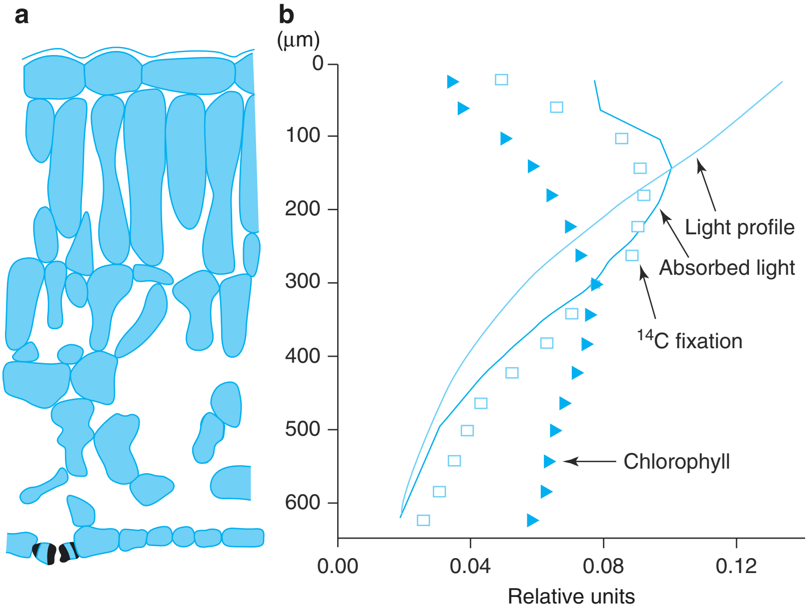

Fig. 3.7 Gradients of chlorophyll, light absorption and photosynthetic activity across a spinach leaf. **a** Thin cross-section (Modified from Munns et al. (2010)). **b** Profiles of light intensity, absorbed light, chlorophyll and photosynthetic $^{14}CO_2$ fixation across a spinach leaf. CO_2 fixation follows best the profile of absorbed light (based on Nishio et al. (1993) and Evans (1995))

The range of light energies known to be used for photosynthesis is huge. A champion of using low photosynthetic light intensities is a green sulphur bacterium (*Chlorobium phaeobacteroides*) from the Black Sea, collected from an 80-m depth, where the light intensity is 3–10 nmol quanta $m^{-2}\ s^{-1}$. Thus, a single bacterium receives no more than 300 photons per second, whereas 10^{16} photons per second impinge on a medium-sized leaf of a terrestrial plant. Owing to high concentrations of light-harvesting pigments and very low maintenance energy requirements, the sulphur bacterium can survive but takes years to double (Overmann et al. 1992). In spite of its acclimation to the low-light environment, the efficiency of energy transfer in its photosynthetic apparatus (**chlorosomes**) is no more than about 60% of the absorbed radiation. Even fast-growing terrestrial plants with optimised photosynthetic membranes use less than 50% of the absorbed photosynthetic active radiation for photosynthetic CO_2 assimilation (Scholes et al. 2011) (Fig. 3.7).

On average, a dorsiventral leaf (e.g. of spinach) absorbs about 85% of the incident light between 400 and 700 nm. This is mainly due to extension of the light path in the leaf by scattering; depending on the epicuticular fine structure, up to 10% is reflected and the remaining (~5%) is transmitted (Munns et al. 2010) (Chap. 9).

3.2.2 Overexcitation and Damage to Photosynthetic Membranes

Radicals generated by overexcitation of PS II (Chap. 2, Sect. 2.2) result first in **photoinhibition** (destruction of the D1 protein of the affected reaction centre). Prolonged photoinhibition leads to greater damage and finally to the destruction of the photosynthetic membranes. The potential for radical formation and photodamage is even enhanced by the oxygen-rich micro-environment of the chloroplast and the strong oxidising conditions needed for the crucial reaction of photosynthesis—the oxidation of water.

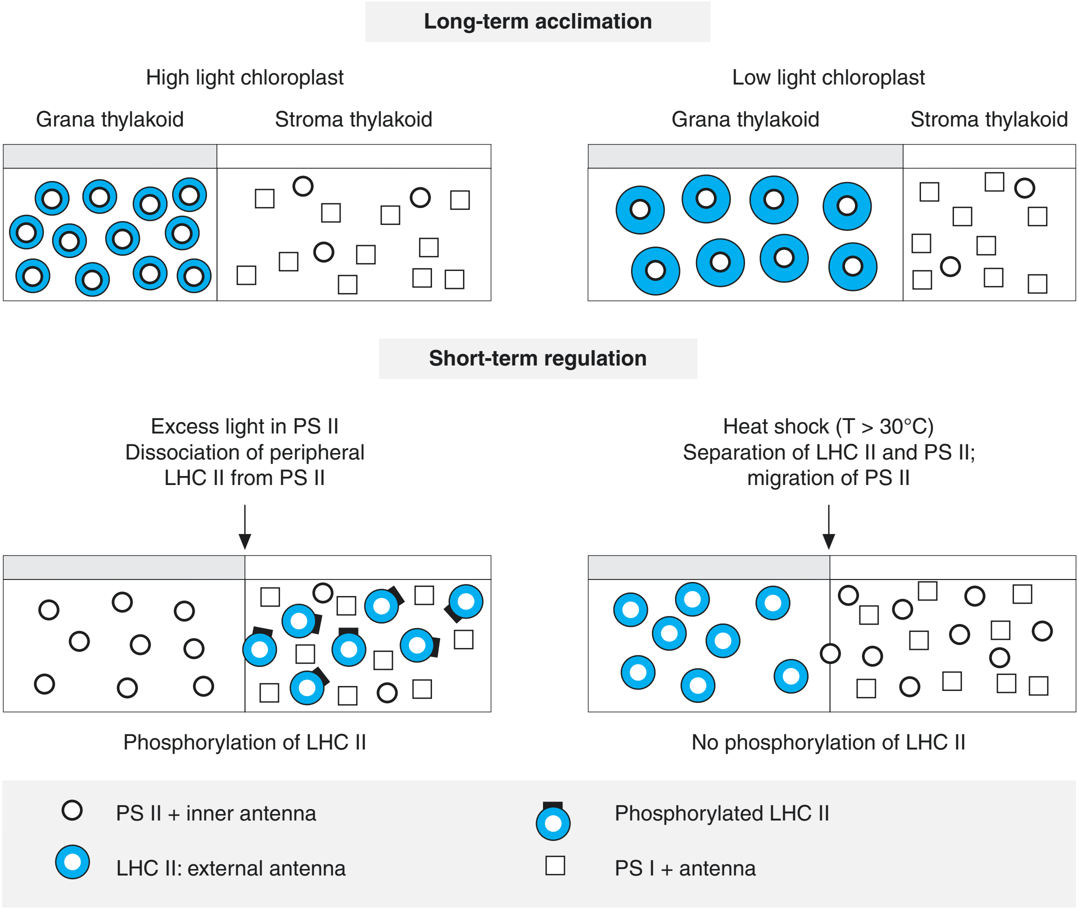

Fig. 3.8 Long- and short-term acclimation of photosynthetic membranes in response to the light environment and to a heat shock. As long-term acclimation under high-light conditions the antennae of photosystem II (PS II) are smaller than those under low-light conditions, thereby reducing light absorption. Short-term regulation: overexcitation of PS II due to excessive light triggers the state transition, a rapid change in the antennae sizes of PS I and PS II. Light-harvesting complex II (LHC II) becomes phosphorylated and partly associates with PS I instead of PS II. (Modified from Anderson and Andersson (1988))

3.2.3 Flexible Acclimation to Changes in Light Intensity

The photosynthetic apparatus of higher plants serves two seemingly opposing functions: (a) harvesting of light and transfer of the excitation energy to the reaction centre; and (b) dissipation of excessively absorbed light harmlessly as heat in order to prevent **photodestruction** of the thylakoids. Not only can the ratio of the antennae to the reaction centres vary but also the dimensions of the antenna complexes can change in response to the light intensity (Fig. 3.8).

The so-called major antenna of PS II, LHC II (**light-harvesting complex II**, usually organised as trimeric complexes), together with the minor peripheral light-harvesting complexes CP26 and CP29 (chlorophyll proteins, named after their molecular weights in kDa), can dissociate from the core antenna complexes, which are also chlorophyll-containing proteins (CP43 and CP47) surrounding the reaction centre of PS II. When the energy pressure on the reaction centre is high and **PS II** is overexcited relative to **PS I**, the so-called **state transition** occurs (Fig. 3.8). The plastoquinone pool becomes over-reduced. This activates protein kinases that phos-

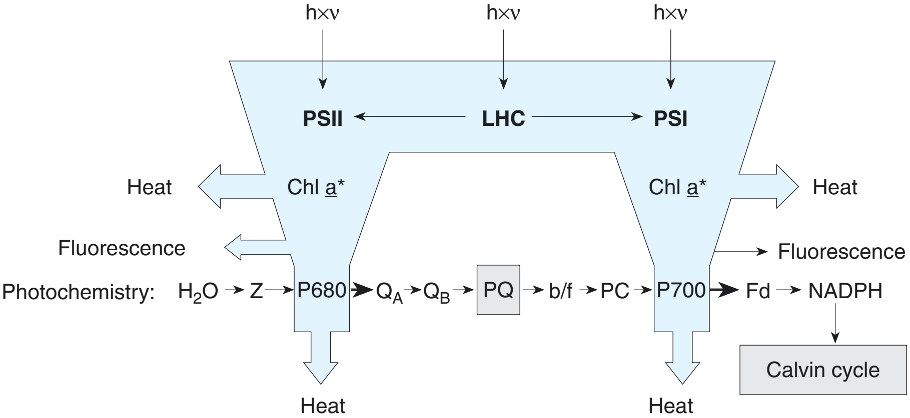

Fig. 3.9 Linear photosynthetic electron transport (from water to nicotinamide adenine dinucleotide phosphate ($NADP^+$)) in the context of utilisation of absorbed energy, and dissipation of excess energy as fluorescence and heat. Acclimation of the photosynthetic machinery to high excitation by the so-called state I–state II transition (dissociation of the light-harvesting complex (LHC) from photosystem II (PS II)) is also shown. The majority of the absorbed light energy is dissipated as heat, and a small proportion (<5%) is emitted as fluorescence. A variable proportion can be used for photochemical work (oxidation of water and electron transport). Under strong illumination the peripheral antennae of PS II can dissociate from the photosystem and at least in part associate with PS I (state transition; Fig. 3.8). In this way, PS II absorbs less and PS I absorbs more light energy. Since the entire system is dynamic, the rate constants (*thickness of arrows*) can change—for example, by overexcitation. Photochemistry: presented are the constituents of the linear electron transport (After Schreiber et al. (1994))

phorylate threonine residues in the peripheral antenna proteins. Phosphorylation leads to an accumulation of negative charges and a dissociation of the peripheral antennae from the core antennae. At the same time, the connection of the appressed regions loosens, allowing lateral movement of the peripheral antennae and thus a diminution of the PS II supercomplex (Minagawa 2013). Simultaneously, the extent (as well as the efficiency) of light harvesting of PS I increases, because part of the peripheral antennae of PS II can associate with PS I, thereby balancing the excitation of both photosystems (Fig. 3.9). Such a balance is essential for optimal utilisation of the light energy and is likewise important for the avoidance of PS II overexcitation (over-reduction of the pools of its redox compounds such as Q_B).

Even in the balanced electron flow, light intensity frequently exceeds the capacity of its utilisation for photosynthesis. According to theoretical considerations, 8 mole quanta are required for assimilation of 1 mole of CO_2. However, because of the way in which ATP synthesis is coupled to the linear electron flow, slightly more quanta are necessary. The highest measured **quantum efficiency** (lowest quantum requirement) is 9.4 mole quanta per mole of assimilated CO_2. For such measurements, the light intensity must be limiting, as is the case in the linear range of the light response curve (Fig. 3.10, curve a).

When the light response curve of CO_2 uptake deviates from the linear relationship (Chap. 12), more light is absorbed than can be used for photosynthesis and the plant is confronted with the need for energy dissipation. At the light intensity of a sunny day (800–1000 μmol quanta m^{-2} s^{-1}), already 500–600 μmol quanta m^{-2} s^{-1} are in excess. The problem of **de-energisation** of the photosynthetic membranes is aggravated when water shortage necessitates closure of stomata and concomitant lowering of the intercellular CO_2 concentration. Similarly, on a bright day in winter, stress arises when the low ambient temperatures greatly decelerate metabolism and metabolite fluxes while high radiation intensities impinge on the leaves. Plants have evolved several mechanisms to cope with this challenge.

In Fig. 3.10, curve d shows the excessive photon flux density that needs to be dissipated. Less

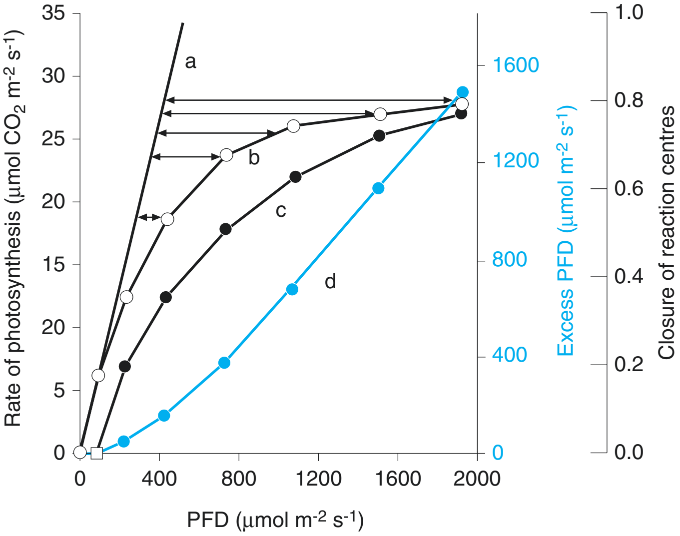

Fig. 3.10 Interpretation of a light response curve of photosynthetic CO_2 uptake. Curve **a**: linear increase of the photosynthetic rate in low light (limitation of photosynthesis by light intensity). Curve **b**: measured photosynthetic rate indicating light saturation at high photon flux density (PFD). Curve **c**: calculated proportion of reduced (closed) photosystem II (PS II) reaction centres with excessive light. Curve **d**: Excess light energy (corresponding to the *horizontal arrows* between curves **a** and **b**). (Modified from Björkman and Demming-Adams (1994))

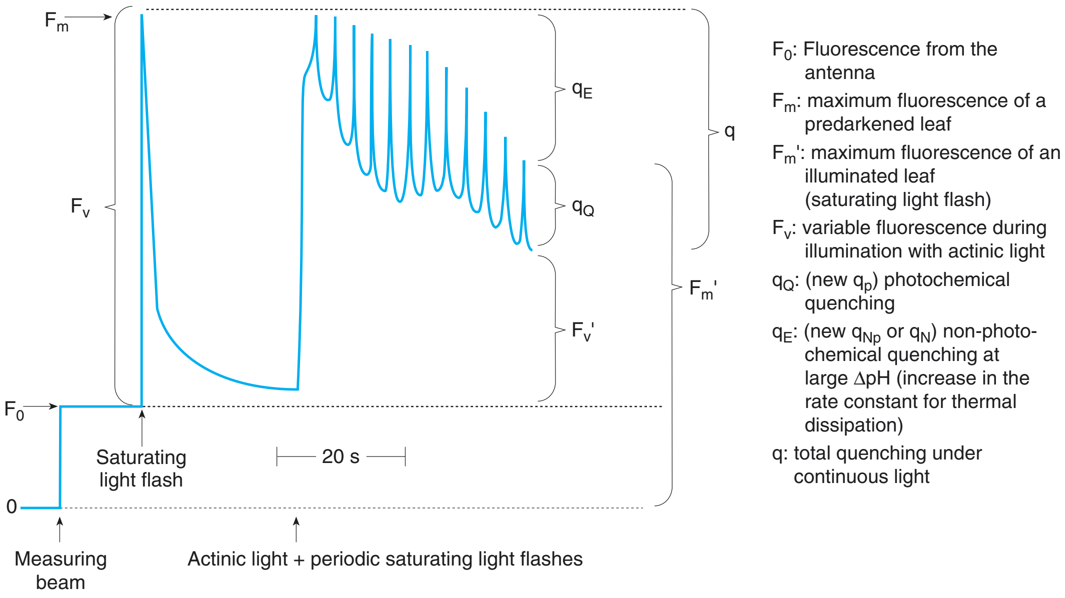

Fig. 3.11 Analysis of chlorophyll a fluorescence from photosystem II (PS II) of a pre-darkened leaf. The first peak reflects the time course of chlorophyll a fluorescence intensity triggered by a single saturating flash on a pre-darkened leaf. A series of saturating flashes results in a decrease of fluorescence by two mechanisms: q_P is the quench of fluorescence by photosynthetic electron flow and reoxidation of the reaction centres, while q_E reflects a quench resulting from an increasing rate of energy dissipation in the antennae of PS II. F_0 is understood to result from fluorescence of some antenna chlorophylls, while F_V is the fluorescence that is complementary to photosynthetic electron flow. Actinic light (low intensity) is necessary to maintain the photosystems in an activated state. (After Schreiber et al. (1986))

than 5% of the absorbed energy can be dissipated as **chlorophyll a fluorescence** (Fig. 3.9), which is complementary to the portion that can be utilised for photochemistry (photosynthesis). Because of this relation, photosynthesis can be followed indirectly by measurement of chlorophyll a fluorescence. This is illustrated in Fig. 3.11.

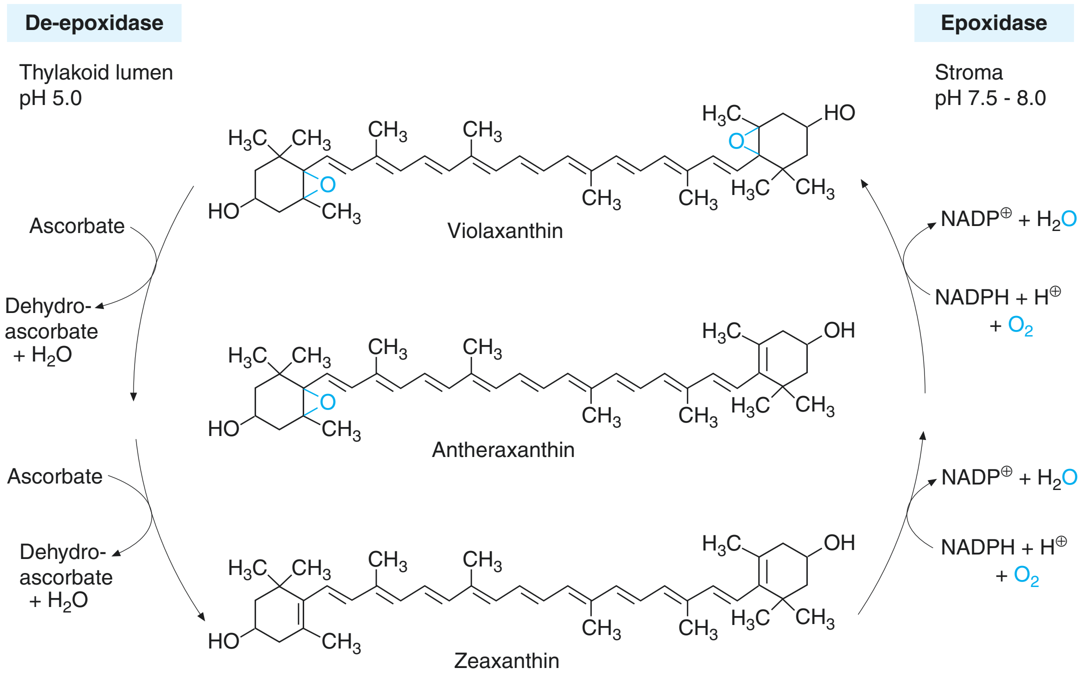

Fig. 3.12 The xanthophyll cycle in chloroplasts. In high light and an acidic luminal pH of the thylakoids, violaxanthin is converted into zeaxanthin by the de-epoxidase; in darkness and a slightly alkaline luminal pH, reoxidation of zeaxanthin to violaxanthin is catalysed by the epoxidase (Heldt and Piechulla 2010)

The intensity of fluorescence is composed of a small contribution from the antennae (termed F_0) and a major component from chlorophyll a of the reaction centre. The latter is termed variable fluorescence (F_V). When the photosystem is completely reduced—that is, when there is no acceptor of electrons available—F_V is maximal ($F_{max} = F_0 + F_V$). A return of F_V to the ground state (F_0) takes about 30 s. A series of subsequent saturating light flashes decreases F_m to F_m' because of a quench of the fluorescence of the fully reduced ("closed") reaction centres. This quench is again composed of several components: q_p is the portion of fluorescence that is quenched by photochemistry (i.e. photosynthesis); q_E is the so-called **non-photochemical quenching** (**NPQ**) or energy-dependent quenching, which depends on the trans-thylakoid pH gradient, on the concentrations of the xanthophyll zeaxanthin and on the antenna-associated protein PsbS. NPQ is the major mechanism of photoprotection. Excess light energy absorbed by the antennae of PS II is thermally dissipated. As Fig. 3.11 shows, this quench increases with increasing saturation/reduction of PS II.

The mechanism of **NPQ** is complicated insofar that the same ensemble of compounds has to mediate antagonistic reactions—namely, feeding of excitation energy to the reaction centre (of PS II) as well as dissipation of excess light energy by de-energisation of excited chlorophyll molecules. Conformational changes by protonation of the involved proteins, especially of PsbS by an acidic thylakoid lumen pH, result in switching from excitation to dissipation mode (Ahn et al. 2008; Correa-Galvis et al. 2016; Fan et al. 2015). The dissipative conformation is stabilised by **zeaxanthin**, which is a product of the **xanthophyll cycle** (Fig. 3.12). In high light and correspondingly low thylakoid lumen pH, **violaxanthin de-epoxidase** is activated, which catalyses the formation of zeaxanthin from violaxanthin. A model has been proposed that integrates the fast component of NPQ via protonation of PsbS and the slow component, the formation of zeaxanthin by the de-epoxidation of violaxanthin and

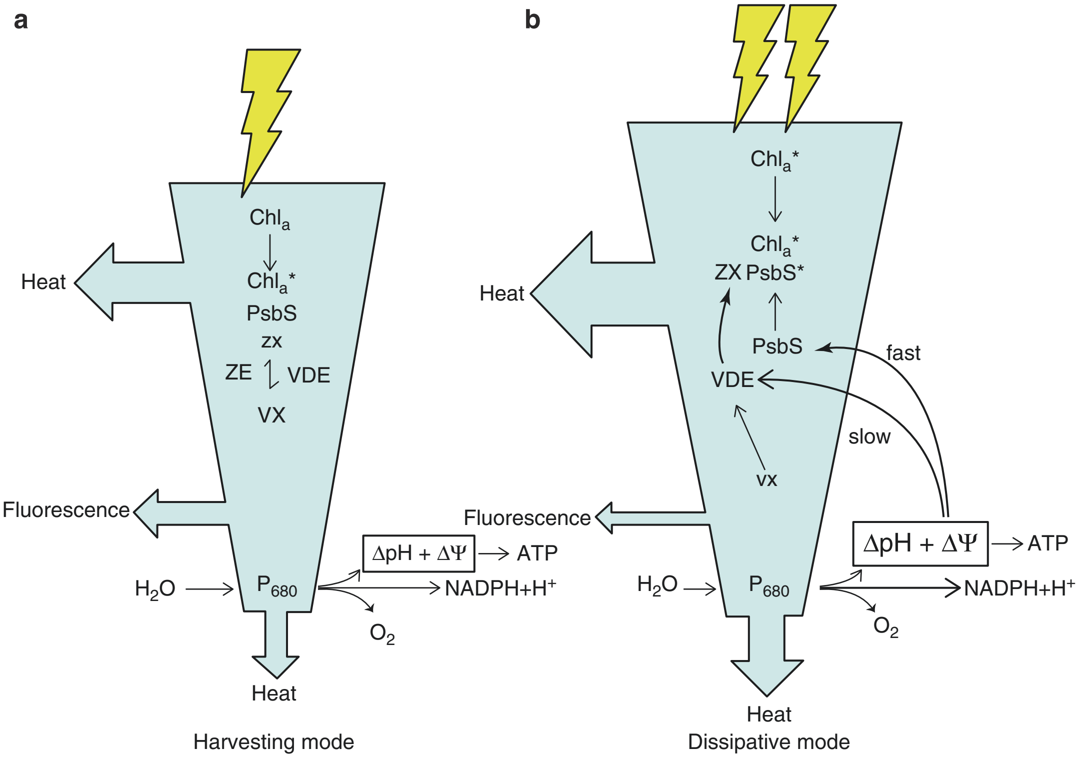

Fig. 3.13 Model for the switching of the photosystem II (PS II) antenna from light harvesting into the energy dissipation mode by non-photochemical quenching (NPQ). **a** Excitation and flow of energy in PS II under moderate light. The protein PsbS is inactive; the xanthophyll pool consists mainly of violaxanthin (VX) with a very small amount of zeaxanthin (ZX). **b** Excitation of PS II with high irradiance creates a high proton motive force (ΔpH and ΔΨ). Acidic pH activates (protonates) PsbS, which associates with the antenna, leading to an attenuation of energy transfer to the active centre of PS II and higher dissipation of energy as heat. The Chla*–PsbS* complex is stabilised by zeaxanthin, which is produced from violaxanthin by the pH-activated violaxanthin de-epoxidase (VDE). In low light, NPQ is small or even almost absent and the energy is used for photosynthesis (harvesting mode)

subsequent association with PsbS (Zaks et al. 2012, Fig. 3.13). The fast component may be restricted to the already detached antennae, whereas the slow component appears to happen in the core antennae, including the minor chlorophyll proteins, and thus protects PS II from overexcitation (Holzwarth et al. 2009). The quantitatively dominant xanthophyll of the thylakoid membranes, **lutein**, can react in a way similar to zeaxanthin (Li et al. 2009). A **lutein-5,6 epoxide cycle** has been reported, which is driven by light-activated violaxanthin de-epoxidase and **zeaxanthin epoxidase** under low light (Matsubara et al. 2008). The physiological importance of the xanthophyll cycles is underlined by the increase and decrease in the concentrations of their components upon transfer of a plant from low light to high light, and vice versa (Fig. 3.14). Also, one of the first common garden experiments with *A. thaliana* wild-type and mutant plants demonstrated that plants with defects in NPQ suffer a significant loss of fitness (determined as seed yield) under naturally fluctuating light conditions (Kühlheim et al. 2002).

At the metabolic level of the Calvin cycle, even under conditions of closed stomata, a possibility to avoid or at least reduce overexcitation arises from the oxidative photosynthetic carbon cycle (**photorespiration**) which, under low CO_2 (due to decreased conductance of the stomata)

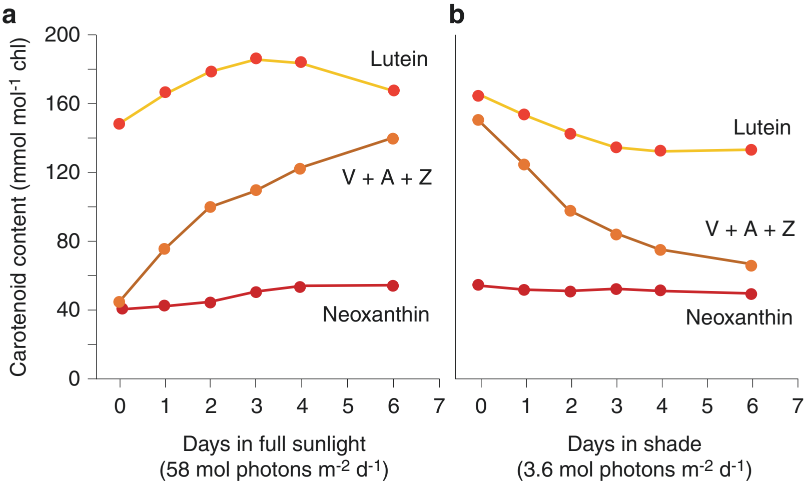

Fig. 3.14 Dynamic changes in xanthophyll pools of young cotton leaves upon changes of the light intensity from low to high **a**, and vice versa **b**. In contrast to the xanthophyll neoxanthin, for which no cycle is known, the xanthophylls undergoing de-epoxidation and epoxidation, respectively, respond readily to a change in the light environment. (Modified from Björkman and Demming-Adams (1994))

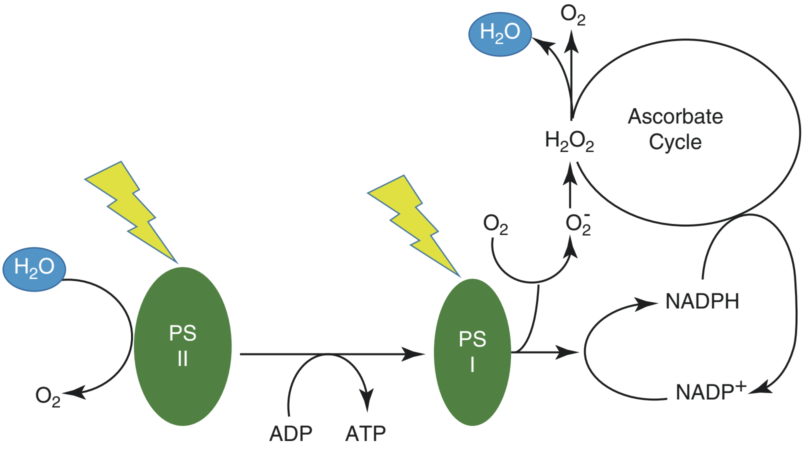

Fig. 3.15 The so-called water–water cycle or pseudocyclic photosynthetic electron transport. This occurs as a recourse of the electron flow when the chloroplastic pools of nicotinamide adenine dinucleotide phosphate ($NADP^+$) and nicotinamide adenine dinucleotide (NAD^+) are depleted because of an over-reducing environment and no electron acceptor other than oxygen is available. Reduction of oxygen produces the oxygen anion (superoxide). The oxygen anion dissociates to oxygen and peroxide, which is reduced to oxygen and water by ascorbate peroxidase. (For more details on the responsible enzymes, Chap. 2, Sect. 2.2)

and high light, releases CO_2 from glycine decarboxylation. This internal CO_2 keeps the photosynthetic electron flow running through consumption of NADPH and ATP in the Calvin cycle (for the reactions and compartmentation of the oxidative carbon cycle, see plant biochemistry textbooks). Likewise, photosynthetic reduction of nitrite or sulphate and the subsequent formation of amino acids require these photosynthetic primary products. However, the rates of the latter pathways are comparatively small. Oxygen may also be reduced photosynthetically in the so-called **Mehler reaction** (Chap. 2, Sect. 2.2), giving rise to ROS, which can be detoxified by a sequence of reactions, finally resulting in the consumption of NADPH (the "**water–water cycle**" or **pseudocyclic photosynthetic electron flow**) (Fig. 3.15).

Box 3.1: A Day in the Life of a Tree Leaf: Dynamic Acclimation of Leaf Performance to Short-Term Environmental Changes

The effect of **sunflecks** on the photosynthetic performance of leaves (e.g. of a tree crown) has been discussed controversially with respect to the question as to whether a frequent change in the light intensity enhances or decreases their photosynthetic efficiency. The basis of such considerations is the observation that once a leaf is in a photosynthetically active state, the increase in the rate of photosynthesis is fast (occurring in a few seconds), while the return to the "shade state" is in the range of minutes, resulting in overall elevated efficiency (Fig. 3.16c). On the other hand, such a consideration must also take note of the nonlinear quantum efficiency of varying light intensities, which is described by the light response curve of net CO_2 uptake (Figs. 3.10 and 3.16a). Sunflecks from direct sunlight commonly surpass the range of the linear or nearly linear relation between light intensity and photosynthetic CO_2 uptake. In the examples shown in Figs. 3.16a and 3.17a for the tropical gymnosperm *Podocarpus falcatus*, the increase in photosynthetic CO_2 uptake was minimal beyond a photosynthetically active radiation (PAR) intensity of about 400 µmol quanta m^{-2} s^{-1}. The sunflecks, however, reached up to 1500 µmol quanta m^{-2} s^{-1} (Fig. 3.17a). Therefore, the sunflecks were of lower **photosynthetic quantum efficiency** than low light. When the same amount of PAR was supplied to a *Podocarpus* leaf over the same time period as continuous radiation of low intensity (Fig. 3.16b) or as artificial sunflecks (termed lightflecks; Fig. 3.16c), the photosynthetic gain was obviously higher under continuous low light. Under natural conditions, not only the light intensity varies (Fig. 3.17) but also the conductivity (g_s) of the stomata responding to the water status of the leaves (Chaps. 10 and 12). When stomatal conductivity is low, as it generally is in the afternoon, the photosynthetic efficiency of sunflecks is even lower because of a low internal CO_2 concentration. This in turn indicates the importance of energy dissipation by the chloroplasts. The actual quantum efficiency of CO_2 assimilation over an entire day was only 72% of the (theoretical) **quantum efficiency** of the same amount of quanta administered over the same time period, when provided as continuous low light

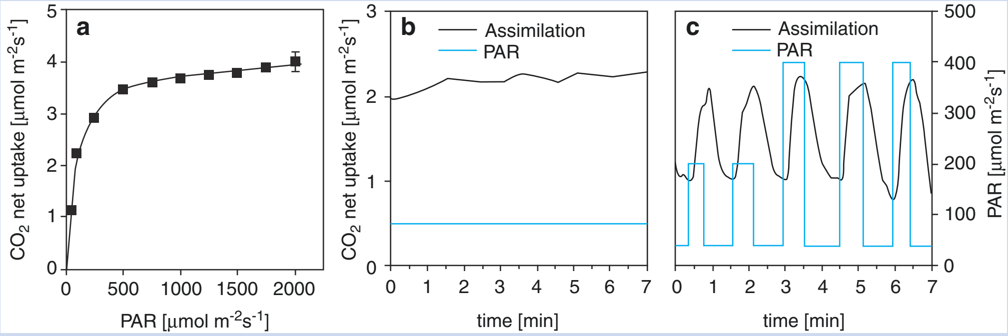

Fig. 3.16 Photosynthetic CO_2 net uptake by leaves of young *Podocarpus* trees (shade leaves) under the canopy of an old evergreen tropical forest. **a** Light response curve. The data show the mean values for 2–5 saplings per site with three repetitions per leaf (± standard error (S.E.)). **b**, **c** Analysis of the sunfleck effect on photosynthetic CO_2 uptake by two artificial light conditions, providing the same amount of photosynthetically active radiation (PAR) over an identical time span. **b** PAR provided as a constant photon flux density of 83 µmol m^{-2} s^{-1}. **c** PAR provided as intermittent lightflecks lasting 30 s at an intensity of 200 or 400 µmol m^{-2} s^{-1} superimposed on a basic intensity of 40 µmol m^{-2} s^{-1}. (Modified from Strobl et al. (2011))

(Table 3.2). This difference is, of course, not a constant. However, it indicates the extent to which the real light climate is less effective than artificial illumination. Continuous artificial low light mimics, to some extent, the diffuse radiation in the shade of a tree canopy which, for an entire forest canopy, is photosynthetically more efficient than direct irradiation (Mercado et al. 2009). In comparison with the mentioned minimal quantum requirement for photosynthetic CO_2 assimilation of 9.2 μmol quanta per μmol CO_2, the data in Table 3.2 suggest a sixfold lower quantum efficiency (54 mole quanta per mole of CO_2). Under adverse environmental conditions the apparent quantum efficiency can further decrease tremendously—for example, when stomata are closed under drought and merely 1–2% of the incident visible light can be used for photosynthesis (Osmond et al. 1997). It is important to note that quantum efficiency has a different meaning in the ecological context than it does in the photosynthetic light reaction, where only those quanta that conduct photochemistry are counted. The difference is due to the energy of a high proportion of absorbed quanta being dissipated as heat under natural conditions.

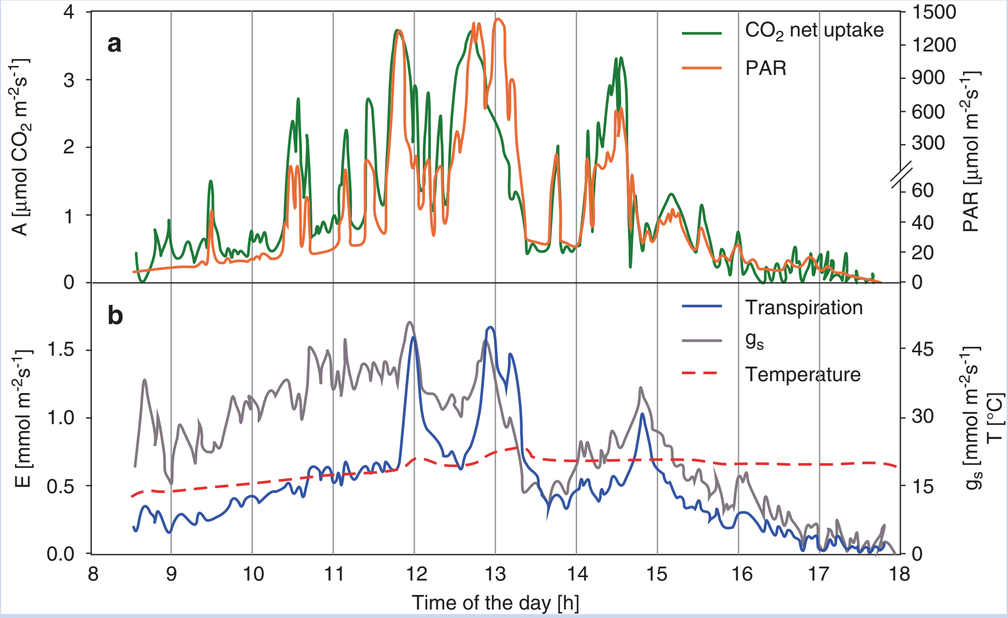

Fig. 3.17 A day under the canopy in the natural forest. Daily courses of **a** CO_2 net uptake and ambient photosynthetically active radiation (PAR), and **b** stomatal conductance (g_s) and transpiration (E) of young *Podocarpus* leaves and of air temperature on a sunny day (24 November 2006). (Modified from Strobl et al. (2011))

Table 3.2 Effect of sunflecks on the photosynthetic gain of a tree. Photosynthetic efficiency of the subcanopy light climate compared with virtual constant illumination of the same PAR magnitude applied over the same time period to leaves of *Podocarpus falcatus* (Modified from Strobl et al. (2011))

Daily sum of PAR [mol m^{-2} day^{-1}]	Calculated PAR_{av} over the day (μmol m^{-2} s^{-1})	Theoretical daily CO_2 net uptake on the basis of PAR_{av} (mmol m^{-2} day^{-1})	Measured daily CO_2 net uptake (mmol m^{-2} day^{-1})	Apparent efficiency of actual PAR (%)
1.5	50.5	38.3	27.7	72

PAR photosynthetically active radiation, *PAR_{av}* average PAR intensity

3.2.4 Continuous Light

In greenhouses, plants are frequently cultivated under continuous light for enhancement of biomass production. On the other hand, continuous light can induce severe injury in many plants. Plants sensitive to continuous light (e.g. eggplant, peanut, some cultivars of potato and many cultivars of tomato, but also some lichens and mosses) react with lower rates of photosynthesis, leaf chlorosis and necrosis (Velez-Ramirez et al. 2011). Several reasons have been identified for that damage. Some of it results from a disturbance in photosynthetic carbohydrate metabolism. Assimilatory starch accumulates during the daily light period between the grana of the chloroplasts. Suppression of nocturnal starch degradation leads to continuous deposition of starch and finally destruction of the chloroplast ultrastructure. Enhanced formation of radicals and ROS are other reasons, in particular when the applied light contains a high proportion of blue light. Usually the natural day/night cycle is accompanied by an oscillation in the temperature. Continuous light in combination with a constant temperature can disturb the circadian clock and affect the development of the plant. Is continuous light not a natural phenomenon of the polar summer beyond the polar circles, one might ask? By no means! Even in the polar summer, the light intensity (and light spectral distribution) oscillates in the daily rhythm concomitantly with the temperature. Thus, artificial continuous light (and temperature) provided in a greenhouse represents an environment without an analogy in nature. It is therefore maybe more surprising that some plants can grow well in continuous light than that many plants cannot.

3.2.5 Light Triggers Plant Adaptation and Acclimation to the Environment

3.2.5.1 Photoreceptors

Because of its role as an energy source, light is arguably the most important environmental factor for a plant. Consequently, perception of light and translation of the respective signals control many aspects of plant development and are crucial for adaptation to diverse habitats. The sensing of light conditions is enabled by a range of receptors, which are specific for particular wavelengths of the visible spectrum (Fig. 3.18). **Phytochromes** are receptors for red and far-red light, **cryptochromes** and **phototropins** are receptors for blue light. The photoreceptors for red and blue light principally consist of a protein and a chromophore. The chromophores are molecules absorbing light of the respective wavelengths (for example, flavin adenine dinucleotide (FAD) and tetrapyrroles). During evolution they have been recruited for a wide range of biological functions. Upon photon absorption the chromophores undergo conformational changes that are transmitted to the protein and thereby change its activity. For UV light a special photoreceptor has

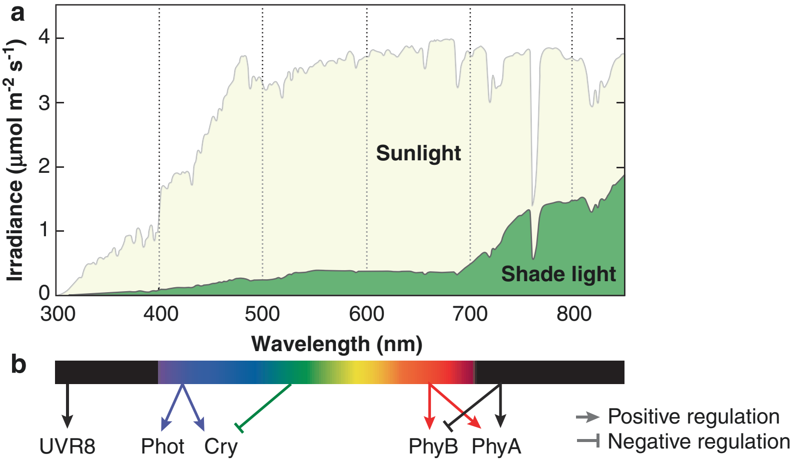

Fig. 3.18 Spectrum of visible light and the respective photoreceptors of terrestrial plants. Perception of shade light signals by photosensory receptors. **a** Spectral photon distribution of sunlight and shade light. **b** Impact of different wavebands on the status of phytochromes, cryptochromes, phototropins and UVR8 (Casal 2013)

recently been identified (**UVR8**) which, because of the UV absorption by aromatic amino acid residues, does not require a chromophore.

Phytochromes

Phytochromes are proteins with an open-chain tetrapyrrole as a chromophore that changes its configuration upon absorption of red or far-red light. The effective **ratio of red to far-red**, ζ, refers to the broad spectral peaks of phytochrome in the red and far-red and can be calculated by Eq. 3.1 (Chelle et al. 2007):

$$\zeta = \frac{E_{\mathrm{R}}}{E_{\mathrm{FR}}} = \frac{E_{\mathrm{R\,direct}} + E_{\mathrm{R\,diffuse}}}{E_{\mathrm{FR\,direct}} + E_{\mathrm{FR\,diffuse}}} \tag{3.1}$$

where E_{R} and E_{FR} are the spectral irradiances from the sun and the sky and the complex radiative transfer reactions within the canopy. E_{R} comprises the radiation between 655 and 665 nm and accordingly E_{FR} comprises that between 725 and 735 nm. Whereas ζ of the sunlight is around 1.2, it decreases in the understorey space to less than 0.2. Reactions that are triggered by (red) light (e.g. light-dependent seed germination) thus do not take place in the shade of a dense canopy. The situation changes in forest gaps where, because of the direct irradiation, ζ is high and seeds of pioneers can germinate rapidly (Chap. 2, Sect. 2.4). In contrast, the time span of sunflecks is too short to initiate red light–triggered morphogenic reactions, because the **activation** of phytochrome is reversible by a rapid return to low ζ.

The scheme in Fig. 3.19 shows two **phytochromes** (A and B). Phytochrome B represents several phytochromes (B through E), which react in the same way and have been identified from several plant sources. While the interconversion of the physiologically inactive form (“$\mathrm{P_r}$” for $\mathrm{P_{red}}$) to the active form (“$\mathrm{P_{fr}}$” for $\mathrm{P_{far\text{-}red}}$) by respective irradiation follows the same mechanism in all phytochromes, the inactivation mechanisms for $\mathrm{P_{fr}}$ differ. $\mathrm{PhyA_{fr}}$ inhibits its own synthesis, and irradiation with red light as well as with blue light triggers its degradation. Synthesis and degradation play a secondary role in PhyB biochemistry as compared with **photoconversion** and slow reversion in the dark (Fig. 3.19). Note that photoconversion of phytochromes is associated with transport into ($\mathrm{P_{fr}}$) and out of ($\mathrm{P_r}$) the nucleus. The existence of a photoreceptor in two different states with distinct absorption maxima allows the monitoring of spectral quality (similar to colour vision in animals). Sunlight comprises both red and far-red light. Hence, the ratio of red to far-red light is crucial for the concentration of $\mathrm{P_{fr}}$ and the formation of a cellular signal.

Cryptochromes

Three cryptochromes have been found in *A. thaliana*, two acting primarily in the nucleus and one (Cry3) in mitochondria and chloroplasts. Cry3 is a photolyase with potentially some cryptochrome activity too (Liu et al. 2011). Cryptochrome 1 is the photoreceptor for high blue light intensity, while cryptochrome 2 is a sensitive blue light receptor that reacts at low fluence rates. The photoactive domains of the cryptochromes are homologous to those of the photolyases (N-terminal photolyase-homologous region (PHR)). However, because of their C-terminal extensions, cryptochromes do not exhibit pho-

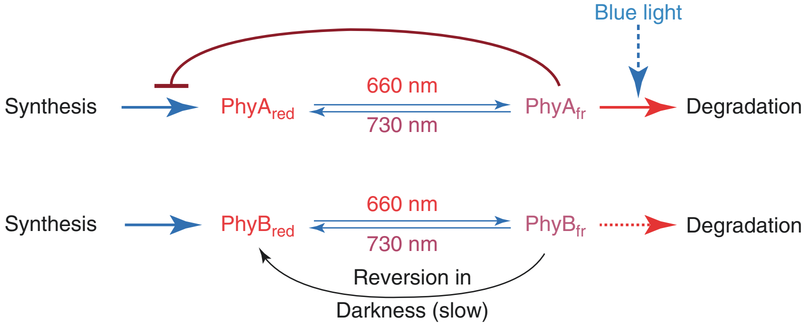

Fig. 3.19 The red-light switch mediated by phytochrome. $\mathrm{Phy_{fr}}$ is the active form of all phytochromes. (Modified from Weiler and Nover (2008))

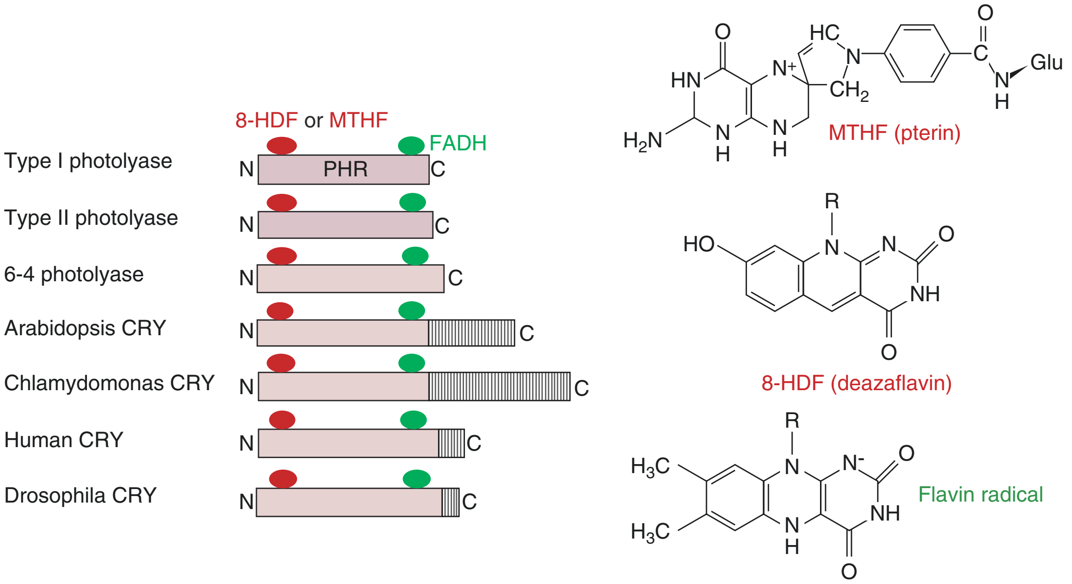

Fig. 3.20 Cryptochromes are evolutionarily derived from ultraviolet (UV)-activated photolyases involved in DNA damage repair. Photolyases (type I: *Escherichia coli*; type II and 6–4 photolyase: *Arabidopsis thaliana*), their substrates and co-substrates. A blue-light-triggered intrinsic energy transfer from pteridine to reduced flavin adenine dinucleotide (FADH) leads to an energisation of the pyrimidine residues of the dimers (in a DNA strand) and to a rearrangement of the carbon bonds, resulting in the cleavage of the dimers and restoration of the original DNA helix. Structures of pterin (MTHF), deazaflavin (8-HDF) and the intermediate flavin radical ($FADH^-$). (Modified from Cashmore et al. (1999))

tolyase activity (Fig. 3.20) but instead act as kinases. The photochemical mechanism(s) of cryptochrome light activation are not yet completely understood and the mechanisms of **photoactivation** and inactivation of both cryptochromes may differ to some extent (Li et al. 2011; Liu et al. 2011). Binding of the chromophores (5,10-methenyltetrahydrofolate (MTHF)) and FAD to the protein is non-covalent and the formation of an FAD radical anion (by electron transfer from MTHF) and a reduced FAD (FADH) radical (by subsequent proton transfer from the protein) appears obligatory in both cryptochromes. For activity, *A. thaliana* cryptochromes have to be phosphorylated. Upon additional (auto)phosphorylation after exposure to blue light, Cry2 (but not Cry1) is ubiquitinated and degraded. This mode of action resembles the situation in the phytochrome systems where PhyA is readily degraded, while PhyB is not (Liu et al. 2011).

Phototropins

Phototropins (Phot 1 and Phot 2 in *A. thaliana*) are blue light receptors of the plasma membrane with two flavin mononucleotides (FMNs) as chromophores. In darkness, their C-terminal protein kinase domain is sterically inhibited. Absorption of blue light changes the protein conformation, leads to dissociation from the plasma membrane and unlocks the kinase activity. In the activated state, the FMN becomes covalently bound to a cysteine residue of the protein chain. This state of the protein is unstable and is readily reversed in the dark, whereupon the covalent bond breaks up. Along with cryptochromes and phytochromes, phototropins allow plants to respond to their light environment. For instance, they are important for the opening of stomata and mediate phototropic responses, e.g. the movements of chloroplasts (Fig. 3.4). Phot 1 is required for blue light–mediated transcript destabilisation of specific messenger RNAs (mRNAs) in the cell. For detailed chemical structures of the photoreceptors and mechanisms of gene regulation by light, see plant biochemistry textbooks (e.g. Buchanan et al. 2015).

3.2.5.2 Signal Transduction: The Signalling Centre COP1

Growth of plants in the dark, known as **etiolation** or **skotomorphogenesis**, requires suppression of

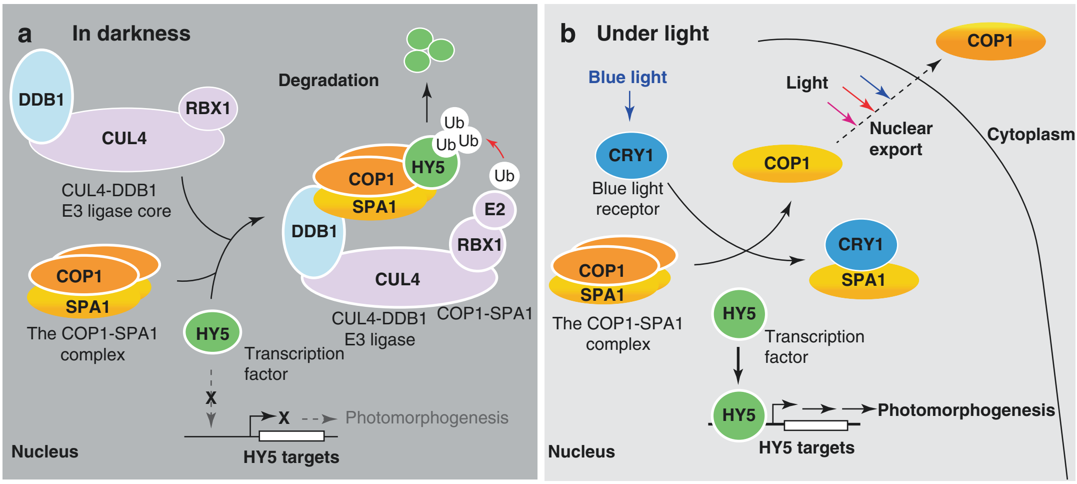

Fig. 3.21 Action of COP1 in the dark (**a**) and its inactivation by interaction with activated Cry1 in the light (**b**). The core protein complex for ubiquitination of proteins for degradation is composed of three proteins, which interact with the targeting dimer complex $(COP1–SPA1)_2$ on the one hand and with the ubiquitinating enzyme E2 on the other. In the dark the transcription factor HY5 is ubiquitinated and degraded in the proteasome. Light-activated Cry1 dissociates the COP1–SPA1 interaction, releasing COP1 which, as a monomer, is exported from the nucleus. HY5 accumulates and initiates photomorphogenesis (Lau and Deng (2012))

photomorphogenesis, which is initiated by illumination. Activation of the above described photoreceptors - phytochromes and cryptochromes in particular - by irradiation triggers signal transduction cascades, which converge at a protein termed COP1 (CONSTITUTIVE PHOTOMORPHOGENIC 1). COP1 is a central switch which, because of its complex structure, can interact with several other proteins. In the dark, COP1—by its function as an E3 ubiquitin ligase—targets photomorphogenesis-promoting transcription factors for degradation by the ubiquitin-proteasome system, thus preventing photomorphogenesis. One of these proteins is the transcription factor ELONGATED HYPOCOTYL 5 (**HY5**) which, together with others, is responsible for the onset of photomorphogenesis (e.g. the inhibition of hypocotyl elongation growth). In the dark, it is degraded in the proteasome, giving rise to the well-known etiolated hypocotyls. Light-activated photoreceptors inactivate COP1 by mediating its export from the nucleus, thereby suspending its activity against transcription factors that are located in the nucleus. For a further understanding of the interaction of COP1 with the photoreceptors, it is necessary to introduce another protein, **SPA1** (**SUPPRESSOR OF PHY A 1**), which forms a complex with COP1 to enable its association with the E3 ligase core complex; this finally ubiquitinates the proteins, targeting them for degradation (Fig. 3.21a). In the light, activated Cry1 and 2 interact with SPA1, dissociating it from COP1, which can now be exported from the nucleus (Fig. 3.21b). Further targets of the COP1 E3 ubiquitin ligase are the phytochromes—in particular $PhyA_{fr}$ and cryptochrome 2.

While COP1 is a negative regulator of photomorphogenesis, it promotes UV-B-triggered reactions of plants, hence acting as a positive regulator (Fig. 3.22). To understand this difference, it is important to note that in **skotomorphogenesis**, COP1 acts as a homodimer, and also the COP1–SPA1 complex is dimeric. Dissociation of the COP1–SPA1 complex by sequestration of SPA1 through interaction with cryptochrome also monomerises the COP1 homodimer. In the cytosol, monomeric COP1 can bind to the monomeric activated UVR8 receptor and the heterodimer migrates back into the nucleus, where it activates HY5 and other transcription factors and effectors (Chap. 3).

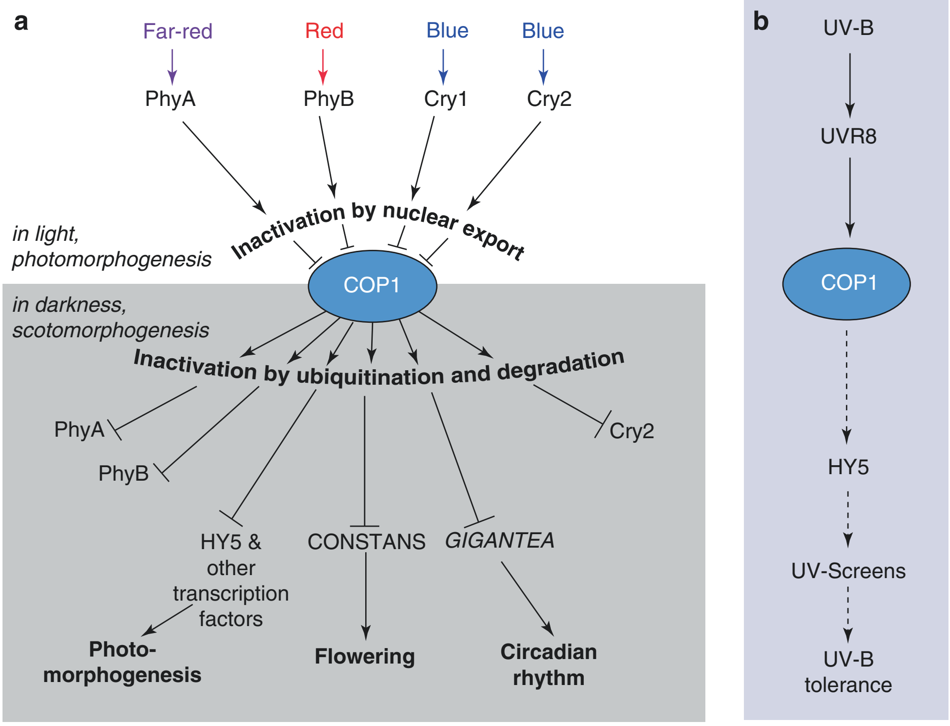

Fig. 3.22 Roles of the central regulator COP1 in signal transduction of skotomorphogenesis, photomorphogenesis **a** and ultraviolet (UV)-triggered responses **b**. In addition to photomorphogenesis, COP1 is involved in other developmental events (regulation of flowering, with the transcriptional regulator CO (CONSTANS)) and the circadian rhythm (by regulating the abundance of the circadian-associated protein GI (GIGANTEA)). (Modified from Lau and Deng (2012))

3.3 UV-B Radiation

3.3.1 Ranges of Ultraviolet Radiation and Biological Activity

The spectrum of solar **ultraviolet light** is continuous but is commonly divided into three wavelength bands: **UV-C** (200–290 nm), **UV-B** (290–320 nm) and **UV-A** (320–400 nm). UV-C is the most energetic of the three and is known as "germicidal UV" because of its potency against microorganisms (Yin et al. 2016). It is used to disinfect fresh fruit and vegetables to preserve their quality. However, since it is effectively absorbed by oxygen and ozone in the stratosphere, only a very small fraction reaches the Earth's surface. UV-A, on the other hand, is not attenuated by atmospheric ozone, and this less damaging type of radiation plays an important role in plant photomorphogenesis. Although a sizeable amount of UV-B is absorbed by atmospheric ozone, its impact on life on our planet is considerable.

The development of the ozone hole—that is, the decrease in stratospheric ozone concentrations due to ozone decomposition by reaction with anthropogenic gases such as halogenated hydrocarbons or nitrogen oxides (IPCC/TEAP Special Report on Ozone and Climate 2005) is therefore observed with much concern. While the seasonally fluctuating ozone hole is particularly pronounced in the polar and subpolar regions, the UV radiation emitted by the sun crosses the atmosphere in regions of high geographical latitude at an angle and thus encounters a significantly "thicker" ozone layer than at the equator, where it takes the shortest path through the atmosphere. Therefore, in spite of the high latitudinal ozone hole, the UV radiation is high in the tropics and relatively low in the polar regions. The well-known altitudinal increase in UV radiation is caused by an attenuation of the tropospheric ozone layer, concomitant with a decrease in the intensity of haze.

UV-B radiation can damage cells and thus is dangerous to organisms (Table 3.3). In particular, plants—as sessile organisms—have developed mechanisms to cope with the ubiquitous and inescapable natural flux density of UV radiation through **repair mechanisms** for damaged cellular components (such as DNA). Protective measures are accumulation of UV-absorbing pigments in the epidermal layers, thick layers of hairs (Holmes and Keiller 2002; Manetas 2003) and cuticular waxes (Barnes et al. 1996). Generally, plants show **adaptation to the UV-B** load of their habitat. Plants growing along a latitudinal or an elevation gradient exhibit increased UV-B tolerance (Robberecht et al. 1980, Fig. 3.23). Problems caused by UV may arise for crop cultivars that are not well adapted to the natural UV-B stress occurring at their sites of cultivation, or for mobile organisms such as plankton. **Phytoplankton**, especially of the cold oceans, appear to be very sensitive to UV-B. In spite of the shallow depth to which UV light penetrates in a body of water (Fig. 3.24), significant reductions in phytoplankton biomass have repeatedly been observed as a consequence of the ozone hole. Likewise, decreases in yields have been reported for UV-sensitive crop cultivars (e.g. of maize and soybeans (Rius et al. 2016)). However, although statistically significant, these reductions were relatively small (usually <10%).

Morphological–anatomical symptoms indicating a still tolerable **UV-B stress** are swollen and shortened internodes, reduced leaf expansion, curling up of leaf edges and enhanced branching of the shoot through promotion of lateral buds. Leaves tend to show succulence

Table 3.3 Physiological effects of increased ultraviolet (UV)-B radiation. (Modified from Jansen et al. (1998))

Damage	
DNA damage	Dimerisation of thymine; strand breaks
Biomembranes	Lipid peroxidation
Photosynthetic apparatus	Inactivation of photosystem II; acceleration of D1 turnover; damage to thylakoid membranes; bleaching of pigments; decrease in the activity of photosynthetic enzymes (particularly RubisCO); inactivation of photosynthetic genes
Phytohormones	Photo-oxidation of auxin
UV avoidance	
Activation of secondary metabolism	Activation of expression of the key genes of phenylpropanoid metabolism and accumulation of flavonoids; accumulation of alkaloids, waxes and polyamines
Production of radical scavengers	Increased capacity of the anti-oxidative system (ascorbate peroxidase, superoxide dismutase, glutathione reductase and others, e.g. mycosporines)

RubisCO ribulose-1,5-bisphosphate carboxylase/oxygenase

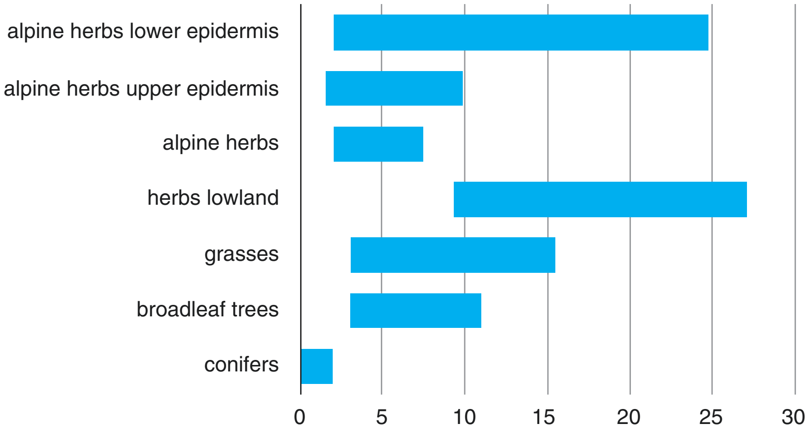

Fig. 3.23 Efficiency of ultraviolet (UV)-B screening (percent transmittance of impinging UV-B radiation) through the epidermis of several plant life forms from various provenances. (Modified from Munk (2009), Körner (1999) and Day et al. (1993))

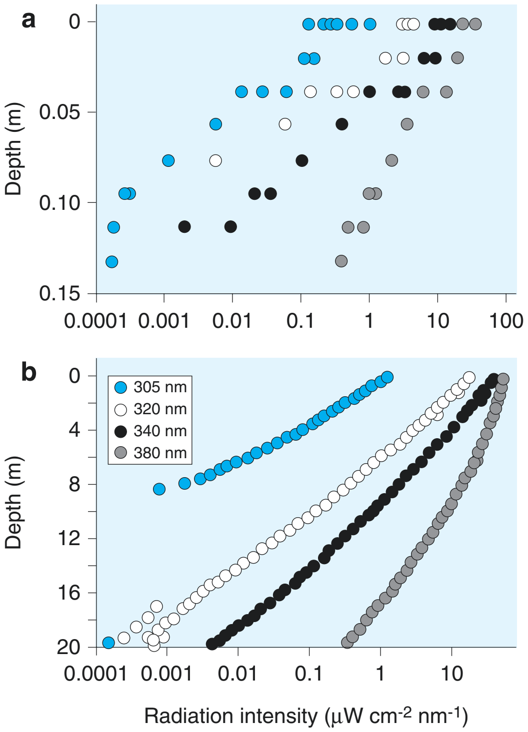

Fig. 3.24 Decrease in ultraviolet (UV) radiation with depth of water **a** in the northern Adriatic and **b** in the humin-rich Lake Neusiedler (Austria). Both measurements were conducted on a cloud-free August day. The intensity of the UV radiation at a depth of 5 cm in Lake Neusiedler corresponded approximately to a depth of 5 m in the Adriatic. (Modified from Herndl (1996))

with a particularly thick, usually pigmented epidermis and low density of stomata. Tolerated UV stress often results in accumulation of vitamin C and soluble sugars in fruits as radical scavengers, thereby also increasing the quality of food. However, the transition from UV-B-triggered "normal morphogenetic reactions" to those that have to be considered as stress responses is not clearly apparent, inasmuch as other natural stresses such as drought, nutrient deficiency or low temperature can interact with UV-B effects at the molecular level. Nevertheless, differentiation between normal development of UV-B tolerance and stress responses is clear when above-ambient levels of UV-B cause damage to DNA, proteins and membrane lipids, and inhibit protein synthesis and photosynthetic reactions. However, since UV-B also generates **ROS** (mainly the superoxide radical O_2^-) through its impact on photosynthesis, respiration and on enzymes such as peroxidases and oxidases, the origin of UV-B triggered damage is not always obvious.

Investigation of UV-B effects on plants is not trivial, because of the omnipresence of this radiation in nature and, to a lesser extent, in artificial light sources. Many experiments have therefore applied pulses of UV-B overdoses or longer than natural exposure periods. Such treatment can easily overstretch the tolerance—for example, the capacity for repair—of the plants, causing unnatural reactions and even necroses and death. Also, different reactions have been observed, depending on whether the same total overdose of UV-B was applied either in high intensity pulses or as a slightly elevated constant flux over a long period. With the UV stress applied in short pulses, damage and repair are the dominant effects, while continuous but low-intensity stress leads to acclimation and damage avoidance.

3.3.2 Ultraviolet-B Damage and Repair Mechanisms

DNA has a broad absorption peak between 235 and 315 nm and thus is photoactivated by UV. Since the effects of UV-B radiation on DNA affect all kinds of organisms, they have been particularly well studied. Several types of UV-triggered damage are known: strand breaks and cross-linking, as well as modifications of pyrimidine bases. In plants, dimerisation of thymine—resulting in cyclobutane pyrimidine dimers (CPDs) and, to a smaller extent, in pyrimidinone dimers (known as 6–4 photoproducts)—is a common reaction to irradiation with UV-B. Less packaged DNA of mitochondria and probably also of chloroplasts is particularly sensitive. UV irradiation of yeast cells caused a 10% loss of nuclear DNA, but at the same time a 50–60% loss of mitochondrial DNA.

There are several **mechanisms to repair** such damage (for details, see biochemistry textbooks, e.g. Berg et al. (2015)), of which two are mentioned here: the DNA photolyase reaction, which requires blue light/UV-A; and light-independent reactions such as base excision and recombination. Repair usually takes only a few hours. Interestingly, UV-activated photolyases represent the evolutionary origin of the blue light receptor **cryptochrome** (Fig. 3.20). Strong UV stress leads directly to irreparable chromosome breakage and deletions resulting in the death of the organism. This is the basis for sterilisation of rooms and instruments with intense UV light.

Irrespective of the repair mechanisms, **DNA damage** signalling involves a UV-damaged DNA-binding protein complex (UV–DDB complex), which recognises UV-induced DNA damage and recruits proteins of the nucleotide excision repair pathway. It also induces several other UV-B responses, such as the formation of protective pigments.

In addition to UV damage to DNA, **photo-oxidation** of UV-absorbing pigments is known: yellowing and complete bleaching of leaves of indoor plants after abrupt transfer to the open air are frequent phenomena. Here the protective effect of the chloroplast pigments (energy dissipation) on their protein environment can be seen. Photodestruction of the thylakoid pigments leads to a significant decline in the amount of ribulose-1,5-bisphosphate carboxylase/oxygenase (RubisCO).

3.3.3 Avoidance of Ultraviolet-B-Induced Stress

Plants synthesise a range of compounds in order to avoid damage by UV-B radiation. The rate of accumulation in different plant types correlates well with the average **UV exposure** associated with the respective habitat (Fig. 3.23). **Phenylpropanes**, as aromatic compounds, exhibit strong absorbance of shortwave radiation and are thus able to function as effective **UV filters** or sunscreen pigments. Many compounds in this family of secondary plant metabolites absorb light only in the UV range and cannot be recognised as pigments by the human eye. Others, such as the anthocyanins, absorb light also in the visible range and therefore appear as pigments (Figs. 3.25 and 3.26).

Glycosylation renders phenylpropanes water soluble so they can be sequestered in the vacuoles primarily of the epidermis. In certain purple varieties such as copper beech (*Fagus sylvatica*), the vacuoles of the mesophyll cells contain such pigments too. They absorb in the UV spectrum (Fig. 3.26) and in the green region of the visible spectrum and thus do not interfere with the absorption of light by the chlorophylls. Protective colouration of the leaves by anthocyanins is frequently observed in unfolding young leaves (called "**juvenile anthocyanin**") and again during senescence.

Fig. 3.25 Anthocyanins in flushing leaves of the tropical Sapotacea *Inhambanella henriquesii* in the coastal forests of Kenya. The anthocyanin is located in the vacuoles of the leaf epidermis and protects the leaves, which are not yet fully green, from radiation damage. The close-up (*right*) shows the mixture of colours between the red anthocyanins and the chlorophyll. (Photos: E. Beck)

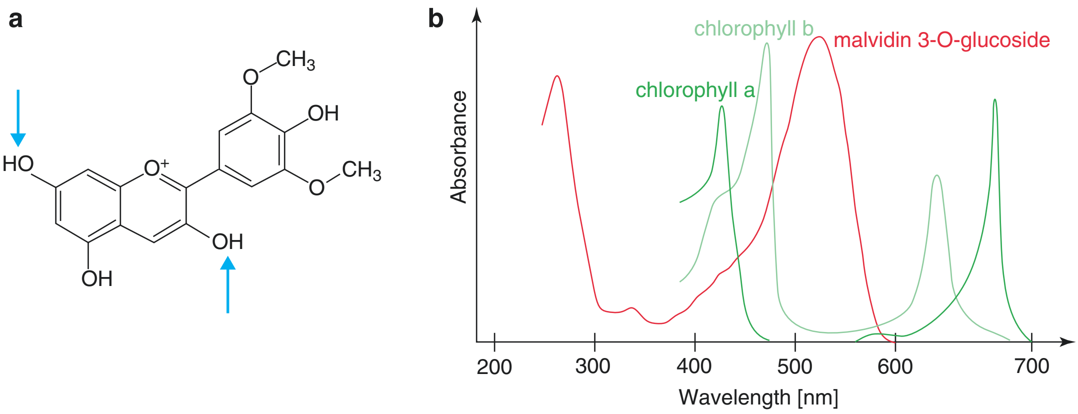

Fig. 3.26 After glycosylation, phenylpropanes are accumulated in the vacuoles of the epidermal cells. **a** Chemical structure of the anthocyanidin malvidin (at acidic pH, *arrows* indicate the positions for glycosylation) and **b** the absorption spectrum of its 3-O-glucoside (which is nearly identical to that of the aglycone malvidin) in comparison with the absorption spectra of chlorophylls a and b

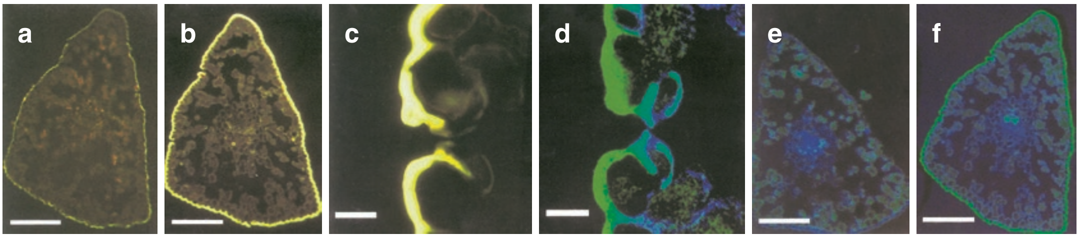

Fig. 3.27 Histochemical evidence for ultraviolet (UV)-absorbing substances in the epidermis of pine needles. **a–c** Fluorescence (excited by light of 450–490 nm wavelength, determined at >520 nm): **a** control; **b**, **c** after treatment with a reagent that intensifies flavonoid fluorescence. **d–f** Observation with a confocal laser microscope (which shows the cells and their content more clearly): (**e**) control; **d**, **f** after staining, as above. **a**, **b**, **e**, **f** Transverse section of a needle; **c**, **d** stomata. (Modified from Schnitzler et al. (1996))

In young leaves the additional pigments protect the developing photosynthetic machinery until the energy dissipation mechanisms are fully functional. The "**autumn anthocyanin**" is well known from the Indian-summer aspect of deciduous trees. Its ecological function, however, is not well understood. Most likely it protects the controlled degradation of leaf constituents—in particular, the chlorophylls—and the export of degradation products to the overwintering parts of the plant. The key enzyme in the flavonoid metabolism is chalcone synthase, whose formation is strongly induced by UV-B as well as by UV-A/blue light.

Other examples of compounds—out of the great variety of aromatic secondary metabolites—that accumulate upon UV-B exposure include 3″,6″-**DCA** and 3″,6″-**DCI** (=3″,6″-di-*para*-coumaroyl-astragalin and 3″,6″-di-*para*-coumaroyl-isoquercitrin) in pine needles and 2″,2″-di-*para*-coumaroylkaemperol-3α-ᴅ-arabinoside in beech leaves (Figs. 3.27 and 3.28). The non-conjugated phenylpropanes (e.g. *p*-coumaric acid and its derivatives) are primarily localised in the epidermal cell wall, while the conjugates are mainly sequestered in the vacuoles of the same cells. It has been calculated that the accumulation of aromatic compounds in the outer epidermis cell wall of pine needles allows only about 4% of the incoming UV-B to pass through. Diacylated flavonoids in the vacuole are able to filter out the residual UV-B, leaving the mesophyll completely unaffected. This explains the exceptional UV protection that needles of coniferous trees are known for (Fig. 3.23).

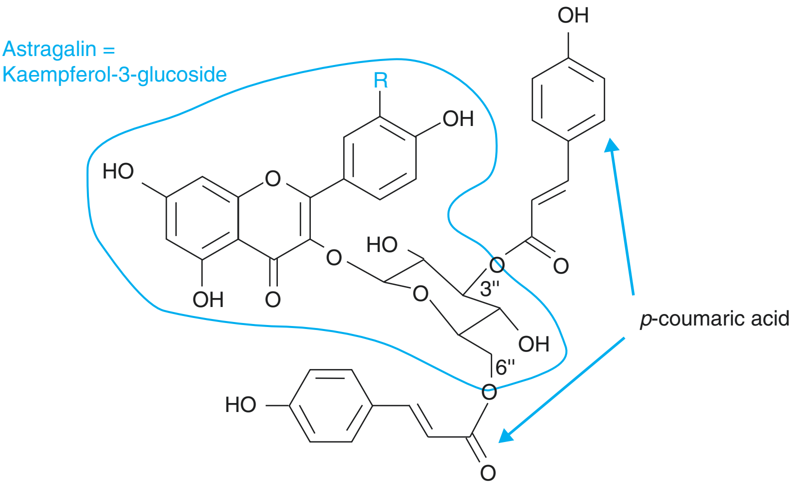

Fig. 3.28 Examples of diacylated flavonoids. 3″,6″-Di-*p*-coumaroyl-astragalin (DCA, R=H) and 3″,6″-Di-*p*-coumaroyl-isoquercitrin (DCI, R=OH)

The association between concentrations of UV screens and UV exposure in the natural habitat is apparent when comparing, for instance, alpine herbs with herbs from the lowlands (Filella and Peñuelas 1999; Fig. 3.23). Moreover, because synthesis of UV-B screening phenols and phenylpropanes is stimulated by UV-B radiation, variations in their concentrations can be expected also when leaves of the same species but from locations with contrasting UV-B radiation intensities are compared. One example of such a **local adaptation** is mountain avens (*Dryas octopetala*) from the Arctic, from southern Norway and from the French Alps, where the average UV-B radiation is three times higher than in the Arctic. UV-B transmittance in the epidermis of *Dryas* from the French Alps was only 2.5% versus 5% in plants from Norway and 7% in Arctic plants (Nybakken et al. 2004). It was also shown that depending on the weather conditions during the year, the screening capacities of the leaf epidermis may change, indicating a dynamic acclimation response (Barnes et al. 1996).

3.3.4 Ultraviolet-B Perception and Signalling

Many transcriptional responses to increased doses of UV-B are non-specific and shared with, for instance, defence responses against pathogen attack (Stratmann 2003). The respective signalling has been associated with UV-B as a severe stressor of plant life, is triggered by DNA damage and ROS production, and involves typical plant stress hormones (Fig. 3.29). Responses result in repair and in protection by the same classes of chemical compounds, which can act either as sunscreen pigments or as components for defence (phytoalexins). In particular, induction or reinforcement of radical scavenging systems such as glutathione reductase, ascorbate peroxidase and glutathione peroxidase are very important for avoidance and alleviation of UV-triggered stress. Overall, responses to UV-B stress are dependent on signalling pathways triggered by non-specific secondary stress (Chap. 2, Sect. 2.2), while **photomorphogenic acclimation responses** are more UV-B specific and are triggered by low levels of UV. It is important to note that both contribute to survival. The specific responses can—depending on the wavelength, intensity or duration—also represent acclimation and avoidance reactions. During the past decade, much progress has been made in the elucidation of signal transduction chains resulting in UV-B tolerance of plants.

Photomorphogenic signalling requires perception of radiation. While the photoreceptors for visible light contain chromophores, the **UV-B photoreceptor** lacks such a component. It absorbs shortwave radiation by a series of aromatic amino acid residues—in particular, 14 tryptophan residues (Trp, W). The UV-B receptor was originally described as a regulatory protein

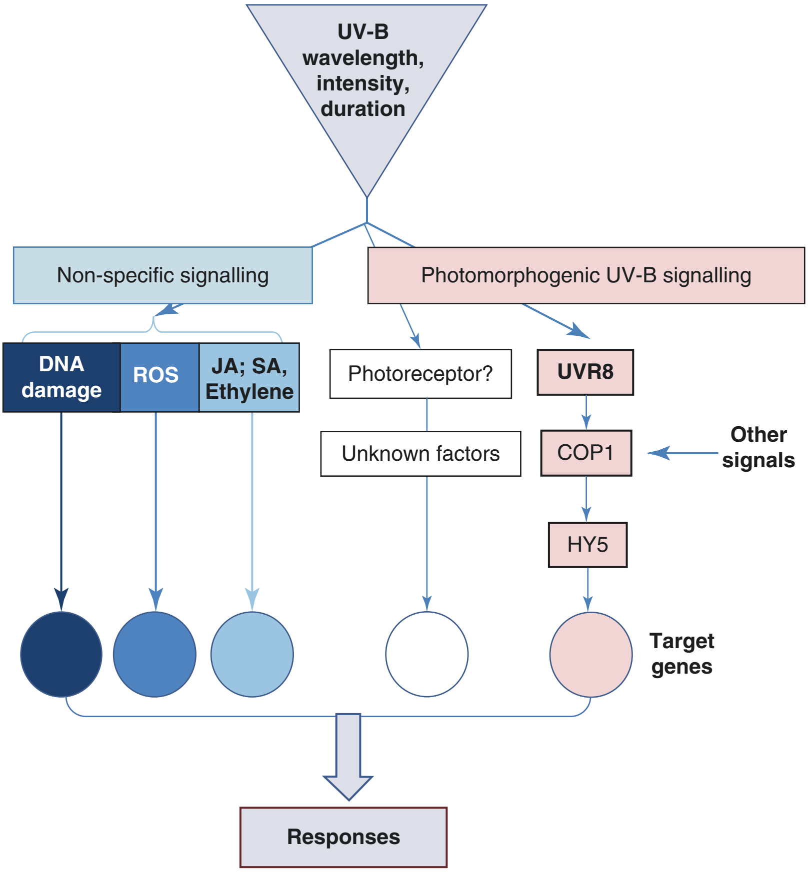

Fig. 3.29 Ultraviolet (UV)-B signal transduction pathways. UV-B induces UV-B-specific and non-specific signal production and transduction. The UV-B wavelength, intensity and duration of exposition trigger the induction of specific sets of target genes and downstream responses that result in repair of UV-triggered damage and adaptation to UV-B. *JA* jasmonic acid, *SA* salicylic acid. (Modified after Jenkins (2009))

in UV-triggered signal transduction in *A. thaliana* (Kliebenstein et al. 2002) and was termed UV RESISTANCE LOCUS 8 (**UVR8**). In 2011, Rizzini et al. identified this protein as the long-sought-after UV-B photoreceptor which, by a special arrangement of tryptophan residues and positively charged arginine residues, can convert UV-B radiation into a chemical signal. Other authors contributed the detailed photochemical and biochemical mechanisms of that process (Christie et al. 2012; Wu et al. 2012). In all investigated species, from algae to higher plants, this type of UV-B photoreceptor has been found (Rizzini et al. 2011).

In the energetic ground state (e.g. in the dark), UVR8 is a doughnut-shaped homodimer whose monomers are linked by a network of salt bridges and aromatic side-chain interactions (Gardner and Correa 2012) (Fig. 3.30). Each monomer consists of 440 amino acid residues with 14 Trp residues, which are clustered at the top surface where the dimer forms. Three of them form a triad, which interacts with another tryptophan of the counterpart analogue (Fig. 3.30). Excitation of the tryptophan residues by UV-B results in the dissociation of the salt bridges and releases the monomers. The active UVR8 monomer then binds to the multifunctional **COP1 protein**, which is a central regulator in UV-B and visible light signalling (Oravecz et al. 2006) (Fig. 3.22). At this point the question of “normal photomorphogenesis” versus the UV stress response arises again but cannot be conclusively answered. It is, however, clear that UV-B-specific responses—whether they are contributing to the normal development of a plant or are excited by an unusual dose of UV radiation—are mediated by the **UVR8–COP1 signalling pathway**

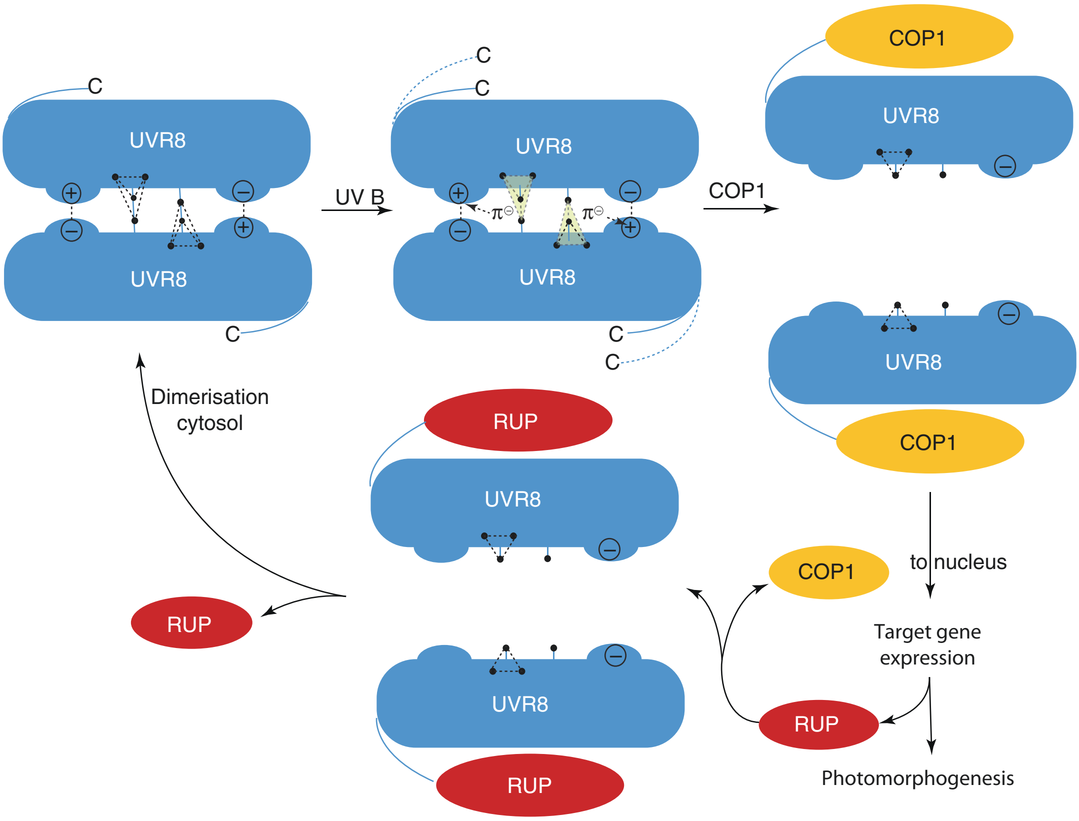

Fig. 3.30 Plant ultraviolet (UV)-B sensing by the UVR8 photoreceptor. UVR8 exists as a stable dimer in the dark through salt bridges and interactions of tryptophan residues forming a Trp-pyramid (3 + 1 trp residues •). Excitation of the tryptophan residues by UV-B results in the donation of π electrons to the arginine residues of the salt bridges, leading to charge neutralisation and dissociation of the dimer. Monomeric UVR8 binds to COP1 which, as a complex, can migrate into the nucleus for expression of the HY5 transcription factor and other genes that lead to the formation of, for example, UV screens. Among these genes is that for RUP proteins (REPRESSOR OF UV-B PHOTOMORPHOGENESIS), which can replace COP1 and finally, by dissociation from UVR8, facilitate dimerisation of (inactive) UVR8. (Modified from Gardner and Correa (2012); for details, see Jenkins (2014))

(Heijde and Ulm 2012). The central protein of this pathway is COP1, best known as a negative regulator or repressor of photomorphogenesis (Fig. 3.22). However, in UV-B signalling, COP1 is a positive regulator. The interaction complex of monomeric UVR8 with COP1 migrates from the cytosol into the nucleus, where it activates *HY5* gene expression. The **transcription factor HY5** triggers the expression of a great variety of UV-B-responsive genes. Among these are genes that encode proteins required for UV-B tolerance or protection, such as photolyases for DNA repair, and enzymes of the phenylpropanoid pathway, such as chalcone synthase, by which phenolic UV-B scavengers are produced.

3.3.5 Crosstalk Between Ultraviolet-B and Visible Light Responses

COP1 interacts with all known photoreceptors for visible and UV-B light in specific ways, thereby enabling crosstalk between the photoreceptors. The multifunctionality of the **COP1 protein** is based on its complex structure, which consists of three major domains: a RING finger, a coiled coil domain and a so-called WD40 (TrpAsp) repeat domain. COP1 can dimerise through the coiled coil domain. Furthermore, the photoreceptors for red/far-red (phytochromes), blue (constitutive cryptochrome effect) and UV-B (UVR8) interact with specific sites of the WD40 domain. By the versatility of the interactions of photoreceptors with the same central regulatory protein, COP1 specificity of signalling can be achieved. While, for example, the ubiqitination and degradation of the photolabile receptors Cry2 and PhyA is mediated by COP1 (Fig. 3.22), it does not impair the stability of PhyB, Cry1 and UVR8. Further regulation of COP1 activity and specificity is achieved by interaction of the coiled coil domain with proteins of the SUPPRESSOR OF PHYTOCHROME A family (SPA1–SPA4; Fig. 3.21), which are required for COP1 function in the dark and visible light but not for the UV-B response. On the other side, REPRESSOR OF UV-B PHOTOMORPHOGENESIS 1 and 2 (RUP1 and RUP2, Fig. 3.30) have been identified as negative feedback regulators of UVR8 signalling (Gruber et al. 2010).

Summary

- For plants, light has a dual function as an energy source and as a signal crucial for plant development and adaptation to the environment. The two basic functions are mediated by light-absorbing molecules, which differ in spectral sensitivity, biological activity and subcellular localisation: the light-harvesting systems for photosynthesis are in the chloroplasts, and the light sensors regulating developmental processes are predominantly cytosolic and/or in the nucleus.
- Light as a stressor: An unfavourable light environment may result from low and high light intensity, as well as from rapid changes between both radiation intensities. Plants can acclimate to their light environment at the level of life strategies, by positioning, morphology and structure of leaves and chloroplasts, as well as by physiological, biochemical and biophysical adjustments.
- While the interpretation of morphological, structural and physiological acclimations to a stressful light environment is obvious, the mechanisms by which the permanent or dynamic acclimations are achieved are understood in less detail, except in a few cases, such as light harvesting and energy dissipation, or the shade avoidance response of juvenile plants as an example of development guided by the light conditions.
- Only a small portion of the visible radiation absorbed by photosynthetic pigments can be used for photosynthetic CO_2 assimilation. Under otherwise adverse environmental conditions such as a shortage of water, this portion may be as low as 1% or 2%. Overexcitation results in damage to the photosystems—mainly photosystem II—either directly or by the formation of radicals and reactive oxygen species (ROS). Several mechanisms are known for avoidance of overexcitation or for dissipation of excess light energy.
- The most important mechanism for energy dissipation is the so-called non-photochemical quenching (NPQ or q_E), which takes place in the antenna system. Conformational change of the proton-sensing protein PsbS of the thylakoid membrane switches between the light harvesting and energy dissipation modes of photosystem II. The xanthophyll cycle participates in the latter reaction. Energy-dependent dissipation of the peripheral antennae from photosystem II and partial association with photosystem I (the state I–state II transition) provide for a balanced excitation of both photosystems in the case of high irradiation.
- Acclimative changes between the harvesting and the dissipative modes of the photosystem are necessary for leaves of a tree crown during the course of a day. Acclimated to a moderate light intensity, they are transitorily stressed by direct radiation, termed sunflecks. The photosynthetic gain from such a changing light environment is lower than from continuous illumination.
- Continuous light, as applied in greenhouses, is injurious for many plant species, as it is not natural. Even in the polar summer, light intensities oscillate considerably in a circadian rhythm.
- Perception of light by a range of receptors and subsequent translation of the respective signals control many aspects of plant development and are crucial for acclimatisation to environmental stressors in diverse habitats. Phytochromes are receptors for red and far-red

light, and cryptochromes and phototropins are receptors for blue light. The photoreceptors for red and blue light principally consist of a protein and a chromophore. Because of the UV absorption by aromatic amino acid residues, the photoreceptor for UV-B light does not require a chromophore.

- Two classes of phytochromes are known—PhyA and PhyB—the latter comprising several species, which are differentiated by their proteins (PhyB–E). Physiologically inactive phytochromes (Phy_{red}) of both classes absorb red light by an open-chain tetrapyrrole chromophore and change their structure to the physiologically active form with an absorption peak in the infrared ($\text{Phy}_{\text{far-red}}$). $\text{Phy}_{\text{far-red}}$ migrates into the nucleus for triggering activity, while Phy_{red} is localised in the cytosol. Both classes of phytochromes are differentiated by their mode of inactivation: $\text{PhyA}_{\text{far-red}}$ inhibits its own synthesis, and irradiation with red as well as with blue light triggers its degradation. $\text{PhyB}_{\text{far-red}}$ slowly reconverts into PhyB_{red} (in the dark) or is degraded.
- Cryptochrome 1 is the photoreceptor for high blue light intensity, while cryptochrome 2 is a sensitive receptor that reacts at low intensities. The photoactive domains of cryptochromes apparently evolved from photolyases but, because of their C-terminal extensions, they act as kinases and do not exhibit photolyase activity. Their chromophores are pterins and flavins. For activity, cryptochromes must become phosphorylated. Further (auto)phosphorylation triggers degradation in the proteasome and thus stops cryptochrome activity.
- Phototropins are blue light receptors of the plasma membrane with two flavin mononucleotides (FMNs) as chromophores. Absorption of blue light changes the protein conformation, leads to dissociation from the plasma membrane and unlocks a kinase activity, which activates regulatory proteins. Phototropins are important for many blue-light-dependent reactions of the plant—for example, opening of stomata (activation of the proton pump) and phototropic responses.
- Activation of the photoreceptors triggers signal transduction cascades, which merge at the central protein COP1 (CONSTITUTIVE PHOTOMORPHOGENIC 1) which, as a homodimer, can interact with several other proteins. In the dark, COP1 exhibits activity as E3 ubiquitin ligase, targeting photomorphogenesis-promoting transcription factors for degradation in the proteasome and thus preventing photomorphogenesis. Light-activated photoreceptors inactivate COP1 by mediating its monomerisation and export from the nucleus, thereby suspending its activity against transcription factors in the nucleus. Further targets of the COP1 E3 ubiquitin ligase are also the phytochromes—in particular, $\text{PhyA}_{\text{far-red}}$ and cryptochrome 2.
- Under irradiation with UV-B, monomeric COP1 associates with the activated UV-B receptor. The heterodimer is transported back into the nucleus, where it triggers expression of genes for photomorphogenesis and UV protection.
- The spectrum of ultraviolet radiation comprises three wavelength ranges according to the energy level: UV-C (100–280 nm), UV-B (260–315 nm) and UV-A (315–400 nm). The shorter the wavelength is, the stronger is its destructive effect, but the more is also absorbed by ozone in the stratosphere and the troposphere. UV-C is almost completely absorbed when passing through the atmosphere; UV-A passes through the atmosphere but hardly damages organisms. The biologically most effective UV light is UV-B. Due to the fluctuating attenuation by stratospheric ozone (the “ozone hole”), the intensity of UV-B reaching the Earth’s surface can increase temporarily.
- Strong UV-B radiation damages plants, particularly DNA (breakage of strands and deletions) in the nucleus, the chloroplasts and mitochondria. It also damages the photosynthetic apparatus (bleaching of photosynthetic pigments, destruction of photosynthetic proteins). Organisms have very efficient repair systems, particularly for damaged DNA (photolyases and nucleotide excision).
- Plants have a high potential to develop protection against UV-B stress. By accumulating UV-B screen compounds, plant can adapt and/or acclimate to UV-B impact. The degree of

UV protection correlates well with the extent of UV exposure typical of the respective habitats.

- UV-B screens consist, above all, of strongly UV-absorbing phenylpropanoid pigments in the walls and vacuoles of epidermal cells. Common radical scavengers, such as the ascorbate peroxidase system or glutathione, are also boosted because of the ROS production elicited by UV stress.
- UV responses involve non-specific and specific signalling pathways. The latter are triggered by damaged DNA or ROS. Specific responses depend on UV-B-specific receptors such as *Arabidopsis thaliana* UVR8. Morphogenetic UV-B signalling can interact with signals from phytochrome and cryptochrome. Crosstalk is integrated by the multifunctional COP1 protein, which controls protein degradation.

References

Ahn TK, Avenson TJ, Ballottari M, Cheng Y-C, Niyogi KK, Bassi R, Fleming GR (2008) Architecture of a charge-transfer state regulating light harvesting in a plant antenna protein. Science 320:794–797

Anderson JM, Andersson B (1988) The dynamic photosynthetic membrane and regulation of solar energy conversion. Trends Biochem Sci 13:351–355

Barnes JD, Percy KE, Paul ND, Jones P, McLaughlin CK, Mullineaux PM, Creissen G, Wellburn AR (1996) The influence of UV-B radiation on the physicochemical nature of tobacco (Nicotiana tabacum L.) leaf surfaces. J Exp Bot 47:99–109

Berg JM, Tymoczko JL, Gatto Jr. CJ, Stryer L (2015) Biochemistry, Internatl edn. Springer, Berlin, Heidelberg

Björkman O, Demming-Adams B (1994) Regulation of photosynthetic light capture, conversion, and dissipation in leaves of higher plants, Ecol Stud. Springer, Heidelberg, New York; 100:17–47.

Björkman O, Powles SB (1981) Leaf movement in the shade species Oxalis oregana. I. Response to light level and quality. Carnegie Inst Wash Year B 80:59–62

Buchanan BB, Gruissem W, Jones RL (2015) Biochemistry and molecular biology of plants, 2nd edn. Wiley, Hoboken

Casal JJ (2013) Photoreceptor signaling networks in plant responses to shade. Annu Rev Plant Biol 64:403–427

Cashmore AR, Jarillo JA, Wu Y-J, Liu D (1999) Cryptochromes: blue light receptors for plants and animals. Science 284:760–765

Chelle M, Evers JB, Combes D, Varlet-Grancher C, Vos J, Andrieu B (2007) Simulation of the three-dimensional distribution of the red:far-red ratio within crop canopies. New Phytol 176:223–234

Christie JM, Arvai AS, Baxter KJ, Heilmann M, Pratt AJ, O'Hara A, Kelly SM, Hothorn M, Smith BO, Hitomi K, Jenkins GI, Getzoff ED (2012) Plant UVR8 photoreceptor senses UV-B by tryptophan-mediated disruption of cross-dimer salt bridges. Science 335:1492–1496

Correa-Galvis V, Poschmann G, Melzer M, Stühler K, Jahns P (2016) PsbS interactions involved in the activation of energy dissipation in Arabidopsis. Nat Plants 2:15225

Day TA, Martin G, Vogelmann TC (1993) Penetration of UV-B radiation in foliage: evidence that the epidermis behaves as a non-uniform filter. Plant Cell Environ 16:735–741

Evans JR (1995) Carbon fixation profiles do reflect light absorption profiles in leaves. Austral J Plant Physiol 22:865–873

Fan M, Li M, Liu Z, Cao P, Pan X, Zhang H, Zhao X, Zhang J, Chang W (2015) Crystal structures of the PsbS protein essential for photoprotection in plants. Nat Struct Mol Biol 22:729–735

Filella I, Peñuelas J (1999) Altitudinal differences in UV absorbance, UV reflectance and related morphological traits of Quercus ilex and Rhododendron ferrugineum in the Mediterranean region. Plant Ecol 145:157–165

Gardner KH, Correa F (2012) How plants see the invisible. Science 335:1451–1452

Gruber H, Heijde M, Heller W, Albert A, Seidlitz HK, Ulm R (2010) Negative feedback regulation of UV-B–induced photomorphogenesis and stress acclimation in Arabidopsis. Proc Natl Acad Sci U S A 107:20132–20137

Hall DO, Rao KK (1994) Photosynthesis. Cambridge University Press, Cambridge

Heijde M, Ulm R (2012) UV-B photoreceptor-mediated signalling in plants. Trends Plant Sci 17:230–237

Heldt HW, Piechulla B (2010) Plant biochemistry, 4th edn. Spektrum Akad. Verl, Heidelberg

Herndl GH (1996) Ultraviolett-Strahlung und Bakterioplankton. Biologie unserer Zeit 26:234–239

Holmes MG, Keiller DR (2002) Effects of pubescence and waxes on the reflectance of leaves in the ultraviolet and photosynthetic wavebands: a comparison of a range of species. Plant Cell Environ 25:85–93

Holzwarth AR, Miloslavina Y, Nilkens M, Jahns P (2009) Identification of two quenching sites active in the regulation of photosynthetic light-harvesting studied by time-resolved fluorescence. Chem Phys Lett 483:262–267

Jansen MAK, Gaba V, Greenberg BM (1998) Higher plants and UV-B radiation: balancing damage, repair and acclimation. Trends Plant Sci 3:131–135

Jenkins GI (2009) Signal transduction in responses to UV-B radiation. Annu Rev Plant Biol 60:407–431

Jenkins GI (2014) The UV-B photoreceptor UVR8: from structure to physiology. Plant Cell 26(1):21–37

Jiao Y, Lau OS, Deng XW (2007) Light-regulated transcriptional networks in higher plants. Nature Rev 8:217–230

Kami C, Lorrain S, Hornitschek F, Fankhauser C (2010) Light-regulated plant growth and development. Curr Top Dev Biol 91:29–66

Kim G-T, Yano S, Kozuka T, Tsukaya H (2005) Photomorphogenesis of leaves: shade-avoidance and differentiation of sun and shade leaves. Photochem Photobiol Sci 4:770–774

Kitajima K, Hogan KP (2003) Increases of chlorophyll a/b ratios during acclimation of tropical woody seedlings to nitrogen limitation and high light. Plant Cell Environ 26:857–865

Kliebenstein DJ, Lim JE, Landry LG, Last RL (2002) Arabidopsis UVR8 regulates ultraviolet-B signal transduction and tolerance and contains sequence similarity to human Regulator of Chromatin Condensation 1. Plant Physiol 130:234–243

Körner C (1999) Alpine plant life: functional ecology of high mountain ecosystems. Springer, Berlin, Heidelberg, New York

Kühlheim C, Ågren J, Jansson S (2002) Rapid regulation of light harvesting and plant fitness in the field. Science 297:91–93

Lambers H, Chapin FS III, Pons TL (2008) Plant physiological ecology, 2nd edn. Springer, Berlin

Lau OS, Deng XW (2012) The photomorphogenic repressors COP1 and DET1: 20 years later. Trend Plant Sci 17:584–593

Li Z, Ahn TK, Avenson TJ, Ballottari M, Cruz JA, Kramer DM, Bassi R, Fleming GR, Keasling JD, Niyogi KK (2009) Lutein accumulation in the absence of zeaxanthin restores nonphotochemical quenching in the Arabidopsis thaliana npq1 mutant. Plant Cell 21:1798–1812

Li X, Wang Q, Yu X, Liu H, Yang H, Liu X, Tan C, Klejnot J, Zhong D, Lin C (2011) Arabidopsis cryptochrome 2 (CRY2) functions by the photoactivation mechanism distinct from the tryptophan (trp) triad-dependent photoreduction. Proc Natl Acad Sci USA 108:20844–20849

Liu H, Liu B, Zhao C, Pepper M, Lin C (2011) The action mechanisms of plant cryptochromes. Trend Plant Sci 16:684–691

MacIntyre HL, Kana TM, Anning T, Geider RJ (2002) Photoacclimation of photosynthesis irradiance response curves and photosynthetic pigments in microalgae and cyanobacteria. J Phycol 38:17–38

Manetas Y (2003) The importance of being hairy: the adverse effects of hair removal on stem photosynthesis of Verbascum speciosum are due to solar UV-B radiation. New Phytol 158:503–508

Matsubara S, Krause GH, Seltmann M, Virgo A, Kursar TA, Jahns P, Winter K (2008) Lutein epoxide cycle, light harvesting and photoprotection in species of the tropical tree genus Inga. Plant Cell Environ 31: 548–561

Mercado LM, Bellouin N, Sitch S, Boucher O, Huntingford C, Wild M, Cox PM (2009) Impact of changes in diffuse radiation on the global land carbon sink. Nature 458:1014–1018

Minagawa J (2013) Dynamic reorganization of photosynthetic supercomplexes during environmental acclimation of photosynthesis. Front Plant Sci 4:513

Munk K (ed) (2009) Taschenlehrbuch Biologie Botanik. Thieme, Stuttgart

Munns R, Schmidt S, Beveridge C (2010) Plants in Action 2nd edition, Copyright © Australian Society of Plant Scientists, New Zealand Society of Plant Biologists, and New Zealand Institute of Agricultural and Horticultural Science. http://plantsinaction.science.uq.edu.au/edition1/?q=content/1-1-2-light-absorption

Nishio JN, Sun J, Vogelmann TC (1993) Carbon fixation gradients across spinach leaves do not follow internal light gradients. Plant Cell 5:953–961

Nultsch W (2001) Allgemeine Botanik, 11th edn. G. Thieme, Stuttgart, New York

Nybakken L, Aubert S, Bilger W (2004) Epidermal UV-screening of arctic and alpine plants along a latitudinal gradient in Europe. Polar Biol 27:391–398

Oikawa K, Kasahara M, Kiyosue T, Kagawa T, Suetsugu N, Takahashi F, Kanegae T, Niwa Y, Kadota A, Wada M (2003) CHLOROPLAST UNUSUAL POSITIONING1 is essential for proper chloroplast positioning. Plant Cell 15:2805–2815

Oikawa K, Yamasato A, Kong SG, Kasahara M, Nakai M, Takahashi F, Ogura Y, Kagawa T, Wada M (2008) Chloroplast outer envelope protein CHUP1 is essential for chloroplast anchorage to the plasma membrane and chloroplast movement. Plant Physiol 148:829–842

Oravecz A, Baumann A, Máté Z, Brzezinska A, Molinier J, Oakeley EJ, Ádám É, Schäfer E, Nagy F, Ulm R (2006) CONSTITUTIVELY PHOTOMORPHOGENIC 1 is required for the UV-B response in Arabidopsis. Plant Cell 18:1975–1990

Osmond B, Badger M, Maxwell K, Björkman O, Leegood R (1997) Too many photons: photorespiration, photoinhibition and photooxidation. Trends Plant Sci 2:119–120

Overmann J, Cypionka H, Pfennig N (1992) An extremely low-light-adapted phototrophic sulphurbacterium from the Black Sea. Limnol Oceanogr 37:150–155

Prior SA, Pritchard SG, Runion GB (2004) Leaves and the effects of elevated carbon dioxide levels. Encyclopedia of Plant and Crop Science, Marcel Dekker Inc

Pritchard SG, Rogers HH, Prior SA, Peterson CM (1999) Elevated CO_2 and plant structure: a review. Glob Change Biol 5:807–837

Rastogi RP, Richa SRP, Singh SP, Häder DP (2010) Photoprotective compounds from marine organisms. J Ind Microbiol Biotechnol 37:537–558

Rius SP, Emiliani J, Casati P (2016) P1 epigenetic regulation in leaves of high altitude maize landraces: effect of UV-B radiation. Front Plant Sci

Rizzini L, Favory J-J, Cloix C, Faggionato D, O'Hara A, Kaiserli E, Baumeister R, Schäfer E, Nagy F, Jenkins GI, Ulm R (2011) Perception of UV-B by the Arabidopsis UVR8 protein. Science 332:103–106

Robberecht R, Caldwell MM, Billings WD (1980) Leaf ultraviolet optical properties along a latitudinal gradient in the arctic–alpine life zone. Ecology 61: 612–619

Schäfer KVR, Dirk VW (2011) The physical environment within forests. Nat Educ Knowl 2(12):5

Schnitzler JP, Jungblut TP, Heller W, Köfferlein M, Hutzler P, Heinzmann U, Schmelzer E, Ernst D, Langebartels C, Sandermann H Jr (1996) Tissue localization of

UV-B screening pigments and of chalcone synthase mRNA in needles of Scots pine seedlings. New Phytol 132:247–258

Scholes GD, Fleming GR, Olaya-Castro A, van Grondelle R (2011) Lessons from nature about solar light harvesting. Nat Chem 3:763–774

Schreiber U, Schliwa U, Bilger W (1986) Continuous recording of photochemical and non-photochemical chlorophyll fluorescence quenching with a new type of modulation fluorometer. Photosynth Res 10:51–62

Schreiber U, Bilger W, Neubauer C (1994) Chlorophyll fluorescence as a nonintrusive indicator for rapid assessment on in vivo photosynthesis, Ecol Studies. Springer, Berlin, Heidelberg, New York; 100:49–70.

Strasburger F (1983) Lehrbuch der Botanik. 32nd edn. Fischer, Stuttgart

Stratmann J (2003) Ultraviolet-B radiation co-opts defense signalling pathways. Trends Plant Sci 8:526–533

Strobl S, Fetene M, Beck EH (2011) Analysis of the "shelter tree-effect" of natural and exotic forest canopies on the growth of young Podocarpus falcatus trees in southern Ethiopia. Trees 25:769–783

Taiz L, Zeiger E et al (2015) Plant physiology and development, 6th edn. Sinauer Associates Inc., Sunderland

Usami H, Maeda T, Fujii Y, Oikawa K, Takahashi F, Kagawa T, Wada M, Kasahara M (2012) CHUP1 mediates actin-based light-induced chloroplast avoidance movement in the moss Physcomitrella patens. Planta 236:1889–1897

Velez-Ramirez AI, van Ieperen W, Vreugdenhil D, Millenaar FF (2011) Plants under continuous light. Trends Plant Sci 16:310–318

Wada M (2013) Chloroplast movement. Plant Sci 210:177–182

Weiler E, Nover L (2008) Allgemeine und molekulare Botanik. Georg Thieme Verlag Stuttgart, New York

Wu D, Hu Q, Yan Z, Chen W, Yan C, Huang X, Zhang J, Deng H, Wang H, Deng XW, Shi Y (2012) Structural basis of ultraviolet-B perception by UVR8. Nature 484:214–220

Yin X, Singer SD, Qiao H, Liu Y, Jiao C, Wang H, Li Z, Fei Z, Wang Y, Fan C, Wang X (2016) Insights into the mechanisms underlying ultraviolet-C induced resveratrol metabolism in grapevine (V. amurensis Rupr.) cv. "Tonghua-3". Front Plant Sci 7:503

Zaks J, Amarnath K, Kramer DM, Niyogi K, Fleming GR (2012) A kinetic model of rapidly reversible nonphotochemical quenching. Proc Natl Acad Sci U S A 109:15757–15762

Temperature

4

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Water freezes not only on the surface of a plant at sub-zero temperatures but also in the plant tissues. Freezing-tolerant plant organs limit intra-organ ice formation to the intercellular spaces, extracting water from the cells, mainly their vacuoles. Aspects that are not well understood are the ice nucleation process and the significance of cellular components—in particular, special cell wall–bound proteins as potential catalysts of heterogeneous nucleation. Extra-organ ice may propagate—for example, via the stomata, hydathodes or lenticels—into the interior, triggering the freezing of extracellular water. (Photo: www.fotocommunity.de/photo/hagebutten-im-raureif)

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4.1 The Temperature Challenge

Temperature is the second dominant factor (after precipitation) that determines the global structure of vegetation. On more than 60% of the continental surface of the Earth, frost can occur at least temporarily. Because of the fundamental importance of water for life, frost (i.e. temperatures below the freezing point of water) is a major threat for any type of organism. This applies in particular to poikilothermic organisms such as plants, which equilibrate with the temperature of their environment. Therefore, frost tolerance is a major factor for the distribution of the terrestrial vegetation on Earth. On the other side, even in the hottest regions (with the exception of volcanoes)—Al'Aziziyah in Libya and Death Valley in California, USA, with the highest ever recorded temperatures of 57.8 °C and 56.7 °C, respectively—higher plant life is possible, provided that moisture is available. Extreme temperatures are commonly accompanied by other stresses—in particular, a shortage of water, which is either frozen at sub-zero temperatures or simply not available in hot places.

4.1.1 Temperature Dependence of Life

For most organisms, **temperature ranges** of active life can be determined, as well as **temperature limits** beyond which life is not possible. Since metabolism requires water, active life is confined to conditions under which water is in the liquid state, and only under high pressure (e.g. in the deep sea) is life possible at temperatures around and even above 100 °C. On the other side, freezing of cellular liquids can be avoided—for example, by high concentrations of compatible solutes or antifreeze compounds, such as specialised proteins—and therefore life processes can continue even in a small temperature range below zero, albeit at low intensity. A dose–response diagram for temperature usually shows an asymmetrical curve with an optimum range of about 10 K, a steep drop towards higher temperatures and a smooth decline towards lower temperatures (Fig. 4.1). Imbalances of metabolism increase with deviation from the optimal range, thereby hampering cellular and developmental processes such as growth and reproduction. On the high-temperature side, heat damage to proteins contributes the most to such imbalances, while on the low-temperature side, membrane functions and different rates of deceleration of enzymatically catalysed reactions are the main reasons for the occurrence of imbalances. For each organism a temperature range of hardly detectable life functions can be derived. Extreme temperatures beyond this range result in lethal damage. Within the tolerable temperature range, the extent of damage does not exceed the capacity of a plant for repair at more favourable temperatures. This status of "latent life" is known as one of the five **cardinal points of temperature tolerance** of an organism (cold death, cold latent life, temperature optimum for active life, heat latent life and heat death) (Fig. 4.1).

4.1.2 Plants as Poikilothermic Organisms

Only very few examples of plant organs that can produce heat by alternative respiration are known. One of these is the spadix of Aracean flowers. Plants are **poikilothermic organisms**, which cannot maintain their temperature at a level different from that of their immediate environment (Chap. 9). However, as the exterior temperatures can vary substantially for different organs such as roots (soil temperature) or leaves (air temperature, local heating by sunrays), temperatures within one individual plant can be very different at any given time. Furthermore, environmental temperatures can change rapidly. Thus, plant cells, tissues and organs require the ability to autonomously respond to temperature fluctuations.

4.1.2.1 Temperature Dependence of Metabolism

In contrast to homeothermic organisms, which maintain a stable inner temperature, plants need to balance the biochemical reactions of their

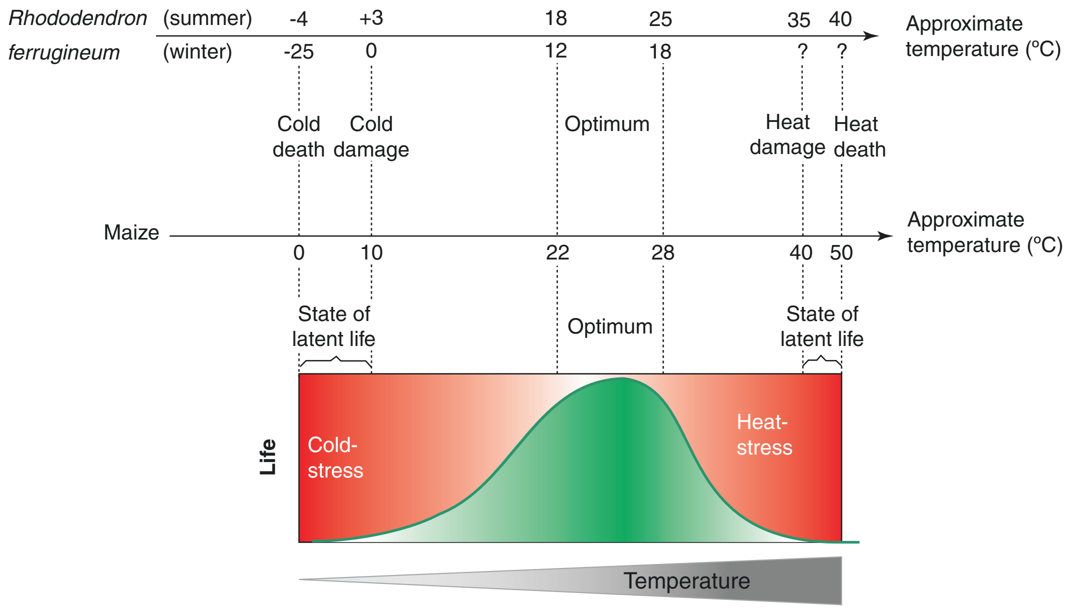


Fig. 4.1 Life processes of an organism, described as a function of temperature. The relative growth rate (*R*) or percentage of survival, respectively, may be used as a measure of life:

$$R = \frac{\Delta \text{biomass}}{\Delta t} \times \frac{1}{\text{biomass}} \qquad (4.1)$$

metabolism. This is not a trivial task, as the rate even of an enzyme-catalysed reaction depends on the temperature, just like any non-catalysed reaction (with the only difference being that the enzyme lowers the activation energy). The simple measure for the temperature dependency of a reaction is the so-called $\mathbf{Q_{10}}$ (the quotient of the rates (V) of a reaction at two temperatures (T) differing by 10 K):

$$\mathrm{Q}_{10} = \frac{V_{T+10}}{V_T} \qquad (4.2)$$

An increase in the temperature speeds up the reaction; a decrease slows it down. The Q_{10} is a direct indicator of the **temperature dependence** of a reaction. The Q_{10} for enzymatic reactions lies between 1.4 and 2.5, while for biophysical processes it is between 1.03 and 1.3. Both the range of Q_{10} values for enzymatic reactions and the difference between biochemical and biophysical reactions pose fundamental problems for plants.

When the rate constants, k_{T_1} and k_{T_2}, are inserted instead of the rate (V) of the reaction, the **activation energy** (E_a) can be calculated:

$$\ln \frac{k_{T_1}}{k_{T_2}} = \frac{E_a}{R}\left(\frac{1}{T_1} - \frac{1}{T_2}\right) \qquad (4.3)$$

where R is the universal gas constant.

Because of variations in the efficiency of catalysis, not all biochemical reactions that take place at the same time in a plant cell require the same activation energy. Therefore, a change in the temperature could easily disturb the metabolic balance in reaction chains—in particular, those involving steps with a high Q_{10}. Plants must be able to compensate for potential temperature-caused **metabolic imbalances**—that is, changes of pool sizes of metabolites.

The challenges arising from the much lower temperature dependence of biophysical reactions apply to photosynthesis in particular. Absorption of light energy is barely affected by temperature, while the **$\mathbf{CO_2}$ fixation** in the **Calvin cycle** is

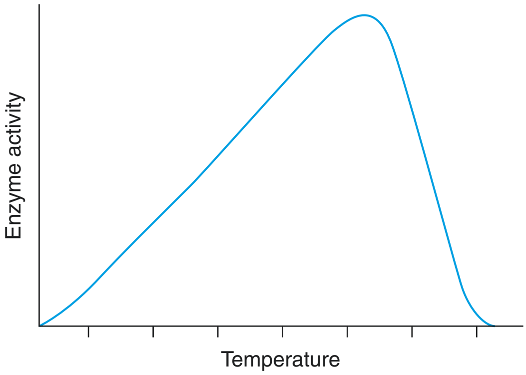


Fig. 4.2 Temperature dependence of an enzyme-catalysed reaction. While at temperatures below the optimum the Q_{10} rule is applicable, temperatures higher than the optimum progressively inactivate the enzyme by affecting its molecular structure (denaturation). Therefore, the temperature response curve of a biochemical reaction is asymmetrical with a strong decline towards higher temperatures

substantially slower at cooler temperatures. This leads to an excess of energy, which has to be dissipated in order to prevent injury (Sect. 4.1.2.2 and Chap. 3) (Fig. 4.2).

Since the cellular metabolism is composed of a large number of individual reactions whose reaction rates are dependent not only on the temperature but also on the equilibrium constants and sizes of the substrate pools, heat inactivation of the cellular metabolism is not as sudden as that of individual enzymes. Comparably strong inactivation does not take place at temperatures below the optimum.

4.1.2.2 Temperature and Photosynthesis

Practically any type of stress that impairs CO_2 assimilation in the Calvin cycle under high light can cause oxidative damage and **photoinhibition** (of photosynthesis). Low temperatures are among the most prominent of these stresses (Chap. 12). Essentially, two processes account for oxidative damage. First, excitation energy cannot be channelled efficiently into the reduction of nicotinamide adenine dinucleotide phosphate ($NADP^+$), because the balance is disturbed between photosynthetic thylakoid reactions (the so-called light reactions, which are virtually not decelerated), and the biochemical CO_2 fixation reactions which, in contrast, are slowed down considerably in the cold. As a consequence, reduced NADP (NADPH) is not oxidised at a sufficient rate in the reducing phase of the Calvin cycle, leading to a shortage of the electron acceptor $NADP^+$. Under such conditions, electrons are transferred to O_2 instead and thereby radicals and **reactive oxygen species** (**ROS**) are produced. Depending on the scavenging capacity of the cell, ROS can be detoxified or cause damage. In addition, they can act as signals activating pathways that target genes for ROS-detoxifying proteins such as ascorbate peroxidase, glutathione reductase or superoxide dismutase (Chap. 2, Sect. 2.2).

ROS generation can inhibit the repair of the **D1 protein**, which is the primary site of photoinhibition due to excessive light intensity (Yamamoto 2016). The D1 protein is a component of **photosystem II** (**PS II**), which contains—in addition to the paired P_{680} reaction centre—several other photopigments, as well as the quinones Q_A and the mobile Q_B (plastoquinone in the bound state). During unlimited electron drainage from PS II to plastoquinone the excited chlorophylls of P_{680} are in the singlet state $^1P_{680}$, which readily dissipates its energy through Chl_{D1} and $pheophytin_{D1}$ to Q_A. Impaired reoxidation of $Q_A^{\ominus}$—e.g. because of over-reduction of plastoquinone or other components of the linear photosynthetic electron transport—results in a spin conversion of $P_{680}^+Q_A^{\ominus}$ to $^3[P_{680}^+Q_A^{\ominus}]$ (**triplet state**) (Chap. 2, Sect. 2.2). This triplet state of P_{680} reacts readily with molecular oxygen $^3O_2$, producing the extremely reactive **singlet oxygen** $^1O_2$. (Quenching of singlet oxygen formed at a low rate by carotenoids is described in detail in Chap. 2, Sect. 2.2.3). At low temperatures, quenching cannot keep pace with the production of singlet oxygen. This is the second process (besides ROS production) that causes photoinhibition of PS II. A similar process has also been described for **photosystem I** (**PS I**), albeit with ROS species other than singlet oxygen. Here the equivalent to the D1 protein, PsaB, is damaged when ROS production (in particular, the hydroxyl radical) exceeds detoxification. Photoinhibition

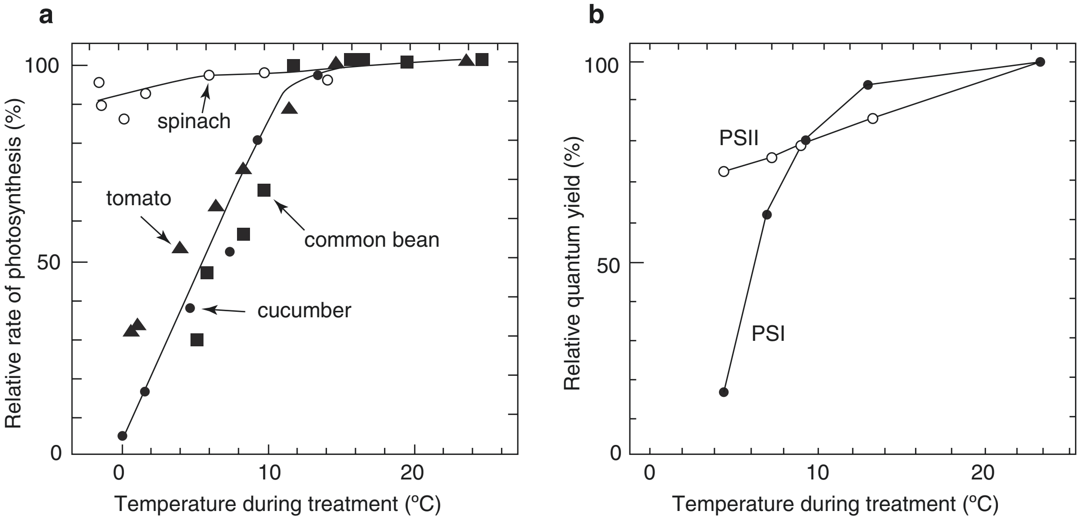


Fig. 4.3 Photoinhibition by chilling at a photon flux density (PFD) of about 450 µmol quanta m^{-2} s^{-1} upon exposure for 2.5 h to the indicated temperatures. The rate of photosynthesis by leaf slices maintained at 25 °C at the same PFD is 100%. **a** Photosynthetic CO_2 net uptake. **b** Photosynthetic quantum yield of photosystem II (H_2O → 2,6-dimethyl-*p*-quinone) and photosystem I (diaminodurene → methylviologen/O_2), respectively, measured in potato leaves. Cucumber, common bean, tomato and potato are chilling sensitive; spinach is chilling tolerant (Sonoike 1996)

of PS I is particularly pronounced in tropical species sensitive to chilling—that is, cold temperatures above freezing (Fig. 4.3). The difference in the damage to D1 and PsaB is the time required for repair. Recovery from photoinhibition of PS II requires only hours, whereas restoration of PS I takes several days.

4.1.2.3 Membrane Fluidity

In addition to its influence on the rates of metabolic processes, temperature has a strong effect on cellular membranes. Biomembranes consist of a bilayer of bipolar lipids with embedded proteins such as transporters, ion channels or receptors, as well as photosynthetic and respiratory multi-protein complexes. Their structure is described in the fluid mosaic model (see biochemistry textbooks such as Buchanan et al. 2015; Heldt and Piechulla 2010). This lipid bilayer has to maintain a fluid state for functionality. Also, signal transduction events and localised responses of cells require horizontal mobility of proteins in a membrane or the production of signal compounds from membrane lipids. The fluidity of these lipids depends, in the first approximation, on the solid (crystallised) or liquid state of the **fatty acids** which, at a given temperature, depends on the chain length and the degree of unsaturation. The longer the chain length and the smaller the number of double bonds, the higher the melting point (Table 4.1). Polyunsaturated fatty acids need more space than saturated fatty acids because of the rotational movement of the carbon chain at the double bonds. Therefore, membranes with a high proportion of unsaturated fatty acids are less tightly packed and hence more fluid than those where saturated fatty acids dominate. On the other hand, the thickness of the lipid bilayer decreases with an increasing proportion of unsaturated fatty acids.

4.1.2.4 Freezing

A fourth temperature-related stress phenomenon—besides metabolic imbalances, changes in membrane fluidity and heat denaturation of proteins—is the freezing of water (i.e. the formation of ice crystals) within an organism (Boxes 4.1 and 4.2). This represents a severe additional threat. Thus, **chilling stress** (exposure to low positive

Table 4.1 Chemical structures and melting points of the most common fatty acids in biomembranes

Carbon skeleton	Structure	Common name	Melting point (°C)
16:0	$CH_3(CH_2)_{14}COOH$	Palmitic acid	63.1
18:0	$CH_3(CH_2)_{16}COOH$	Stearic acid	69.6
20:0	$CH_3(CH_2)_{18}COOH$	Arachidic acid	76.5
16:1 (Δ^9)	$CH_3(CH_2)_5CH{=}CH(CH_2)_7COOH$	Palmitoleic acid	−0.5
18:1 (Δ^9)	$CH_3(CH_2)_7CH{=}CH(CH_2)_7COOH$	Oleic acid	13.4
18:2 ($\Delta^{9,12}$)	$CH_3(CH_2)_4CH{=}CHCH_2CH{=}CH(CH_2)_7COOH$	α-Linoleic acid	−5.0
18:3 ($\Delta^{9,12,15}$)	$CH_3CH_2CH{=}CHCH_2CH{=}CHCH_2CH{=}CH(CH_2)_7COOH$	α-Linolenic acid	−11
20:4 ($\Delta^{5,8,11,14}$)	$CH_3(CH_2)_4CH{=}CHCH_2CH{=}CHCH_2CH{=}CHCH_2CH{=}CH(CH_2)_3COOH$	Arachidonic acid	−49.5

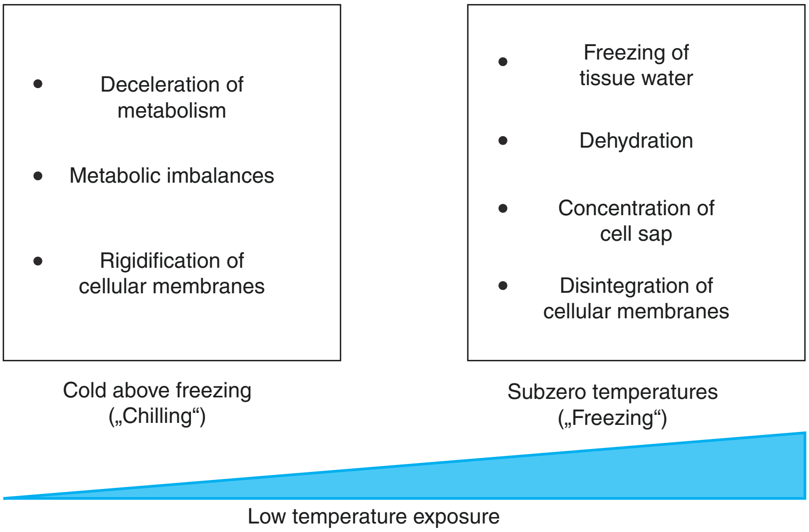


Fig. 4.4 Stress from cold and frost at the cellular level. Low temperatures below the optimal range but above the melting point of water (= chilling) slow down enzymatic reactions. Because these are not equally affected by temperature changes (i.e. they have different Q_{10} values), metabolic imbalances (Jones et al. 1998; Janská et al. 2010) occur. Cellular membranes rigidify as a result of reduced movement of lipids. A further decrease in temperature below the melting point (= freezing) can lead to the freezing of extracellular water. This causes dehydration because of a massive reduction in water availability owing to crystallisation. Cells lose water to the exterior and cell sap becomes more concentrated. Intracellular formation of ice crystals causes disintegration of cellular membranes and thereby ion leakage

temperatures) is distinguished from **freezing stress** (exposure to sub-zero temperatures) (Fig. 4.4). Massive injury can occur because of severe dehydration upon formation of ice crystals (Box 4.2). Ice crystals predominantly build up in the apoplast because of the lower concentration of solutes relative to the cytosol. Ice formation in the apoplast leads to a drastic drop in water availability. The concomitant decrease in the water potential to extremely negative values causes damage to membranes and in turn the cellular compartmentation. Ice, in contrast to liquid water, is hydrophobic, and ice crystals at the surface of a biomembrane cannot exert the membrane-forming forces required for the formation of a lipid bilayer. Amphiphilic lipids unite with micelles or membranes only when they are in a sufficiently hydrophilic medium—that is, stabilised by an ordered water film. If this film disappears, the stabilising effect of the hydrophobic interaction vanishes and the lipids aggregate into droplets. This is then called the “lipid hexagonal II phase” (Fig. 4.5).

Thus, intracellular crystallisation of water, which inevitably brings ice into contact with biomembranes, results in membrane disintegration and collapse of the cellular compartmentation. Loss of membrane integrity is indicated by electrolyte leakage, a parameter commonly used to quantify freezing tolerance (Box 4.3). Furthermore, freezing of water in xylem vessels and subsequent thawing causes air breakage of the water column, called an **embolism**.

4.1.3 Variations in Temperature Range

A classification most commonly used in microbiology sorts organisms into three categories based on their temperature optima: **psychrophiles**, **mesophiles** and **thermophiles**. **Psychrophiles** are organisms adapted to cold habitats where water frequently changes from the liquid to the crystalline state. Most of them are unicellular snow and

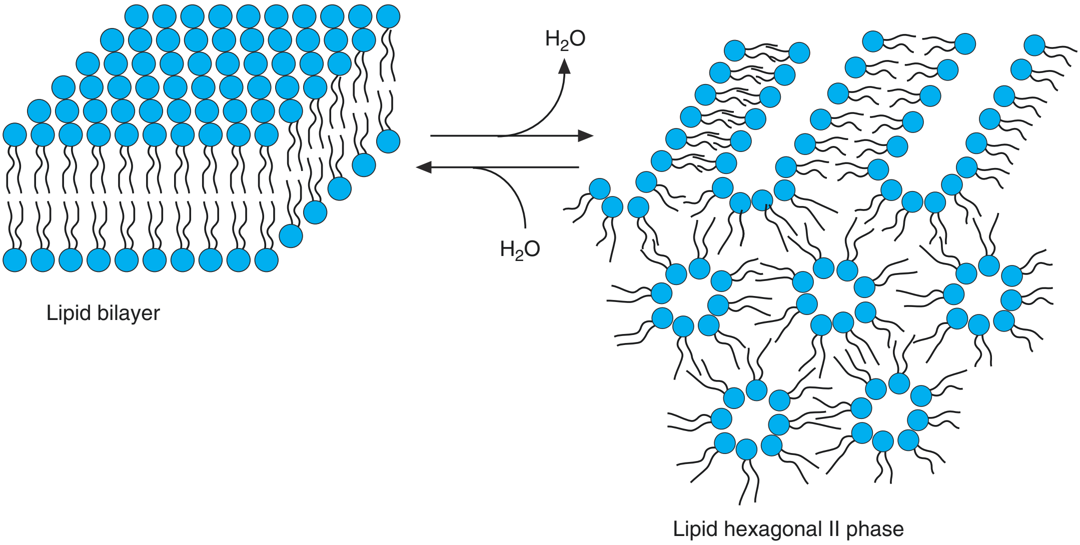


Fig. 4.5 Disintegration and reconstruction of a phospholipid bilayer by water removal (e.g. freeze dehydration) and rehydration. Phospholipids form lipid droplets or threads in the hexagonal II phase. (Modified from Crowe et al. (1983))

Box 4.1: The Physics of Freezing: Homogeneous and Heterogeneous Ice Nucleation

A droplet of purest water, not disturbed by any agitation, can supercool to around −40 °C before instant nucleation takes place (Lorv et al. 2014). In that case, the Brownian molecular movement of the water molecules is so slow that larger clusters of molecules form, which initiate solidification in a hexagonal crystal lattice. As the nucleation in this case originates from water itself, it is called **homogeneous nucleation**. The cooling energy expended to achieve crystallisation is released as the heat of crystallisation, which can be recorded on a thermogram as the **freezing exotherm** (Fig. 4.6). The melting process requires energy as well, referred to as the heat of fusion, and is recognised by a delay in warming during the thawing process (melting point (MP) in Fig. 4.6). When nucleation of crystallisation is initiated in other ways (e.g. by seeding with ice crystals), **supercooling** to a less negative temperature than for homogeneous nucleation is sufficient for crystallisation. This is called **heterogeneous nucleation** because elements of the environment trigger

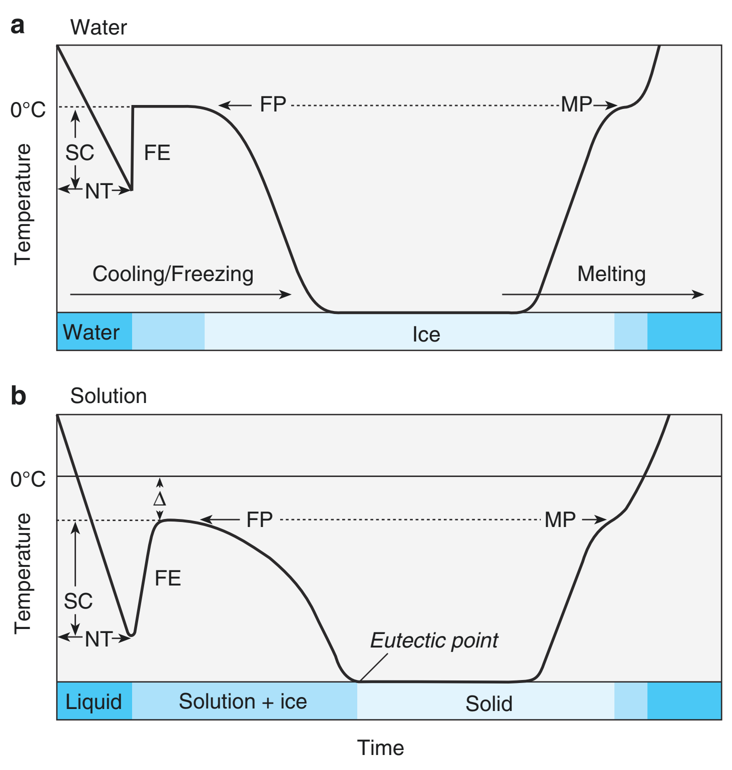


Fig. 4.6 Thermograms of the freezing and thawing processes of pure water **a** and of an aqueous solution of a low molecular weight compound **b**. Δ denotes freezing point depression. *FE* freezing exotherm, *FP* freezing point, *MP* melting point, *NT* nucleation temperature, *SC* supercooling

crystallisation. These elements can be particular surface structures (e.g. of an ice crystal or a cell wall), whose microstructures can force the water clusters into a lattice-like structure which, together with the sub-zero temperature, facilitates crystallisation. Thus, heterogeneous nucleation requires less supercooling and, considering the situation in a plant tissue, with the physicochemical equilibrium between the extracellular ice and the cellular solutions, the proportion of water that crystallises is smaller and the **freeze desiccation** is less dramatic. This is important for preventing freezing damage by sudden ice formation.

The water vapour pressure over ice is less than that over supercooled liquid water at the same sub-zero temperature (Table 4.2). In line with the lower water vapour pressure is the more negative water potential of ice compared with supercooled water. Both are directly dependent on the sub-zero temperature. The water potential of ice (Ψ_{ice}) can be calculated from the vapour pressures over liquid water (P_{water}) and over ice (P_{ice}) by the following equation:

$$\Psi_{\text{ice}} = \frac{RT}{V_{\text{w}}} \times \ln \frac{P_{\text{ice}}}{P_{\text{w}}}, \qquad (4.4)$$

where V_{w} is the mole volume of water at the particular temperature. Therefore, at sub-zero temperatures, ice is thermodynamically more stable than supercooled water.

The water vapour pressure is also lower over aqueous solutions than over pure water and depends on the concentration of the solution—more precisely on the mole fraction (M) of water in the solution (**Raoult's law**):

$$P = P_0 \times M_{\text{water}} \qquad (4.5)$$

$$\text{where } M_{\text{water}} = \frac{\text{mol}_{\text{solvent}}}{\text{mol}_{\text{solvent}} + \text{mol}_{\text{solute}}}. \qquad (4.6)$$

Table 4.2 Partial pressure of water vapour (in millibars) above ice and supercooled water

°C	Vapour pressure of ice (mbar)	Vapour pressure of liquid water (mbar)
0	6.1	6.1
−5	4.0	4.2
−10	2.6	2.9
−15	1.7	1.9
−20	1.0	1.3
−30	0.38	0.51

For dilute solutions it is the concentration of a solute(s):

$$c_s = \frac{n_s}{V_{\text{water}}}, \tag{4.7}$$

where n = number of moles in a particular volume of water and the osmotic potential (water potential of the solution, π) is:

$$\pi = -\text{RT} \times c_s. \tag{4.8}$$

It follows that the freezing/melting point of a solution is lower than that of pure water (Fig. 4.6b) and that the depression (Δ_{Tm}) is proportional to the concentration of the solution, whereby the molar Δ_{Tm} = 1.86 °C; thus the actual $\Delta_{\text{Tm}} = 1.86 \times n_s$ (mole solute in 1 kg water (molality)).

This applies strictly to dilute (i.e. "ideal") solutions. In concentrated solutions, interactions occur between the dissolved particles, resulting in an apparent reduction in the concentration. The factor α, by which the concentrations appears to decrease, is the activity factor.

The following considerations are important for the **freeze dehydration** of plant cells. Cooling of dilute solutions to sub-zero temperatures results first in freezing of pure water and an increase in the concentration of the cellular liquid. Separated by the cell wall, extracellular ice coexists with the liquid content of the cell, the proportions responding to the water potential of both compartments (within the cell, equilibrium of the water potentials of the organelles must also be assumed, otherwise considerable intracellular fluxes of water would occur between the organelles).

ice algae (e.g. *Haematococcus pluvialis* and various diatoms) or bacteria that prevent freezing of cellular water. At the other end of the scale are the **thermophiles** (and extremophiles) with optimal temperatures for growth between +80 °C and above 100 °C. They comprise certain unicellular algae such as *Cyanidioschyzon merolae*, cyanobacteria, bacteria and archaea, most of them living in hot springs, in geysers or on the black smokers of the deep sea. Most organisms, including practically all plants—in particular, the (homoiohydric) terrestrial and the marine species—belong to the **mesophiles**, which thrive at day temperatures between 15 °C and 25 °C and (in the case of terrestrial species) night temperatures about 10 K lower.

However, while temperature optima are not that different between plants, the tolerable temperature range varies widely (Tables 4.3 and 4.4). Most of the variation is attributable to differences in the ability to withstand temperatures below the optimum. The temperature at which cold damage occurs largely corresponds to the **geographical distribution** of a species. For instance, plants from temperate zones are usually more cold tolerant than plants from tropical regions. They are able to withstand sub-zero temperatures, whereas many tropical plants already show damage when exposed to temperatures slightly above freezing (chilling) (Fig. 4.3). Palms, mangroves, and tropical ornamental plants such as the African violet (*Saintpaulia ionantha*) (Fig. 4.8) or the coffee tree (Fig. 4.9) have been studied intensively. They are all adapted to a temperature range of between +5 and about 50 °C. Many other crops are chilling sensitive as well (e.g. cotton, soybean, maize and rice).

The chilling sensitivity of the African violet has been used to demonstrate that the strength or quantity of stress is composed of its intensity and its duration (Fig. 4.8). **Chilling damage**, visible as necroses, starts at temperatures below 8 °C. Fifty per cent damage results from 6 h of exposure to +1 °C or maintenance at +5 °C for

Box 4.2: How Much of the Tissue Water Can Freeze?

Liquid water can be distinguished from ice by nuclear magnetic resonance (NMR) spectroscopy. The frozen and the still liquid portions of the water content of a leaf, for example, can thus be determined by running the NMR scans at a series of sub-freezing temperatures. Plotting the portion of liquid water versus the temperature produces so-called **freezing curves** (Fig. 4.7). The lower the temperature, the more cellular water is deposited as ice in the intercellular cavities. The nearly hyperbolic freezing curve of ivy (*Hedera helix*) can be transformed into a straight line by plotting the residual liquid water against the reciprocal of the temperature. The line cuts the *y* axis at a value, *K*, which is the amount of water that, because of its binding to macromolecules, cannot freeze. In the example shown in Fig. 4.7, $K \approx 5\%$. Interestingly, at a normal winter temperature of −10 °C, about 80% of the water in an ivy leaf is already frozen outside the cells and accordingly shrinkage of the cell volumes is dramatic and can result in considerable negative turgor (Zhu and Beck 1991). The concomitant increase in the concentration of the intracellular solutes is likewise dramatic (e.g. fivefold in the presented example). A highly concentrated solution has a substantially lower freezing point than the original cellular solutions, thus counteracting intracellular ice formation.

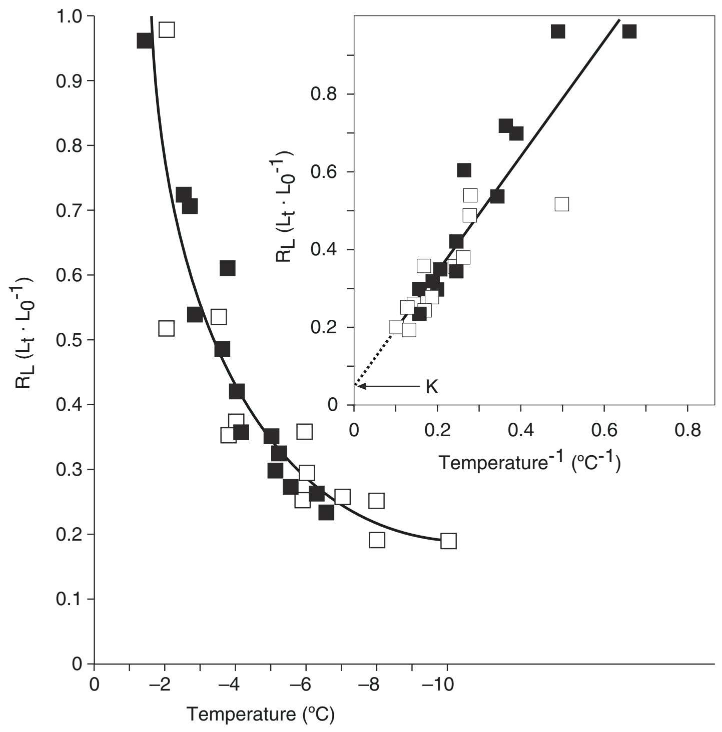


Fig. 4.7 Freezing curve of frost-hardened ivy (*Hedera helix*) leaves. The curve shows the liquid water proportion (R_L) of the total water content (L_0) as dependent on the frost temperature (t)

$$R_L = \frac{L_t}{L_0} \tag{4.9}$$

Upon ideal equilibrium freezing, a rectangular hyperbola is obtained, which can be transformed into a simple linear relationship (*insert*). The point at which this line cuts the *y* axis is the *K* point, indicating the non-freezable portion of tissue water (Hansen and Beck 1988).

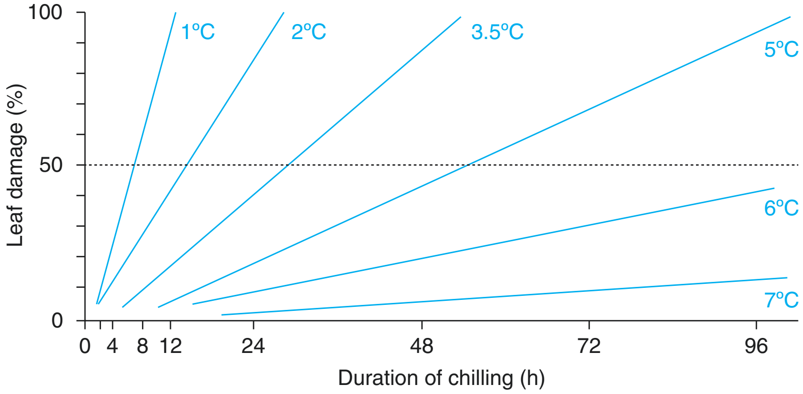
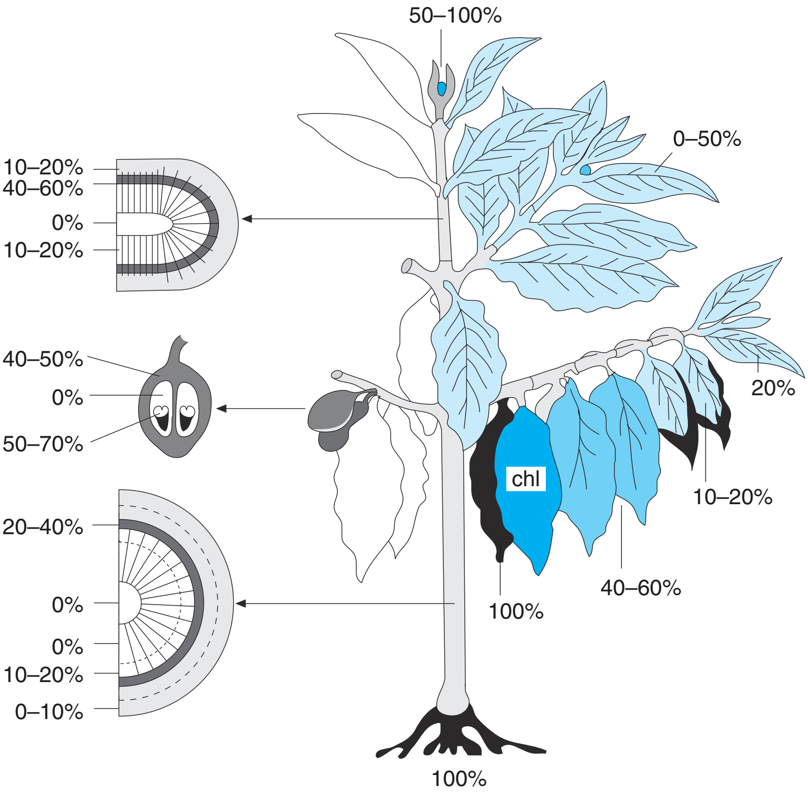


Fig. 4.8 Damage to the African violet (*Saintpaulia ionantha*) by various chilling treatments. Below the threshold temperature of +8 °C, necrosis occurs. The strength of the chilling stress can be estimated as the product of cold (above the freezing point) multiplied by the duration of the exposure to the temperatures, as indicated in the figure. (Modified from Larcher (1994))

Fig. 4.9 Differences in the cold sensitivity of the organs of a coffee tree. Visual damage after 3 days of continuous cooling to +1 °C is shown. *Black* denotes complete damage. *Chl* chlorotic (Larcher 2003)



50 h. In this case, the low rate of repair allows comparative quantification of stress damage.

The variation in the ability to tolerate temperature extremes is far less pronounced at the other end of the temperature scale. Critical temperatures causing heat damage barely vary between plants, and hardly any correlation with the climatic zone of origin is apparent (Tables 4.3 and 4.4).

Not all life processes of a plant have the same optimum temperature, because the individual developmental steps may take place in different ambient conditions. Winter cultivars of cereals, for instance,

Table 4.3 Maximum temperature resistance of microorganisms and poikilohydric seed plants in the moist turgescent state and in the dry rigid state caused by desiccation. (Modified from Larcher (2003))

	Temperature at which cold damage occurs after at least 2 h (°C)		Temperature at which heat damage occurs after 30 min (°C)	
Organisms/plant type	Moist	Dry	Moist	Dry
Bacterial spores		Liquid nitrogen	80 to 120	Up to 160
Fungi				
Plant pathogenic fungi			45 to 65 (70)	
Saprophytic fungi	0 to below −10		40 to 60 (80)	75 to 100
Fungal fruiting bodies	−5 to −10 (−30)			
Fungal spores		Liquid nitrogen	50 to 60 (100)	Above 100
Marine algae				
Tropical sea algae	+14 to +5 (−2)		32 to 35 (40)	
Temperate sea algae (tidal zone)	−8 to −40		30 to 35	
Polar sea algae	−10 to −60		(15) 20 to 28	
Freshwater algae	−5 to −20 (−30)		35 to 45 (50)	
Airborne algae	−10 to −30	Liquid nitrogen	40 to 50	
Lichens				
From polar regions, high mountains, deserts	−80	Liquid nitrogen		
From temperate climate zones	−50	Liquid nitrogen	33 to 45	70 to 100
Mosses				
From humid tropics	−1 to −7			
From temperate climates				
From humid locations	−5 to 15		40 to 45	
From forest floors	−15 to −25		40 to 50	80 to 95
Epiphytic and epipetric	−15 to −35	Liquid nitrogen		100 to 110
From polar regions	−50 to −80	Liquid nitrogen		
Poikilohydric ferns	−20	Liquid nitrogen	47 to 50	60 to 100
Seed plants				
Ramonda myconi	−9	Liquid nitrogen	48	56
Myrothamnus flabellifolia		Liquid nitrogen		80

germinate at temperatures considerably lower than those required for growth (in spring and summer). Nevertheless, the rates of germination show typical temperature dependence with Q_{10} values between 1.5 and 2.5. In that context it is also important to mention that not all organs of a higher plant are similarly cold sensitive or tolerant. Those most sensitive are the roots and meristems of the shoots, while axial tissues and mature leaves are the most tolerant parts (Fig. 4.9). Also, certain stages in the development of a plant are particularly vulnerable—namely, seed germination and fruit ripening.

Also relevant for plant survival is the fact that the temperature tolerance of a cell is strongly influenced by its water status. When dry, poikilohydric plants, prokaryotes and fungi can survive freezing in liquid nitrogen and exposure to temperatures close to 100 °C, while in the hydrated state the range of their temperature tolerance is much narrower. Table 4.3 presents some examples of the temperature tolerance of poikilohydric lower and higher plants, bacteria and fungi in the dry state and the hydrated state.

The correlation between the cold/frost tolerance of a species and the average minimum temperature of the climatic zone it inhabits shows the adaptive importance of mechanisms to cope with temperatures near and especially below the freezing point. Likewise, **within-species variation** in frost tolerance is associated with distribution of **ecotypes** along temperature gradients. The frost tolerance of *Arabidopsis thaliana* accessions correlates well with the mean minimum temperature at the site of origin. Individuals from Sweden or Russia, for instance, survive exposure to two consecutive nights of −10 °C much better than

Table 4.4 Temperature tolerance of the leaves of vascular plants from various climate zones. (Modified from Larcher (2003))

Plant functional type	Temperature at which cold damage occurs in a hardened state (°C)	Temperature at which heat damage occurs during vegetative growth (°C)
Tropical plants		
Trees	+5 to −2	45 to 50
Tropical alpine plants	−5 to −15 (−20)	About 45
Subtropical plants		
Evergreen woody plants	−8 to −12	50 to 60
Palms	−5 to −14	55 to 60
Succulents	−5 to −10 (−15)	58 to 67
C_4 grasses	−1 to −5 (−8)	60 to 64
Annual desert grasses	−6 to −10	50 to 55
Temperate plants		
Evergreen plants of mild winter	−7 to −15 (−25)	46 to 50 (55)
Herbaceous plants	−10 to −20 (−30)	47 to 52 (sun), 40 to 45 (shade)
Halophytes	−10 to −20	
Water plants	−5 to −12	38 to 44
Homoiohydric ferns	−10 to −40	46 to 48
Winter-cold areas		
Evergreen conifers	−40 to −90	40 to 52
Boreal deciduous trees	Liquid nitrogen (vegetative buds)	42 to 45
Arctic alpine dwarfs shrubs	−30 to −70	48 to 54

The data quoted correspond to the limiting temperatures causing 50% damage (TL_{50} in °C) after at least 2 h of exposure to cold or 30 min of heat treatment

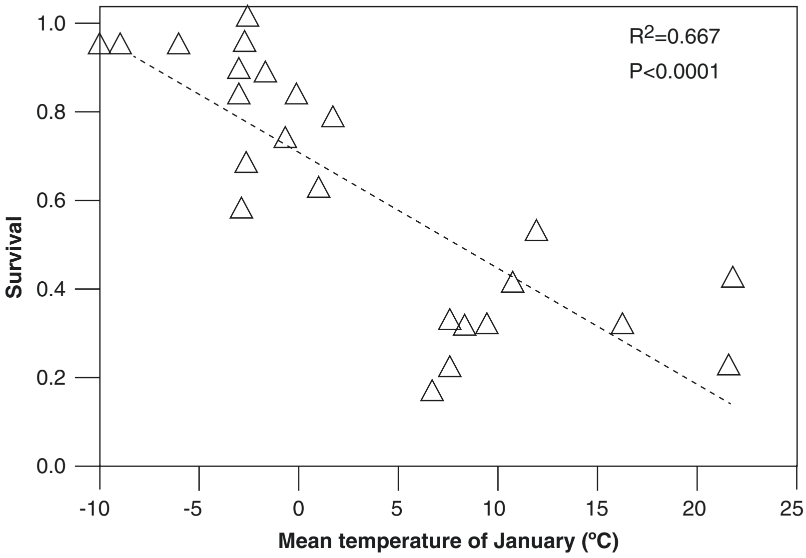


Fig. 4.10 Clinal variations in the freezing tolerance of *Arabidopsis thaliana* accessions. Survivorship is plotted against the January mean temperature at the site of origin for 24 *A. thaliana* accessions cooled to −10 °C for two consecutive nights. All plants were first cold acclimated for 7 days at 4 °C. The data are based on 20 replicates per accession (Zhen and Ungerer 2008)

individuals from Spain, Libya or Morocco (Zhen and Ungerer 2008, Fig. 4.10). Similarly, there are pronounced differences in freezing tolerance between winter cereals and spring cereals.

Depending on the temperature climate of their habitat, plants must be adapted to and acclimate to not only the extremes of the temperature range (i.e. to seasonal variations) but also to smaller or greater diurnal temperature fluctuations. Considerable **diurnal temperature oscillations** are typical of deserts and the alpine and nival vegetation belts of high mountains, especially in

Box 4.3: Measurement of Cold Hardiness and Damage by Cold and Freezing of Plant Tissue

The degree of cold/frost hardiness of a plant or plant tissue can be experimentally examined by subjecting the sample to a so-called freeze–thaw cycle with subsequent quantification of the induced damage. To warrant full equilibration of the sample with the applied temperature, low rates of cooling and rewarming must be applied (Wisniewski et al. 2014). A frequently used rate is 2 K/h. The protocol for a freeze–thaw cycle is shown in Fig. 4.11. For quantification of the damage, which can result from cooling as well as from rewarming, the sample is kept after rewarming at room temperature for at least 24 h to allow development of potential damage. Commonly used assays for the degree of damage and cold resistance, respectively, are biochemical activity tests such as the **triphenyl-tetrazolium test** for dehydrogenase activity or the electrical conductivity test for membrane leakage (Fig. 4.12). Controls are undamaged as well as completely killed (by dipping in liquid nitrogen) samples. Cold hardiness is commonly expressed as the LT_{50}—the temperature at which 50% damage (e.g. ion leakage of 50%) becomes apparent.

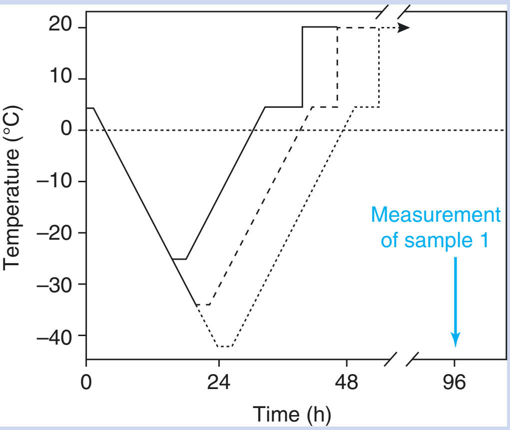


Fig. 4.11 Temperature course of a freeze–thaw cycle experiment. In order to determine the degree of cold hardiness or damage, the samples must be cooled to several defined final temperatures, where they remain for 2 h. Rewarming then occurs at the same rate as cooling. After rewarming, the sample is kept for 5 h at +5 °C and subsequently for 24 h or even longer at ambient temperature

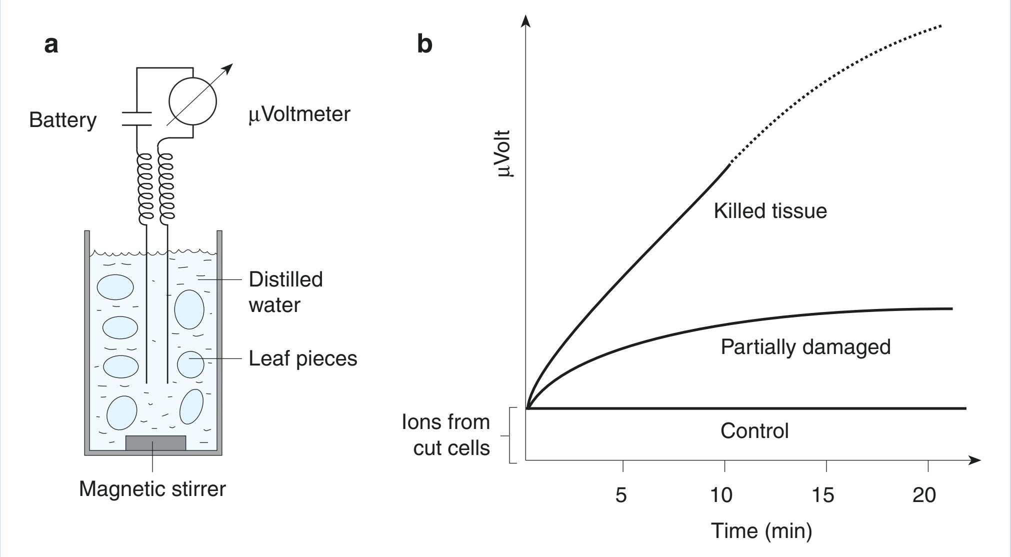


Fig. 4.12 Electrical conductivity assay. Damage to plant tissues leads to loss of selective membrane permeability—that is, inactivation of ion channels and transporters in plant membranes. Consequently, solutes leak out of the tissue. When, for example, excised leaf discs are floated in distilled water **a**, low molecular weight compounds diffuse into the medium, among them several ions. The increase in the conductivity of the water can be measured conductometrically. The more cells have been damaged, the higher the resulting conductivity is **b**

the tropics. The air temperature during daytime may reach 20–30 °C, whereas the nocturnal temperature usually falls below the freezing point and the leaves may be stiffly frozen at the end of the night. While freezing of leaf tissue water is a process of several hours, thawing takes place within minutes once the tropical morning sun hits the leaves (Sect. 4.2.6). These plants have developed mechanisms to slow down freezing or even avoid it. They have to be frost tolerant all year round.

On a sunny day in temperate regions (e.g. in Central Europe) the surface of bare soil may become as hot as +50 °C, while the air temperature above the soil decreases rapidly with the distance from the soil surface. The gradient in the soil itself is even steeper. Reverse temperature gradients occur also during clear nights when no cloud cover mitigates radiation emission from horizontal and slightly inclined surfaces of the vegetation or from the soil. Young plants whose shoots or leaves are close to the ground are therefore exposed to a stronger temperature stress during both day and night than plants whose leaves are supported by a stem, which experience a considerably less challenging temperature microclimate (for details of the energy balance of leaves, Chap. 9).

4.1.4 Strategies to Cope with Temperature Fluctuations and Temperature Extremes

Seasonally varying temperature extremes can be avoided through various escape strategies (Chap. 2). Annual plants can endure unfavourable conditions as dry seeds that are far less frost or heat sensitive. A new life cycle then starts with germination only after a cold winter or a hot, dry summer, depending on the habitat. Alternatives for perennial plants are the shedding of cold-sensitive organs such as the leaves or the overwintering only of the subterranean plant parts (rhizomes, bulbs) (Chap. 12). Tropical alpine plants have developed mechanisms of short-term freezing avoidance, as the daily periods of sub-zero temperatures are usually shorter than 12 h (Sect. 4.2.6).

Besides such escape strategies, every plant needs to be able to adjust metabolic fluxes and membrane fluidity to fluctuating temperatures and to protect cellular structures during short periods of temperature extremes. In the absence of homeostatic temperature regulation, most of the mechanisms involved operate at the cellular level and protect the tissues directly exposed to an unfavourable temperature.

In the case of temperatures below the optimum, adjustments result in **cold acclimation** or **cold hardening**. Many plant species acquire frost tolerance by exposure to low yet non-freezing temperatures (**frost hardening**) (the temperature ranges depicted in Table 4.4 take the acclimation into account). Plant organs (e.g. evergreen leaves) become tolerant of freezing of a considerable portion of their tissue water. Such acclimation offers effective protection in most habitats because decreases in temperature are usually slower than the kinetics of cellular responses. Moreover, frost hardening is often initiated even before the onset of cold temperatures, owing to the ability to anticipate the coming winter on the basis of environmental cues such as decreasing day length (Beck et al. 2004). In addition, non-damaging cold can also induce or, as in the case of evergreen conifers, boost an ongoing cold-hardening process. Since frost hardening is associated with a change or even a halt of metabolic activity (Nagler et al. 2015), acclimated plants must undergo a **de-hardening process** at the beginning of the warm season (Sect. 4.2).

Acclimative changes in heat tolerance (= **acquired thermotolerance**), albeit not nearly as pronounced as cold hardening, are also well established. The underlying mechanisms are only partly specific to the stressor heat (Sect. 4.3); rather, they provide general stress tolerance. This is important, as heat stress (a) occurs in a temperature range of high metabolic activity and (b) is almost always accompanied by or associated with other stresses such as drought, high light intensity and generation of ROS.

4.2 Cold Acclimation and Freezing Tolerance

A complex array of cellular mechanisms (a cold tolerance syndrome) counteracts the negative consequences of exposure to low non-freezing

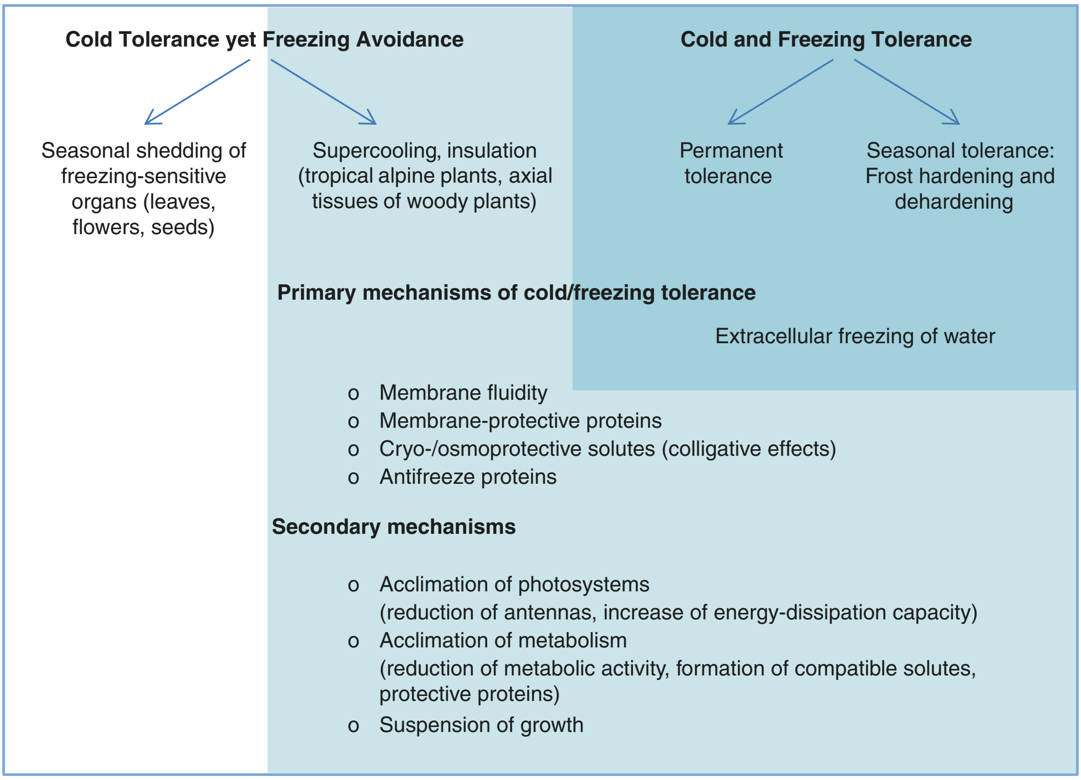


Fig. 4.13 Mechanisms that allow plants to survive in habitats characterised by permanently, transitorily or seasonally occurring cold and frost

temperatures and to temperatures below 0 °C. The efficiencies and relative contributions of different mechanisms vary between plant species, as well as depending on the mode of stress (e.g. acute versus chronic freezing stress). Also, the amount of direct evidence supporting the function of a particular mechanism for survival at low temperatures varies. Clearly of central importance is the adjustment of membrane fluidity through the modulation of lipid compositions. Furthermore, metabolic imbalances causing, for instance, the risk of **photoinhibition** need to be buffered. Various proteins and metabolites that protect cellular structures are synthesised during cold acclimation.

With respect to stress caused by sub-zero temperatures, mechanisms can be divided into **tolerance** and **avoidance** strategies—that is, those enabling plants to endure the formation of ice crystals versus those suppressing or even promoting the formation of ice crystals. Several reactions upon freeze dehydration resemble those observable during drought or salinity stress (Chaps. 6 and 7). At the molecular level, signal transduction networks activated by the three different types of stress target partly the same genes because some protective mechanisms are the same (Yamaguchi-Shinozaki and Shinozaki 2006; Huang et al. 2012) (Chap. 2). This explains the so-called **cross-protection**: exposure to drought improves cold tolerance, and *vice versa*. The same applies to osmotic strain caused by salt.

Avoidance mechanisms involve synthesis of so-called **antifreeze proteins**, which inhibit the growth of ice crystals, or other measures to at least partially suppress the formation of ice crystals (Moffatt et al. 2006) (Fig. 4.13).

4.2.1 Adjustment of Membrane Fluidity

A very important aspect of cold stress physiology is the increase of membrane fluidity with decreasing temperatures (Sect. 4.1.2.3). Cold/

frost hardening and de-hardening are therefore strongly associated with changes in the chemical composition of the cellular membranes to maintain the fluidity required for proper functioning. Acclimation to a particular temperature involves modification of the lipid composition with respect to the proportions of saturated and unsaturated fatty acids—that is, changes in the **desaturation index** (double-bond index (DBI)):

$$\mathrm{DBI} = \frac{\sum\begin{pmatrix}\text{mol\% fatty acid content}\\ \times\ \text{number of double bonds}\end{pmatrix}}{100}. \tag{4.10}$$

At lower growth temperatures, membrane fluidity is maintained by a higher proportion of unsaturated fatty acids. The respective acclimative responses (Fig. 4.14) have been documented for many different plant species.

Membrane **sterols** play a special role, due to an amphipathic structure that differs from that of the glycerolipids. Since their hydrophobic moiety is much larger relative to the polar heads than in glycerolipids, they are able to diffuse rapidly horizontally as well as vertically (the so-called flip-flop mechanism). They serve as buffers for membrane fluidity. At low temperatures, they increase membrane fluidity by disrupting gelling of phospholipid domains and thus preventing the formation of semi-crystalline patches. At high temperatures, they decelerate the motion of the fatty acid tails and thus stiffen the membrane (Buchanan et al. 2015).

Unsaturated fatty acids originate from saturated ones by the oxygen-dependent action of **desaturases**. Although desaturation is an oxidative process, it requires, in addition, two electrons from electron donors such as ferredoxin (in plastids) or reduced cytochrome b_5 (in the endoplasmic reticulum (ER); for more details, see plant physiology and plant biochemistry textbooks). Each fatty acid desaturase introduces a double bond at a specific position—for example, at the Δ6, Δ9 or Δ12 position. In the ER of plants and in cyanobacteria, desaturation is commonly catalysed by acyl-lipid desaturases, which introduce unsaturated bonds into fatty acids that are in a lipid-bound form. Various types of membrane-bound and soluble desaturases are also present in the plastids of plant cells. The importance of desaturases for cold acclimation is demonstrated by the inability of desaturase mutants to survive at low non-freezing temperatures. In contrast, overexpression of the ω-3 fatty acid desaturases *FAD3* (localised in the ER) and *FAD7* (localised in the chloroplasts), which catalyse the conversion of linoleic acid (18:2) to linolenic acid (18:3) in tomato, increased the chilling tolerance of the plants (Domínguez et al. 2010) but also affected the photosynthetic performance in a different way, depending on the intracellular localisation of the respective desaturase (Fig. 4.15).

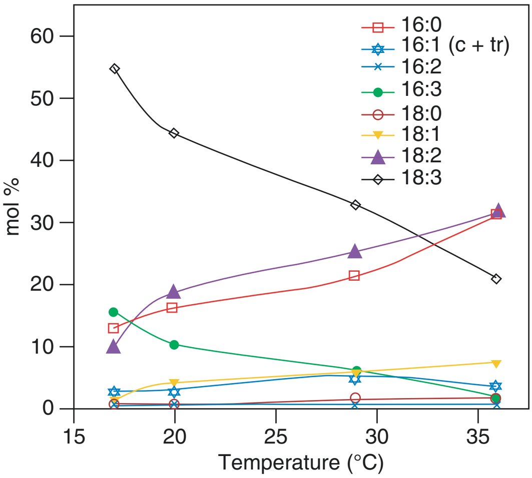


Fig. 4.14 Fatty acid composition of membranes of *Arabidopsis thaliana* leaves grown at various temperatures from 17 °C to 36 °C. *c* + *tr* cis and trans isomers. (Modified from Falcone et al. (2004))

Adjustment of the lipid composition of membranes takes time, as degradation, synthesis and trafficking of lipids are required. Temperature changes during the course of a day/night cycle are probably too rapid, as changes in membrane composition usually take several days. Still, during a day/night cycle associated with a corresponding **diurnal temperature cycle**, the plasma membranes of *Arabidopsis* seedlings showed slightly lower fluidity during the cold phase. Whether this was due to a reorientation of the membrane domains (van Meer et al. 2008) or to small changes in lipid desaturation was not clear. The fluidity buffer function exerted by the membrane sterols may play an important role in compensating for diurnal fluidity fluctuations (Martinière et al. 2011).

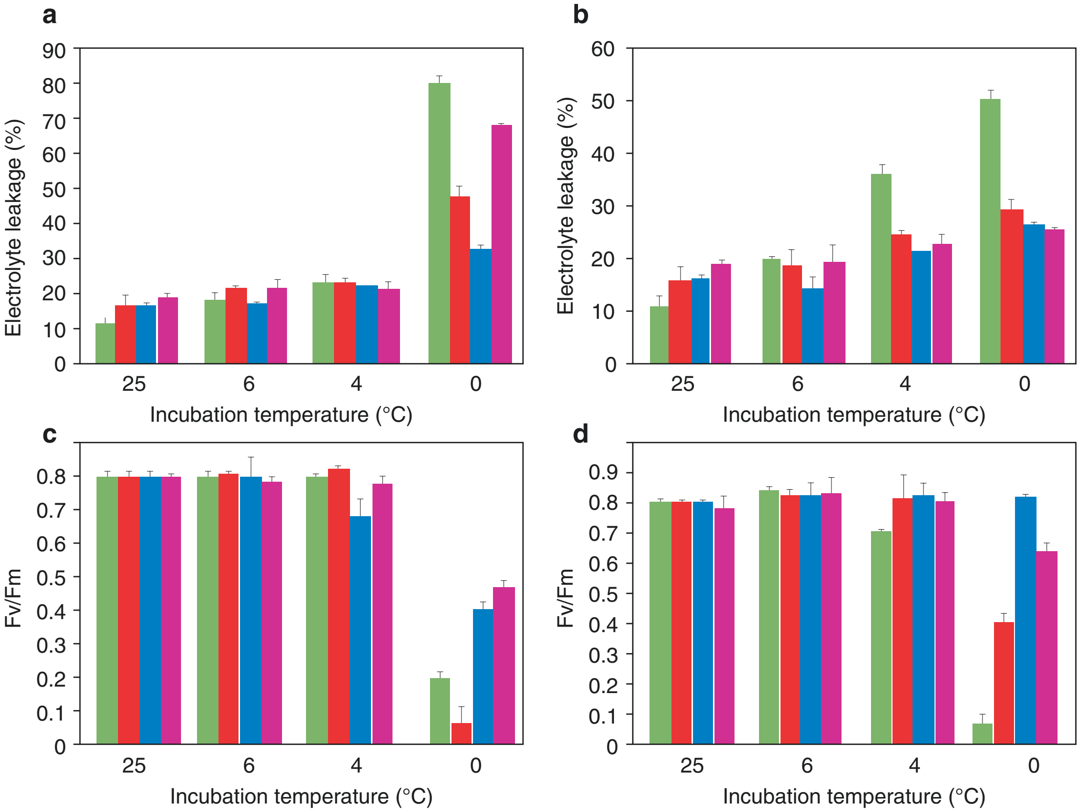


Fig. 4.15 Chilling tolerance and photosynthetic performance of fatty acid desaturase–overexpressing transgenic tomato plants. **a**, **b** Chilling tolerance of non-acclimated plants **a** and acclimated plants **b** determined with the electrolyte leakage assay (Box 4.3). *Green bars* represent the untransformed wild type; *other colours* represent independent transgenic lines. Relative conductance was measured before cold treatment and after a 24-h recovery period subsequent to chilling in the dark for 3 days at 6 °C, 4 °C and 0 °C. **c**, **d** Photosynthetic performance determined by the chlorophyll a fluorescence assay (F_v/F_m; Chap. 3, Fig. 3.11) of wild-type and fatty acid desaturase–overexpressing tomato before cold treatment (25 °C) and after chilling, as described for **a** and **b**. All measurements were taken on the youngest fully expanded leaves. Acclimation was achieved by progressive cooling of the plants to a temperature of 10 °C. (Modified from Domínguez et al. (2010))

Evergreen plants of temperate and cold regions are able to seasonally adjust the fluidity of their biomembranes by exchanging certain types of fatty acids for others (homeoviscous or homeophasic acclimation). Such exchanges are a major part of the processes of cold hardening and de-hardening (Vogg et al. 1998). Table 4.5 shows this for a specific membrane—the chloroplast envelope of spruce needles. The proportions of unsaturated and polyunsaturated fatty acids increase dramatically in the phospholipid as well the galactolipid fractions upon cold hardening and decrease upon de-hardening.

Table 4.5 Changes in the composition of the lipids of a defined biomembrane (the chloroplast envelope of spruce needles) during the course of frost hardening ("winter") and de-hardening ("summer") (Senser and Beck 1992)

Lipids	Fatty acids (%) 16:0 + 18:0 + 18:1^{tr}	Fatty acids (%) 16:3 + 18:1 + 18:2 + 18:3 + 18:4 + 18: 2-hydroxy +20:3
Phospholipids		
Summer	55.4	41.2
Winter	25.6	66.0
Galactolipids		
Summer	33.4	64.4
Winter	9.4	84.8

4.2.2 Prevention of Photoinhibition

Cold hardening has to include not only modifications of the lipid/protein composition of the biomembranes but also adjustments of other metabolic processes. The foremost adjustment is the reduction in the light-harvesting capacity of the chloroplasts. The decelerated metabolism in the cold can lead to dramatically increased rates of ROS formation, since light absorption by the photosynthetic pigments takes place irrespective of the temperature, while the biochemical utilisation of the absorbed energy cannot keep pace with the pigment excitation. Thus, in cold-hardened plants the chlorophyll content is lower and the photosynthetic apparatus is partially degraded (Fig. 4.16). Conversely, xanthophyll concentrations are higher, so the capacity for **non-photochemical quenching** is higher.

The limitation of photosynthesis does not necessarily result in a shortage of plant reserve material, as respiration is also markedly restricted at lower temperatures (Hansen and Beck 1994). Concomitantly with the slowdown in photosynthesis, frost hardening of evergreens is associated with a change in **carbohydrate metabolism** in favour of the production and accumulation of oligosaccharides instead of starch (Hansen et al. 1997).

4.2.3 Cryoprotective Proteins

In the course of cold acclimation, the proteome of plant cells undergoes pronounced changes. Many proteins increase in abundance upon exposure to low temperature. Collectively they are often referred to as cold-responsive proteins (**COR proteins**). Among them are isoforms of housekeeping enzymes with a lower temperature optimum, as well as enzymes involved in the biosynthesis of **cryoprotectants** (Sect. 4.2.4.1). The integrity and function of biomembranes have to be protected against damage resulting from freeze dehydration and the concomitant increase in the solute concentrations of the intracellular fluids. Such protection has been associated with the synthesis of **dehydrins** (**DHNs**) and **dehydrin-like proteins** (Late Embryogenesis Abundant (LEA) proteins and Responsive to ABA (RAB)

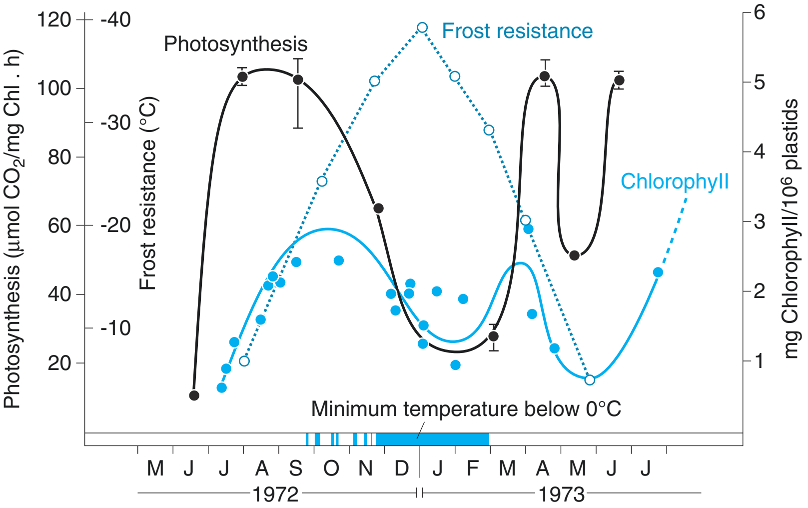


Fig. 4.16 Frost resistance and photosynthetic capacity (CO_2 uptake at saturating light and 1% CO_2 concentration) of one generation of spruce (*Picea abies* Karst.) needles measured under identical conditions over the course of 2 years. Note that the annual fluctuation in photosynthesis follows the dynamics of the chlorophyll content of the chloroplasts. Needles were taken from a 50-year-old spruce tree in the Botanical Garden in Munich. (After Senser and Beck (1979))

proteins; for more details, Chap. 6). These proteins are all extremely hydrophilic glycine-rich proteins of a wide range of molecular weights. They lack enzymatic activity, are heat and acid stable and possess a high proportion of a random coil secondary structure, which binds water intramolecularly (Hanin et al. 2011). Interaction with biomembranes is enabled by a hydrophobic domain while the hydrophilic domain(s) face the cytosol. Attachment to the biomembranes displaces low molecular weight solutes, such as ions, from the membrane, thus avoiding changes in the membrane potential and disintegration or inactivation of ion pumps and transporters.

In unstressed plants, only low concentrations of dehydrins are present. Stress by drought, salt and cold leads to rapid up-regulation of gene expression and steady accumulation of dehydrins in all compartments of the cell. As for the majority of the COR proteins, formation of dehydrins can be triggered by abscisic acid (ABA) or can be activated independently of ABA. The promoter of the *COR* gene, *RD29A* (also known as *COR78* or *LTI178*) contains *cis*-acting elements for ABA-independent signalling (cold response, osmotic stress) as well as for ABA-dependent (osmotic) signalling (Chaps. 2 and 6). Enhanced frost tolerance of *A. thaliana* was achieved by overexpression of *RcDHN5* from *Rhododendron catawbiense* (Peng et al. 2008) and was attributed to maintenance of enzyme activity upon water deficiency. Nonetheless, the question as to whether particular dehydrins directly contribute to chilling and freezing tolerance remains unanswered.

Another type of proteins has been described as **Cold Shock Domain Proteins** (**CSPs**), suggesting cryoprotective properties (Sasaki et al. 2007). The typical Cold Shock Domain (CSD) contains a five-stranded β-barrel sheet with two consensus motifs, which bind to single-stranded DNA/RNA (Sasaki et al. 2013). The CSDs are found in bacteria, as well as in eukaryotes, and are considered RNA chaperones. Upon cold treatment, RNA forms unfavourable secondary structures that could interfere with RNA functions such as transcription and translation. CSPs are able to resolve these structures and restore RNA functionality. Although they are associated with cold adaptation, CSPs regulate many biological processes such as growth and flowering, thus exhibiting pleiotropic effects (Sasaki and Imai 2012).

4.2.4 Control of Ice Formation

To survive sub-freezing temperatures, organisms have developed a variety of mechanisms to maintain at least a minimum portion of their cellular liquids unfrozen. Variations in frost tolerance between acclimated and non-acclimated plants are at least partly explained by differences in the onset temperature of detrimental **intracellular ice formation**. Figure 4.17 shows the example of rye.

Whether crystallisation takes place inside or outside the cells depends on the cooling rate. When tissue is cooled slowly, water can move or leak out of the cells and crystallise outside the cell membranes in the extracellular spaces. This is a reversible process following the equilibrium between the water potentials of ice and of the cellular solutions. The water potential of ice is more negative than that of supercooled pure water (Box 4.1). The lower the sub-zero temperature is, the more negative the water potential of ice is and the more cellular water crystallises in the intercellular space. At a high cooling rate, there is not sufficient time for water export, and freezing takes place intracellularly, thereby killing the cells. In that case, ice crystals can grow through plasmodesmata and pits from cell to cell and rapidly expand to wider areas of the tissue.

For crystallisation, the liquid accumulating in the apoplastic space requires a **nucleation** trigger. Ice spreading from nearby xylem vessels could play such a role. In frost-sensitive dicots, ice spreads from only one nucleation event rapidly through the entire plant, while in graminoids, because of the polystele, each grass leaf requires separate nucleation. Thus, the shoot structure and vascular system are important for the spreading of ice and freezing damage (Hacker and Neuner 2007, 2008). Otherwise, so-called **ice nucleation–active bacteria** (**INA bacteria**; Box 4.4) in the substomatal cavity or on the surface of a leaf could trigger nucleation. With potato and cauliflower, it has been shown that even water droplets

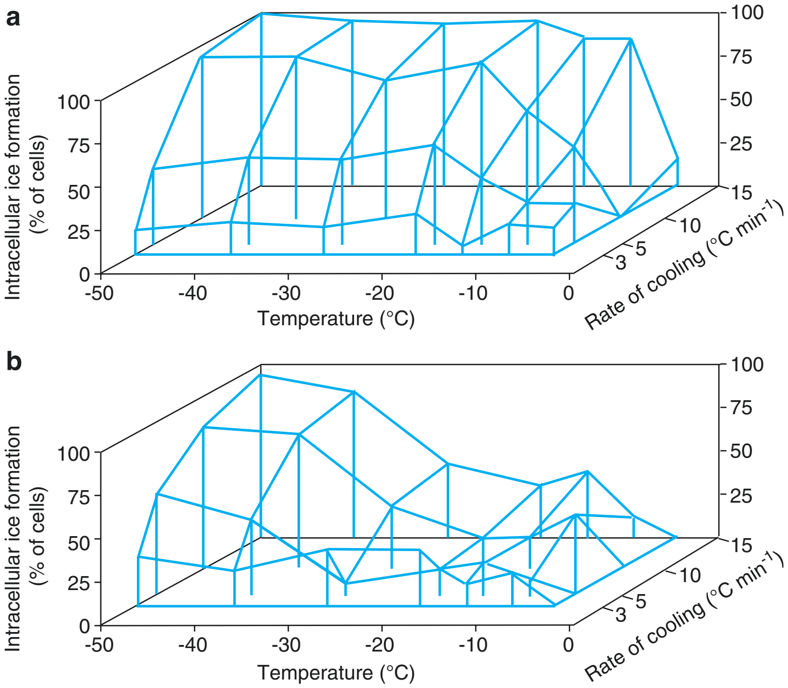


Fig. 4.17 Formation of intracellular ice in protoplasts from frost-sensitive **a** and frost-hardened **b** rye leaves as a function of the cooling rate and the minimum temperature (*x axis*). Protoplasts from frost-sensitive leaves do not deposit **plasma membrane material** on the outer surface upon shrinking by extracellular ice formation. Intracellular ice formation is lethal for the cells. (Modified from Dowgert and Steponkus (1983))

Box 4.4: Ice Nucleation Proteins

The so-called **ice nucleation–active bacteria** (**INA bacteria**) produce cylindrical surface proteins, which facilitate heterogeneous nucleation (ice nucleation proteins (INPs)). These bacteria are commonly gram-negative, epiphytic and pathogenic (Lorv et al. 2014). An example is *Pseudomonas syringae*. The effect of the "decoration" of the outer membrane with INPs is shown in Table 4.6 in comparison with other bacteria, which do not produce these proteins.

The INP from *P. syringae* consists of a particular octapeptide in up to more than 100-fold repetition (Fig. 4.18). The N terminus is anchored with transmembrane spans to a glycosylphosphatidylinositol patch of the outer membrane of the bacterium (Turner et al. 1991; Sarhan 2011).

Deletion mutants show that a 68-fold repetition of the motif is sufficient to effectively trigger ice seeding. A change in the octapeptide sequence abolishes ice nucleation activity (Green and Warren 1985). A model of the protein predicts a largely planar molecule with a molecular mass around 150 kDa, serving as a

Table 4.6 Ice nucleation activity of bacterial cultures (Maki et al. 1974)

Species	Ice nucleation temperature (°C)	
	T_1	T_{90}
Pseudomonas syringae C9	−2.9	−3.5
Pseudomonas syringae wt	−3.2	−3.9
Pseudomonas aeruginosa	−7.5	−17.8
Staphylococcus epidermidis	−6.9	−19.5
Escherichia coli	−8.3	−17.1
Proteus mirabilis	−8.0	−19.4
Bacillus subtilis	−10.6	−18.0
Pure culture medium	−9.2	−17.0

Thirty droplets (each 0.01 mL) of test material were placed on a controlled surface, and the temperature was slowly lowered from room temperature to −25 °C. The temperature at which the first crystal formed (T_1) and the temperature at which 90% of the droplets were frozen (T_{90}) were recorded

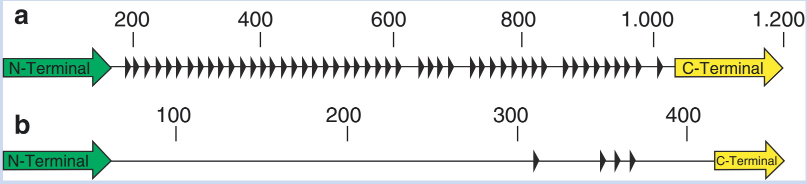


Fig. 4.18 Blueprints of the ice nucleation protein (INP) from *Pseudomonas syringae* **a** and INP-F from the fungus *Fusarium acuminatum* **b**. *Triangles* represent the repetitive motif. The N-terminal domain (about 15%) of the *Pseudomonas* INP consists of three or four potential transmembrane spans; the C-terminal tail makes up 4% of the protein (Shimazu et al. 2003). The smaller number of the IN motifs in the fungal protein result in lower ice nucleation activity: *P. syringae*: −2 °C, *F. acuminatum*: −5 °C. (Lagzian et al. 2014)

Table 4.7 Analysis of bacterial ice nucleators (INPs) from *Pseudomonas syringae*. (Hew and Yang 1992)

Nucleation temperature (°C)	Estimated molecular mass (kDa)	Number of INPs required for nucleation
−12 to −13	150	1
−3	870	60
−2	19,800	132
−1	83,700	558

Table 4.8 Antagonists (mutants) of ice nucleation–active (INA) bacteria inhibiting noxious ice formation during moderate frost. (After Lindow (1982))

Bacterial culture	Damage (% change in leaf colour after 1 week)
Control (*Pseudomonas syringae*)	95
Mutant A 510	12
Mutant A 509	18
Mutant A 507	27
Mutant A 506	33
Mutant A 508	51

Pear leaves were inoculated with the respective bacterial culture 3 weeks prior to frost to give the bacteria time to establish themselves. Frost damage was quantified by assessing necrosis

template for forcing water into an ice lattice. This quasi-crystalline fixation of the water molecules minimises the degree of supercooling that is required to “quiet” the water clusters (Kajava and Lindow 1993) (Table 4.7).

As mentioned above, ice seeding activity has been observed with plant cell walls from blueberry stems and also with cell walls from rye leaves (Brush et al. 1994). Apart from a general chemical composition (proteins, carbohydrates and phospholipids (Gusta et al. 2004)), the mode of function and mechanism of plant ice nucleators are not yet known.

The effects of INA bacteria are double edged. In frost-tolerant plants they trigger “high-temperature” ice seeding, thus avoiding strong supercooling and potential intracellular ice formation. On the other hand, they cause frost damage to many crops, such as maize, strawberry and citrus fruits, which are not freezing resistant but can tolerate supercooling to some extent. Attempts have been made to dilute out the INA bacterial infestation of crop plants by replacement with antagonists (Table 4.8). These are obtained by plating out wash solutions from leaves and cooling them to −5 or −9 °C. Antagonists of INA bacteria should be present wherever ice formation does not take place. These organisms are mostly natural mutants of the original bacterial strains.

INA bacteria have found several technical and biotechnical applications: artificial snow making, cloud seeding and rain making in warmer regions, and use as part of a fusion protein of the N-terminus with a protein of interest (e.g. an enzyme (Gao et al. 2014)) or binding of cancer cells by an antibody or antibody mimetic protein displayed on the surface of engineered *Escherichia coli* cells (Zahnd et al. 2007).

on a leaf or a flower bud surface can catalyse ice formation inside the plant, and it takes only a few minutes for the entire plant to be frozen (Fuller and Wisniewski 1998). Ice nucleation activity has recently been reported in plant cell walls of bark tissue from blueberry stems, with outstanding activity (ice nucleation at −1.0 °C). This activity showed seasonal changes, peaking in November shortly before the onset of frost (Kishimoto et al. 2014). The mechanism underlying this INA principle is not yet known.

4.2.4.1 Osmotic Adjustments

For the sake of survival during freezing, ice formation should take place outside the cell walls in the intercellular spaces and should be suppressed intracellularly by furnishing of the cells with compatible solutes, which allow them to supercool, thereby preserving their cell plasma in the liquid state. Both strategies entail benefits and stresses or risks. Extracellular freezing of cellular water results in cellular desiccation proportional to the frost temperature. At the same time, intracellular solutions concentrate and may exert ionic stress on biomembranes and protein complexes. Accumulation of compatible solutes counteracts problems caused by **freeze desiccation**, but this mechanism carries a high risk as ice formation by overstretching the capacity for **supercooling** leads to instantaneous death, as there is no time for water export. For both mechanisms, stress increases with the strength of the frost. Possible damage is gradual upon **extracellular freezing** but is sudden and absolutely detrimental upon intracellular ice formation.

Accordingly, frost hardening of plants is regularly associated with the accumulation of **compatible solutes** (also termed **osmolytes** or **cryoprotectants**) in the cells, predominantly in the vacuoles which, however, have to equilibrate their osmotic potential with the cytoplasm and other cellular organelles. These low molecular weight solutes are carbohydrates, amino acids (e.g. proline), polyamines and many more. Among the carbohydrates that accumulate during frost hardening, sucrose and its galactosides raffinose and stachyose are prominent. Also, **polyols**, as the reduced forms of monosaccharides, are frequently found. For winter and summer cereals, for instance, a strong correlation between freezing tolerance and the sugar accumulation rate was determined.

Compatible solutes, in addition to their colligative effects, are known also as soft ROS detoxifiers (e.g. mannitol) (Tarczynski et al. 1993). Upon extracellular freezing of cell water, these non-charged but weakly polar (like water) compounds “dilute” the ionic charge at the membrane surfaces (which results from the concentration of cellular ionic compounds) and thus stabilise the bilayer structure.

Their colligative (physicochemical) effect on the freezing point of the cellular liquids comes into play when freeze dehydration progresses. For example, the cell sap of frost-hardened spruce needles is only 1.5 osmolar, corresponding to a freezing point depression of 2.8 K. This is physiologically insignificant because ice nucleation requires stronger supercooling than −2.8 °C. Upon extracellular freezing of cellular water the concentration of the cryoprotectants increases significantly, and with a 10% remaining liquid volume, the **freezing point depression** attains 28.5 K, which could prevent freezing of the residual liquid water.

An example of the cold-hardening effect of cryoprotectants is the branched-chain polyol hamamelitol and its galactoside clusianose, which accumulate under natural or artificial cold stress in the leaves of the alpine primrose *Primula clusiana* (Sellmair et al. 1968, 1969) (Fig. 4.19). Both compounds are not degradable by the plant itself and finally reach the soil when leaves decay.

Besides the formation of cryoprotectants, the release of water from the cell into the apoplast can further reduce the probability of intracellular freezing, albeit at the cost of potentially stronger ionic stress for the cell. Membranes of frost-hardened cells allow water to exit from the cell into the apoplast more easily than frost-sensitive membranes do. This has been demonstrated with protoplasts isolated from frost-sensitive and frost-hardened rye leaves (Fig. 4.17). The mechanisms behind this facilitated efflux are not known. The simplest explanation assumes cold inhibition of ion pumps and H^+-ATPases, leaking of low molecular weight solutes and passive water efflux, following the solutes.

4.2.4.2 Antifreeze Proteins

In particular, unicellular organisms such as bacteria are endangered by intracellular crystallisation of water. Three strategies have been recognised in frost-tolerant organisms including prokaryotes, lower and higher plants, and special groups

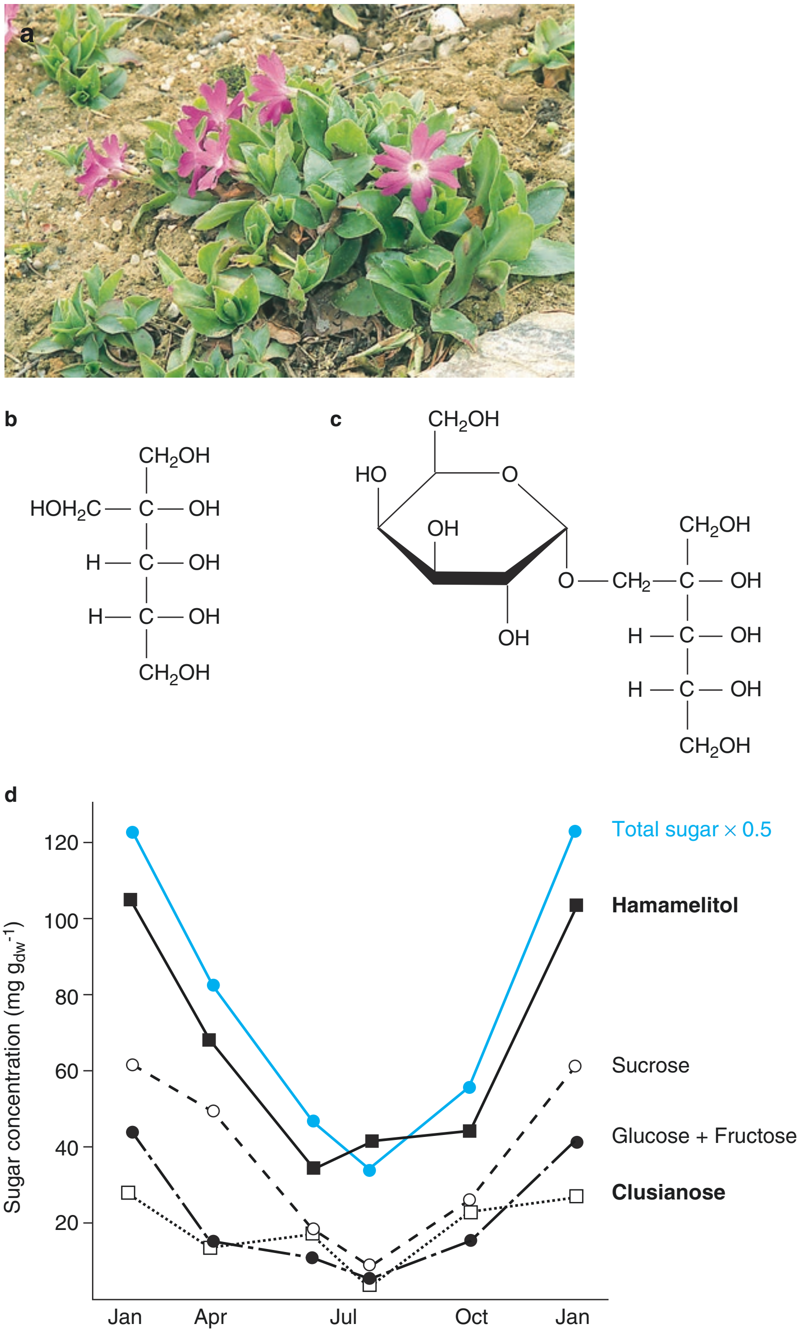


Fig. 4.19 Frost protection in the alpine *Primula clusiana* Tausch **a**. **b** The branched-chain polyol hamamelitol. **c** The disaccharide clusianose (D-galactosyl-hamamelitol). **d** Annual course of the concentration of carbohydrates in the leaves of that primrose. Accumulation of carbohydrates can also be induced by cooling of the plants in summer for 1 week at 5 °C. (Photo: E. Beck)

of animals—for example, insects or inhabitants of the Arctic and Antarctic Oceans. Apart from the accumulation of compatible solutes and the activation of their biosynthetic machinery, three functional types of proteins can be differentiated in relation to the formation of ice crystals at the cellular level: proteins that promote ice formation (**ice nucleation proteins** (**INPs**)), proteins that inhibit ice nucleation (**anti-nucleating proteins** (**ANPs**)) and proteins that control the growth and recrystallisation of ice crystals (the classical **anti-freeze proteins** (**AFPs**)). ANPs and AFPs are often considered one group of proteins because there is some evidence that AFPs might also bind to nucleation-promoting structures (Griffith and Yaish 2004). Up to now, INPs have been known only from prokaryotes—mainly gram-negative bacteria (Box 4.4)—while ANPs and AFPs are also known from plants.

AFPs have been detected in all types of organisms—for example, vertebrates and invertebrates, plants, fungi and prokaryotes (Table 4.9). Their presence can be monitored microscopically by examining the shape of the ice crystals. These are round and flat in water or diluted solutions. Upon binding of AFPs to their prism faces, developing ice crystals acquire a hexagonal structure (Fig. 4.20). AFPs have been extracted from the leaves of frost-hardened plants, but barely from non-acclimated frost-sensitive leaves. For instance, one of the two flowering plants found naturally in Antarctica, *Deschampsia antarctica*, secretes AFPs into the apoplast (Bravo and Griffith 2005). Thus, the ability to produce AFPs appears to be part of the cold-hardening process at least in some plant species.

AFPs are also known as **thermal hysteresis proteins** (**THPs**) because they lower the freezing point but not the melting point (thermal hysteresis activity). Thus, the freeze–thaw characteristic appears as a hysteresis curve (Griffith and Yaish 2004) which can be monitored in a temperature-controlled microscope. AFP interaction with tiny ice crystals suppresses their growth, at least at moderate freezing temperatures (ice recrystallisation inhibition (IRI)); considerably deeper supercooling is required for the crystallisation of that portion of water, which corresponds to the equilibrium between the water potentials of ice and the supercooled cellular solutions (Box 4.1). As they are efficient at very low concentrations (μM), it is clear that AFPs act in a non-colligative (non-physicochemical) manner. AFPs adsorb to the surface of ice crystals by forces that are not yet fully clear; hydrogen bonds, hydrophobic interactions or a particular structure of the hydration layer of the AFPs have been discussed (Lorv et al. 2014). One common character of all AFPs is a flat, hydrophobic ice-binding surface (Smolin and Daggett (2008). Another common feature are amino acid tandem repeats (X-Gly-Thr-Gly-Asn-Asp-X-U-X-U-Gly-Gly-X-U-X-Gly-X-U-X, in which X = hydrophilic and U = hydrophobic residue), which are aligned on one side forming that surface (Fig. 4.20a). Adsorption inhibits both further growth of the ice crystal and recrystallisation into harmful shapes, such as long needles. Probably the IRI activity is the more important since the actual effect on the freezing point depression (Table 4.9) is small. In recrystallisation assays with rye leaf extracts, AFPs present in cold-acclimated plants have been demonstrated to inhibit the growth of ice crystals (Fig. 4.20). AFPs are a mixture of small to medium-sized proteins, which can bind to both planes of an ice crystal, covering most of its surfaces. The binding is irreversible until the ice melts.

Table 4.9 Lowering of the freezing point by antifreeze proteins, as measured by thermal hysteresis

Organism	Tissue	Lowering of freezing point, thermal hysteresis (°C)
Bony fish	Muscle	0.7–1.5
Insects	Digestive tract, muscle	3–6
Bacteria	–	0.3–0.35
Fungi	Fruiting body	0.3–0.35
Mosses	Whole plant	0.3–0.68
Horsetails (*Equisetum hyemale*)	Rhizome	0.2
Ferns	Shoot	0.25
Winter wheat	Leaves	0.2
Carrot	Root	0.4
Carrot	Shoot	0.15
Poplar	Twig	0.22

The efficacy of AFPs in lowering the freezing point differs greatly between organisms. Plant AFPs, although not very effective in lowering the freezing temperature (less than 1 K; Table 4.9) are very efficient in inhibiting recrystallisation of ice nuclei. Because of multiple ice-binding domains of individual plant AFPs or AFP oligomers, the same protein can bind simultaneously to different planes of the ice crystals (Griffith and Yaish 2004). Intracellular AFPs, when binding to ice nucleators, can prevent intracellular ice formation. Furthermore, they can be secreted into the apoplast, where they interfere with growth and recrystallisation of extracellular ice. Thus, they have a dual task.

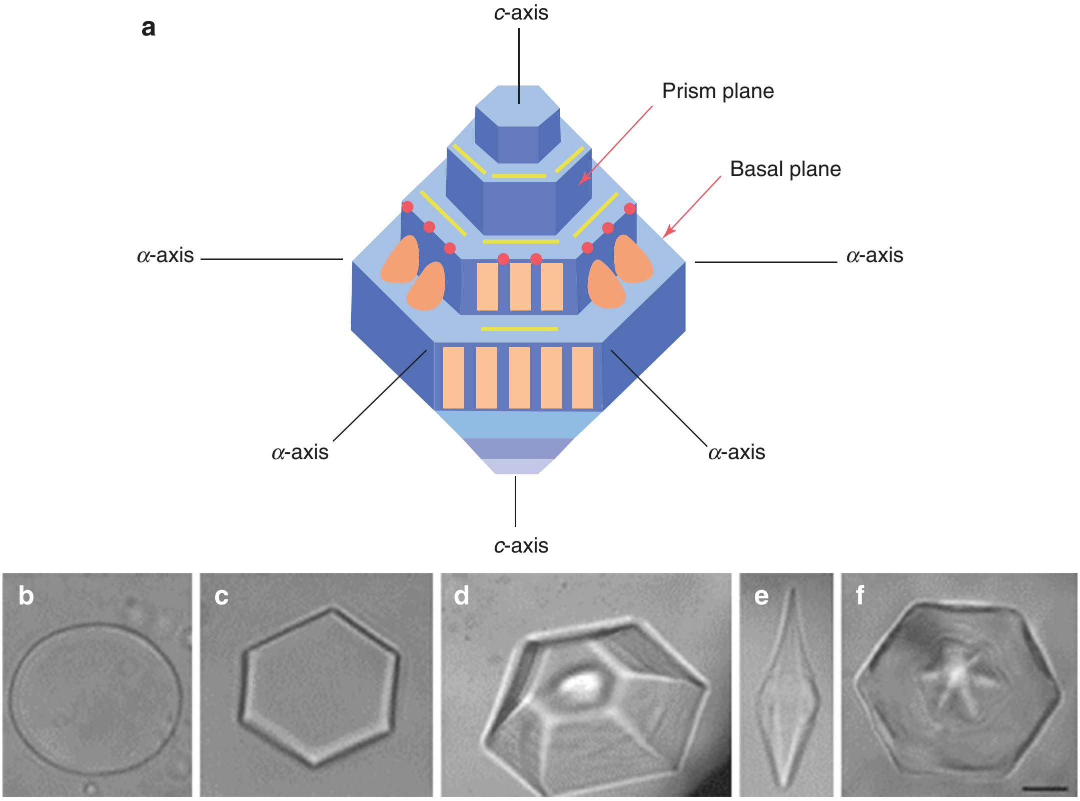


Fig. 4.20 **a** Hexagonal ice crystal (*blue*) that forms in the presence of antifreeze proteins (AFPs) showing the *α* (basal) and *c* (prism) axes and the modes of interaction with AFPs. Binding of AFPs (*brown symbols*) to the "vertical" prism plane inhibits growth of the crystal's basal plane (width), while binding to the basal plane prevents growth along the *c* axis (crystal length). **b** In pure water, ice grows as a round and flat crystal. **c** In a dilute solution, most types of AFP bind to the prism face of ice creating the hexagonal crystals. **d** Adsorption of AFPs to the prism face inhibits the binding of additional water molecules, making it energetically favourable for water to bind to the basal plane so that the crystal grows along the *c* axis (towards the viewer). **e** At high concentrations of AFPs, the ice crystals form bipyramids **a**, which are hexagonal in cross-section. **f** When the temperature is cooled and warmed in slow cycles, it is possible to see ridges on the surface of the ice crystal where the AFPs have bound. *Scale bar* = 10 μm. (**a** From Lorv et al. (2014); **b**–**f** from Griffith and Yaish (2004))

Amino acid sequences of plant antifreeze proteins do not establish them as a distinct protein family. Instead, AFPs are highly variable and display similarities to a wide range of proteins. Some AFPs—in particular, those from cereals—are highly homologous to pathogenesis-related (PR) proteins produced upon pathogen attack. They include chitinases, β-1,3-glucanases, polygalacturonase inhibitors, and osmotin- and thaumatin-like enzymes (Griffith and Yaish 2004; Gupta and Deswal 2014)—that is, enzymes that degrade fungal cell walls and inhibit fungal enzymes. In cold-acclimated winter rye, AFPs exhibit both antifungal and antifreeze activity. In contrast, PR proteins induced by pathogens at room temperature in non-acclimated plants lack antifreeze activity. The dual function of the PR-AFPs has been interpreted with respect to resistance against low-temperature pathogens such as snow mould. The excreted PR-AFPs form hetero-oligomers that inhibit growth of such fungal pathogens (Hiilovaara-Teijo et al. 1999).

4.2.4.3 Supercooling

Supercooling refers to the phenomenon where aqueous solutions remain in the liquid state even below the melting point (Box 4.1). **Freezing avoidance** by supercooling preserves the water relations of the turgescent tissue and prevents considerable export and import of water upon extracellular freezing. In woody tissues of boreal plants, water can supercool to the temperature of **homogeneous ice nucleation**. The classical example of deep or extreme supercooling is the xylem of dogwood (*Cornus sericea*, syn. *Cornus stolonifera*) (Byard et al. 2010). Several woody species have been shown to exhibit the phenomenon of deep supercooling, while others of similar geographical distribution do not (e.g. *Acer* supercools, whereas the majority of the investigated *Betula* species freeze) (Byard et al. 2010). Anti-nucleating substances such as flavonoids and hydrolysable tannins have been proposed to contribute to deep supercooling (Wisniewski et al. 2014). However, at present the mechanisms enabling deep supercooling are not known: "The properties of a cell, tissue or organ that allow it to deep supercool remain enigmatic despite the widespread prevalence of this ability in many plant species" Gusta and Wisniewski 2013 (see also Kasuga et al. 2008; Wang et al. 2013).

4.2.5 Signalling Networks Involved in Cold Acclimation

Drought, high salinity and freezing stress all pose osmotic challenges for plants. Accordingly, there is considerable overlap in the molecular responses of cells to these different stress conditions (Chap. 2). When one is judging by the hundreds to thousands of changes elicited in the *A. thaliana* transcriptome, however, there are also highly complex responses specific to cold acclimation.

A large number of ***COR* genes** belong to the CBF (for C-REPEAT BINDING FACTOR) regulon—that is, they are activated under the control of **CBF transcription factors** (also termed **DRE-Binding proteins** (**DREB**)) (Yamaguchi-Shinozaki and Shinozaki 2006). The promoters of these COR genes, which encode many of the proteins discussed above (i.e. dehydrins, antifreeze proteins, ROS-detoxifying enzymes, fatty acid desaturases, lipid transfer proteins, sugar and proline transporters, osmolyte producing enzymes) share a 5-bp consensus sequence (CCGAC), the so-called **Dehydration Responsive Element** (**DRE**), which is known also as **Low Temperature Responsive Element** (**LTRE**) or **C-Repeat** (**CRT**). Binding of CBFs rapidly activates transcription of COR genes.

The **CBF regulon** is present in many if not all higher plants (Box 4.5). Its central role in cold acclimation has been demonstrated by overexpression studies. Constitutive strong transcription of CBF genes results in the formation of COR proteins and a permanent cold-acclimated state even in the absence of low-temperature exposure. Such plants can survive transfer to freezing temperatures even without prior acclimation (Jaglo-Ottesen et al. 1998) (Fig. 4.21). *CBF* overexpression leads, on the other hand, to a strong reduction in the growth rate

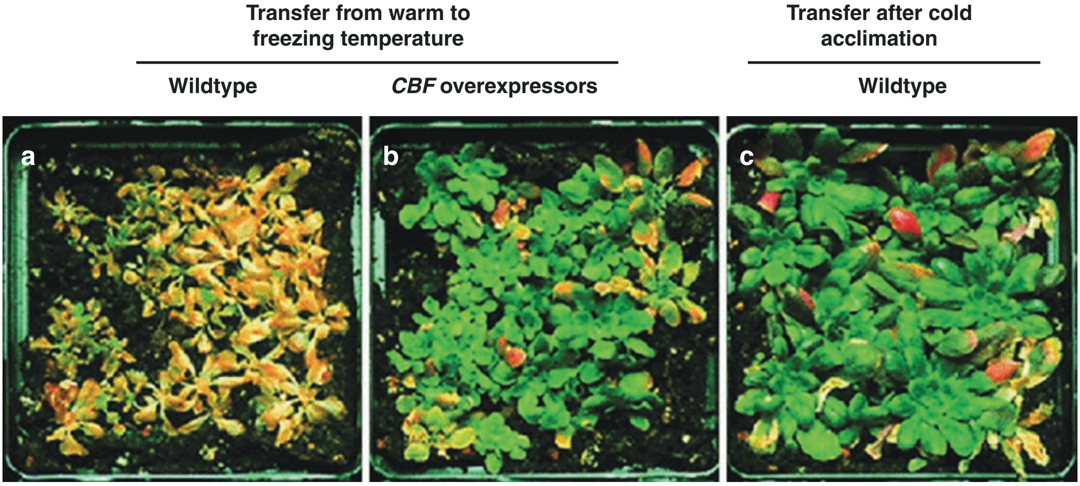


Fig. 4.21 Effect of *CBF* overexpression on the cold sensitivity of *Arabidopsis thaliana*. Wild-type plants **a** require several days of acclimation at low non-freezing temperatures to withstand freezing temperatures **c**, while plants overexpressing *CBF* genes survive transfer from warm temperatures directly to sub-zero temperatures **b**. Note the smaller size of the CBF-overexpressing plants in **b**. (Modified from Jaglo-Ottesen et al. (1998))

because CBFs stimulate the production of **DELLA proteins**, which are central negative regulators of growth (Fig. 4.21b). This is one of many examples for the active dampening of growth as an integral part of stress acclimation responses (Chap. 2).

Activation of **cold acclimation** involves a cascade of regulatory steps that have been unravelled in *A. thaliana* (Fig. 4.22). *CBF* genes are rapidly up-regulated upon exposure to low non-freezing temperatures. Their expression is controlled by transcription factors that are themselves predominantly controlled at the posttranslational level. The **transcription factor ICE1** (Inducer of CBF Expression 1) triggers the transcription of *CBF* genes by binding to *cis* elements in the *CBF* promoters. The stability of ICE1 is controlled by ubiquitination. The ubiquitin E3 ligase HOS1 targets ICE1 for proteasomal degradation, which prevents the expression of *CBF* genes in the absence of cold. HOS1-antagonistic regulation of ICE1 stability is mediated by SUMO-Ligase-mediated (SIZ1) sumoylation—that is, the addition of SUMO proteins, which protect ICE1 from degradation (Knight and Knight 2012).

Events upstream from ICE1 are less well defined. The primary sensor of cold temperature is still unknown (Sect. 4.4). What is clearly established is a rapid increase in **cytosolic Ca^{2+}** levels upon transfer of plants to cold conditions, which activates proteins that inhibit ICE1 degradation and activate ICE1 sumoylation. In addition, Ca^{2+} influences *CBF* expression via a calmodulin-binding transcription factor (CAMTA). The same regulatory steps leading to enhanced ICE1 activity are triggered by a cold-responsive Ca^{2+}-independent **MAP kinase phosphorylation cascade**.

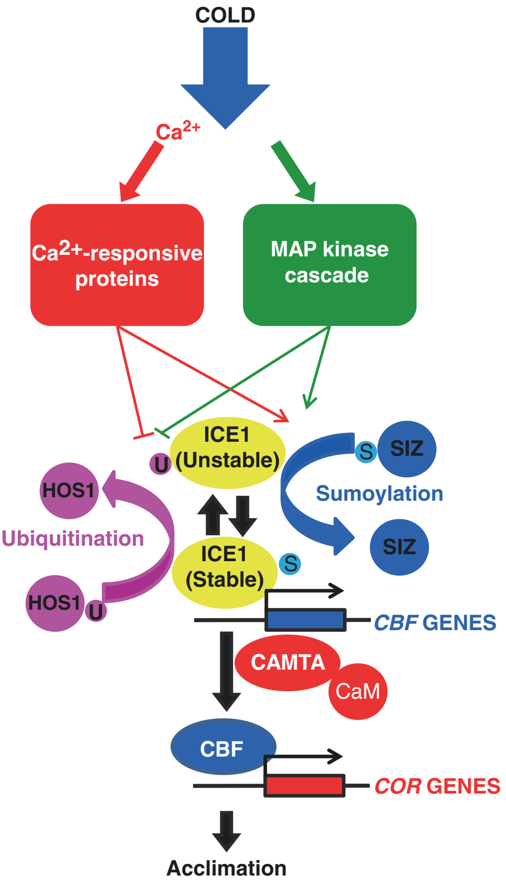


Fig. 4.22 Cold acclimation pathway. Model for signalling leading from cold to the expression of *COR* genes regulated by CBF transcription factors in *Arabidopsis*. Transcription factors are represented by *solid ellipsoids*; other proteins are represented by *circles*. Red symbolises Ca-dependent processes, green symbolises processes controlled by MAP kinase cascades. *S* sumoylation, *U* ubiquitination, *CaM* calmodulin. (Modified from Knight and Knight (2012))

Box 4.5: The Role of the CBF Regulon in Cold Tolerance and Cold Acclimation

The CBF regulon is present even in chilling-sensitive species such as tomato (Chap. 2 and Sect. 4.2.1), and tomato *CBF* genes can trigger cold acclimation when expressed in *Arabidopsis thaliana*. Thus, the responses activated by CBFs appear to vary between species that are able to cold acclimate (e.g. *Arabidopsis*) and those that cannot (e.g. tomato). In addition, however, differences in *CBF* expression can be linked to **natural variations in freezing tolerance** (Fig. 4.23). The higher sensitivity to freezing temperatures of *A. thaliana* accessions from North Africa and Southern Europe (Fig. 4.23) correlates with lower CBF expression and concomitantly lower *COR* gene expression relative to accessions from Northern and Eastern Europe. Comparative sequencing of *CBF* genes from these accessions indicated relaxed selection on these genes in accessions from habitats that have a much lower incidence of frost events (Zhen and Ungerer 2008). However, not for all *CBF* genes expression can be directly linked with cold tolerance or cold acclimation (Fig. 4.23e).

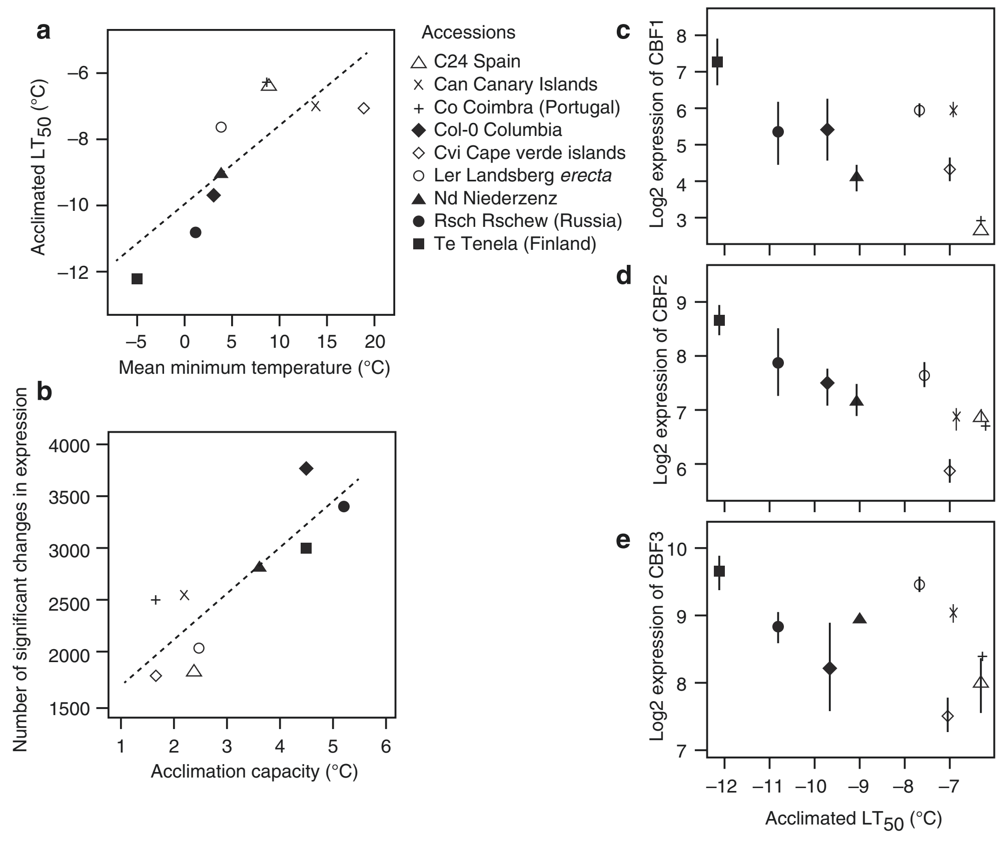


Fig. 4.23 Correlation between habitat temperature, acclimated freezing tolerance **a** and gene expression **b** in particular, of the CBF regulon **c–e** of *Arabidopsis thaliana* accessions from different climates. The temperature data for the accessions are the average minimum temperature during January for winter annuals and April for summer annuals, obtained from the nearest weather station. Freezing tolerance is given as the temperature at which 50% electrolyte leakage occurred from detached leaves (LT_{50}) of plants. For cold acclimation the plants were subjected to a temperature of 4 °C for 14 days. The data are means from 4–6 independent experiments. The acclimation capacity **b** was measured as the difference between the non-acclimated and acclimated LT_{50} of detached leaves. It correlates nearly linearly with the extent of changes in gene expression. Changes were classified as significant when the gene-wise false discovery rate–corrected F test and *t* test *p* values were both less than 0.05. **c–e** Expression of the CBF transcription factor genes *CBF1–3* in cold-acclimated plants. Scatterplots of GCRMA (guanine cytosine robust multi-array analysis) on a log2 scale, where a doubling of expression intensity corresponds to a unit of 1. Expression estimates are shown against the LT_{50} of detached leaves from the nine accessions after 14-day cold acclimation. The data are means ± standard errors (SEs) from three independent experiments (Hannah et al. 2006)

4.2.6 Freezing Avoidance and Freezing Tolerance in Tropical High Mountain Plants

Cold hardening and de-hardening is observed only in plants of regions with seasons characterised by temperature changes. Tropical plants are not known to harden, which corresponds to virtually invariable high temperatures throughout the year. Nevertheless, plants of the tropical high mountains (e.g. the Andes, the East African and Hawaiian volcanoes, and the high mountains of New Guinea) are frost hardy. Furthermore, their frost hardiness is maintained throughout the entire year because they are subjected to the so-called Frostwechsel climate, described as summer every day and winter every night (Hedberg 1964) (Fig. 4.24). The regularly occurring frosts are only moderate (temperatures below −15 °C are rare and occur mostly in topographic depressions) and may last for a maximum of 12 h, and the life forms of the vegetation are adapted to cope with this recurrent temperature stress (Hedberg 1964; Beck 1994a). Adaptation to this type of climate requires mechanisms of freezing avoidance in addition to acclimative reactions. The plants are frost tolerant throughout the whole year but are not tolerant of an uninterrupted frost period.

Several types of response to sub-freezing temperatures can be recognised in the five common functional plant types of the **tropical high alpine flora** (Chap. 19): grass tussocks, sclerophyllous shrubs, acaulescent rosette plants, cushion plants and the spectacular giant rosette plants. All rely on the principle of daily changes between the nocturnal frost and the "summer" temperatures during the day, caused by the intense tropical sunshine. Mechanisms to overcome the different primary and secondary abiotic stress factors (climate, high light intensities and ultraviolet radiation, seasonal shortage of water during the dry season, low partial pressure of CO_2 and oxygen) imposed on the tropical alpine plants by their environment have been discussed in some detail, but the molecular level has hardly been touched upon (Beck 2011). Ecophysiological data show that separate investigation of the impact of one abiotic stressor on these plants cannot sufficiently explain the real situation, and a more holistic consideration of their performance is required, as claimed by Gusta and Wisniewski (2013), for the understanding of plant cold hardiness. The example of the "giant rosette plant" life form (Fig. 4.25) shows that more than one "strategy" may be adopted by a plant individual—namely, freezing tolerance as well as freezing avoidance by permanent insulation (Fig. 4.25) or nocturnal insulation, thermal buffering by liquids, or supercooling. Each of these "strategies" may be considered to meet a special physiological requirement. While the stems, inflorescences and roots follow the "strategy" of freezing avoidance, the leaves of the African *Senecio* and *Lobelia* are freezing tolerant and are stiffly frozen in the morning before sunrise. **Extracellular freezing** of cellular water has been documented, concomitant with freeze cytorrhysis of mesophyll cells or intravacuolar emergence of gas bubbles, which disappear upon thawing in the hypodermis (Beck 1994a). In nature the mesophyll cells produce sucrose as a **cryoprotectant**, and only a minor accumulation of starch can be detected in the chloroplasts. While the mature leaves of the giant rosette freeze every night, the young leaves in the central leaf bud, despite being freezing resistant as well, are protected from freezing through the formation of a so-called night bud (Hedberg 1964) by the outer rosette leaves. Since extracellular crystallisation of cell water results in a loss of cell turgor, growth of the young leaves would be interrupted every night. The night bud prevents nocturnal sub-zero temperatures and concomitant freezing of the meristematic tissue, thus enabling uninterrupted growth. A question still to be solved is how propagation of ice from the frozen leaves to the other parts of the plants is prevented. Fast spreading of ice has been observed by infrared differential thermal analysis in dicotyledonous alpine plants, starting from the xylem vessels and spreading into the rest of the plants (Hacker

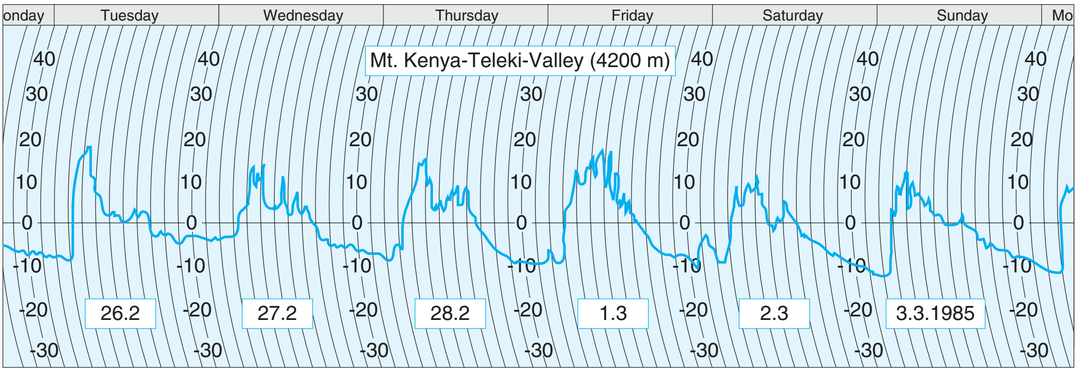


Fig. 4.24 Temperature courses in a tropical "Frostwechselklima" recorded on Mt Kenya at 4200 m altitude during the dry season. The temperature sensor was about 20 cm above the soil surface

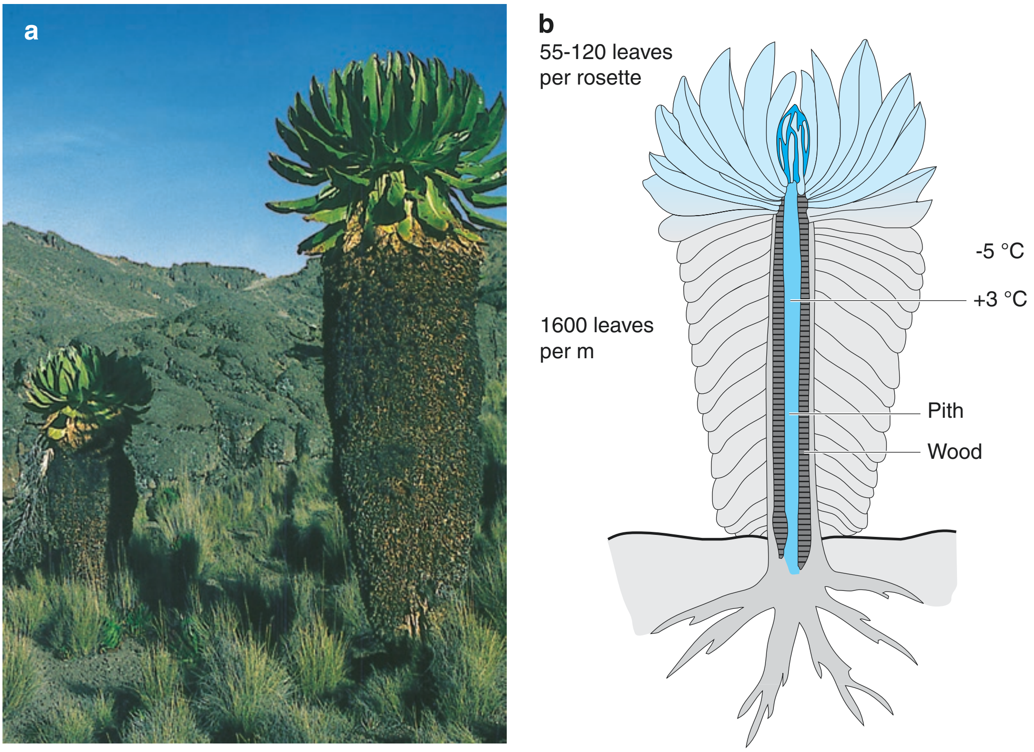


Fig. 4.25 Young specimens of the giant rosette plant *Senecio* (*Dendrosenecio*) *keniodendron* in the Afro-alpine zone of Mt Kenya (at 3500–4800 m). These plants carry a single terminal leaf rosette of up to 1 m diameter with around 100 big leaves surrounding the terminal leaf bud (*dark blue in the sketch*) in the centre of the rosette. At least the first half of the leaf development takes place in that cone-shaped leaf bud, from which the leaves separate after greening. After senescence, the dead, now outer leaves of the rosette remain attached to the stem and the resulting leaf cloak of shrivelled leaves delays nocturnal cooling of the stem until the tropical sun warms it up again. Maintenance of the stem temperature well above the freezing point is important, as a large share of the water required by the leaves is supplied by the living pith cells, while the amount of water delivered by the extremely narrow vessels of the weakly developed xylem is inferior. Water transport via living cells depends strongly on the temperature. A similar "strategy" is known from the corresponding plant life form, *Espeletia*, in the tropical Andes, where the "cloak" of dead leaves has inspired the plant's popular name, *frailejones* ("thick monks"). Interestingly, the cloak is densely rooted by adventitious roots from the stem, which absorb water and nutrients from the decaying leaf material. (Beck 1994b)

and Neuner 2007, 2008). In the case of *Senecio*, ice formation is confined to the leaves and cannot be triggered from the xylem, because of the existence of a kind of "thermal ice barrier" (Hacker et al. 2011). Interestingly, the leaves of the corresponding giant rosette plants of the neotropical Andes (*Espeletia* spp.) are reported to supercool to about 8–12 °C below the ambient temperature and to be killed by intracellular ice formation (Goldstein et al. 1984, 1985).

4.3 Heat Stress

Heat is understood here as the upper temperature range in which active life is possible (Fig. 4.1). In this range, stress increases with increasing temperature, and organisms (in particular, plants) that cannot escape the heat stress respond with a diverse set of reactions. Not all of them are specific to heat; they can also be observed under drought, salt and heavy metal strain—that is, whenever proteins are denatured. Nevertheless the heat stress response in plants has distinctive features and is very complex. In the tolerable temperature range it appears to follow the **stress dose rule** (the product of the severity of stress and exposure time: $\Delta T \times t$) (Nover and Höhfeld 1996). In mesophilic plants a slight heat stress response can be observed beyond 35 °C. Above 40 °C, strong reactions take place. Such temperatures can be reached in many plant habitats. On a sunny day in Central Europe, for instance, topsoil temperatures can transitorily exceed 50 °C, which can severely damage or even kill seedlings that have just emerged from the soil surface. Also, solar irradiation can cause very rapid increases in temperature by easily 20 °C within minutes (McClung and Davis 2010).

Heat damage (Fig. 4.26) is predominantly a consequence of **protein misfolding** and **protein denaturation** (Fig. 4.2). Additionally, the functionality of membranes is negatively affected by excessive fluidity. Molecular interactions between membrane components are weakened, which can cause ion leakage. Some processes, including photosynthesis, are more sensitive to heat than others. Among the developmental stages of plants, seedling development and reproduction are particularly vulnerable (Bita and Gerats 2013).

Fig. 4.26 Heat damage on a leaf of *Cannabis sativa*, resulting in collapsed leaf patches. The pale colour indicates disintegration of the chloroplasts and photobleaching of chlorophyll liberated from their protein environment in the thylakoids. (Source: http://forum.sensiseeds.com/images/plant_problems/heat_stress_rd_c2727.html)

When one is considering the exposure of a plant to potentially dangerous elevated temperatures, **heat shock** should be differentiated from heat stress. A heat shock (even if it is not injurious) refers to a sudden and short-term exposure that triggers a transient short-term response, while heat stress refers to a long-term exposure to elevated and potentially damaging temperatures. Both heat shock and heat stress can lead to the so-called **acquired thermotolerance** (Sect. 4.3.2)—that is, the ability to withstand higher temperatures because of acclimation. The major difference at the cellular level is the rapid deceleration of housekeeping metabolism (apparent in the down-regulation of housekeeping genes) and the subsequent revival of this metabo-

Table 4.10 Effects of elevated temperatures on growth, tuber formation and starch content of a heat-tolerant potato (*Solanum tuberosum*) variety ("Norchip") and a heat-sensitive variety ("Up-to-date") (Lafta and Lorenzen 1995)

Cultivar	Temperature (°C)	Shoot (g/plant)	Tuber (g/plant)	Total weight (g/plant)	Plant height (cm)	Starch content (mg/g dry weight)
Norchip	19/17	244 ± 6	134 ± 3	378 ± 4	35 ± 1	290 ± 9
	31/29	253 ± 4	5 ± 3	258 ± 4	45 ± 2	129 ± 2
Up-to-date	19/17	197 ± 17	131 ± 14	328 ± 13	42 ± 1	24 ± 14
	31/29	96 ± 2	0.6 ± 0.6	96 ± 3	57 ± 0.5	99 ± 12

Control plants were grown under a day/night temperature regime of 19/17 °C; plants exposed to elevated temperatures grew at 31/29 °C. Biomass production and growth of the potato plants were determined after 4 weeks of heat stress, which started at the onset of tuber formation. The starch content of fully developed leaves was measured 8 days after the temperature increase at the end of the daily light period

lism after a return to the normal temperature in the heat shock reaction, while in long-term heat stress exposure the housekeeping metabolism has to maintain its function at the elevated temperature. Both sets of reactions, however, depend on the strongly enhanced expression of genes encoding transcription factors (**heat shock factors**) and protective proteins (**heat shock proteins**), many of which serve essential cellular functions also at optimal temperature.

Even in the absence of actual heat stress, temperature optima of plants differ both between and within species. Temperatures beyond the optimal range not only accelerate but also redirect metabolic processes and lead to changes in metabolite pools, thereby affecting growth and many other developmental processes. A good example of differential responses to elevated temperatures below the heat stress threshold is provided by potatoes (*Solanum tuberosum*; Table 4.10) (Lafta and Lorenzen 1995), which originate from the tropical Andes. Despite being cultivated for ~13,000 years, potatoes still have a rather narrow range of optimal growth temperatures. As tropical upland plants, potatoes grow best at temperatures around 20 °C. More than 5000 potato cultivars are currently known, some of which are considered heat tolerant (e.g. cv. "Norchip"), while others are heat sensitive (e.g. cv. "Up-to-date"). Growth at elevated temperature results in a change in the developmental control system of both cultivars, as shown in Table 4.10. "Norchip" was less affected than "Up-to date" but tuber formation was strongly suppressed in both varieties along with a drastically reduced starch formation and storage. Instead, elongation growth of the shoots was increased.

Table 4.11 Activities of the enzymes starch synthase and ADP-glucose pyrophosphorylase (AGPase) in the potato tubers of "Norchip" and "Up-to-date" after 2 weeks of exposure to an elevated temperature regime (from Lafta and Lorenzen (1995)

Cultivar	Temperature (°C)	Sucrose synthase (mg sucrose/g × h)	AGPase (µmol ADP-glucose/g × min)
Norchip	19/17	33.4 ± 11.9	1.2 ± 0.11
	31/27	13.7 ± 3.8	0.93 ± 0.05
Up-to-date	19/17	15.0 ± 4.2	1.17 ± 0.12
	31/27	4.2 ± 2.3	0.84 ± 0.08

Sucrose synthase: Sucrose + UDP → UDP-glucose + fructose

UDP-glucose pyrophosphorylase: UDP-glucose + PP_i → Glucose-1-P + UTP

AGPase: Glucose-1-P + ATP → ADP-glucose + PP_i

Starch synthase: ADP-glucose + primer →→→ starch + ADP

Starch formation in the tubers ("sink") requires phloem unloading by sucrose synthase and formation of the starch synthase substrate adenosine diphosphate (ADP)-glucose by ADP-glucose pyrophosphorylase. Both enzyme activities were significantly decreased by heat stress (Table 4.11). In contrast, sucrose metabolism was slightly increased or at least not attenuated.

Such effects of temperatures below the threshold of heat stress will not be discussed further here. The main focus of this chapter is the variety

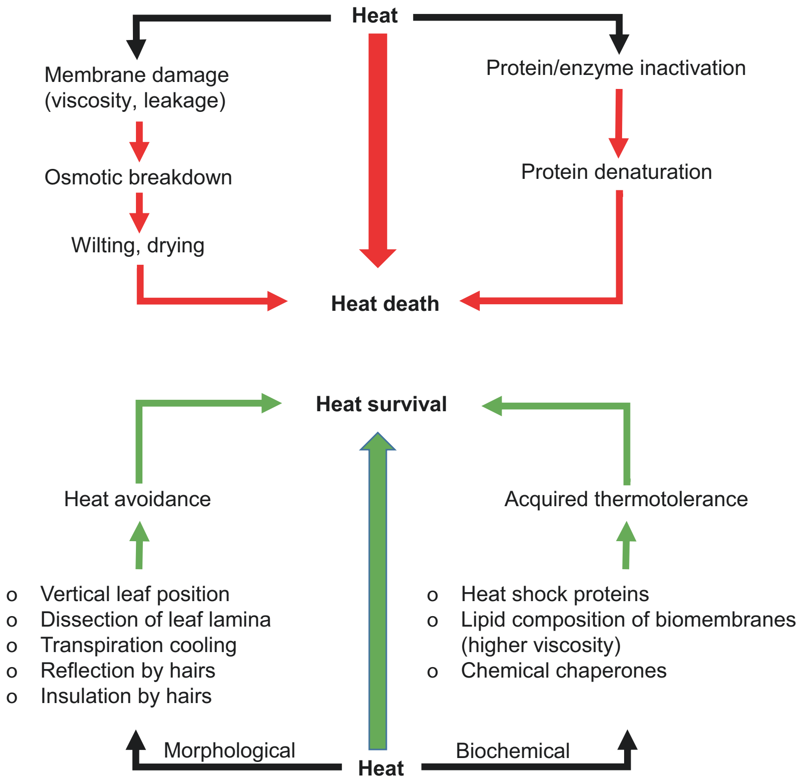


Fig. 4.27 Effects of heat on plants and their reactions to it

of cellular mechanisms of heat survival, which are summarised in Fig. 4.27.

4.3.1 Heat Stress Avoidance

The timing of key developmental steps such as germination and sexual reproduction can help plants reduce the probability of heat exposure and damage (Chap. 2). Besides that, not many different mechanisms of heat stress avoidance have been demonstrated. At the morphological level, positioning of the leaves in a tree crown or canopy and the leaf angle may reduce heating by sunrays. Segmentation of large leaf areas into narrower parts can have a similar effect. **Transpiration cooling** (Chap. 10) appears to be an effective mechanism. However, heat frequently coincides with low water availability, and then the necessary closure of stomata greatly reduces the cooling potential. More details about heat avoidance are presented in Chap. 9.

Generally, however, because of the extreme fluctuations in temperature that can occur daily or seasonally and at the micro-scale (Sect. 4.1), it is in most habitats virtually impossible for terrestrial plants, as sessile organisms, to avoid heat stress altogether. Accordingly, all plants are capable of mounting a response to heat stress (Vierling 1991).

4.3.2 Acquired Thermotolerance

It is well documented that exposure to either a continuously applied non-lethal heat stress or single heat shocks results in the acquisition of **thermotolerance** or, in other words, **heat hardening**. These types of heat exposure elicit cellular processes that enhance the ability of plants to survive a later and more severe heat stress. Acquired thermotolerance therefore represents a classic acclimation. After just 15 min of exposure to heat, plants start to acclimatise, as

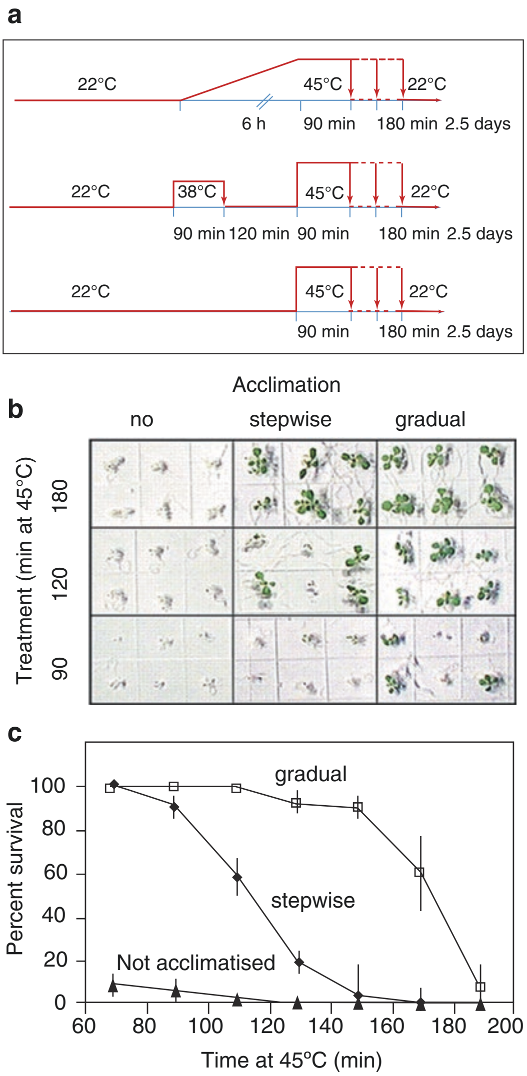


Fig. 4.28 Effect of hardening on the survival of heat-stressed *Arabidopsis thaliana* seedlings. **a** Protocol of the hardening experiment. Gradual hardening was accomplished by slow elevation of the ambient temperature from 22 °C to the heat shock temperature of 45 °C. Stepwise hardening was performed by application of a moderate heat shock (38 °C for 90 min) 2 h prior to the actual heat shock. No hardening treatment was applied in the control set of seedlings. Samples were returned to the ambient temperature and analysed for survival after 2½ days **b**. (**c**) Quantitative analysis of the acclimation effect. (Modified from Larkindale and Vierling (2008))

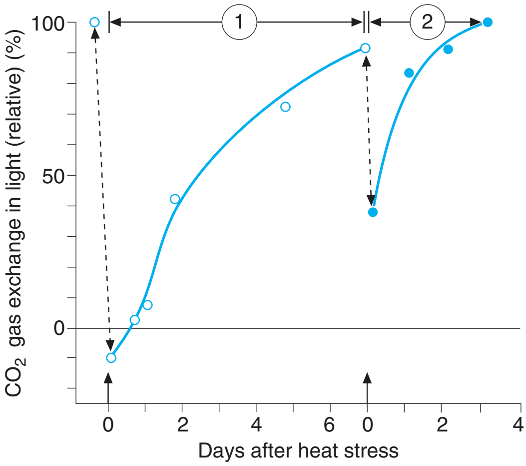


Fig. 4.29 Acquisition of thermotolerance in fir needles after heat stress treatment. Damage and hardening were assessed by measurement of the photosynthetic activity of the needles. (1) Recovery and hardening phase after the first heat stress. (2) After the second heat treatment (44 °C for 30 min). The extent of damage and the duration of the recovery phase are clearly reduced after the second stress (Larcher (1987))

indicated by a steady rise in the maximum tolerated temperatures (Kaplan et al. 2004). Fig. 4.28 shows the differences in survival rates of *A. thaliana* seedlings after heat stress of 45 °C, depending on the temperature exposure prior to the heat stress.

Similarly, heat exposure is less damaging to the photosynthetic capacity of fir needles when they have been exposed to a previous non-lethal heat stress (Fig. 4.29).

The most important mechanism underlying acquired thermotolerance is the massive production of **heat shock proteins** (**HSPs**) (Sect. 4.3.3.1) (Vierling 1991). Regardless of the optimal growing temperature, this response is highly conserved not only among plants but also among prokaryotes, animals and fungi. According to recent genome-wide analyses in *A. thaliana*, however, not only the expression level of HSP genes changes. Up to 2% of all genes are affected in their activity (Kotak et al. 2007). For many of them the contribution to thermotolerance is functionally not understood. What is evident is an up-regulation of **anti-oxidative defences** to counteract the increased production of ROS under heat stress. Documented is also the accumulation of so-called **chemical chaperones**, which can increase the heat resistance of cells and shift the onset of the heat stress response to higher temperatures. These chemical chaperones

Box 4.6: Chaperones and Chaperonins Repair Misfolded Proteins

The HSP70 cycle (Fig. 4.30): The heat shock protein 70 (Hsp70) (DnaK) proteins contain three functional domains; the N-terminal domain has ATPase activity. Hydrolysis of adenosine triphosphate (ATP), as well as the exchange of ATP for adenosine diphosphate (ADP), changes the conformation of the other domains. The C-terminal domain functions as a lid for the interior domain, which binds the misfolded protein(s). The lid is open whenever ATP is bound to the N-terminal domain. Misfolded proteins bind weakly to the substrate-binding domain by hydrophobic interaction (1). Binding of a co-chaperone (J-domain protein) activates ATP hydrolysis, whereupon the lid closes and refolding of the protein can take place in the groove of the substrate-binding domain (2). The J-domain protein dissociates from the Hsp70–ADP complex. By interaction with a nucleotide exchange factor (NEF), ADP is replaced by ATP and the lid opens (3) to release the completely (4) or partially repaired protein which, in the latter case, can undergo another HSP cycle (5). Under normal conditions, the HSP70 cycle is also operative in preventing misfolding of hydrophobic stretches of a nascent protein protruding from the ribosome.

The prokaryotic chaperonin GroEL/GroES cycle operates in the plastids and mitochondria of a plant cell in a mechanism that resembles that of the HSP70 system but also shows some differences, as the GroEL forms a back-to-back double chamber, with each chamber consisting of seven GroEL subunits, which all show ATPase activity. Both chambers work alternately. GroES is the lid protein and DnaJ replaces the J-domain protein. One GroEl cycle consumes seven ATPs. Step 3, as the rate-limiting step, requires about 10 s.

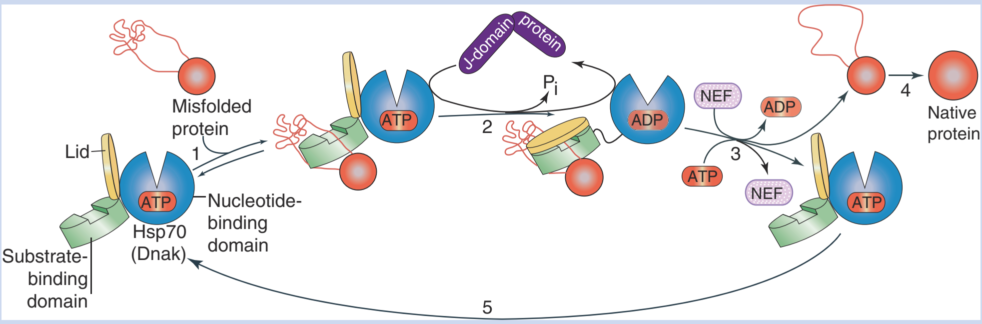


Fig. 4.30 Model of the mechanism of action of heat shock protein 70 (HSP70) chaperones in protein rescue. (Modified from Doyle et al. (2013))

are **compatible solutes** such as glycerol, proline and betaines (Chap. 6). They stabilise the folding and structure of mature proteins, and they can buffer the cellular redox potential. Another critical response is the modulation of membrane lipids towards a higher saturation level of fatty acids. Some of the reactions may initiate signalling cascades that result in the induction of HSPs. For instance, the dehydration-responsive transcription factor DREB2A (Chap. 6) regulates the heat shock factor Hsf3A (Sect. 4.3.3.2 and Box 4.7). ABA concentrations rise in heat-stressed tissues.

4.3.3 The Heat Shock Response

Heat stress causes the unfolding (denaturation) of proteins (Sect. 4.3.3) (Qu et al. 2013). In eukaryotic cells this triggers a reaction sequence termed the **unfolded protein response** (**UPR**). Stress-induced accumulation of unfolded proteins activates transcription factors (**heat shock transcription factors** (**HSFs**)), which then bind to specific *cis* elements (**heat shock elements** (**HSEs**)) in the promoters of genes encoding heat shock proteins (HSPs).

4.3.3.1 Heat Shock Proteins

HSPs are named after their enhanced production upon heat treatment. However, they are essential for prokaryotic as well as eukaryotic cells, both in the absence of stress and for heat stress survival. HSPs act as chaperones required for correct folding of (unglycosylated) nascent proteins upon release from the ribosome or after stress-induced misfolding, unfolding or aggregation of unfolded proteins (Box 4.6). This essentiality is the reason why the contribution of HSPs to heat stress survival—while not in doubt—cannot be accurately assessed genetically. Loss-of-function mutants are not viable.

HSPs are constitutively expressed and involved in protein and membrane stabilisation, in protein assembly into functional complexes, in intracellular transport of protein precursors to their target organelles and as part of cellular signalling processes. In plants they occur in plastids, mitochondria, peroxisomes, the nucleus, the cytosol and the ER. However, not all chaperones occur in all of these plant cell organelles. Prokaryotic HSPs such as HSP60 are known only from mitochondria and chloroplasts—plant organelles of prokaryotic origin. HSPs are classified by their molecular weight (Wang et al. 2004) and only in the bacterial (*Escherichia coli*) system do they have specific designations (in brackets). The most important classes are HSP100 (Clp), HSP90, HSP70 (DnaK), HSP60 (GroEL, the so-called GroE chaperonins) and the small HSPs (sHSPs): the HSP40 (DnaJ), HSP10 (GroES) and HSP23 (GroE) families. HSPs can cooperate with co-chaperones (e.g. HSP70 with HSP40 and HSP23).

Chaperones, particularly of the HSP70 type, are also involved in the removal of irreversibly denatured proteins. After a strong heat stress, some unfolded proteins cannot be repaired anymore. They are irreversibly denatured and tend to form—or have already formed—aggregates via their exposed hydrophobic domains. Such proteins have to be removed from the cell. They are tagged for degradation in the 26S proteasome by the attachment of several units of the small protein ubiquitin (**poly-ubiquitination**). Targeting to the proteasome where the adenosine triphosphate (ATP)-consuming degradation takes place is then dependent on HSP activity.

4.3.3.2 Heat Stress Transcription Factors

Transcriptional activation of *HSP* genes is dependent on **heat stress transcription factors** (**Hsfs**). Hsfs have a modular structure (Box 4.7) which, irrespective of variations in size, is conserved in the entire eukaryotic kingdom (Scharf et al. 2012). The mode of interaction with the promoters is equally conserved. Plant genomes are particularly rich in Hsfs: in *A. thaliana*, 21 *Hsf* genes are known; in soybean there are 52 such genes. According to similarities and differences in their sequences, plant Hsfs have been classified into HsfA, HsfB and HsfC, each class consisting of a number of members (e.g. HsfA1–A8). Further grouping is indicated by lower-case letters (e.g. HsfB4a–h). In comparison with plants the diversity of Hsfs in other organisms is smaller.

Hsfs mediate the acute heat shock response, as well as the acquisition of thermotolerance. Thus, responses of different magnitude can be controlled by Hsfs. This is exemplified by representatives of the A1, A2 and B1 groups in tomato (Fig. 4.31). Under normal conditions (Fig. 4.31a), monomeric HsfA1 is inactive because of its association with HSP70 and HSP90, while HsfB1 is targeted to the 26S proteasome for degradation. Acute heat stress and concomitant denaturation of proteins results in the dissociation of the chaperone–Hsf complexes and association of the HSPs with the misfolded or unfolded proteins. The liberated Hsfs (particularly HsfA1 as a master regulator) oligomerise (trimerise), and HsfA1 and HsfB1 bind to the heat stress elements in the promoters of heat stress–activated genes, which usually harbour more than one HSE. The HsfA1–HsfB1 complex further recruits a histone acetyltransferase

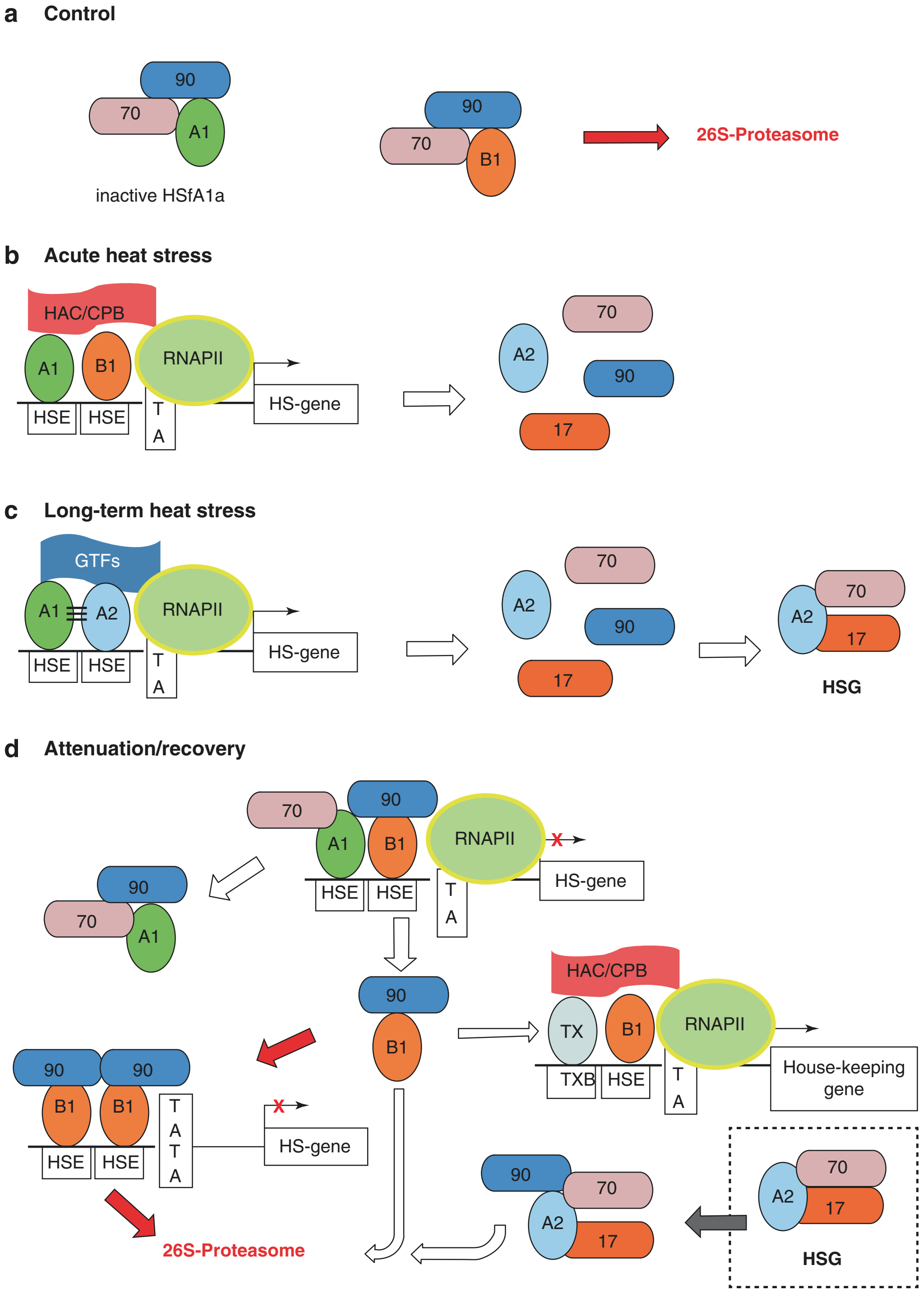


Fig. 4.31 Regulation of the heat stress response in tomato. **a** The unstressed state. **b** Acute heat stress; free Hsfs oligomerise and bind to the heat stress elements of the promoters of the HSPs. More HSPs are produced, as well as more HsfA2, the key regulator in the plant heat stress response. **c** Prolonged heat stress leads to acquired thermotolerance; Hsfs A1 and A2, together with other general transcription factors (GTFs), form a superactivator for the expression of more HSPs and the formation of heat stress granula (HSG). **d** Recovery from heat shock and enhanced thermotolerance; expression of *HSP* genes is strongly attenuated and the Hsfs are either degraded in the proteasome or conserved by binding to HSPs. (Modified from Scharf et al. (2012))

Box 4.7: The Structure of Heat Stress Transcriptions Factors

In all investigated heat stress transcription factors (Hsfs), the DNA-binding domain is close to the N-terminus (Fig. 4.32). The hydrophobic core of that domain of about 100 amino acids specifies the selectivity of the interaction with the repetitive heat shock elements (HSEs) on the promoters of the heat shock genes. Since usually more than two HSEs are required for a proper heat stress response, oligomerisation of the Hsfs is also necessary for promoter activation.

Downstream from the DNA-binding domain is the Hsf oligomerisation domain (OD). Depending on the structure of this domain, homo-oligomerisation—as well as hetero-oligomerisation—is possible. The classification of HsfA, B or C results from sequence differences of the OD, which is therefore also termed the HR-A/B region. Clusters of basic amino acids downstream from the OD represent the nuclear localisation signal (NLS), which mediates import into the nucleus. For acclimation of the Hsf concentration in the nucleus, import must be balanced by export, and a nuclear export signal (NES) has also been identified in many plant Hsfs. Depending on the rates of import and export into and out of the nucleus, the intracellular distribution of the free Hsfs changes dynamically between the nucleus and the cytoplasm.

Activator elements (AHA motifs)—consisting of aromatic, large hydrophobic and acidic amino acids—are typical of the members of the HsfA class, except for the HsfA8 types. The activator elements can interact with the transcription apparatus and thereby activate it. Similar activator motifs are known from other transcription factors (Baniwal et al. 2004). Hsfs of the B class contain a characteristic tetrapeptide (LFGV, Leu-Phe-Gly-Val) in their C-terminal domains which, by comparison with other transcription factors, is interpreted as a repressor-binding motif. However, the corresponding transcription repressor is not yet known.

Specific roles of the plant heat stress transcription factors: The high diversity and multitude of the principally similar plant Hsfs suggest specific functional roles of these proteins. For instance, in tomato, HsfA1a is a master regulator of the heat stress response and recovery, interacting with Hsfs A2 and B1 in a functional triad upon extended heat stress (Fig. 4.31c). In this triad, HsfA2 functions as an enhancer of heat stress–induced thermotolerance. HsfB1 acts as a synergistic co-activator of HsfA1, whereas in the presence of a co-repressor, class B Hsfs can attenuate the activation of the HS genes. HsfA3 is involved in drought stress signalling, and HsfA9 controls *HSP* gene expression during seed development (Scharf et al. 2012).

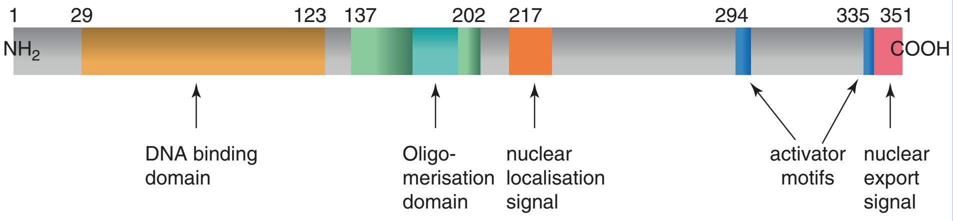


Fig. 4.32 Domains of the tomato HsfA2. (Modified from Scharf et al. (2012))

(HAC1-CBP in Fig. 4.31) as a co-regulator, and this ternary complex enhances the expression of the HSPs (70, 90 and 17) and, in particular, that of Hsfs B1 and A2, which play a crucial role in the acquisition of thermotolerance. HsfA2 is expressed only in stressed plants and accumulates to high levels upon long-term heat stress. Loss-of-function and overexpression experiments have revealed HsfA2 as one of the key elements in the plant stress response.

HsfA2 is involved in protection against heat, ROS, salt stress and even anoxia. It hetero-oligomerises with HsfA1, forming a kind of **superactivator complex** (a so-called enhancosome) for the expression of HS genes (Fig. 4.31c). Apparently, the combination of the HsfA2 activator domains (AHA in Fig. 4.32) with the HAC1-CBP results in strongly enhanced activation of the transcription machinery. Hetero-oligomerisation with HsfA1a is also necessary for the import of HsfA2 into the nucleus in order to overcome the strong C-terminal nuclear export signal (NES) of this Hsf.

Upon abatement (Fig. 4.31d) of the heat stress, the heat stress response is switched off. HsfA2 is inactivated by association with small HSPs (e.g. HSP17-CII and HSP70). This complex accumulates in the so-called **heat stress granula** (**HSGs**; Sect. 4.3.3.3). Release of HsfA2 from these granula requires another small heat stress protein, HSP17C-1, which is important for long-term heat stress. Prolonged heat stress results in high levels of heat stress proteins and of HsfA2. This is the state of acquired thermotolerance. Fading of the heat stress releases HSPs because of the decreasing level of misfolded proteins. An increase in the concentrations of free HSPs leads to monomerisation and thus inactivation of the Hsfs because of their reassociation with the HSPs. HsfA1 binds again to HSPs 70 and 90, and HsfB1 binds accordingly to HSP90. This complex can elicit degradation of HsfB1. Furthermore, it can interact with transcription factors of housekeeping genes and reactivate their expression. HSP90 interacts with HSGs, whereupon HsfA2 is released and degraded.

The interaction between heat shock factors and heat shock proteins exerts effective control over the up-regulation of HSP synthesis. The presence of more denatured proteins than under non-stressed conditions triggers the interaction of Hsfs with *HSP* gene promoters, and a decline in the number of denatured proteins gradually tunes out the extra HSP synthesis. Nonetheless, other factors are known to contribute to the activation of the heat shock/heat stress response (Kotak et al. 2007; Saidi et al. 2011). These include ROS and the plant hormones ABA, ethylene and salicylic acid. A change in the **ROS homeostasis** resulting from ROS production and detoxification appears to be a signal. Several mechanisms of ROS sensing have been proposed—for example, unidentified receptor proteins and redox-sensitive transcription factors (Chap. 2), including heat shock transcription factors (Mittler et al. 2004). However, neither ROS signalling under heat stress nor the roles of signalling molecules are understood nearly as well as the Hsf-dependent activation of HSP synthesis triggered by protein denaturation.

A second mode of sensing protein denaturation is described for the ER. One of the sensors is an ER membrane–associated transcription factor for chaperones. It is a basic leucine zipper protein, bZIP28 (Srivastava et al. 2012) (Fig. 4.33), with a single-pass transmembrane domain (TMD), a cytosolic N-terminus containing the bZIP element and a C-terminus protruding into the ER lumen. The RRIL site (Arg-Arg-Ile-Leu) on the luminal part serves the processing by specific proteases in the Golgi vesicles. bZIP28 is arrested in the ER by association of its C-terminal domain with the major luminal ER chaperone, the "binding immunoglobulin protein" (BIP). Upon stress-induced accumulation of misfolded proteins in the ER, BIP is competed away from the C-terminus of bZIP28 and associates with the accumulating misfolded proteins. Dissociation of the bZIP28–BIP complex enables the transcription factor to leave the ER and enter the Golgi. Processing by specific proteases in the Golgi removes the C-terminal part, liberating the cytosolic part of the bZIP28, which can now enter the nucleus as a transcription factor. For binding to the heat shock elements in the promoter of the heat

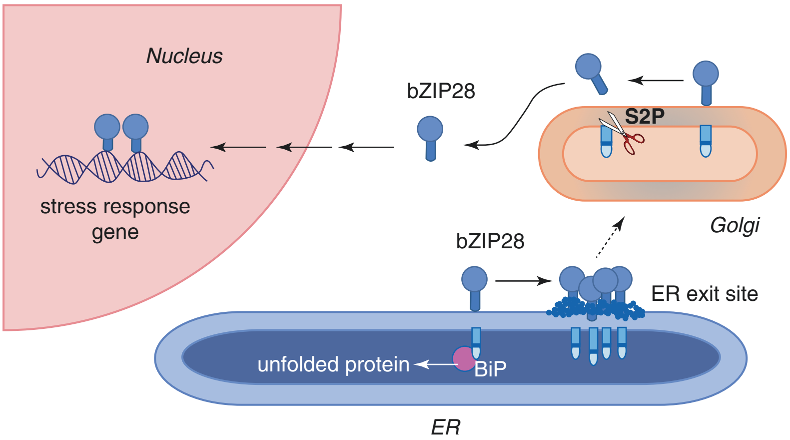


Fig. 4.33 Activation of the bZIP28 transcription factor by stress, such as heat stress. *BiP* binding protein, a member of the HSP70 family. (Modified from Srivastava et al. (2014))

shock genes, oligomerisation of the transcription factor is necessary.

4.3.3.3 Cell Biological Aspects of the Heat Stress Response

Organisms can acquire thermotolerance by maintaining a high level of HSPs while the normal “housekeeping metabolism” continues. During an acute heat shock, in contrast, the cell redirects its activity to almost exclusive synthesis of HSPs. Several mechanisms contribute to that rearrangement of the cellular processes: the activation of the heat stress transcription factors and the transcription of the unique *HSP* genes, the inhibition of the processing of the pre-messenger RNAs (pre-mRNAs) of the housekeeping genes combined with preferential translation of the heat stress gene mRNAs, and the conservation of housekeeping pre-mRNA in the nucleus or the surrounding cytosol in the form of **heat stress granula** (Fig. 4.34). Since housekeeping mRNAs are not functional under acute heat stress, they would be predestined for rapid degradation by RNAses. By association with small heat stress proteins and HSP70, as well as accumulated HsfA2 protein, these mRNAs are protected from degradation and stored in the multi-chaperone granula of 40 nm diameter. This might promote a return to normal cell physiology after the heat shock or upon development of the acquired thermotolerance. Dissociation of these heat stress granula requires ATP-dependent interaction with further HSPs.

4.4 Temperature Sensing

It is evident from the existence of effective acclimative processes such as cold hardening and acquired thermotolerance that plant cells are able to sense the temperature and convert this information into changes in gene expression that confer enhanced stress tolerance. Furthermore, many developmental processes are known to be responsive to ambient temperature changes in the absence of any stress response (Fig. 4.35). The transition from vegetative to reproductive growth, for instance, is induced in *A. thaliana* by a temperature shift from 23 °C to 27 °C (Capovilla et al. 2015)—that is, a modest, non-damaging change in environmental conditions. The right timing of germination, bud break or flowering confers a fitness advantage and is crucial for adaptation to particular habitats and their fluctuating conditions. The same applies to the entrainment of the circadian clock by temperature changes (Chap. 2).

Some responses to temperature changes are rapid (e.g. many responses to stressful temperatures), while others depend on the monitoring of temperatures over weeks and months (e.g. **vernalisation**; Chap. 2). Some processes are controlled by the rate of temperature change, others by the absolute temperature. An example of the latter is the transcriptional activation of *CBF* genes (Sect. 4.2.5). It is not the cooling that is the trigger but a certain absolute temperature. Another differentiation of temperature perception is that between the sensing of extreme (= potentially damaging) temperatures (frost, cold and heat) and the sensing of non-stressful changes of the ambient temperature within the range of active development (Fig. 4.35).

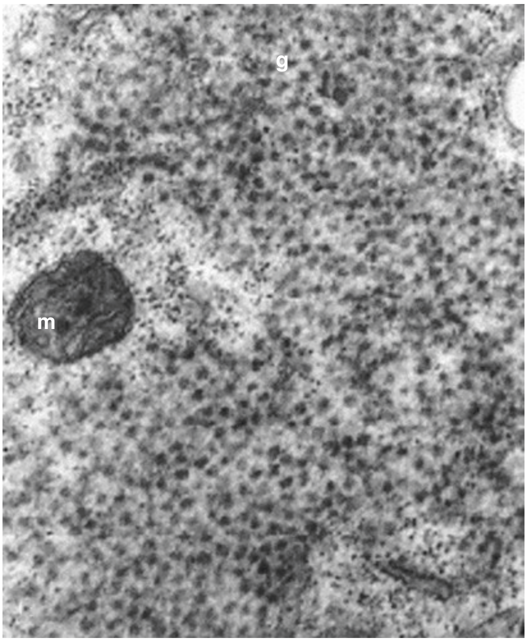


Fig. 4.34 Heat stress granula (*g*) in a tomato cell culture after heat shock (20 → 40 °C within 2 h). (*m*) mitochondria (Bucka 1999)

While a wealth of information is available on transcriptional regulatory networks in plant cells exposed to temperature fluctuations, our understanding of the primary processes of temperature sensing is still like viewing a black box faintly illuminated by a few beams of light. The nature of temperature sensors has been among the great unknowns of molecular plant biology (Penfield 2008). In recent years, several critical components involved in temperature sensing have been identified and functionally characterised. However, the actual molecular thermometers remain to be found (Wigge 2013). Many differences between the sensing of potentially stressful versus ambient temperature changes indicate that several thermometers

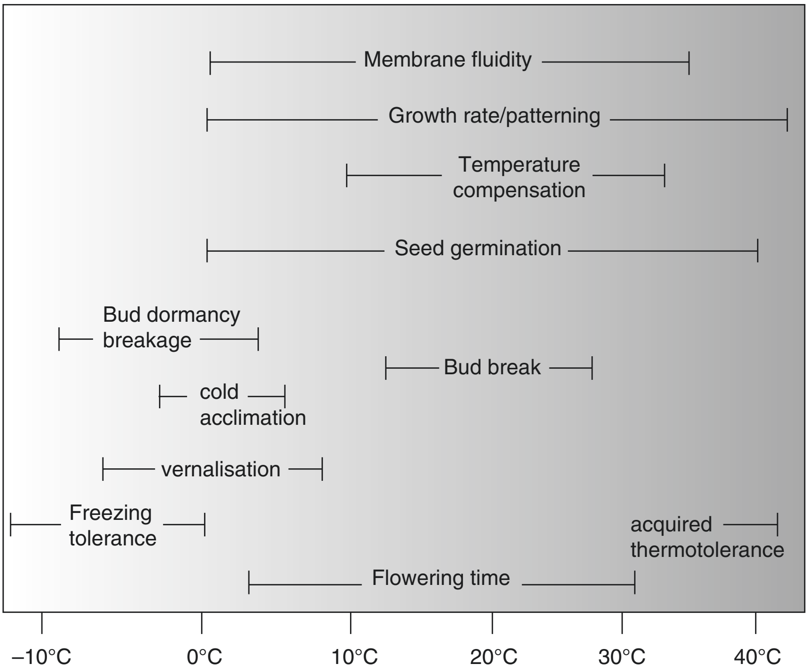


Fig. 4.35 Temperature ranges of plant responses to the ambient temperature; for example, the "bud break" responds to the ambient temperature in a range between 12 °C and 28 °C. "Temperature compensation" refers to the circadian clock. (Modified from Penfield (2008))

may exist in plants (Knight and Knight 2012). One that has been shown to trigger **thermomorphogenesis** is associated with the **phytochrome** system (PhyB), especially with the nocturnal inactivation of Phy_{fr} by reversion to Phy_r (Chap. 3, Fig. 3.19). Phy_{fr}, together with another transcription repressor complex, represses the activity of the **transcription factor PIF4** (phytochrome interacting factor 4) which positively controls *ATHB2*, a homeobox gene promoting hypocotyl elongation growth. The half-life of $PhyB_{fr}$ is 2.09 h at 22 °C and 1.59 h at 27 °C. Thus, the inhibitory effect of Phy_{fr} on the activity of PIF4 and the expression of ATHB2 lasts longer at lower temperatures, and this holds also for another transcription-repressing complex (ELF3 in Fig. 4.36) (Jung et al. 2016).

4.4.1 Sensing of Extreme Temperatures

Biological membranes are strongly affected in their biophysical properties by cold or heat. For this reason and because the respective mechanisms have been revealed in bacteria, yeast and animal cells, changes in membrane fluidity or (alternatively, at least in the case of cold) disturbance and destabilisation of the microfilaments—as cytoskeletal elements are associated with the biomembranes (Orvar et al. 2000; Knight and Knight 2012)—have long been hypothesised to play a primary sensory role in temperature perception by plant cells (Saidi et al. 2011). In these cells, the list of messengers used by signalling pathways includes Ca^{2+}, lipids, pH, and cyclic guanosine monophosphate (cGMP). However, no other messenger has been found that responds to more stimuli than **cytosolic free Ca^{2+}** (Sanders et al. 1999). Such Ca^{2+} signals have been well documented in many plant species as the earliest measurable events (within seconds) in response to both cold (Knight et al. 1996) and heat (Gong et al. 1998) (Fig. 4.37). It is assumed that temperature-dependent membrane or cytoskeleton changes are translated into transient increases in cytosolic Ca^{2+} concentrations, mediated by Ca^{2+} channels in the plasma and the tonoplast membranes.

Evidence exists for distinct **Ca signatures** (Chap. 2)—that is, specific kinetics of the transient $[Ca^{2+}]$ increases that carry information and enable specificity of the downstream events (Plieth et al. 1999). In mammalian systems, different classes of Ca^{2+}-permeable channels have been identified as essential sensors for cold or heat, respectively. However, no Ca^{2+} channels orthologous to the ones identified outside the plant kingdom are present in plants, according to genome analyses.

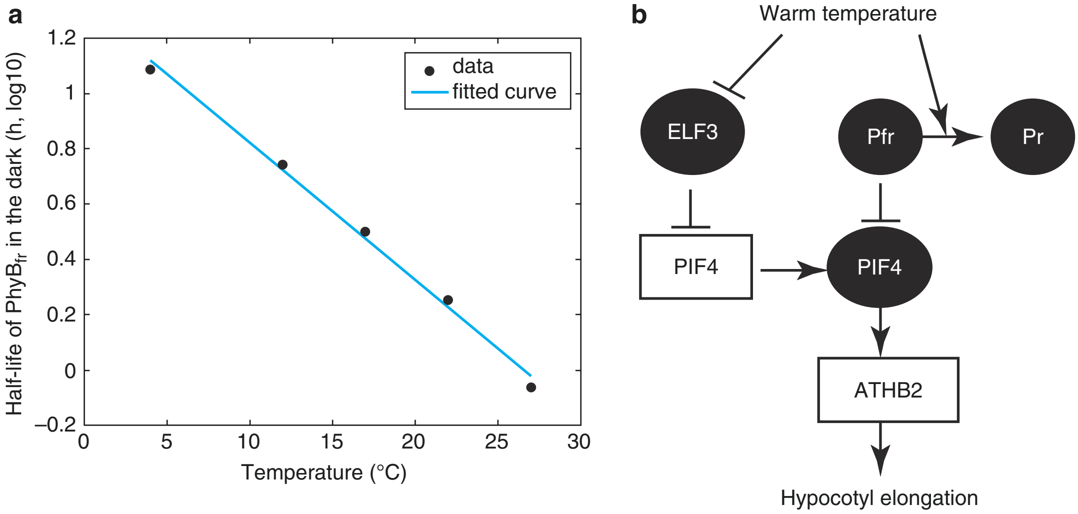


Fig. 4.36 Involvement of phytochrome in ambient temperature sensing. The kinetics of the P_{fr} inactivation (reversion to P_r) in the dark depends on the temperature **a** and temperature sensing **b** by phytochrome- and ELF3-dependent regulation of the transcription factor PIF4, which in turn activates the homeobox gene ATHB2 as a master regulator of (hypocotyl) growth of *Arabidopsis thaliana* (Jung et al. 2016)

4.4.2 Sensing of Ambient Temperature Changes

Changes in temperature within the sub-extreme range, which act as important environmental cues for the modulation of developmental processes (Fig. 4.35), are apparently sensed by mechanisms that are different from the ones involved in sensing a shift to potentially stressful temperatures. A component of the ambient temperature sensing is dependent on **histone H2A.Z**, which can be dynamically replaced by the canonical histone 2A in the nucleosome, and vice versa (Kumar and Wigge 2010). H2A.Z-containing nucleosomes wrap DNA more tightly, which renders the DNA less accessible to RNA polymerases and in turn mRNA synthesis. Upon a shift to higher temperatures, H2A.Z is evicted from nucleosomes. This then enables key regulators such as PIF4 (Fig. 4.36) to bind to regulatory sequences and initiate the transcription of genes that activate developmental transitions. In the case of flowering, this is the florigen-encoding gene, *FT* (Kumar et al. 2012) (Fig. 4.38). However, while these components are clearly

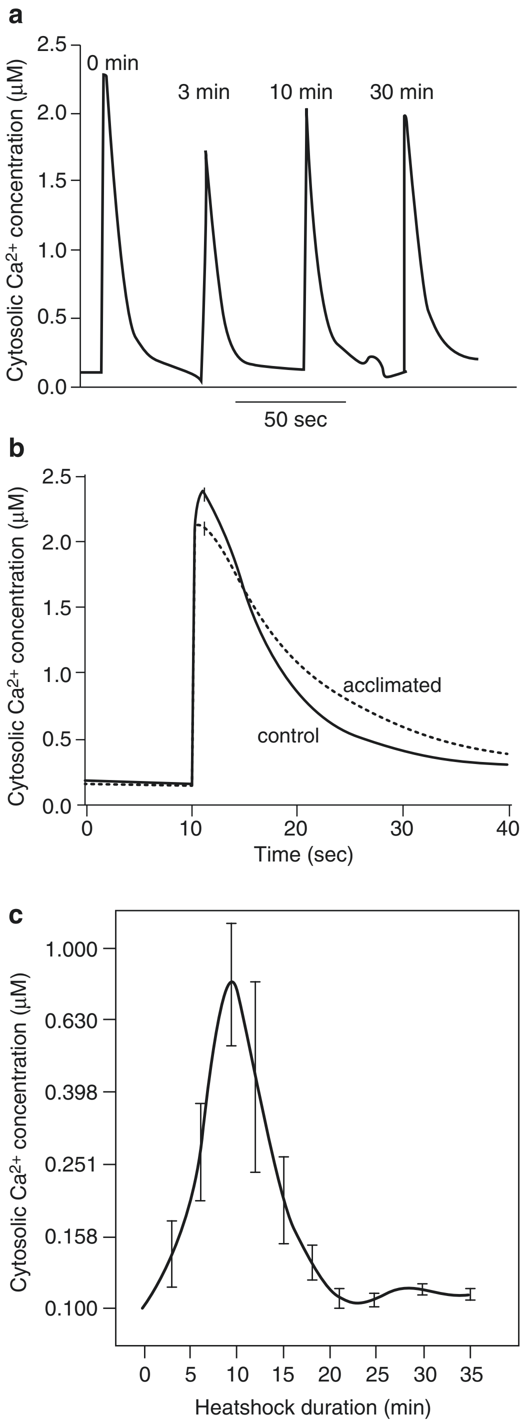


Fig. 4.37 Cold and heat shock–induced momentary changes in the cytosolic free Ca^{2+} concentration in *Arabidopsis thaliana*. **a** Repeated cold shocks applied to non-acclimated control plants. **b** Comparison of Ca^{2+} signals following a cold shock (21 → 0 °C) in non-acclimated and acclimated (3 days with a cooling period: 3 h at 4 °C) 7-day-old *A. thaliana* seedlings. In acclimated seedlings the transitory increase in cytosolic [Ca^{2+}] lasts longer (redrawn after Knight et al. (1996)). **c** Ca^{2+} signal after a heat shock (21 → 47 °C for 35 min) (Modified from Gong et al. (1998)). Note the different time scales, indicating different sensing mechanisms for cold and heat. Changes in [Ca^{2+}] can be visualised by means of the Ca^{2+}-sensitive luminescent protein aequorin. To that end, transgenic experimental plants stably expressing apoaequorin were used. (Knight et al. 1996)

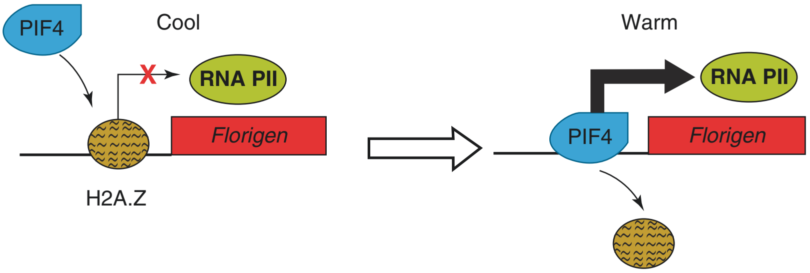


Fig. 4.38 H2A.Z and PIF4 as critical components of ambient temperature sensing in *Arabidopsis thaliana*. Upon an increase in ambient temperature, H2A.Z is evicted from nucleosomes, making DNA more accessible for binding by regulatory factors such as the key regulator PIF4 and activation of genes such as *FT*. The FT protein (= florigen) triggers a more rapid transition to flowering. (Modified from Kumar et al. (2012))

important in mediating temperature-controlled changes, they do not represent the primary thermosensory mechanisms. These remain to be uncovered (Wigge 2013).

Summary

- Active life requires water in the liquid state, but not the entire temperature range where this applies is equally convenient for organisms. Organisms such as plants, which (apart from a few exceptions) cannot produce heat themselves and thus equilibrate with the ambient temperature, are characterised as either psychrophilic when adapted to low temperatures, as thermophilic when thriving at temperatures above 40 °C and as extremophilic when living in and around hot springs. However, the vast majority of plants are mesophilic, with temperature optima between 20 °C and 30 °C.
- As so-called poikilothermic organisms, plants can thrive at temperatures above and below the optimal temperature range, experiencing increasing stress with escalating deviation from the optimum. The absolute limits of life—set by cold and heat death, respectively—are generally species-specific. Nevertheless, the habitats colonised by a species can select individuals that are genetically better adapted, yielding ecotypes with different temperature requirements.
- The vast majority of tropical and subtropical plants are not adapted to cold. Exceptions are tropical alpine plants, which are cold tolerant all year round.
- Perennial plants bound to habitats that are subject to temperature-induced seasons such as winter and summer can acclimatise. As a result the so-called cardinal points of life (temperature optimum, cold or heat death as points of no return) can shift considerably (by 10–20 °C) to lower temperatures or, less pronounced (<10 °C), to higher temperatures. Seasonal acclimation (hardening and de-hardening) is triggered by environmental cues (e.g. the length of the photoperiod) or by mild forms of the respective stress.
- Hardening and de-hardening are syndromes encompassing a variety of changes at the biochemical and ultrastructural levels. A principle that applies likewise to cold or heat acclimation is the adjustment of the viscosity (and functionality) of the biomembranes to the altered temperature ranges by an increase (cold hardening) or decrease (acquisition of thermotolerance) in the proportion of desaturated fatty acids in the membrane lipids. This is associated with a change in the expression of the genes encoding fatty acid desaturases.
- As poikilothermic organisms, plants do not have physicochemical or biochemical

thermometers. Nevertheless, they are able to quantify deviations from the optimal temperature range. This kind of temperature sensing is coupled either to the incidence of damage, such as protein inactivation by heat, or simply attainment of a particular temperature range where selected genes are expressed, such as *CBF* genes in cold hardening. The biochemical mechanisms by which plants can sense temperature are still unknown. However, it appears more likely that there are several thermosensors for particular processes in a plant's life and acclimation to its environment. One of these is temperature-dependent phytochrome B reversion from the physiologically active Phy_{fr} to the inactive Phy_r.

- An early response to temperature stress is the transient increase of the cytosolic concentration of free Ca^{2+}—that is, its immediate release from cellular pools and fast sequestering into presumably other organelles such as the vacuole. However, such Ca^{2+} spikes are signals, not thermometers.
- Apart from the adjustment of the membrane viscosity, the processes of cold hardening/de-hardening and acquisition or loss of thermotolerance differ fundamentally. The impacts of cold are associated not only with a slowdown of (bio)chemical reactions and rigidification of non-acclimatised biomembranes (cold damage by "chilling" at still positive temperatures) but also with a change of liquid water to (hydrophobic) ice at sub-zero temperatures. Intracellular ice formation results in the disintegration of the cellular membranes because of the loss of the hydrophobic interaction of the amphiphilic lipids with liquid water.
- Therefore, frost hardening triggers either the capability of the cells for extracellular ice nucleation, most probably provoked by so-called antifreeze proteins in the apoplast which, in contrast to their name, control ice formation. A physicochemical equilibrium across the cell membrane between the water potential of ice and that of the cellular solutions results in temperature-dependent progressive cell dehydration by apoplastic crystallisation of cellular water. Freeze dehydration to a residual volume of less than 20% of liquid cellular water is not uncommon.
- An alternative strategy is an increase in the cell's capability for supercooling—that is, the avoidance of ice formation by colligatively effective cryoprotectants. These are hydrophilic low molecular weight solutes such as carbohydrates, amino acids and quaternary ammonium compounds which, even at higher concentrations, do not lose their cellular compatibility. Increased production and accumulation of cryoprotectants require a rearrangement of the preferential biochemical routes of the de-hardened state from energy metabolism for growth towards synthesis of less readily metabolisable compounds. Extreme supercooling to the temperature of homogeneous ice nucleation (−40 °C) is known from the xylem tissue of some woody species. However, the mechanisms enabling this physically unlikely phenomenon are not known.
- The formation of amphiphilic, membrane-protecting proteins (dehydrins), which accumulate also under drought and salt stress, is a common component of the frost-hardening process. Cryoprotectants are produced in plant tissues, which are capable of extracellular ice formation as well. A more negative osmotic potential upon extracellular ice deposition diminishes the degree of freeze dehydration.
- Cold hardening is accompanied by changes in the chloroplast ultrastructure and a reduction in the photosynthetic efficiency. A substantial decrease in the chlorophyll content indicates the downsizing and even complete degradation of parts of the photosystems. This prevents over-excitation of the photosynthetic light reactions with respect to the utilisation of the end products, reduced nicotinamide adenine dinucleotide phosphate (NADPH) and adenosine triphosphate (ATP). Overstretching of the photosystem's capacity of de-energisation leads to the formation of reactive oxygen species, causing further damage. Upon de-hardening in spring, the photosystems and antenna complexes are restituted.
- Not all parts of a plant can harden (and de-harden) to the same extent and at the same

time. Roots, old leaves, and growing leaves and twigs are the most temperature-sensitive organs. In the absence of homeostatic temperature regulation, most of the mechanisms involved are operating at the cellular level and protect the tissues directly exposed to an unfavourable temperature.

- Stress by freezing, drought and high salinity poses osmotic challenges to plants. Accordingly, there is considerable overlap in the molecular responses of cells to these different stress conditions. However, there are also highly complex responses specific to cold acclimation. Many proteins increase in abundance upon exposure to low temperature. They are known as cold-responsive proteins (COR proteins). A large number of *COR* genes are activated under the control of the CBF transcription factors summarised under the term "CBF regulon". Binding of CBFs rapidly activates transcription of *COR* genes. Constitutive strong transcription of *CBF* genes results in a permanent cold-acclimated state without an exposure to cold. *CBF* overexpression leads, on the other hand, to a strong reduction in the growth rate as an integral part of stress acclimation responses.
- Cold acclimation involves rapid up-regulation of the *CBF* genes. Their expression is controlled by transcription factors that are themselves predominantly controlled at the posttranslational level. A specific transcription factor for cold acclimation is ICE1 which, by binding to *cis* elements in the *CBF* promoters, triggers the transcription of *CBF* genes. Events upstream from ICE1 are less well defined. What is clearly established is a rapid increase in cytosolic Ca^{2+} levels upon transfer of plants to cold. Another regulatory mechanism leading to enhanced ICE1 activity involves a cold-responsive but Ca^{2+}-independent MAP kinase phosphorylation cascade.
- Elevated temperatures above the optimal range not only accelerate but also redirect metabolic processes, leading to changes in metabolite pools, thereby affecting growth and many other developmental processes. Apart from such biochemical responses and the aforementioned membrane viscosity problems, denaturation of proteins is the major challenge of heat stress which, for mesophilic organisms, starts at around 35 °C. In many habitats, even in temperate climate zones, temperatures of 40 °C and more are frequently encountered—in particular, during direct sunshine. Even if these events are transitory, they trigger strong heat shock responses, targeted at rescuing misfolded or degrading aggregated proteins in the 26S proteasome. The short-term heat shock must be differentiated from longer-lasting heat stress with a greater potential for heat damage. Both heat shock and heat stress can lead to the so-called acquired thermotolerance: the ability to withstand higher temperatures owing to acclimation.
- At the cellular level, the major response to a heat shock is the rapid deceleration of housekeeping metabolism, apparent in the down-regulation of housekeeping genes, and the subsequent revival of this metabolism after a return to the normal temperature. During long-term heat stress the housekeeping metabolism has to maintain its function at the elevated temperature. Both sets of reactions, however, depend on the strongly enhanced expression of genes encoding transcription factors (heat shock factors) and heat shock proteins, many of which serve essential cellular functions also in the optimal temperature range.
- There are several ways in which plants can avoid or at least mitigate heat stress—for example, by timing of sensitive processes and phases such as germination, by dissection of large leaf laminas (e.g. in banana), by covering the leaf surface with a felt of trichomes or by transpiration cooling. Since plants, as sessile organisms, cannot avoid heat stress altogether, all are capable of mounting a response to heat stress.
- The most important mechanism underlying acquired thermotolerance is the massive production of heat shock proteins (HSPs). However, not only does the expression level of *HSP* genes change but also up to 2% of all genes are affected in their activity. For many

of them the contribution to thermotolerance is functionally not understood. What is evident is an up-regulation of anti-oxidative defences to counteract the increased production of reactive oxygen species under heat stress. Also, the concentrations of compatible solutes increase, which can protect proteins from unfolding and thus shift the onset of the heat stress response to higher temperatures.

- The classical heat shock reaction requires stress-induced accumulation of misfolded proteins activating heat shock transcription factors (Hsfs), which then bind to specific elements (heat shock elements (HSEs)) in the promoters of genes encoding heat shock proteins (HSPs). HSPs—named after their enhanced production upon heat treatment—are essential components of both prokaryotic and eukaryotic cells for life and stress survival as well. HSPs act as chaperones required for correct folding of nascent proteins upon release from the ribosome or after stress-induced misfolding, unfolding or aggregation of unfolded proteins. They do not exhibit enzymatic activity and are classified by their molecular weights. The two types (prokaryotic and eukaryotic) differ in the details of their modes of action in the so-called HSP cycle. The misfolded protein is bound via an exposed hydrophobic stretch to the interior (also hydrophobic) domain of the HSP which, by consumption of ATP, is converted into a hydrophilic microenvironment; this in turn forces the misfolded protein back into its natural conformation with a hydrophilic surface. After release of the repaired protein, the HSP is ready for a new round either with the same protein (if the repair was not yet complete) or with another misfolded protein. Several co-chaperones are required for the function of the HSP cycle.
- Chaperones are, in addition, involved in the removal of irreversibly denatured proteins. The function of HSPs in the removal of such proteins is the targeting of the poly-ubiquitinated candidates to the 26S proteasome.
- The normal heat shock response starts with the transcriptional activation of *HSP* genes by Hsfs. Hsfs have a modular structure, which is conserved in the entire eukaryotic kingdom. Plant genomes are particularly rich in Hsfs: in *Arabidopsis thaliana* 21 *Hsf* genes, in soybean even 52 *Hsf* genes are known. Hsfs mediate the acute heat shock response, as well as the acquisition of thermotolerance. Under normal conditions, Hsfs are inactive because of their association with heat shock proteins, which prevent their oligomerisation. Heat denaturing of proteins results in dissociation of the chaperone–Hsf complexes because of the association of the HSPs with the mis- or unfolded proteins. The liberated Hsfs oligomerise and bind to the heat stress elements (HSEs) in the promoters of heat stress genes, which usually harbour more than one HSE. The transcriptions factor HsfA2 has turned out to be one of the key elements in the plant stress response. It is involved in protection against heat, reactive oxygen species, salt stress and even anoxia, and accumulates to high levels upon long-term heat stress. The interaction between heat shock factors and heat shock proteins exerts an effective control over the up-regulation of HSP synthesis. The presence of more denatured proteins than under non-stressed conditions triggers the interaction of Hsfs with *HSP* gene promoters, and a decline in the number of denatured proteins gradually tunes out the extra HSP synthesis.
- In the heat shock response, sensing of high temperature occurs via the abundance of inactivated, misfolded or even aggregated proteins. A second mode of sensing of protein denaturation has been described for the endoplasmic reticulum (ER), where one of the sensors is an ER membrane–associated basic leucine zipper protein, bZIP28, as a transcription factor for chaperones. It is arrested in the ER by association with the major ER chaperone, the “binding immunoglobulin protein” (BIP). Upon accumulation of misfolded proteins in the ER, BIP is competed away from bZIP28 and associates with the accumulating misfolded proteins. After several modifications, bZIP28 enters the nucleus as a transcription factor binding to the heat shock elements in the promoters of heat shock genes.

- Organisms can acquire thermotolerance by maintaining a high level of HSPs while the normal "housekeeping metabolism" continues. During an acute heat shock, in contrast, the cell redirects its activity to almost exclusive synthesis of HSPs. Processing of the pre-messenger RNAs (pre-mRNAs) of the housekeeping genes is stopped with the preferential translation of the heat stress gene mRNAs. To avoid degradation of unprocessed pre-mRNAs and thus allowing immediate resumption of housekeeping gene expression, the pre-mRNAs associated with heat shock proteins are conserved in the nucleus or the surrounding cytosol in the form of heat stress granula.

References

Baniwal SK, Bharti K, Chan KY, Fauth M, Ganguli A, Kotak S, Mishra SK, Nover L, Port M, Scharf K-D, Tripp J, Weber C, Zielinski D, von Koskull-Döring P (2004) Heat stress response in plants: a complex game with chaperones and more than twenty heat stress transcription factors. J Biosci 29:471–487

Beck E (1994a) Cold tolerance in tropical alpine plants. In: Rundel P, Smith AP, Meinzer FC (eds) Tropical alpine environments: plant form and function. Cambridge University Press, Cambridge. pp 77–110

Beck E (1994b) Turnover and conservation of nutrients in the pachycaul Senecio keniodendron. In: Rundel P, Smith AP, Meinzer FC (eds) Tropical alpine environments: plant form and function. Cambridge University Press, Cambridge. pp 215–222.

Beck E (2011) Abiotischer Stress pur: Überlebensstrategien von (tropischen) Hochgebirgspflanzen. Rundgespr. Kommission für Ökologie, Bayer. Akad Wissensch 39:93–110

Beck E, Heim R, Hansen J (2004) Plant resistance to cold stress: mechanisms and environmental signals triggering frost hardening and dehardening. J Biosci 29: 449–459

Bita CE, Gerats T (2013) Plant tolerance to high temperature in a changing environment: scientific fundamentals and production of heat stress-tolerant crops. Front Plant Sci 4:273

Bravo LA, Griffith M (2005) Characterization of antifreeze activity in Antarctic plants. J Exp Bot 56:1189–1196

Brush RA, Griffith M, Mlynarz A (1994) Characterization and quantification of intrinsic nucleators in winter rye leaves. Physiol Plant 104:725–735

Buchanan BB, Gruissem W, Jones RL (2015) Biochemistry and molecular biology of plants, 2nd edn. Wiley, Hoboken

Bucka A (1999) Charakterisierung kleiner cytoplasmatischer Hitzeschockproteine der Wildtomate (Lycopersicon peruvianum L.) PhD thesis, Martin Luther University Halle-Wittenberg

Byard S, Wiesniewski M, Li J (2010) Interspecific analysis of xylem freezing responses in Acer and Betula. Hort Science 45:65–68

Capovilla G, Schmid M, Posé D (2015) Control of flowering by ambient temperature. J Exp Bot 66:59–69

Crowe JH, Crow LM, Mouradian R (1983) Stabilization of biological membranes at low water activities. Cryobiology 20:346–356

Domínguez T, Hernández ML, Pennycooke JC, Jiménez P, Martínez-Rivas JM, Sanz C, Stockinger EJ, Sánchez-Serrano JJ, Sanmartín M (2010) Increasing ω-3 desaturase expression in tomato results in altered aroma profile and enhanced resistance to cold stress. Plant Physiol 153:655–665

Dowgert ME, Steponkus PL (1983) Effect of cold acclimation on intracellular ice formation in isolated protoplasts. Plant Physiol 72:978–988

Doyle SM, Genest O, Wickner S (2013) Protein rescue from aggregates by powerful molecular chaperone machines. Nat Rev Mol Cell Biol 14:617–629

Falcone DL, Ogas JP, Somerville CR (2004) Regulation of membrane fatty acid composition by temperature in mutants of Arabidopsis with alterations in membrane lipid composition. BMC Plant Biol 4:17

Fuller MP, Wisniewski M (1998) The use of infrared thermal imaging in the study of ice nucleation and freezing of plants. J Thermal Biol 23:81–89

Gao F, Ding H, Feng Z, Liu D, Zhao Y (2014) Functional display of triphenylmethane reductase for dye removal on the surface of Escherichia coli using N-terminal domain of ice nucleation protein. Bioresour Technol 169:181–187

Goldstein G, Meinzer F, Monasterio M (1984) The role of capacitance in the water balance of Andean giant rosette species. Plant Cell Environ 7:179–186

Goldstein G, Rada F, Azocar A (1985) Cold hardiness and supercooling along an altitudinal gradient in Andean giant rosette species. Oecologia 68:147–152

Gong M, van der Luit AH, Knight MR, Trewavas AJ (1998) Heat-shock-induced changes in intracellular Ca^{2+} level in tobacco seedlings in relation to thermotolerance. Plant Physiol 116:429–437

Green RL, Warren GJ (1985) Physical and functional repetition in a bacterial ice nucleation gene. Nature 317:645–648

Griffith M, Yaish MWF (2004) Antifreeze proteins in overwintering plants: a tale of two activities. Trends Plant Sci 9:399–405

Gupta R, Deswal R (2014) Antifreeze proteins enable plants to survive in freezing conditions. J Biosci 39:931–944

Gusta LV, Wisniewski M (2013) Understanding plant cold hardiness: an opinion. Physiol Plant 147:4–14

Gusta LV, Wiesniewski M, Nesbitt MT, Gusta ML (2004) The effect of water, sugars, and proteins on the pattern of ice nucleation and propagation in acclimated and nonacclimated canola leaves. Plant Physiol 135:1642–1653

Hacker J, Neuner G (2007) Ice propagation in plants visualized at the tissue level by infrared differential thermal analysis (IDTA). Tree Physiol 27:1661–1670

Hacker J, Neuner G (2008) Ice propagation in dehardened alpine plant species studied by infrared differential thermal analysis (IDTA). Arct Antarct Alp Res 40:660–670

Hacker J, Ladinig U, Wagner J, Neuner G (2011) Inflorescences of alpine cushion plants freeze autonomously and may survive subzero temperatures by supercooling. Plant Sci 180:149–156

Hanin M, Brini F, Ebel C, Toda Y, Takeda S, Masmoudi K (2011) Plant dehydrins and stress tolerance: versatile proteins for complex mechanisms. Plant Signal Behav 6:1503–1509

Hannah MA, Wiese D, Freund S, Fiehn S, Heyer AG, Hincha DK (2006) Natural genetic variation of freezing tolerance in Arabidopsis. Plant Physiol 142:98–112

Hansen J, Beck E (1988) Evidence for ideal and non-ideal equilibrium freezing of leaf water in frost hardy ivy (Hedera helix) and winter barley (Hordeum vulgare). Bot Acta 101:76–82

Hansen J, Beck E (1994) Seasonal changes in the utilisation and turnover of assimilation products in 8-year-old Scots pine (Pinus sylvestris L.) trees. Trees 8: 172–182

Hansen J, Türk R, Vogg G, Heim R, Beck E (1997) Conifer carbohydrate physiology: updating classical views. In: Rennenberg H, Eschrich W, Ziegler H (eds) Trees—contributions to modern tree physiology. SPB Academic Publication, The Hague. pp 97–108

Hedberg O (1964) Features of Afro-alpine plant ecology. Acta Phytogeogr Suecica 48:1–144

Heldt HW, Piechulla B (2010) Plant biochemistry. Academic Press, London

Hew CL, Yang DSC (1992) Protein interaction with ice. Eur J Biochem 203:33–42

Hiilovaara-Teijo M, Hannukkala A, Griffith M, Yu XM, Pihakaski-Maunsbach K (1999) Snow-mold-induced apoplastic proteins in winter rye leaves lack antifreeze activity. Plant Physiol 121:665–674

Huang GT, Ma SL, Bai LP, Zhang L, Ma H, Jia P, Liu J, Zhong M, Guo ZF (2012) Signal transduction during cold, salt, and drought stresses in plants. Mol Biol Rep 39:969–987

Jaglo-Ottesen KR, Gimour SJ, Zarka DG, Schabenberger O, Thomashow MF (1998) Arabidopsis CBF1 overexpression induces COR genes and enhances freezing tolerance. Science 280:104–106

Janská A, Marsik P, Zelenkova S, Ovesniá J (2010) Cold stress and acclimation—what is important for metabolic adjustment? Plant Biol 12:395–405

Jones TL, Tucker DE, Ort DR (1998) Chilling delays circadian pattern of sucrose phosphate synthase and nitrate reductase activity in tomato. Plant Physiol 118:149–158

Jung J-H, Domijan M, Klose C, Biswas S, Ezer D, Gao M, Khattak AK, Box MS, Charoensawan V, Cortijo S, Kumar M, Grant A, Locke JCW, Schaefer E, Jaeger KE, Wigge PA (2016) Phytochromes function as thermosensors in Arabidopsis. Science 27

Kajava AV, Lindow SE (1993) A model of three-dimensional structure of ice nucleation proteins. J Mol Biol 232:709–717

Kaplan F, Kopka J, Haskell DW, Zhao W, Schiller KC, Gatzke N, Sung DY, Guy CL (2004) Exploring the temperature-stress metabolome of Arabidopsis. Plant Physiol 136:4159–4168

Kasuga J, Hashidoko Y, Nishioka A, Yoshiba M, Arakawa K, Fujikawa S (2008) Deep supercooling xylem parenchyma cells of katsura tree (Cercidiphyllum japonicum) contain flavonol glycosides exhibiting high anti-ice nucleating activity. Plant Cell Environ 31:1335–1348

Kishimoto T, Sekozawa Y, Yamazaki H, Murakawa H, Kazuyaki K, Ishikawa M (2014) Seasonal changes in ice nucleation activity in blueberry stems and effects of cold treatments in vitro. Environ Exp Bot 106: 13–23

Knight MR, Knight H (2012) Low-temperature perception leading to gene expression and cold tolerance in higher plants. New Phytol 195:737–751

Knight H, Trewavas AJ, Knight MR (1996) Cold calcium signalling in Arabidopsis involves two cellular pools and a change in calcium signature after acclimation. Plant Cell 8:489–503

Kotak S, Larkindale J, Lee U, von Koskull-Döring P, Vierling E, Scharf K-D (2007) Complexity of the heat stress response in plants. Curr Opin Plant Biol 10:310–316

Kumar SV, Wigge PA (2010) H2A.Z-containing nucleosomes mediate the thermosensory response in Arabidopsis. Cell 140:136–147

Kumar SV, Lucyshyn D, Jaeger KE, Alós E, Alvey E, Harberd NP, Wigge PA (2012) Transcription factor PIF4 controls the thermosensory activation of flowering. Nature 484:242–245

Lafta AM, Lorenzen JH (1995) Effect of high temperature on plant growth and carbohydrate metabolism in potato. Plant Physiol 109:637–643

Lagzian M, Latifi AM, Bassami MR, Mirzaei M (2014) An ice nucleation protein from Fusarium acuminatum: cloning, expression, biogeochemical characterization and computing modeling. Biotechnol Lett 36(10):2043–2051

Larcher W (1987) Stress bei Pflanzen. Naturwissenschaften 74:158–167

Larcher W (1994) Ökophysiologie der Pflanzen 5. Aufl. Eugen Ulmer Stuttgart

Larcher W (2003) Physiological plant ecology, 4th edn (Plants under stress). Springer, Berlin

Larkindale J, Vierling E (2008) Core genome responses involved in acclimation to high temperature. Plant Physiol 146:748–761

Lindow SE (1982) Population dynamics of epiphytic ice nucleation active bacteria on frost sensitive plants and frost control by means of antagonistic bacteria. In: Li PH, Sakai A (eds) Plant cold hardiness. Academic Press, New York. pp 395–416

Lorv JS, Rose DR, Glick BR (2014) Bacterial ice crystal controlling proteins. Australas Sci 2014:976895

Maki LR, Galyan ME, Chien ME, Caldwell DR (1974) Ice nucleation induced by Pseudomonas syringae. Appl Microbiol 28:456–459

Martinière A, Shvedunova M, Thomson AJ, Evans NH, Penfield S, Runions J, McWatters HG (2011) Homeostasis of plasma membrane viscosity in fluctuating temperatures. New Phytol 192:328–337

McClung CR, Davis SJ (2010) Ambient thermometers in plants: from physiological outputs towards mechanisms of thermal sensing. Curr Biol 20(24): R1086–92

van Meer G, Voelker DR, Feigenson GW (2008) Membrane lipids: where they are and how they behave. Nat Rev Mol Cell Biol 9:112–124

Mittler R, Vanderauwera S, Gollery M, van Breuseem F (2004) Reactive oxygen gene network of plants. Trends Plant Sci 9:490–498

Moffatt B, Ewart V, Eastman A (2006) Cold comfort: plant antifreeze proteins. Physiol Plant 126:5–16

Nagler M, Nukarinen E, Weckwerth W, Naegele T (2015) Integrative molecular profiling indicates a central role of transitory starch breakdown in establishing a stable C/N homeostasis during cold acclimation in two natural accessions of Arabidopsis thaliana. BMC Plant Biol 15:284

Nover L, Höhfeld I (1996) Hohe Temperaturen. In: Brundol C, Rueggisegger A, Brändle R (eds) Stress bei Pflanzen. Paul Haupt, Bern. pp 49–70.

Orvar BL, Sangwan V, Omann F, Dhindsa RS (2000) Early steps in cold sensing by plant cells: the role of actin cytoskeleton and membrane fluidity. Plant J 23:785–794

Penfield S (2008) Temperature perception and signal transduction in plants. New Phytol 179:615–628

Peng Y, Reyes JL, Wei H, Yang Y, Karlson D, Covarrubias AA et al (2008) RcDhn5, a cold acclimation responsive dehydrin from Rhododendron catawbiense rescues enzyme activity from dehydration effects in vitro and enhances freezing tolerance in RcDhn5-overexpressing Arabidopsis plants. Physiol Plant 134:583–597

Plieth C, Hansen U-P, Knight H, Knight MR (1999) Temperature sensing by plants: the primary characteristics of signal perception and calcium response. Plant J 18:491–497

Qu A-L, Ding Y-F, Jiang Q, Zhu C (2013) Molecular mechanisms of the plant heat stress response. Biochem Biophys Res Commun 432:203–207

Saidi Y, Finka A, Goloubinoff P (2011) Heat perception and signalling in plants: a tortuous path to thermotolerance. New Phytol 190:556–565

Sanders D, Brownlee C, Harper JF (1999) Communicating with calcium. Plant Cell 11:691–706

Sarhan MAA (2011) Ice nucleation protein as a bacterial surface display protein. Arch Bio Sci (Belgrade) 63:943–948

Sasaki K, Imai R (2012) Pleiotropic roles of cold shock domain proteins in plants. Front Plant Sci 2:116

Sasaki K, Kim M-H, Imai R (2007) Arabidopsis COLD SHOCK DOMAIN PROTEIN2 is a RNA chaperone that is regulated by cold and developmental signals. Biochem Biophys Res Commun 364:633–638

Sasaki K, Imai R, Kim M-H, Imai R (2013) Arabidopsis COLD SHOCK DOMAIN PROTEIN 2 is a negative regulator of cold acclimation. New Phytol 198:95–102

Scharf K-D, Berberich T, Ebersberger I, Nover L (2012) The plant heat stress transcription factor (Hsf) family: structure, function and evolution. Biochim Biophys Acta 1819:104–119

Sellmair J, Beck E, Kandler O (1968) Isolierung und Identifizierung von Hamamelit aus Primula clusiana Tausch. Z Pflanzenphysiol 59:70–79

Sellmair J, Beck E, Kandler O (1969) Zur Physiologie der Clusianose. Z Pflanzenphysiol 61:338–342

Senser M, Beck E (1979) Kälteresistenz der Fichte. Ber Dtsch Bot Ges 92:243–259

Senser M, Beck E (1992) Frost resistance in spruce [Picea abies (L.) Karst]: IV. The lipid composition of frost resistant and frost sensitive spruce chloroplasts. Z Pflanzenphysiol 105:241–253

Shimazu M, Nguyen A, Muchandani A, Chen W (2003) Cell surface display of organophosphorus hydrolase in Pseudomonas putida using an ice-nucleation protein anchor. Biotechnol Prog 19:1612–1614

Smolin N, Daggett V (2008) Formation of ice-like water structure on the surface of an antifreeze protein. J Phys Chem B 112:6193–6202

Sonoike K (1996) Photoinhibition of photosystem I: its physiological significance in the chilling sensitivity of plants. Plant Cell Physiol 37:239–247

Srivastava R, Chen Y, Deng Y, Brandizzi F, Howell SH (2012) Elements proximal to and within the transmembrane domain mediate the organelle-to-organelle movement of bZIP28 under ER stress conditions. Plant J 70(6):1033–1042

Srivastava R, Deng Y, Howell SH (2014) Stress sensing in plants by an ER stress sensor/transducer, bZIP28. Front Plant Sci 5:59

Tarczynski MC, Jensen R, Bohnert HJ (1993) Stress protection of transgenic tobacco by production of the osmolyte mannitol. Science 259:508–510

Turner A, Arellano E, Kozloff LM (1991) Components of ice nucleation structures of bacteria. J Bacteriol 173:6515–6527

Vierling E (1991) The roles of heat shock proteins in plants. Annu Rev Plant Physiol Plant Mol Biol 42:579–620

Vogg G, Heim R, Gotschy B, Beck E, Hansen J (1998) Frost hardening and photosynthetic performance of Scots pine (Pinus sylvestris L.). II Seasonal changes in the fluidity of thylakoid membranes. Planta 204:201–206

Wang W, Vinocur B, Shoseyov O, Altman A (2004) Role of plant heat-shock proteins and molecular chaperones in the abiotic stress response. Trends Plant Sci 9:244–252

Wang D, Kubawara C, Endoh K, Fukushi Y, Fujikawa S, Arakawa K (2013) Supercooling-facilitating hydrolyzable tannins isolated from xylem tissues of Cercidiphyllum japonicum. In: Imai R, Yoshida M, Matsumoto N (eds) Plant and microbe adaptations to cold in a changing world. Springer, Berlin. pp 179–188

Wigge PA (2013) Ambient temperature signalling in plants. Curr Opin Plant Biol 16:661–666

Wisniewski M, Gusta L, Neuner G (2014) Adaptive mechanisms of freeze avoidance in plants: a brief update. Environ Exp Bot 99:133–140

Yamaguchi-Shinozaki K, Shinozaki K (2006) Transcriptional regulatory networks in cellular responses and tolerance to dehydration and cold stresses. Annu Rev Plant Biol 57:781–803

Yamamoto Y (2016) Quality control of photosystem II: the mechanisms for avoidance and tolerance of light and heat stresses are closely linked to membrane fluidity of the thylakoids. Front Plant Sci 7:1136

Zahnd C, Wyler E, Schwenk JM, Steiner D, Lawrence MC, McKern NM, Pecorari F et al (2007) A designed ankyrin repeat protein evolved to picomolar affinity to HER 2. J Mol Biol 369:1015–1028

Zhen Y, Ungerer MC (2008) Clinal variation in freezing tolerance among natural accessions of Arabidopsis thaliana. New Phytol 177:419–427

Zhu JJ, Beck E (1991) Water relations of Pachysandra leaves during freezing and thawing: evidence for a negative pressure potential alleviating freeze-dehydration stress. Plant Physiol 97:1146–1153

Oxygen Deficiency

5

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Nelumbo nucifera, the lotus flower, is a typical swamp plant in the monsoon climate of northern Australia. The rhizomes grow in oxygen-deficient mud and are supplied with oxygen via an aerenchyma. Because of crocodiles, researchers in this area should exercise caution (Kapalgam, Northern Territories). (Photo: E.-D. Schulze)

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Two thirds of the Earth's land mass can at least occasionally be flooded (e.g. the monsoon regions of South East Asia or the areas at the lower reaches of the large Siberian rivers). Thus, many plants are exposed to varying degrees of **inundation with water**. In waterlogged soils, only the roots are affected. However, sometimes even the above-ground organs can be partially or completely submerged. The duration and frequency of flooding range from continuous (for instance, in swamps), to sporadic (for instance, on riverbanks). Flooding can cause severe stress due to inhibition of energy provision, as well as drastic changes in the availability of minerals. Survival under such conditions therefore requires specific adaptations, modifications and acclimations (Bailey-Serres et al. 2012a). Pronounced differences in survival between species represent an important factor determining plant distribution on Earth. In fact, hydrologically defined niches have been suggested to structure plant communities such as those found in meadows (Silvertown et al. 1999). The influence of **waterlogging** and **submergence** as one form of extreme water availability has been on the rise over the past 50 years because, as a consequence of anthropogenic influences such as climate and land use change, the incidence of flooding events has increased six- to eightfold on all continents except for Australia (Millennium Ecosystem Assessment, cited in Bailey-Serres et al. (2012a)).

5.1 Conditions of Flooded Soil

Common soils consist of four components: soil particles, water, air and organisms (including plant roots) (Fig. 5.1). Freely draining soils can retain water only in pores with diameters smaller than 10–60 μm. Even at water saturation up to the field capacity, the air-filled pore volume is 10–30% of the total soil volume. However, in partially or permanently waterlogged soils, there are almost no air-filled pores, as the air dissolves in the soil water.

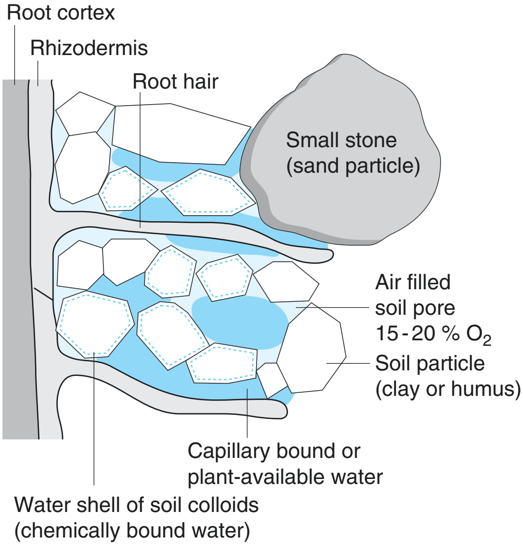

Fig. 5.1 A four-component system: root/soil organism, soil particle, soil water (solution) and soil air

Gas exchange in well-aerated soils occurs mainly through diffusion in the continuum of the air-filled pores. It is accelerated by a number of active processes in the soil and thus becomes a relatively fast process. For example, when oxygen is consumed by the respiratory activity of microorganisms and plant roots, oxygen from the atmosphere flows quickly into the soil, following the concentration gradient. As a result, the partial pressure of O_2 in the soil air, at least in pore-rich soils, remains in the range of 15–20%. Similarly, CO_2 that accumulates in the soil pores quickly leaks out from the soil. The situation is completely different when gas exchange occurs via the water-filled pores of waterlogged soils. **Fick's first law of diffusion** describes the amount of gas diffusing per unit of time (i.e. the net gas flux) as being dependent on the diffusion coefficient, D, the size of the exchange area and the concentration gradient. At the same temperature, the **diffusion coefficient of oxygen** in water is about 10,000 times (exactly 11,300 times) smaller than in air. Furthermore, oxygen has very low solubility in water (0.03 mL O_2 L^{-1} H_2O). Thus, gas exchange in waterlogged soils is very slow and oxygen becomes one of the limiting factors for growth and the development of plants. Similar considerations apply for CO_2 supply to submerged photosynthetic tissues. Photosynthesis under such conditions can, in addition, be hampered by low availability of light when the floodwater is turbid.

Long-term waterlogged soils have a negative redox potential because of the **low oxygen**

partial pressure—that is, they exhibit reducing properties. Oxygen entering such soils (e.g. through root or earthworm channels) is readily consumed by soil organisms. The dramatic decrease in the redox potential is already observed after only a few days of flooding (Fig. 5.2). Microaerophilic and anaerobic microorganisms start to grow. They mainly utilise the organic matter of the soil as an energy source and require ions as electron acceptors. When nitrate is used as an electron acceptor in a process termed nitrate respiration, it is reduced to nitrite, N_2O and finally N_2 (**denitrification**). Correspondingly, in **sulphate respiration**, sulphide is formed from SO_4^{2-}. These processes reduce the nutrient availability for plants. Similarly, oxidised forms of iron (Fe(III)) and manganese (Mn(IV)) can be reduced to their respective divalent ions. In addition, CO_2 may be used as an electron acceptor, resulting in the production of methane. Table 5.1 shows the sequence of redox reactions occurring in the soil when the redox potential decreases. Such reactions often consume protons—that is, they result in alkalinisation of the soil.

Reduced heavy metal ions such as Fe(II) and Mn(II) are more toxic to plants because their availability for uptake is higher relative to the oxidised forms. Thus, the growth of roots not only is inhibited by the lack of oxygen, which is the major stress factor, but can also be affected by toxic ions in the vicinity of the roots (Fig. 5.3).

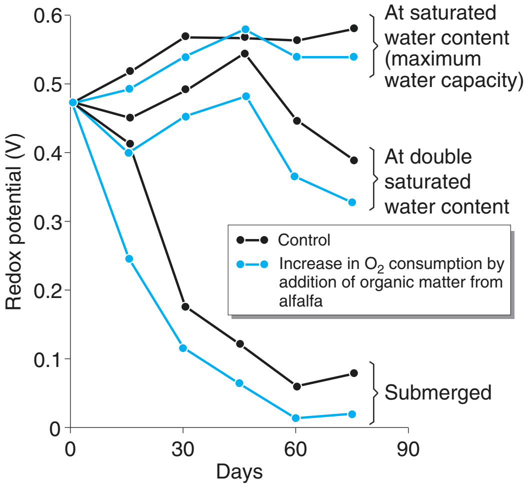

Fig. 5.2 Development of the redox potential of a loamy clay soil as influenced by the water content and the amount of organic matter. (After Amberger (1988))

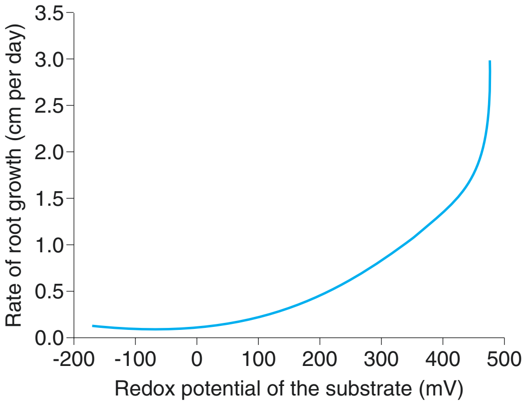

Fig. 5.3 Dependence of root growth of the grass *Spartina patens* on the redox potential of the soil. (After DeLaune et al. (1993))

Table 5.1 Sequence of soil-bound redox reactions (After Marschner (1986))

Redox reaction		Redox potential E (mV) at pH 7
Start of nitrate reduction (denitrification)	$NO_3^- \rightarrow NO_2^-$	450–550
Start of manganese reduction	$MnO_2 + 4H^+ + 2e^- \rightarrow Mn^{2+} + 2H_2O$	350–450
Absence of free oxygen (due to respiration)	$O_2 + 4H^+ + 4e^- \rightarrow 2H_2O$	350
Absence of nitrate	$(\rightarrow N_2O \rightarrow N_2)$	250
Start of Fe^{2+} formation	$Fe(OH)_3 + 3H^+ + 1e^- \rightarrow Fe^{2+} + 3H_2O$	150
Complete consumption of Fe^{3+}		120
Start of sulphate reduction	$SO_4^{2-} + 10H^+ + 8e^- \rightarrow H_2S + 4H_2O$	−50
Complete consumption of sulphate		−180
Methane formation	$CO_2 + 8H^+ + 8e^- \rightarrow CH_4 + 2H_2O$	< −180

The redox potential provides important information about the reactions in the soil, as these reactions take place in the sequence listed (i.e. sulphate is not reduced as long as Fe(III) ions are still present)

Furthermore, the symbiosis of plant roots with mycorrhizal fungi can be severely compromised in waterlogged soil, thereby further decreasing nutrient acquisition and growth.

Regarding the relationship between oxygen concentration and metabolism, a situation where biochemical reactions are not limited by partial oxygen pressure is called **normoxia**. When mitochondrial adenosine triphosphate (ATP) synthesis is affected but not completely inhibited by low O_2, it operates under **hypoxia**. In the absence of oxygen (**anoxia**), oxidative phosphorylation in the mitochondria is negligible and ATP synthesis is restricted to substrate phosphorylation in **glycolysis**. The necessary reoxidation of reduced nicotinamide adenine dinucleotide (NADH) is achieved by **fermentative pathways**.

Physiologically, **primary** and **secondary hypoxia** (or **anaerobiosis**) should be differentiated. In primary hypoxia, germination of a plant already takes place in an oxygen-deficient environment, which does not change during the whole lifetime of the plant. This applies, for example, to obligate marsh plants. Secondary hypoxia occurs when plants that normally grow in well-aerated soils are temporarily flooded. This hypoxia gradually develops, allowing plants to acclimate. Accordingly, one has to differentiate constitutively expressed mechanisms to survive prolonged inundation from those induced by flooding events. A second distinction should be made between responses to waterlogging (which affects only root respiration) and submergence (which in addition affects photosynthesis and respiration in the shoot).

5.2 Hypoxia-Induced Damage: Energy Metabolism of Plants Under Oxygen Deficiency

Root cells need to produce ATP via respiration in order to support transport processes and biosyntheses—for example, the uptake of nutrient anions from the soil solution against a negative membrane potential or the activation of sugars to build cell wall polysaccharides, respectively. The daily oxygen demands of soils during the growth period of plants are in the range of 10–20 L/m^2, depending on the density of the roots and the activity of soil microbes. There is a direct positive correlation between O_2 partial pressure and root growth. The minimum oxygen partial pressure in the soil for the growth of flooding-sensitive plants is 2–3% (about 5 kPa). Inhibition of growth under hypoxic conditions is a multifactorial phenomenon, which is basically caused by the very low efficiency of the energy metabolism. During inhibition of **mitochondrial respiration**, many heterotrophic organisms and plant tissues are able to switch to **fermentative metabolism**, which can be regarded as an acclimative response to oxygen deficiency. This type of metabolism, however, requires increased throughput of energy carriers such as glucose because of the much lower energy yield (2 moles of ATP per mole of glucose via glycolysis, compared with 34–36 moles of ATP per mole of glucose via oxidative phosphorylation). Under these conditions, reserve material is quickly consumed. Despite stimulation of glycolysis and fermentation—the so-called **Pasteur effect**—the **energy charge** of cells remains low, so during extended periods of hypoxia, or even short-term anoxia, values below 0.5 result (Fig. 5.4). These values are too low for anabolic metabolism (i.e. for growth). Inhibition of phloem transport and phloem unloading is another consequence of the low energy charge of the plant tissues. Thus, cells are depleted not only because of the faster turnover of storage material but also because of a drop in supply of photosynthates.

In addition to the energy deficit caused by hypoxia and anaerobiosis, fermentation leads to the accumulation of toxic metabolic products. The first product is **lactate**, produced by **lactate dehydrogenase** (**LDH**), which is rapidly activated upon O_2 deficiency. A rise in lactate concentrations causes acidification of the cytosol, with potentially detrimental effects on metabolism. The next acclimative response, therefore, is inactivation of LDH by acidic pH (Sect. 5.4.2). As the pH optimum of LDH is in the neutral range, it inhibits itself upon acidification of the cytosol. **Pyruvate decarboxylase** is less susceptible to acidity and therefore takes over, producing

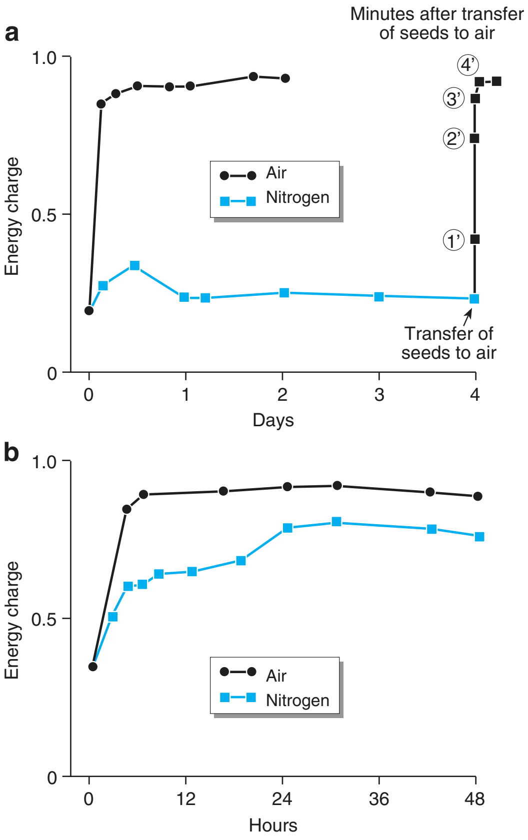

Fig. 5.4 Energy charge (EC) of lettuce seeds **a** or rice grains **b** during germination in air or under nitrogen. The energy charge of cells is usually determined by the degree of phosphorylation of the adenylate system. The following formula is applied: EC = ([ATP] + 0.5[ADP])/([ATP] + [ADP] + [AMP]). By definition, the maximum EC equals 1. Since ADP possesses only one energy-rich phosphate bond, its concentration has to be multiplied by the factor 0.5. A cell supplied with sufficient oxygen has an EC between 0.8 and 0.95. Under anaerobic conditions the energy charge may drop to 0.2. (After Pradet et al. (1985))

acetaldehyde, which is converted to **ethanol** by **alcohol dehydrogenase**. Higher concentrations of this poisonous compound destroy the selective permeability of membranes and prevent formation of proton gradients and, in turn, the gain of energy. On the other hand, ethanol easily permeates through cellular membranes and cell walls and thus only rarely reaches damaging concentrations of 50–100 nM in the cell. This limits toxicity but results in a loss of reduced carbon. Acetaldehyde, the biochemical precursor of ethanol, is much more toxic than ethanol but is usually reduced immediately. It accumulates only when alcohol dehydrogenase is nonfunctional or switched off by mutation or regulation, respectively.

Fine root systems and root meristems are particularly sensitive to oxygen deficiency. In species not tolerant of flooding, those parts of the root system used for water and ion uptake die off at oxygen partial pressures below 0.5–5 kPa and, as a consequence, the plant becomes stressed as if exposed to drought even though it is standing in water. This is indicated by stomatal closure. The rates of photosynthesis and growth decrease. Finally, the plants become stunted, while their leaves show strong **epinasty** (downward bending of the leaves and petioles because of increased relative growth of the upper side; this response is hypothesised to limit transpirational water loss because exposure to light is reduced). Such phenomena are often observed in indoor plants that are watered too much. Hypoxia in the water-saturated soil leads to death of the root system and withering of the shoot. In fact, most plants are more sensitive to flooding than to **desiccation**.

5.3 Natural Variation in the Ability to Endure Inundation by Water

Strong variation exists in the ability to withstand conditions of low oxygen availability. Many terrestrial plant species, including nearly all crops, are sensitive and do not survive longer than a few days of waterlogging. At the other extreme are plants adapted to life in **wetlands** (swamps, marshes, bogs, etc.), such as *Iris pseudacorus*, *Typha latifolia*, *Phragmites australis* and *Rorippa sylvestris*. They can tolerate submergence for months (Bailey-Serres et al. 2012b) and thus are adapted to primary hypoxia. Many other species show moderate tolerance of secondary hypoxia that reflects the hydrological signature of their natural environments—that is, variation in flooding tolerance determines, to a large extent, the distribution of plant species in the many areas worldwide that can be exposed to flooding. This can easily be seen in **riparian vegetation**, which shows pronounced **zonation** attributable to variation in **flooding tolerance**. A well-documented case is represented by the genus *Rumex*. It comprises species that are more hypoxia tolerant (e.g. *R. maritimus* and *R. palustris*) and thrive in zones prone to extended flooding—for instance, in the Rhine Valley (Fig. 5.5, Table 5.2)—as well as more hypoxia-sensitive species (e.g. *R. acetosa* and *R. acetosella*), which are found in zones with less frequent and lower-amplitude flooding events. Similarly, certain tree species (e.g. of the genera *Alnus*, *Populus*, *Salix* and *Quercus*) dominate along rivers and in alluvial forests.

In contrast to most cultivated plants, rice is flooding tolerant, and lowland rice varieties are normally grown in paddy fields (i.e. parcels of land covered with water 5–50 cm deep). Still, considerable intraspecific variation exists. Several low-yielding landraces are able to withstand particularly severe floods. Others can be directly planted as seeds into shallow paddies and develop despite low oxygen availability (Bailey-Serres and Voesenek 2008) (Sect. 5.6).

A wide range of mechanisms explains the distribution of plants in flood-prone environments. Some species (e.g. *Chenopodium rubrum*) are able to circumvent the adverse effects of hypoxia by completing their life cycle between floods—which in many habitats occur with certain regularity—and by enduring flooding events as dormant life

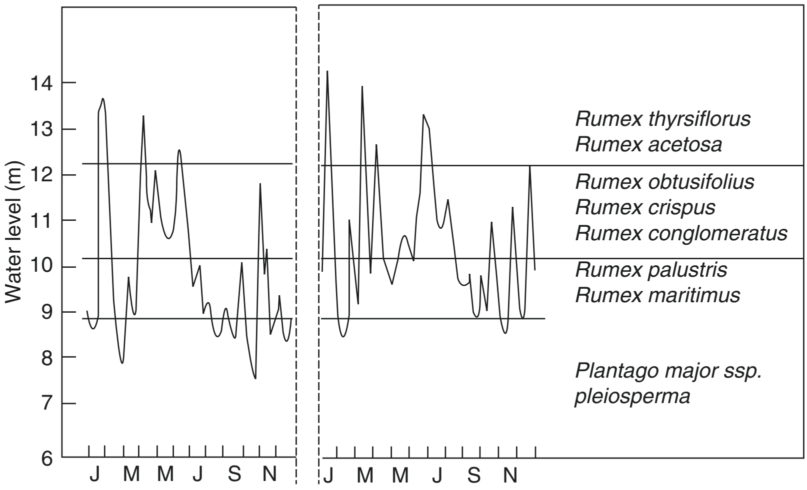

Fig. 5.5 Water level changes of the Rhine river near Nijmegen (the Netherlands) over 2 years, and vertical zonation of species differing in submergence tolerance. (Redrawn after Blom et al. (1993))

Table 5.2 Effect of flooding on biomass production and on nutrient content of the leaves of two flooding-sensitive representatives and one flooding-tolerant representative of the genus *Rumex* (After Laan et al. (1989))

Species/ conditions for growth	Dry weight of shoot (g)	Nutrient content of leaves (μmol g^{-1} dry weight)				
		Nitrogen	Phosphorus	Sodium	Calcium	Magnesium
R. thyrsiflorus						
Dry site	15.2 ± 1.4	1878 ± 45	143 ± 10	1238 ± 37	323 ± 11	435 ± 22
Flooded site	7.2 ± 1.4	1006 ± 64	44 ± 2	355 ± 15	190 ± 2	218 ± 3
R. crispus						
Dry site	13.6 ± 1.4	1372 ± 54	90 ± 5	857 ± 39	532 ±27	311 ± 7
Flooded site	12.7 ± 2.5	702 ± 35	58 ± 10	347 ± 23	315 ± 13	160 ± 8
R. maritimus						
Dry site	24.8 ± 2.6	1018 ± 91	59 ± 2	478 ± 11	615 ± 19	401 ± 4
Flooded site	25.4 ± 3.9	1052 ± 52	59 ± 2	272 ± 10	761 ± 40	398 ± 11

The data are average values of five identical experiments ± standard deviations

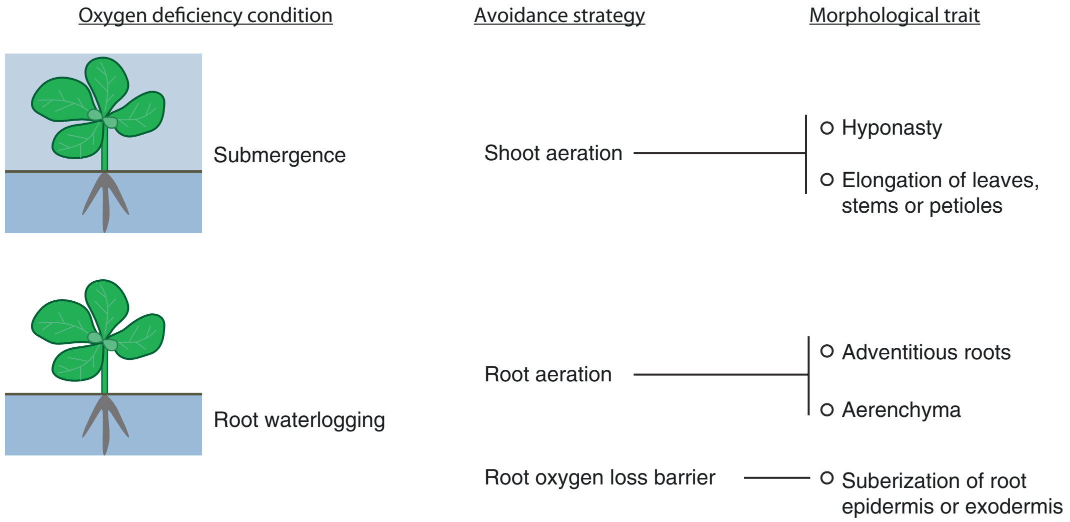

Fig. 5.6 Morphological and developmental adaptations or acclimative modifications that help flooding-tolerant plant species avoid anoxic conditions (for details, Sect. 5.4.1)

stages (Blom and Voesenek 1996). Most other plants show morphological, anatomical, developmental and metabolic characteristics that help them to avoid or truly tolerate oxygen deprivation (Voesenek and Bailey-Serres 2015) (Fig. 5.6).

Hypoxia survival traits represent a very good example of how plant stress endurance strategies have in recent years been elucidated from the organismic level to the molecular level, and from model plants to species initially studied purely ecophysiologically. This has been possible thanks to the fruitful collaboration of ecologists with molecular biologists. The current level of understanding has implications for agriculture too, as mechanistic insights can now be used in breeding programmes aimed at developing plant varieties better adapted to conditions that are becoming more prevalent because of climate change (Xu et al. 2006) (Box 5.1).

5.4 Adaptations to Flooding-Prone Habitats

5.4.1 Anatomical–Morphological Adaptations and Modifications

An obvious way to alleviate the consequences of inundation with water is the formation of structures that supply oxygen to the roots or, in the case of submergence, to the shoot as well. A hallmark of **helophytes** (marsh plants) are large intercellular channels extending from the shoot and leaves into the roots. Such gas-filled tissues (termed **aerenchyma**) maintain a sufficiently high oxygen concentration in the roots.

In plants adapted to conditions of primary hypoxia, the formation of aerenchymas is a constitutive trait. Many other hypoxia-tolerant species (both monocots and dicots) are able to develop aerenchymas in roots and the basal part of the shoot in response to flooding. Documented examples include maize (Fig. 5.7), the coastal grass *Spartina patens* or sunflower (Drew et al. 2000). Formation of aerenchyma not only guarantees the aeration of tissues but also reduces the number of oxygen-consuming cells in those tissues.

While, during development, aerenchyma arise by separation of cells at the middle lamella (**schizogeny**), inducible aerenchyma formation requires **programmed cell death** (**PCD**) and disintegration of cells (**lysigeny**). PCD does not take place in differentiated older cells. Rather, an aerenchyma is initiated near the elongation zone of the organ. The competence to produce aerenchyma has been directly linked to flooding survival. A large-scale investigation of wetland,

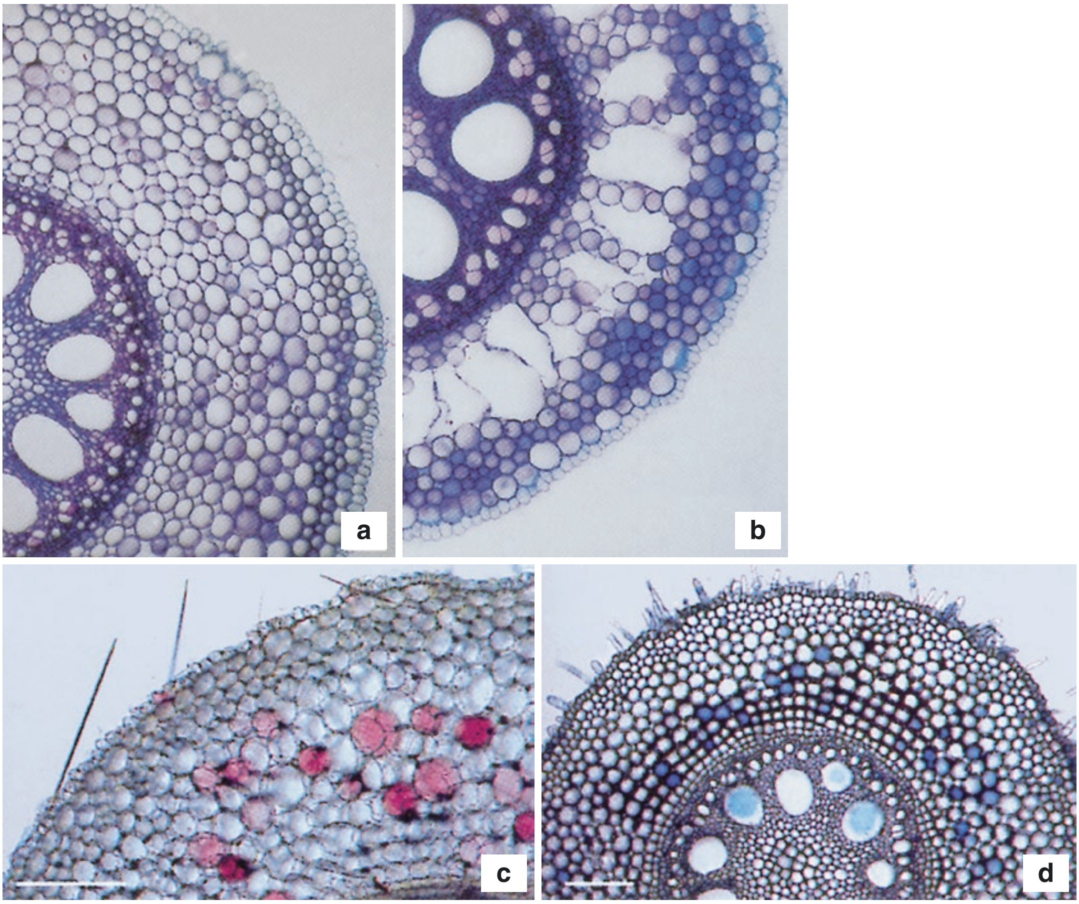

Fig. 5.7 Aerenchyma formation in a maize root: **a** normoxia; **b** hypoxia; **c** hypoxia + neutral red (disintegrating cells are coloured purple by neutral red); **d** hypoxia + Evans blue (Evans blue accumulates in dying cells). (After He et al. (1996) and Drew et al. (2000))

non-wetland and intermediate species found a clear positive correlation between flooding survival and root porosity (Justin and Armstrong 1987). Such correlations apply also to petioles when partial or complete submergence is considered (Mommer et al. 2006), showing that the formation of longitudinally interconnected pathways for gas flow extends from leaves to root tips.

Another way to enhance oxygen supply is initiation of **adventitious roots** with a well-developed aerenchyma. Some plants (e.g. maize, ash, willow, *Forsythia* and *Rumex palustris*) are able, within a few days, to produce them from basal shoot parts or the lower nodes (Fig. 5.8). These roots do not penetrate as deeply into the soil as the primary root system does into a well-aerated substrate. Formation of adventitious roots involves programmed cell death too. The epidermal cell layer covering adventitious root primordia has to be weakened to allow emergence of the adventitious roots. The mechanical force exerted by the growth stimulation of the primordial cells is sufficient to trigger programmed cell death (Steffens et al. 2012).

Oxygen reaching root cells via aerenchyma should be available for respiration and not diffuse out. Radial loss of oxygen from the interior of the root to the surrounding anaerobic soil is often reduced by the formation of a **diffusion barrier**. This is found, for instance, in deepwater rice, which produces a suberin-impregnated **exodermis**. Many wetland species show suberised and lignified secondary cell walls very close (within a few millimetres) to the root tip. If such a diffusion barrier

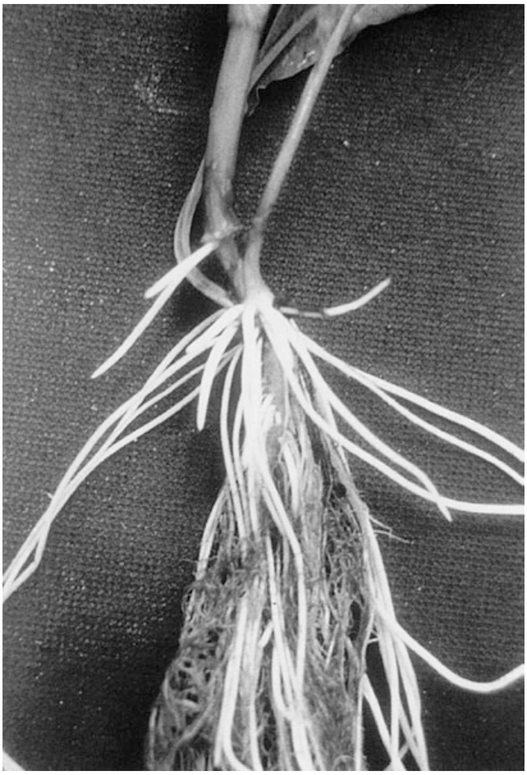

Fig. 5.8 Formation of adventitious roots in the flooding-tolerant *Rumex palustris* upon flooding of the root bed. The newly formed roots appear white as a consequence of the air-filled spaces in the aerenchyma and are thus clearly distinguished from roots grown under aerobic conditions, which senesce under prolonged hypoxia (Laan et al. 1991)

tissue is missing, oxygen leaks out of the aerenchyma to the surrounding soil, where the heavy metal ions in the immediate proximity of the roots are oxidised, forming rusty spots and root channels in pseudogley (or stagnosol), the main soil type of wetlands. The oxidation detoxifies the metals for soil organisms—an effect that can also be beneficial for the roots themselves.

Submerged plants additionally show typical leaf modifications that enhance photosynthesis and gas exchange. Leaves of *Rumex palustris* developing under water have a greater specific leaf area and a thinner cuticle, and the chloroplasts are oriented towards the leaf surface (Voesenek et al. 2006). Complete submergence of plants abolishes access to atmospheric O_2. Supply of O_2 then is largely dependent on photosynthesis, which explains why light availability can support submergence survival. Some plants, however, show a pronounced "snorkel response" under these conditions—that is, they massively elongate internodes and petioles to escape the hypoxic environment. This reaction has been termed the **low-oxygen escape syndrome** (**LOES**). Applying the definitions used throughout this book (Chap. 2), it would be more appropriately termed an avoidance syndrome, because the consequences (hypoxia) of a stress (submergence) are mitigated by expanding parts of the plant so they reach the surface and have access to oxygen. LOES has been particularly well studied in **deepwater rice**, where the submerged shoots elongate by up to 25 cm/day (Fig. 5.9). Alternatively, **hyponastic growth** of leaves (i.e. a change in the orientation of petioles to vertical) can elevate them above the water surface (Voesenek et al. 2006). Such a response is well documented for *R. palustris* (Fig. 5.10).

The strategy to escape low oxygen availability by stimulated growth involves substantial metabolic costs. For instance, cell wall material has to be synthesised, which requires carbohydrates and ATP. Especially given the metabolic constraints that submerged plants are subjected to, these investments can be fatal when the atmosphere is not reached. Indeed, it has been found that the escape is associated with a particular type of flooding—namely, prolonged but rather shallow floods that can be outgrown by internode elongation or hyponastic growth. In the Rhine Valley, elongating species are exclusively found in areas with slow drainage (Voesenek et al. 2004) (Figs. 5.5 and 5.17).

When floods are more transient or deep, escape via accelerated growth as an inducible avoidance strategy is not viable. Instead, species and genotypes exposed to submergence caused by these types of floods display an alternative strategy, the **low-oxygen quiescence syndrome** (**LOQS**). They tolerate hypoxic conditions in an **energy-saving mode**—that is, they restrict growth until the water recedes to a level where above-ground tissues are in direct contact with the atmosphere again. This has been documented best for a limited number of rice accessions

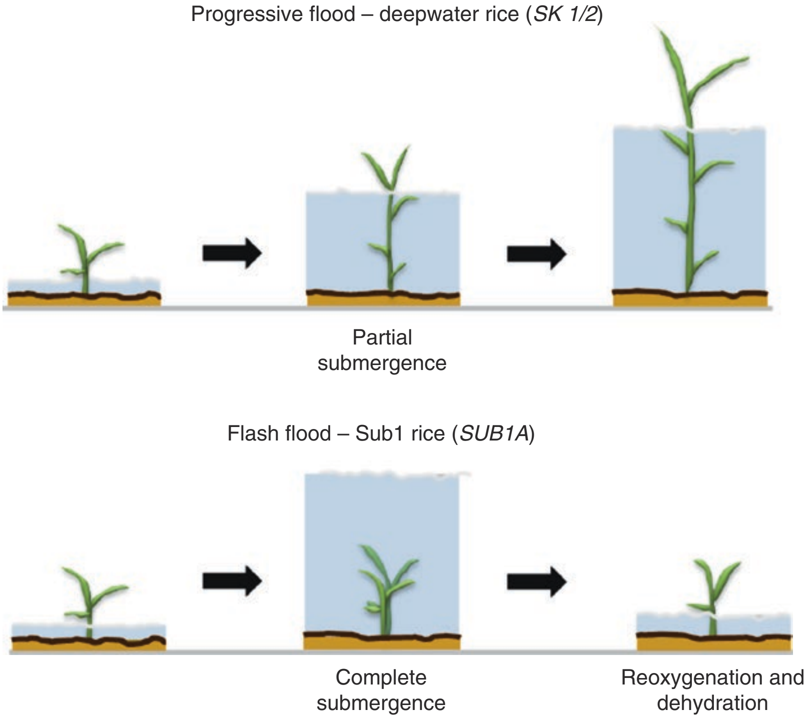

Fig. 5.9 Contrasting flooding survival strategies of rice. Among flooding-tolerant plant species, a continuum of survival strategies can be observed. The extremes of this continuum are represented here by rice accessions. *Top:* Low-oxygen escape syndrome (LOES); deepwater rice can cope with a slow progressive and long-lasting flood by rapid elongation of internodes. *Bottom:* Low-oxygen quiescence syndrome (LOQS); some rice accessions endure deep but transient flash floods through a strong reduction of growth and metabolic adjustments that maintain cell viability under anoxic conditions. LOES is controlled by *SNORKEL* genes (*SK1* and *SK2*); LOQS is controlled by the *SUB1A* locus. Interestingly, both *SK1/2* and *SUB1A* encode ethylene response factors (ERFs). These ERFs trigger contrasting responses in the respective rice accessions induced by the same signal transduction pathway (Fig. 5.14). (Modified from Bailey-Serres et al. (2012a))

Fig. 5.10 *Rumex palustris* shows hyponastic growth upon submergence. Leaves of a submerged plant (*right*) re-orient into a more vertical position. Strong petiole growth then moves the leaves towards the water surface. On the *left*, a plant that was not submerged is shown for comparison (Voesenek et al. 2006)

(Fig. 5.9) but can also be observed in many other species successfully colonising flooding-prone habitats—for example, other *Rumex* species such as *R. acetosa* (Fig. 5.17). LOES and LOQS can be regarded as the extremes of a continuum of survival strategies employed by flooding-tolerant plant species (Voesenek and Bailey-Serres 2015).

5.4.2 Biochemical Modifications

Reoxidation of NADH to NAD$^+$ in **fermentative reactions** is an absolute requirement to sustain energy provision by glycolysis in low-O$_2$ conditions, since without NAD$^+$ as a substrate, glycolytic reactions cannot take place (Sect. 5.2). Correspondingly, up-regulation of enzymes such as lactate dehydrogenase and alcohol dehydrogenase belongs to the first acclimative responses elucidated molecularly. In flooding-tolerant plants, hypoxia—which under natural flooding stress conditions precedes anoxia—triggers increases in the levels of "anaerobic polypeptides" (ANPs). This process has been intensively studied in maize roots. Besides fermentative proteins, glycolytic enzymes such as aldolase, enolase and glyceraldehyde-3-phosphate dehydrogenase have been predominantly identified (Drew 1997). Higher concentrations of these proteins are a combined result of stronger gene expression and preferential translation. The promoters of the anaerobic genes share a consensus sequence, the so-called anaerobic response element (ARE) (Christopher and Good 1996). The presence of this *cis*-element allows coordinated regulation. In addition, it has been well documented, at least for alcohol dehydrogenase (ADH) messenger RNA (mRNA), that under hypoxia stress it is more efficiently translated than mRNAs of housekeeping genes. While overall protein synthesis is strongly reduced under low-O_2 conditions in spite of continuous gene expression, ADH protein is synthesised at high rates. This is dependent on specific sequence motifs in the 5′ and 3′ untranslated regions of the *ADH* mRNA.

Inability to mount these responses is detrimental. Mutant plants with compromised fermentative and glycolytic activities are unable to acclimate to decreasing O_2 availability and thus die more rapidly when exposed to anoxia (Bailey-Serres and Voesenek 2008). This has been demonstrated for maize as an example of a flooding-tolerant species. Plants lacking ADH1 are more flooding sensitive than near-isogenic lines with functional ADH1.

An immediate threat of **lactate fermentation** is a potentially damaging drop in pH (cytosolic acidosis). Therefore, an essential component of metabolic responses to hypoxia and anoxia is the switch to **ethanol fermentation**. This is brought about by a characteristic of pyruvate decarboxylase—namely, the marked increase in activity at a pH below the usual physiological value. As a consequence, cytosolic acidification due to lactate synthesis switches on ethanol fermentation. Conversely, lactate fermentation is reduced because lactate dehydrogenase becomes progressively less active with the lowering of cytosolic pH. This type of regulation is sometimes referred to as pH-stat (Fig. 5.11). In addition, pyruvate decarboxylase gene expression is induced. An alternative way of counteracting acidification is the activation of lactate efflux in hypoxic root cells. This has been documented in maize.

Several additional metabolic responses that support survival of flooding conditions have been discovered in subsets of hypoxia-tolerant plant species (Bailey-Serres et al. 2012a). For instance, more biochemical modifications are known that help prevent some of the negative consequences of fermentation. The loss of carbon due to ethanol formation and its diffusion out of cells is reduced when pyruvate is converted to alanine instead. The amino group is provided by glutamate, which is converted to α-ketoglutarate. Metabolism of α-ketoglutarate to succinate in the citric acid cycle provides extra ATP. In addition to lactate and ethanol, rice seedlings and sweet flag (*Acorus calamus*) rhizomes mainly produce basic amino acids (asparagine, arginine and γ-aminobutyric acid (GABA)) as fermentation end products. Synthesis of GABA from glutamate releases CO_2 and consumes protons, thereby reducing the risk of cytosolic acidosis (Fig. 5.11).

Reliance solely on **glycolysis** and the ensuing **energy crisis** necessitate a suite of modifications to optimise ATP production and to minimise energy consumption. Contributing to the latter is the aforementioned down-regulation of housekeeping protein synthesis. An example of ATP-saving metabolism is a switch in sucrose mobilisation from the invertase pathway to sucrose synthase, which reduces the amount of ATP needed to channel sucrose into glycolysis from 2 moles of ATP per mole of sucrose to 1 mole of pyrophosphate per mole of sucrose (Fig. 5.11).

Because of the low ATP gain of glycolysis in comparison with mitochondrial respiration, energy provision under O_2 deficiency is dependent on the rapid **mobilisation of starch** and other reserves. However, in accordance with the contrasting escape and quiescence strategies, flooded plants differ in the rate of starch mobilisation. Two different metabolic modes of anoxia

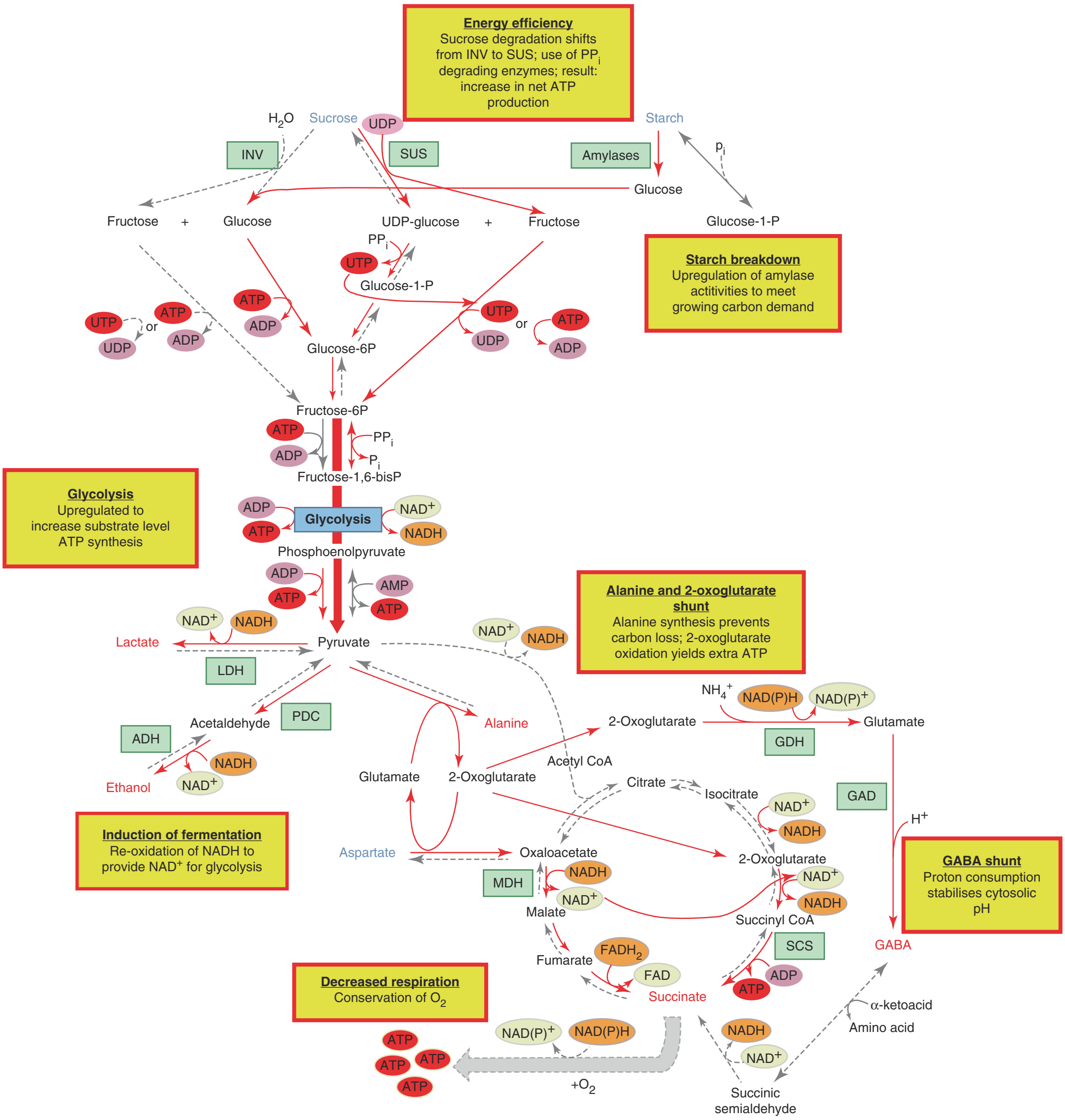

Fig. 5.11 Metabolic adjustments under hypoxic conditions. When respiration is decreased because of reduced oxygen availability, metabolic changes occur that maximise substrate-level adenosine triphosphate (ATP) production and counteract negative consequences of this shift. The processes that are shown have been reported in flooding-tolerant plant species. Please note that they do not necessarily occur all or with the same rates in every species. Sucrose metabolism may be stimulated to meet an increase in carbon demand. Flux through glycolysis is enhanced to at least partially compensate for the much lower ATP yield compared to respiration. Lactate and ethanol fermentation provide nicotinamide adenine dinucleotide (NAD$^+$) to maintain glycolytic activity. Alanine production reduces the carbon loss of ethanol fermentation. The γ-aminobutyric acid (GABA) shunt consumes protons and thus stabilises cytosolic pH (which can be lowered by lactate fermentation). *Yellow boxes* summarise prominent metabolic adjustments; *red lines* indicate pathways enhanced during hypoxia; *grey dashed lines* indicate reactions that are inhibited during hypoxia. Metabolites that accumulate under these conditions are shown in *red*; metabolites that decrease in abundance are shown in *blue*; important enzymes are shown in *green boxes*. *ADH* alcohol dehydrogenase, *GAD* glutamic acid decarboxylase, *GDH* glutamate dehydrogenase, *INV* invertase, *LDH* lactate dehydrogenase, *MDH* malate dehydrogenase, *PDC* pyruvate decarboxylase, *SCS* succinyl CoA ligase, *SUS* sucrose synthase. (Modified from Bailey-Serres et al. (2012a))

tolerance can be distinguished, one based on high rates of anaerobic carbohydrate metabolism to supply ATP (energy consumption), and one based on reduced rates of anaerobic carbohydrate metabolism (energy saving) allowing a low rate of energy provision to be sustained for extended periods (Gibbs and Greenway 2003). Over time, many O_2-deprived cells move from the first to the second strategy.

Differences in the ability to grow in conditions of primary hypoxia are already apparent at the germination stage and are associated with starch metabolism. Neither wheat nor barley seeds are able to germinate under anaerobic conditions, but rice can because of differences in starch mobilisation (Fig. 5.4). Dry cereal seeds contain reserve carbohydrates, mainly in the form of starch. In order to germinate, they require catabolising enzymes: α- and β-amylase, amylopectin-debranching enzymes and α-glucosidases (maltase, diastase). In the rice grain, starch debranching enzymes and α-glucosidases are present as inactive precursors, which are activated during germination, even without oxygen. Upon germination in the absence of oxygen, α- and β-amylases are synthesised de novo (Guglielminetti et al. 1995). This happens during the first 2 days of germination when the soluble carbohydrates already present serve as the energy source. After this, starch-catabolising enzymes become active, starch is hydrolytically degraded and the degradation products become available for further metabolism, predominantly as glucose-6-P and fructose-6-P.

An additional aspect of metabolism under hypoxic conditions is post-anoxic stress. Tissues tolerating hypoxic stress are often damaged by subsequent aeration because the sudden availability of oxygen triggers reactive oxygen species (ROS) production (Chap. 2, Sect. 2.2). Cells that are metabolically acclimated to hypoxic or anoxic conditions have a comparatively negative redox potential—that is, high electron pressure from a high NADH to NAD^+ ratio. In the presence of O_2 this leads to oxygen reduction and to the formation of ROS. During the hypoxic phase, activities of enzymes detoxifying ROS are decreased and the pools of scavenger metabolites are reduced, so the tissue is not capable of coping with increased oxidative stress. However, some plants (e.g. *Iris pseudacorus*, an ornamental aquatic plant native to Europe, western Asia and northern Africa but invasive in the USA) are known to tolerate post-anoxic stress well, owing to the up-regulation of enzymes such as superoxide dismutase in response to hypoxia.

5.5 Sensing of Flooding and Ensuing Signal Transduction

Elongation growth, programmed cell death and metabolic adjustments all represent acclimations and modifications that are activated upon waterlogging and/or submergence, and often depend on changes in gene expression. This clearly implies the existence of sensing and signalling mechanisms. The gaseous hormone **ethylene** plays a central role as a response mediator under O_2 deficiency. The key modifications—aerenchyma formation, adventitious root emergence, hyponastic growth and stem elongation—are all controlled by ethylene as the trigger. Ethylene is constitutively produced in all cells of a plant. Upon flooding, ethylene immediately (within 1 h) accumulates in and around roots and submerged shoots because of the strongly reduced gas exchange under water. Thus, it represents an early and very reliable indicator of flooding. As detailed in Sect. 5.6, ethylene is employed for controlling contrasting strategies via the regulation of differential gene expression through **ethylene response factors** (**ERFs**).

5.5.1 Ethylene Signal Transduction

The simple alkene ethylene regulates a multitude of developmental processes in plants, including seed germination, leaf abscission and fruit ripening, as well as many responses to abiotic and biotic stresses. The **ethylene signalling** pathway has been elucidated in *Arabidopsis thaliana* (Fig. 5.12). In dark-grown *A. thaliana* seedlings, ethylene induces the so-called **triple response**:

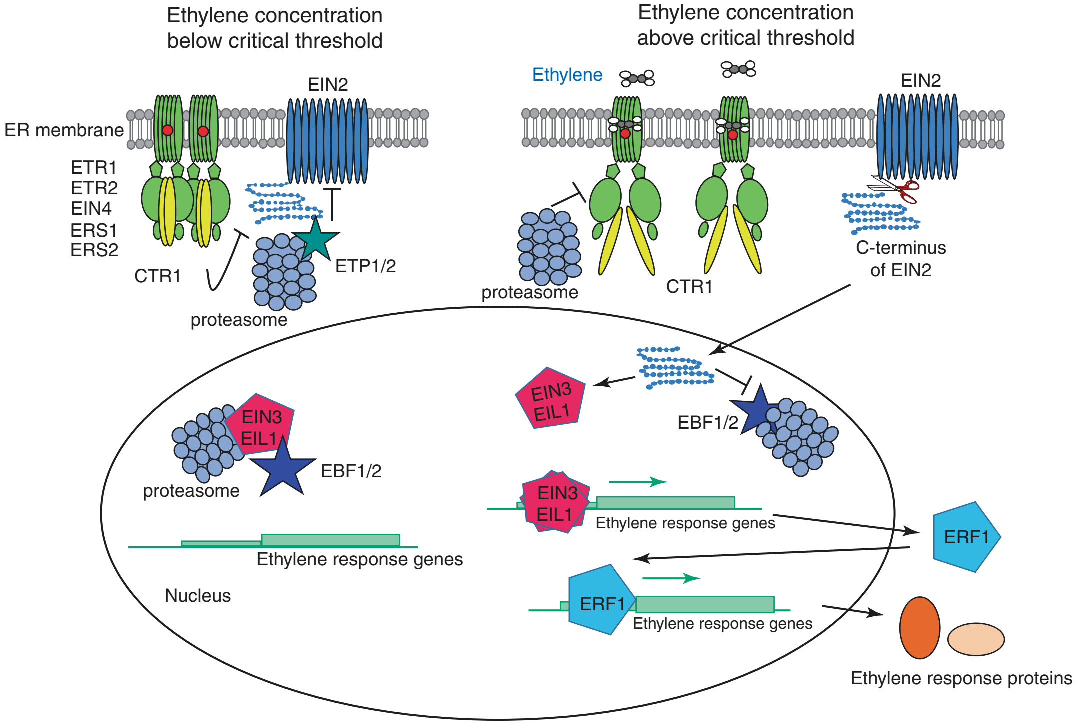

Fig. 5.12 Ethylene signal transduction. According to the current model of ethylene signal transduction in *Arabidopsis thaliana*, the five ethylene receptors (ETR1, ERS1, ETR2, ERS2 and EIN4) (shown as *green structures*; two receptors are shown exemplarily) reside in the membrane of the endoplasmic reticulum as homodimers. Copper (shown as *red circles*) serves as a cofactor for ethylene binding. The ethylene receptors are negative regulators. In the absence of a critical ethylene concentration (*left side*), the receptors activate the kinase CTR1 (shown in *yellow*), which suppresses the response. The positive regulator EIN2 (shown in *blue*) is inactivated by phosphorylation through CTR1 and is tagged for degradation in the 26S proteasome by the F-box proteins ETP1 and ETP2. Two other F-box proteins, EBF1 and EBF2, mediate degradation of the transcription factors EIN3 and EIL1 (shown in *red*) in the nucleus. No transcription of the ethylene response genes occurs. When the ethylene concentration rises above a critical threshold—for example, because of strongly reduced diffusion out of plant tissues into flooded soil—the receptors bind the hormone and become inactivated. This switches off CTR1 and prevents the phosphorylation of EIN2. The C-terminal end of EIN2 moves to the nucleus after cleavage, stabilises the transcription factors EIN3/EIL1 and induces degradation of EBF1/2. The transcription factors dimerise and bind to *cis* elements in the promoters of ethylene response genes such as *ERF1*, thereby activating their expression. ERF1 and other products of early genes then activate expression of hundreds of additional ethylene response genes. Their combined activities bring about acclimative changes in morphology and metabolism. (Modified from Merchante et al. (2013))

an increased apical hook of the cotyledons, thickening of the hypocotyl instead of extension growth, and reduced root elongation. The triple response is easy to score and allows the isolation of mutants showing either ethylene insensitivity (*etr*, *ein*) or constitutive responses in the absence of ethylene (*ctr*). Molecular analysis of these mutants has defined the core pathway of ethylene signalling, which has since been found to be highly conserved in the plant kingdom.

The ethylene signal is perceived by **ethylene receptors**. They share sequence similarity with the bacterial two-component histidine kinases, which indicates their evolutionary origin. Interaction with the extremely simple ligand C_2H_4 requires Cu as a cofactor. Apparently, all terrestrial plants, including mosses, possess several receptors that can homodimerise and form higher order complexes. *A. thaliana* has five ethylene receptors, with ETR1 being the most studied. Ethylene receptors are negative regulators that suppress responses in the absence of the signal. They do this by activating another negative regulator, the serine/threonine kinase CTR1, which inactivates the next downstream component, EIN2, through phosphorylation of its C-terminus (Fig. 5.12).

Ethylene receptors reside in the membrane of the endoplasmic reticulum. This is possible because ethylene freely diffuses through aqueous and lipid phases. Upon binding of the ligand, the receptors become inactivated and switch off CTR1. The positive regulator EIN2 is thus no longer phosphorylated, which triggers cleavage of the C-terminus of EIN2, its movement into the nucleus and the triggering of the transcriptional cascade constituting the ethylene response. The EIN2 C-terminus stabilises the transcription factors EIN3 and EIL1, which in the absence of ethylene are tagged for proteasomal degradation by EBF1 and EBF2. EIN3/EIL1 dimerise and activate transcription of genes encoding transcription factors such as the ERFs (e.g. *SUB1A* in rice; Fig. 5.14 and Box 5.1), which then activate hundreds of other ethylene-responsive genes.

This linear core pathway is modulated by various additional mechanisms. For instance, Cu supply to the ethylene receptors is dependent on the Cu-ATPase RAN1. More recently discovered regulatory components promote, for example, the transition of the ethylene receptors from the inactive to the active state (RTE1), or they influence the stability of EIN2 (ETPs) (Merchante et al. 2013).

5.5.2 Oxygen Sensing

A second indicator of flooding is, of course, the O_2 status. However, while ethylene concentrations rapidly increase in all organs upon submergence, the situation is more complex for O_2. In contrast to root cells, which can become anoxic quite rapidly, shoot O_2 levels can show a pronounced diurnal pattern with comparatively high concentrations during the light period because of photosynthetic O_2 generation (Voesenek and Sasidharan 2013). The existence of a **direct oxygen-sensing mechanism** in plants has long been debated. The alternative scenario postulated an indirect sensing of O_2 levels through the perception of, for instance, the energy charge of cells or the cytosolic pH. However, an oxygen sensor was finally discovered in *A. thaliana* (Licausi et al. 2011; Gibbs et al. 2011). It regulates ethylene response factors, which are important for low-oxygen survival. In this way the two important indicators of flooding stress are integrated. It is important to note, however, that acclimations and modifications differ with respect to the relative roles that ethylene and low O_2 play in activating them. Overall, oxygen sensing is mainly important for metabolic changes, while ethylene signalling has a broader role and is essential for most responses upon flooding, including morphological modifications.

The sensor uses the oxygen dependence of the amino (**N**)-**end rule pathway** for targeted proteolysis of proteins that carry a cysteine at the N-terminus right after the first amino acid, methionine (Fig. 5.13). Following cleavage of the methionine, the cysteine can be oxidised enzymatically. This enables arginylation, that is, the addition of an arginine residue, which tags the proteins for proteasomal degradation. Thus, under normoxic conditions in a cell, these proteins are destabilised. Among the proteins with a methionine–cysteine combination at the N-terminus in *A. thaliana* are the class VII ERFs, which mediate various hypoxia responses (Sect. 5.6). Thus, they are rapidly degraded when O_2 for the cysteine oxidation is available and cannot activate hypoxia responses. In contrast, under low-oxygen conditions, this oxidation of the cysteine no longer occurs, resulting in greater stability of the response factors and the activation of metabolic and developmental changes supporting survival of flooding or submergence.

5.6 Regulation of Avoidance and Tolerance Strategies

The metabolic and morphological plasticity of flooding-tolerant plants enables a wide range of survival strategies, of which escape and quiescence can be regarded as the extreme poles. Molecular dissection of these contrasting

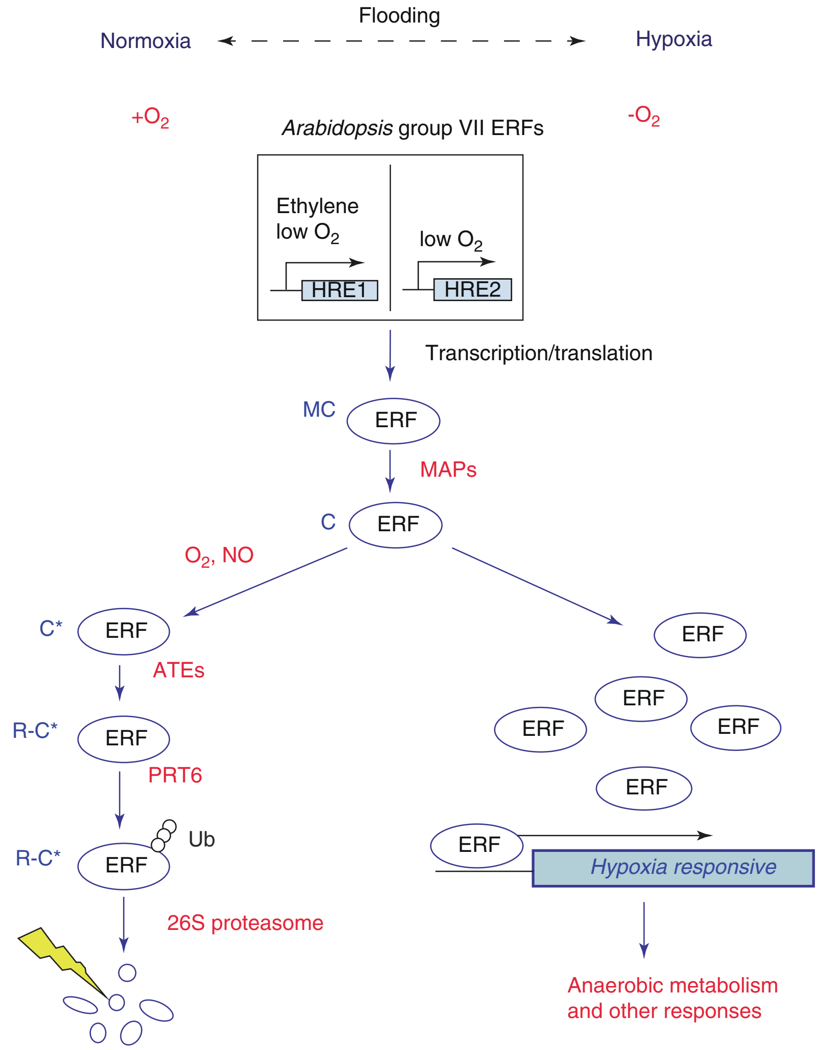

Fig. 5.13 The oxygen sensor in *Arabidopsis thaliana*. Under hypoxic conditions, ethylene signalling activates transcription of group VII ethylene response factors (ERFs; Fig. 5.12). These ERFs (HRE1 and HRE2 are shown as examples) all share the N-terminal sequence Met-Cys (MC) and are thus substrates of the N-end rule pathway. Methionine (M) is cleaved by a methionine aminopeptidase (MAP). In the presence of O_2 (normoxic conditions) or NO, the cysteine is oxidised. After addition of an arginine (R) by arginyl transfer RNA (tRNA) transferase (ATE), the protein is recognised by the E3 ligase PRT6, which tags the arginylated ERF for degradation in the 26S proteasome by adding several ubiquitins (Ub). Thus, the ERFs cannot activate expression of ethylene response genes. However, when the cellular O_2 concentration drops, the cysteine oxidation eventually cannot occur. ERFs are not degraded and now activate the hypoxia responses. (Modified from Bailey-Serres et al. (2012a))

strategies in rice has revealed that they are regulated by very similar factors. This provides direct insights into how, during evolution, successful adaptation to a variety of habitats can arise within a species or a genus. Several low-yielding rice landraces cultivated in flood-prone areas carry loci that are responsible for the rapid shoot elongation trait (*SNORKEL1* and *SNORKEL2* (*SK1* and *SK2*) (Hattori et al. 2009)) or the energy-saving mode (*SUBMERGENCE TOLERANCE1A* (*SUB1A*) (Xu et al. 2006)) (Fig. 5.9). Encoded by these loci are group VII ethylene response factors—that is, members of the family that in *A. thaliana* has been shown to be regulated by the oxygen-sensing pathway (Fig. 5.13). Thus, the integration of the ethylene signal and the O_2 sensing is utilised to trigger very different responses to oxygen deprivation through variation in the targets of ethylene and low-oxygen signalling. The underlying circuitry and its recruitment for contrasting strategies exemplify the central role of differential growth control for the adaptation to stress conditions (Chap. 2, Sect. 2.3).

Shoot growth is dependent on the plant growth hormone **gibberellic acid** (**GA**). One of its classic activities is stimulation of internode elongation. Accordingly, the *SNORKEL* genes stimulate the GA response (Fig. 5.14). In addition, ethylene triggers the decrease in the endogenous abscisic acid (ABA) level and thus

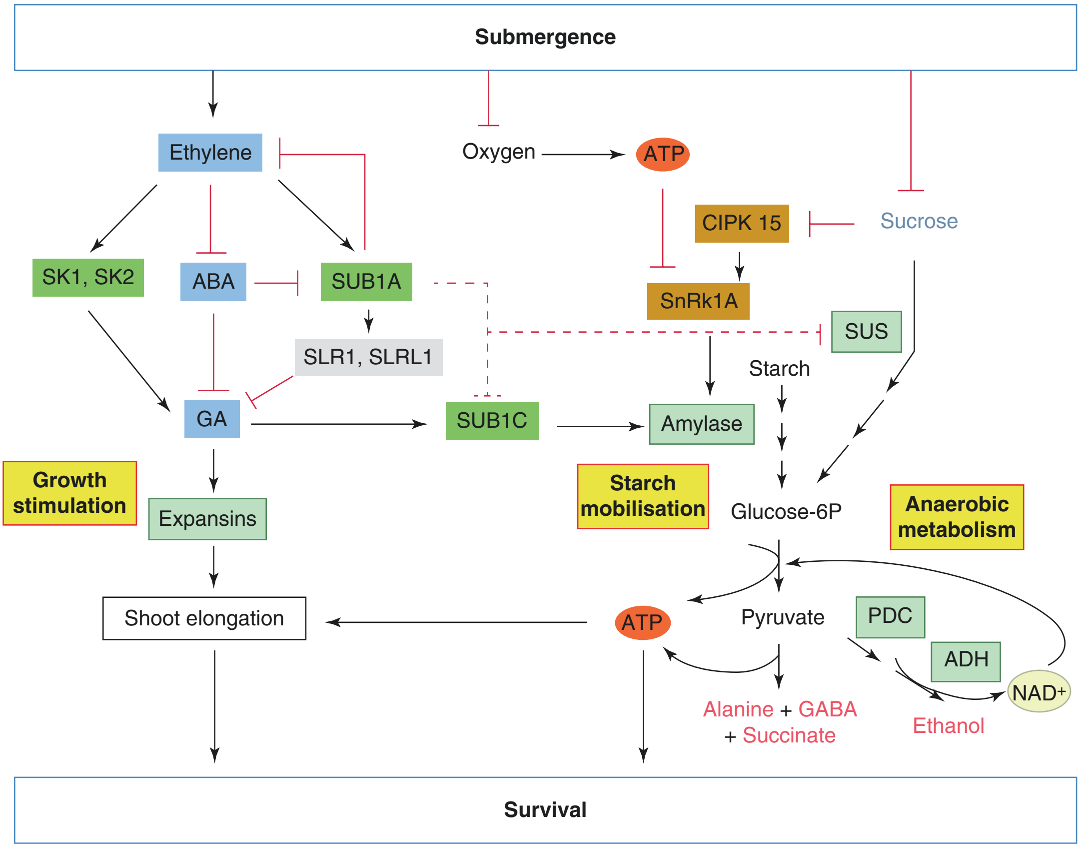

Fig. 5.14 Contrasting submergence survival strategies are mediated by ethylene response factors in rice accessions. Upon submergence of aerial organs, ethylene concentrations rise, adenosine triphosphate (ATP) becomes depleted and sucrose is rapidly consumed. These events trigger contrasting strategies in different rice genotypes: either promotion of elongation growth in deepwater rice (escape) or repression of growth in accessions tolerant of deep submergence (quiescence). The escape strategy is controlled by the ethylene response factors SNORKEL1 (SK1) and SNORKEL2 (SK2). They stimulate gibberellic acid (GA)–dependent elongation of internodes. Among the activated proteins are expansins. GA also induces another ethylene response factor, SUB1C, which activates starch mobilisation and the provision of ATP through anaerobic metabolism (Fig. 5.11; *ADH* alcohol dehydrogenase, *PDC* pyruvate decarboxylase, *SUS* sucrose synthase). Depletion of ATP and sucrose pools trigger these metabolic processes through kinases such as CIPK15 and SnRK1A. By contrast, in rice genotypes carrying the *SUB1A* gene, ethylene leads to an increased accumulation of the GA response inhibitors SLENDER RICE 1 (SLR1) and SLENDER RICE-LIKE 1 (SLRL1). Furthermore, the consumption of sucrose and starch, as well as the synthesis of ethylene, are inhibited. (Modified from Bailey-Serres and Voesenek (2010))

in turn increases the effectiveness of GA. Part of the GA response is the induction of **expansins**—small proteins that are involved in the loosening of hydrogen bonds between cellulose and hemicelluloses in the cell wall. This is a prerequisite for cell expansion. In the shoots of deepwater rice, submerged internodes accumulate considerably more expansins than those in air. The proteins occur in the intercalary meristem and in the adjacent extension zone but not in the differentiation zone (Cho and Kende 1997). Auxin also plays a role in shoot expansion: it stimulates acidification of the cell wall by activating the ATP-dependent proton pumps in the plasma membrane.

Conversely, when the *SUB1A* gene is present in rice, the GA response is inhibited through the activation of negative regulators. *SLENDER RICE 1* and a related gene in rice encode **DELLA proteins**, which repress the induction of GA response genes such as expansins. The energy conservation is further supported by reducing the mobilisation of carbohydrate reserves—for instance, through the inhibition of sucrose synthase activity. *SUB1A* also supports recovery from post-anoxic shock upon subsidence of floodwater by up-regulating antioxidant defences. The function of *SUB1A* as a major regulator of flooding responses has enabled successful breeding approaches (Box 5.1).

Box 5.1: Molecular Breeding for Enhanced Flooding Tolerance

Molecular elucidation of stress tolerance mechanisms and adaptation greatly facilitates the breeding of elite cultivars, using the available diversity. The *SUB1A* gene represents an impressive example of the potential of this approach. Some rice cultivars are highly tolerant of prolonged and complete submergence. This ability is linked to a major quantitative trait locus (QTL), *SUBMERGENCE TOLERANCE1*. It has been molecularly identified and found to carry three genes (*SUB1A*, *SUB1B* and *SUB1C*) (Fig. 5.15) encoding ethylene response factors (Xu et al. 2006). While

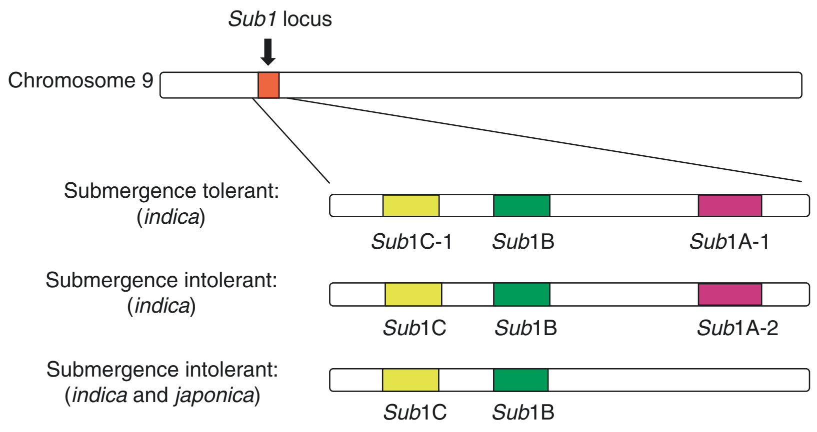

Fig. 5.15 Structure of the *SUB1* locus in rice. *SUB1* is a major quantitative trait locus explaining some of the natural variation in submergence tolerance among rice accessions. The SUB1 locus comprises a set of genes encoding ethylene response factors. They activate contrasting submergence survival strategies upon a rise in ethylene concentrations (Fig. 5.14) (Fukao et al. 2009)

SUB1B and *SUB1C* are ubiquitously present in rice cultivars, there is variation for *SUB1A*. First, it is present only in a subset of rice cultivars. Second, two different alleles have been found to be associated with submergence intolerance (*SUB1A-2*) or submergence tolerance (*SUB1A-1*). Using **marker-assisted breeding**, *SUB1* has been introgressed into several flooding-sensitive elite rice cultivars. In all cases examined, it was found that varieties can be generated that show substantial increases in flooding tolerance yet retain yield potential and other desired agronomic traits (Xu et al. 2006; Septiningsih et al. 2009) (Fig. 5.16).

Variation at the *SUB1* locus and the involvement in contrasting strategies (Fig. 5.9) suggest that duplication and divergence of group VII ERFs underlie distinctions in flooding responses in rice, as well as in many other flooding-tolerant species (Bailey-Serres and Voesenek 2010).

Fig. 5.16 Generation of more flooding-tolerant varieties by SUB1 introgression. The SUB1 haplotype from a flooding-tolerant variety (R49830, *right*) was introduced into an intolerant variety (Swarma, *left*) by marker-assisted selection, and confers submergence tolerance. In the *centre*, two individual plants selected from backcrosses that carried the *Sub1* haplotype with the least IR49830 background are shown. Fourteen-day-old seedlings were submerged for 14 days and photographed 14 days after de-submergence (Xu et al. 2006)

The differential developmental and metabolic response to ethylene is not unique for rice but conserved among flooding-tolerant plants. Species of the genus *Rumex*, as well as other plant species in the Rhine Valley floodplain, display varying degrees of flooding tolerance, and their growth behaviour can be placed at different positions along the continuum between escape and quiescence (Fig. 5.5). *R. palustris* tries to reach the atmosphere by hyponastic leaf growth (Fig. 5.10); the closely related species *R. acetosa* does not. Ethylene invariably accumulates in submerged tissues, yet only *R. palustris* shows activation of cell expansion. These differences can also be seen when more species are tested. Ethylene treatment stimulates growth in only a subset of the species (Fig. 5.17). All of them—for example, *Ranunculus sceleratus* and *Rumex maritimus* (Fig. 5.5)—belong to the same niches in the Rhine Valley. These niches are defined mostly by gradients in flooding duration and the speed of soil drying after a flooding event. The escape strategy is associated with long-lasting floods and slow drainage.

According to **genome-wide transcriptome analyses** of the two model *Rumex* species *R. palustris* and *R. acetosa*, using RNA sequencing, the differential behaviour can be associated with the activation of different processes similar to what has been found in rice (van Veen et al. 2013). Submerged *R. acetosa* undergoes metabolic reprogramming consistent with quiescence, while *R. palustris* activates photomorphogenesis and shade avoidance pathways to support the growth response (i.e. escape).

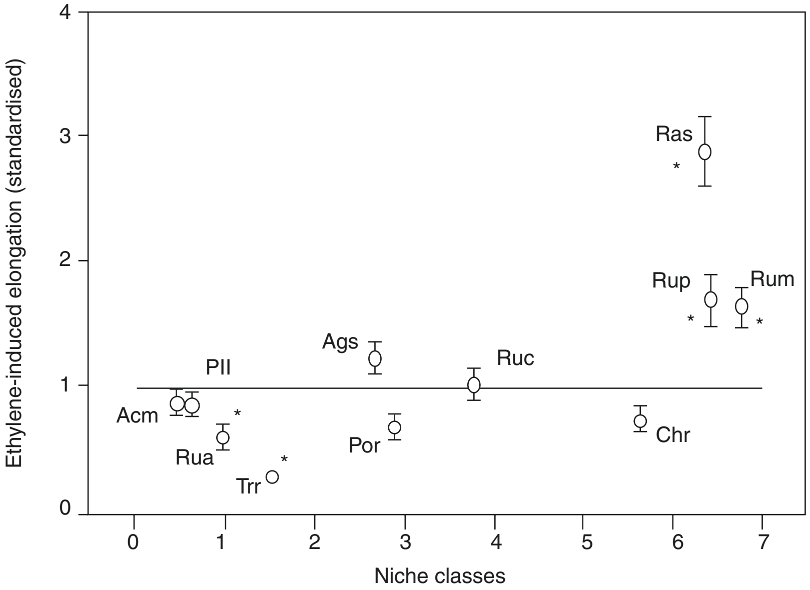

Fig. 5.17 Differential responses to ethylene in herbaceous species from floodplains of the Rhine River. For 11 species belonging to different niche classes, ethylene-induced shoot elongation (5-day treatment with air containing 10 µL/L ethylene) was determined relative to the mean elongation under control conditions (treatment with air) (standardised at 1). *Asterisks* indicate significant differences ($p < 0.05$) between ethylene and control treatments. The niche classes are characterised by differences in the duration of flooding and in the speed of run-off and drying after a flooding event. The elongating species are found in sites with long-lasting and slowly receding floods. Abbreviated species names: Acm, *Achillea millefolium*; Ags, *Agrostis stolonifera*; Chr, *Chenopodium rubrum*; Pll, *Plantago lanceolata*; Por, *Potentilla reptans*; Ras, *Ranunculus sceleratus*; Rua, *Rumex acetosa*; Ruc, *Rumex crispus*; Rum, *Rumex maritimus*; Rup, *Rumex palustris*; Trr, *Trifolium repens*. (Modified from Voesenek et al. (2004))

Summary

- Many plants are exposed to varying degrees of inundation with water. Both waterlogging and submergence cause a lack of oxygen because the diffusion of oxygen in water is about 10,000 times slower than in air. Normoxia, hypoxia and anoxia refer to conditions of sufficient oxygen supply, reduced oxygen supply affecting mitochondrial respiration, and lack of oxygen, respectively. Hypoxia and anoxia produce negative redox potentials of the soils. Under these conditions, oxidised heavy metal ions become reduced and in this form can be toxic, thereby adding to the stress caused by inundation.
- Low oxygen partial pressure affects the energy metabolism of plant organs. Adenosine triphosphate (ATP) synthesis is restricted to substrate phosphorylation in glycolysis. The necessary reoxidation of reduced nicotinamide adenine dinucleotide (NADH) is achieved by fermentative pathways but results in accumulation of the potentially toxic products lactate and ethanol. Thus, prolonged oxygen deficiency results in the death of root tissue in non-adapted plants. Adapted plants are capable of metabolic adjustments that limit the damage caused by fermentation.
- Strong variation exists in the ability to withstand conditions of low oxygen availability. Many plant species have evolved the ability to tolerate primary hypoxia—for example, helophytes (swamp-inhabiting plants) are able to thrive in continuously oxygen-limited conditions. Other species withstand secondary hypoxia caused by flooding and can therefore colonise flooding-prone habitats.
- A hallmark of helophytes are aerenchyma—large intercellular channels extending from the shoot and leaves into the roots. Such gas-filled

tissues supply roots and rhizomes with oxygen. The formation of suberin-impregnated diffusion barriers in the root limits oxygen loss to the surrounding soil or water.

- Secondary hypoxia triggers morphological, anatomical, developmental and metabolic changes that help the plant avoid or truly tolerate oxygen deprivation. The gaseous phytohormone ethylene plays a key role in activating these processes. Its concentration rises rapidly in roots and submerged shoots upon flooding, because of the strongly reduced gas exchange under water.
- The inducible formation of aerenchyma and adventitious roots provides better root aeration. Both processes require programmed cell death.
- The extremes of a continuum of survival strategies employed by submergence-tolerant plant species are the low-oxygen escape syndrome (LOES) and the low-oxygen quiescence syndrome (LOQS). LOES refers to a “snorkel response”—the stimulation of rapid shoot elongation or hyponastic growth of leaves in order to reach the water surface. LOQS, on the other hand, summarises mechanisms that suppress growth and restrict energy consumption to survive until a flood recedes. Both extremes can be observed within one species (e.g. rice) or between closely related species (e.g. in the genus *Rumex*).
- Growth stimulation in LOES is dependent on another phytohormone, gibberellic acid. In LOQS the gibberellic acid response is inhibited and the metabolism of carbohydrate reserves is suppressed.
- Ethylene controls these contrasting strategies via the regulation of differential gene expression through ethylene response factors (ERFs). The presence of particular sets of *ERF* genes in the genome determines the survival strategy. Therefore, transfer of alleles via marker-assisted breeding can confer increases in flooding tolerance.
- Ethylene signal transduction proceeds via the inactivation of ethylene receptors, which act as negative regulators of signalling.
- Ethylene signalling is integrated with a second mode of perception, the sensing of intracellular oxygen levels. Oxygen sensing depends on the N-end rule pathway, an O_2-dependent protein degradation pathway that results in the rapid degradation of ERFs and other proteins when the oxygen supply is sufficient.

References

Amberger A. Pflanzenernährung, 3rd edn, Ulmer. 1988.

Bailey-Serres J, Fukao T, Gibbs DJ et al (2012a) Making sense of low oxygen sensing. Trends Plant Sci 17:129–138.

Bailey-Serres J, Lee SC, Brinton E (2012b) Waterproofing crops: effective flooding survival strategies. Plant Physiol 160:1698–1709.

Bailey-Serres J, Voesenek LA (2010) Life in the balance: a signaling network controlling survival of flooding. Curr Opin Plant Biol 13:489–494.

Bailey-Serres J, Voesenek LACJ (2008) Flooding stress: acclimations and genetic diversity. Annu Rev Plant Biol 59:313–339.

Blom C, Voesenek L (1996) Flooding: the survival strategies of plants. Trends Ecol Evol 11:290–295.

Blom CWPM, Voesenek LACJ, van der Sman AJM (1993) Responses to total submergence in tolerant and intolerant riverside species. In: Jackson MB, Black CR (eds) Interacting stresses on plants in a changing climate, NATO ASI Series 1, vol 16. Springer, Berlin.

Cho HT, Kende H (1997) Expansins in deepwater rice internodes. Plant Physiol 113:1137–1143.

Christopher ME, Good AG (1996) Characterization of hypoxically inducible lactate dehydrogenase in maize. Plant Physiol 112:1015–1022.

DeLaune RD, Pezeshki SR, Patrick WH Jr (1993) Response of coastal vegetation to flooding and salinity: a case study in the rapidly subsiding Mississippi River deltaic plain, USA. In: Jackson MB, Black CR (eds) Interacting stresses on plants in a changing climate, NATO ASI Series 1, vol 16. Springer, Berlin. pp 211–229.

Drew MC (1997) Oxygen deficiency and root metabolism: injury and acclimation under hypoxia and anoxia. Annu Rev Plant Physiol Plant Mol Biol 48:223–250.

Drew MC, He CJ, Morgan PW (2000) Programmed cell death and aerenchyma formation in roots. Trends Plant Sci 5:123–127.

Fukao T, Harris T, Bailey-Serres J (2009) Evolutionary analysis of the Sub1 gene cluster that confers submergence tolerance to domesticated rice. Ann Bot 103:143–150.

Gibbs DJ, Lee SC, Isa NM et al (2011) Homeostatic response to hypoxia is regulated by the N-end rule pathway in plants. Nature 479:415–418.

Gibbs J, Greenway H (2003) Mechanisms of anoxia tolerance in plants. I. Growth, survival and anaerobic catabolism. Funct Plant Biol 30:1–47.

Guglielminetti L, Perata P, Alpi A (1995) Effect of anoxia on carbohydrate metabolism in rice seedlings. Plant Physiol 108:735–741.

Hattori Y, Nagai K, Furukawa S et al (2009) The ethylene response factors snorkel1 and snorkel2 allow rice to adapt to deep water. Nature 460:1026–1030.

He CJ, Morgan PW, Drew MC (1996) Transduction of an ethylene signal is required for cell death and lysis in the root cortex of maize during aerenchyma formation induced by hypoxia. Plant Physiol 112:463–472.

Justin SHFW, Armstrong W (1987) The anatomical characteristics of roots and plant response to soil flooding. New Phytol 106:465–495.

Laan P, Clement J, Blom C (1991) Growth and development of Rumex roots as affected by hypoxic and anoxic conditions. Plant Soil 136:145–151.

Laan P, Smolders A, Blom C, Armstrong W (1989) The relative roles of internal aeration, radial oxygen losses, iron exclusion and nutrient balances in flood tolerance of Rumex species. Acta Bot Neerl 38:131–145.

Licausi F, Kosmacz M, Weits DA et al (2011) Oxygen sensing in plants is mediated by an N-end rule pathway for protein destabilization. Nature 479:419–422.

Marschner H (1986) Mineral nutrition of higher plants. Academic Press, San Diego.

Merchante C, Alonso JM, Stepanova AN (2013) Ethylene signaling: simple ligand, complex regulation. Curr Opin Plant Biol 16:554–560.

Mommer L, Lenssen JPM, Huber H et al (2006) Ecophysiological determinants of plant performance under flooding: a comparative study of seven plant families. J Ecol 94:1117–1129.

Pradet A, Mocquot B, Raymond P, Morisset C, Aspart L, Delseny M (1985) Energy metabolism and synthesis of nucleic acids and protein under anoxic stress. In: Key JL, Kosuge T (eds) Cellular and molecular biology of plant stress. Liss, New York. pp227–245.

Septiningsih EM, Pamplona AM, Sanchez DL et al (2009) Development of submergence-tolerant rice cultivars: the Sub1 locus and beyond. Ann Bot 103:151–160.

Silvertown J, Dodd ME, Gowing DJG, Mountford JO (1999) Hydrologically defined niches reveal a basis for species richness in plant communities. Nature 400:61–63.

Steffens B, Kovalev A, Gorb SN, Sauter M (2012) Emerging roots alter epidermal cell fate through mechanical and reactive oxygen species signaling. Plant Cell 24: 3296–3306.

van Veen H, Mustroph A, Barding GA et al (2013) Two Rumex species from contrasting hydrological niches regulate flooding tolerance through distinct mechanisms. Plant Cell 25:4691–4707.

Voesenek LACJ, Colmer TD, Pierik R et al (2006) How plants cope with complete submergence. New Phytol 170:213–226.

Voesenek LACJ, Sasidharan R (2013) Ethylene—and oxygen signalling—drive plant survival during flooding. Plant Biol 15:426–435.

Voesenek LACJ, Rijnders J, Peeters AJM et al (2004) Plant hormones regulate fast shoot elongation under water: from genes to communities. Ecology 85:16–27.

Voesenek LACJ, Bailey-Serres J (2015) Flood adaptive traits and processes: an overview. New Phytol 206:57–73.

Xu K, Xu X, Fukao T et al (2006) Sub1A is an ethylene-response-factor-like gene that confers submergence tolerance to rice. Nature 442:705–708.

6

Water Deficiency (Drought)

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A flowering ocotillo (*Fouquieria splendens*) in the Anza-Borrego desert in Southern California. The picture was taken in spring after a rainfall. Ocotillos escape unfavourable conditions. They appear almost dead during the extended dry periods but quickly form a large number of small leaves when water becomes available. The red-orange flowers are pollinated by hummingbirds and bees. (Photo: Stephan Clemens)

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Water accounts for up to 90% of a plant's fresh weight. Furthermore, since the experiments of Stephan Hales in the eighteenth century it has been known that a large fraction of the water taken up by plants from the soil is lost to the air, that is, it is transpired. This water loss is an inevitable consequence of the need for terrestrial plants to take up CO_2 from the atmosphere. For every molecule of CO_2 that enters a plant through stomata by diffusion, several hundred molecules of H_2O leave the plant via this same pathway. The concentration gradient across the leaf surface is much greater for water loss than for CO_2 uptake, but a membrane or other material that would allow selective passage of CO_2 has never evolved in plants. Thus, not only is water the most abundant of the resources needed by a plant for functioning and growth—a characteristic that plants share with animals—but CO_2 uptake and thereby photosynthesis require large fluxes of water through the plant, which is the reason why water availability very often limits productivity (Chap. 10). The strict correlation between CO_2 uptake and water loss is sometimes referred to as the **central dilemma of plants**: dying of thirst or dying of hunger?

A second distinctive feature of plant–water relations is based on a major difference in the structure of plant and animal cells. Plant cell walls can withstand considerable **hydrostatic pressures and tensions**. The ability to build up **turgor pressure** is essential for growth via cell expansion and for the rigidity of tissues not stabilised by lignified cells.

Besides temperature, precipitation is the most dominant environmental factor determining the distribution of vegetation on the global scale. Vast differences exist between plant species in the ability to grow and reproduce in water-limited habitats, estimated to represent more than 50% of the Earth's surface area. Following a consideration of the unique properties of water, this chapter will address cellular aspects of **plant–water relations** such as the driving forces for water movement, the water conductivity of membranes and cellular responses to water scarcity. Plants synthesise a range of protective molecules, regulate their osmotic potentials and—most importantly—control the rate of water loss through stomata (Fig. 6.1). Also covered are the molecular mechanisms underlying growth responses to drought and the photosynthesis variants (**C_4 photosynthesis** and **Crassulacean Acid Metabolism** (CAM)) that result in higher **water use efficiency**, i.e., a more favourable ratio of water loss to CO_2 fixation. Plant–water relations at the whole-plant level are described in Chap. 10.

6.1 The Properties of Water

The biochemistry of life requires water in the liquid state and is thus dependent on the physicochemical properties of the water molecule. These are often referred to as anomalies (Box 6.1) and result from the **dipole nature** of the molecule $H^{\delta+}$-$O^{\delta-}$-$H^{\delta+}$ (Fig. 6.2a). The water molecule is bent (at an angle of around 104°) and therefore has an asymmetrical charge distribution. The dipoles produce **hydrogen bonds** between the individual molecules, and this guarantees a high degree of cohesion with, at the same time, low viscosity. The water molecules form flickering (mobile) clusters or aggregates, which continuously exchange individual molecules. That explains why water is in the liquid rather than the gaseous state at temperatures between 0 and 100 °C and at standard air pressure, despite the low molecular mass of the water molecule. Related consequences of the dipole nature of water are **adhesion** to polar surfaces such as cell

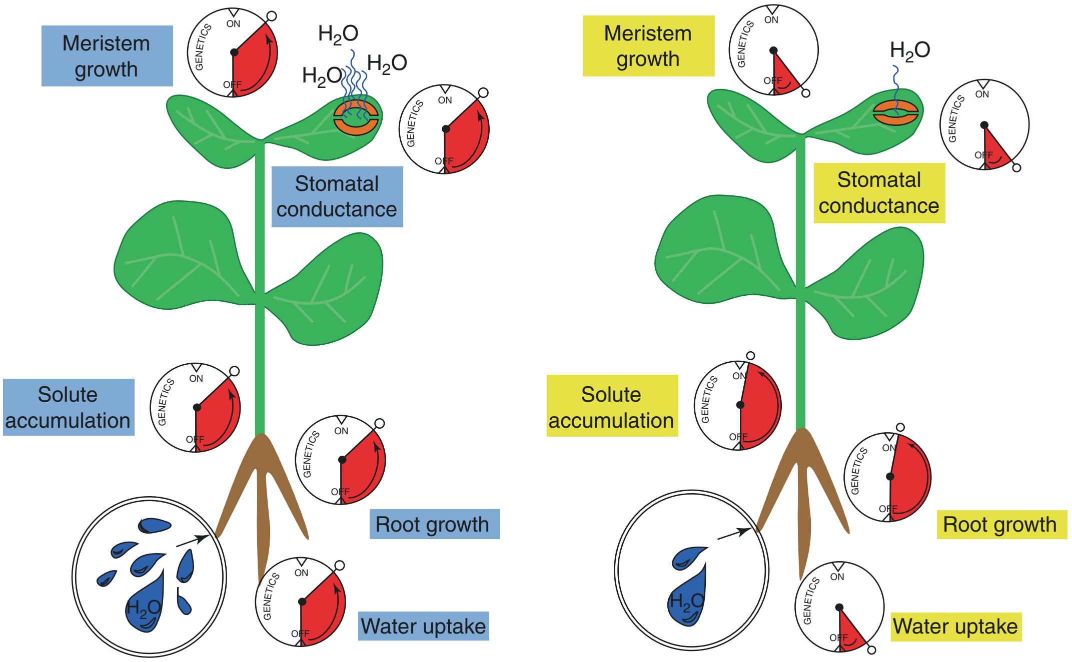


Fig. 6.1 A plant before (*left*) and during (*right*) drought stress. Major control points of acclimation are indicated as valves. (Modified from Maggio et al. (2006))

walls, and **capillary forces** caused by the high surface tension. Adhesion, capillary forces and **cohesion**, as well as low viscosity, are decisive factors for the transport of water from roots to leaves (the **cohesion–tension theory** of water conductance; Chap. 10 and plant physiology textbooks). Another consequence of the dipole nature of the water molecule is its suitability as a solvent for polar and polarisable compounds. In addition, water exerts a structuring force in amphiphilic systems (hydrophilic–hydrophobic) giving rise to lipid micelles and contributing to the tertiary structures of proteins. Furthermore, water is a very effective heat buffer for organisms because of its relatively high heat of crystallisation (freezing avoidance) and very high heat of vaporisation (transpiration cooling). As its radiation absorption is outside the boundaries of the visible spectrum, water does not absorb visible light and thus does not interfere with photosynthesis or processes regulated by blue or red light.

Box 6.1: The Physico-chemical Properties (Anomalies) of Water

Because of their dipole nature, water molecules (Fig. 6.2a) associate via hydrogen bonds to a three-dimensional lattice (clusters, Fig. 6.2b), which is in a permanent molecular rearrangement. The physico-chemical anomalies of water (e.g. high melting and boiling temperatures in comparison with molecules such as H_2S or ethanol, Table 6.1) can be attributed to this cluster formation.

The properties of water are also the reason for hydrophobic interactions. Non-polar molecules in an aqueous environment are forced into aggregates in order to minimise the energetically unfavourable interaction with water molecules. Amphiphilic molecules (i.e. molecules with polar and non-polar groups) such as phospholipids and glycolipids form ordered structures (= biomembranes) with the hydrophilic part interacting with water molecules and the hydrophobic part excluding water (Fig. 6.2c) (Larcher 2003).

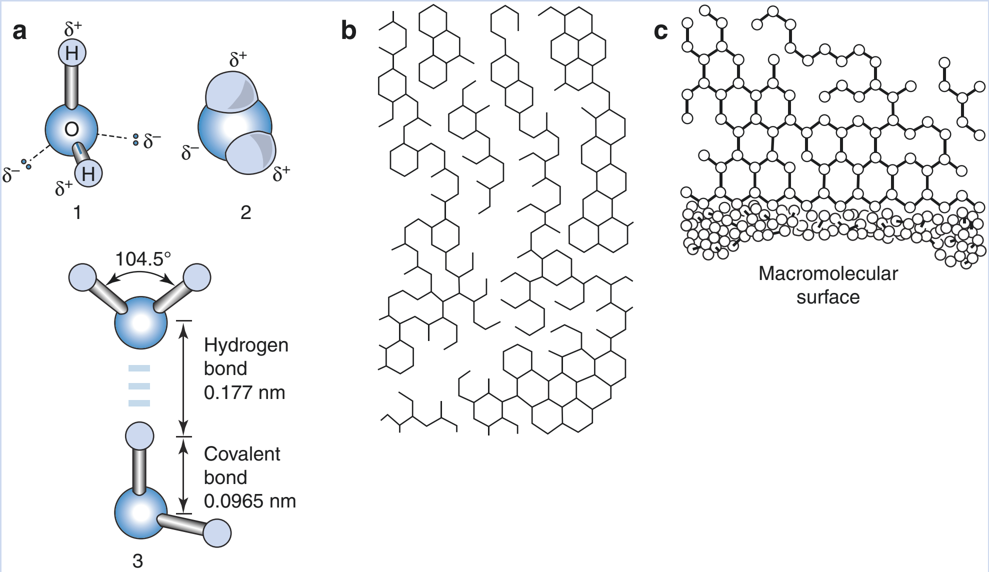


Fig. 6.2 Dipole, clusters, hydrophobic interaction

Table 6.1 Physico-chemical anomalies of water

Compound	Molecular weight	Melting point (°C)	Boiling point (°C)
H_2O	18	0	100
H_2S	34	−86	−61
Further biologically important physical properties of water			
Specific heat capacity		$1\ \mathrm{cal\ g^{-1}} = 4.2\ \mathrm{J\ g^{-1}}$	
Latent heat of crystallisation		$333.6\ \mathrm{J\ g^{-1}}$	
Latent heat of evaporation		$2441\ \mathrm{J\ g^{-1}}$	
Surface tension (at 15 °C)		$73.5\ \mathrm{g\ s^{-1}}$	

6.2 Water Acquisition and Movement: Cellular Aspects

Life is so strictly dependent on water that the search for traces of extraterrestrial life (e.g. on Mars) is essentially a search for signs of water. The evolution of life on land has required key innovations allowing organisms to acquire water. In addition, most animal and plant species have to maintain a hydrated state; that is, they are **homoiohydric**. Only few species of vascular plants can withstand dehydration and are able to resume physiological activity after rehydration. Together with lichens and many mosses, they are referred to as **poikilohydric**.

The needs to take up water and to stay hydrated demand acclimations and adaptations to cope with fluctuations in water supply and, in particular, with a shortage of water supply. Many plant habitats are characterised by either temporary or permanent water scarcity. Not only does this threaten photosynthesis and the functions of all kinds of metabolic processes that take place in the aqueous environments of cells, but water is also physically important for the growth of plants. Growth is a function of cell division and cell expansion. The expansion growth of plant cells is dependent on **turgor pressure**, i.e. on **water influx**. The modulation of cell wall properties such as their extensibility controls the expansion rate, but the build-up of hydrostatic pressure is what drives the expansion.

Thus, practically every facet of terrestrial plant life is dependent on the uptake of water from the soil at sufficient rates and the tightly controlled movement of water within the plant.

Water uptake by roots and water movement are dependent on a driving force—that is, pressure differences—and on the facilitation of passage through biological membranes. We consider **cellular water homeostasis** and short-distance transport here. Long-distance transport of water is covered in Chap. 10.

6.2.1 The Water Potential

The thermodynamic state of water is described by the **water potential** (**Ψ_w**), which is, figuratively speaking, a measure of the energy required to remove water molecules from any water-containing system. The (chemical) potential of pure water under standard conditions of pressure and temperature is defined as zero and used as a reference. Any system that requires more energy to remove water from it has a negative water potential. Commonly, the water potential of a system is expressed in the dimension of pressure and not of energy: relating the chemical potential of water to the molar volume results in the dimension of "pressure". Thus, Ψ_w of pure water under standard conditions is 0 MPa. Other details and the derivation of the definition of water potential are given in Chap. 10 (see also plant physiology textbooks).

The water potential of a solution, and correspondingly that of a cell, is influenced by three major components: concentration of solutes, pressure and gravity. When one is considering water potential beyond the cellular level or in cells and other structures in an at least partially dehydrated state, the **matrix potential** (**Ψ_m**) is often included as a fourth component. It describes the reduction in the free energy of water when it is adsorbed in a thin layer to surfaces of cell walls, soil particles or other structures. In the analysis of cellular processes it becomes apparent only after the cell has been desiccated to such an extent that only the water bound to cellular and subcellular structures remains. Removal of that portion of cellular water requires either extremely low (negative) water potentials or extremely high pressures. Because of very small values of the matrix potential in hydrated cells, it can be neglected for the discussion of cellular water relations, with the exception of freezing dehydration (Chap. 4, Box 4.1).

The concentration of solutes translates into the **osmotic potential** (**Ψ_s**). Jacobus H. van 't Hoff (who received the Nobel Prize for Chemistry in 1901) was the first to quantitatively describe the linear relationship between solute concentrations and the osmotic pressure exerted by water flowing through a semipermeable membrane separating two aqueous solutions (semipermeable = permeable for water molecules but not for the ions and molecules dissolved in water). **Osmotic pressure** is positive, while osmotic potential has a negative sign. It describes the negative effect of dissolved ions or molecules on the water potential. In other words, solutes reduce the probability of a water molecule moving across a semipermeable membrane into another compartment. The net flow of water between two solutions is directed towards the solution with the higher solute concentration.

The **pressure potential** (**Ψ_p**) refers to the hydrostatic pressure of a solution. A positive value raises the water potential—that is, the tendency of a water molecule to move from one place (e.g. a cell) to another. A positive hydrostatic pressure in a plant cell is equivalent to the **turgor pressure**. It is generated by the osmotically driven influx of water into a cell and the limited extensibility of the cell wall. Some cells in a plant can have negative hydrostatic pressure (tension). This applies, for instance, to xylem vessels. Both positive and negative pressures are made possible by the rigidity of cell walls.

The influence of gravity, which forces water molecules downward towards the Earth's centre, is expressed with the term **Ψ_g**. When analysing plant–water relations the water potential is mathematically often described as:

$$\Psi_w = \Psi_s + \Psi_p + \Psi_m + \Psi_g$$

An alternative formula to describe the water potential is explained in Chap. 10.

Ψ_g needs to be included when vertical movement of water over long distances (such as in tall trees) is analysed. Near the base of a plant, Ψ_g is negligible, so a discussion of plant–water relations at the cellular level can focus on Ψ_s and Ψ_p. In order to understand the movement of water into a plant, within a plant and out of a plant, one has to determine $\Delta\Psi_w$ (i.e. the water potential difference) between relevant places—for example, the soil and root cells, root cells and mesophyll cells, or mesophyll cells and the atmosphere.

6.2.2 Facilitation of Intercellular and Intracellular Water Flow: Aquaporins

Water movement in a plant is always passive. It follows gradients in potential. A water potential difference between two systems (e.g. two cells) can be compared to a voltage in an electrical circuit. It causes the flux of water in the direction of the system with the more negative potential, provided that a water conductive pathway exists between the systems. In accordance with the analogy to an electrical circuit, the pathway for water corresponds to a resistance. While long-distance movement of water occurs mostly through vascular cells (Chap. 10), three pathways for the flux of water through a tissue exist. Let us, for instance, consider the radial movement of water through the root towards the vasculature. The cells through which this radial movement occurs represent an important resistance for water flow (Steudle and Peterson 1998). It is therefore physiologically very important under conditions of transpiration when water has to be replenished from the soil solution. The flux of water may occur in the apoplast—that is, through and along the cell walls (the **apoplastic path**)—or from cell to cell via plasmodesmata (the **symplastic path**). The third path is **transcellular** and requires membrane passages (Fig. 6.3). The different pathways and respective forces driving the water flux are integrated into the "**composite water transport model**" (Steudle 2001). Apoplastic water flux is mostly due to hydrostatic forces (pressure or tension). In contrast, the symplastic and transcellular paths are additionally driven by osmotic pressure, as osmotic gradients can establish across the cellular membranes. The relative contributions of the three pathways vary widely depending on the species, developmental stage or environmental conditions. For instance, in a transpiring plant, hydrostatic forces dominate, while in the absence of transpiration, osmotic pressures are more important (Javot and Maurel 2002).

Movement of water through cellular membranes is largely controlled by water channels—the **aquaporins** (Chaumont and Tyerman 2014). Their crucial role for water flow within tissues has been clearly determined. A widely used method to differentiate between the movement of water molecules directly through the membranes (which is the essence of the semipermeability of biological membranes) and aquaporin-dependent water movement is to compare conductivities in the absence and presence of mercury ions (Hg^{2+}). Hg^{2+} oxidises crucial cysteine residues in aquaporins and thereby inactivates them. The effect can be reversed by thiol reagents (Fig. 6.4). Hg^{2+} exposure strongly reduces the water flow through roots. Thus, a large (yet variable) fraction of root water permeability is attributable to aquaporins.

Aquaporins represent an ancient family of small membrane proteins. They consist of six membrane-spanning helices connected by five loops (Fig. 6.6). The N– and C–termini are cytosolic. Their molecular mass lies between 21 and 34 kDa. Shortly after their unexpected discovery in the early 1990s in animal cells (for which Peter Agre received the 2003 Nobel Prize in Chemistry; Agre 2004), they were also identified in plants and microorganisms. Aquaporins transport water

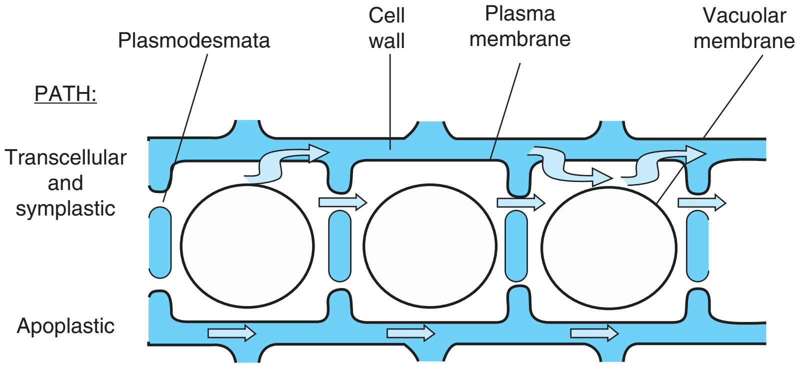


Fig. 6.3 Three pathways of water flow through living plant tissues: apoplastic, symplastic and transcellular. (Modified from Javot and Maurel (2002))

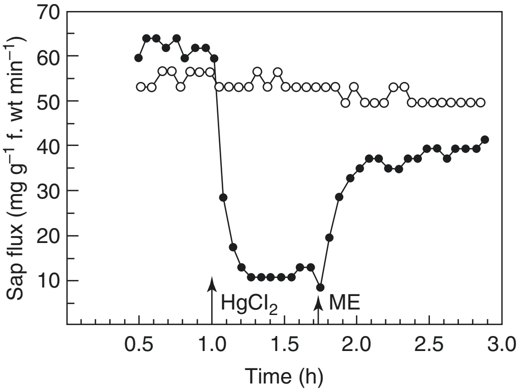


Fig. 6.4 Effects of mercury (Hg^{2+}) on pressure-induced water transport in excised tomato roots. Sap flux through roots of de-topped tomato plants was continuously monitored. The plants were held under constant pressure. $HgCl_2$ (0.5 mM) and the reductant β-mercaptoethanol (ME; 60 mM) were applied at the times indicated. Hg^{2+} blocks aquaporins via the interaction with conserved cysteines; β-mercaptoethanol reverses this effect. The sap fluxes were recorded in an $HgCl_2$-treated root system (*closed circles*) and a corresponding untreated control root system (*open circles*). $HgCl_2$ reduced the intensity of sap flux in a partially reversible manner by about 70%. This reduction was assumed to reveal the contribution of aquaporins to root conductivity in this experiment. (From Javot and Maurel (2002), after Maggio and Joly (1995))

molecules and also a range of other substrates such as CO_2, boron and silicon (Maurel et al. 2015). In accordance with the importance of controlled water movement in all types of cells at every developmental stage, plants possess a large number of isoforms (e.g. 35 in the eudicot *Arabidopsis thaliana* and 33 in the monocot rice) with distinct expression patterns and subcellular localisations (Maurel et al. 2008). Most abundant are aquaporins in the plasma membrane (**PIPs** (**plasma membrane intrinsic proteins**)) and in the tonoplast (**TIPs** (**tonoplast intrinsic proteins**))—that is, the two membranes that most of the transcellular water movement goes through. However, they are also found in all other membranes of the endomembrane system.

The principal ways of controlling aquaporin-dependent water flow are modulation of aquaporin abundance and permeability (= gating). Across a plant organ, aquaporin expression levels are not equal in all cell types. Instead, it can be observed that certain cells and cell types show higher abundance of aquaporins. These are cells of particular importance for controlling the flow of water. They function as gatekeepers (Chaumont and Tyerman 2014) and include the stomata (Sect. 6.3.3), bundle sheath and xylem parenchyma cells in the leaves. In roots, **gatekeeper cells** are located near the endodermis and the exodermis. The apoplastic pathway through the root is blocked by these cell layers. Suberised and lignified cell walls (referred to as the **Casparian strip** in the case of the endodermis) prevent movement of water molecules along the cell wall. Entry into the symplastic pathway requires a membrane passage that is facilitated by aquaporins.

Especially given the existence of gatekeeper cells, it is evident that the passive flow of water through a plant can be regulated by the abundance and activity of aquaporins. Coming back to the electrical circuit analogy, aquaporins represent variable resistances. The voltage (the water potential gradient) cannot be influenced, but the current (the flow of water) can. One way of modulating the “resistance” is transcriptional control over aquaporin expression levels. For instance, diurnal and circadian rhythms in the conductivity of roots and leaves can be well explained by corresponding changes in the transcription of major PIP genes (Maurel et al. 2008) (Fig. 6.5). Such rhythmicity couples tissue water conductivity to stomatal functions. During the light period when stomata are open, the tissue conductivity is increased (the resistance is lowered) through higher expression levels of aquaporins, thereby preventing the emergence of extreme xylem tension due to transpiration. Various environmental stresses, including drought, affect aquaporin expression, often in complex ways. In addition to transcriptional control, several mechanisms for regulating aquaporin activity are known. Aquaporin residence time in the plasma membrane is influenced by constitutive recycling; that is, aquaporin molecules are trafficked not only in vesicles from the endoplasmic reticulum and Golgi to the plasma membrane but also in the reverse direction. In this way a cell can finely adjust the number of active aquaporins.

Furthermore, the stability of aquaporins is modified by phosphorylation and ubiquitination. Gating

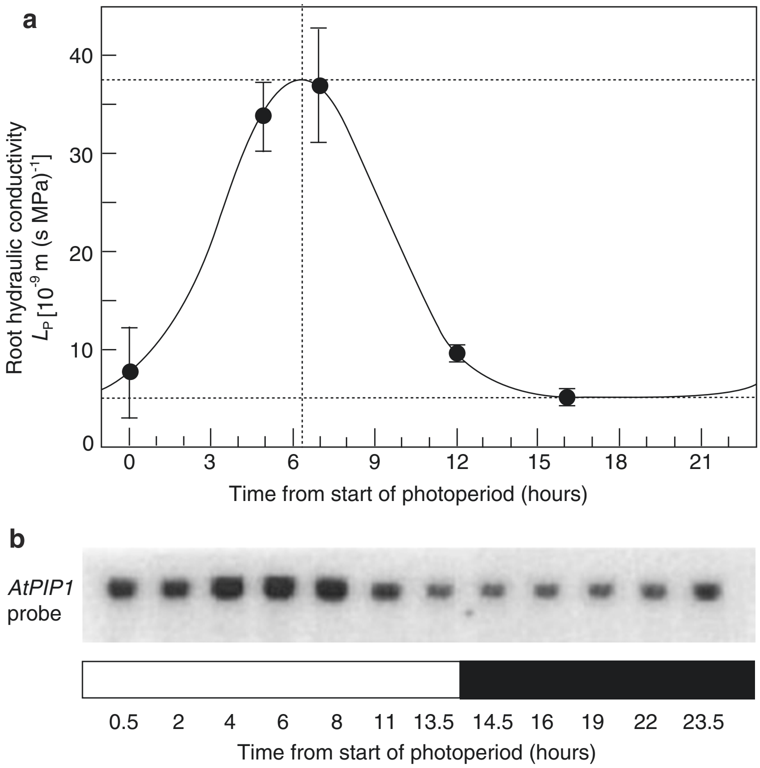


Fig. 6.5 Diurnal rhythm of *Lotus japonicus* root conductivity and aquaporin expression. **a** A peak in root water conductivity near the middle of the light period, when stomata are open and transpiration is high, coincides with higher levels of aquaporin transcripts. **b** Northern blot showing changes in the abundance of a major plasma membrane aquaporin transcript, detected with a probe derived from the *Arabidopsis thaliana* homologue. This illustrates the coordination between transpiration and water conductivity of tissues, which is achieved by transcriptional regulation of aquaporins. (From Javot and Maurel (2002), adapted from Henzler et al. (1999))

of the water channels is modulated through heteromerisation, Ca^{2+} levels, pressure or pH. All of these processes can be influenced by environmental cues (Fig. 6.6) (Chaumont and Tyerman 2014). In summary, the multitude of aquaporin isoforms in a plant and the many ways of regulating them provide the means to acclimate to fluctuations in water availability and demand by adjusting resistance for water flow across tissues as well as into and out of cells and cellular compartments.

6.3 Drought Stress Responses: Avoidance and Tolerance

Under conditions of drought, plants lose water to the atmosphere. When water uptake cannot keep pace with water loss, transpiration is fed mainly from the vacuoles. Usually the water permeability of the tonoplast is considerably higher than that of the plasma membrane. This allows fast equilibration of the intracellular water potentials upon changes in the cell's water status. Water flows via the plasma membrane into the apoplast, from where it evaporates into the intercellular spaces. Because of the decrease in volume caused by water loss, the osmotic pressure in the protoplast is increased; that is, the osmotic potential becomes more negative. At the same time, the hydrostatic pressure decreases. When the so-called **turgor loss point** is reached, the cell wall is completely relaxed and the pressure (Ψ_p) is zero. Consequently, the water potential of the cell is then equal to its osmotic potential (Ψ_s). In this state a plant shows substantial wilting. With further loss of water, wilting increases, as the cell walls not only are

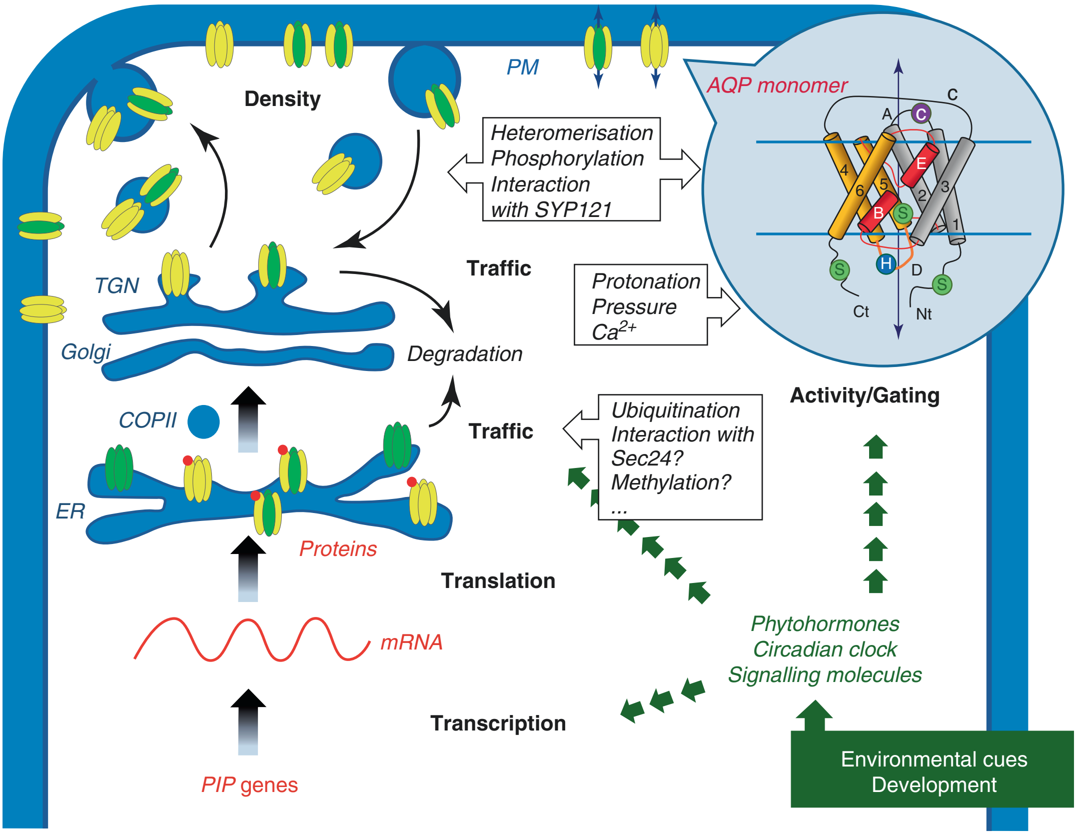
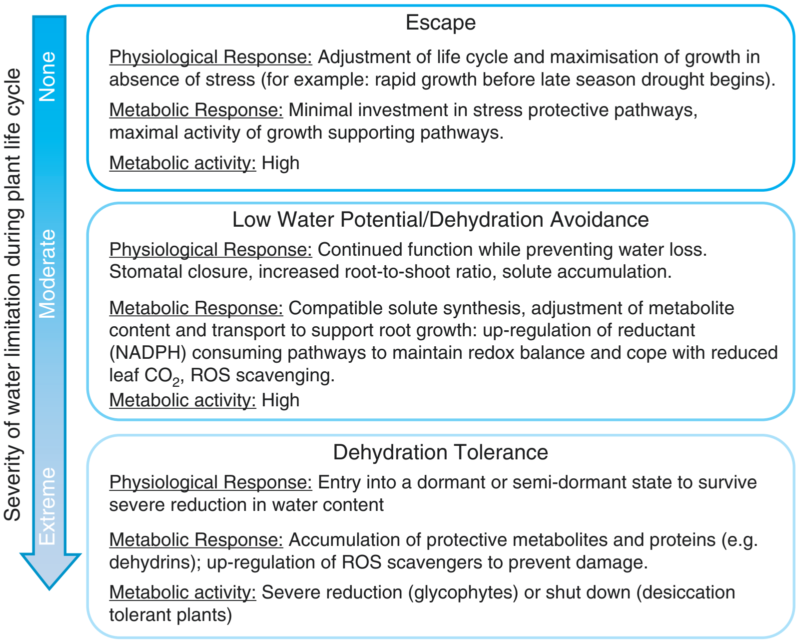


Fig. 6.6 Regulation of plasma membrane aquaporin (plasma membrane intrinsic proteins (PIPs)) abundance and activity within the cell. *PIP* genes are transcribed, their messenger RNA (mRNA) translated in the rough endoplasmic reticulum (ER) and the proteins targeted at the plasma membrane (PM). PIPs of different classes (depicted in *yellow* and *green*) can form homo- or hetero-oligomers. PIP oligomers transit through the Golgi apparatus via the trans-Golgi network (TGN) and are then routed to the plasma membrane in secretory vesicles. Transcription and trafficking are modulated depending on the developmental stage and various environmental cues. Insertion of PIPs into the plasma membrane is mediated by the syntaxin SYP121. Internalisation of plasma membrane–localised PIPs occurs as a result of constitutive recycling. Once internalised in vesicles, PIPs are delivered to the TGN before being routed back to the plasma membrane or directed into lytic vacuoles for degradation. Under stress conditions, PIPs can be dephosphorylated and internalised, or ubiquitinated and then degraded in the proteasome. The water channel activity or gating of PIPs is regulated by different mechanisms (heteromerisation, phosphorylation, interaction with SYP121, protonation, the pressure gradient and the Ca^{2+} concentration). In the *upper right corner* the topological structure of an aquaporin monomer is shown (Murata et al. 2000), which consists of six membrane-spanning α-helices (1–6) connected by five loops (A–E) and N– and C–termini facing the cytosol. The loops B and E, together with the membrane-spanning helices, create a pore with high specificity. The transcription, translation, trafficking and gating of PIPs are regulated by environmental and developmental factors involving signalling molecules, phytohormones and the circadian clock. (Chaumont and Tyerman 2014)

relaxed but also, in responding to the intracellular suction, bend inwards. This will finally result in **cytorrhysis**—that is, the complete collapse of the cell—provided that the cell wall rigidity is low enough to allow folding. As described for the case of freezing dehydration, this happens because the water-imbibed cell wall (Sect. 4.2.6 in Chap. 4) does not allow any air to penetrate. Suction develops and, correspondingly, a negative water potential (−1 to −2 MPa) of the cell arises.

Besides the escape of water-limited conditions through the timing of, for instance, germination



Escape

Physiological Response: Adjustment of life cycle and maximisation of growth in absence of stress (for example: rapid growth before late season drought begins).

Metabolic Response: Minimal investment in stress protective pathways, maximal activity of growth supporting pathways.

Metabolic activity: High

Low Water Potential/Dehydration Avoidance

Physiological Response: Continued function while preventing water loss. Stomatal closure, increased root-to-shoot ratio, solute accumulation.

Metabolic Response: Compatible solute synthesis, adjustment of metabolite content and transport to support root growth: up-regulation of reductant (NADPH) consuming pathways to maintain redox balance and cope with reduced leaf CO_2, ROS scavenging.

Metabolic activity: High

Dehydration Tolerance

Physiological Response: Entry into a dormant or semi-dormant state to survive severe reduction in water content

Metabolic Response: Accumulation of protective metabolites and proteins (e.g. dehydrins); up-regulation of ROS scavengers to prevent damage.

Metabolic activity: Severe reduction (glycophytes) or shut down (desiccation tolerant plants)

Fig. 6.7 Drought adaptation strategies ranging from escape to tolerance of severe dehydration. (Modified from Verslues and Juenger (2011))

or flowering (Fig. 6.7) (Chap. 2), principally two different strategies to cope with water scarcity can be distinguished: **avoidance** and **tolerance**. It is important to note, however, that these categories merely represent distinct areas within a continuum of responses. They can even both be displayed by the same plant, depending on the severity of the water limitation (Fig. 6.7). Avoidance refers to a balancing of water uptake and water loss that maintains the water status. This can be achieved by restricting water loss, by increasing the water supply or by water storage. It has been argued that avoidance is an idealised concept. In reality, avoidance mechanisms achieve later onset of drought stress (Lawlor 2013). Tolerance mechanisms help a plant endure a moderate lowering of the water potential. They protect cells against damage potentially arising from water loss—for instance, by compatible solute accumulation (Sect. 6.3.1). Key cellular functions are maintained, enabling resumption of growth after resupply of water.

An extreme form of drought tolerance is shown by **poikilohydric plants**, which withstand near complete tissue dehydration (**desiccation**). Lichens and certain mosses, on the one hand, and resurrection plants such as *Craterostigma plantagineum* and *Xerophyta humilis*, on the other hand, have evolved specific adaptations that allow them to enter a dormant or quiescent state under dry conditions. These adaptations are substantially different from those that allow **homoiohydric plants** to continue their physiological activity during less severe water limitation. Owing to the accumulation of protective proteins (Sect. 6.3.2) and osmolytes, cells of poikilohydric plants survive a very low water status and are able to resume metabolic activity following rehydration. This enables poikilohydric plants to inhabit extremely dry environments such as the deserts in Southern Africa, where a diversity of resurrection plants is found.

Finally, another useful categorisation of strategies similar to the avoidance–tolerance distinction is the differentiation between **isohydric** and **anisohydric** plant species. It refers to two different types of stomatal regulation (Sect. 6.3.3) in response to soil drying. Isohydric plants such as maize or poplar maintain the water potential of their cells at relatively constant values (at around −2 MPa) by reducing stomatal conductance early upon the onset of water shortage. In contrast, anisohydric species (e.g. sunflower) allow a decline in cellular water potential upon a drought-induced drop in soil water potential. The two strategies are associated with different physiological risks. Rapid stomatal closure can lead to early onset of a **negative carbon balance** because of the reduced CO_2 assimilation. On the other hand, the decrease in water potential can result in **hydraulic failure**. When water loss through transpiration is substantially greater than the uptake of water by roots, high xylem water tension can develop, which eventually leads to cavitation of xylem vessels and conductivity loss (McDowell et al. 2008) (Chap. 10). Overall, anisohydric species tend to be more common in drought-prone habitats than isohydric species.

6.3.1 Control of the Osmotic Potential

When the water potential outside a cell is more negative than the water potential of the cell itself, a net flux of water out of the cell will occur. Thus, in order for the plant to take up water from the soil solution, the water potential of its root cells has to be more negative than that of the surrounding soil; that is, the cells have to establish a water potential difference. Under conditions of drought the soil water potential decreases substantially because of the adhesion of the remaining water to soil particles (a strongly negative matrix potential (Ψ_m) develops). This poses the challenge to maintain a water potential gradient. It is important to note that several other environmental conditions cause a very similar problem. The water potential of wet soil can become too negative when high concentrations of salt are present (Chap. 7). Likewise, freezing of extracellular water causes an extreme drop in the water potential (Chap. 4).

Plant cells can lower their water potential by **osmotic adjustment**. Increasing the concentration of solutes makes the **osmotic potential** (**Ψ_s**), and thereby the water potential of the cell, more negative. Osmolality increases which are achieved in this way exceed the solute-concentrating effect of partial dehydration. The process of preventing cellular water loss by achieving a more negative water potential than that of the surrounding solution is an acclimative response and is referred to as **osmoprotection**. It is known from all kinds of organisms (Yancey 2005). The solutes accumulating for osmotic adjustment are called "**compatible solutes**" or "**osmolytes**". They are mostly organic low molecular weight compounds. Accumulation of ions would principally have the same effect on the osmotic potential of a cell. However, elevated concentrations of ions may affect the hydration shell of proteins and thereby inactivate them. In contrast, many organic molecules are compatible with cell functioning because they are either uncharged or zwitterionic at physiological pH. They do not enter the hydration shell of proteins and, owing to their hydrophilicity, they can become a constituent of the structured portion of the water film on the membrane surface. Compatible solutes accumulate predominantly in the cytosol and in metabolically active organelles such as the chloroplasts to maintain an osmotic balance with the vacuoles where ions can be stored and lower the osmotic potential without disturbing metabolism.

The osmotic potential of a cell is a function of the concentrations of a vast number of dissolved molecules and ions. Only a few of them accumulate massively (up to about 10% of the dry weight) for osmotic adjustment and therefore function as osmolytes. They are chemically diverse and predominantly belong to the soluble sugars (e.g. glucose, sucrose), sugar alcohols (e.g. mannitol, sorbitol), oligosaccharides (raffinose, stachyose), amino acids (e.g. proline), quaternary ammonium compounds (e.g. glycine betaine) or polyamines (e.g. putrescine, spermidine) (Table 6.2). Some of these metabolites accumulate in many different plant species of diverse phylogeny. Proline is a prominent example (Fig. 6.8). Other osmolytes are typical for particular plant families. For instance, β-alanine betaine as an osmolyte is largely confined to Plumbaginaceae; glycine betaine is common in Chenopodiaceae. Thus, different molecules have been recruited during evolution for the purpose of osmotic adjustment.

The protective function of osmolytes goes beyond the osmotic effect (Table 6.2). Unlike the lowering of the osmotic potential, however, other activities cannot generally be ascribed to all osmolytes. Instead, they are more specific to particular

Table 6.2 Accumulation of molecules in organs of terrestrial plants under drought stress, and their physiological effects

Type of molecule	Examples	Function under drought
Ions	K^+	Osmotic adjustment
Proteins	LEA/dehydrins	Membrane and protein protection
	SOD, catalase	ROS detoxification
Metabolites		
Amino acids	Proline	Membrane and protein protection
Sugars	Raffinose	ROS scavenging
Polyols	Mannitol (acyclic)	Osmotic adjustment, ROS scavenging
	Pinitol (cyclic)	
Polyamines	Spermine	ROS scavenging, membrane protection
	Spermidine	
Quaternary amines	Glycine betaine	Membrane and protein protection
	β-Alanine betaine	Osmotic adjustment under hypoxia
Tertiary sulphonium compounds	Dimethyl sulphonopropionate	ROS scavenging
Pigments	Carotenoids	Protection against overexcitation, photoinhibition
	Anthocyanins	

LEA late embryogenesis abundant, *ROS* reactive oxygen species, *SOD* superoxide dismutase

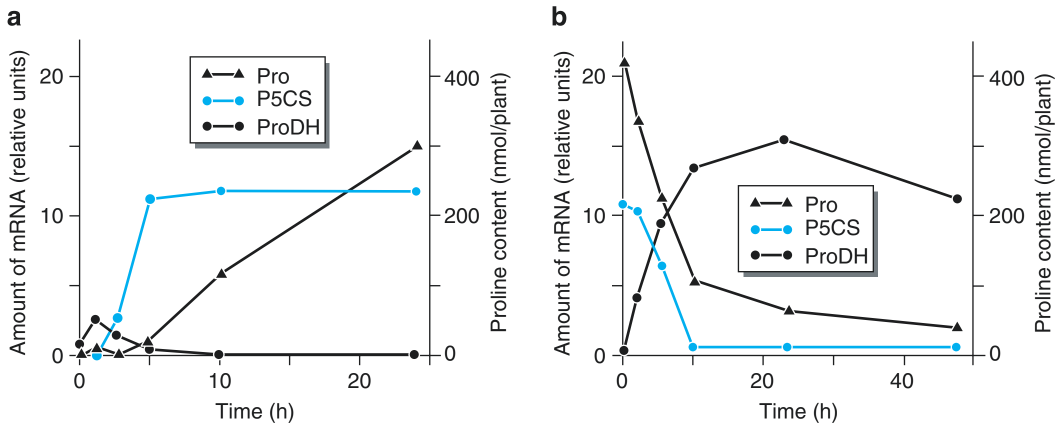


Fig. 6.8 The compatible solute proline. Time course of accumulation and decrease in proline (Pro) concentration and the messenger RNAs for D1-pyrroline-5-carboxylate synthase (P5CS) and for proline dehydrogenase (proline oxidase (ProDH)) in *Arabidopsis thaliana* during the development of drought **a** and 10 h after rehydration **b**. (After Yoshiba et al. (1997))

compound classes (Yancey 2005). Some osmolytes—for example, mannitol and other sugar alcohols—are believed to act as **antioxidants**—that is, to scavenge reactive oxygen species (ROS) generated during drought or freezing. Others, such as proline and β-alanine betaine, have been implicated in **redox balancing**. In this case it is not a characteristic of the solute itself that explains this protective function; rather, the synthesis of proline and other solutes is reductive. The oxidation of reduced nicotinamide adenine dinucleotide phosphate (NADPH) regenerates $NADP^+$ as an electron acceptor. This reduces the risk of electron transfer from photosystem I to O_2 and thereby lowers the probability of photoinhibition. Proline may also function as a molecular chaperone, stabilising proteins and other macromolecules. Protection of enzymes involved in detoxification of ROS would then offer yet another explanation for the documented antioxidant effect of proline (Szabados and Savouré 2010). Similar protective effects on enzymes that are important either for stress tolerance or for metabolic activity under stress have been described for glycine betaine too.

The accumulation of osmolytes under conditions of drought and other stresses such as **freezing** (Chap. 4) and **osmotic stress** (Chap. 7) has been documented in countless studies for a wide range of plant species. Nevertheless, direct unequivocal evidence demonstrating the importance of these acclimative responses—for example, through a loss-of-function mutation and concomitant stress hypersensitivity—has not been possible to obtain. This is different from the modulation of stomatal conductance. Inability to close stomata under drought stress dramatically accelerates the wilting of plants (Sect. 6.3.3). The importance of compatible solute accumulation has initially been mostly inferred from similar responses in microorganisms such as *Saccharomyces cerevisiae*, *Escherichia coli* or salt-tolerant cyanobacteria and the demonstrated contribution of compatible solutes to survival in these biological systems. Experimental support in plants has predominantly come from studies with **transgenic plants** engineered to overproduce particular compatible solutes. Very often such plants showed moderate gains in stress tolerance. Analyses of **extremophile species** with extraordinary levels of abiotic stress tolerance have provided some additional indirect evidence. The salt-tolerant Brassicaceae *Eutrema salsugineum* (formerly *Thellungiella halophila*), for instance, has higher proline levels already in the non-stressed state and accumulates proline more strongly under stress than other related Brassicaceae species (Chap. 7). Similarly, levels of pinitol are higher in some drought- and salt-tolerant species such as *Mesembryanthemum crystallinum*. It cannot be generalised, however, that particularly stress tolerant plant species always display stronger accumulation of compatible solutes.

The strong increase in osmolyte accumulation requires many changes in the transcriptome, proteome and metabolome of plants exposed to water deficit stress. Accumulation can arise in different ways. Monosaccharide concentrations can be adjusted through the breakdown and synthesis of starch and other polysaccharides. For sugar alcohols such as mannitol the utilisation of the hexose phosphate pool is diverted away from sucrose synthesis by the induction of enzymes that use fructose-6-phosphate for sugar alcohol synthesis. Proline concentrations are a function of synthesis and degradation rates (Fig. 6.8). Their regulation has been studied intensively. As mentioned earlier, proline is a multitasking molecule with many physiological functions besides its role as one of the 20 amino acids found in proteins. Correspondingly, several different environmental cues influence the rates of synthesis from glutamate and the degradation back to glutamate. Some of them are shown in Fig. 6.9 (the alternative biosynthetic pathway from ornithine is not depicted). The major hormone eliciting drought responses is abscisic acid (ABA) (Sect. 6.5). When it accumulates in cells, pyrroline-5-carboxylate synthetase (P5CS)—the enzyme catalysing the first step in the synthesis from glutamate to proline—becomes transcriptionally upregulated. In *A. thaliana* the drought responsive gene is *P5CS1*. The second isoform, *P5CS2*, is not activated even though it is highly similar to *P5CS1*. It has housekeeping functions; that is, it is responsible for the proline synthesis that is needed in the absence of stress. Under salt stress, *P5CS1* is activated via a different signal transduction pathway (Szabados and Savouré 2010). Catabolism is repressed under drought stress conditions, while it is stimulated upon stress relief—for instance, by rehydration. Control is exerted on two enzymes, proline dehydrogenase (PDH) and pyrroline-5-carboxylate dehydrogenase (P5CDH).

6.3.2 Protective Proteins

The function of proteins accumulating under conditions of drought have been mostly studied in the context of desiccation—that is, a lowering of the relative water content of a tissue or organ to 10% or less. **Desiccation tolerance** represents an adaptation to extreme environmental conditions and requires specific mechanisms dis-

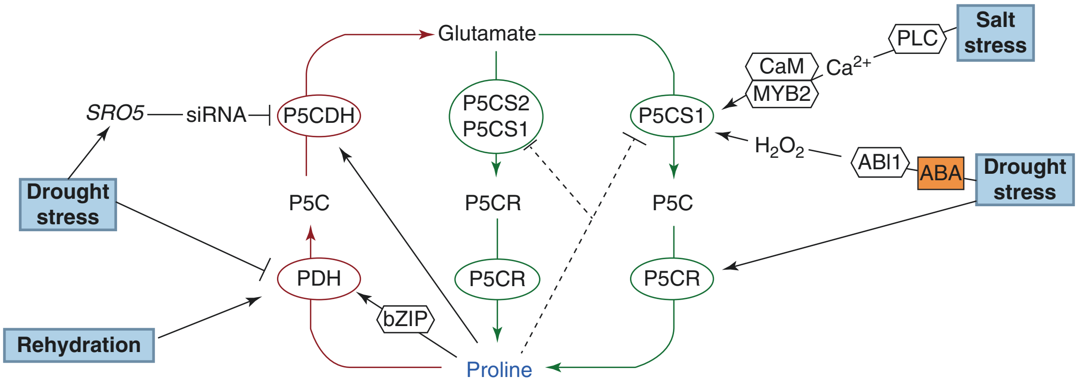


Fig. 6.9 Proline synthesis and degradation in *Arabidopsis thaliana* are responsive to several environmental cues. The cues depicted here are water status and salt stress. The influences of other factors such as light, the photoperiod and pathogen attack, as well as the complex cellular compartmentation of proline metabolism, are not shown. Synthesis of proline (*green lines*) from glutamate is stimulated by the transcriptional up-regulation of one particular pyrroline-5-carboxylate synthetase isoform (*P5CS1*) via different signal transduction cascades depending on the type of water deficit stress (drought versus high salt concentrations in the soil). Activation under drought stress is mediated by abscisic acid (ABA) and reactive oxygen species (ROS) as signalling molecules. Pyrroline-5-carboxylate reductase (P5CR) is up-regulated under drought stress. The end product proline feedback-inhibits P5CS1. Proline degradation (*red lines*) to glutamate by proline dehydrogenase (PDH) and pyrroline-5-carboxylate dehydrogenase (P5CDH) is inhibited under drought stress and stimulated upon rehydration. The *P5CDH* transcript is targeted by a natural small interfering RNA (siRNA) upon drought activation of *SRO5* transcription. Regulatory proteins involved in signal transduction cascades are shown in *hexagons*: transcription factors of the bZIP and MYB class, calmodulin (CaM), the phosphatase ABI1 and phospholipase C (PLC). (Modified from Szabados and Savouré (2010))

played by only a small number of plant species (around 300 within the angiosperms). This makes it different from the acclimative control of osmotic potential or the stomatal aperture (Sect. 6.3.3), which essentially every plant is capable of. It involves a state of **dormancy** of the whole plant, which is reminiscent of seeds. In fact, it has been proposed that in resurrection plants the developmental programmes underlying seed maturation have been recruited for the desiccation tolerance of the whole plant (Farrant and Moore 2011).

During the early phase of **dehydration**, **osmotic adjustment** occurs through the accumulation of sucrose and other osmolytes. Progressive water loss concentrates the cellular content and causes mechanical as well as metabolic stress. The risk of protein denaturation and unwanted biochemical reactions increases. Osmolytes replace water molecules and can eventually accumulate to levels such that **vitrification** occurs; that is, the sucrose solution adopts a glassy, almost solid state (Fig. 6.10). Proteins that have the capacity to protect cellular structures strongly accumulate. They are called **late embryogenesis abundant** (**LEA**) **proteins**. The name indicates that these proteins were first described as accumulating during the later stages of seed maturation, when desiccation tolerance is acquired. However, they are found not only in plants but also in bacteria, archaea, fungi and certain invertebrates (e.g. nematodes, arthropods).

Within the plant kingdom, LEA proteins are not specific to resurrection plants. They accumulate in the seeds of most other plants during ripening. Also, their expression is induced under conditions of water limitation such as drought, freezing and high salt concentrations in the vegetative tissue of many non-desiccation-tolerant plant species. Some of the *COR* (COld-Regulated) genes up-regulated during cold acclimation (Chap. 4) encode LEA proteins. Genome-wide analyses in model species have shown that different subsets of *LEA* genes are expressed during seed maturation and abiotic stress with very little overlap. **Resurrection plants** (Fig. 6.11) are special with respect to LEA proteins only in that they often show much stronger accumulation of these proteins. Also, in some species, these proteins are constitutively expressed at high levels

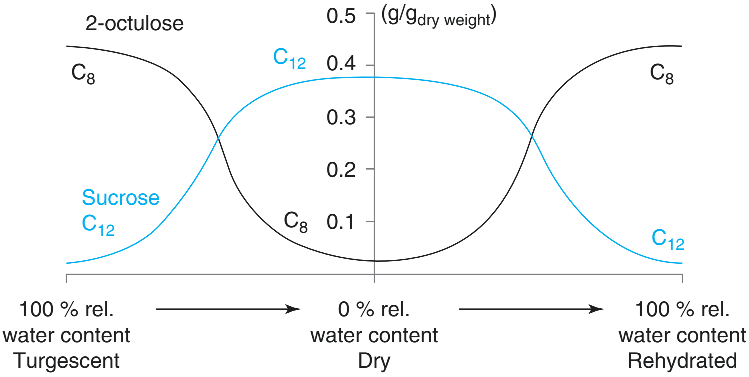


Fig. 6.10 Changes in the proportions of soluble carbohydrates, corresponding to the water relations of the resurrection plant *Craterostigma plantagineum*. In the fully hydrated state, leaves mainly contain the C8 sugar octulose which, upon desiccation, is almost quantitatively converted to sucrose, a compatible solute. This reaction is reversible. (After Bartels et al. (1993))

Fig. 6.11 The resurrection plant *Craterostigma plantagineum*, which recovers fully from drying out: a plant in the hydrated state (*left*), in the dry state (*centre*) and after rehydration (*right*). (Photos courtesy of Dorothea Bartels, University of Bonn, Germany)

even in the absence of water deficit. The latter is interpreted as a way of priming these plants for dehydration upon the arrival of severe drought events.

LEA proteins are highly hydrophilic. On the basis of their amino acid composition (for instance, a high content of glycine and other small amino acids) and supported by biochemical investigations of a few examples, most of them are assumed to be intrinsically disordered proteins—that is, lacking a tertiary structure. Large numbers of genes encoding LEA proteins are found in plant genomes (>50 in *A. thaliana*, for example). LEA proteins are divided into several classes according to sequence similarities. The annotation and categorisation of LEA proteins are not consistent throughout the literature. They largely overlap with another group of proteins named “hydrophilins”, which are defined as glycine rich and hydrophilic. Among the different classes of LEA proteins there are some that carry alternative names such as “**dehydrins**”.

The increase in LEA protein abundance under water deficit conditions has been documented for a large number of plant species, organs, tissues and cell types. LEA proteins have thus been firmly associated with abiotic stress tolerance. Still, the functional understanding of LEA proteins is limited. How exactly their accumulation promotes cell survival under stress is unknown (Wise and Tunnacliffe 2004). Enzymatic activities have never been described. Many LEA proteins become structured—that is, partially folded—upon dehydration and may exert their protective effects in this state. On the other hand, the accumulation in water-limited vegetative tissues not undergoing desiccation suggests functions of LEA proteins also in the hydrated state. Several hypotheses exist as to the actual physiological and biochemical activities, including the stabilisation of proteins and membranes, anti-oxidative activities or a function as space-filling molecules in cells with low water content to prevent collapse.

In vitro it has been shown for several enzymes that the presence of LEA proteins preserves activity, probably because the hydrophilicity of LEA proteins prevents the formation of protein aggregates. This is sometimes referred to as a “molecular shield” mechanism and is different from the chaperone activity of heat shock proteins (Chap. 4), as LEA proteins cannot protect proteins from heat denaturation. According to this hypothesis the unstructured LEA proteins would sterically hinder the interaction between partially denatured proteins. The anti-aggregate function is supported by in vivo data obtained for cells co-expressing LEA proteins and aggregation-prone target proteins. Evidence for an interaction of LEA proteins with membranes exists as well. Binding may occur concomitantly with the formation of α-helices upon drying or alternatively in a hydrated state. Certain dehydrins have been found to electrostatically interact with membrane lipid head groups in solution. Direct evidence for stress protection conferred by LEA proteins is rare. Numerous studies with plants ectopically expressing LEA proteins have reported comparatively modest gains in stress tolerance.

Besides LEA proteins, other protective proteins accumulate in resurrection plants and generally in plant cells affected by water loss. The most prominent ones are **small heat shock proteins** (**sHSPs**). They show true chaperone characteristics in addition to a general stabilising effect on cellular macromolecules and membranes. A third group of protective proteins comprises **ROS scavenging enzymes** such as aldehyde dehydrogenases and peroxiredoxins (Chap. 2) to counteract the production of ROS in cells affected by water loss.

6.3.3 Regulation of the Stomatal Aperture

Leaf surfaces sealed by a cuticle and wax deposition represent a key innovation for the evolution of land plants. Without an effective barrier against water loss the maintenance of a relatively constant internal water status (**homoiohydry**) would not be possible in most terrestrial habitats. While there is considerable variation in the effectiveness of the sealing—for example, between plants inhabiting wetlands and xerophytes thriving in arid habitats—the cuticular water conductance rarely accounts for more than a small fraction (10% or less—much less in the case of xerophytes with a thick cuticle and massive wax deposition) of total evaporation. Most of the gas exchange and, with that, most of the water loss are due to **stomatal conductance**. It has been estimated that about 60% of all terrestrial rainfall globally is returned to the atmosphere through stomata. In water-limited ecosystems this proportion can be even higher (Katul et al. 2012) (Chap. 9). Because of the large difference in water potential between leaves and air (with the air having very negative values), the control of the **stomatal aperture** is the most important response to conditions of low water availability—for example, a more negative soil water potential. Regulation of stomatal conductance therefore plays a key role in a plant’s response to water deficit and drought stress tolerance. Plants that are unable to close their stomata die quickly when water is withheld.

Several internal and environmental cues are integrated by **guard cells** (which form the stomatal pore) in order to optimally adjust the stomatal aperture for any given physiological situation. Stomatal opening is in most plants (with the exception of CAM plants; Sect. 6.6) triggered by light. Stomatal closure under conditions of water limitation is elicited by the phytohormone **abscisic acid** (**ABA**) (Fig. 6.12) (for ABA signal transduction, Sect. 6.5). Other factors influencing the stomatal aperture are temperature (with lower temperatures favouring opening) and internal CO_2 (with higher CO_2 partial pressure favouring

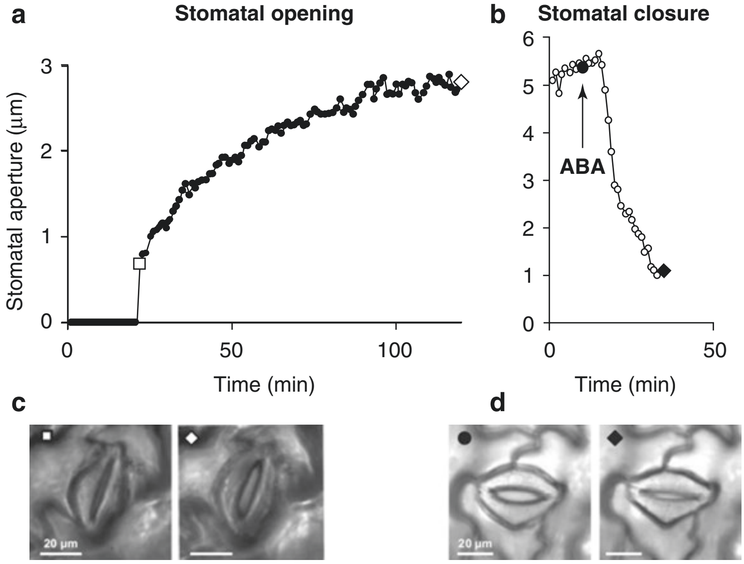


Fig. 6.12 Light-induced and abscisic acid (ABA)–induced stomatal movement in the abaxial epidermis of intact tobacco leaves. **a** At *t* = 0 the leaves were illuminated with white light. The images shown in **c** correspond to the open symbols on the graph in **a**. **b** ABA (10 µM) was applied to the leaf cuticle. The images shown in **d** correspond to the closed symbols in **b**. Note the different response kinetics. (Kollist et al. 2014)

closing). Recognition of microorganisms via microbe-associated molecular patterns (MAMPs; Chap. 8) leads to stomatal closure because stomata represent important entry sites for pathogens.

The **stomatal aperture** is nearly linearly correlated with the **guard cell turgor pressure**. Guard cells are built in such a way that higher turgor pressure leads to a bending of the cells and thereby an opening of the pore between them. The turgor pressure is a function of the osmotic potential of the cells. A more negative value relative to the apoplast results in water influx, and vice versa. Thus, the concentration of solutes in guard cells determines stomatal conductance. **Stomatal movement** is driven by the transport, as well as the synthesis and degradation, of solutes. Most important are K^+ ions and their counter ions Cl^- and malate^{2-}. Changes in K^+ and Cl^- concentrations are brought about by ion channel–mediated exchange between guard cells and the surrounding apoplast, as well as between guard cell vacuoles and the cytosol. Malate, in contrast, is either synthesised from starch or degraded via mitochondrial respiration either in guard cells or in neighbouring epidermal cells. Because the majority of solutes are stored in the vacuoles, the control of stomatal movement depends on the modulation of transport activities in both the plasma membrane and the tonoplast.

The principal classes of transporters are described in Chap. 7. Negative membrane potentials across the plasma membrane and the tonoplast are generated by different types of proton pumps: P-type H^+-ATPases in the plasma membrane and V-type ATPases and pyrophosphatases in the tonoplast (Fig. 6.13). K^+ influx and efflux is mediated by K^+ channels, whose activity is dependent on the plasma membrane potential. **Inward-rectifying channels** (i.e. channels allowing the passage of ions more easily into the cell) open at membrane potentials more negative than the resting potential for K^+ (i.e. upon **hyperpolarisation**) and mediate K^+ influx. **Outward-rectifying K^+ channels** (i.e. channels allowing the passage of ions more easily out of the cell) open at membrane potentials more positive than the resting potential for K^+ (i.e. upon **depolarisation**) and mediate K^+ efflux. K^+ uptake into the vacuole occurs against a concentration gradient and the electrical potential difference. Thus, it is assumed to require K^+/H^+ symport. Efflux from the vacuole is channel mediated.

Because of the **voltage dependence** of K^+ channels in the plasma membrane, K^+ movement into and out of guard cells is controlled by the

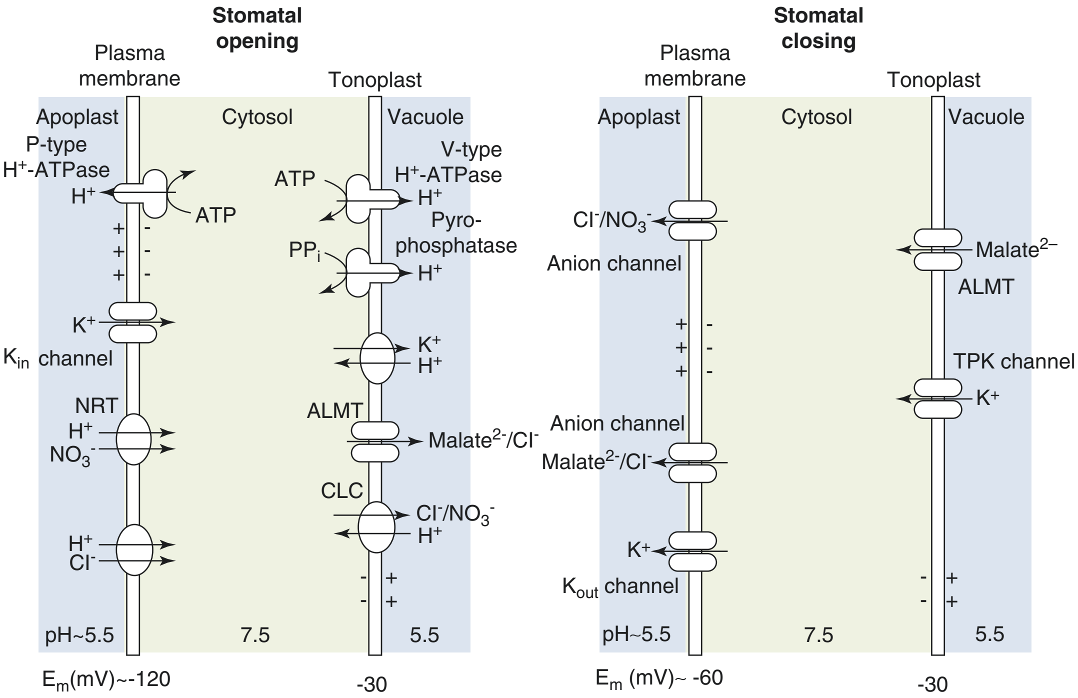


Fig. 6.13 Plasma membrane–localised and tonoplast-localised channels and transporters involved in opening and closing of stomata. Proton pumping activities of P-type H$^+$-ATPases, V-type H$^+$-ATPases and pyrophosphatases result in an acidic pH of the vacuole and the apoplast. Opening of stomata is triggered by a stimulation of proton pumping that renders the potential of the plasma membrane more negative (approximately −120 mV), which activates inward-rectifying K$^+$ channels (K$_{in}$ channels). Influx of anions is dependent on H$^+$-driven symporters such as the NRTs in the case of NO_3^-. The K$^+$ ions taken up into the cytosol are transported into the vacuole by NHX transporters—antiporters driven by H$^+$ flux. Anions and malate are stored in the vacuole, following passage through anion channels (ALMT) or transporters (CLC). Stomatal closure is initiated by the activation of anion channels. The efflux of anions out of the cell depolarises the plasma membrane to about −60 mV. Outward-rectifying K$^+$ channels open and K$^+$ efflux occurs. (Modified from Kollist et al. (2014))

plasma membrane potential. **Hyperpolarisation** is achieved by increases in proton pumping activity. Light-triggered stomatal opening is dependent on blue light receptors (phototropins), which further activate H$^+$-ATPases, leading to hyperpolarisation, K$^+$ influx and, finally, osmotically driven water uptake. There is also evidence for an opening in response to photosynthetically active radiation, which is mechanistically poorly understood. The actual signal sensed by the guard cells could be the lowering of the CO_2 concentration in the sub-stomatal cavity owing to active photosynthesis. In this way, CO_2 demand would be coupled to the stomatal aperture.

ABA-triggered stomatal closure is mediated by an inactivation of proton pumps and a concomitant activation of Cl$^-$ channels (such as SLAC1) in the plasma membrane. The resulting depolarisation opens the outward-rectifying K$^+$ channels and thereby causes K$^+$ efflux and water loss into the apoplast (Fig. 6.14). ABA signal transduction is discussed in Sect. 6.5. Other factors triggering stomatal closure include low humidity and elevated atmospheric CO_2 levels (Chap. 10).

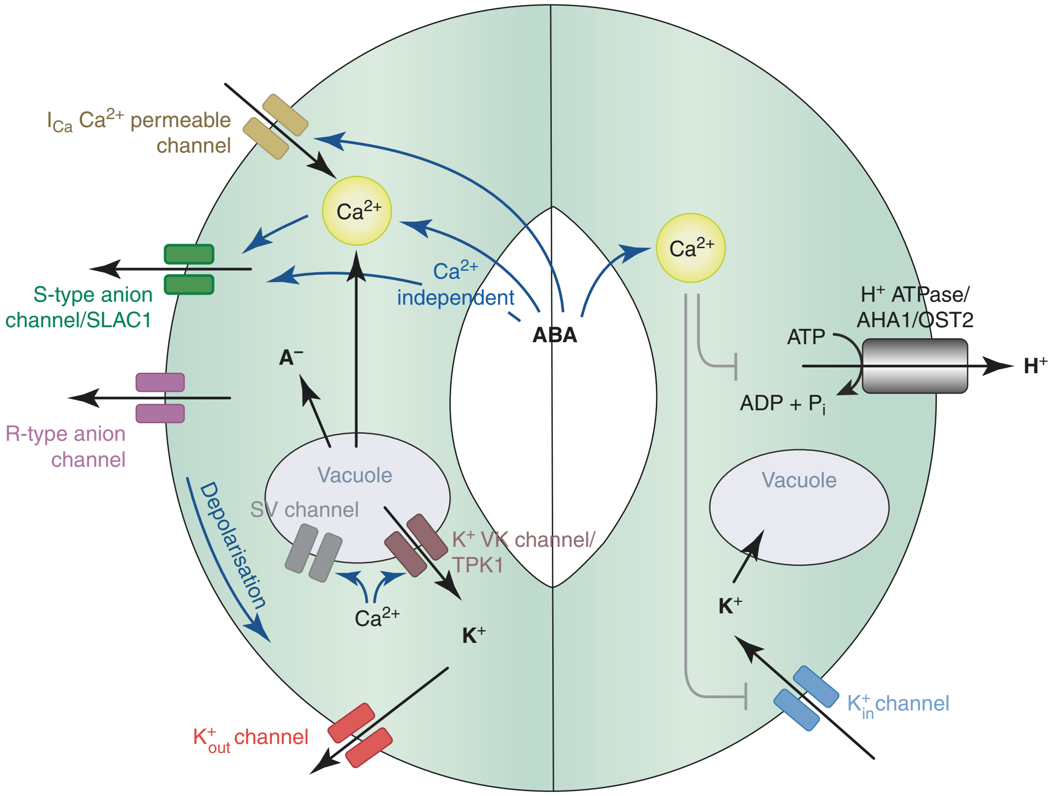


Fig. 6.14 Abscisic acid (ABA)–dependent guard cell ion channel regulation. ABA triggers stomatal closure (shown on the *left*) and inhibits stomatal opening mechanisms (shown on the *right*), which are activated, for instance, by blue light. *AHA1* ARABIDOPSIS H+ ATPASE 1, I_{Ca} inward Ca^{2+} current, *OST2* OPEN STOMATA 2, *R-type* rapid-type, *SLAC1* SLOW ANION CHANNEL 1, *S-type* slow-type, *SV* slow vacuolar, *TPK1* TWO PORE K^+ CHANNEL 1, *VK* vacuolar K^+ selective. (Kim et al. 2010)

6.4 Acclimation of Growth

An integral part of a plant's acclimation to water deficit caused by drought or high salt—and essentially an avoidance strategy—is the reduction of leaf area relative to biomass. In this way the loss of water via transpiration is reduced and the water status of the plant is improved. Indirectly this strategy also lowers the risk of overheating that accompanies the closing of stomata. Unfortunately for a plant, this water-saving strategy comes with the cost of potentially lower reproductive success because fewer resources can be accumulated during the vegetative stage to produce viable seeds. The other problem is the risk of being outgrown by faster-growing competitors. It therefore represents one of the fundamental challenges for plants to find the right balance between investment in stress tolerance on the one hand and growth on the other hand (Fig. 6.15) (Claeys and Inzé 2013) (Chap. 2). Accordingly, a wide natural variation exists between species, and even within species, with respect to the thresholds of water supply that trigger a strong reduction or even halt of leaf growth. Depending on the extent of the stress, different strategies can be successful. Continued growth can be beneficial in comparatively mild water limitation scenarios but detrimental when a plant is exposed to a longer drought.

A second **acclimation of growth** under conditions of water scarcity is the stimulation of root growth in order to improve the water uptake capacity and to access additional water resources.

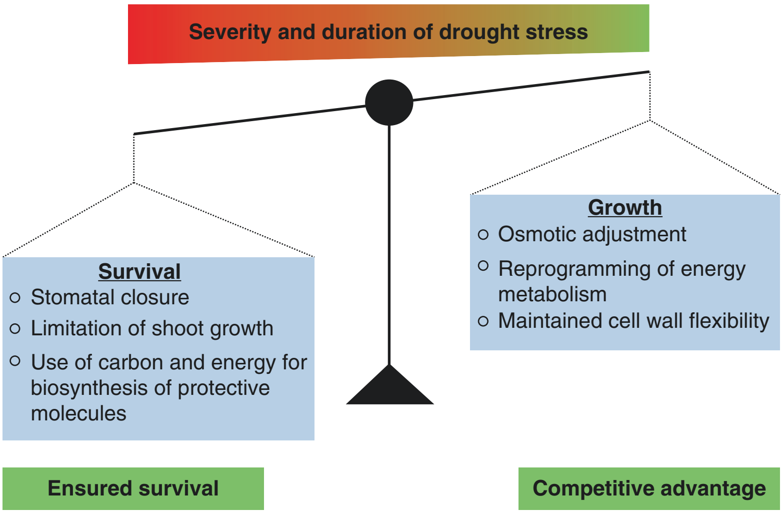


Fig. 6.15 The trade-off between stress tolerance and maintained growth. In response to water limitation, stress avoidance and tolerance mechanisms are activated to ensure survival in case the stress is prolonged or becomes more severe, resulting in growth limitation and a potential competitive disadvantage. On the other hand, acclimative mechanisms exist that allow continued growth in situation where the stress is less severe. (Modified from Claeys and Inzé (2013))

This strategy is viable as long as there is soil water available. Under more severe drought, root growth also becomes inhibited. The plasticity of roots in response to drought goes beyond the size. The **root system architecture**—that is, the combination of the primary root length, lateral root formation, and root hair density and length, as well as root diameters—is highly flexible and can be adjusted in response to environmental fluctuations (Chaps. 2 and 7).

It is one of the major principles of plant stress tolerance that **growth reduction** under unfavourable conditions is not simply a consequence of disturbance or damage but, rather, an active modulation of resource utilisation (Chap. 2). The slowing of growth is a result of balanced **hormonal control**. Molecular understanding of underlying mechanisms has developed rapidly and is summarised in this chapter with regard to drought.

6.4.1 Inhibition of Shoot Growth

Shoot growth responds very rapidly to water deficit. Acclimative slowing of growth can be observed within 20–30 min. The response occurs even in the absence of any changes in the water potential of the elongating cells. Thus, it is not a mere consequence of turgor loss. Furthermore, growth halts much faster than photosynthesis under drought conditions. A shortage of reduced carbon can therefore be ruled out as the cause of the growth reduction as well. In fact, sugars often accumulate after the onset of stress, meaning that growth is uncoupled from the availability of carbon under these conditions, once more indicating controlled processes rather than simple supply-driven processes. An important inference from active growth modulation is that growing tissues and mature tissues—for example, young sink leaves and old source leaves—respond differentially to stress (Fig. 6.16). This principal difference is indicated by many observations but has not been systematically dissected yet at the molecular level (Claeys and Inzé 2013).

Growth is determined by the **cell division rate** and **cell expansion rate**. Under water-limited conditions, both processes are actively modulated in shoots. **Cell cycle** activity, which determines the cell division rate, is triggered by cyclin-dependent kinases and associated cyclins (see molecular biology and biochemistry textbooks). The major pathways controlling cyclin-dependent kinases are all responsive to drought. For instance, repression of the anaphase-promoting complex/cyclosome (APC/C), a master negative regulator of cell cycle activity in eukaryotes, is down-regulated, leading to reduced cyclin-dependent kinase activity. The cell cycle control pathways themselves are controlled by **DELLA proteins** as central regulators of **gibberellic acid** signalling and growth (Chap. 2). The stress hormone **ethylene** has also been implicated in cell cycle arrest. A very early transcriptional response to osmotic stress specifically in

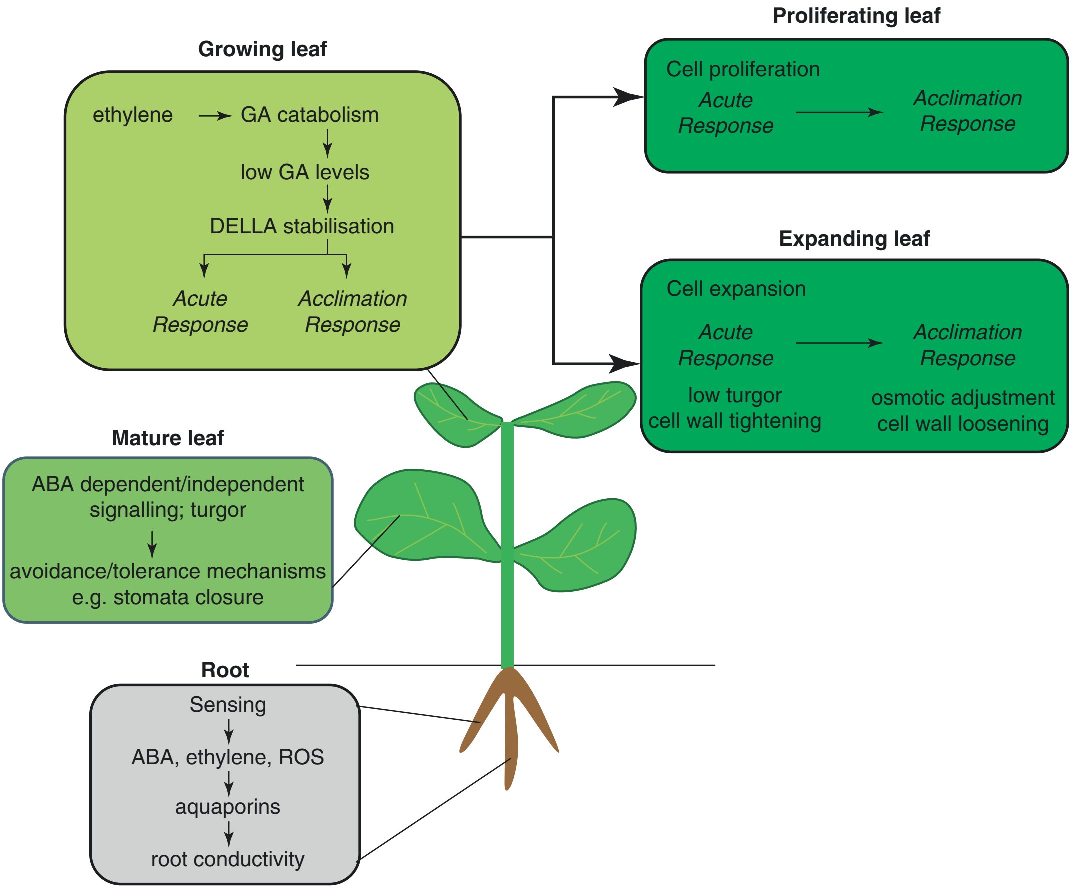


Fig. 6.16 Processes involved in growth regulation upon drought. The responses differ between mature and growing leaves and, in the latter, between proliferating leaves (growth by cell division) and expanding leaves (growth by cell expansion). Soil drying is sensed in roots, activating a combination of hydraulic and chemical signals, which are transported through the xylem to the leaves (Fig. 6.18), where they initiate a number of tolerance mechanisms. The response of mature leaves can be described by the avoidance/tolerance concept. In growing leaves, stress leads to acute growth inhibition followed by growth acclimation, both mediated by DELLA signalling—that is, the inhibition of gibberellic acid signalling. Ethylene promotes DELLA stabilisation and growth inhibition. While hormonal signalling is common between expanding and proliferating leaves, effector genes are distinct. In proliferating leaves, inhibitors of the cell cycle might play a role in the acute response. In expanding leaves, cell wall tightening and changes in cell turgor lead to growth cessation, while osmotic adjustment and cell wall loosening are important for growth acclimation. (Modified from Skirycz and Inzé (2010))

growing leaves is the up-regulation of ethylene response factors that stimulate the catabolism of gibberellin (Claeys and Inzé 2013).

Cell expansion requires turgor pressure and sufficient extensibility of the cell wall. Aquaporin-facilitated water uptake can lead to cell enlargement, provided that the osmotic driving force for water uptake—that is, the intracellular concentration of solutes such as K^+—is strong enough. The higher the rigidity of the cell (the lower the extensibility of the cell), the higher the pressure required to expand the cell. The dynamics of **cell wall** characteristics therefore play a central role in plant growth processes. Cell wall flexibility is modulated, on the one hand, by ROS-dependent cross-linking and cleavage reactions and, on the other hand, by enzymes modifying the structure of pectins or influencing the interaction between cellulose microfibrils and hemicelluloses (for cell wall structure, see plant biochemistry and plant physiology textbooks). Such enzymes include pectin methylesterases, xyloglucan endotransglucosylases/hydrolases and expansins. Their expression patterns change substantially under conditions of drought (Tenhaken 2015). The precise and high-resolution description of **cell wall dynamics** and growth processes at the cell, tissue and organ levels is a complex systems biology problem, which is very actively studied and far from being solved. However, three aspects can be singled out to help illustrate the shoot growth responses under conditions of water scarcity. First, osmotic adjustment can maintain the turgor pressure to enable continued growth under stress and may thus have different significance for cells of growing leaves than for those of mature leaves. In the latter, the main purpose of osmotic adjustment is avoidance of water loss. Second, cell expansion with reduced turgor pressure can be achieved by increasing the flexibility of the cell wall. Third, growth can be effectively stopped by a stiffening of the cell wall. Shoot growth under drought often goes through two different phases. During the acute phase, growth ceases as a consequence of cell wall stiffening. In a second phase of **growth acclimation** the cell wall becomes more flexible again to support new expansion growth (Skirycz and Inzé 2010). Depending on the severity of stress and on the genetic variation selected for in habitats varying in the extent of water limitation, different processes can be dominant to establish the right balance for the fundamental **trade-off** between growth and stress tolerance. For instance, a detailed study of *A. thaliana* responses showed that under mild drought stress the expression of expansins was up-regulated (that is, cell walls became more extensible and growth was maintained) whereas under more severe drought, expansins were down-regulated (Harb et al. 2010) (that is, cell walls were more rigid and growth was halted).

Plants not only reduce the growth of evaporative surfaces when they are water limited; they also lower the density of **stomata** per epidermal cell and per unit of leaf area to further reduce water loss. In developing leaves the divisions of epidermal cells are controlled in such a way that under drought conditions, fewer stomata arise. This process is under the control of the mature leaves and their perception of water status. **ABA** is a key molecule also in regulating stomatal development (Chater et al. 2014).

6.4.2 Stimulation of Root Growth

The root system architecture belongs to the "hidden half" of plant biology. **Plasticity of root growth** has, for a long time, not been studied as extensively as the plasticity of shoot growth. This changed only recently (Chap. 7), at least partly fuelled by the expectation that major advances in sustainable agriculture may be achievable by breeding for relevant root traits.

A general shift in plant growth under water limitation is the increase in the root to shoot biomass ratio. This applies at least to situations of mild stress. More pronounced drying of the soil inhibits root growth as well, in part because of high **soil impedance**—that is, an increase in the force needed to penetrate the soil. Overall, the plasticity of the root system is even greater than that of the shoot. For instance, the surface area can vary more widely because of the tremendous influence of root hairs on the total surface. Mechanistically, the modulation of root system architecture in response to soil water is barely understood. **Auxin** gradients and **cytokinins** play a major role in controlling root morphology. **ABA** is known to influence the respective pathways.

6.5 Sensing of Water Status and Signal Transduction

As described above, a multitude of responses and acclimations is triggered by water deficit. Since the plant is part of the hydraulic soil–plant–air continuum and the cells are symplastically connected (with the exception of guard cells) (Steudle 2001), responses have to be coordinated in the entire organism. The stomatal aperture, for instance, has to be synchronised with the resistance of leaf and root tissue to water flow. Water shortage is translated into the stimulation of root growth. There is ample evidence for rapid responses of shoots to the root water status, and vice versa. Thus, **long-distance signalling** has to be in operation.

The most important endogenous signalling molecule mediating these responses is **ABA**. Its synthesis is rapidly and strongly up-regulated under drought stress (Fig. 6.17). Mutants lacking

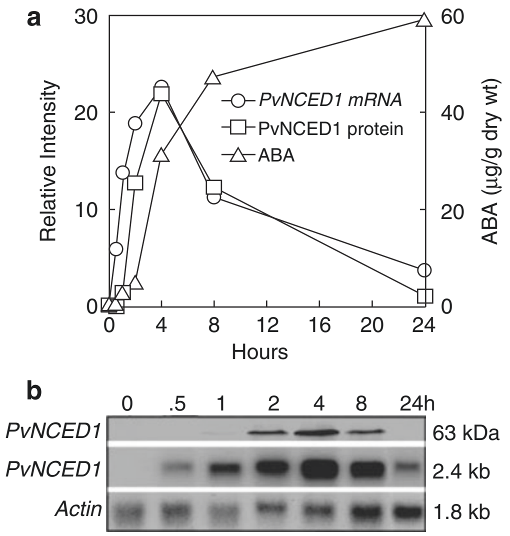


Fig. 6.17 Abscisic acid (ABA) synthesis is rapidly upregulated upon dehydration of leaves. Upon water deficit, genes encoding the nine-*cis*-epoxycarotenoid dioxygenases (*NCEDs*) are transcriptionally activated. NCEDs catalyse the rate-limiting step in ABA synthesis. This activation results in a rapid rise in ABA concentrations. **a** Time course of changes in *NCED* messenger RNA (mRNA) and NCED protein abundance, as well as ABA concentrations occurring in detached, wilting *Phaseolus vulgaris* leaves. **b** Western blot and northern blot analysis of NCED protein and *NCED* mRNA, respectively. (Qin and Zeevaart 1999)

the ability to synthesise ABA are not able to withstand even a mild water deficit. ABA activates the majority of avoidance and tolerance mechanisms, including stomatal closure, the regulation of aquaporin abundance and activity, synthesis of protective proteins and osmoregulation. There is, however, also ABA-independent drought stress signalling. Furthermore, the rapid signalling of water status from the roots to the shoots, and vice versa, cannot be explained by ABA alone. ABA increases have frequently been detected in the xylem sap. However, grafting experiments with tomato and *A. thaliana* plants have demonstrated that leaves can respond normally to water deficit perceived by roots even when the roots are unable to synthesise ABA, so no ABA can travel to the shoot with the transpiration stream (Christmann et al. 2007).

ABA is an ancient molecule, detectable in all organisms with the exception of Archaea. Still, phylogenetic analysis of the main components of the core ABA signalling module (Fig. 6.20) suggests that ABA-dependent signalling apparently evolved in land plants (Hauser et al. 2011). Most drought stress avoidance and tolerance mechanisms are ABA dependent. Also, ABA triggers both rapid responses (within minutes), such as the closing of stomata, and responses that require changes in gene expression—that is, responses that depend on the interaction of transcription factors with *cis* elements in the promoters of stress tolerance genes and take hours to days. Three layers of ABA action can be differentiated: synthesis and transport, perception, and signal transduction (Hauser et al. 2011).

6.5.1 Sensing of Water Status

How a plant cell senses its water status and converts this into a signal has not been fully elucidated yet. Principally, two modes are discussed: the sensing of mechanical forces exerted on the plasma membrane by changes in turgor pressure or the sensing of osmotic potential by proteins sensitive to osmotic changes. The former could be mediated by mechanosensitive ion channels, the latter by osmosensitive kinases or other proteins able to transduce signals. Examples of both types of sensing are known from bacteria and yeast.

One current model assumes the sensing of a long-distance **hydraulic signal** (low water potential) by cells in the vasculature that would locally be transformed into a chemical signal—namely, ABA. Sensing of the water status and stimulated **ABA synthesis** are connected by a signal transduction pathway involving transient increases in cytosolic Ca^{2+} (Fig. 6.18) (Christmann et al. 2013). Recently, a first plant osmosensor may have been identified in *A. thaliana* (Yuan et al. 2014). Through a genetic screen for mutants with an impaired cytosolic Ca^{2+} response upon exposure to hyperosmolality, a Ca^{2+}-permeable channel gated by hyperosmolality was found. When this channel (OSCA1) is defective, both rapid cellular responses and long-term whole-plant responses to osmotic stress are compromised.

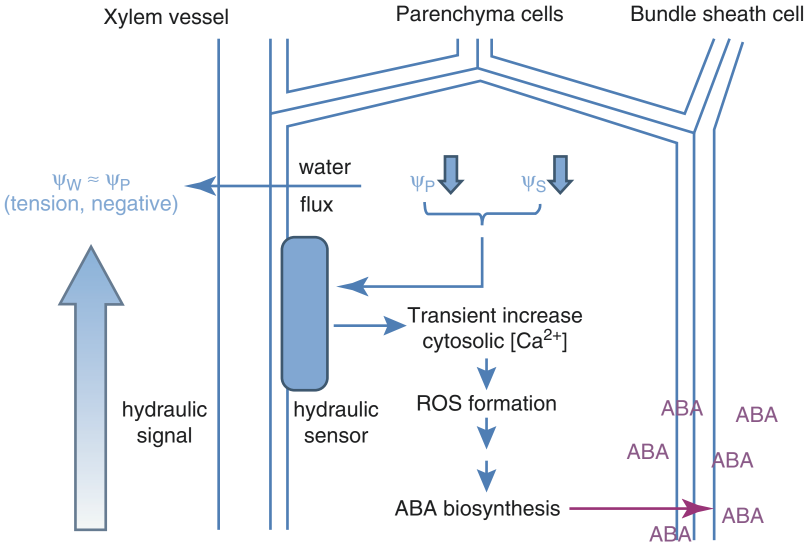


Fig. 6.18 Model of hydraulic signalling: a long-distance hydraulic signal (decrease in water potential (Ψ_w)) travels through the plant in the xylem and is locally converted into a biochemical signal. The decrease in Ψ_w causes water flux along the Ψ_w gradient out of the parenchyma cells within, for example, the shoot vasculature, as shown here. The resulting decrease in turgor pressure (Ψ_p) and osmotic potential (Ψ_S) is sensed by an unidentified receptor, which triggers a signalling cascade (a transient increase in cytosolic Ca^{2+} and production of reactive oxygen species (ROS)). The signalling activates ABA biosynthesis. ABA synthesised in parenchyma cells is exported to bundle sheath cells and beyond to trigger acclimative responses. (Modified from Christmann et al. (2013))

Plants can still respond to ABA normally, yet stomatal closure upon water deficit is impaired. This places OSCA1 upstream of ABA signalling and fulfils the criteria for the hypothetical **osmosensor** depicted in Fig. 6.18.

6.5.2 ABA Signal Transduction

ABA biosynthesis is known to occur predominantly in vascular parenchyma cells of roots and shoots (Fig. 6.18). Both the responsible enzymes and the expression of the respective genes have been detected there. Plasma membrane–localised **ABC-type transporters** such as ABCG25 in *A. thaliana* can export ABA. Cells respond to ABA synthesised by the cell itself and to ABA taken up from the apoplast. Uptake of ABA into guard cells is mediated by another ABC-type transporter (ABCG40 in *A. thaliana*). Lack of its activity reduces the responsiveness of guard cells to ABA (Fig. 6.19).

The earliest events in **ABA signalling** are mediated by a central regulatory module, which consists of three protein classes, the soluble **ABA receptor PYR** (PYRABACTIN RESISTANCE; also called RCAR, for REGULATORY COMPONENTS OF ABA RECEPTORS), protein phosphatases 2C (PP2C) and protein kinases (SnRK2s for SNF1-related protein kinases 2) (Fig. 6.20). Several isoforms of each of these proteins are encoded by plant genomes. This provides flexibility for the ABA signalling, which occurs in all kinds of cells and during all developmental stages. The signalling pathway formed by the three types of proteins is double negative. In the inactive state the protein SnRK2, which triggers the ABA responses, is inhibited by PP2C. Upon binding of ABA the receptor PYR interacts with PP2C and thereby inactivates it. This releases SnRK2 from the inhibition and enables the phosphorylation of several possible target proteins.

The comparatively slow transcriptional responses to ABA are brought about by the phosphorylation of **transcription factors** such as AREB1 and AREB2. In the phosphorylated state these proteins are able to interact with ABA

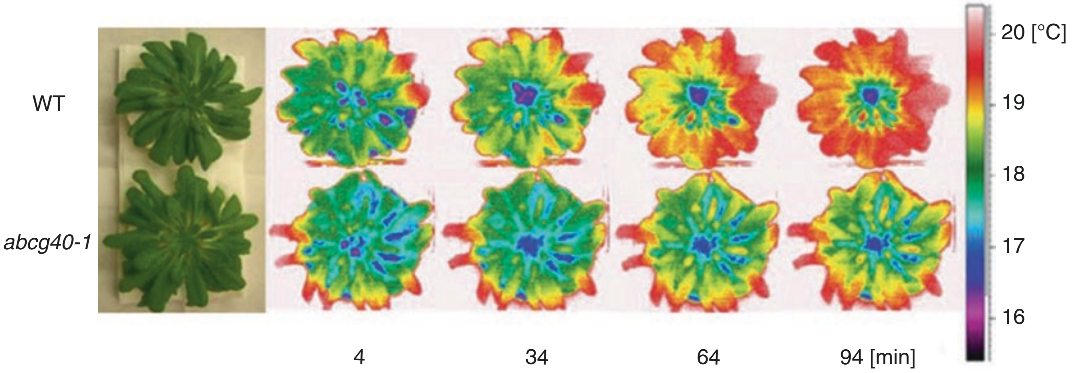


Fig. 6.19 Abscisic acid (ABA) import into guard cells is required for the normal ABA response, emphasising the importance of ABA uptake into guard cells and intracellular ABA sensing. Elevation of leaf temperature due to stomatal closure and a concomitant decrease in transpirational cooling can be detected after ABA treatment. The response is delayed in *atabcg40* plants defective in an ABA-importing ABC-type transporter. Less ABA reaches the inside of the guard cells per unit of time. The leaf temperature was monitored using an infrared thermal imaging camera after the addition of ABA. (Kang et al. 2010)

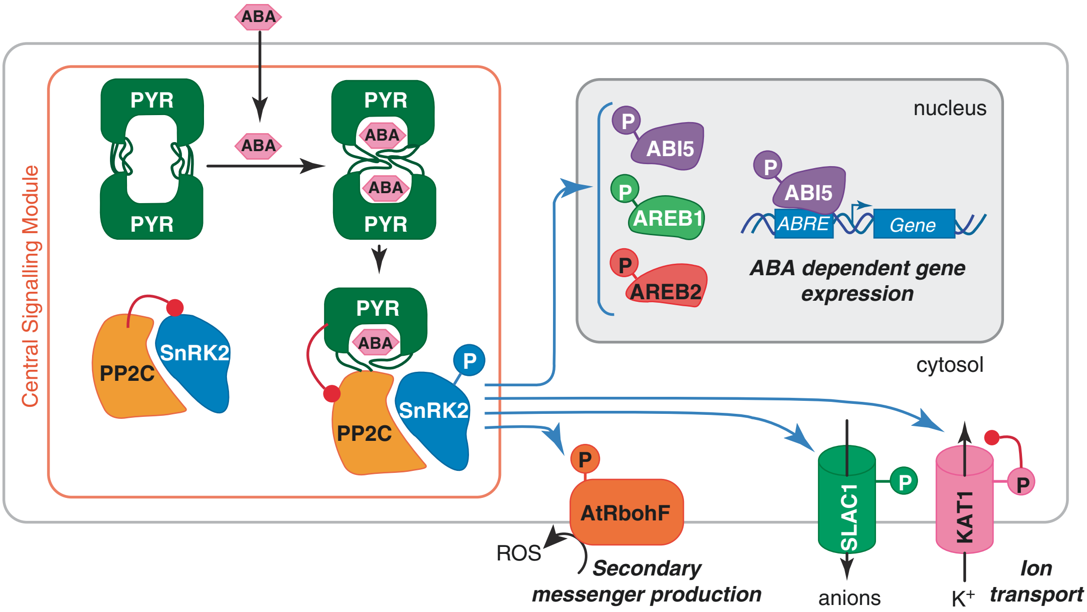


Fig. 6.20 The core abscisic acid (ABA) signalling module. Protein phosphatases 2C (PP2Cs, *yellow*) inhibit protein kinases (SnRKs) (indicated by the *red symbol*) in the absence of ABA. ABA is bound by intracellular receptors (PYR dimers), which dissociate and form ABA receptor–PP2C complexes. This complex formation inhibits PP2Cs and allows activation of SnRKs. SnRKs then phosphorylate (indicated by *blue arrows*) target proteins. Several SnRK targets are known, of which only a subset are depicted here. ABA can activate both fast and slow responses because the SnRKs can modulate either ion channel activity or transcription factor activity, respectively. In addition, SnRKs can trigger downstream signalling events—for instance, by activating reduced nicotinamide adenine dinucleotide phosphate (NADPH) oxidases (AtRbohF), which produce reactive oxygen species. (Hubbard et al. 2010)

response elements (ABRE) in the promoters of ABA-responsive genes and to activate transcription. Target genes of these and related transcription factors encode, for instance, protective proteins such as LEA proteins and enzymes involved in compatible solute synthesis.

ABI5 is a transcription factor whose target genes maintain **seed dormancy**—one of the developmental processes under ABA control. Thus, the core signalling module is important for all types of ABA-dependent processes.

Rapid responses of guard cells are elicited by the activation of the anion channel SLAC1 and the inactivation of the **inward-rectifying K^+ channel** KAT1. The resulting **depolarisation** of the plasma membrane opens **outward-rectifying K^+ channels**, resulting in K^+ efflux, turgor loss and stomatal closure (Figs. 6.13 and 6.14). SnRK2 also triggers additional signalling events such as the formation of ROS by NADPH oxidases (e.g. RbohF).

Besides **ROS**, other **second messengers** are involved in ABA signalling. Transient increases in **cytosolic Ca^{2+}** concentrations, as a very common element of signalling cascades (Chap. 2), are observed in ABA-treated guard cells too. The central **ABA signalling module** (Fig. 6.20) is not Ca^{2+} dependent. Instead, Ca^{2+} signalling modulates targets of the core pathway. ROS production stimulates a cytosolic Ca^{2+} increase which, via the action of Ca^{2+}-dependent protein kinases, affects the activity of **anion channels** such as SLAC1. It is conceivable that the necessary integration of various environmental and physiological cues in guard cells, which is essential for a plant responding to many simultaneously changing aspects of its natural environment, is at least in part achieved by the convergence of several signalling pathways on the anion channels as central control points for the plasma membrane potential. Anion channel phosphorylation in multiple sites by different kinases controlled by distinct signalling pathways could provide a mechanism for such **signal integration** (Kollist et al. 2014).

6.5.3 ABA-Independent Signalling

ABA is clearly the central stress hormone controlling water deficit responses. Still, in mutant plants unable to respond to ABA, there can be induction of drought stress-responsive genes. This demonstrates the existence of signalling pathways that do not require ABA. A known pathway activates **transcription factors** of the CBF/DREB class, which are involved in ABA-independent signalling during cold acclimation (Chap. 4). Some of these proteins trigger dehydration responses instead. The promoters of their target genes contain a *cis* element called the dehydration responsive element (DRE) or C-repeat.

6.6 Photosynthesis Variants with Improved Water Use Efficiency

Plants are dependent on the uptake of CO_2 through stomata, which inevitably results in evaporation of H_2O. Two major variants of photosynthesis have evolved that reduce the amount of water vapour lost per unit of carbon fixed. In other words, they increase the **water use efficiency**—that is, the ratio of dry weight gained (= growth) to water lost. In regular **C_3 photosynthesis**, about 500 g of H_2O is spent per gram of carbon assimilated. The cost is reduced to about 250 g of H_2O per gram of carbon in plants displaying **C_4 photosynthesis** and to only 50–100 g of H_2O in **CAM plants** (Table 6.3). Both mechanisms share a first fixation of CO_2 by the enzyme phosphoenolpyruvate carboxylase (**PEP carboxylase**) prior to a second ribulose-1,5-bisphosphate carboxylase/oxygenase (**RubisCO**)–dependent fixation of CO_2 after its release through decarboxylation of the storage molecule malate. The competitive advantage of higher water use efficiency is evident from the fact that plants showing these photosynthesis variants are predominantly found in arid and dry regions of the world (Chap. 10).

6.6.1 C_4 Photosynthesis

In every plant, CO_2 is fixed by **RubisCO**. This enzyme, which represents by far the most abundant protein on Earth, catalyses the first reaction of the **Calvin cycle** between an activated pentose phosphate, ribulose-1,5-bisphosphate and

Table 6.3 Water use efficiency, photosynthesis and biomass production of C_3, C_4 and CAM plants. Crassulacean acid metabolism (CAM) plants are superior to other photosynthetic types in their water use efficiency[a], but their photosynthetic rates and growth rates are much lower (Lüttge et al. 1994)

Type of photosynthesis	C_3	C_4	CAM
Water use efficiency (g water/g C)	450–950	250–350	18–100 (night-time) 150–600 (daytime)
Maximum rate of net photosynthesis (μmol CO_2 m^{-2} s^{-1})	9–25	25–50	0.6–8
Growth (g biomass m^{-2} day^{-1})	50–200	400–500	1.5–1.8

[a] Water use efficiency is defined as the ratio of dry weight gained (= growth) to water lost

CO_2 (the **carboxylase activity**), yielding two molecules of 3-phosphoglycerate—a molecule with three C atoms (hence the term **C_3 photosynthesis**). In conditions of a vast excess of O_2 versus CO_2, RubisCO also catalyses the reaction of ribulose-1,5-bisphosphate with O_2 (the **oxygenase activity**), yielding one molecule of 3-phosphoglycerate and one molecule of 2-phosphoglycolate. This side reaction poses a problem, as 2-phosphoglycolate is a useless toxic metabolite that should not accumulate. 2-Phosphoglycolate is converted to 3-phosphoglycerate via **photorespiration**, a pathway that requires the metabolic activity of three organelles—namely, peroxisomes and mitochondria, besides chloroplasts where 2-phosphoglycolate is produced (see plant physiology and plant biochemistry textbooks). Of the carbon in 2-phosphoglycolate, 75% is returned to the Calvin cycle as 3-phosphoglycerate.

The efficiency of ribulose-1,5-bisphosphate carboxylation is about 100-fold higher than that of the oxygenation. Thus, only gradually with the accumulation of oxygen in the atmosphere did this side reaction of RubisCO become relevant. RubisCO evolved in an atmosphere that was essentially devoid of molecular oxygen.

Furthermore, it is ecologically important that the carboxylation to oxygenation ratio of RubisCO is influenced by temperature. With higher temperature the oxygenase activity becomes more relevant because RubisCO specificity decreases. Therefore, the need for photorespiration, which negatively affects photosynthetic efficiency in plants with C_3 photosynthesis, grows with increasing temperatures.

At a time about 30 million years ago, when atmospheric CO_2 reached a critically low level, C_4 photosynthesis arose. It has evolved independently many times since then (>60 times according to current counts) in multiple plant families. Through a series of anatomical and biochemical modifications, C_4 photosynthesis achieves a higher concentration of CO_2 in the vicinity of RubisCO, thereby effectively suppressing the oxygenase activity. This results in higher photosynthetic efficiency under conditions that promote photorespiration (low CO_2, high temperature). Typically, two consecutive fixations of CO_2 occur in separate cell types. In mesophyll cells, which in C_4 plants often surround the vascular bundles (including the bundle sheath cells) in a circular arrangement called the **Kranz anatomy**, CO_2 is fixed by **PEP carboxylase** and not by RubisCO, as in C_3 plants. In C_4 plants, RubisCO activity is restricted to the bundle sheath cells which, in contrast to C_3 plants, are more prominent and contain chloroplasts. Fixation of CO_2 as bicarbonate by PEP carboxylase (which does not catalyse a reaction with O_2) produces a C_4 acid, which is then shuttled into the bundle sheath cells where decarboxylation releases CO_2. This CO_2 is utilised by RubisCO in the Calvin cycle (Fig. 6.21). Concentration of CO_2 in the vicinity of RubisCO by primary CO_2 fixation via PEP carboxylase and shuttling of carbon into bundle sheath cells can be seen as the core of C_4 photosynthesis. Variations between plant species exist with respect to the type of C_4 acid (e.g. malate or aspartate) and the nature of the decarboxylating enzymes (malic enzyme in Fig. 6.21).

The **CO_2 pumping** allows RubisCO to operate at near substrate saturation. This offers the potential for very high photosynthetic rates. Furthermore, it enables C_4 plants to reduce

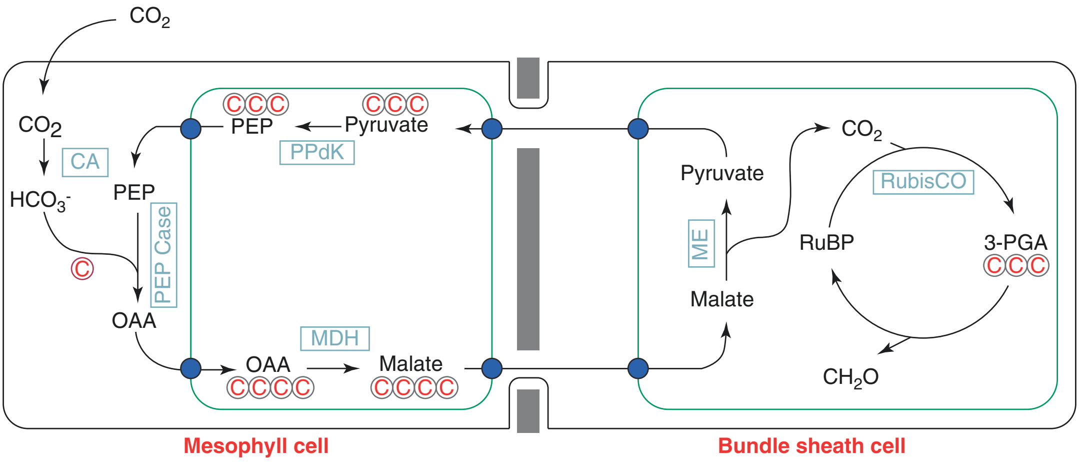


Fig. 6.21 The C_4 photosynthesis core mechanism. The *green boxes* represent the chloroplasts. *Blue dots* represent active transport steps. *CA* carbonic anhydrase, *MDH* malate dehydrogenase, *ME* malic enzyme, *PEPCase* phosphoenolpyruvate carboxylase, *PPdK* pyruvate orthophosphate dikinase, *PEP* phosphoenolpyruvate, *OAA* oxaloacetate, *RuBP* ribulose-1,5-bisphosphate, *3-PGA* 3-phosphoglycerate. (Modified from Langdale (2011))

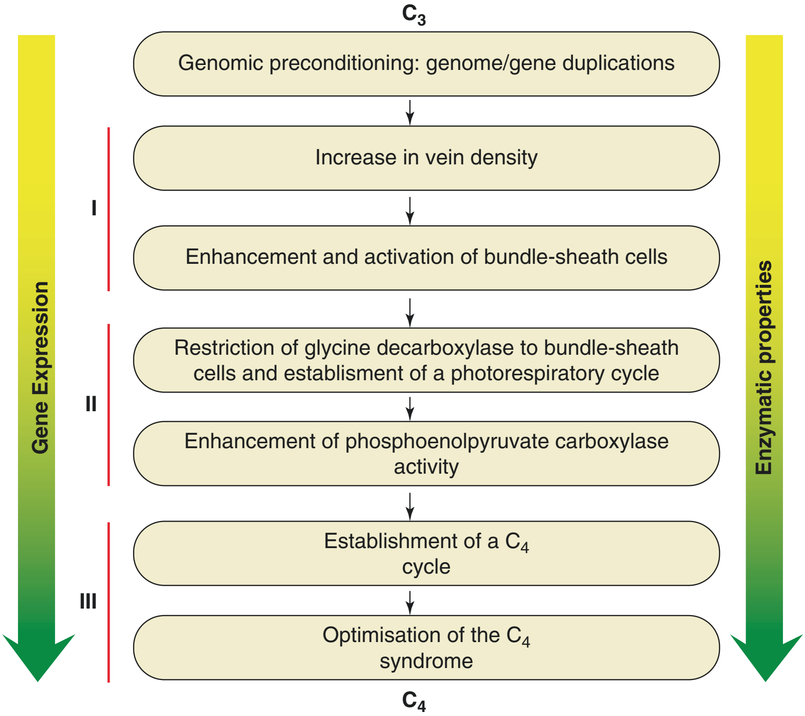
stomatal conductance, which decreases water loss and improves **water use efficiency**. An additional advantage is the lower nitrogen requirement of C_4 plants. Much less investment in RubisCO protein is needed. Higher efficiency of photosynthesis and lower demand for water explain why, today, many biomes—especially in the tropics and subtropics (such as the African savannas)—are dominated by C_4 plants. Of today's vascular plant species, 3% use C_4 photosynthesis. They account for about 25% of total terrestrial photosynthesis. Nevertheless, the distribution of C_4 plants clearly shows that by no means all biomes favour C_4 photosynthesis (Chap. 12, Sect. 12.1). The primary CO_2 fixation consumes extra metabolic energy because the substrate PEP has to be regenerated from pyruvate, a reaction that consumes adenosine triphosphate (ATP). Thus, C_4 plants have lower **quantum use efficiency** than C_3 plants under conditions where photorespiration is low (low light, low temperature).

6.6.2 Evolution of C_4 Photosynthesis

C_4 photosynthesis is characterised by a suite of distinct anatomical, morphological, physiological and biochemical features. Therefore, it is, at first sight, surprising that C_4 photosynthesis has evolved independently so many times from ancestral C_3 photosynthesis. Owing to a large body of research work, we can today describe C_4 photosynthesis as an excellent example of how the evolution of a key adaptation can be understood in an ecological context (Christin and Osborne 2014). Conceptual models have been proposed as to how C_4 photosynthesis developed (Fig. 6.22). Evolution along this path is plausible because for every step, distinct selective advantages can be inferred and factors priming C_3 lineages for the evolution of these steps can be identified. Moreover, some of the steps can be seen in extant **C_3–C_4 intermediate species** (e.g. in the genus *Flaveria*), which represent different stages on the evolutionary trajectory towards C_4 photosynthesis.

All enzymes employed in C_4 photosynthesis are of ancient bacterial origin. A first preconditioning step towards C_4 photosynthesis was the duplication of respective enzyme-coding genes or of whole genomes. The existence of more than one gene copy enabled diversification with respect to localisation, timing and strength of expression. This occurred predominantly via changes in promoter sequences. Furthermore, kinetic properties could change through alterations in coding sequences (right arrow in Fig. 6.22). For example, PEP carboxylases of C_4 plants are less inhibited by malate. This is

Fig. 6.22 Model of the stepwise evolution of C_4 photosynthesis from C_3 photosynthesis (Gowik and Westhoff 2011); see also a similar model in Sage et al. (2012)



functionally important, as CO_2 fixation by PEP carboxylases has to function in the presence of high malate concentrations (Fig. 6.21). The PEP carboxylase genes in C_4 plants show signs of strong positive selection in their sequences, meaning there is evidence that amino acid changes affecting the kinetic properties of the encoded enzymes were selected during the evolution of C_4 photosynthesis.

The efficient exchange of metabolites between mesophyll and bundle sheath cells is promoted by high vein density, as this reduces the distances between the two cell types. The high vein density typical of many C_4 lineages offers advantages for C_3 plants too. For example, there are more pathways for water transport into and through the leaves. This could improve drought tolerance and photosynthetic rates in arid, high-light environments.

The higher proportion of leaf volume occupied by bundle sheath cells with only a few chloroplasts and therefore low photosynthetic capacity could have exerted selective pressure to increase the number of chloroplasts and other organelles in these cells. Related to the higher metabolic activity of bundle sheath cells in C_4 plants is the **photorespiratory CO_2 pump** found in extant **C_3–C_4 intermediates**. Restriction of the glycine decarboxylase activity (for details of the photorespiration pathway, see plant biochemistry or plant physiology textbooks) to mitochondria of bundle sheath cells forces the processing of all photorespiratory glycine in these cells (sometimes this is referred to as the "C_2 cycle"). The decarboxylation releases CO_2 at a site more distant from the leaf surface, thus improving the chances for refixation by RubisCO, whose oxygenation activity is suppressed by the extra CO_2. Molecularly the photorespiratory CO_2 pump can arise easily. It takes only two genes encoding a subunit of the glycine decarboxylase complex with expression restricted to either mesophyll or bundle sheath cells by the right *cis* elements in the promoters. Loss of function of the mesophyll-expressed version would then result in glycine decarboxylase activity only in the bundle sheath cells and thereby establish the CO_2 pump.

Conversely, the levels of carbonic anhydrase and PEP carboxylase had to massively increase in the cytosol of the mesophyll cells. The C_4 cycle is then completed through the spatial separation of the two carboxylase reactions, PEP carboxylase in the mesophyll and RubisCO in the bundle sheath cells. In the course of **C_4 cycle optimisation**, many other metabolic changes have evolved that can mostly be explained by changes in transcriptional regulation too. A recent modelling of the biochemical fitness landscape between C_3 and C_4 photosynthesis—based on kinetic parameters of enzymes, gas exchange rates, etc.—demonstrated that indeed every step along the different evolutionary trajectories from C_3 to C_4 photosynthesis is associated with a **fitness gain** (Heckmann et al. 2013). This leaves the question as to why not all angiosperm lineages have evolved C_4 photosynthesis. A possible explanation could be that certain potentiating factors such as high vein density are not present in all lineages.

6.6.3 Crassulacean Acid Metabolism

CAM represents an important metabolic adaptation to water scarcity. It is characterised by highly efficient **water use**, coming at the expense of slow growth. CAM photosynthesis has been found in at least 36 taxonomically diverse plant families and has therefore most probably also evolved multiple times independently, like C_4 photosynthesis. About 6% of all flowering plant species are **CAM plants**. They thrive mostly in dry and hot regions, or are confronted with water scarcity because they live as **epiphytes**—for instance, orchids on trees in tropical forests. CAM plants restrict water loss by a reversal of **stomatal regulation** in comparison with non-CAM plants. Stomata are closed during the day and opened at night when the air is much cooler and more humid; that is, when the vapour pressure deficit between leaf and air is lower (Fig. 6.23). CAM photosynthesis usually is combined with several anatomical and morphological features that further minimise water loss. They include highly efficient sealing of above-ground surfaces by thick cuticles, low surface to volume ratios, **succulence** (i.e. large cells and vacuoles with enhanced water storage capacity) and lower stomatal density (Cushman 2001; Silvera et al. 2010).

Usually the CAM metabolism is divided into four phases (Fig. 6.24). Because of the nocturnal stomatal conductance, CO_2 is taken up in the dark. Primary carbon fixation is catalysed by **PEP carboxylase** but, in contrast to C_4 photosynthesis, primary and secondary carbon fixations are separated temporally, not spatially. Phosphoenolpyruvate reacts with HCO_3^- to yield oxaloacetate. Oxaloacetate is then reduced in the cytosol to malate by NAD(P)-dependent malate dehydrogenase and stored in the vacuole as the protonated form, malic acid. As a result the vacuoles of CAM plants strongly acidify (up to pH 3) (by the end of phase I). Early in the light period, stomata may still be open and some CO_2 fixation by RubisCO can occur (in phase II). Later during the day, malate is released from the vacuole (deacidification) and converted by the NADP-dependent malic enzyme or PEP carboxykinase into CO_2, reduction equivalents (NADPH) and pyruvate. CO_2 is assimilated by RubisCO in the reductive photosynthetic carbon cycle (Calvin cycle)—that is, the regular C_3 photosynthesis path. However, in contrast to C_3 plants, the RubisCO operates at saturating CO_2 concentrations and oxygenation of ribulose-1,5-bisphosphate is strongly reduced (end of phase III). Phase IV comprises the second transition when organic acid stores are depleted and stomata open again if environmental conditions permit. Liberated C_3 acids are converted into storage carbohydrates. The primary CO_2 acceptor, PEP, is synthesised from storage carbohydrates. One of the main enzymes catalysing this reaction is pyruvate orthophosphate dikinase (PPdK). Typical **diurnal rhythms** of gas exchange, as well as malic acid and starch concentration, are shown in Fig. 6.24. In contrast to C_3 and C_4 plants, the rate of CO_2 uptake by CAM plants is limited by mesophyll processes—such as the provision of acceptor molecules for carboxylation derived from storage carbohydrates or vacuolar storage capacity—and not by stomatal conductance. The need for malic acid storage is

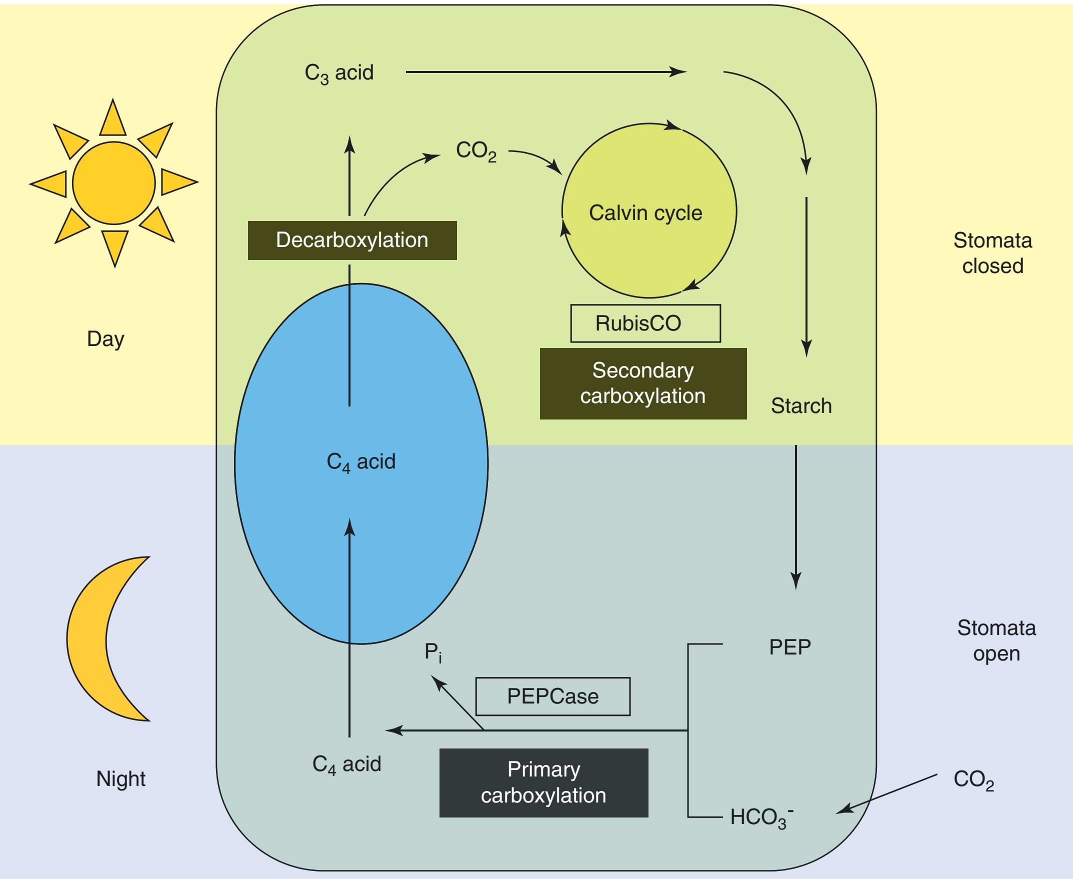
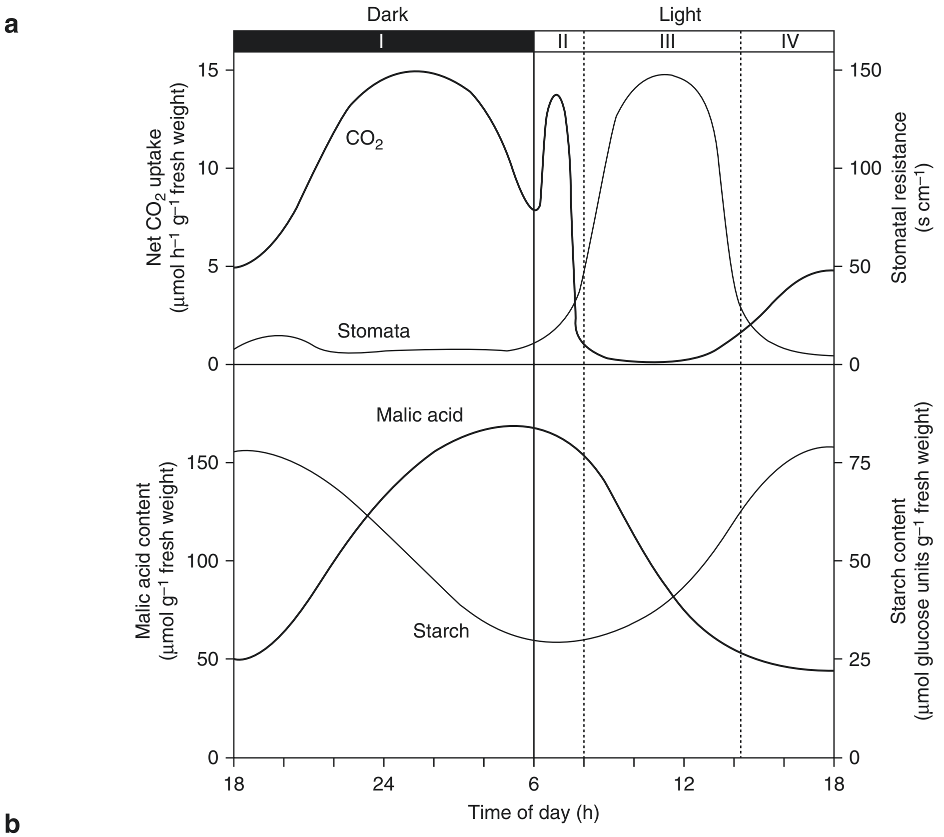


Fig. 6.23 Key steps in crassulacean acid metabolism (CAM) photosynthesis. (Modified from Borland et al. (2014))

one additional reason for the frequent association of CAM photosynthesis with **succulence**.

The regulation of **PEP carboxylase activity** in CAM plants represents an illustrative example of the importance of the **biological clock** and controlled day/night cycles in adaptation (Chap. 2). During the day, the refixation of CO_2 by PEP carboxylase has to be down-regulated in order to prevent competition with RubisCO for the substrate and a concomitant futile cycle of malate synthesis and decarboxylation. Regulation occurs via phosphorylation of the enzyme by a kinase whose activity oscillates with a **circadian rhythm**. When the N-terminus of the enzyme is phosphorylated, PEP carboxylase is less feedback inhibited by the end product malate and can thereby provide sustained primary CO_2 fixation during the night. The nonphosphorylated form is inhibited by about ten times lower malate concentrations. Due to these properties, a rhythmic alternation between a more active “night form” and a less active “day form” of the enzyme is achieved through circadian transcriptional regulation of the responsible kinase, PEPC kinase. The gene is more actively transcribed during the night, resulting in the presence of the more active phosphorylated form of PEPC during nighttime. Other processes such as the provision of PEP are also under circadian control.

CAM shows pronounced physiological plasticity and ecological diversity. Depending on the environmental conditions, different manifestations of CAM are distinguished. During long periods of drought, stomata remain continuously closed, even at night. Fixation and assimilation of CO_2 are limited to CO_2 generated internally in the plant tissue by respiratory processes. This state is



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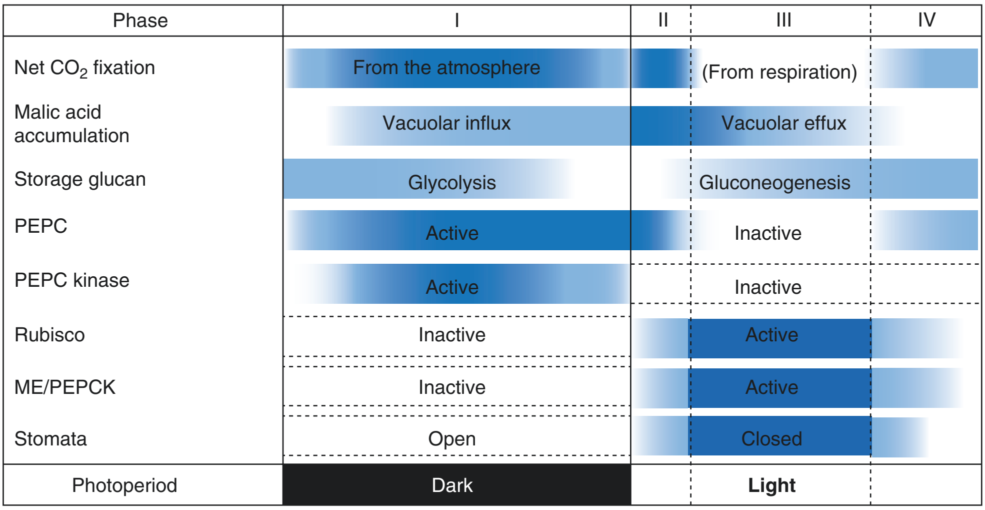


Phase	I	II	III	IV
Net CO_2 fixation	From the atmosphere		(From respiration)	
Malic acid accumulation	Vacuolar influx		Vacuolar effux	
Storage glucan	Glycolysis		Gluconeogenesis	
PEPC	Active		Inactive	
PEPC kinase	Active		Inactive	
Rubisco	Inactive		Active	
ME/PEPCK	Inactive		Active	
Stomata	Open		Closed	
Photoperiod	Dark		**Light**	

Fig. 6.24 Typical diurnal rhythms of a crassulacean acid metabolism (CAM) plant. **a** Gas exchange curve (CO_2 uptake rate and stomatal resistance = stomatal conductance^{-1}) (*upper panel*) and changes in the concentrations of the typical metabolites starch and malate (*lower panel*). The gas exchange shows phase I: nocturnal CO_2 fixation; phase II: dawn, with the start of CO_2 fixation by ribulose-1,5-bisphosphate carboxylase/oxygenase (RubisCO); phase III: assimilation of the internally released CO_2 by RubisCO with the stomata closed; and phase IV: stomata begin to open after the internal CO_2 has been depleted and daytime temperatures are dropping. In **b** the time courses of the different reactions are indicated by different shades of *blue*. **a** Lüttge et al. (1994); **b** Cushman and Bohnert (1999)

called **CAM idling**. The photosynthetic assimilation of internal CO_2 provides some protection against photoinhibition. However, the low internal CO_2 content, combined with the usually extremely high radiation, is not sufficient to allow a substantial flow of electrons and full relief of the photosystems. Consequently, oxygen radicals are formed and oxidative stress occurs. Therefore, CAM idling is of only limited use, as it cannot be sustained for extended periods of time.

Many bromeliads show diurnal CAM metabolism, even though no or very little nocturnal CO_2 fixation by PEP carboxylase occurs. This is called **CAM cycling** or weak CAM (meaning an evolutionarily early form of CAM). An extreme example of CAM cycling occurs in usually submerged water plants such as *Isoëtes howellii*, a lycophyte. The epidermis of this plant, of course, has no stomata, and the plant does not experience water deficit stress (Keeley 1998). The reason for the CO_2 fixation during the night is assumed to be the lack of CO_2 in the usually acidic waters where *Isoëtes* grows. CAM cycling has also been found in flowering aquatic plants (e.g. the genus *Sagittaria*). **Latent CAM** refers to high but not diurnally cycling organic acid concentrations and is thought to represent a C_3–CAM intermediate stage.

CAM can also be facultative—that is, induced upon exposure to low water availability—in species that in the presence of sufficient water supply show normal C_3 photosynthesis. This represents an effective acclimation to salt or drought stress conditions and has been most intensively studied in the common ice plant *M. crystallinum* (Cushman 2001). **CAM induction** can be irreversible, as in *M. crystallinum*, or reversible. In some facultative CAM plants, only certain leaves or developmental stages display CAM photosynthesis. The succulent stem of *Frerea indica* (an asclepiad) performs CAM, while the green leaves—at least in rainy periods—photosynthesise in the C_3 mode. In tropical *Clusia* species with opposite leaves at a node, one leaf may perform C_3 photosynthesis while the opposite leaf uses CAM (Lüttge 1987).

The magnitude of the transition is strongly influenced by the degree of water scarcity and other environmental factors, including light intensity, temperature and humidity. This ecophysiological **plasticity** allows the C_3–CAM intermediates optimal acclimation of their photosynthetic capacity to the prevailing conditions, making effective use of the humid season or of sporadic precipitation. The shift to CAM photosynthesis in response to drought or salinity involves transcriptional up-regulation of many genes encoding enzymes involved in CAM. The first example was a **PEP carboxylase** gene in *M. crystallinum*. More recent transcriptome studies have revealed changes in >2000 genes during the transition from C_3 to CAM photosynthesis (Cushman et al. 2008).

Whether a facultative CAM plant, or a part of the plant, follows C_3 photosynthesis or CAM photosynthesis can be determined using the **$\delta^{13}C$ value**. Of the carbon dioxide in the air, 98.89% consist of the ^{12}C isotope and 1.11% consist of ^{13}C. The content of the radioactive isotope ^{14}C is, in comparison with those values, negligible ($10^{-10}\%$). **RubisCO** consumes CO_2 as a substrate and discriminates more strongly between ^{12}C and ^{13}C than does **PEP carboxylase**, which uses HCO_3^- instead of CO_2. Carbon assimilated only by RubisCO thus contains less ^{13}C than that fixed first by PEPC. The change of ^{13}C in the biomass therefore allows determination of the mode of CO_2 fixation. The ratio of ^{13}C to ^{12}C is determined by mass spectrometry and calculated with the following formula:

$$\delta^{13}\left[‰\right] = \left[\frac{^{13}C/^{12}C \text{ of sample}}{^{13}C/^{12}C \text{ of standard}} - 1\right] \times 1000$$

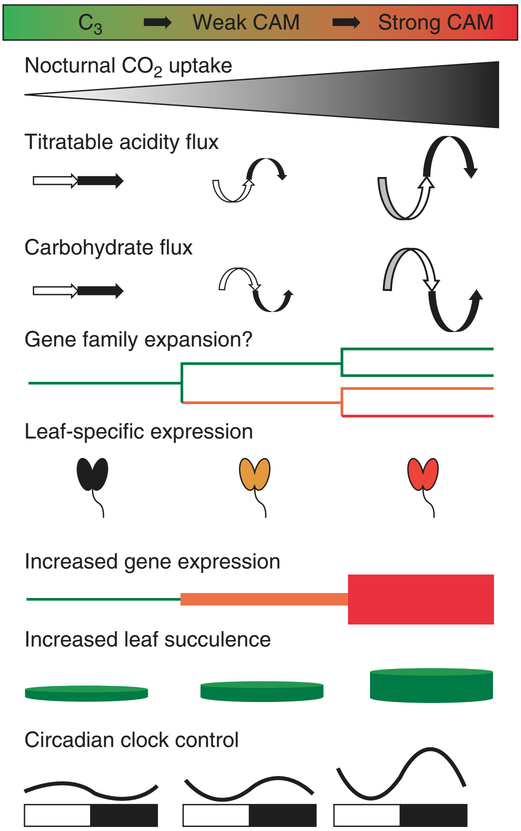
The standard is a defined limestone. The $\delta^{13}C$ values of C_3 plants are around −28‰; those of C_4 plants are around −14‰; and those of CAM plants with predominantly nocturnal CO_2 fixation are between −10 and −20‰, and for daytime CO_2 fixation, between −25 and −34‰.

6.6.4 Evolution of Crassulacean Acid Metabolism Photosynthesis

The physiological plasticity of CAM corresponds to its evolutionary diversity. CAM manifestation is strongly influenced by the history of a species and its habitat context (Silvera et al. 2010). CAM is taxonomically more broadly distributed than C_4 photosynthesis and is most likely evolutionarily older. The presence of CAM in ancient groups such as the *Isoëtes* (see *I. howellii* above) suggests a first appearance of CAM already in the Triassic (250–200 million years ago). Further CAM evolution was then probably driven by selection for increased carbon gain and better **water use efficiency** after the global reduction in atmospheric CO_2 concentration about 30 million years ago during the Oligocene (see evolution of C_4 photosynthesis, Sect. 6.6.2). CAM has evolved many times independently and to varying degrees. The extent of CAM manifestation shows a positive correlation with the dryness of the site; that is, the stronger the water scarcity of a habitat, the higher the likelihood of full CAM expression in the plants populating it.

Several characteristics of CAM can be distinguished, as described above (Borland et al. 2014). Accordingly, CAM requires a number of evolutionary changes in basal mechanisms that principally are present in all higher plants (Fig. 6.25):

- First, a reversal of stomatal regulation enables nocturnal CO_2 uptake. The control of the stomatal aperture by light has to be overridden by other control mechanisms. One factor could be the low internal leaf CO_2 partial pressure at night, due to the activity of **PEP carboxylase**
- Second, **diurnal fluctuations** in organic acids and (reciprocally) in storage compounds and soluble sugars, plus respective transport activities, are established (e.g. malate into the vacuole and malic acid out of the vacuole)
- Third, key elements of CAM photosynthesis, e.g. carboanhydrase and PEPC, as well as



All or most of the CO_2 uptake occurs at night when the water potential gradient between leaves and air is much smaller than during the day. This requires an inverse day-night pattern of stomatal opening.

The primary carboxylation reactions result in the nocturnal accumulation of C_4 organic acids (mainly malate). Their subsequent degradation provides an internal CO_2 source during the following photoperiod.

Storage carbohydrates such as starch exhibit accumulation patterns that are reciprocal to the pattern of C_4 organic acid accumulation. A large fraction is used for the synthesis of PEP.

Expansion of gene families made the evolution of CAM-specific isoforms possible.

Several genes encoding, for instance, PEP carboxylase and decarboxylating enzymes show strong expression predominantly in leaves.

Enzymes catalysing key steps in CAM photosynthesis are overall more strongly expressed than in C_3 plants.

CAM evolution is well correlated with increased leaf succulence: mesophyll cells with increased size, increased mesophyll tissue and leaf thickness due to large storage vacuoles.

Circadian clock control is essential. One example is the control of PEP carboxylase activity.

Fig. 6.25 Evolutionary changes required for crassulacean acid metabolism (CAM) photosynthesis. (After Silvera et al. (2010))

decarboxylating enzymes—are more strongly expressed. Prerequisites here are the duplication and diversification of genes encoding the respective enzymes. As in plants with C_4 photosynthesis, there are CAM plant–specific isoforms of PEP carboxylase with very high leaf expression
- Fourth, enhanced gluconeogenic and glycolytic activities supply substrates for carboxylation and decarboxylation
- The fifth element is leaf **succulence**. A clear correlation exists between the degree of leaf succulence and the strength of CAM. Plants with thicker leaves show lower $\delta^{13}C$ values, which is indicative of stronger CAM (see the range of $\delta^{13}C$ values in Table 6.3). This is explained not only by the greater storage capacity of larger cells (with vacuoles taking up 90–95% of the volume) but also by the tight packing of cells in succulent tissues, which restricts the intercellular gas space and thereby the gas exchange rates, and consequently limits C_3 photosynthesis during phases II and IV
- Finally, the sixth key mechanism is the **circadian clock** control over CO_2 fixation. Comparative studies with four *Clusia* species (one C_3 species, two C_3–CAM intermediates and one strong, constitutive CAM species) have revealed an association of the circadian control of *PEPCK* transcript abundance with CAM strength—that is, with day/night changes in malate and soluble sugar content

As indicated in Fig. 6.25, all of these mechanisms can vary in their extent along a continuum of CAM manifestations.

Summary

- The strict association between CO_2 uptake and water loss can be referred to as the central dilemma of plants: dying of thirst or dying of hunger?
- Life requires liquid water and is thus dependent on particular physico-chemical properties that result from the dipole nature of the water molecule (the so-called anomalies of water).
- The water potential (Ψ_w) is a measure of the thermodynamic state of water in any system and is given in the dimension of pressure. Figuratively speaking, it is a measure of the energy required to remove water molecules from any water-containing system. The potential of pure water under standard conditions of pressure and temperature is defined as zero and used as a reference. Any system that requires more energy to remove water from has a negative water potential. Thus, water moves towards the lower (more negative) potential.
- The water potential of a solution, and correspondingly that of a cell, is influenced by three major components: the concentration of solutes, termed the osmotic potential (Ψ_s), the pressure potential (Ψ_p) and gravity (Ψ_g). When considering water potential beyond the cellular level or in cells and other structures in an at least partially dehydrated state, the matrix potential (Ψ_m) is often included as a fourth component.
- Water movement in a plant follows gradients in potential. It is always passive, as no mechanical pump is in operation. The plant, however, actively influences the direction and the steepness of these gradients.
- In order to take up water from the soil solution, the water potential of root cells has to be more negative than that of the surrounding soil. Plant cells can lower their water potential by osmotic adjustment. Increasing the concentration of solutes makes the osmotic potential (Ψ_s), and thereby the water potential of the cell, more negative.
- Three pathways for the flux of water through a tissue exist: apoplastic, symplastic, and transcellular. Uptake into the symplasm and transcellular flux both require membrane passages. The resistance of biomembranes for water flux is lowered by water channels, the aquaporins. Plants possess a large number of aquaporin isoforms with distinct expression patterns and subcellular localisations. The principal ways of controlling aquaporin-dependent water flow are modulation of aquaporin abundance and permeability (= gating).

- The multitude of aquaporin isoforms in a plant and the many ways of regulating them (e.g. transcription, subcellular localisation, phosphorylation, ubiquitination) provide the means to acclimate to fluctuations in water availability and demand by adjusting resistance for water flow across tissues, as well as into and out of cells and cellular compartments.
- Principally two different strategies to cope with water scarcity can be distinguished: avoidance and tolerance. However, these categories merely represent the extreme poles of a continuum of responses that are dependent on the plant and the severity of the drought stress. Avoidance refers to a balancing of water uptake and water loss that maintains the water status (in isohydric plant species). Tolerance mechanisms help a plant endure a moderate lowering of the water potential (in anisohydric plant species).
- Osmotic adjustment is achieved by the accumulation of "compatible solutes" or "osmolytes"—organic low molecular weight compounds of different chemical classes. The protective function goes beyond the osmotic effect. Some compatible solutes can scavenge reactive oxygen species; others stabilise proteins and membranes.
- Protective proteins accumulate under drought stress to shield cellular structures from damage caused by water loss. Among them are the late embryogenesis abundant (LEA) proteins, which are also formed during seed maturation as part of a plant's regular developmental programme.
- An extreme form of drought tolerance is shown by poikilohydric plants, which withstand near complete tissue dehydration (desiccation). Desiccation tolerance represents an adaptation to extreme environmental conditions. It involves a state of dormancy characterised by massive accumulation of protective proteins.
- Most of the transpirational water loss occurs via the stomata. Therefore, control of the stomatal aperture plays a key role in a plant's response to water deficit and in drought stress tolerance. Several internal and environmental cues (e.g. water status, humidity, CO_2 concentration) are integrated by guard cells (which form the stomatal pore) in order to optimally adjust the stomatal aperture for any given physiological situation.
- The stomatal aperture is nearly linearly correlated with guard cell turgor pressure. Thus, the concentration of solutes in guard cells determines stomatal conductance. Changes in K^+ and Cl^- concentrations are brought about by ion channel–mediated exchange between guard cells and the surrounding apoplast, as well as between guard cell vacuoles and the cytosol. Control over stomatal movement is exerted by control over these ion fluxes.
- An integral part of a plant's acclimation to water deficit caused by drought, and essentially an avoidance strategy, is the reduction of leaf area relative to biomass; that is, a trade-off exists between stress tolerance and maintained growth. A second acclimation of growth under conditions of water scarcity is the stimulation of root growth in order to improve the water uptake capacity and to access additional water resources. Thus, a general shift in plant growth under water limitation is the increase in the root to shoot biomass ratio.
- Growth control is regulated at the level of cell division and cell expansion.
- Drought responses have to be coordinated in the entire organism, requiring long-distance signalling between organs.
- The phytohormone abscisic acid (ABA) activates the majority of avoidance and tolerance mechanisms, including stomatal closure, the regulation of aquaporin abundance and activity, synthesis of protective proteins and osmoregulation.
- Three layers of ABA action can be differentiated: synthesis and transport, perception, and signal transduction.
- The earliest events in ABA signalling are mediated by a central regulatory module, which consists of three protein classes: receptors, protein phosphatases and protein kinases. This module triggers rapid responses—such as the activation and inactivation of ion channels—and slower responses at the transcriptional level.

- Two major variants of photosynthesis have evolved that increase water use efficiency—that is, they reduce the amount of water vapour lost per unit of carbon fixed: C_4 photosynthesis and Crassulacean Acid Metabolism (CAM).
- C_4 photosynthesis and CAM employ a first fixation of CO_2 (as bicarbonate) by PEP carboxylase before CO_2 is fixed a second time by ribulose-1,5-bisphosphate carboxylase/oxygenase (RubisCO). In C_4 plants these CO_2 fixations are separated spatially; in CAM plants they are separated temporally.
- Both variants achieve a higher CO_2 concentration in the vicinity of RubisCO. This suppresses the oxygenase activity of RubisCO and thereby the need for photorespiration.
- C_4 plants can achieve efficient photosynthesis with a reduced stomatal aperture, which limits water loss. Provision of the substrate for the first CO_2 fixation requires extra energy. Taken together, these restrict the natural occurrence of C_4 plants essentially to environments characterised by water scarcity, high light and high temperature.
- CAM plants reduce water loss even more. They open stomata at night so that less transpiration occurs. CO_2 is taken up and stored after fixation as malate in the vacuole for later use by RubisCO.
- C_4 photosynthesis and CAM have evolved many times independently in different plant lineages. Models have been developed that describe the stepwise evolution of these major adaptations to arid environments.

References

Agre P (2004) Aquaporin water channels (Nobel lecture). Angew Chem Int Ed Engl 43:4278–4290

Bartels D, Alexander R, Schneider K et al (1993) Desiccation-related gene products analyzed in a resurrection plant and in barley embryos. In: Close TJ, Bray EA (eds) Plant responses to cellular dehydration during environmental stress, Current topics in plant physiology, vol 10, pp 119–127. American Society of Plant Physiologists, Rockville

Borland AM, Hartwell J, Weston DJ et al (2014) Engineering crassulacean acid metabolism to improve water-use efficiency. Trends Plant Sci 19:327–338

Chater CCC, Oliver J, Casson S, Gray JE (2014) Putting the brakes on: abscisic acid as a central environmental regulator of stomatal development. New Phytol 202:376–391

Chaumont F, Tyerman SD (2014) Aquaporins: highly regulated channels controlling plant water relations. Plant Physiol 164:1600–1618

Christin P-A, Osborne CP (2014) The evolutionary ecology of C_4 plants. New Phytol 204:765–781

Christmann A, Grill E, Huang J (2013) Hydraulic signals in long-distance signaling. Curr Opin Plant Biol 16:293–300

Christmann A, Weiler EW, Steudle E, Grill E (2007) A hydraulic signal in root-to-shoot signalling of water shortage. Plant J 52:167–174

Claeys H, Inzé D (2013) The agony of choice: how plants balance growth and survival under water-limiting conditions. Plant Physiol 162:1768–1779

Cushman JC (2001) Crassulacean acid metabolism. A plastic photosynthetic adaptation to arid environments. Plant Physiol 127:1439–1448

Cushman JC, Bohnert HJ (1999) Crassulacean acid metabolism: molecular genetics. Annu Rev Plant Physiol Plant Mol Biol 50:305–332

Cushman JC, Tillett RL, Wood JA et al (2008) Large-scale mRNA expression profiling in the common ice plant, Mesembryanthemum crystallinum, performing C_3 photosynthesis and crassulacean acid metabolism (CAM). J Exp Bot 59:1875–1894

Farrant JM, Moore JP (2011) Programming desiccation-tolerance: from plants to seeds to resurrection plants. Curr Opin Plant Biol 14:340–345

Gowik U, Westhoff P (2011) The path from C-3 to C-4 photosynthesis. Plant Physiol 155:56–63

Harb A, Krishnan A, Ambavaram MMR, Pereira A (2010) Molecular and physiological analysis of drought stress in Arabidopsis reveals early responses leading to acclimation in plant growth. Plant Physiol 154: 1254–1271

Hauser F, Waadt R, Schroeder JI (2011) Evolution of abscisic acid synthesis and signaling mechanisms. Curr Biol 21:R346–R355

Heckmann D, Schulze S, Denton A et al (2013) Predicting C_4 photosynthesis evolution: modular, individually adaptive steps on a Mount Fuji fitness landscape. Cell 153:1579–1588

Henzler T, Waterhouse RN, Smyth AJ et al (1999) Diurnal variations in hydraulic conductivity and root pressure can be correlated with the expression of putative aquaporins in the roots of Lotus japonicus. Planta 210:50–60

Hubbard KE, Nishimura N, Hitomi K et al (2010) Early abscisic acid signal transduction mechanisms: newly discovered components and newly emerging questions. Genes Dev 24:1695–1708

Javot H, Maurel C (2002) The role of aquaporins in root water uptake. Ann Bot 90:301–313

Kang J, Hwang J-U, Lee M et al (2010) PDR-type ABC transporter mediates cellular uptake of the phytohormone abscisic acid. Proc Natl Acad Sci U S A 107:2355–2360

Katul GG, Oren R, Manzoni S et al (2012) Evapotranspiration: a process driving mass transport and energy exchange in the soil–plant–atmosphere–climate system. Rev Geophys 50:RG3002

Keeley JE (1998) CAM photosynthesis in submerged aquatic plants. Bot Rev 64:121–175

Kim T-H, Böhmer M, Hu H et al (2010) Guard cell signal transduction network: advances in understanding abscisic acid, CO_2, and Ca^{2+} signaling. Annu Rev Plant Biol 61:561–591

Kollist H, Nuhkat M, Roelfsema MRG (2014) Closing gaps: linking elements that control stomatal movement. New Phytol 203:44–62

Langdale JA (2011) C_4 cycles: past, present, and future research on C_4 photosynthesis. Plant Cell 23:3879–3892

Larcher W (2003) Physiological plant ecology, 4th edn. Springer, Berlin

Lawlor DW (2013) Genetic engineering to improve plant performance under drought: physiological evaluation of achievements, limitations, and possibilities. J Exp Bot 64:83–108

Lüttge U (1987) Carbon dioxide and water demand: crassulacean acid metabolism (CAM), a versatile ecological adaptation exemplifying the need for integration in ecophysiological work. New Phytol 106: 593–629

Lüttge U, Kluge M, Bauer G (1994) Botanik. Weinheim, VCH

Maggio A, Joly RJ (1995) Effects of mercuric chloride on the hydraulic conductivity of tomato root systems (evidence for a channel-mediated water pathway). Plant Physiol 109:331–335

Maggio A, Zhu J-K, Hasegawa PM, Bressan RA (2006) Osmogenetics: Aristotle to Arabidopsis. Plant Cell 18:1542–1557

Maurel C, Boursiac Y, Luu D-T et al (2015) Aquaporins in plants. Physiol Rev 95:1321–1358

Maurel C, Verdoucq L, Luu D-T, Santoni V (2008) Plant aquaporins: membrane channels with multiple integrated functions. Annu Rev Plant Biol 59:595–624

McDowell N, Pockman WT, Allen CD et al (2008) Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? New Phytol 178:719–739

Murata K, Mitsuoka K, Hirai T et al (2000) Structural determinants of water permeation through aquaporin-1. Nature 407:599–605

Qin X, Zeevaart JA (1999) The 9-cis-epoxycarotenoid cleavage reaction is the key regulatory step of abscisic acid biosynthesis in water-stressed bean. Proc Natl Acad Sci U S A 96:15354–15361

Sage RF, Sage TL, Kocacinar F (2012) Photorespiration and the evolution of C_4 photosynthesis. Annu Rev Plant Biol 63:19–47

Silvera K, Neubig KM, Whitten WM et al (2010) Evolution along the crassulacean acid metabolism continuum. Funct Plant Biol 37:995–1010

Skirycz A, Inzé D (2010) More from less: plant growth under limited water. Curr Opin Biotechnol 21:197–203

Steudle E (2001) The cohesion–tension mechanism and the acquisition of water by plant roots. Annu Rev Plant Physiol Plant Mol Biol 52:847–875

Steudle E, Peterson CA (1998) How does water get through roots? J Exp Bot 49:775–788

Szabados L, Savouré A (2010) Proline: a multifunctional amino acid. Trends Plant Sci 15:89–97

Tenhaken R (2015) Cell wall remodeling under abiotic stress. Front Plant Sci 5:771

Verslues PE, Juenger TE (2011) Drought, metabolites, and Arabidopsis natural variation: a promising combination for understanding adaptation to water-limited environments. Curr Opin Plant Biol 14(3):240–245

Wise MJ, Tunnacliffe A (2004) POPP the question: what do LEA proteins do? Trends Plant Sci 9:13–17

Yancey PH (2005) Organic osmolytes as compatible, metabolic and counteracting cytoprotectants in high osmolarity and other stresses. J Exp Biol 208:2819–2830

Yoshiba Y, Kiyosue T, Nakashima K et al (1997) Regulation of levels of proline as an osmolyte in plants under water stress. Plant Cell Physiol 38:1095–1102

Yuan F, Yang H, Xue Y et al (2014) OSCA1 mediates osmotic-stress-evoked Ca^{2+} increases vital for osmosensing in Arabidopsis. Nature 514:367–371

7 Adverse Soil Mineral Availability

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Salt lakes are almost uninhabitable for plants because of the enormously negative osmotic potential of the substrate, which is often also very alkaline because of the high soda ($NaCO_3$) content. The white expanses in this picture of Lake Magadi in southern Kenya are not snow but salt incrustations. Nevertheless, plant life can be found in such habitats. The banks of sediment in the lake are overgrown with thick layers of algae. In some parts, the shoreline supports vegetation of halotolerant bushes. (Photo: E. Beck)

E.-D. Schulze et al., *Plant Ecology*, https://doi.org/10.1007/978-3-662-56233-8_7

A number of elements, but in fact only a fraction of the elements found in the Earth's crust, have been recruited for biological functions during evolution. Recruitment is governed by three factors: abundance, availability and reactivity. Life depends mostly on the lighter, more abundant elements. However, not all of the abundant elements have biological functions. Titanium, for instance, is practically not available in ionic form. Usage of the available and abundant elements depends on their chemical properties, as detailed below. Among the first-row transition metals, for example, Ni is found in only one plant enzyme, while Zn is a cofactor of hundreds of enzymes.

Plant mineral composition and requirements were among the earliest questions addressed by plant physiologists. Nicolas Theodore de Saussure realised that the dry weight gain of plants during growth is not fully explained by the carbon fixed in photosynthesis (Hart 1930). **Hydroponic cultivation** of plants, i.e., with the roots drawing minerals from a defined liquid medium—has enabled the systematic investigation of nutrient requirements. Among the first insights derived from such experiments was the realisation by Julius von Sachs that Fe is an essential nutrient.

7.1 Mineral Nutrients

An element is essential when an organism cannot complete its life cycle without that element. Depending on the concentration found in tissues, mineral nutrients are divided into **macroelements** (approximately 1000–15,000 µg/g of dry weight (d.w.)) and **microelements** (approximately 0.005–100 µg/g d.w.) (Table 7.1). A third category comprises the **beneficial elements** that have positive effects on plant growth and/or fitness but are not essential.

Table 7.1 Adequate concentrations of macronutrients and micronutrients

Element	Chemical symbol	Content (µg/g of dry weight)
Macronutrients		
Nitrogen	N	15,000
Potassium	K	10,000
Calcium	Ca	5000
Magnesium	Mg	2000
Phosphorus	P	2000
Sulphur	S	1000
Micronutrients		
Iron	Fe	100
Manganese	Mn	50
Zinc	Zn	20
Copper	Cu	6
Molybdenum	Mo	0.1
Nickel	Ni	0.005
Chlorine	Cl	100
Boron	B	20

After Marschner (2012) and Buchanan et al. (2015)

Silicon is accumulated by many plant species, sometimes to very high levels, and accounts for up to 10% of the dry weight of leaves of grass species such as *Oryza sativa*. Silicon accumulation protects against several abiotic and biotic stresses because deposition in the cell walls strengthens the physical barrier against invading pathogens, enhances tolerance of mechanical stresses and reduces cuticular transpiration (Ma and Yamaji 2006). Still, there is no evidence that a plant cannot exist without this element.

Generally not counted as nutrient elements are H, C and O, which are by far the most abundant elements in organisms. They are obtained not from the soil but from CO_2 and H_2O.

Not all types of organisms have the same mineral requirements. For instance, while sodium (Na) is an essential element for mammals, it is considered merely beneficial for plants. The same applies to cobalt (Co). Plants do not require fluorine (F); mammals do. On the other hand, boron (B) is essential for plants but not for other organisms. In total, 14 elements (besides C, H and O) have been determined as being essential for plants (Fig. 7.1). It was a fundamental insight that in principle every mineral element can become limiting for plant growth, independently of the amount that is required. What matters is the ratio between the requirement for and the availability of every nutrient. This is described as Justus Liebig's **law of the minimum**. In an extreme case an element could become limiting if it is used by only a single indispensable protein but is not available in sufficient amounts to supply this one enzyme. Deficiencies cause symptoms characteristic of the element that is limiting. For example, Mn deficiency causes yellowing of

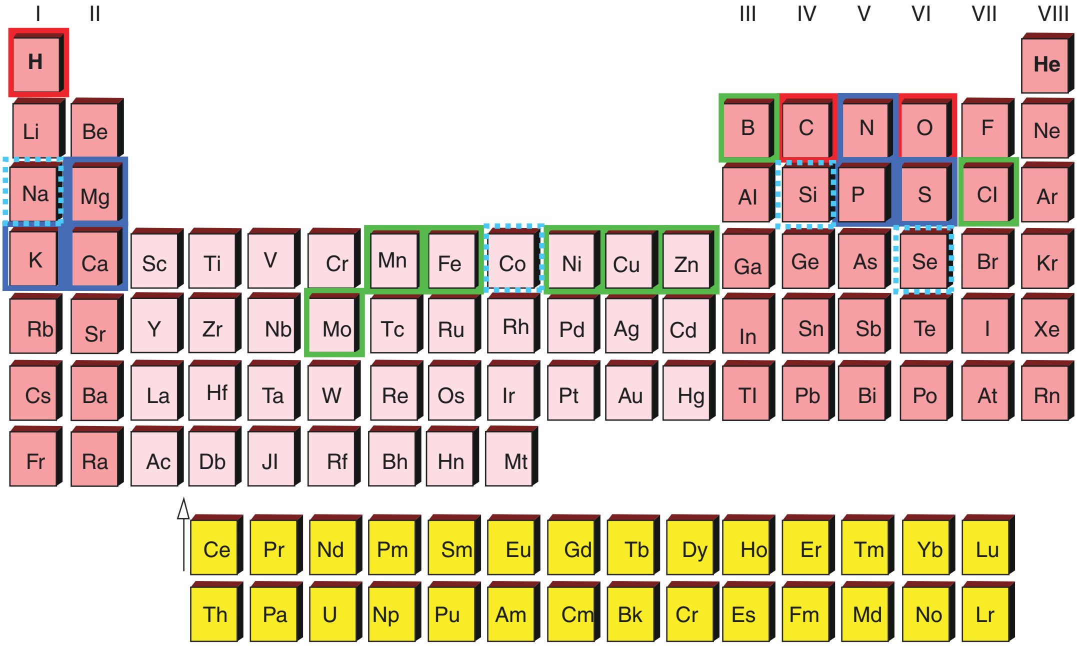

Fig. 7.1 The elements of life from a plant's perspective: macroelements (*blue frame*), microelements (*green frame*) and beneficial elements (*dotted line*)

the young leaves in dicotyledonous plants, while the major symptom in cereals is the development of grey specks in the mature leaves (Marschner 2012). Since practically every natural ecosystem responds to mineral nutrient input, normally by enhanced biomass production, it can be inferred that nutrient limitation is very common or, in other words, that plants are practically always under stress from suboptimal availability of mineral nutrients (Sect. 7.3). Depending on the habitat, different elements tend to become limiting. Alkaline soils are often Fe limited because of very low Fe availability (Sect. 7.3.1). However, the predominant limitations for plants are nitrogen and phosphate deficiency. The use of N and P fertilisers is one major reason for the enormous yield increases seen in many regions of the world over the past 100 years.

The functions of essential and beneficial mineral elements in plants are very diverse. They are usually categorised into four groups based on their physiological context and biochemical properties (Taiz and Zeiger 2006). Group 1 contains nitrogen and sulphur as the elements that are incorporated (assimilated) into carbon compounds. N is the most abundant of the mineral elements, since it is part of proteins and nucleic acids. S is part of two amino acids and of several essential metabolites such as coenzyme A or glutathione (GSH). Group 2 elements are P, B, and Si, which are important for energy storage or structural integrity. P is a component of nucleotides, nucleic acids and phospholipids. Myriad small molecules and macromolecules in cells can become phosphorylated. Boron is complexed by several components of the cell wall. Group 3 comprises the elements that remain in ionic form inside plants: the macroelements K, Ca and Mg; the microelements Mn and Cl; and the beneficial element Na. K^+ ions are the major osmoticum in plant cells at concentrations around 100 mM. Ca^{2+} ions are components of the cell wall and inside cells are involved in a vast number of signal transduction processes as second messengers (see, for instance, the common sym pathway, discussed in Sect. 7.4.3). Finally, group 4 encompasses microelements involved in redox reactions: Fe, Cu, Zn, Ni and Mo. Fe and Cu are redox-active metals, which can exist in two different oxidation states under physiological conditions. This is the reason why they have been recruited for electron transfer reactions in biological systems, most prominently seen in photosynthesis and respiration (e.g. Fe–S proteins, plastocyanin, cytochrome c). Zn is a widely used cofactor in enzymes from all six enzyme classes. Mo plays a key role in the global nitrogen cycle as a cofactor of nitrate reductases and nitrogenases (Sect. 7.4.2). The predominant use of microelements in enzymes explains why they are required in smaller amounts than the main osmotica (K) or the components of all major macromolecules (N).

7.2 The Mineral Nutrition Challenge

Plants are unique among multicellular organisms in their ability to build every organic molecule from inorganic parts, namely, CO_2, H_2O and mineral nutrients. Terrestrial plants have to acquire most mineral nutrients from the soil—an extremely complex, diverse and heterogeneous substrate. With the exception of carnivorous plants, uptake of nutrients by the leaves plays only a minor role and will not be described in detail here. Volatile N- and S-containing molecules can enter the plant via stomata and then be utilised. Another source of nutrients can be the rainwater on leaves of plants such as mosses and epiphytes.

Unlike heterotrophic organisms, which ingest biological material with an elemental composition that is already close to physiological requirements and is fairly balanced with respect to the relative quantities of mineral nutrients (e.g. more N than S, more Zn than Mo), plants depend on a soil solution that under most circumstances shows very low and unbalanced concentrations of nutrients. Thus, a fundamental characteristic of plant nutrition is the enrichment of nutrients relative to the environment. For some elements the enrichment factors exceed 1000—that is, the concentration is 1000-fold higher in the plant than in the soil solution (e.g. K^+; the soil solution concentration can be below 0.1 mM; the cellular concentration is around 100 mM). Furthermore, the nutrients are present in the environment in extremely fluctuating ratios that can be very far from the ratios needed physiologically.

When the relationship between the supply of a particular nutrient and the growth response is plotted, three regions of the curve can be distinguished: the deficiency range, where the growth response to supply is essentially linear; the adequate range, where an additional supply does not result in further growth stimulation; and the toxicity range, where the concentration of a nutrient is too high and causes growth reduction (Fig. 7.2). Both the deficiency and the toxicity ranges repre-

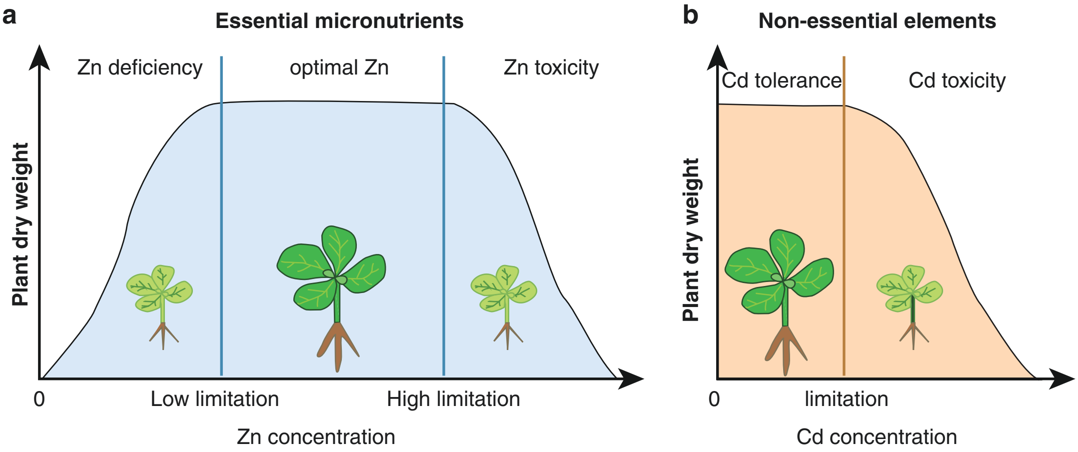

Fig. 7.2 Growth response of plants to the supply of essential elements and non-essential toxic elements. **a** Zn as an example of an essential microelement. **b** Cd as an example of a non-essential toxic element. (Modified from Lin and Aarts (2012))

sent a stress condition that plants have to cope with. Hence, both are topics discussed in this chapter.

In the following sections we will first describe the challenges arising from the characteristics of the soil substrate. Then the strategies of plants to cope with nutrient scarcity are discussed, including the two major **symbioses**: **mycorrhizae** and **biological N_2 fixation**. Next are responses to toxicity. Molecular mechanisms underlying the adaptations to particular adverse soil conditions are explained along the way.

Because of their charge, ions cannot pass through biological membranes passively. Thus, transport across membranes plays key roles in mineral nutrition. Consequently, basic features of plant ion transport, as well as the sensing of nutrient status and the regulation of ion transport, are major themes throughout this chapter.

7.2.1 Elements in the Soil

The soil represents an immensely complex physical, chemical and biological substrate (Chap. 11, Sect. 11.1.1 for a more detailed description). **Nutrient availability** strongly varies in space and time. Soil types differ tremendously in mineral content. Large and element-specific fluctuations occur within a soil—for instance, depending on changes in pH (Fig. 7.3), water status or microbial activity. Gradients develop horizontally and vertically. Elements can be found in patches because of uneven distribution of factors influencing availability—for example, litter fall and decomposition. Mobility within the soil is strongly element-specific.

Soil consists of solid, liquid and gaseous phases. The mineral nutrient supply is influenced by all three phases. The solid phase contains most of the nutrients. Inorganic soil matter is a reservoir for nutrients such as K and Fe, and organic soil matter is the main N reservoir. Minerals originate mostly from the weathering of bedrock—the sediments that give rise to soil. The exception is nitrogen, which predominantly stems from nitrogen fixation (Sect. 7.4.2). Weathering rates are strongly influenced by age and environmental factors. For instance, many tropical soils are highly weathered and the soils are therefore depleted in plant-available phosphorus.

The liquid phase contains ions available for uptake by roots. Only a very small fraction of total soil minerals are in soil solution. The bulk is bound to soil particles (e.g. clay, humic acids) that carry mostly negative charges, thus providing binding sites for cations. Minerals are in a dynamic equilibrium between the two phases. Ion exchange processes result in slow release into the soil solution. The binding capacity of the particles is an important **soil fertility** factor, and the average particle diameter is therefore a parameter used for soil classification. The high binding capacity of smaller particles reduces leaching and thus increases reserves.

While roots tap nutrient resources by growth (Sect. 7.3.5), nutrient ions ultimately have to reach the root surface via mass flow and diffusion. Elements differ strongly in their mobility within the soil solution. Phosphate is about three orders of magnitude less mobile than nitrate or sulphate (Lambers et al. 2015) because of stronger interaction with soil particles. This has major consequences for the biology of nutrient acquisition. About 90% of all plant species live in a **mycorrhizal symbiosis** with fungi. The fungal hyphae greatly enhance the capacity to unlock immobile phosphate in the soil (Sect. 7.4.1).

Soil particles form pores that differ in size between macro- and micropores. They are partly filled with water and partly with air, depending on the type of the soil and the amount of precipitation (Fig. 5.1). Air-filled pores are important for the gas exchange of the respiring roots (**autotrophic respiration**) and of other soil organisms (**heterotrophic respiration**). Gas exchange of roots and soils influences nutrient availability. For example, CO_2 released from roots as the product of respiration dissolves in H_2O and forms hydrogen carbonate (HCO_3^-) and H^+. These ions can desorb nutrient ions from soil particles through ion exchange and thereby enhance bioavailability.

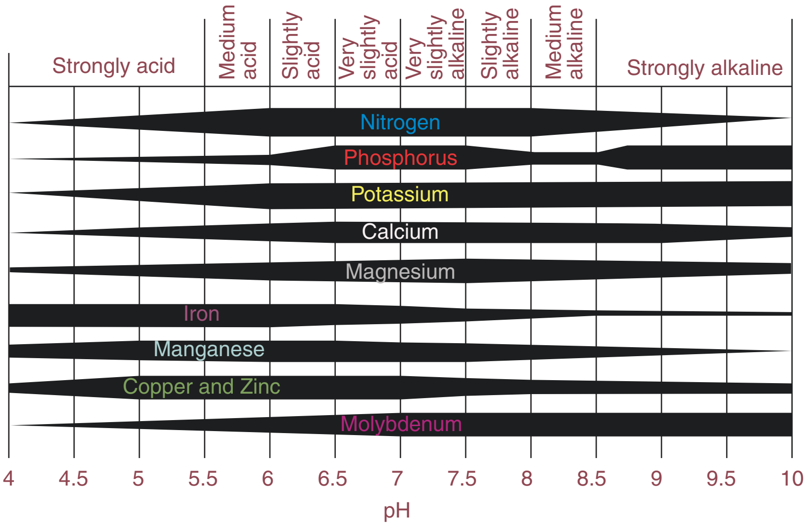

Fig. 7.3 Influence of soil pH on the availability of different mineral nutrients. (Lambers et al. 2008)

Box 7.1: Redox Potential of the Soil

The redox potential of soil results from the ratios between the oxidised forms and the reduced forms of metals:

$$E = E_0 + \frac{RT}{nF}\ln\frac{a_{\mathrm{Ox}}}{a_{\mathrm{red}}}[V]$$
$$E = E_0 + \frac{0.059}{n}\log\frac{a_{\mathrm{Ox}}}{a_{\mathrm{red}}}[V] \quad (7.1)$$

where n denotes the number of electrons exchanged between the oxidised and the reduced form, a_{Ox} is the activity of the oxidised form and a_{red} is the activity of the reduced form.

Well-aerated soils have redox potentials of up to +0.8 V, and poorly aerated soils at the level of groundwater or peat soils have redox potentials of up to −0.35 V.

The **reductive potential** of the soil is characterised by the $\mathbf{p_e}$ value. The p_e value (analogous to pH) is the negative log of the “concentration of electrons (n)” in the soil:

$$\text{e.g.}\quad \begin{matrix} p_e = 2 & [e] = 10^{-2}\,\mathrm{M} \\ p_e = -1 & [e] = 10^{1}\,\mathrm{M} \end{matrix} \quad (7.2)$$

The conversion factor between E and p_e is: $p_e = E\,(V) \times 16.9$.

The p_e values of a paddy rice field are between +4 (surface) and −3 (middle layer).

Strong variation exists between species and also within species (i.e. between ecotypes, cultivars, varieties) in their ability to acquire nutrients from soil. Thus, soil **mineral availability** has a strong influence on the distribution and composition of natural vegetation (Marschner 2012) (compare global soil map Fig. 11.2). This is illustrated by widely used classifications such as **calcicoles** versus **calcifuges**—that is, plants thriving on alkaline lime-rich soil versus plants with a preference for acidic soil. Some plant species have evolved specific adaptations to particularly nutrient-impoverished soils—for example, highly weathered ancient soils in Australia and South Africa, or soils in cold climates with very slow mineralisation of organic matter.

7.2.2 Element Toxicity

For macroelements the adequate range is usually very broad. This is different for some micronutrients. Their reactivity is the reason why they can easily become toxic (Fig. 7.2). Thus, the concentration range between deficiency and toxicity is comparatively narrow. Mn availability can become very high in acidic soils, and the resulting Mn toxicity is a secondary problem of low pH besides the (far more important) Al toxicity (Sect. 7.5.4). A negative redox potential of flooded soil is another reason for high Mn availability and toxicity (Box 7.1). Plants in many arid regions such as southern Australia suffer from boron toxicity (Sect. 7.5.1).

Similarly, beneficial elements are quite often available in the soil at a concentration that exceeds the toxicity threshold. Unlike silicon, aluminium and sodium are required in only very small quantities for growth stimulation. Many soils and soil conditions exist, however, that are associated with high availability of these elements and their respective toxicities. Survival of plants in salt marshes entails the expression of particular salt tolerance mechanisms (Sect. 7.5.3). Growth in acidic soils where Al^{3+} becomes available for uptake by plant roots requires specific adaptations to cope with the associated toxicity (Sect. 7.5.4).

Another relevant aspect to consider is the potential availability of elements that have no biological function and are potentially highly toxic (Clemens 2006). Some are taken up into cells because of their chemical similarity to essential elements. The most important examples are arsenic (As) and Cd. The arsenate anion $[(AsO_4)^{3-}]$ closely resembles the phosphate anion and cannot be discriminated against accurately enough by phosphate uptake systems. Cd is below Zn in the periodic table and therefore shares many chemical characteristics with this essential element. Again, transporters for the essential Zn^{2+} ion are not perfectly selective and transport Cd^{2+} ions as well.

Some plants have evolved the capacity to survive in soils with very high levels of toxic elements that far exceed the concentrations tolerable for most terrestrial plants. In the case of Na they are referred to as **halophytes** (Sect. 7.5.3). Vegetation on metal-rich sites is dominated by **metallophytes** (Sect. 7.5.2). The adaptations to such extreme habitats represent very instructive models for rapid **evolution in action** and will therefore be described from this angle.

7.3 Nutrient Acquisition and Responses to Nutrient Scarcity

As mentioned, nutrient scarcity is a general theme of a plant's life. The hidden half of plant biology—that is, the biology of the root—can, by and large, be explained by the need to acquire—besides water—the mineral nutrients essential for growth. A whole array of physiological, biochemical and developmental processes operate to modulate the availability of nutrients, to allow uptake from the soil solution, to store and to distribute to other organs or to engage in symbioses that greatly facilitate nutrient acquisition.

There are common themes applicable to most or all nutrients (e.g. the existence of specialised transporters in the plasma membrane), as well as mechanisms specific to one or a few nutrients (e.g. the modulation of the rhizosphere to mobilise scarcely available Fe(III)). Those molecularly best understood are the acquisition of the macroelements P, N and K, and the microelement Fe. They will therefore be the main focus of Sect. 7.4 and will be discussed to illustrate the principles of plant root responses to the stress of nutrient scarcity.

Four principal strategies that plant roots use to ensure adequate nutrient acquisition can be distinguished (Fig. 7.4):

- They influence the availability of nutrients in the rhizosphere
- They tightly regulate ion transport capacities
- They modulate their architecture—that is, the three-dimensional morphological structure
- They establish symbioses with fungi (mycorrhizae) and bacteria (biological N_2 fixation)

The molecular aspects of these strategies are detailed in Sects. 7.3.1–7.4.3.

7.3.1 Modulation of Nutrient Availability

Plant roots actively influence the **rhizosphere**—that is, the immediate vicinity of the roots—in order to change the availability of nutrients. Because of the important role of soil pH, acidification by proton pumping is one prevalent mechanism that enhances availability of Fe, Zn, B and Mn. Organic acids such as malate and citrate are among the major components of **root exudates**. Deposition of carbohydrates in the rhizosphere accounts for a substantial fraction of the 20–60% of photosynthetically fixed carbon that

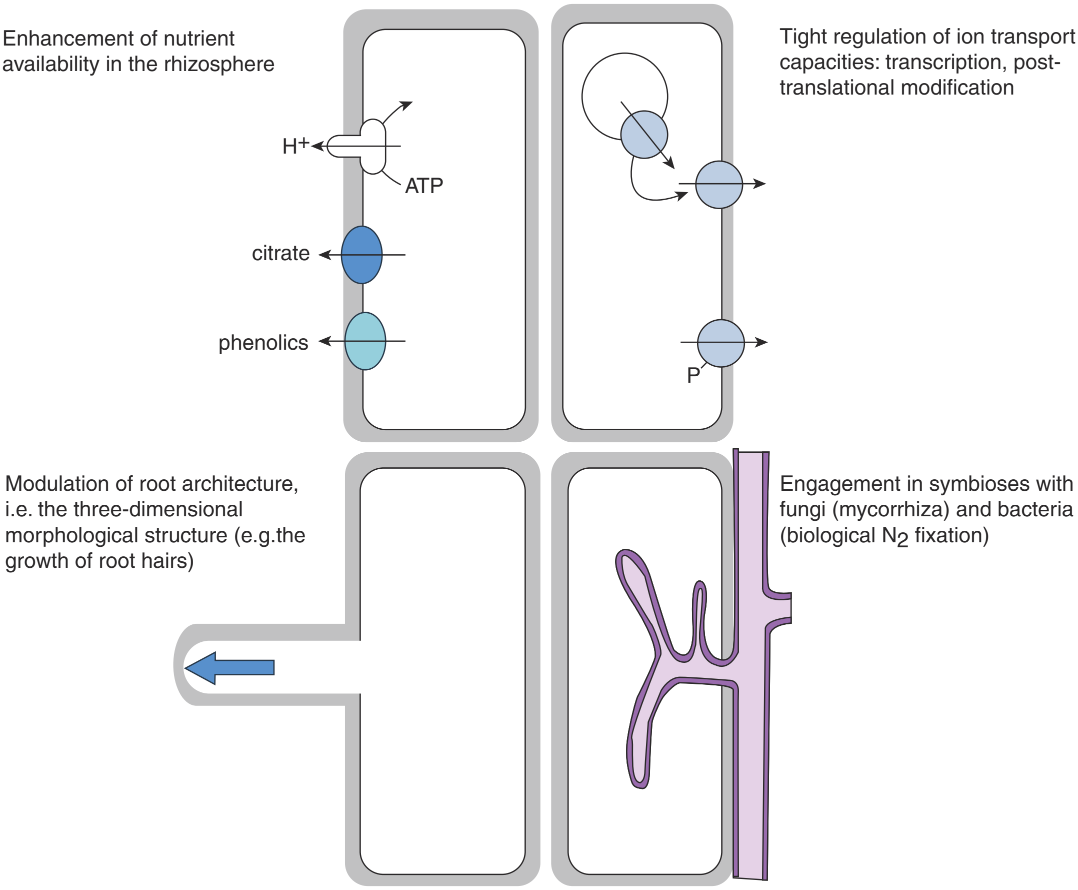

Fig. 7.4 Strategies for nutrient acquisition

is transferred below-ground by plants (Kuzyakov and Domanski 2000). Release of organic acids can occur passively through damaged root cells and via controlled secretion through anion channels in the plasma membrane. Stimulation of the latter has been observed especially in response to phosphate deficiency. Citrate and other carboxylates can mobilise sparingly soluble phosphate adsorbed to Fe or Al oxides. Their exudation is particularly pronounced in cluster roots of certain plants adapted to phosphate-poor soils (Fig. 7.19). Phosphate can in addition be mobilised by the secretion of enzymes (e.g. phosphatases) that can hydrolyse organic P esters (Fig. 7.5).

Because of the complexity of the processes and the difficulties in experimentally accessing the rhizosphere, detailed molecular understanding of root exudates and their contribution to nutrient availability is still limited. In contrast, a well-understood and very important example not only of nutrient mobilisation is **Fe acquisition** (Kobayashi and Nishizawa 2012), which will therefore be a recurring theme throughout this chapter. Iron is a particularly problematic element with respect to bioavailability. The usage of Fe as a redox-active element in biological systems evolved at a time when conditions in the Earth's atmosphere were reducing, making Fe readily available because Fe sulphides are highly soluble (Frausto da Silva and Williams 2001). With the advent of oxygenic photosynthesis, the bioavailability of Fe gradually and dramatically dropped by about eight orders of magnitude. In an oxidising atmosphere, Fe is mostly present as insoluble Fe oxides. Massive Fe precipitation resulted in the formation of red bands in sedimentary rock about 2.5 billion years ago. Thus, Fe is one of the most abundant elements in the Earth's crust, yet it is scarcely available in many

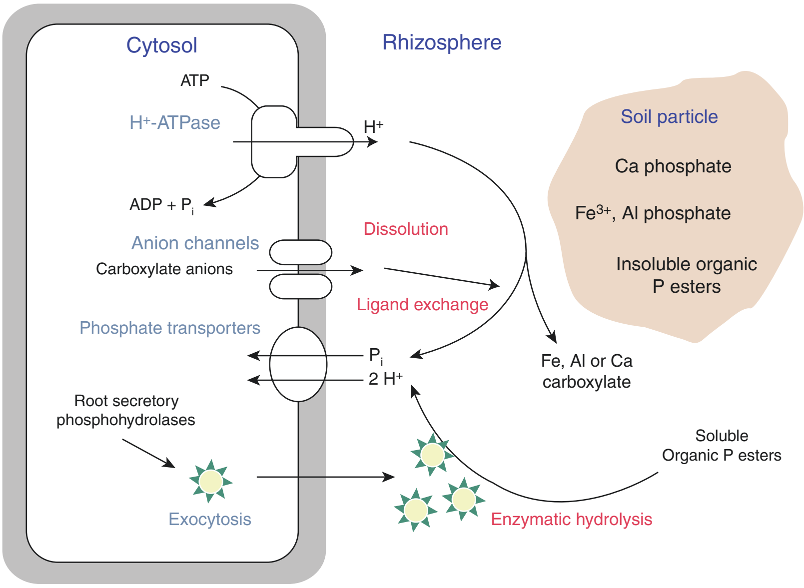

Fig. 7.5 Roles of root exudation in phosphate acquisition. (Modified from Neumann and Martinoia (2002))

habitats because it is mostly present in the oxidised form Fe(III), which is barely soluble, especially at pH values above neutral (Fig. 7.3).

Terrestrial plants evolved two distinct strategies to mobilise and to take up Fe (Römheld and Marschner 1986). **Strategy I**, expressed by dicots and non-graminaceous monocots, consists of subsequent acidification, reduction and uptake steps. Protons are secreted into the rhizosphere by **proton pumps** (**P-type H^+-ATPases**) to enhance solubility of Fe(III). Plasma membrane–localised **ferric reductases** reduce Fe(III) chelate complexes to Fe(II), which is then taken up into root epidermal and cortex cells. This strategy is supplemented by the secretion of phenolic compounds such as coumarins, which may act as chelators and/or reductants of Fe(III) (Clemens and Weber 2016). **Strategy II** is characteristic for grasses. Fe(III)-chelating **phytosiderophores** such as mugineic acids are secreted by root cells. Phytosiderophores form complexes with Fe(III), which are substrates for specialised transporters that mediate the uptake of these complexes. Many of the proteins mediating these processes have been molecularly identified in *Arabidopsis thaliana* and maize. Loss-of-function mutants have demonstrated the essentiality of the different steps for growth under Fe-limited conditions. Maize mutants lacking the phytosiderophore uptake transporter Yellow stripe 1 (*ys1*) show characteristic Fe deficiency–caused chlorosis phenotypes of the leaves (Curie et al. 2001) (Fig. 7.6).

Fig. 7.6 Chlorosis of the *Yellow stripe1* maize mutant. The *ys1* mutant (*left*) suffers from Fe deficiency because of a defect in an Fe(III)–phytosiderophore complex transporter. (Photo courtesy of University of Massachusetts Amherst)

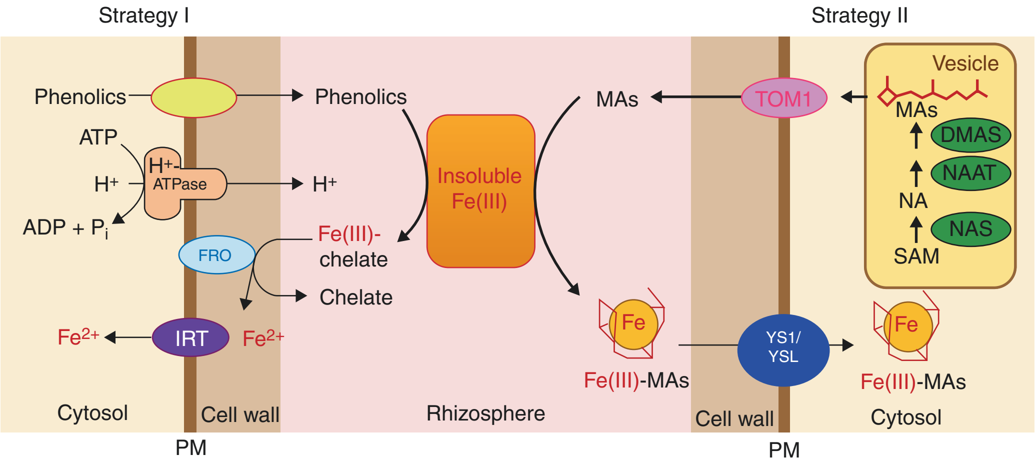

Fig. 7.7 The two strategies for Fe acquisition. Higher plants, with the exception of grasses, use strategy I: a combination of acidification by protein pumping, the reduction of Fe(III) by ferric reductases (FRO) and uptake by Fe(II) transporters (IRTs). Especially when the soil pH is alkaline and acidification is difficult, the secretion of phenolics helps improve Fe availability. Grasses employ strategy II: the secretion of Fe(III)-chelating molecules—the phytosiderophores of the mugineic acid (MA) family—by transporters such as TOM. Fe(III)–MA complexes are then taken up by transporters of the YS1/YSL family. *SAM* S-Adenosylmethionine, further explanations in the text. (After Kobayashi and Nishizawa (2012))

The synthesis and secretion of Fe-chelating molecules is strongly activated under Fe limitation. In rice, barley and maize, as representative grass species, several genes encoding enzymes of the mugineic acid synthesis pathway are up-regulated. Examples include nicotianamine synthase (NAS), nicotianamine aminotransferase (NAAT) and deoxymugineic acid synthase (DMAS) (Fig. 7.7). The same applies to the transporters for mugineic acid or Fe(III)–mugineic acid complexes. Variations within and between grass species in the ability to thrive on alkaline soil have been explained by differences in phytosiderophore secretion rates. Barley shows much stronger mugineic acid release than rice. When rice was engineered to produce more phytosiderophores through transfer of a more strongly expressed nicotinamine aminotransferase gene from barley, growth and yield on alkaline soil was significantly improved (Takahashi et al. 2001)—an example for the engineering of stress tolerance.

It is important to note that P and Fe are merely the two best-understood examples of active modulation of nutrient availability. The aforementioned **rhizodeposition** of organic compounds strongly influences the density and the activities of microbial communities around the root. These activities in turn have pronounced effects on nutrient chemistry (Sect. 7.3.2.1, the conversion of N sources). The questions as to whether and how plant roots actively recruit certain microbial populations (the **rhizosphere microbiome**) can only now begin to be addressed, owing largely to the revolution in DNA sequencing technologies (Bulgarelli et al. 2013).

7.3.2 Cellular Ion Transport Mechanisms

Mineral nutrients in the soil solution are practically always present as ions and carry an electric charge. Thus, they cannot cross biological membranes at sufficiently high rates without the involvement of proteins that form specialised pores allowing passage through the membranes. Ions can move into the cytosol and out of the cytosol. Movement from the exterior into the cytosol is called uptake; transport into the extracellular space is called efflux. All other transport processes occur across organellar membranes. Most relevant for mineral nutrition are uptake, efflux and transport into and out of the vacuole (Fig. 7.8). A large number of transport proteins mediating these processes are encoded in plant genomes, as we know from the

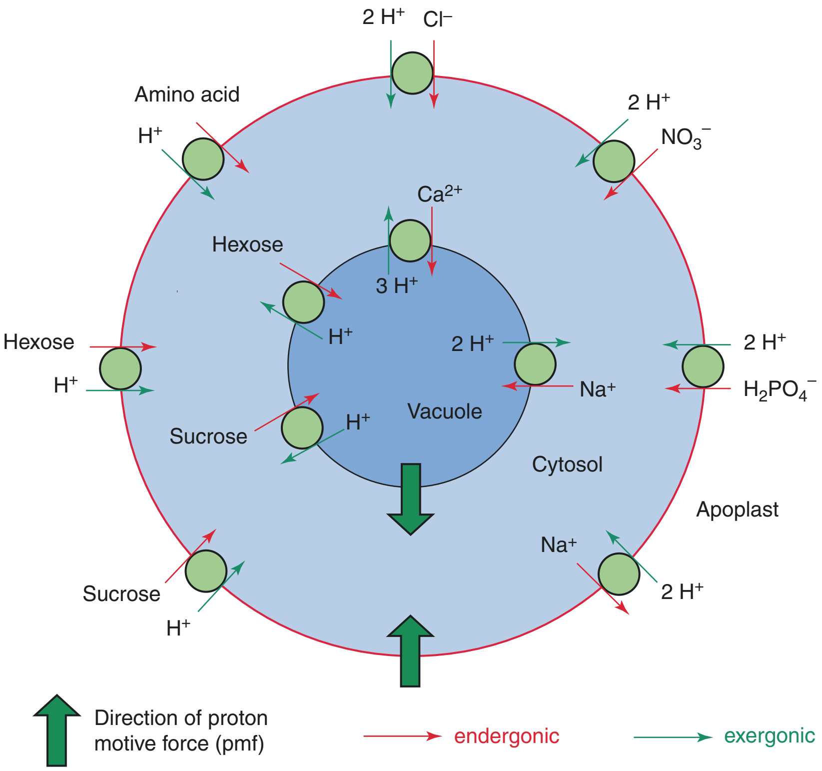

Fig. 7.8 Secondary active transport across the plasma membrane and the tonoplast. The proton motive force (pmf) generated by proton pumps and pyrophosphatases provides the energy for transport against an electrochemical potential gradient. A few examples of myriad transport processes in a plant cell are shown. (Modified from Weiler and Nover (2008))

model species *A. thaliana* and rice. For example, around 50 genes encode K^+ channels and K^+ transporters in *A. thaliana* alone (Ward et al. 2009).

Depending on the driving force, three categories of transporters are distinguished (Fig. 7.9). Facilitated diffusion refers to transport that is energetically favourable because it occurs along an electrochemical potential gradient. Typical proteins enabling facilitated diffusion are channels such as K^+ channels (Figs. 7.11 and 7.12). Active transport moves an ion (or a metabolite) against an electrochemical potential gradient—for example, from the soil solution with a low concentration to the cytosol of a root cell with a high concentration (enrichment)—or an anion against the negative potential of the plasma membrane (by definition, the membrane potential of a cell is negative when there is a surplus of negative charges on the cytosolic side). **Primary active transport** is directly energised by the hydrolysis of adenosine triphosphate (ATP). **Secondary active transport** uses the energy supplied by a gradient in electrochemical potential through coupling of the energetically favoured movement of one molecule to the unfavourable movement of another (Fig. 7.9).

The dominant primary active transport in plant cells is the establishment of a **proton gradient** across the plasma membrane and the tonoplast by the activity of **H^+-ATPases** (and additionally of pyrophosphatases in the case of the tonoplast). This proton gradient, the **proton motive force**, provides the driving force for myriad transport processes in plants (Fig. 7.10). It can be used by carrier proteins (Fig. 7.9). Many of them co-transport protons with ions or metabolites. This co-transport can be a **symport** (i.e. both molecules move in the same direction) or an **antiport** (i.e. the molecules move in opposite directions). While most carriers involved in nutrient acquisition couple transport to the movement of protons and are therefore secondary active, there are many others that couple the transport of two metabolites or of a metabolite and an ion and are passive. Examples are the phosphate translocator in the inner plastid membrane, which exchanges phosphate with 3-phosphoglycerate, or the malate/oxaloacetate shuttle. A third type of

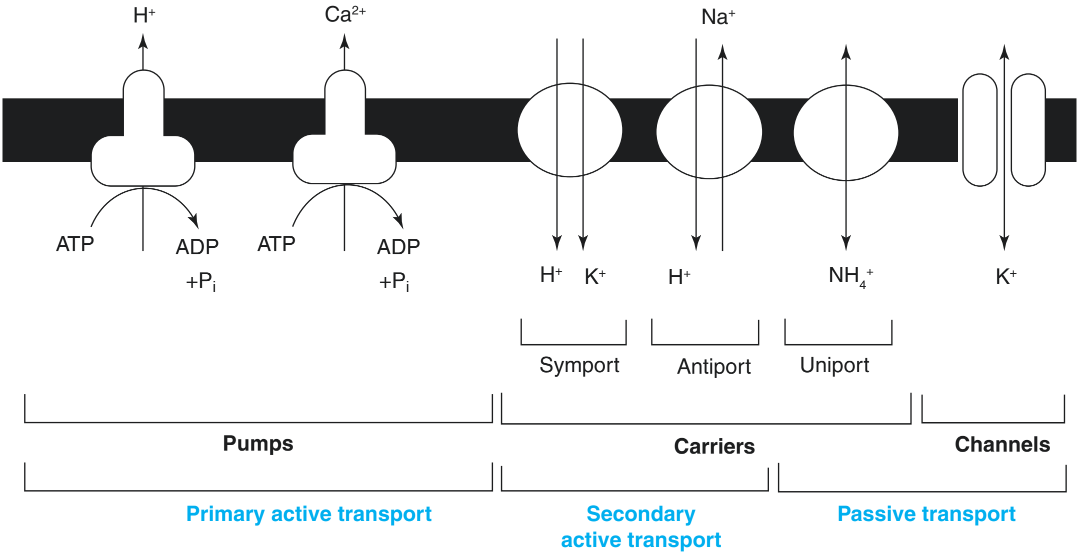

Fig. 7.9 Different categories of transport. (Modified from Marschner (2012))

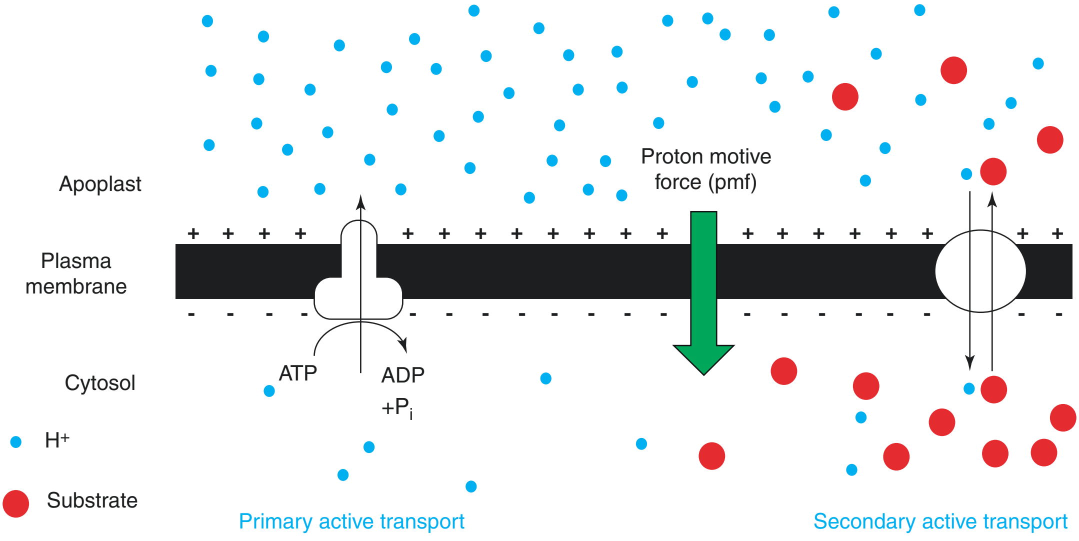

Fig. 7.10 Primary active transport fuels secondary active transport. The pumping of protons from the cytosol to the apoplast is a primary active transport, directly energised by ATP and mediated by P-type H^+-ATPases. It contributes to the particularly negative membrane potential of plant cells. The resulting proton motive force can drive secondary active transport through the coupling of energetically favoured proton influx with, for example, efflux of a positively charged substrate against an electrochemical potential difference

carrier—and passive too—is the uniporter that mediates transport of one molecule along a potential gradient.

The activities of cation and anion channels depend on the cell's external and internal ion concentrations, which establish a specific **membrane potential** (Fig. 7.10). The so-called rectifying channels allow charges (ions) to pass more easily either into the cells (inward rectifier) or in the outward direction (outward rectifier), thus also affecting the membrane potential (Fig. 7.11). The same holds for channels in the tonoplast membrane. At a membrane potential negative to the equilibrium potential of, for example, K^+, inward

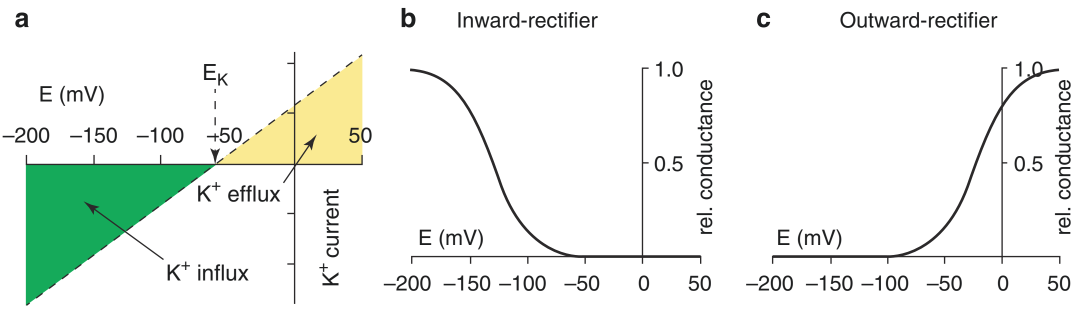

Fig. 7.11 Dependency of K$^+$ channels on the membrane potential (voltage). **a** The *dashed line* shows the degree to which a K$^+$ channel population is open for inward or outward K$^+$ fluxes. At the equilibrium voltage (E_K) no net flux of potassium takes place. The E_K depends on the potassium concentrations on both sides of the membrane. In principle, and given a respective membrane potential, an inward rectifier can also export K$^+$ ions, and vice versa. The activity of the voltage-gated channels changes gradually with a change in the membrane potential. Inward-rectifying K$^+$ channels **b** open upon hyperpolarisation of the membrane potential (i.e. a shift to more negative values), and outward-rectifying K$^+$ channels **c** open upon depolarisation of the membrane potential (i.e. a shift to less negative values). (Dreyer and Blatt 2009)

potassium rectifiers support the flow of the potassium cation into the cell, rendering the membrane potential more positive until the equilibrium potential (also termed the **Nernst potential**) of K$^+$ is reached. Anion-rectifying channels operate in a similar way with anions. Channels whose activities change the membrane potential can, on the other hand, be controlled by that potential. They are termed **voltage-gated channels**, in contrast to channels that are controlled by specific ligands (**ligand-gated channels**). Gating of these channels can control K$^+$ mineral nutrition (Sect. 7.3.2.2), signalling, and abiotic as well as biotic stress responses. The regulation of inward- and outward-rectifying K$^+$ channels plays a key role in controlling the turgor of guard cells and the apertures of stomata (Sect 6.3.3).

Depending on the nutrient ion in question, uptake into the root symplast—that is, the cytosol—has to be either energised or not. The plasma **membrane potential** of plant cells is negative (around −150 mV), owing largely to the proton pumping activity of H$^+$-ATPases. Thus, cations such as K$^+$ or Fe^{2+} can in principle move passively into the cytosol along an electric potential gradient through channels or uniporters. In contrast, anions such as phosphate, nitrate and sulphate enter a root cell against a potential gradient. This is enabled by H$^+$-coupled symport (Figs. 7.8 and 7.10). Conversely, efflux out of the symplast into the apoplast for xylem loading requires energisation for the cations and is energetically favourable for the anions.

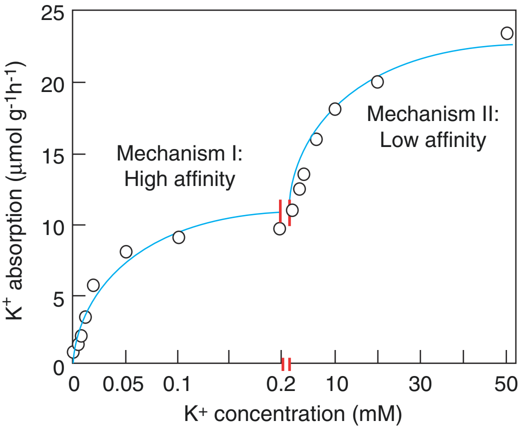

Fig. 7.12 Multiphasic nutrient uptake systems. Usually two types of uptake systems for nutrients such as K$^+$ can be expressed in plants, depending on availability and the physiological state; a high-affinity system is induced when nutrient availability is limited, and a low-affinity system operates when the nutrient supply is good

One of the hallmarks of plant mineral uptake is the existence of multiphasic uptake systems with varying affinities, as classically shown for K$^+$ (Epstein et al. 1963). Depending on the concentration in the soil solution, **low-affinity** or **high-affinity** transport systems with affinities in the millimolar or micromolar range, respectively, are in operation (Fig. 7.12). As for enzymes, the affinity for the substrate is expressed

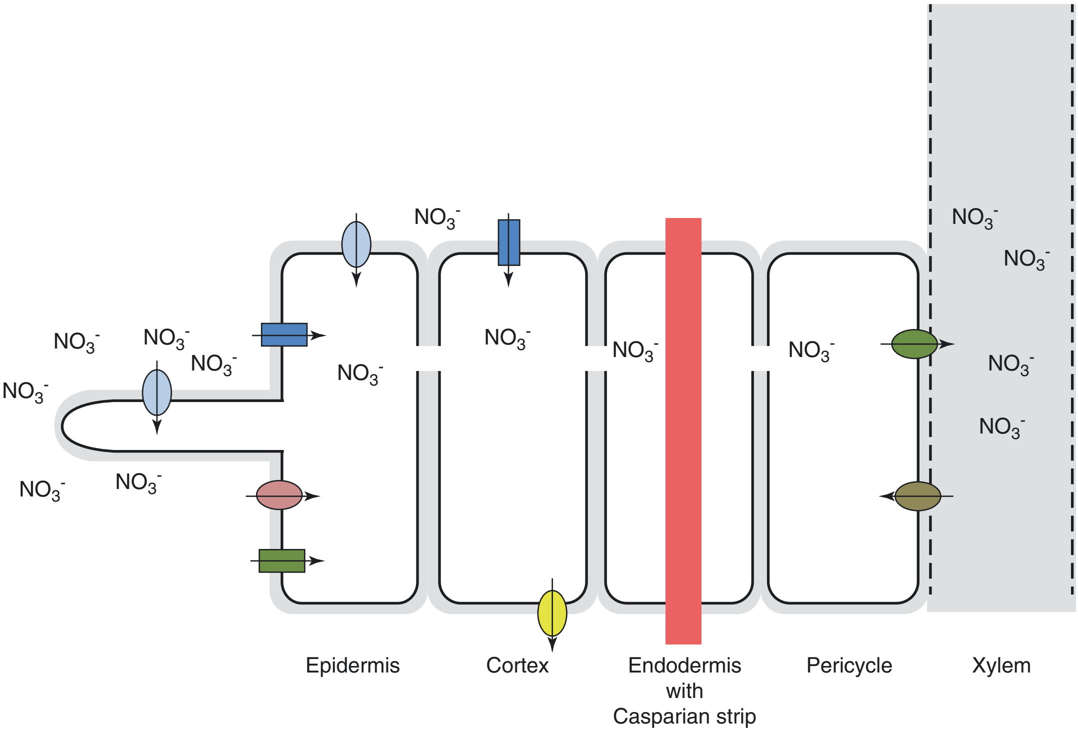

Fig. 7.13 Nutrient acquisition by the plant root is dependent on families of transporters differing in affinity, expression level and localisation. The example of nitrate is shown. Both uptake and efflux activities are involved in supplying nitrate in the right concentrations to roots and—via the xylem—shoots. *Ovals* represent members of the low-affinity NRT1 transporter family; *rectangles* represent members of the high-affinity NRT2 transporter family. The storage of nitrate in root cell vacuoles is not shown

as a K_M (**Michaelis–Menten**) value—that is, the substrate concentration at which the transport rate is half maximal. Typically, a plant possesses several isoforms of both low-affinity and high-affinity transporters, which vary in localisation and timing of expression (Fig. 7.13). This applies to both monocot and dicot plants.

7.3.2.1 Nitrogen Uptake

Nitrogen is present in the soil in many different chemical forms. The three most abundant ones are **nitrate** (**NO_3^-**), **ammonium** (**NH_4^+**) and **amino acids**. Their relative contributions can vary widely depending on environmental conditions and competition by soil microorganisms. Ammonium is the main N source under anoxic reducing conditions (e.g. in wetlands) or at low pH, when nitrification by microorganisms is impaired. Rice plants in paddy fields, for instance, utilise mostly ammonium. Nitrate dominates at higher pH values and in more oxidising aerobic soils. Amino acids are released by the breakdown of proteins in soil organic matter. When mineralisation is slow—for instance, because of low temperatures in high-altitude habitats or boreal forests—organic N in the form of amino acids can represent a substantial nitrogen source. Microbial competition is further dependent on mobility of the different N forms in the soil. Nitrate is more mobile in the soil solution because of its negative charge and is therefore less prone to utilisation by microorganisms before it reaches the surface of a plant root (Miller and Cramer 2005) (Sect. 11.2.2).

Plants possess multiple uptake transporters to be able to optimally exploit the hugely varying N sources. Transporters differ in substrates, substrate affinities, localisation of expression and regulation. In this way they provide a set of tools to fine-tune uptake activity in response to external supply. Nitrate concentrations in the soil solution can vary between micromolar and millimolar. Low-affinity transporters for nitrate uptake at high external supply belong to the NRT1 protein family. Their K_M values are in the millimolar range. NRT2 family members are high-affinity transporters with a K_M value for nitrate of around 50 µM. They are structurally not related to NRT1 transporters and mediate nitrate/H^+ antiport (Fig. 7.13).

Transporters accounting for low-affinity ammonium uptake have not been identified yet. High-affinity uptake is dependent on AMT1 proteins. They function as uniporters (see overview scheme in Fig. 7.9). Typically for nutrient uptake transporters, different isoforms (six in *A. thaliana*) are expressed in root hairs, the root cortex and endodermis cells.

The molecular understanding of amino acid uptake is much more limited than that of nitrate and ammonium uptake. Transporters with varying substrate spectra exist. Little is known about their contribution to N acquisition (Svennerstam et al. 2011, Chap. 11, Sect. 11.2.2.1).

Nitrogen is one of two nutrients (besides sulphur) that have to be assimilated into organic compounds. While ammonium can be directly assimilated, nitrate has to be reduced first to nitrite and then to ammonium. Nitrate assimilation can, depending on the plant species, occur preferentially in root cells or in leaf cells. The first product of nitrogen assimilation is glutamate. All other N-containing molecules are synthesised from this amino acid (for more details, see plant physiology and plant biochemistry textbooks).

7.3.2.2 Potassium Uptake

While K^+ uptake is driven by the negative membrane potential, external concentrations can be so low—that is, the concentration gradient between inside and outside can be so high—that energisation is required. Thus, in contrast to the **low-affinity systems**, which are channels enabling passive diffusion, the **high-affinity systems** are usually symporters co-transporting K^+ and protons. In *A. thaliana* the K^+ channel AKT1 accounts for much of the K^+ root uptake. AKT1 is a representative of the Shaker-type of K^+ channels (named after a *Drosophila* mutant), which are present in a wide range of species across kingdoms and are involved in processes as diverse as action potentials in neurons, potassium nutrition and stomatal regulation (Chérel et al. 2014).

Low external K^+ causes an even more negative membrane potential than normal because K^+ influx into cells is a major force attenuating the surplus of positive charges on the outside of cells. This more negative membrane potential further enhances the electrical potential gradient, which can drive K^+ into cells. This is the reason why AKT1, as a channel mediating only facilitated diffusion, is still able to support growth even at rather low external K^+. Still, below such concentrations, proton-coupled import is required. The responsible proteins are designated KUP/HAK (K^+ uptake permease/High affinity K^+). They account for the high-affinity uptake (mechanism I in Fig. 7.12).

7.3.2.3 Phosphate Uptake

Phosphate availability is one of the major constraints of plant growth. In the soil, P is present in the inorganic oxidised form (P_i; orthophosphate) or as part of organic molecules. Only inorganic phosphate can be utilised. Phosphate in organic molecules has to be liberated by enzymes such as plant or microbial phosphatases (Fig. 7.5). Concentrations of inorganic phosphate in the soil solution are often very low (around 1 µM) because of the poor solubility of phosphate and its tendency to adsorb to soil particles. Its low mobility relative to other macronutrients is explained by these characteristics too.

The negative membrane potential and a steep concentration gradient between the soil solution and the cytoplasm (with a concentration of around 5 mM) under most conditions demand energised high-affinity uptake systems for the uptake of phosphate anions such as the major form $H_2PO_4^-$. The systems mainly responsible in both mycorrhized and non-mycorrhized plants are the **Pht1 family transporters**, of which several are encoded in the genomes of higher plants (López-Arredondo et al. 2014).

7.3.2.4 Uptake of Other Nutrient Elements

Sulphate acquisition shows many similarities to nitrate acquisition. High-affinity uptake by proton-coupled symporters (in the case of sulphate these are referred to as sulphate permeases) mediate entry into the cytosol. All steps of sulphate assimilation occur in plastids. The metabolite that is analogous to glutamate in N assimilation is cysteine for S assimilation.

Uptake of Fe(II) by strategy I plants such as *A. thaliana* is mainly dependent on IRT1. The absence of this uniporter causes severe growth inhibition when Fe availability in the soil is low (Fig. 7.14).

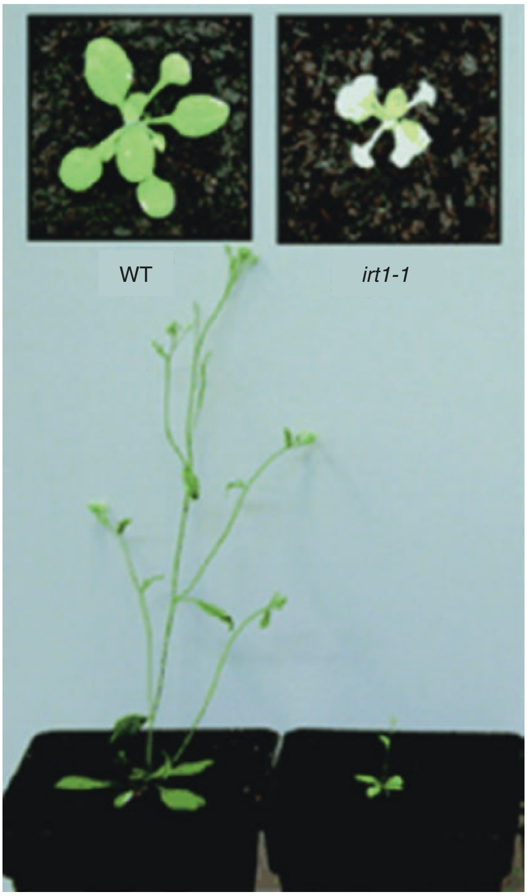

Fig. 7.14 The transporter IRT1 is essential for Fe(II) uptake in *Arabidopsis thaliana*. Loss of the functional transporter causes severe growth inhibition and chlorosis. *Left:* Wild-type plants. *Right: irt1* mutant plants. (Vert et al. 2002)

Boron and the beneficial element Si are taken up as boric acid and silicic acid, respectively, by **aquaglyceroporins** of the nodulin 26–like intrinsic protein (NIP) family. These proteins form pores in the membrane for facilitated diffusion. The protein responsible for boron uptake in *A. thaliana* is NIP5;1. The very pronounced uptake of Si in rice is mediated by Lsi1. This transporter represents an example of the polar localisation of at least some nutrient transporters in root cells. Lsi1 is exclusively localised on the distal side facing the soil (Ma et al. 2006).

7.3.3 Modulation of Nutrient Uptake in Response to Deficiency

Plants need to be able to respond and acclimate to strongly fluctuating external nutrient availability. The major targets of acclimation are nutrient uptake capacities and the root architecture (described in Sect. 7.3.5). Generally relevant factors are the external supply of a particular nutrient and the internal status. Both can in principle be sensed and translated into a response. A second distinction is that between a **local response** (i.e. a cell or a tissue perceives a problem and triggers countermeasures) and a **systemic response** (i.e. leaves or another organ distant from the site of nutrient acquisition monitor the nutritional status and send a signal down to the root, where uptake is modulated appropriately).

A basal feature of plant nutrient acquisition is the switching from low-affinity uptake to high-affinity uptake when external concentrations drop below certain thresholds (Fig. 7.12). The activities of the different systems often correlate quite strongly with the expression levels of the genes encoding the transporters. Thus, **transcriptional regulation** is one key to the adjustment of uptake capacities. While low-affinity systems tend to be expressed constitutively, many high-affinity transporter genes (e.g. NRT2, AMT1, Pht1, KUP/HAK) have been shown to be up-regulated upon nutrient deficiency (Miller et al. 2009).

Another aspect of transcriptional control is activation in the presence of a substrate and repression by an end product. Nitrate serves as an important signal for nutrient availability and elicits the transcription of nitrate uptake transporter genes. Conversely, glutamine—as the product of ammonium transfer onto glutamate during nitrate assimilation—represents a **negative feedback** signal for nitrate uptake.

The P deficiency response is a relatively well-understood example of **systemic signalling**. Studies on *A. thaliana* and rice mutants with deregulated P_i acquisition (i.e. with low shoot P levels even when external supply is high) or with excessive P accumulation regardless of P status led to the identification of a systemic regulation of P uptake which, in its principal form, is present in many plants. PHO2 is a regulatory protein crucial for the down-regulation of Pht1-dependent high-affinity uptake. *pho2* mutants over-accumulate P in their shoots. The *PHO2* messenger RNA (mRNA) carries target sites for microRNA (miRNA) 399. This miRNA represents a phloem-mobile signal of P status in the leaves. Low P levels stimulate miRNA399 synthesis. In roots, miRNA399 then suppresses *PHO2* expression, which in turn results in higher expression of Pht1 transporters and thus higher transport capacity (Fig. 7.15). The abundance of miRNA399 is under the control of a transcription factor, Phr1, which controls many P deficiency responses.

Locally controlled transcription and systemically controlled transcription do not fully explain the **plasticity** of nutrient uptake. The responsible transporters are also regulated post-translationally. The attribution of low- and high-affinity uptake to distinct classes of transporters is in fact not without exceptions. CHL1/NRT1.1, the first nitrate transporter identified in plants, can switch between a low-affinity state and a high-affinity state. In response to low external nitrate concentrations, a threonine residue is phosphorylated by a kinase (Fig. 7.16). Similar affinity switching is known to occur in high-affinity K^+ uptake transporters in the HAK/KUP family. The K^+ channel AKT1 is activated by phosphorylation when external K^+ is low.

Ammonium is a nutrient that can be toxic to cells and therefore should not accumulate. Thus, uptake of ammonium needs to be controlled by a mechanism that allows rapid shut-off if a critical ammonium concentration is exceeded. AMT proteins are oligomeric proteins. Their C-terminal domain functions as an allosteric regulator of activity, which is controlled by phosphorylation.

Also, transporter activity can cause problems when the substrate specificity is not very high. This is illustrated by the Fe(II) uptake system

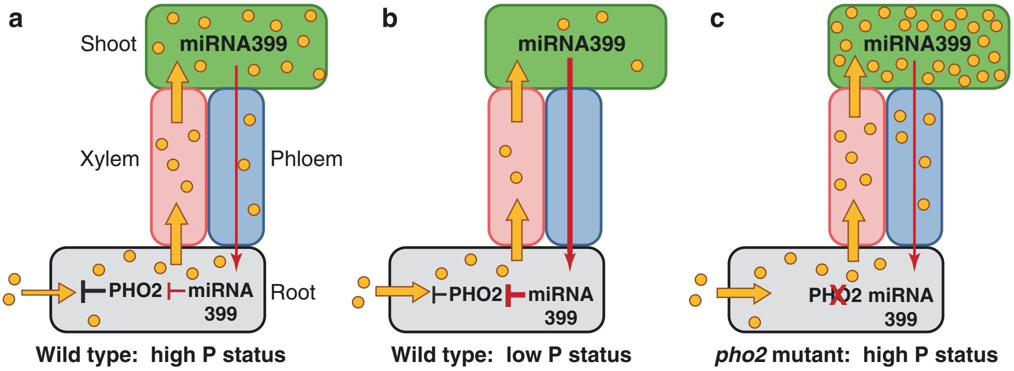

Fig. 7.15 The phosphate nutritional status of the shoot is signalled to the root by a microRNA. PHO2 is a protein that controls protein stability. When phosphate (*yellow dots*) supply to the shoot is sufficient **a**, phosphate uptake transporters (the Pht1 family) are down-regulated in a PHO2-dependent manner. However, when the shoot phosphate status is low **b**, microRNA (miRNA) 399 is expressed more strongly in leaf cells, travels via the phloem to the root and causes the degradation of PHO2 messenger RNA. This in turn results in higher phosphate transporter expression and hence uptake. In the pho2 mutant **c**, phosphate over-accumulates to toxic levels in the shoots because phosphate uptake by roots is not controlled any more. (Modified from Buchanan et al. (2015))

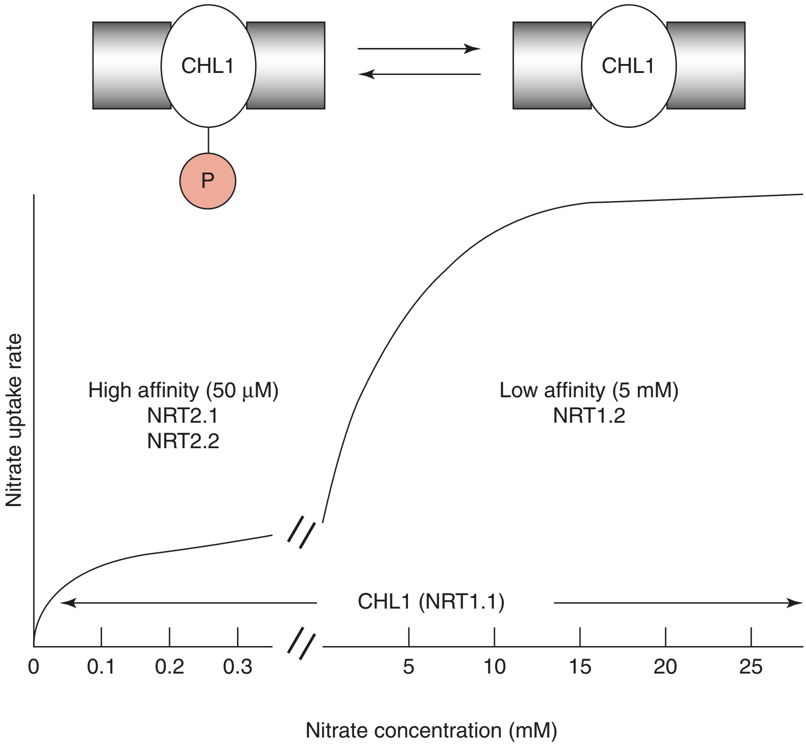

Fig. 7.16 Switching of the nitrate uptake transporter CHL1/NRT1.1 by phosphorylation from a low-affinity status to a high-affinity status (Tsay et al. 2007)

IRT1. IRT1 expression is transcriptionally upregulated when the plant's Fe status is low. Because IRT1 mediates entry also of Zn, Ni and Cd ions, among others, Fe deficiency can lead to supraoptimal uptake of these metal ions, resulting in toxicity. In the case of IRT1, the tight control through the Fe status and rapid shutdown when enough Fe is present intracellularly is brought about by cycling of the transporter within the endomembrane system (see aquaporin cycling in Chap. 6, Sect. 6.2 for a similar phenomenon). The residence time in the plasma membrane and protein stability respond immediately to Fe via post-translational mechanisms (Brumbarova et al. 2015), again enabling rapid inactivation of uptake capacity.

7.3.4 Intracellular Transport and Cellular Aspects of Long-Distance Transport

Nutrient supply to organelles and vacuolar storage require transporters too. Principally the same transporter types responsible for uptake also mediate transport into organelles (Miller et al. 2009). Examples are phosphate transporters in the **Pht family**. While Pht1 resides in the plasma membrane and takes up P_i, Pht2 is localised to the plastid inner membrane, Pht3 to the mitochondrial inner membrane and Pht4 to the Golgi compartment to mediate P_i transport into these organelles (López-Arredondo et al. 2014). The vacuole is an important storage site for some nutrient ions, including nitrate and phosphate. **Vacuolar storage** of nitrate is dependent on NRT2 nitrate transporters and nitrate/H^+ antiporters of the CLC family (see also stomatal regulation in Chap. 6, Sect. 6.3).

Not all nutrients are present in the cytosol as hydrated ions that can readily be accepted as substrates for transporters in organellar membranes. Many micronutrients, with Cu as the most extreme example, are too reactive to be available in this form for interaction with proteins and other molecules (Clemens 2001). According to the Irving–Williams series—that is, the observation that the stability of transition metal complexes with organic ligands generally follows the

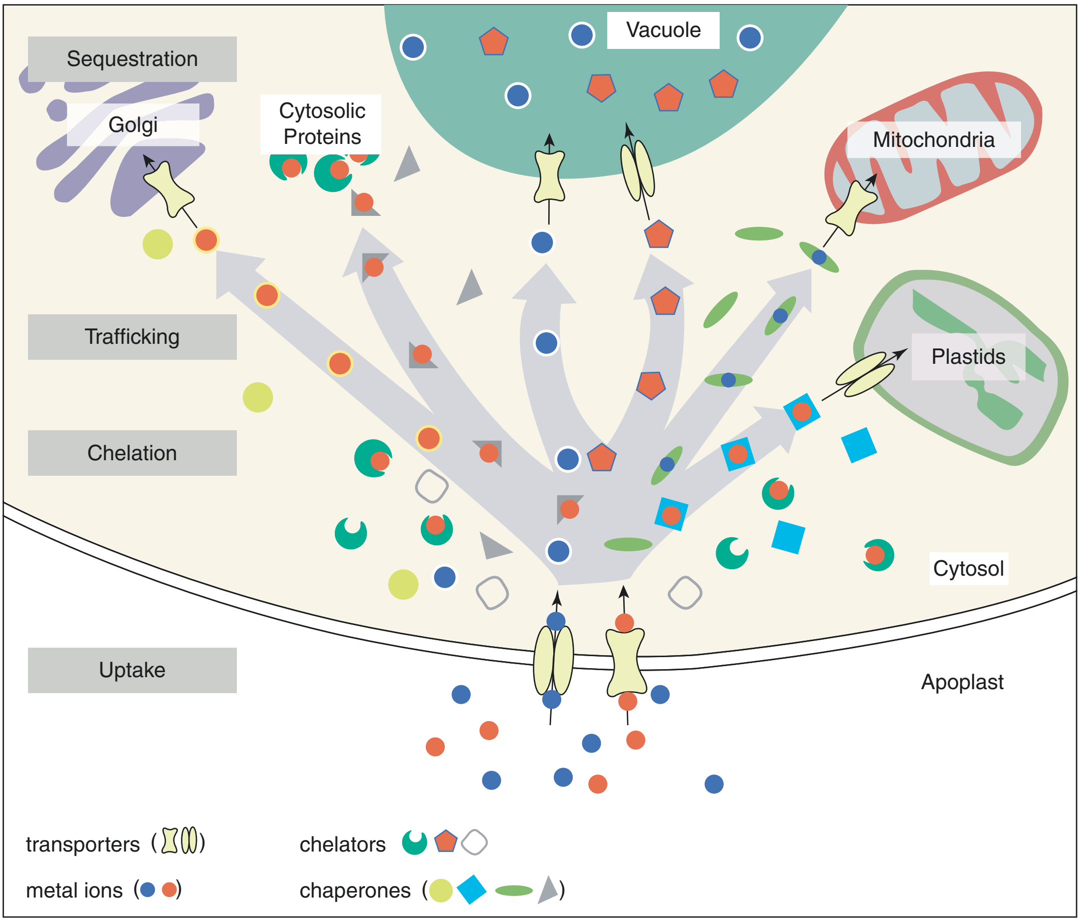

Fig. 7.17 Cellular metal homeostasis. Following uptake through plasma membrane–localised transporters, the ions of Cu and Zn in particular are bound by chelators and chaperones. Chelators buffer cytosolic metal concentrations and chaperones are involved in trafficking metals to target sites—that is, organelles and proteins requiring the metal in question. In particular, Cu chaperones directly interact with metal pumps that transport the metals into organelles. (Clemens 2001)

order Mn(II) < Fe(II) < Co(II) < Ni(II) < Cu(II) > Zn(II) (Irving and Williams 1948)—Cu(II) has a higher affinity for organic ligands than any other divalent cation in biology. This applies to N-, O- and S-ligands—for example, amino acids, organic acids or thiols such as GSH. Therefore, Cu(II) (and Cu(I) after reduction) have to be chelated by designated **metallochaperones** that deliver Cu ions to various pumps (proteins in the Heavy Metal ATPase (HMA) family) residing in the membranes of cellular compartments (or the plasma membrane for efflux). It has been estimated that in fact not a single hydrated Cu ion is present in the cytosol of a prokaryotic or eukaryotic cell. For Zn(II) the concentration of the so-called labile pool of ions that can readily be transported or bound is in the picomolar range—that is, several orders of magnitude below the total cellular concentration, which is in the micromolar range. Thus, most Zn(II) ions are chelated either by proteins or by low molecular weight ligands (Sect. 7.5.1). Estimates for the other micronutrients including Fe are less precise (Fig. 7.17).

Following **symplastic passage** from sites of uptake in the root cortex (Fig. 7.13), nutrients are loaded for long-distance transport into the xylem. The xylem is apoplastic. Thus, efflux across the plasma membrane of the xylem parenchyma or pericycle cells is necessary. Energetically the situation is reversed in comparison with uptake. Anions can be loaded via facilitated diffusion; cations may require active transport. Many transporters involved in this loading process are known in the model systems *A. thaliana* and rice. Loss of function leads to reduced **xylem sap** concentrations of the nutrient in question. This results in lower shoot concentrations.

In *A. thaliana*, nitrate, which can (in contrast to ammonium) be transported over long distances, is loaded into the xylem by the low-affinity transporter NRT1.5. The cytosolic nitrate concentration is high enough for this type of transport. NRT1.5 shows the typical localisation of expression in pericycle cells adjacent to the protoxylem to fulfil its loading function (Fig. 7.13). Similarly, borate is exported into the xylem by transporters known from *A. thaliana* and rice (BOR1). K^+ ions reach the xylem through outward-rectifying Shaker-type channels—SKOR in *A. thaliana*. Its opening probability decreases with rising external K^+ concentrations. This ensures that only efflux is mediated (Chérel et al. 2014). Zn is an example of a nutrient that is actively pumped into the xylem. The proteins responsible are HMAs. In *A. thaliana*, HMA2 and HMA4 load Zn into the xylem (Sect. 7.5.2 for the role of HMAs in metal hyperaccumulation).

7.3.5 Plasticity of Root Architecture and Responses to Nutrient Deficiency

Roots are the plant organs with the highest developmental **plasticity**. This plasticity helps roots to efficiently explore and exploit their heterogeneous soil habitat. Uptake of water and nutrients occurs predominantly near the root tips. Continuous root growth is required to access fresh and often immobile nutrient sources. The size of the root surface that is competent to take up water and nutrients determines the capacity of a plant individual to acquire these resources. For a given species or even for a given genotype, the spatial arrangement of roots and root systems (i.e. the **root architecture**) can be highly variable. It is mostly determined by:

- The number and lengths of root axes, including the length of the primary root
- The position, angle, density and growth of lateral roots
- The density and elongation of root hairs

New cells arise through cell division in the root meristem near the root tip. The root tip itself is protected by a root cap. In many species the root cap releases cells (border cells) that influence the rhizosphere—for example, by enhancing nutrient availability. Cells formed in the meristem differentiate into the epidermis, the cortex, the endodermis and the stele with its pericycle, xylem and phloem. Lateral roots are initiated in the pericycle; adventitious roots are initiated in the stem. Root hairs, which are particularly important for increasing the root surface, arise through the tip growth of designated epidermal cells, the **trichoblasts**.

Root architecture plasticity is governed by a variety of processes that occur in response to either the **nutrient availability** in the soil or the **nutritional status** of the plant (Fig. 7.18). Responses to nutrient availability are predominantly those triggered by the presence of nutrients. Responses to the nutritional status are triggered by **nutrient deficiency**. Detailed investigations have revealed clear nutrient specificity of the root architecture modulation. For instance, the strong inhibition of primary root growth and the stimulation of root hair development and elongation in phosphate-deficient plants are very well documented. Conversely, phosphate availability stimulates growth of lateral roots. Phosphate resources tend to be concentrated in the topsoil. The root architecture responses enhance exploitation of this soil layer. Perhaps the most striking response to phosphate deficiency is the formation of cluster roots—for instance, in a range of plants native to nutrient-poor soils in Australia (Lambers et al. 2015) (Fig. 7.19).

Stimulation of **lateral root growth** by a lack of adequate nitrogen or Ca supply represents a

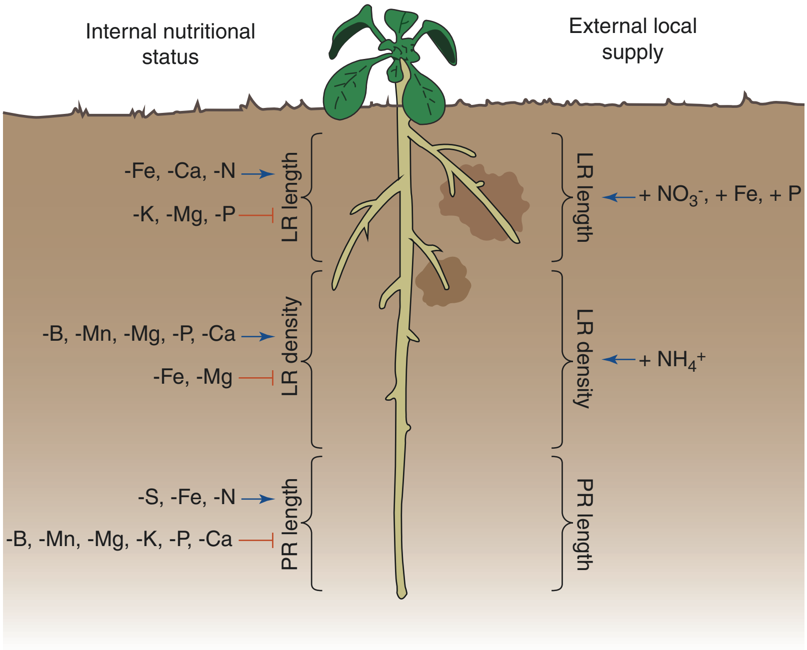

Fig. 7.18 Root developmental processes and nutrient availability responses. Blue symbols indicate stimulation, red symbols indicate inhibition. Minus (-) means deficiency of an element, plus (+) availability of an element. The root of a typical dicotyledonous plant is shown as an example. *LR* lateral root, *PR* primary root. (Giehl et al. 2014)

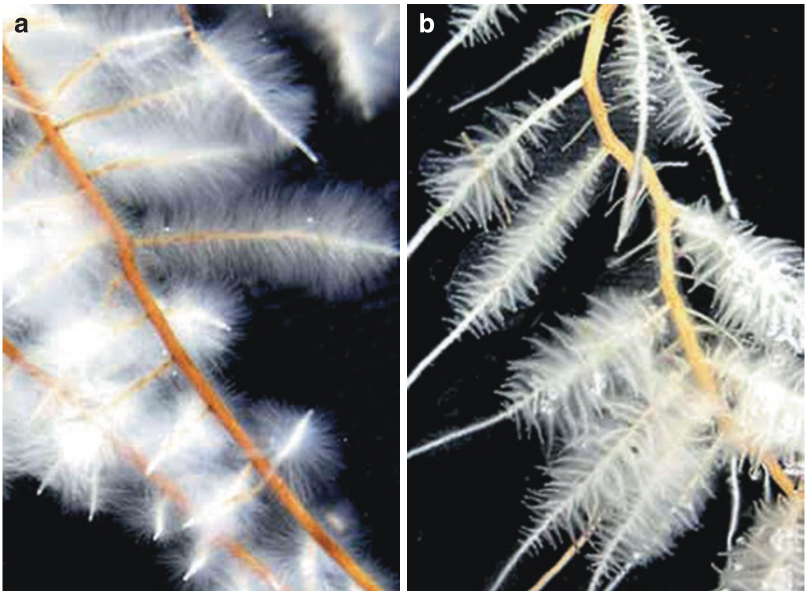

Fig. 7.19 Cluster roots of Proteaceae

foraging behaviour of roots. This strategy is physiologically limited inasmuch as a minimum nutrient supply has to be available to sustain the foraging (Giehl et al. 2014). When a nutrient-rich patch of soil is found, the growth of lateral roots is further stimulated. This has been shown for nitrate, phosphate and Fe (Fig. 7.18). In many experiments with various plant species, localised supply of nitrate in the substrate triggered growth of lateral roots located near or in the nutrient patch. In contrast, the **systemic response** of the lateral roots as a whole to conditions of ample nitrogen supply is a reduction in the growth rate. Less investment in root biomass is needed, thus more resources can be channelled into shoot growth. The **local response** enables rapid exploitation of a nutrient resource and thereby gives a plant a distinct competitive advantage over its neighbours. It is dependent on the perception of nitrate as a signal and not a mere consequence of nutrient supply. Generally, phosphate and nitrogen supply elicit the strongest responses of the root system development (Osmont et al. 2007). For many **root architecture responses**, however, it remains to be determined whether they represent strategies to mitigate the deficiency or symptoms of either the nutrient deficiency stress or the availability of nutrients to one part of the root but not another.

Like all plant developmental processes, the formation of the root system is controlled by the delicate, fine-tuned interaction of hormones (for detailed descriptions, see plant physiology and plant molecular biology textbooks). Key events are **cell cycle activity**, **cell differentiation** and **cell elongation**. The interplay between **auxin** and **cytokinin** in controlling root architecture is well documented. One important aspect is the balance between cell division and cell differentiation in the root meristem (Petricka et al. 2012). An auxin gradient establishes in the root and controls stem cell maintenance, cell proliferation and differentiation. Cytokinin, on the other hand, antagonistically inhibits cell division and reduces the size of the root meristem.

Emergence of lateral roots originates from pericycle cells adjacent to the xylem poles. Auxin triggers the formation of lateral roots. The sensing of phosphate deficiency, for instance, may sensitise pericycle cells to auxin, possibly through the up-regulation of auxin receptor expression. Overall, the exact mechanisms underlying the nutrient status–dependent modulation of root architecture by the **hormonal network** are not well understood yet.

7.3.6 Sensing of Nutrient Availability and Nutrient Status

Regulation of nutrient acquisition and modulation of root system architecture require accurate sensing of external nutrient availability and internal nutritional status. The latter is monitored both locally and systemically (Chap. 2, Sect. 2.2.4). The respective sensing then has to be translated into transcriptional changes (for instance, the up-regulation of genes encoding high-affinity transporters), post-translational control of transporters or regulatory proteins, and changes in the concentrations and distribution of hormones.

As alluded to in previous chapters, the molecular understanding of the primary sensing of environmental parameters generally lags behind the insight into the downstream signal transduction events. This is no different for the sensing of nutrient availability in the rhizosphere or the monitoring of the nutritional status. Local and systemic sensing of phosphate status, for instance, is not understood, while the regulation via miRNAs is well established (Fig. 7.15). The knowledge on **nitrate perception** is most advanced and can therefore serve as an example. The nitrate transporter **NRT1/CHL1**, already introduced as a protein able to switch affinity in a phosphorylation-dependent manner (Fig. 7.16), functions, in addition, as a **nitrate sensor** (Ho et al. 2009). Both the primary response to nitrate availability (the up-regulation of nitrate transporter, nitrate reductase and nitrite reductase genes) and the stimulation of lateral root growth in nitrate-rich soil patches (Fig. 7.18) are dependent on NRT1/CHL1 in *A. thaliana*. This association is not explained by transporter activity of NRT1/CHL1. Instead, external nitrate regulates the phosphorylation status of the protein and its ability to activate responses to high external nitrate availability. NRT/CHL1 is the first plant example of a so-called **transceptor**, a transporter protein that in fact functions like a receptor. The nutrient is not a substrate but a ligand with a signalling function. Many similar proteins may be involved in other nutrient-sensing processes.

7.4 Nutrient Acquisition Symbioses

For most plants in natural habitats, **symbiotic associations** with microorganisms are an essential part of their nutrient acquisition. Plants provide reduced carbon to the microorganisms and receive macro- and micronutrients in return. The importance of these symbioses (mycorrhizal associations between plant roots and fungi, and the biological N_2 fixation by symbiotic bacteria living within plant tissues) for global biogeochemical cycles cannot be overestimated (Chap. 19, Sect. 19.4). Here, we will describe:

- The mechanisms of nutrient and carbon exchange between the symbiotic partners
- The molecular events leading to establishment of the symbioses, which share so many features that the concept of a "**common sym pathway**" has emerged (Sect. 7.4.3)

7.4.1 Mycorrhizae

About 90% of all land plants—most monocots and dicots, and nearly 100% of gymnosperms—engage in a mycorrhizal association with fungi. On the fungal side, tens of thousands of different taxa are involved. Mycorrhizae are present in most terrestrial habitats colonised by plants. Rare exceptions include very dry soils, waterlogged soils or extremely phosphorus-impoverished areas where plants with cluster roots dominate (Fig. 7.19). Also, most members of a few plant families (e.g. Brassicaceae, Chenopodiaceae) do not form mycorrhizae. Mycorrhizae are evolutionary ancient and most likely were already instrumental when plants first colonised land about 450 million years ago (van der Heijden et al. 2015). This is suggested by fossils of the earliest land plants, which show signs of mycorrhizae.

Two major types are distinguished, which vary in morphology, type of partner and physiology. An **endomycorrhiza** is characterised by growth of fungal hyphae within the root cortex of the plant host and the formation of structures within cortex cells, while in an **ectomycorrhiza** the fungal hyphae do not grow into root cortical cells. Ectomycorrhizal fungi sheath the root with a mantle of tightly woven hyphae and grow between cortical cells (Hartig's net) (Fig. 7.20). Within the endomycorrhizal symbioses, three types are differentiated further: the **arbuscular**

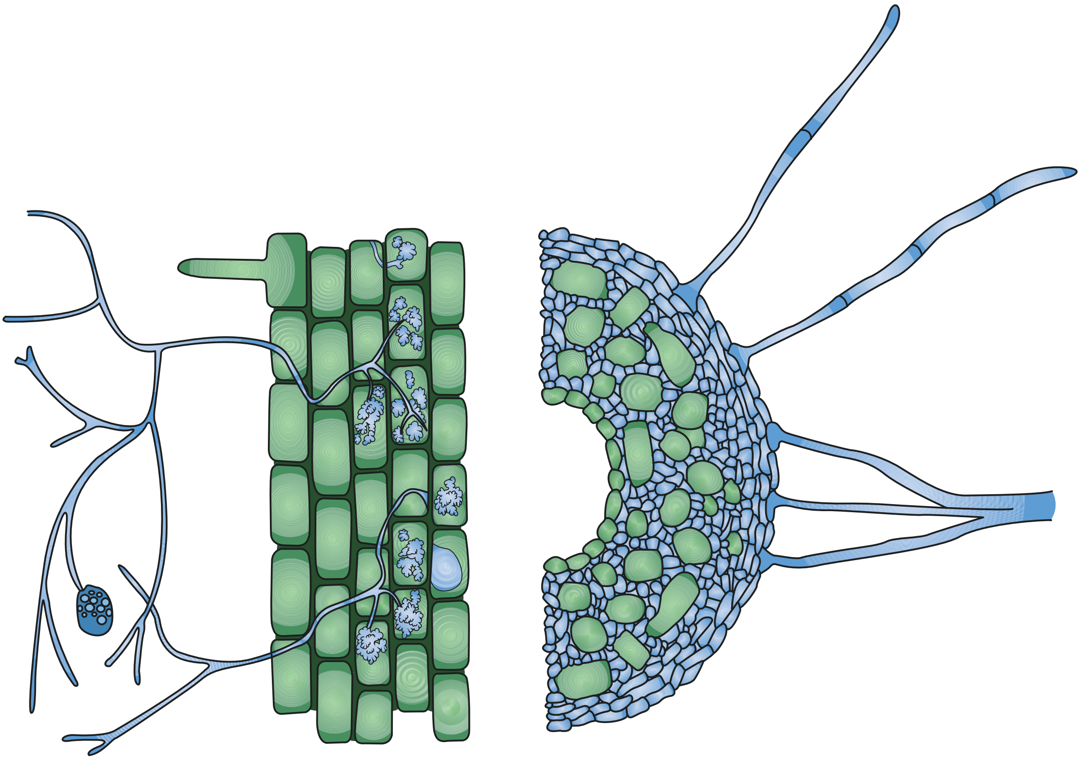

Fig. 7.20 Structural features of an arbuscular mycorrhiza (*left*) and an ectomycorrhiza (*right*). (Marschner 2012)

mycorrhiza, **ericoid mycorrhiza** and **orchid mycorrhiza**. By far the most common form (occurring in around 75% of all plant species) and evolutionarily the oldest is the arbuscular mycorrhiza. It is also the one that has been studied intensively at the molecular level and will thus be the focus of this section.

A large fraction (up to 80%) of the main limiting macronutrient, phosphorus, is provided to plants by mycorrhizal fungi. **Phosphorus** is much less mobile in the soil solution than nitrogen or other macronutrients. Therefore, the ability of fungal hyphae to grow into soil micropores that are too small for the diameter of plant roots makes more phosphorus available for uptake. Like plant roots (Fig. 7.5), mycelia actively mobilise phosphorus bound to soil particles—for instance, by the secretion of phosphatases. Zn is another comparatively immobile nutrient that is supplied to the host by the fungal partner. However, this is not well understood. The contribution of the arbuscular mycorrhiza to nitrogen supply for the host is much less pronounced. This is different for ericoid mycorrhizae and ectomycorrhizae. In addition to nutrients, the fungal symbiont supplies water to the host.

Both the molecular physiology of mycorrhizal transport processes and the events that enable symbiosis formation are being investigated predominantly in the **model systems** *Medicago truncatula* and *Lotus japonicus*. These species are studied in place of *A. thaliana* which, as a member of the Brassicaceae, does not engage in mycorrhizal symbioses. The added benefit of *M. truncatula* and *L. japonicus* as model species is that they are legumes; therefore, biological N_2 fixation can be studied as well.

Fungal **arbuscules** are structures with a large surface within root cortical cells (Fig. 7.21). Thus, the exchange of nutrients and sugars between the fungus and the plant occurs through two membranes that are in close vicinity: the invaginated plant-derived **periarbuscular membrane**, which is continuous with the plasma membrane of the host cell; and the plasma membrane of the arbuscule. Nutrient transfer from the soil into host cells requires uptake by the fungal mycelium, efflux into the symbiotic interface (the **periarbuscular space**) and uptake by the plant cell. Transfer of sugars arriving via the phloem from the plant to the fungal partner entails two membrane passages: efflux across the

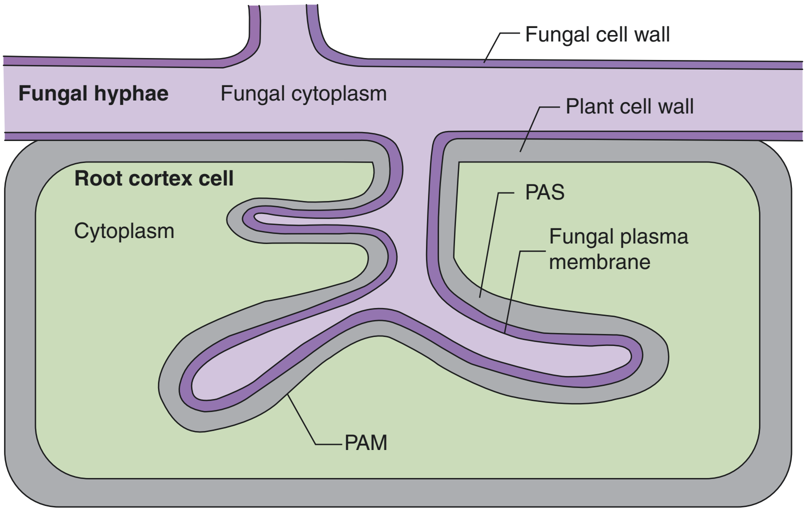

Fig. 7.21 Structure of an arbuscule. An arbuscular mycorrhiza is characterised by arbuscules developing inside root cortex cells. Exchange of sugars and mineral nutrients between the symbiotic partners occurs across the fungal plasma membrane, the periarbuscular space (PAS) consisting of plant and fungal cell wall material, and the plant-derived periarbuscular membrane (PAM), which is continuous with the plant plasma membrane. (Modified from Parniske (2008))

root cell plasma membrane and uptake by the arbuscular membrane.

Experimentally it is extremely challenging to detect and identify the transporters mediating these different steps. Consequently, a molecular dissection of the exchanges between the symbiotic partners is far from achieved. Sequencing of the genomes of plants and mycorrhizal fungi, as well as transcriptomes of mycorrhized and non-mycorrhized plants, is establishing inventories of transporters that are potentially involved (Garcia et al. 2016). The understanding of phosphate transport is most advanced. In host plants, genes encoding specific subgroups of phosphate transporters (the **Pht1 family**; Sect. 7.3.4) are up-regulated upon fungal colonisation of the root. In turn, other transporters involved in direct phosphate uptake from the soil solution are down-regulated. This indicates that phosphate supply through the symbiosis is prioritised. How this regulation occurs molecularly is not known. The up-regulated phosphate transporters in colonised root cells take up phosphate from the interface. Energy is provided, as in the case of anion uptake from the soil solution, by the pumping of protons. The proteins involved in the release of phosphate from the arbuscules are unidentified. Uptake of phosphate from the soil solution into the mycelium is mediated by high-affinity transporters similar to the ones expressed by plants (Harrison and van Buuren 1995). An equally fragmentary aspect is the assignment of essential sugar transport steps—that is, efflux of glucose out of the colonised root cell and uptake into the fungal mycelium—to particular proteins.

Even less is known at the molecular level about the possible exchange of reduced carbon, macronutrients and micronutrients between neighbouring plants via **mycorrhizal connections**. The host specificity—especially of the fungi involved in arbuscular mycorrhizae, the **Glomeromycota**—is low. Thus, they can be simultaneously associated with individuals of several different plant species. Also, many plant roots are colonised by more than one fungal species. The resulting underground hyphal network may well enable, for example, the support of shaded tree saplings with assimilates supplied by connected adult trees (van der Heijden et al. 2015). Also, the first direct evidence of **carbon trading** between trees has recently been found through carbon **isotope labelling**. A substantial fraction of the carbon isotope label introduced via photosynthesis into one tree was later found in neighbouring trees, suggesting an exchange mediated by ectomycorrhizal connections (Klein et al. 2016). The exact fluxes in such underground networks, however, have not really been determined yet, and the relevant molecular knowledge (e.g. about responsible transporters) is not yet available.

7.4.2 Nitrogen Fixation

Biological nitrogen fixation represents the major route of nitrogen supply to plants in natural terrestrial environments (an estimated 80–90%), while input into agricultural ecosystems originates largely from industrial production of NH_3 through the **Haber–Bosch process**. The conversion of inert atmospheric N_2 into organic nitrogen is of utmost importance for the global N cycle. The enrichment of soils with nitrogen has a massive impact on ecosystems (Chap. 23, Sect. 23.2).

A limited number of bacteria are able to fix atmospheric N_2 to NH_3. These bacteria are either free-living in the soil, associated with plants or partners in a symbiosis with plants. Those quantitatively most important with respect to the total nitrogen supplied to plants are symbiotic N_2 fixers. They account for approximately 80% of the biologically fixed nitrogen. Different types of nitrogen-fixing symbioses exist:

- Fabaceae establish symbioses with bacteria of the genus *Rhizobium*
- Woody shrubs and trees (e.g. *Alnus*) live in symbiosis with actinomycetes (*Frankia*)
- Diverse plant species such as certain gymnosperms or the fern *Azolla* host cyanobacteria

Molecularly the **Fabaceae–rhizobia symbiosis** is the best-understood symbiosis and will therefore be the focus here.

The symbiotic bacteria live in specialised structures (**nodules** in the case of the Fabaceae–rhizobia symbiosis) within the plant host. These provide suitable conditions for the supply of reduced carbon to the bacteria and the transfer of fixed nitrogen to the host. Another essential requirement is protection of the feature enzyme of all N_2-fixing bacteria—**nitrogenase**—from oxygen. Nitrogenase catalyses the reaction:

$$N_2 + 8e^- + 16ATP + 8H^+ \rightarrow 2NH_3 + 16ADP + 16Pi + H_2 \qquad (7.3)$$

It is immediately clear how energy demanding the nitrogenase reaction is. This probably explains why symbiotic N_2 fixation has such a dominant role in nature. For free-living bacteria it is extremely difficult to provide the ATP needed for NH_3 production. In contrast, symbiotic bacteria are supplied with assimilates by the host. The oxidation through respiration produces enough ATP to ensure efficient nitrogen fixation. A major challenge is the co-occurrence of respiration and oxygen-sensitive nitrogenase reaction. The mechanisms involved in generating a low-oxygen atmosphere in the vicinity of the nitrogenase are a bacterial cytochrome oxidase with an unusually high O_2 affinity and the synthesis of O_2-binding **leghemoglobins** by the host cells.

Within root nodule cells, rhizobia live as **bacteroids** in a specialised structure, the **symbiosome** (Fig. 7.22). The symbiosome is separated from the cytosol of the nodule cell by a membrane. Carbohydrates arriving at nodules via the phloem are converted into organic acids.

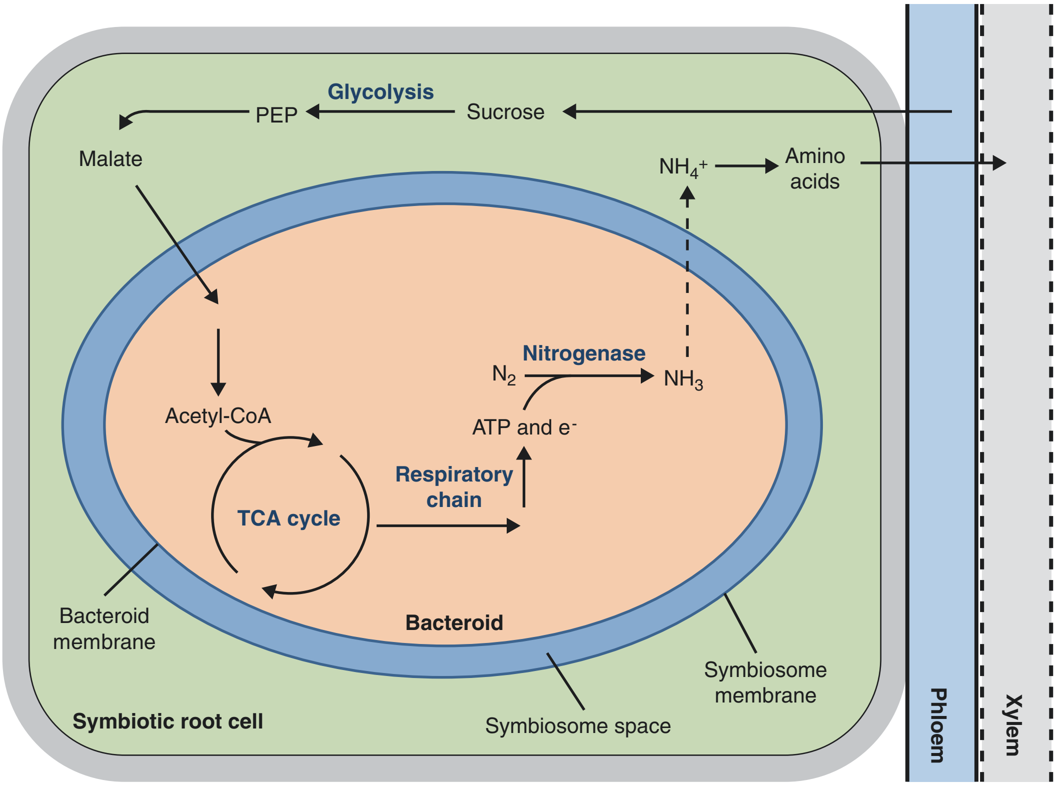

Fig. 7.22 A symbiosome within a nodule cell. The plant-derived symbiosome membrane encloses the bacteroid, a symbiotic form of a rhizobacterium. Exchange of nutrients and metabolites between the cytosol of the nodule cell and the bacteroid occurs across the symbiosome and the bacteroid membrane. The plant cell supplies organic acids such as malate to the bacteroid. Oxidation of these organic acids provides the energy for the N_2-fixing nitrogenase reaction. Ammonia is assimilated via glutamine into amino acids, which are then exported

One fraction of these is taken up by the bacteroids, where they are oxidised in the citric acid cycle (alternatively called the TCA cycle). ATP and reducing equivalents are then used for the nitrogenase reaction. The resulting NH_4^+ is assimilated into glutamine in the cytosol of the nodule cell. The other fraction of the organic acids provides the carbon skeletons for the nitrogen export compounds. Depending on the host plant, either glutamine itself can be exported or it can serve as an amide donor for other metabolites (asparagine, allantoin) supplying organic nitrogen to tissues outside the nodules.

7.4.3 The Common Sym Pathway

Establishment of both a mycorrhiza and nitrogen-fixing symbiosis has to occur for every single plant individually. It requires mutual recognition by the partners through chemical communication. Plant-derived signals perceived by the microorganisms stimulate processes that facilitate formation of the symbiosis. Conversely, signals released by the microbial partner trigger far-reaching developmental changes in the host plant that make entry of the fungal hyphae or the bacteria possible. The command over the process of symbiosis establishment lies entirely on the plant side, as the host has to actively allow infection by the symbiotic partner (Oldroyd 2013). Plants growing in an environment with an ample supply of phosphate do not engage in mycorrhizae, and legumes provided with enough nitrate and/or ammonia do not form nodules. This illustrates why the establishment of these symbioses can be regarded as an **acclimative response** to **nutrient scarcity**.

Flavonoids released by plant roots stimulate rhizobia to synthesise **nod factors**. These are lipo-chito-oligosaccharides, consisting of a chitin oligomer backbone with several modifications. Nod factors are perceived by plant roots and trigger many changes in the host that enable colonisation by the bacteria. First, root hairs curl and thereby build a protected environment for the rhizobia. Following a few bacterial cell division cycles, an infection thread forms inside the root hair. Rhizobia enter the plant root through these threads. Concomitantly, nodule organogenesis occurs in the root cortex. The cell cycle is stimulated, and newly dividing cells develop into the nodule (Fig. 7.23).

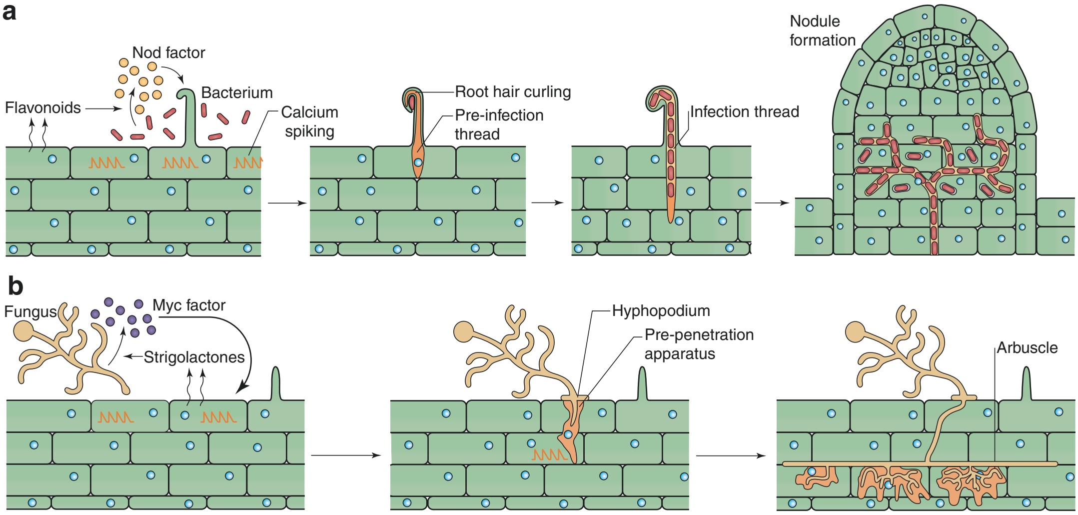

Fig. 7.23 Establishment of rhizobial and mycorrhizal root colonisation. The symbiotic partners recognise each other through the exchange of signals. Upon recognition the plant host undergoes massive developmental changes to allow colonisation. (Oldroyd 2013)

The plant signals that stimulate spore germination and hyphal branching of endomycorrhizal fungi have been identified as **strigolactones** (Akiyama et al. 2005)—that is, root-synthesised phytohormones involved in controlling shoot branching. **Myc factors** are the signals on the fungal side. They are chemically similar to nod factors in that they are lipo-chito-oligosaccharides as well (Maillet et al. 2011). Upon recognition of myc factors, plant roots undergo massive changes to allow penetration of hyphae towards the root cortex. A pre-penetration apparatus is formed in rhizodermal cells. It represents a transcellular “tunnel”, which is then used by the hyphae to grow into the root cortex (Parniske 2008). In the cortex the hyphae grow intercellularly before they form **arbuscules** within cells in the inner cortex (Fig. 7.23).

In spite of the fundamental differences between the symbiotic microorganisms and the plant developmental changes allowing colonisation of the host, the recognition and early signal transduction events in host cells proceed through a pathway shared by arbuscular mycorrhizae and the Fabaceae–rhizobia symbiosis: the **common sym pathway**. Molecular analysis of symbiotic interactions in the legume model systems has revealed that the symbiosis pathway enabling the formation of mycorrhizal associations in most plant species was, much later in evolution (around 150 million years ago), recruited by legumes for the establishment of biological nitrogen fixation. Research using mutants of *M. truncatula* and *L. japonicus* defined several genes that are essential for both mycorrhizae and root nodule symbiosis. A lack of any of these genes (e.g. the *SYMRK* gene) abolishes the early responses of plant roots to the microbial signals (Stracke et al. 2002). The chemically very similar nod and myc factors are perceived by closely related **receptor-like kinases** residing in the plasma membrane of root cells (Fig. 7.24). The receptors and co-receptors, whose exact functions with regard to the recognition of specific ligands are not resolved yet, share LysM domains typical for proteins binding chitin fragments. Early signal transduction event in root cells stimulated by symbiosis signals are **Ca oscillations** (i.e. rapid fluctuations in Ca concentrations, Chap. 2, Sect. 2.2) in the nucleus. Components that have been identified are ion channels of the nuclear envelope (CASTOR and POLLUX) required for the induction of the calcium oscillations, and components of the nuclear pore (Oldroyd 2013). Perception of the Ca signal is mediated by Ca- and calmodulin-dependent kinases (CCaMK), which interact with another common sym pathway component of unknown molecular function, CYCLOPS (Fig. 7.24). Even among the transcription factors downstream from the Ca signalling, overlaps in functional roles between mycorrhizal establishment and nodulation exist.

The common sym pathway exists in mosses and lycophytes, illustrating once more how ancient mycorrhizal associations are in terrestrial plants. Apparently, rather subtle changes in the genomes of legumes enabled them to establish a second symbiosis much later in evolution, this time with rhizobia, by principally employing the same basic mechanisms. It has been shown that many nodulation genes can be replaced by orthologous genes from plant species that are not able to form nodules, indicating that no fundamentally new innovations were required for the legume–rhizobia symbiosis. Nonetheless, a legume root initiates nodule formation in response to nod factors and prepares for penetration of fungal hyphae in response to myc factors. The specificity of the recognition and signalling processes is presumably conferred by specific functions of particular **receptor-like kinases** perceiving the signals and by specific transcriptional regulators.

7.5 Responses to Element Toxicity and Tolerance Mechanisms

Practically all plants exhibit some degree of basal tolerance of element toxicity. This can be easily demonstrated by studying mutants lacking a gene

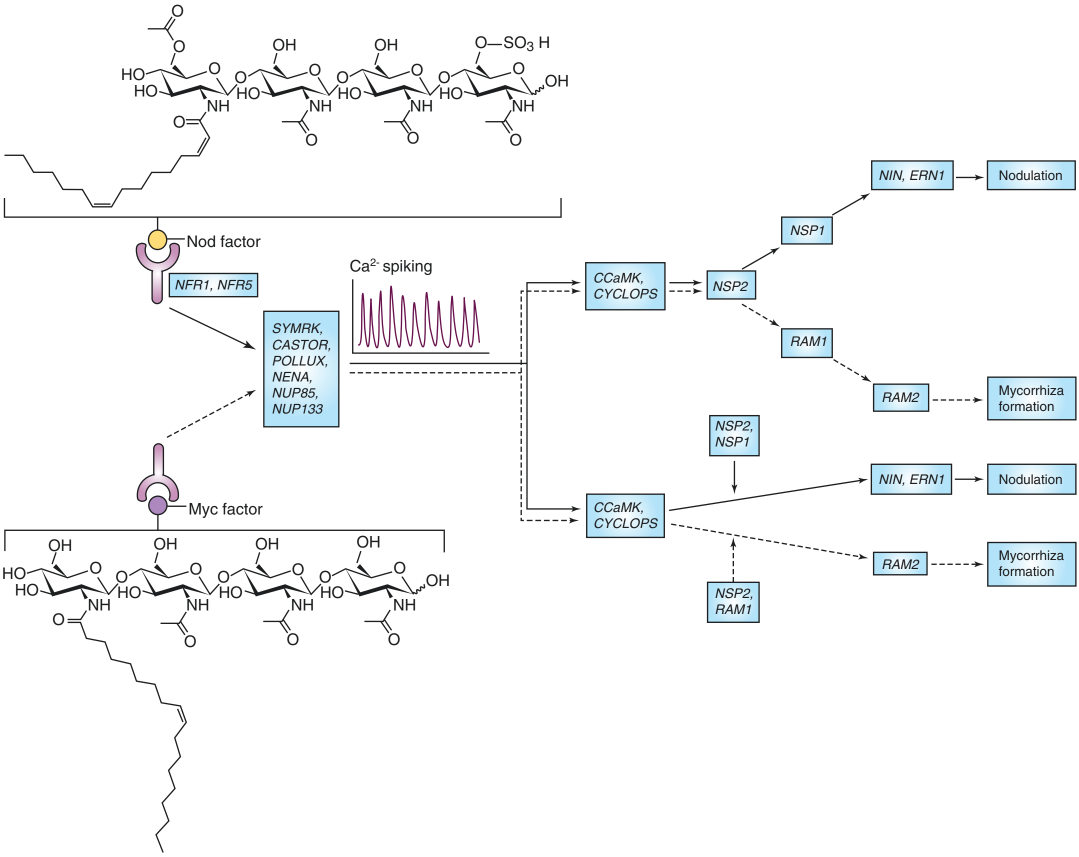

Fig. 7.24 The common sym pathway. Chemically similar bacterial and fungal signals—nod factors and myc factors, respectively—are perceived by similar receptors in the plant host cells. Downstream signal transduction initiating the developmental changes on the host side that allow establishment of either an arbuscular mycorrhiza or nodulation involves Ca oscillations triggered by the same proteins. The Ca signal is perceived by a calcium- and calmodulin-dependent serine/threonine protein kinase (CCaMK). CYCLOPS is a protein interacting with CCaMK. Further transmission of the signal proceeds via several different transcription factors (e.g. NSP1, NSP2, RAM1) and results in either nodulation or mycorrhizal symbiosis. (Oldroyd 2013)

contributing to this basal tolerance. They are hypersensitive because of the gene loss (Fig. 7.25). Responses to toxic concentrations of elements, as well as basal cellular tolerance mechanisms, are described in this chapter. Also included are molecular detoxification pathways underlying within-species differences in tolerance, and adaptations found in plants thriving in habitats characterised by extremely unfavourable soil chemistry. These specialists' tolerance is sometimes referred to as naturally selected **hypertolerance**. In this case, "tolerance" and "hypertolerance" are the preferred terms, rather than "resistance". The latter can be misunderstood as implying that no negative effects occur regardless of the concentrations (this, for instance, applies to antibiotic resistance of bacteria or disease resistance of plants and animals). In contrast, the ability to withstand element toxicity is a gradual phenomenon. At a certain concentration, even the most tolerant organisms will suffer from growth inhibition.

7.5.1 Essential Metal Toxicity and Tolerance

The essential element boron has a particular narrow optimal range (Fig. 7.2a). Like boron defi-

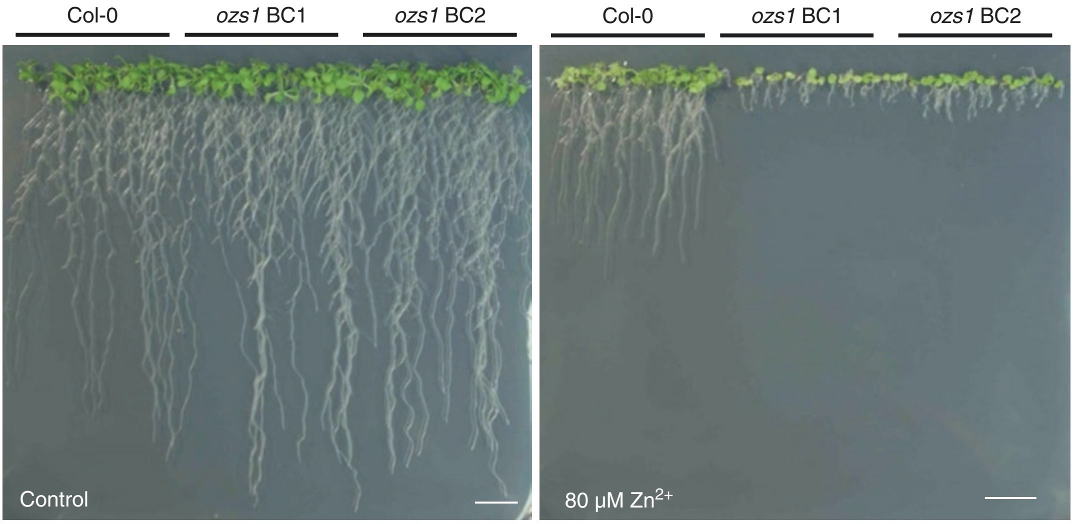

Fig. 7.25 Loss of a basal metal tolerance mechanism results in metal hypersensitivity. A typical metal tolerance assay with *Arabidopsis thaliana* seedlings is shown. In the presence of an excess of Zn^{2+} ions, growth of the mutant *ozs1* is more strongly inhibited than that of the wild type (Col-0). The *ozs1* mutant carries a defect in the transporter MTP1, which mediates vacuolar sequestration of Zn. *BC* backcross. bar = 1 cm (Weber et al. 2013)

ciency, **boron toxicity** limits agricultural productivity in many regions around the world. B toxicity occurs frequently in arid environments on soils rich in B, such as alkaline soils of marine origin. It was first described in southern Australia. Typical symptoms are leaf burns—necrotic spots at the tips of older leaves where higher concentrations of B accumulate because of the transpiration stream that moves mineral nutrients with the water (Nable et al. 1997). Tolerance is conferred by transporters mediating the efflux of boron into the root apoplast (Fig. 7.26). This limits the translocation of boron to the shoot. At high external boron concentrations the efflux transporters can lower cytosolic concentrations (Miwa et al. 2007).

There is a documented **adaptation to boron toxicity** within several crop species, including wheat and barley. Wheat cultivars bred for southern Australia have a yield advantage in their region of origin and perform less well than cultivars from northern Australia when grown there. Genetic loci controlling boron tolerance are known from wheat and barley. Intraspecific differences have been traced to variations in boron efflux transporters. In a highly boron-tolerant barley cultivar this trait is associated with much stronger root expression (>100-fold higher mRNA abundance) of a boron efflux transporter, which is at least partly attributable to an increase in the **gene copy number** (Sutton et al. 2007).

After Fe, Mn is the second most abundant transition metal in the Earth's crust. Mn availability is positively correlated with proton concentrations in the soil solution; thus, in **acidic soils** Mn can become toxic to plants. A second factor causing increasing Mn availability up to potentially growth-inhibitory concentrations is the reducing condition of **waterlogged soils**, which promotes the more bioavailable Mn(II) over the much less available Mn(IV) (Foy et al. 1978). Consequently, plant species adapted to growth under such conditions can tolerate much higher Mn content in their tissues. Rice, for example, can cope with a Mn content of 5000 μg/g d.w. in leaves, while many other plants show toxicity symptoms when the Mn content in the leaves exceeds 150 μg/g d.w. (Marschner 2012).

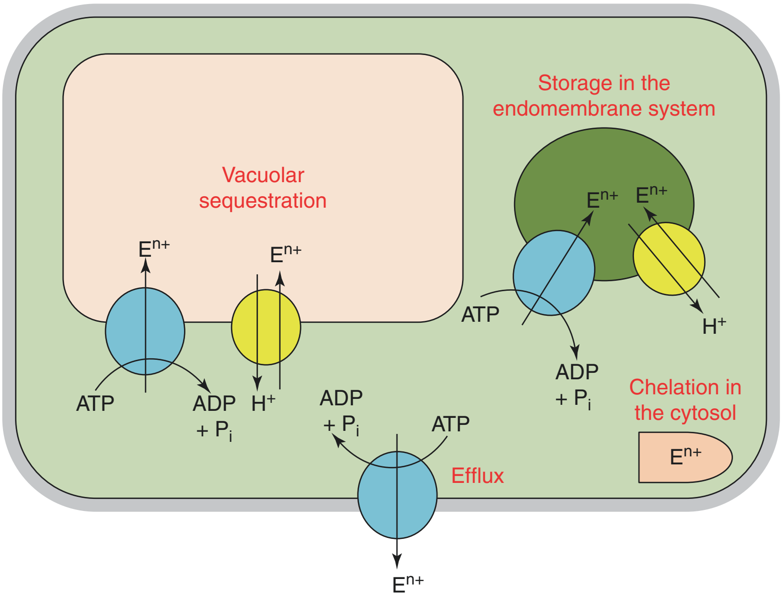

Fig. 7.26 Principal strategies to cope with an excess of a nutrient or a non-essential toxic element. The key is limiting the concentration of a reactive element ion (E^{n+}) in the cytosol by sequestration in the vacuole or vesicles of the endomembrane system (e.g. the endoplasmic reticulum (ER) and Golgi), efflux into the apoplast or chelation in the cytosol

The dominant metal tolerance mechanism is compartmentation. An excess of metal is removed from the cytosol to prevent deleterious effects. In the case of Mn, transporters in the **MTP family** (metal tolerance proteins; the original name is CDF, for **cation diffusion facilitator**) mediate sequestration of Mn in the vacuole as the major storage site or in the endoplasmic reticulum (ER) and Golgi (Fig. 7.26). The transporters are present in plants with **basal tolerance**, as well as those with specific adaptations. Rice is highly Mn tolerant and MTP proteins are involved in **Mn tolerance**. The same applies to *Stylosanthes* species (e.g. *S. hamata*)—tropical legumes thriving in acid soils. However, to date it is not clear whether differences in expression or specific properties of these transporters in the Mn-tolerant species explain adaptation to high-manganese soils. Alternative compartmentations away from the cytosol are accumulation in the apoplast and exclusion from plant tissues. A possible mechanism, similar to the mode of Al tolerance (Sect. 7.5.4), is the secretion of organic acids that form 1:1 complexes with Mn.

7.5.2 Metal Hyperaccumulators as Models for Adaptation to Extreme Environments

Other essential micronutrients such as Zn or Ni can reach toxic concentrations in some soils too. While toxic Zn concentrations are largely restricted to mining-impacted soils, potential Ni toxicity of serpentine soils is more common. A number of plant species have evolved the ability to colonise metal-rich sites. They are called **metallophytes**.

As described in this chapter, the concentrations of metals in plant tissues are under tight physiological control. Many elements are toxic when present in excess. However, approximately 500 taxa (i.e. about 0.2% of all flowering plant species) have evolved the ability to hyperaccumulate metals or metalloids (arsenic, selenium) in their leaves. **Hyperaccumulation** is defined as a metal concentration that is above an element-specific threshold in above-ground tissues of plants grown in the field. This threshold should be a concentration that is two to three orders of magnitude higher than what is normally found in plants growing in soils that are not enriched with particular metals, and one to two orders of magnitude higher than what non-hyperaccumulating species show at a site where the hyperaccumulator grows (Krämer 2010). For example, the hyperaccumulation thresholds are 100 parts per million (ppm) for Cd, 1000 ppm for Ni and As, and 3000 ppm for Zn, while plants normally contain, for example, about 50–100 ppm Zn in their organs. Important aspects of this definition are (a) that extreme accumulation is found in plants grown in the natural habitat (not only in plants cultivated under laboratory conditions) and (b) that the accumulation in above-ground tissues is due to active translocation via the roots and not caused by aerial deposition onto the leaves.

Hyperaccumulators represent a subgroup of the **metallophytes**—that is, plants that are part of a special type of vegetation found on metal-rich sites. Such sites can be rich in metals either naturally (geogenic) or because of human activities such as metal mining or processing (anthropogenic). Typical geogenically metal-rich habitats are serpentine ("ultramafic") soils with high concentrations of Ni; calamine soils rich in Zn; soils in the African copper belts characterised by high concentrations of Co, Cu, Cr, Ni and Zn; and seleniferous soils enriched in Se (Baker 1989). An example of typical metallophyte vegetation is the "Galmei flora" found in calamine soils in Belgium and the region around Aachen in Germany. A characteristic species is the endemic *Viola calaminaria*.

All metallophytes have evolved mechanisms to survive and reproduce on metal-rich soil. They share the ability to tolerate metal or metalloid concentrations that would strongly inhibit or even kill most other plants. With respect to the accumulation of metals, three strategies are distinguished. Many metallophytes are able to grow in the presence of metal/metalloid concentrations that are intolerable for most plants, because they can efficiently exclude the metal from their cells. Even in the presence of high concentrations of bioavailable metal in the soil, the concentration within the plant is maintained at a very low level (Fig. 7.27). Examples are the aforementioned *V. calaminaria* and other more common metallophytes such as *Armeria maritima* and *Silene vulgaris*. Some metallophytes are **bioindicators**. They can tolerate a wider range of concentrations than normal plants, and the accumulation in leaves is linearly correlated with concentrations of available metals in the soil. The third strategy is hyperaccumulation. The plants very efficiently translocate metals from the soil solution via root uptake and long-distance transport into the shoots. Some hyperaccumulator species even hyperaccumulate when growing on sites not enriched in metals at all. They are **pseudometallophytes**, meaning that they occur not only at metal-rich sites but also at sites with normal metal availability in the soil. Examples of such species are the model hyperaccumulators *Arabidopsis halleri* and *Noccaea caerulescens* (in the Brassicaceae; see below).

A given metallophyte species does not tolerate toxic concentrations of any metal. Instead, naturally evolved **hypertolerance**—that is, a degree of metal tolerance exceeding the tolerance found in most plant species—is specific to certain metals. Plants adapted to serpentine soils can thrive in the presence of high Ni concentrations but not necessarily in the presence of high Zn concentrations. There is pronounced variation even within species. Accessions of *N. caerulescens* adapted to calamine soils tolerate Zn and Cd very well but are sensitive to Ni. Conversely, accessions from ultramafic sites are extremely Ni tolerant yet are as sensitive to Zn and Cd as non-metallophytes (Halimaa et al. 2014).

The large majority of hyperaccumulator species—that is, about 450 out of 500—hyperaccumulate nickel and typically occur in serpentine (ultramafic) soil. Hotspots for Ni hyperaccumulators are Cuba and New Caledonia. They are rich in serpentine sites, and more than 150 Ni-hyperaccumulating species grow on these islands. Around 15 taxa hyperaccumulate either Zn, As or Se. A few species accumulate Cd (Krämer 2010). Hyperaccumulating species are strongly overrepresented among the Brassicaceae, indicating a propensity of species in this family

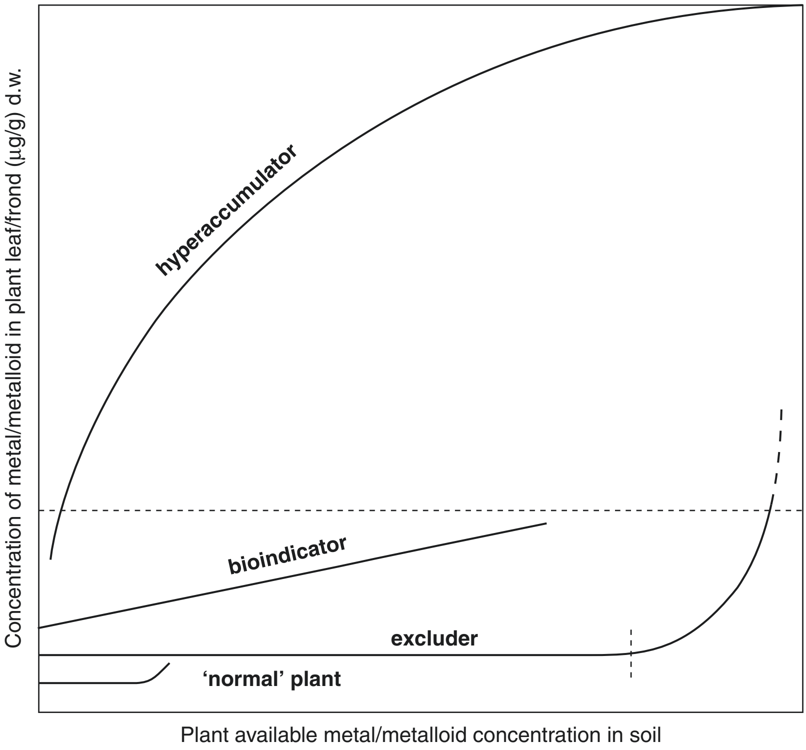

Fig. 7.27 Metal accumulation behaviour of metallophytes and of plants not adapted to metal-rich sites. (van der Ent et al. 2012)

to evolve hyperaccumulation. The adaptation of metallophytes to metal-rich soils has attracted attention from evolutionary biologists and ecologists because the toxicity of metals exerts extreme selective pressure. On serpentine soil a large number of endemic species are found, indicating the need for specific adaptations to cope with such edaphic conditions (which include a high Mg to Ca ratio and scarcity of N, P and K, in addition to high metal concentrations). Colonisation of sites that have been metal contaminated by human activities represents an example of rapid evolution—of "evolution in action", as stated by Antonovics et al. (1971). Within a range of a few metres the environment can differ dramatically, allowing many plants to grow in a meadow and allowing only very few adapted plants to establish themselves on a neighbouring heap of mining waste.

Since the 1990s, research into the ecophysiology and genetics of metallophytes has, in addition, been fuelled by several applications envisioned for metal-hypertolerant plants. They can be used for **phytoremediation** of metal-contaminated areas—for example, mining sites—to enable gradual revegetation. Metallophytes can facilitate the growth of other plants by reducing the bioavailability of toxic pollutants (**phytostabilisation**). Metal-hyperaccumulating plants could even be used for **phytoextraction** to remove metal contaminants (Salt et al. 1998). A related application is **phytomining** to exploit substrates that are too poor for conventional mining.

Mechanistic insights into the evolution of hyperaccumulation can illustrate the path leading to **adaptation to extreme environments** or, more generally speaking, the emergence of new traits in nature. Metal hyperaccumulators show exceptional mobility of metals and metalloids, which enables the transfer to above-ground tissues and thereby a fundamentally different partitioning of metals between below-ground and above-ground tissues. The relatedness of hyperaccumulator species such as *N. caerulescens* and *A. halleri* to the molecular genetics model *A. thaliana* has enabled molecular approaches to the unravelling of metal hyperaccumulation. Intra- and interspecific crosses—for example, between contrasting *N. caerulescens* accessions or between *A. halleri* and its non-hyperaccumulating relative *Arabidopsis lyrata*—have revealed the genetic architecture of metal hypertolerance and metal hyperaccumulation. The two traits are partially independent. Some of the mapped quantitative trait loci are important for both characteristics, others only for one of the two. Several studies compared the transcriptomes of hyperaccumulators with that of *A. thaliana* (Becher et al. 2004; Weber et al. 2004). The fundamental realisation was that many genes involved in metal homeostasis in normal plants show altered regulation in hyperaccumulators. Genes encoding metal transporters and enzymes catalysing the synthesis of metal ligands are constitutively more strongly expressed (Fig. 7.28). The best-documented

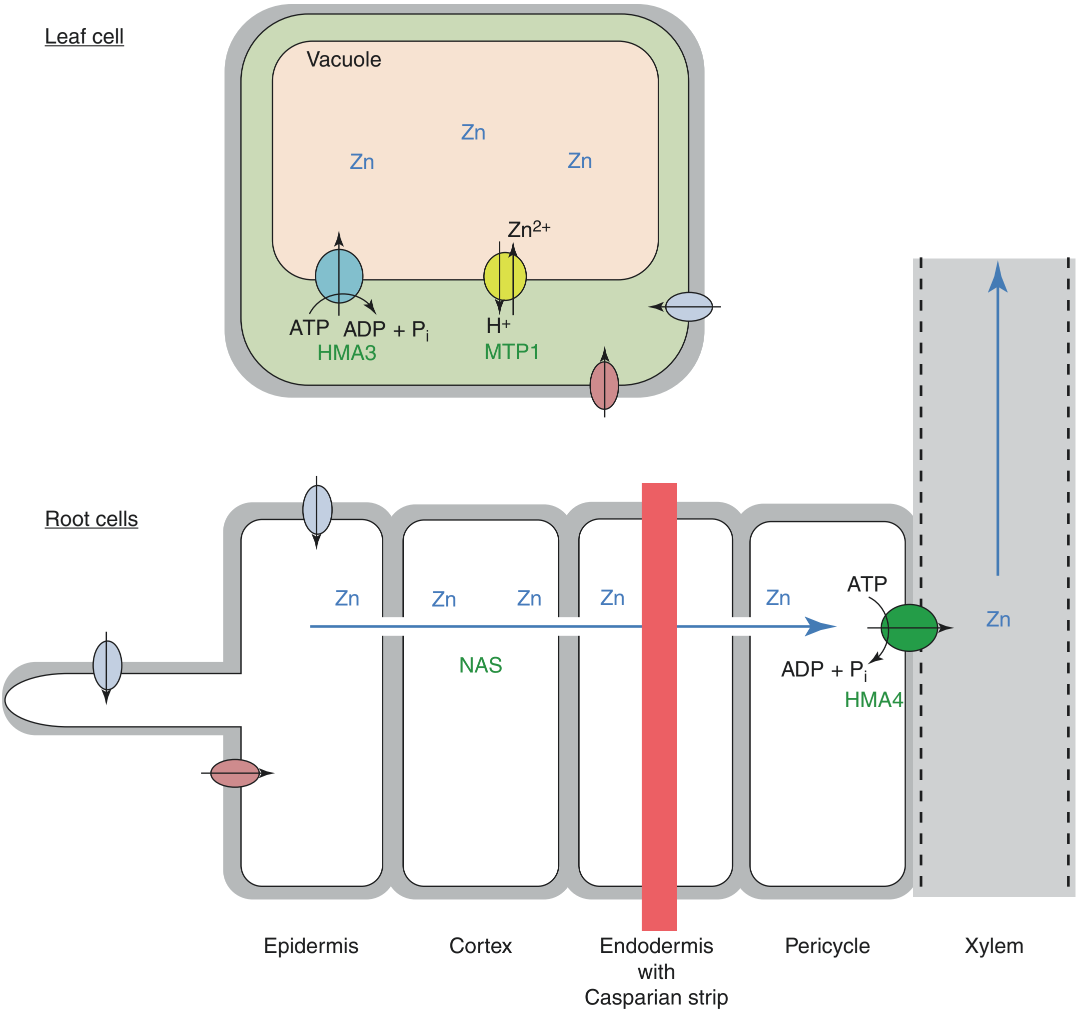

Fig. 7.28 The current model of Zn hyperaccumulation. In Zn-hyperaccumulating species such as *Arabidopsis halleri* and *Noccaea caerulescens*, Zn mobility in the symplast is higher because of greater nicotianamine synthesis by nicotianamine synthases (NAS), more Zn is pumped into the xylem (metal pump HMA4) and more Zn can be transported into the vacuoles of leaf cells (MTP1 and HMA3). The corresponding genes are all more strongly expressed in hyperaccumulators because of copy number expansion and *cis*-regulatory changes. Indicated uptake transporters are molecularly unidentified

example is the metal-pumping ATPase HMA4, a protein that effluxes Zn ions across the plasma membrane (Sect. 7.3.4). In *A. thaliana*, HMA4 loads Zn into the xylem for translocation to the leaves. Much stronger expression of HMA4 in *A. halleri* results in very efficient root-to-shoot translocation of both Zn and Cd. In addition the efflux activity protects root cells from Zn and Cd toxicity (Hanikenne et al. 2008). This difference explains a substantial fraction of the Cd/Zn hypertolerance and hyperaccumulation of *A. halleri*. Higher expression evolved through an expansion of the gene copy number and variation in promoter sequences. The proteins apparently do not differ in affinities, activities or any other functional features. Thus, an important conclusion of general importance is that adaptation has evolved through transcriptional changes via **copy number variation** and changes in *cis*-regulatory sequences—that is, rather subtle changes that can easily occur and then be selected. Indeed, for the triplicated HMA4 locus in the *A. halleri* genome, strong signs of a **selective sweep** were detected (Hanikenne et al. 2013). Among individuals from different populations, nucleotide diversity was strongly reduced around the HMA4 locus. This is indicative of strong **selection** causing rapid spread of this particular allele in *A. halleri* populations.

7.5.3 Sodium Toxicity

The soils of more than 6% of the world's terrestrial surface contain high concentrations of salt, mostly NaCl. To a lesser extent, Na-carbonate and Ca-sulphate are also found, especially in the vicinity of salt lakes. Needless to say, two thirds of the Earth's surface—namely, the oceans—represent saline habitats. Halogenides of alkali and earth alkaline ions are easily soluble in water and thus these ions are washed out from suboceanic or terrestrial minerals of the Earth's mantle and finally accumulate in the sea. From there, saline aerosols are transported landwards by the wind, leading to continuous salt deposition not only in the coastal regions but also further inland. In arid and semi-arid areas, upward movement of the soil water results in deposition of dissolved salt upon evaporation of the solvent, frequently giving rise to salt crusts. This process also takes place in irrigated arid areas. It is estimated that by the middle of the current century, increased salinisation will result in up to 50% arable land loss (Wang et al. 2003). The impact of **soil salinity** on agriculture is enormous, as it affects plants during their entire life cycle and results in huge losses in biomass production and yields.

Soils are considered saline when the electrical conductance exceeds 0.4 Siemens per metre. This value corresponds to approximately 40 mM NaCl and an osmotic potential of −0.2 MPa. The threshold value is derived from agriculture. Many crops react with yield reduction when grown in soils of higher salinity. Salt tolerance is usually determined as the percentage biomass production or crop yield in saline versus control conditions over an extended period of time, or in terms of survival, which is especially useful in experiments with seedlings.

The conductivity of seawater (3% salt: 480 mM Na^+, 50 mM Mg^{2+} and 560 mM Cl^-) is 4.4 S/m—more than ten times the threshold for soil salinity—with an osmotic potential of −2.7 MPa. The conductivity of water used for irrigation must be less than 0.2 S/m, notwithstanding the fact that some plants—for example, glassworts (*Salicornia* species) or even special cultivars of barley (cv. California Mariout)—require or at least tolerate irrigation with seawater. For as yet unknown reasons, salinity in soils is often accompanied by toxic concentrations of boric acid (Tester and Davenport 2003) (Sect. 7.5.1).

Na^+ leaks into plant cells via Ca^{2+}-permeable non-selective cation channels (NSCCs) or K^+/Na^+ transporters. The molecular identities of these proteins are still uncertain. Many K^+ transport systems such as HAK/KUP family members (Sect. 7.3.2.2) have some affinity for Na^+. High-affinity Na^+ uptake has also been observed but is unlikely to play a role under conditions of salt stress with high external Na^+ concentrations (Munns and Tester 2008). The Na^+ electrochemical potential gradient across the plasma membrane suggests that facilitated diffusion is the principal mode of Na^+ influx, while Cl^- is transported against the electrochemical potential.

Uptake therefore requires proton coupling, while efflux can be passive. Anion influx can be passive too, provided that a permeable anion channel is present and the concentration gradient of the ion across the membrane is high enough, as can be the case in saline environments. Furthermore, depolarisation will result from the uptake of cations such as Na^+. This lowers the electrochemical potential gradient and facilitates Cl^- uptake. Thus, exposure of a cell or tissue to high salt concentrations results primarily in passive influx of Cl^-, followed by active uptake after the membrane potential has returned to more negative values.

Salt stresses plants in several ways (Fig. 7.29): by dehydration (Chap. 6), Na^+ (and Cl^-) toxicity, nutrient imbalances and reactive oxygen species production (**ROS production**). Saline soil solutions have a very negative **osmotic potential**, which has to be overcome by the water-absorbing surface of the plant, typically the root. Shortage of water affects growth of cells and plant organs. Thus, for water uptake, the root cells have to produce and maintain an even more negative osmotic potential. Na^+ in particular, but also Cl^-, can be regarded as biologically aggressive solutes on account of their small ionic diameters and the corresponding high surface charge. These properties result in high attraction for water molecules and thus the binding of much water in water shells, which enhances intracellular water scarcity. Also, accumulation of small cations such as Na^+ can strongly interfere with the intracellular balance of ion pools and charges, affecting the membrane potential, which may result in inactivation of voltage-dependent membrane functions. This is especially the case when K^+ is displaced by Na^+ with its higher charge density. Other inorganic plant nutrient relations—for example, of Ca^{2+}, Mg^{2+} and anions such as nitrate and malate—may be affected as well.

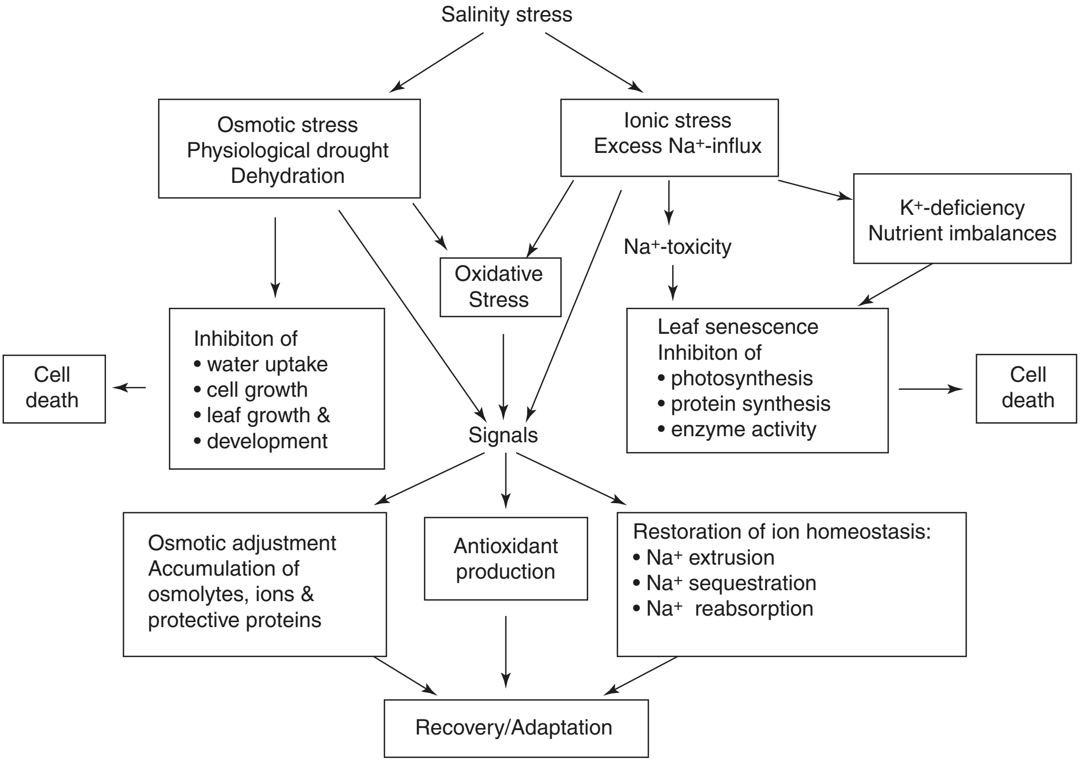

Fig. 7.29 Components and physiological consequences of salinity stress for plants, and mechanisms of adaptation conferring salt tolerance. (Horie et al. 2012)

7.5.3.1 The Osmotic Component of Salt Stress

When a plant, be it salt tolerant or sensitive, is subjected to a sudden increase in the NaCl concentration in the medium or soil, a fast and a slow reaction can be differentiated (Fig. 7.30 and 7.31). Leaves of various cereals and dicots show an instantaneous halt of expansion. Because of its rapidity and the subsequent partial recovery, this fast response must be due to changes in cell water relations. Since the same phenomena can be triggered with KCl, mannitol or polyethylene glycol instead of NaCl, this response is not salt specific (Munns 2002). For most plants, the threshold for that response is around 40 mM NaCl, but it may be lower for particularly salt-sensitive species. Several minutes after the initial decline in leaf growth, a partial recovery takes place and a new steady growth rate is attained after approximately 30 min. The time required for recovery depends on the concentration of the salt solution. Removal of the salt results in an equally sudden overshoot followed by a fast return to the original growth rate.

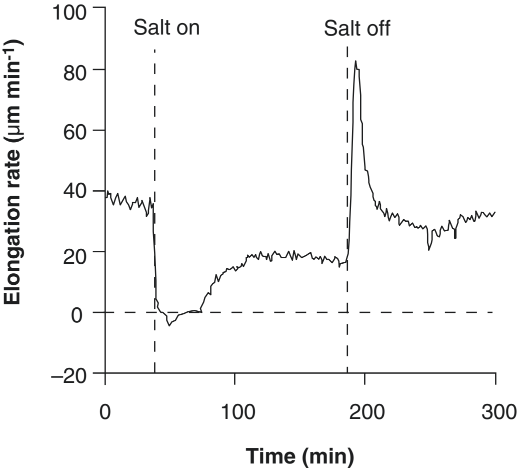

Fig. 7.30 Effects of changes in the salinity of the soil solution on the elongation rate of a barley leaf. A sudden increase in the salt concentration triggers an almost immediate drop in the growth rate, followed by a slower phase of partial recovery. (Munns 2002)

Under long-term salinity stress, inhibition of shoot growth encompasses reduced leaf expansion, delayed formation of new leaves and delayed or even suspended bud break, resulting in fewer branches or lateral shoots. Contrary to the expectation, root growth in saline media is less affected than shoot growth (Chap. 6). This might be due to the fact that a reduction in shoot growth also reduces the water consumption by the plant and mitigates the transpiration-induced increase in salinity in the rooted soil volume.

7.5.3.2 The Ionic Component of Salt Stress

Homeostatic ion concentrations in the cytosol of a non-stressed cell of a **glycophyte**—that is, a plant without adaptation to saline habitats—are 100–200 mM K^+, 1–10 mM Na^+ and Cl^-, and 0.1–0.2 mM Ca^{2+}. These concentrations are maintained in the plant cell mainly through ion

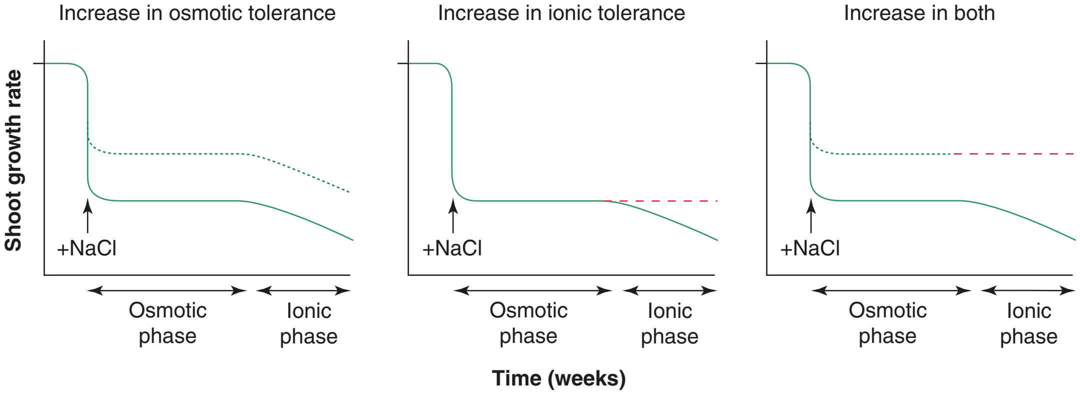

Fig. 7.31 Short- and long-term responses of plants to salinity stress. The *solid green line* indicates the reaction of a plant to the two components of salt stress: an increase in osmolarity and toxicity of NaCl. The *broken green line* represents the reaction of a plant adapted to better tolerate osmotic stress, while the *dashed red line* indicates the reaction of a plant with higher tolerance of the ionic toxicity (Munns and Tester 2008)

transport energised by H^+-ATPases and H^+-pyrophosphatases in the plasma membrane and the tonoplast, respectively. In addition, channels and pumps are involved (Sect. 7.3.2). The combined activities result in a membrane potential of around −150 mV at the plasma membrane and a tonoplast potential between +20 and +50 mV (the cytosolic side is always more negative). These membrane potentials are associated with differences in pH between the cytosol (pH 7.5) on the one hand and the apoplast and the vacuole on the other, whose pH values are around 2 units more acidic (Fig. 7.32).

High salinity subjects this **homeostasis** to considerable strain (Fig. 7.31). In the majority of plant species grown under salinity, Na^+ reaches a toxic concentration before Cl^- does, and so plant chloride relations have attracted much less attention than the plant's response to sodium (Munns and Tester 2008). Chloride is an essential micronutrient (e.g. for photosynthesis), acts as counter anion to stabilise membrane potentials and is involved in turgor and pH regulation. In the presence of high external salt concentrations, large intracellular Na^+ pools build up, partly at the expense of the K^+ pools. More than 50 enzymes are controlled or activated by K^+, and Na^+ cannot substitute for K^+ in this role. High concentrations of Na^+ or high Na^+ to K^+ ratios therefore disturb or even disrupt various enzymatic processes. Photosynthesis and respiration are among the processes that are most sensitive to salt stress. Protein synthesis requires high concentrations of K^+—for example, for the binding of transfer RNA (tRNA) to the ribosomes—and is thus also highly affected by high intracellular Na^+. Finally, ion imbalances (e.g. in photosynthesis and respiration) and water shortage result in oxidative stress which, in combination with the aforementioned impairments, can easily result in cell and organ death.

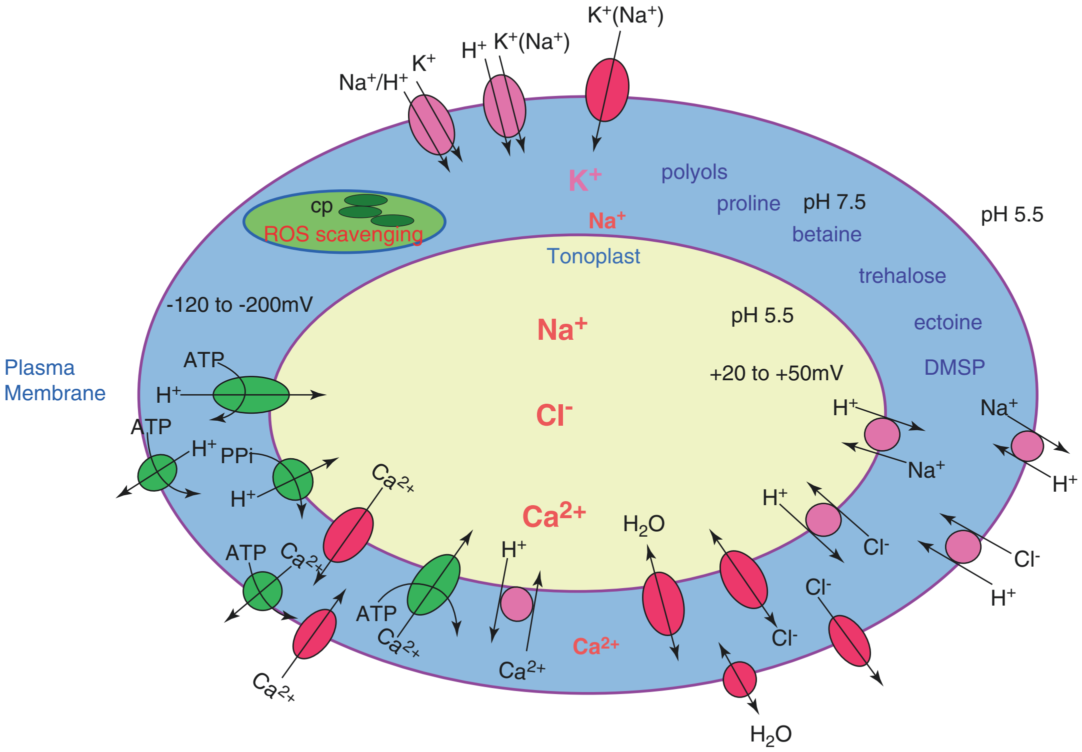

Fig. 7.32 Establishment of cellular homeostasis during salt stress acclimation, showing intracellular ion distribution, membrane potentials and pH values. Ions and osmolytes compartmentalised in the cytosol and vacuole, transport proteins involved in Na^+ and Cl^- homeostasis, and water channels are indicated. ATP- or pyrophosphate-driven pumps are indicated in green (note that for lack of space the products of ATP- or PPi-hydrolysis are not shown); channels gated by the membrane potential are indicated in red while proteins mediating secondary active transport are shown in purple. (Modified from Hasegawa et al. (2000))

7.5.3.3 Variations in Salt Tolerance: Plant Functional Types with Respect to Salinity

Plants vary greatly in their tolerance of salinity (Fig. 7.33). For example, after some time in a 200 mM NaCl solution, a salt-tolerant species such as sugar beet may have a reduction of only 20% in dry weight, a moderately tolerant species such as cotton might have a 60% reduction and a sensitive species such as soybean might be dead. A plant from a salt marsh (e.g. *Suaeda maritima*), however, may be growing at its optimum rate (Flowers and Colmer 2008). Salt-sensitive species such as the monocot rice and the dicot *A. thaliana* are termed **glycophytes**, whereas species with a high salt tolerance or even salt requirement for growth are referred to as **halophytes**. While glycophytes are clearly more salt sensitive than halophytes, they still possess a basal tolerance mechanism, and most molecular knowledge on salt tolerance mechanisms originates from work with *A. thaliana*.

Not all developmental stages of a plant are equally sensitive to salinity. With respect to crops, this provides an opportunity to minimise salt injury at the sensitive stages by using irrigation water of differing salinity during the season. Notwithstanding their relatively high salt tolerance, sugar beet, barley and cotton are relatively sensitive during germination or early seedling growth. In contrast, corn, pea and beans are more sensitive during later stages of development. In tomato, salt tolerance is low in young plants, becomes much higher during vegetative growth and decreases again during flowering.

7.5.3.4 Salt Tolerance Mechanisms

At the cellular level, plants have several principal mechanisms to cope with salinity (Fig. 7.29). They can:

- Minimise initial entry into the root
- Maximise efflux from the root into the soil
- Minimise loading into the xylem or maximise retrieval from the xylem fluid before Na^+ reaches the shoot

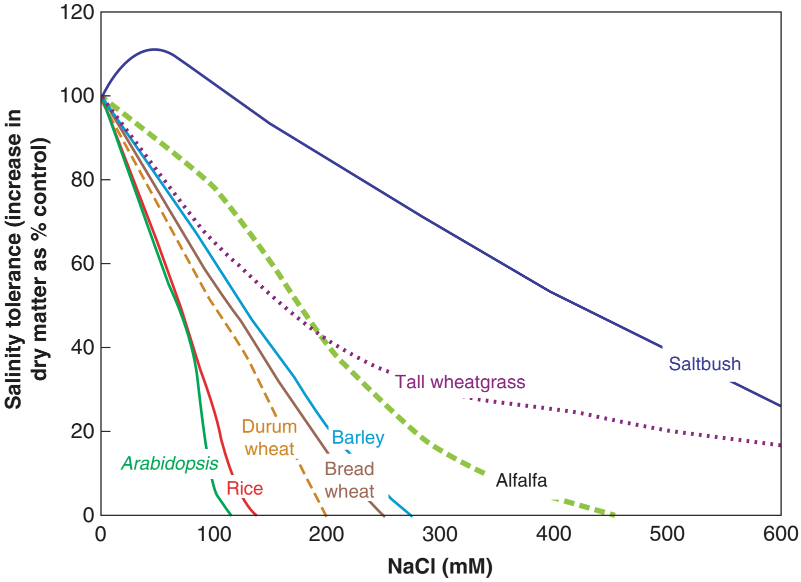

Fig. 7.33 Diversity in salt tolerance between plant species. Salt tolerance is quantified as an increase in shoot dry matter after growth in a solution or sand culture containing NaCl for at least 3 weeks, relative to plant growth in the absence of NaCl (set to 100%). Data are presented for rice (*Oryza sativa*), durum wheat (*Triticum turgidum* ssp. *durum*), bread wheat (*Triticum aestivum*), barley (*Hordeum vulgare*), tall wheatgrass (*Thinopyrum ponticum*, syn. *Agropyron elongatum*), *Arabidopsis thaliana*, alfalfa (*Medicago sativa*) and saltbush (*Atriplex amnicola*). (Munns and Tester 2008)

- Maximise recirculation out of the shoot into the phloem
- Maximise intracellular compartmentation or allocation to particular parts of the shoot (e.g. pith cells or old leaves)
- Secrete salt via glands to the surface of the leaf or into specific bladder hairs

The extent to which these mechanisms operate in plants varies from species to species, and even within species, and depends on the severity of the stress. Because the control—especially of Na^+ influx into the root and efflux from the vascular parenchyma into the xylem apoplast—is weak owing to the limited specificity of many nutrient transporters, the most important cellular aspects of salt stress tolerance are efficient removal of Na^+ from the cytosol especially in young tissues and regulation of Na^+ distribution within the plant (Tester and Davenport 2003).

Maintenance of low cytosolic Na^+ is achieved by secretion into the apoplast or sequestration in the vacuole. This applies to cells in the outer part of the root—that is, the rhizodermis and the cortex—as well as the metabolically active cells in the shoot. Fig. 7.34 shows the basic mechanisms by which the cell can manage its cytosolic Na^+ concentration at the expense of ATP. The dominant systems in the plasma membrane, as well as in the tonoplast, are **Na^+/H^+ antiporters**, which use the proton gradients produced by H^+-ATPases or the vacuolar pyrophosphate-driven proton pump to extrude Na^+ from the cytosol. The transporters were first identified in *A. thaliana* and named **SOS1** (salt overly sensitive, the protein in the plasma membrane) and **NHX** (for Na^+/H^+ exchanger). Their activity is an important component of **Na^+ tolerance** in both **glycophytes** and **halophytes**. Knockout or knock-down of the antiporter expression results in a dramatic increase in

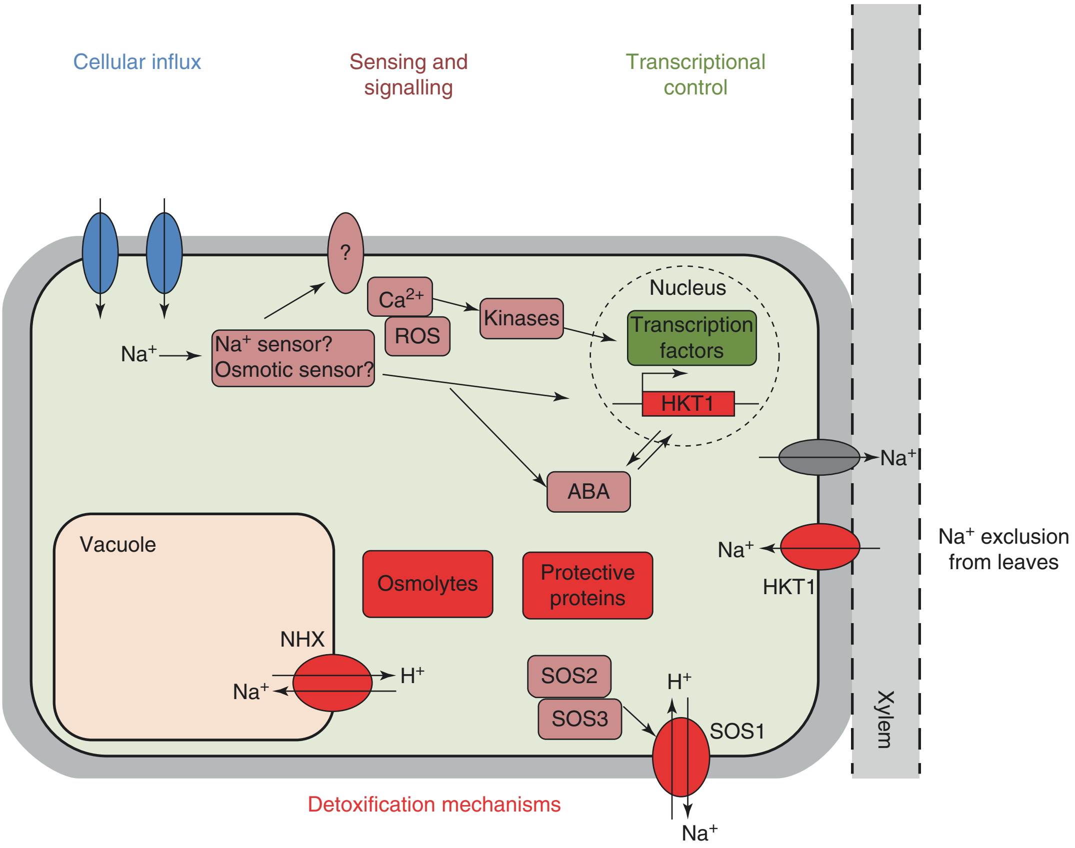

Fig. 7.34 Cellular Na^+ tolerance mechanisms. (Modified from Deinlein et al. (2014))

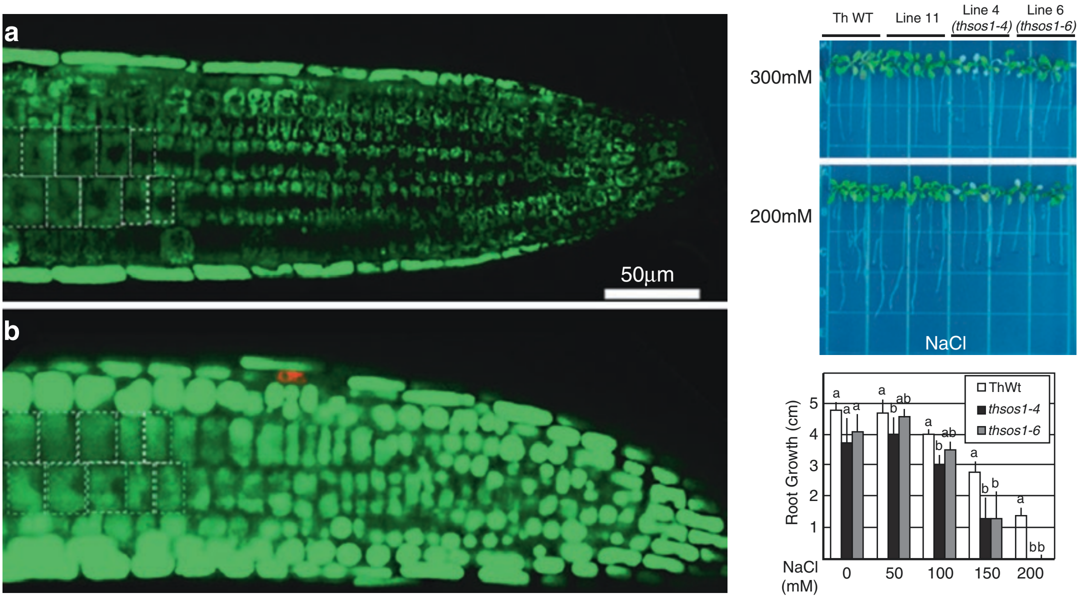

Fig. 7.35 Knock-down of *SOS1* in the halophyte *Eutrema salsugineum* formerly *Thellungiella salsuginea* causes stronger Na^+ accumulation in root cells and compromises Na^+ tolerance. *Left:* Accumulation of Na^+ in root cells visualised with a fluorescent dye (**a** wild type, **b** *SOS1* RNA interference (RNAi) plant). *Right: SOS1* RNAi plants (*thsos1* lines) are more NaCl sensitive than wild-type plants. (Oh et al. 2009)

salt sensitivity in *A. thaliana*, tomato and also the halophyte *Eutrema salsugineum* (formerly known as *Thellungiella salsuginea*) (Fig. 7.35).

NHX antiporters belong to the large cation/proton antiporter 1 (CPA1) family which, by sequence similarity and intracellular localisation, is further subdivided into vacuolar (class I) and endosomal (class II) NHX transporters. Most of the plant species sequenced to date contain both types of NHX (Bassil et al. 2012). The cation selectivity of AtNHX1 represents an instructive example of post-translational transporter modification (Fig. 7.16). It appears to be controlled by the C-terminal domain reaching into the lumen of the vacuole. Depending on the vacuolar Ca^{2+} concentration and the pH, it binds to a calmodulin-like protein, AtCaM15. Interaction with AtCaM15 decreases the Na^+ transport activity of AtNHX1 while maintaining the K^+ transport activity almost unchanged (Yamaguchi et al. 2013). Under normal physiological conditions—that is, a high vacuolar Ca^{2+} concentration and an acidic pH—binding of AtCaM15 favours the K^+/H^+ antiport mode. However, as salinity stress causes vacuolar alkalinisation, AtCaM15 dissociates from AtNHX1, which then exhibits higher Na^+/H^+ antiport activity and promotes sequestration of Na^+ into the vacuole. Overexpression of *NHX* genes improves the salt tolerance of a range of plant species, with a concomitant increase in tissue Na^+ (Apse and Blumwald 2002).

Vacuolar sequestration and efflux into the apoplast are also the cellular mechanisms underlying salt secretion in specialised leaf structures. In **salt bladders** (specialised trichomes), salt accumulates in the large central vacuole of the bladder cells. Bursting of the cells then deposits salt on the leaf surface. In **salt glands** (Fig. 7.36), vacuolar vesicles filled with salt fuse with the plasma membrane for exocytotic release of salt, or Na^+ ions are directly transported out of the cell across the plasma membrane. Thus, it can be postulated that NHX- and SOS1-like proteins play a key role also in these specific adaptations.

Another major mechanism of salt tolerance is the control of **Na^+ translocation** to the shoot. This is largely a function of re-uptake of Na^+ from the xylem into xylem parenchyma cells. The

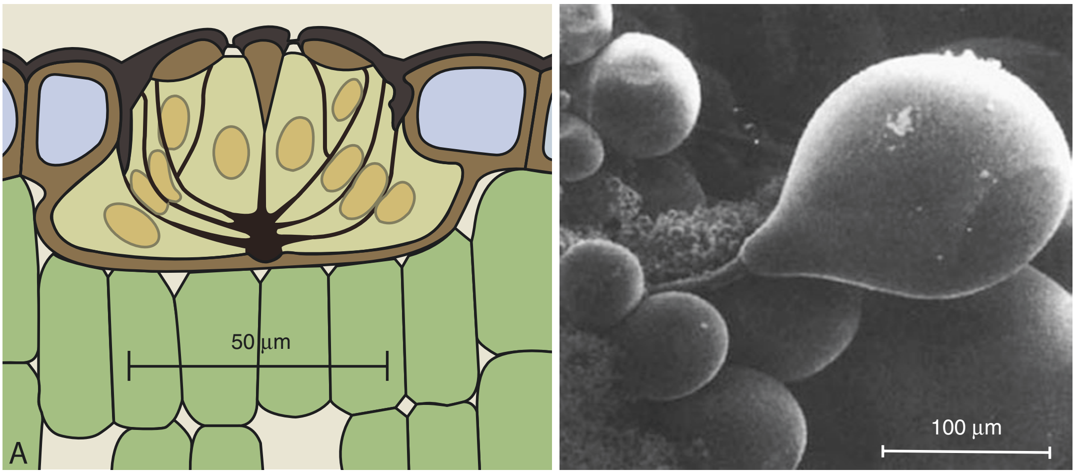

Fig. 7.36 Mechanisms of salt secretion: longitudinal section of a salt gland in a sea lavender (*Limonium vulgare*) leaf and salt hairs as protuberances of the leaf epidermis in *Atriplex hymenelytra* (Chenopodiaceae). (Lüttge et al. 2005)

transporters responsible for this retrieval are those in the **HKT** (**high-affinity K^+ transporter**) family (Deinlein et al. 2014). HKTs belong to a superfamily of potassium transporters, which have been found in microorganisms, yeasts, plant cells and parasites such as trypanosomes (Yamaguchi et al. 2013). Two classes can be differentiated on the basis of functional and structural traits: class I, which is more selective for Na^+; and class II, encompassing K^+/Na^+ co-transporters. *A. thaliana* AtHKT1;1 loss-of-function mutants are Na^+ hypersensitive and accumulate more Na^+ in the leaves. Conversely, overexpression under the control of a stele-specific promoter has been shown to reduce Na^+ transport to the leaves and result in higher salt tolerance (Møller et al. 2009). AtHKT1;1 resides in the plasma membrane of xylem parenchymal cells and phloem tissues. The latter explains recirculation of Na^+ from the shoot to the root via AtHKT1;1, which may contribute to salt tolerance (Box 7.2).

A common acclimative response of a plant to salinity is lowering of the water potential of its cells. This is achieved by accumulation of low molecular weight compounds (the so-called **compatible solutes** or **osmolytes**) in the cell—for example, quaternary ammonium compounds such as glycine betaine, polyamines, open-chain sugar alcohols (polyols) such as mannitol and glycerol, oligosaccharides such as trehalose, and proline (Chap. 6). In addition to their colligative effects, osmolytes can partially replace water, thereby stabilising proteins and cellular substructures. Some osmolytes are rather salinity specific—that is, they are less commonly produced under other stresses such as drought. Very common osmolytes in **halophytes**—for example, mangroves or ice plants—are cyclic sugar alcohols or cyclitols. In contrast to the open-chain polyols, they show slow metabolism, which prevents their consumption in situations of throttled carbohydrate availability (e.g. when stomata are closed), thus safeguarding the osmolyte function. Their biosynthesis starts from glucose-6-phosphate, which is cyclised to inositol-3-P, the basic compound for a variety of cyclitols. They are varied by relatively simple biochemical reactions such as epimerisation (e.g. L-quebrachitol) or transfer of methyl groups (e.g. D-ononitol), which renders them metabolically rather inactive. Because halophytes can tolerate comparatively higher cytosolic salt concentrations owing to compatible solute accumulation and efficient vacuolar sequestration, they can also use Na^+ and Cl^- as osmolytes to lower the osmotic potential.

Like cells affected by low water availability, salt-stressed cells synthesise proteins that are assumed to protect cellular structures such as membranes and protein complexes by associating with them. Typical representatives are the **dehydrins** or **LEA proteins**, whose structural features and functions in cell biology are discussed in Chap. 6.

Box 7.2: Generation of Plants with Increased Salt Tolerance

The genes encoding SOS1, NHX and HKT transporters have been successfully utilised as genetic tools for enhancing the salt tolerance of model and crop plants. The genes *Nax1* and *Nax2*, identified as the sodium transporters *TmHKT1;4-A2* and *TmHKT1;5-A* (Fig. 7.34) in *Triticum monococcum*, were transferred to *Triticum aestivum* (bread wheat), using marker-assisted selection for hexaploid plants containing one or both genes. Expression of *Nax1* reduced the Na^+ content in the leaf blades by 50%, expression of *Nax2* reduced it by 30% and expression of both genes together decreased it by 60%. This decrease was at the expense of sodium accumulation in the leaf sheath; nevertheless, the salt tolerance of the bread wheat was substantially improved (Munns et al. 2012) (Fig. 7.37). However, evidence has been provided that these transporters are also involved in other cellular processes. This limits the possibility of further increasing salt tolerance by stronger overexpression of any of them.

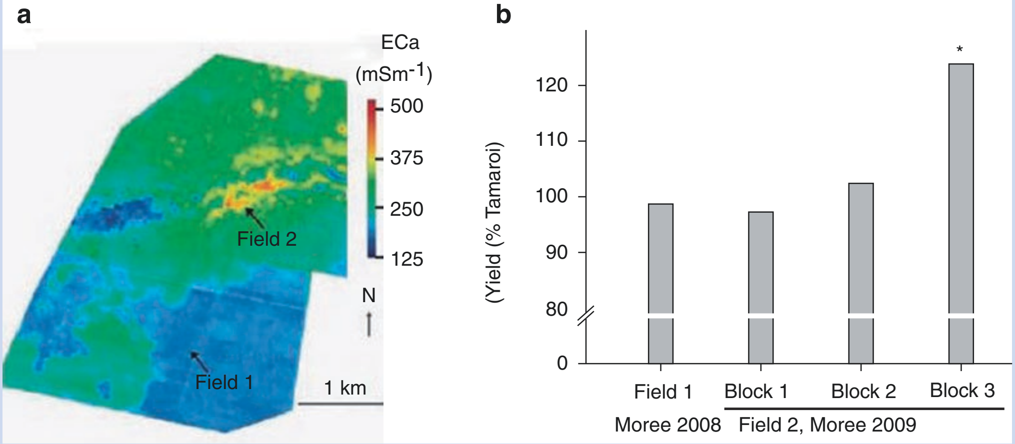

Fig. 7.37 Salinity variation across a commercially farmed field and relative increase in grain yield due to the presence of TmHKT1:5-A. **a** Apparent electrical conductivity (ECa) of a salinity-affected field near Moree in northern New South Wales, Australia. The numbers indicate the locations of field trial sites in 2008 (1) and 2009 (2). **b** Relative increase in grain yield of the cultivar Tamaroi [+] TmHKT1;5-A compared with Tamaroi after cultivation in field 1 and the salinity-affected field 2. $*p < 0.05$. (Munns et al. 2012)

7.5.3.5 Sensing of Salinity Stress and Intracellular Signalling

The overall response of a plant to salt stress is highly complex. It is not only removal of Na^+ from the cytosol and the synthesis of osmolytes that are activated. The transcript abundance of up to several thousand genes changes within hours in the roots of plants exposed to toxic concentrations of NaCl. In *A. thaliana* the majority of these changes occur in the root cortex, where most of the Na^+ accumulates (Deinlein et al. 2014).

Plant cells are able to separately sense the two components of salinity. Osmotic stress elicits responses distinct from those to ionic toxicity. The molecular nature of the sensors is still elusive (Fig. 7.34). A change in osmolality generates a stretch force on the plasma membrane, which may activate **osmosensors**. **Mechanosensitive channels** are known from yeast and other eukaryotes but not from plants. The plant sensors are expected to be closely associated with **Ca^{2+} channels**. Cytosolic Ca^{2+} increases within seconds upon osmotic stress and represents the earliest documented response (also to other stresses such as cold; Chaps. 2 and 4). A recently identified hyperosmolality-gated calcium-permeable channel (OSCA1) is a candidate for an osmosensor (Yuan et al. 2014). Sensing of ionic stress caused by NaCl is less well understood.

The best-characterised salinity-specific signalling pathway is the one leading to the activation of the **H^+/Na^+ antiporter SOS1** (Fig. 7.34). The elevated Ca^{2+} signal is sensed by the calcineurin B–like protein CBL4 (termed SOS3), which responds with dimerisation. The dimer can interact with the protein kinase CIPK24 (CBL-interacting protein kinase), known as SOS2. The SOS3/SOS2 complex is targeted at the plasma membrane, where it phosphorylates the SOS1 protein. Activation of this antiporter requires phosphorylation of its auto-inhibitory domain. Calcium-dependent or calcium-controlled proteins (such as CBL4 or calmodulin) or protein kinases can transduce the salinity signal further downstream and trigger or attenuate gene expression (Fig. 7.34). Some of the calcium-dependent protein kinases regulate the response to abscisic acid (ABA), which accumulates under drought, as well as under salinity stress (Hirayama and Shinozaki 2010) (Chap. 2, Sect. 2.2).

When a plant is subjected to a salt shock, a dramatic but transient increase in ABA takes place, which is similar to the reaction under drought (Fig. 7.38). Under prolonged salt stress the level of ABA might remain elevated or might return to close to the original concentration, depending on the plant species and plant organ, as well as on the experimental conditions. Part of this reaction might indeed be due to the osmotic stress imposed by high salinity. ABA signalling leads via transcription factors to the enhanced formation and accumulation of compatible solutes and protective proteins such as dehydrins. This process is presented in detail in Chap. 6.

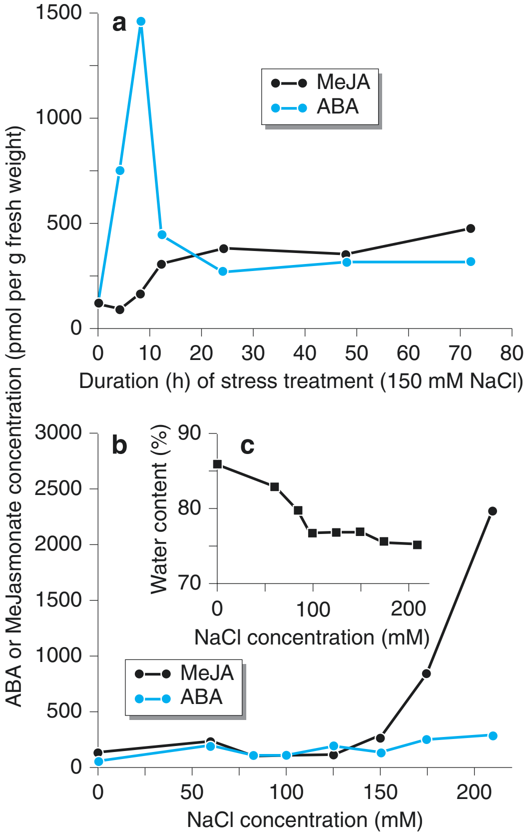

Fig. 7.38 Endogenous concentrations of abscisic acid (ABA) and methyl jasmonate (MeJA) in roots of rice plants subjected to salinity stress. **a** “Salt shock”—that is, transfer of seedlings from a NaCl-free medium to a NaCl-containing medium (150 mM). **b** ABA and methyl jasmonate content in rice seedlings after 2 days of treatment with different salt concentrations. **c** Water content in shoots after 2 days of exposure to salt stresses of different strengths. (After Moons et al. (1997))

7.5.4 Aluminium Toxicity and Tolerance

Aluminium is the most abundant metallic element in the Earth’s crust, where it appears in many (usually insoluble) compounds and complexes. Below a soil pH of around 5, Al becomes available for plant uptake as the highly phytotoxic Al^{3+} ion. This process is the major reason for the limitation of plant productivity in **acidic soils**, which are especially prevalent in tropical and subtropical regions. Around 30% of the global land area is affected by soil acidity.

The primary effect of exposure to the highly reactive Al^{3+} is rapid inhibition of root growth (Kochian et al. 2004). Within 1–2 h, cell elongation is halted. Then, with a delay of several hours, cell division is inhibited too. The apex is the most sensitive part of the root. Only a small fraction of the available Al enters the symplast, via routes that are molecularly not well understood. The larger Al fraction (usually >80%) is bound by the cell wall. Several extra- and intracellular structures and processes are affected by Al^{3+}. In the apoplast, Al^{3+} interacts with the negative charges of pectins. This compromises the cell extensibility and thereby cell expansion. Inhibition of crucial cell wall enzymes such as expansins is another possible cause of extracellular toxicity. Transport of Ca^{2+}, as well as cytosolic Ca signalling, is inhibited. Al^{3+} interferes with Mg^{2+}-dependent processes. For instance, Al-ATP interacts far more strongly with enzymes such as hexokinase than Mg-ATP does. Al^{3+} disrupts the dynamics of the cytoskeleton by interacting with microtubules and actin filaments. It can damage DNA and elicits generation of ROS.

Two major mechanisms allow plants to withstand **Al toxicity**. The first one can be categorised as an **avoidance strategy** and results in effective exclusion of Al^{3+} from the symplast, thereby reducing the actual exposure of cellular sites to the toxicity of Al^{3+}. The second mechanism confers **tolerance**. It comprises processes that detoxify and sequester Al^{3+} ions after they have entered cells.

Considerable variation exists in both exclusion and intracellular detoxification. Because the genetics of **Al exclusion** are comparatively simple in some crop species—including wheat, barley and sorghum—it has been possible to molecularly characterise the responsible loci. Differences in the ability to exclude Al^{3+} from root cells are strongly correlated with differences in the secretion of organic acids, mostly malate and citrate, into the rhizosphere (Fig. 7.39).

The organic acids form complexes with Al^{3+} and thereby prevent uptake of Al^{3+} into the root symplast (Fig. 7.40). The transporters responsible for the efflux of organic acids belong to two different classes. The first Al tolerance locus was cloned from wheat and was found to encode an **aluminium-activated malate-secreting anion channel** (TaALMT1) (Sasaki et al. 2004). The activation is specific to Al^{3+}, as it is not generally triggered by trivalent cations (e.g. La^{3+}, Sc^{3+}). Expression of this channel in other plant species enhances malate secretion and Al^{3+} tolerance. ALMT-like transporters fulfil comparable functions in rye or *A. thaliana*. Proteins of the **MATE** (multidrug and toxic compound extrusion) family account for citrate efflux in sorghum, barley and presumably many other plant species (Magalhaes et al. 2007). MATE proteins represent a large group of secondary active transporters in eukaryotes and prokaryotes. They export a wide variety

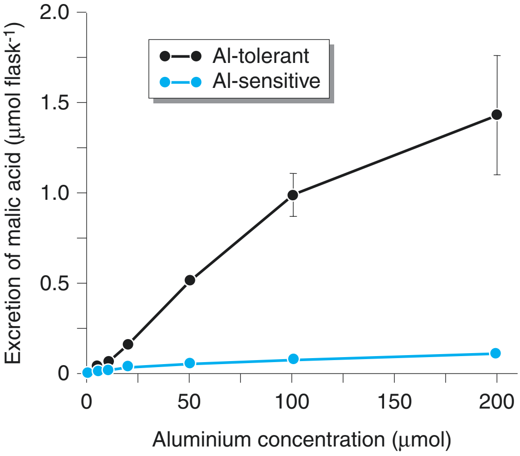

Fig. 7.39 Secretion of malic acid by seedlings of Al-sensitive and Al-resistant wheat varieties. Six-day-old seedlings were exposed for 24 h to different concentrations of an Al^{3+} salt solution. (After Delhaize et al. (1993))

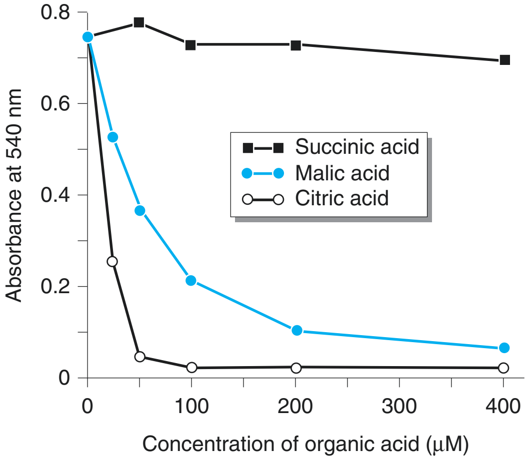

Fig. 7.40 Chelation of Al^{3+} by organic acids. Citric, malic and succinic acid were incubated for 1 h in 3.2 mM Na-acetate buffer (pH 4.2) containing 50 µM Al^{3+} and 250 µM haematoxylin. The formation of Al–haematoxylin complexes was measured by absorption at 540 nm. The reduction of the absorption in the presence of organic acids shows that organic acids chelate part of the aluminium, which is then no longer available for formation of a complex with haematoxylin. (After Delhaize et al. (1993))

of substrates. *Sorghum bicolor* SbMATE, the barley protein HvAACT1 and several orthologues in various species mediate Al-activated citrate secretion. The mechanism of Al^{3+} activation is not understood for any of the ALMT1 and MATE proteins. In addition to this post-translational activation, there is up-regulation of expression in some species. Tight regulation of organic acid secretion helps to limit the carbon costs of this mechanism. Secretion is contingent on the presence of potentially dangerous Al^{3+} concentrations and is apparently restricted to particular zones in the root tip where most of the Al^{3+} damage occurs (Kochian et al. 2015).

Under **aluminium stress**, Al^{3+}-sensitive cultivars excrete malate and citrate too, but much less so than tolerant cultivars (Fig. 7.39). The molecular explanation for natural variation in Al exclusion provides an instructive example of how intraspecific differences in stress tolerance can arise. Variations in ALMT1 and MATE expression at the root tip correlate well with the genotypic variation in Al^{3+} tolerance. Regardless of whether gene expression is responsive to Al^{3+} exposure, tolerant genotypes always show higher transcript levels of the organic acid transporter genes than sensitive genotypes (Delhaize et al. 2012). Different types of promoter polymorphisms have been selected that result in higher expression levels of the version present in the tolerant cultivars. In wheat the ALMT1 promoters differ in the number of repeats. More repeats are correlated with stronger promoter activity (Fig. 7.41). High expression of HvAACT1 at the root apex has been traced to a transposon insertion in the promoter in more tolerant cultivars. Sorghum promoters also differ in repeat numbers.

Resistance to high intracellular Al concentrations is observed in several species adapted to acidic soils. Among them are a few exceptional plants, which can even be referred to as **Al accumulators**, with shoot Al concentrations >10 times higher than those in other plants—that is, up to 3 g/kg of dry biomass. Old leaves of tea accumulate Al to this level and sometimes even higher levels (30 g/kg of dry biomass has been reported). Buckwheat is another example. The accumulation of Al in the vacuoles of *Hydrangea* is remarkable. The sepals turn from red to blue with the addition of Al^{3+} to the irrigation water. The colour change is due to the formation of a complex of Al with delphinidin-3-glucoside and 3-caffeoylquinic acid (Ma et al. 1997) (Fig. 7.42). Corresponding to the high content of soluble Al^{3+} in acidic soils in the

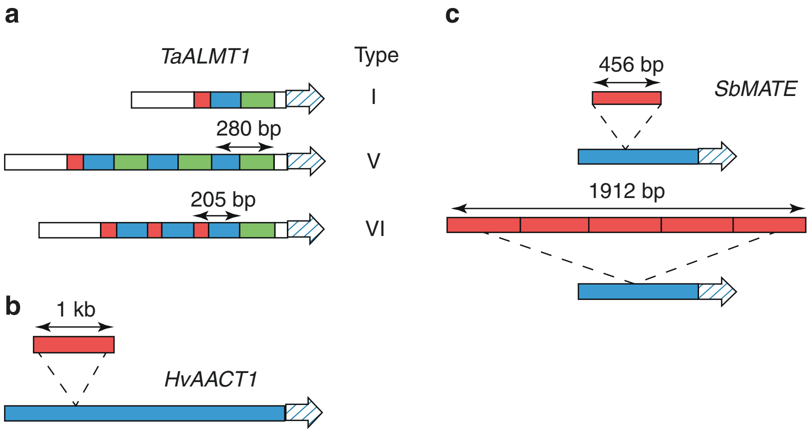

Fig. 7.41 Different types of promoter polymorphisms in Al tolerance genes from wheat, barley and sorghum. **a** The type I allele is associated with weak expression of *TaALMT1* and is found in Al-sensitive cultivars; types V and VI carry repeats in the *TaALMT1* promoter that confer higher expression and Al tolerance. **b** A transposon insertion in the *HvAACT1* promoter is the reason for higher expression. **c** Miniature inverted transposable elements inserted in the *SbMATE* promoter. Between one and five elements are inserted. The number of insertions correlates positively with *SbMATE* transcript abundance. (Modified from Delhaize et al. (2012))

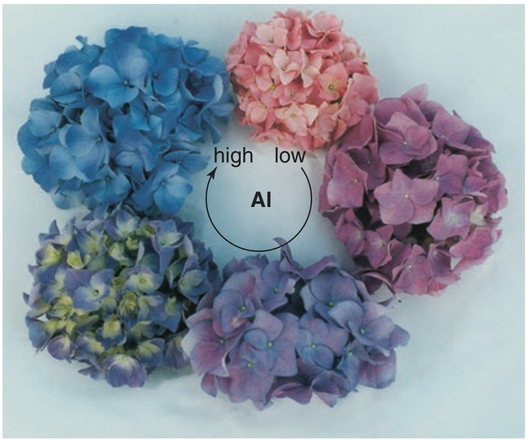

Fig. 7.42 Aluminium ions form complexes with water-soluble vacuolar pigments. Gardeners use this to great effect in the ornamental *Hydrangea* species; different Al^{3+} concentrations change the colour of the flowers from white through red to deep blue. The colours in *Hydrangea* are the result of aluminium complexes with the anthocyanin delphinidin-3-glucoside and with chlorogenic acid (caffeoylquinic acid). The aluminium concentrations in the flowers shown are—from *red* to *blue*—51, 106, 640, 804 and 3959 mg Al/kg of dry weight. (Ma et al. 2001)

tropics, substantial concentrations of Al (up to 1 g/kg) occur in wild plants (e.g. *Melastoma* and *Vaccinium*) in rainforests.

Al tolerance results from effective **sequestration of Al** by formation of cytosolic complexes and transport into vacuoles. Most of this sequestration occurs in root cells and, in Al-accumulating plants, additionally in the leaf symplast. For example, Al accumulates in buckwheat as an Al–oxalate complex. In *Hydrangea* the counter anion for Al^{3+} is citrate.

Mechanistic insight into the intracellular sequestration of Al is predominantly available for rice, the most tolerant cereal species. Al tolerance is genetically much more complex in rice than in the other cereals, which indicates a multitude of factors contributing to tolerance. As in barley and sorghum, rice roots secrete organic acids via a transporter in the MATE family (OsFRDL4). However, the contribution of this transporter to overall Al tolerance is much less pronounced. Instead, a major determinant of natural variation in Al tolerance is allelic variation in the Al transporter NRAT1 (Li et al. 2014). This transporter allows entry of apoplastic Al^{3+} into root cells. The beneficial effect of Al^{3+} uptake in rice demonstrates that at least some of the toxicity of Al^{3+} is explained by interaction with extracellular targets. At the same time it indicates efficient intracellular sequestration of Al^{3+}. Cytosolic Al^{3+} (whose concentration around neutral pH is very low) and/or Al–organic acid complexes are the substrates for tonoplast-localised ABC transporters (e.g. OsALS1 in rice) or aquaporins.

Accumulation of Al in the leaves of a small subset of Al-tolerant species requires **Al mobility**. Al is translocated to the shoot complexed with organic acids, taken up into leaf cells and transported into the vacuoles by aquaporins, as shown for *Hydrangea macrophylla* (Kochian et al. 2015). Transport forms in the xylem of other Al accumulators such as tea, buckwheat and *Melastoma* are of the same chemical nature—that is, Al complexes with citrate, malate or oxalate.

7.5.5 Non-Essential Toxic Metals

Several non-essential and potentially highly toxic metals or metalloids are present in the environment. They can be taken up and accumulated by plants when available in the soil. The most important elements in this category are Cd, As, Pb and Hg. The causes of their release into the environment can be either natural or anthropogenic. Volcanic emissions are important sources of Hg and As. Cd and Pb are present in Zn minerals and become available through weathering. Potentially toxic concentrations, however, are mostly due to human activities. **Metal pollution** is a consequence of mining, metal processing and agricultural practices such as the use of fertilisers with toxic metal impurities (Clemens and Ma 2016). Perhaps surprisingly, all plants apparently express genes conferring non-essential metal tolerance, even those that in their natural habitats are very unlikely to encounter threatening concentrations.

As referred to in Sect. 7.2.2, entry of non-essential metal ions into plant cells is due to hitchhiking on transporters of essential macro- and

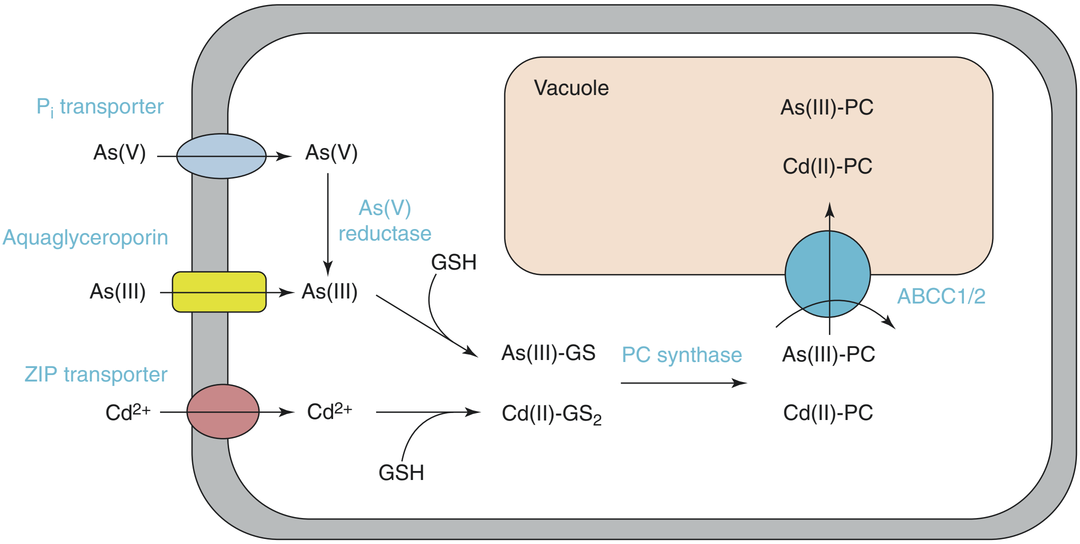

Fig. 7.43 The phytochelatin (PC) metal detoxification pathway. The toxic, non-essential elements As and Cd are taken up into plant cells by transporters of essential or beneficial elements such as phosphate, silicon (aquaglyceroporin) and Zn or Fe (ZIP transporters). Once inside the cells, As(V) is reduced enzymatically to As(III). As(III) and Cd^{2+} form complexes with glutathione (GSH). These complexes are substrates for PC synthase. PC synthase produces metal-binding peptides, which bind As(III) and Cd(II). Their transport into the vacuole by ATP-dependent ABC transporters (ABCC1/2) sequesters the toxic elements away from the cytosol, thereby preventing damage through interaction with the thiols of proteins and other molecules

micronutrients or beneficial elements (Clemens 2006). This is well documented for the two main inorganic As species present in soil, **arsenate** (**AsV**) and **arsenite** (**AsIII**) (Fig. 7.43). The former is taken up by phosphate transporters, the latter by **aquaglyceroporins**. In rice plants the aquaglyceroporin Lsi1 functions as a silicon transporter. In plants with naturally selected As hypertolerance (e.g. the perennial grass *Holcus lanatus*) the suppression of high-affinity phosphate uptake represents an important part of the adaptation.

Cd, As, Pb and Hg are thiophilic elements—that is, they have a high affinity for sulphur groups in biological molecules. Uncontrolled binding renders such molecules inactive and eventually causes damage. Thus, the ability to cope with exposure to toxic non-essential elements is conferred by mechanisms that suppress such unwanted interactions. Like the tolerance of essential metal excess, the detoxification of non-essential metals is predominantly achieved by sequestration and efflux to protect the cytosol. The main sequestration route is the **phytochelatin** (**PC**) **pathway** (Fig. 7.43). PCs are derivatives of GSH with the general formula $(\gamma\text{-Glu-Cys})_n\text{-Gly}$ (n is usually between 2 and 5). PCs are synthesised non-ribosomally by the enzyme PC synthase and bind several metals with high affinity. An excess of metals activates the enzyme in the cytosol. Upon formation of PC–metal complexes, these are transported into the vacuole by ABC-type transporters. A second mechanism to maintain low cytosolic concentrations depends on metal-effluxing **HMAs**—P$_{1B}$-type ATPases localised in the plasma membrane or the tonoplast. They play an important role in Cd hypertolerance in Cd-hyperaccumulating plants (Sect. 7.5.2).

Summary

- Fourteen different mineral nutrients are essential for plants, meaning the plant is not able to complete its life cycle without these nutrients. Depending on the concentrations found in tissues, they are divided into macroelements (approximately 1000–15,000 µg/g of dry weight) and microelements (approximately 0.005–100 µg/g of dry weight).

- The recruitment of elements for biological functions in the course of evolution has been governed by three factors: abundance, availability and reactivity.
- Since practically every natural ecosystem responds to mineral nutrient input, normally by enhanced biomass production, it can be inferred that nutrient limitation is very common or, in other words, that plants are practically always under stress from suboptimal availability of mineral nutrients.
- Terrestrial plants have to acquire most mineral nutrients from the soil—an extremely complex, diverse and heterogeneous substrate.
- Unlike heterotrophic organisms, which ingest biological material with an elemental composition that is already close to physiological requirements, plants depend on a soil solution that under most circumstances shows very low and unbalanced concentrations of nutrients.
- Concerning the relationship between the availability of a particular nutrient and the growth response of a plant, three conditions can be distinguished: deficiency, adequate supply and toxicity. Deficiency and toxicity represent stress.
- Nutrient availability strongly varies in space and time. Soil types differ tremendously in mineral content. Large and element-specific fluctuations occur within a soil—for instance, depending on changes in pH, water status or microbial activity. Gradients develop horizontally and vertically, or element distribution can be patchy. Mobility within the soil is strongly element specific.
- Strong variation exists between species and also within species (i.e. between ecotypes, cultivars and varieties) in their ability to acquire nutrients from soil. Thus, soil mineral availability has a strong influence on the distribution and composition of natural vegetation. Some plant species have evolved specific adaptations to particularly nutrient-impoverished soils.
- The concentration range between deficiency and toxicity is comparatively narrow for some of the microelements. Because of their reactivity, they can easily become growth inhibiting. Also, elements without a biological function in plants, such as arsenic and cadmium, are potentially highly toxic. Some are taken up into cells because of their chemical similarity to essential elements. Numerous plant species have evolved the capacity to survive in soils with very high levels of toxic elements. They are referred to as halophytes in the case of Na and metallophytes in the case of metals.
- The biology of the root can, by and large, be explained by the need to acquire—besides water—the mineral nutrients essential for growth. Four principal strategies can be distinguished that plant roots use to ensure adequate nutrient acquisition: they influence the availability of nutrients in the rhizosphere, they tightly regulate ion transport capacities, they modulate their architecture (i.e. their three-dimensional morphological structure) and they establish symbioses with fungi (mycorrhizae) and bacteria (biological N_2 fixation).
- Plant roots actively influence the rhizosphere to enhance nutrient availability by acidification, as well as the exudation of proteins and small molecules such as organic acids. A large fraction of the photosynthetically fixed carbon is transferred below-ground by plants and feeds microorganisms in the rhizosphere.
- A comparatively well-understood example of nutrient mobilisation is Fe acquisition. Most plants employ acidification, reduction and chelation (strategy I), while grasses secrete FeIII-complexing molecules—the phytosiderophores (strategy II).
- Transporter proteins are essential to mediate the uptake of nutrient ions across the plasma membrane and the efflux out of the cytosol. Several transport proteins encoded in typical plant genomes enable all of the necessary processes.
- Depending on the driving force, three categories of transport are distinguished: facilitated diffusion, primary active transport and secondary active transport. The dominant primary active transport in plant cells is the

establishment of a proton gradient across the plasma membrane and the tonoplast. This proton gradient, the proton motif force, provides the driving force for myriad secondary transport processes.

- The activities of cation and anion channels depend on the cell's external and internal ion concentrations, which establish a specific membrane potential. The plasma membrane potential of plant cells is negative on the cytosolic side (around −150 mV), owing largely to the proton pumping activity of H^+-ATPases. Thus, cations such as K^+ or Fe^{2+} can in principle move passively into the cytosol along an electric potential gradient through channels or uniporters. In contrast, anions such as phosphate, nitrate and sulphate enter a root cell against a potential gradient. This is enabled by H^+-coupled symport.
- One of the hallmarks of plant mineral uptake is the existence of multiphasic uptake systems with varying affinities. Depending on the concentration in the soil solution, low-affinity or high-affinity transport systems with affinities in the millimolar or micromolar range, respectively, are in operation.
- Nitrogen is present in the soil in many different chemical forms. The three most abundant ones are nitrate (NO_3^-), ammonium (NH_4^+) and amino acids. Their relative contributions can vary widely depending on environmental conditions and competition by soil microorganisms. Multiple uptake transporters differing in substrates, substrate affinities, localisation of expression, subcellular localisation and regulation enable optimal exploitation of the hugely varying N sources.
- K^+ and sulphate are taken up by high- and low-affinity systems, while phosphate acquisition demands energised high-affinity uptake systems because the concentration in the soil solution is usually very low (around 1 µM).
- Plants need to be able to respond and acclimate to strongly fluctuating external nutrient availability. Major targets of acclimation are nutrient uptake capacities and the root architecture. Plants sense and respond to the external supply of a particular nutrient and the internal nutritional status. Both local and systemic acclimation occurs.
- Transport capacities are regulated by transcriptional regulation and the post-translational modulation of transporter activities, stability, subcellular localisation and affinities.
- Following symplastic passage from sites of uptake in the root cortex, nutrients are loaded for long-distance transport into the xylem. The xylem is apoplastic. Thus, efflux across the plasma membrane is necessary. Energetically the situation is reversed in comparison with uptake. Anions can be loaded via facilitated diffusion; cations may require active transport.
- Roots are the plant organs with the highest developmental plasticity. The size of the root surface that is competent to take up water and nutrients determines the capacity of a plant individual to acquire these resources. Root architecture plasticity is governed by a variety of processes that occur in response to either the nutrient availability in the soil or the nutritional status of the plant. It is mostly determined by the number and lengths of root axes, including the length of the primary root; the position, angle, density and growth of lateral roots; and the density and elongation of root hairs.
- Root architecture arises from a combination of cell cycle activity, cell differentiation and cell elongation—processes that are under hormonal control. Auxin and cytokinin play key roles.
- The necessary sensing of nutrient availability and nutritional status is poorly understood. Some nutrient transporters can function as sensors of their substrates too.
- For most plants in natural habitats, symbiotic associations with microorganisms are an essential part of their nutrient acquisition. Hence, they are major components of global biogeochemical cycles. Plants provide reduced carbon to the microorganisms and receive macro- and micronutrients in return.

- A mycorrhiza is a symbiosis between plants and fungi. The majority of mycorrhizae are of the arbuscular type. It is evolutionary ancient and most likely was already instrumental when plants first colonised land about 450 million years ago. A large fraction (up to 80%) of the main limiting macronutrient, phosphorus, is provided to plants by mycorrhizal fungi.
- Both the molecular physiology of mycorrhizal transport processes and the events that enable symbiosis formation are being investigated predominantly in the model systems *Medicago truncatula* and *Lotus japonicus*.
- Biological nitrogen fixation represents the major route of nitrogen supply to plants in natural terrestrial environments (an estimated 80–90%). Symbiotic bacteria living within plant tissues account for most of the global nitrogen fixation.
- Establishment of both a mycorrhiza and a nitrogen-fixing symbiosis has to occur for every single plant individually. It requires mutual recognition by the partners through chemical communication. The command over the process of symbiosis establishment lies entirely on the plant side, as the host has to actively allow infection by the symbiotic partner through far-reaching developmental changes.
- In spite of the fundamental differences between the symbiotic microorganisms and the plant developmental changes allowing colonisation of the host, the recognition and early signal transduction events in host cells proceed through a pathway shared by arbuscular mycorrhizae and the Fabaceae–rhizobia symbiosis: the common sym pathway.
- Practically all plants exhibit some degree of basal tolerance of element toxicity. Some specialists adapted to habitats characterised by toxic element concentrations possess naturally selected hypertolerance.
- Tolerance is conferred by transporters mediating efflux or vacuolar sequestration.
- About 0.2% of all flowering plant species have evolved the ability to hyperaccumulate metals or metalloids (arsenic, selenium) in their leaves. They represent a subgroup of the metallophytes—that is, plants that are part of a special type of vegetation found on metal-rich sites. The evolution of hyperaccumulation is an example of adaptation to extreme environments. It has proceeded through transcriptional changes in metal transporter genes via copy number variation and changes in *cis*-regulatory sequences.
- The soils of more than 6% of the world's terrestrial surface contain potentially toxic concentrations of salt, mostly NaCl. Salt stress has an osmotic component and an ion toxicity component. Plants are negatively affected in several ways: by dehydration, Na^+ (and Cl^-) toxicity, nutrient imbalances and production of reactive oxygen species. Na^+ is the more toxic ion. It leaks into plant cells via Ca^{2+}-permeable non-selective cation channels or K^+/Na^+ transporters.
- Plants vary greatly in their tolerance of salinity. Sensitive plants are called glycophytes. Still, they possess a basal tolerance mechanism. Highly salt-tolerant species are called halophytes.
- At the cellular level, plants have several principal mechanisms to cope with salinity: they can minimise initial entry into the root, maximise efflux from the root into the soil, minimise loading into the xylem or maximise retrieval from the xylem fluid before Na^+ reaches the shoot, maximise recirculation out of the shoot into the phloem, maximise intracellular compartmentation or allocation to particular parts of the shoot, or even secrete salt by glands to the surface of the leaf or into specific bladder hairs.
- The most important cellular aspects of salt stress tolerance are efficient removal of Na^+ from the cytosol, especially in young tissues, and regulation of Na^+ distribution within the plant. The former is achieved by secretion to the apoplast or sequestration in the vacuole, the latter largely through re-uptake of Na^+ from the xylem into xylem parenchyma cells.

- Another common acclimative response of a plant to salinity is lowering of the water potential of its cells. This is achieved by accumulation of low molecular weight compounds (the so-called compatible solutes or osmolytes) in the cell.
- Salt stress sensing and signalling involve as yet unknown osmosensors, cytosolic Ca^{2+} increases and abscisic acid responses.
- Aluminium is the most abundant metallic element in the Earth's crust, where it appears in many (usually insoluble) compounds and complexes. Below a soil pH of around 5, Al becomes available for plant uptake as the highly phytotoxic Al^{3+} ion. This process is the major reason for the limitation of plant productivity in acidic soils.
- Two major mechanisms allow plants to withstand Al toxicity. The first one results in effective exclusion of Al^{3+} from the symplast, thereby reducing the actual exposure of cellular sites to the toxicity of Al^{3+} (avoidance). The second mechanism confers tolerance. It comprises processes that detoxify and sequester Al^{3+} ions after they have entered cells.
- Uptake of Al^{3+} into the root symplast is prevented by the secretion of organic acids, mostly malate and citrate, which form complexes with Al^{3+} extracellularly. Differences between plants in the ability to exclude Al^{3+} from root cells are strongly correlated with differences in the rate of organic acid secretion into the rhizosphere. Tolerant genotypes always show higher transcript levels of the organic acid transporter genes than sensitive genotypes. These result from changes in promoter sequences.
- A few exceptional plant species can be referred to as Al accumulators, with shoot Al concentrations >10 times higher than those in other plants.
- Several non-essential and potentially highly toxic metals or metalloids are present in the environment, the most important being As, Cd, Pb and Hg. The detoxification of non-essential metals is predominantly achieved by sequestration and efflux to protect the cytosol. The main sequestration route is the phytochelatin pathway.

References

Akiyama K, Matsuzaki K, Hayashi H (2005) Plant sesquiterpenes induce hyphal branching in arbuscular mycorrhizal fungi. Nature 435:824–827

Antonovics J, Bradshaw AD, Turner RG (1971) Heavy metal tolerance in plants. Adv Environ Sci Technol 7:1–85

Apse MP, Blumwald E (2002) Engineering salt tolerance in plants. Curr Opin Biotechnol 13:146–150

Baker AJMBRR (1989) Terrestrial higher plants which hyperaccumulate metallic elements—a review of their distribution, ecology and phytochemistry. Biorecovery 1:81–126

Bassil E, Coku A, Blumwald E (2012) Cellular ion homeostasis: emerging roles of intracellular NHX Na^+/H^+ antiporters in plant growth and development. J Exp Bot 63:5727–5740

Becher M, Talke IN, Krall L, Krämer U (2004) Cross-species microarray transcript profiling reveals high constitutive expression of metal homeostasis genes in shoots of the zinc hyperaccumulator Arabidopsis halleri. Plant J 37:251–268

Brumbarova T, Bauer P, Ivanov R (2015) Molecular mechanisms governing Arabidopsis iron uptake. Trends Plant Sci 20:124–133

Buchanan B, Gruissem W, Jones R (2015) Biochemistry and molecular biology of plants, 2nd edn. Wiley, Somerset

Bulgarelli D, Schlaeppi K, Spaepen S et al (2013) Structure and functions of the bacterial microbiota of plants. Annu Rev Plant Biol 64:807–838

Chérel I, Lefoulon C, Boeglin M, Sentenac H (2014) Molecular mechanisms involved in plant adaptation to low K(+) availability. J Exp Bot 65:833–848

Clemens S (2006) Toxic metal accumulation, responses to exposure and mechanisms of tolerance in plants. Biochimie 88:1707–1719

Clemens S (2001) Molecular mechanisms of plant metal homeostasis and tolerance. Planta 212:475–486

Clemens S, Ma JF (2016) Toxic heavy metal and metalloid accumulation in crop plants and foods. Annu Rev Plant Biol 67:489–512

Clemens S, Weber M (2016) The essential role of coumarin secretion for Fe acquisition from alkaline soil. Plant Signal Behav 11:e1114197

Curie C, Panaviene Z, Loulergue C et al (2001) Maize yellow stripe1 encodes a membrane protein directly involved in Fe(III) uptake. Nature 409:346–349

Deinlein U, Stephan AB, Horie T et al (2014) Plant salt-tolerance mechanisms. Trends Plant Sci 19:371–379

Delhaize E, Ma JF, Ryan PR (2012) Transcriptional regulation of aluminium tolerance genes. Trends Plant Sci 17:341–348

Delhaize E, Ryan PR, Randall PJ (1993) Aluminum tolerance in wheat (Triticum aestivum L.). II. Aluminum-stimulated excretion of malic acid from root apices. Plant Physiol 103:695–702

Dreyer I, Blatt MR (2009) What makes a gate? The ins and outs of Kv-like K^+ channels in plants. Trends Plant Sci 14:383–390

Epstein E, Rains DW, Elzam OE (1963) Resolution of dual mechanisms of potassium absorption by barley roots. Proc Natl Acad Sci U S A 49:684–692

Flowers TJ, Colmer TD (2008) Salinity tolerance in halophytes. New Phytol 179:945–963

Foy CD, Chaney RL, White MC (1978) Physiology of metal toxicity in plants. Annu Rev Plant Physiol Plant Mol Biol 29:511–566

Frausto da Silva JJR, Williams RJP (2001) The biological chemistry of the elements: the inorganic chemistry of life. Oxford University Press, Oxford

Garcia K, Doidy J, Zimmermann SD et al (2016) Take a trip through the plant and fungal transportome of mycorrhiza. Trends Plant Sci 21:937–950

Giehl RFH, Gruber BD, von Wirén N (2014) It's time to make changes: modulation of root system architecture by nutrient signals. J Exp Bot 65:769–778

Halimaa P, Lin Y-F, Ahonen V et al (2014) Gene expression differences between Noccaea caerulescens ecotypes help identifying candidate genes for metal phytoremediation. Environ Sci Technol 48(6):3344–3353

Hanikenne M, Kroymann J, Trampczynska A et al (2013) Hard selective sweep and ectopic gene conversion in a gene cluster affording environmental adaptation. PLoS Genet 9:e1003707

Hanikenne M, Talke IN, Haydon MJ et al (2008) Evolution of metal hyperaccumulation required cis-regulatory changes and triplication of HMA4. Nature 453:391–395

Harrison MJ, van Buuren ML (1995) A phosphate transporter from the mycorrhizal fungus Glomus versiforme. Nature 378:626–629

Hart H (1930) Nicolas Theodore de Saussure. Plant Physiol 5:424–429

Hasegawa PM, Bressan RA, Zhu J-K, Bohnert HJ (2000) Plant cellular and molecular responses to high salinity. Annu Rev Plant Physiol Plant Mol Biol 51:463–499

Hirayama T, Shinozaki K (2010) Research on plant abiotic stress responses in the post-genome era: past, present and future. Plant J 61:1041–1052

Ho C-H, Lin S-H, Hu H-C, Tsay Y-F (2009) CHL1 functions as a nitrate sensor in plants. Cell 138:1184–1194

Horie T, Karahara I, Katsuhara M (2012) Salinity tolerance mechanisms in glycophytes: an overview with the central focus on rice plants. Rice 5:11

Irving H, Williams R (1948) Order of stability of metal complexes. Nature 162:746–747

Klein T, Siegwolf RTW, Körner C (2016) Belowground carbon trade among tall trees in a temperate forest. Science 352:342–344

Kobayashi T, Nishizawa NK (2012) Iron uptake, translocation, and regulation in higher plants. Annu Rev Plant Biol 63:131–152

Kochian LV, Hoekenga OA, Pineros MA (2004) How do crop plants tolerate acid soils? Mechanisms of aluminum tolerance and phosphorous efficiency. Annu Rev Plant Biol 55:459–493

Kochian LV, Piñeros MA, Liu J, Magalhaes JV (2015) Plant adaptation to acid soils: the molecular basis for crop aluminum resistance. Annu Rev Plant Biol 66:571–598

Krämer U (2010) Metal hyperaccumulation in plants. Annu Rev Plant Biol 61:517–534

Kuzyakov Y, Domanski G (2000) Carbon input by plants into the soil. Review. J Plant Nutr Soil Sci 163:421–431

Lambers H, Chapin FS III, Pons TL (2008) Plant physiological ecology, 2nd edn. Springer, New York

Lambers H, Martinoia E, Renton M (2015) Plant adaptations to severely phosphorus-impoverished soils. Curr Opin Plant Biol 25:23–31

Li J-Y, Liu J, Dong D et al (2014) Natural variation underlies alterations in Nramp aluminum transporter (NRAT1) expression and function that play a key role in rice aluminum tolerance. PNAS 111:6503–6508

Lin Y-F, Aarts MGM (2012) The molecular mechanism of zinc and cadmium stress response in plants. Cell Mol Life Sci 69:3187–3206

López-Arredondo DL, Leyva-González MA, González-Morales SI et al (2014) Phosphate nutrition: improving low-phosphate tolerance in crops. Annu Rev Plant Biol 65:95–123

Lüttge U, Kluge M, Bauer G (2005) Botanik, 5th edn. VCH, Weinheim

Ma J, Ryan P, Delhaize E (2001) Aluminium tolerance in plants and the complexing role of organic acids. Trends Plant Sci 6:273–278

Ma JF, Tamai K, Yamaji N et al (2006) A silicon transporter in rice. Nature 440:688–691

Ma JF, Yamaji N (2006) Silicon uptake and accumulation in higher plants. Trends Plant Sci 11:392–397

Ma JF, Zheng SJ, Matsumoto H, Hiradate S (1997) Detoxifying aluminium with buckwheat. Nature 390:569–570

Magalhaes JV, Liu J, Guimaraes CT et al (2007) A gene in the multidrug and toxic compound extrusion (MATE) family confers aluminum tolerance in sorghum. Nat Genet 39:1156–1161

Maillet F, Poinsot V, Andre O et al (2011) Fungal lipochitooligosaccharide symbiotic signals in arbuscular mycorrhiza. Nature 469:58–63

Marschner P (2012) Marschner's mineral nutrition of higher plants, 3rd edn. Academic Press, Amsterdam

Miller AJ, Cramer MD (2005) Root nitrogen acquisition and assimilation. Plant Soil 274:1–36

Miller AJ, Shen Q, Xu G (2009) Freeways in the plant: transporters for N, P and S and their regulation. Curr Opin Plant Biol 12:284–290

Miwa K, Takano J, Omori H et al (2007) Plants tolerant of high boron levels. Science 318:1417

Møller IS, Gilliham M, Jha D et al (2009) Shoot Na^+ exclusion and increased salinity tolerance engineered by cell type–specific alteration of Na^+ transport in Arabidopsis. Plant Cell Online 21:2163–2178

Moons A, Prinsen E, Bauw G, Van Montagu M (1997) Antagonistic effects of abscisic acid and jasmonates on salt stress-inducible transcripts in rice roots. Plant Cell 9:2243–2259

Munns R (2002) Comparative physiology of salt and water stress. Plant Cell Environ 25:239–250

Munns R, James RA, Xu B et al (2012) Wheat grain yield on saline soils is improved by an ancestral Na^+ transporter gene. Nat Biotechnol 30:360–364

Munns R, Tester M (2008) Mechanisms of salinity tolerance. Annu Rev Plant Biol 59:651–681

Nable RO, Banuelos GS, Paull JG (1997) Boron toxicity. Plant Soil 193:181–198

Neumann G, Martinoia E (2002) Cluster roots—an underground adaptation for survival in extreme environments. Trends Plant Sci 7:162–167

Oh D-H, Leidi E, Zhang Q et al (2009) Loss of halophytism by interference with SOS1 expression. Plant Physiol 151:210–222

Oldroyd GED (2013) Speak, friend, and enter: signalling systems that promote beneficial symbiotic associations in plants. Nat Rev Microbiol 11:252–263

Osmont KS, Sibout R, Hardtke CS (2007) Hidden branches: developments in root system architecture. Annu Rev Plant Biol 58:93–113

Parniske M (2008) Arbuscular mycorrhiza: the mother of plant root endosymbioses. Nat Rev Microbiol 6:763–775

Petricka JJ, Winter CM, Benfey PN (2012) Control of Arabidopsis root development. Annu Rev Plant Biol 63:563–590

Römheld V, Marschner H (1986) Mobilization of iron in the rhizosphere of different plant species. Adv Plant Nutrition 2:155–204

Salt DE, Smith RD, Raskin I (1998) Phytoremediation. Annu Rev Plant Physiol Plant Mol Biol 49:643–668

Sasaki T, Yamamoto Y, Ezaki B et al (2004) A wheat gene encoding an aluminum-activated malate transporter. Plant J 37:645–653

Stracke S, Kistner C, Yoshida S et al (2002) A plant receptor-like kinase required for both bacterial and fungal symbiosis. Nature 417:959–962

Sutton T, Baumann U, Hayes J et al (2007) Boron-toxicity tolerance in barley arising from efflux transporter amplification. Science 318:1446–1449

Svennerstam H, Jämtgård S, Ahmad I et al (2011) Transporters in Arabidopsis roots mediating uptake of amino acids at naturally occurring concentrations. New Phytol 191:459–467

Taiz L, Zeiger E (2006) Plant physiology, 4th edn. Sinauer Associates, Sunderland

Takahashi M, Nakanishi H, Kawasaki S et al (2001) Enhanced tolerance of rice to low iron availability in alkaline soils using barley nicotianamine aminotransferase genes. Nat Biotechnol 19:466–469

Tester M, Davenport R (2003) Na^+ tolerance and Na^+ transport in higher plants. Ann Bot 91:503–527

Tsay Y, Chiu C, Tsai C et al (2007) Nitrate transporters and peptide transporters. FEBS Lett 581:2290–2300

van der Ent A, Baker AJM, Reeves RD et al (2012) Hyperaccumulators of metal and metalloid trace elements: facts and fiction. Plant Soil 362:319–334

van der Heijden MGA, Martin FM, Selosse M-A, Sanders IR (2015) Mycorrhizal ecology and evolution: the past, the present, and the future. New Phytol 205:1406–1423

Vert G, Grotz N, Dedaldechamp F et al (2002) IRT1, an Arabidopsis transporter essential for iron uptake from the soil and for plant growth. Plant Cell 14:1233–1243

Wang W, Vinocur B, Altman A (2003) Plant responses to drought, salinity and extreme temperatures: towards genetic engineering for stress tolerance. Planta 218:1–14

Ward JM, Mäser P, Schroeder JI (2009) Plant ion channels: gene families, physiology, and functional genomics analyses. Annu Rev Physiol 71:59–82

Weber M, Deinlein U, Fischer S et al (2013) A mutation in the Arabidopsis thaliana cell wall biosynthesis gene pectin methylesterase 3 as well as its aberrant expression cause hypersensitivity specifically to Zn. Plant J 76:151–164

Weber M, Harada E, Vess C et al (2004) Comparative microarray analysis of Arabidopsis thaliana and Arabidopsis halleri roots identifies nicotianamine synthase, a ZIP transporter and other genes as potential metal hyperaccumulation factors. Plant J 37:269–281

Weiler E, Nover L (2008) Allgemeine und molekulare Botanik. Thieme, Stuttgart

Yamaguchi T, Hamamoto S, Uozumi N (2013) Sodium transport system in plant cells. Front Plant Sci 4:410

Yuan F, Yang H, Xue Y et al (2014) OSCA1 mediates osmotic-stress-evoked Ca^{2+} increases vital for osmosensing in Arabidopsis. Nature 514:367–371

8

Biotic Stress

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A leaf of broad-leaved dock (*Rumex obtusifolius*), which has been perforated by leaf beetles (Chrysomelidae) and their larvae. Further clutches of eggs are on the leaf lamina. In the right margin of the picture, two spots with red edges (which show the accumulation of anthocyanins) indicate a defence response, probably due to a secondary infection by microbial pathogens. (Photo: E. Beck)

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Plants are constantly under attack. They are surrounded by a wide range of potential enemies—organisms that strive to exploit them as substrates. Spores of fungi and oomycetes land on plant leaves all the time and germinate when conditions are right. Insects seek to make the nearest plant their next meal. The soil abounds with bacteria and nematodes, which roots are exposed to. In light of this, plant disease is amazingly rare in wild populations. If it occurs at all, usually only a few plant individuals are affected and the extent of damage is limited to parts of a leaf or a few leaves at most. Most plants remain healthy because they possess an array of preformed (constitutive) and inducible defence mechanisms that restrict the success of potential pathogens or herbivores. Having said this, there are nonetheless instances in which herbivores or pathogens cause devastating damage to one or several species across large areas. One current example is the mountain pine beetle outbreak, destroying large areas of pine forest in British Columbia, Canada. Another one is sudden oak death, a newly discovered disease caused by the oomycete *Phytophthora ramorum*. Wide areas of California and Oregon in the USA have been affected by the pathogen, which apparently was recently introduced and can colonise not only oaks but approximately 40 other species as well.

As we will see, there are—despite the fundamentally different strategies of, for example, phytopathogenic fungi and chewing insects—many similarities between the strategies plants use to fend off microbial pathogens or herbivores. Both defences can be divided into mechanical/physical and chemical strategies. Both involve recognition events and signalling cascades that result in the induction of defence mechanisms upon the perception of a potential foe or the damage caused by it. There are even common motifs when comparing plant and animal (including human) defence systems. It has in recent years become increasingly clear that they share an **innate immunity** based on the ability to detect the presence of cells that are foreign to the organism.

The observation and analysis of **plant disease** are among the oldest questions in biology. Unlike wild plants in their natural habitats, cultivated crops are far more likely to suffer disease (for reasons that will be considered in Sect. 8.2). Because of the yield losses caused by pathogens and herbivores, the ancient Roman writer Columella examined plant disease. Since the nineteenth century, **phytopathology** has been an active scientific discipline motivated by the goal of reducing susceptibility of cultivated plants to pathogens.

Moreover, plant–pathogen relations serve as an excellent model for the interaction between organisms and their **co-evolution**. Biotic interactions represent a major driver of **biodiversity**, and the "warfare" between plant hosts and their potential pathogens explains why (Sect. 8.2).

This chapter first describes the interaction of plants with predominantly microbial and fungal pathogens that can cause disease in plants. We will look at the types of **pathogens** and their weapons (i.e. **pathogenicity** determinants), at preformed plant defences and, more prominently, at the inducible **plant immune system**. The latter encompasses mechanisms involved in the recognition of potential pathogens or their activities, the ensuing activation of defence responses and the apparent co-evolution between hosts and pathogens. The discussion of defence against **herbivores** (often referred to as **plant pests**) will be focused on insect herbivores. Finally, the chapter covers damage caused by **parasitic plants** and the hostile interaction between plants (i.e. **allelopathy**). Parasitic plants and allelopathic interactions are not nearly as intensively investigated as the plant immune system and herbivore defence. Thus, those parts will present much less molecular insight.

8.1 Plant Disease Caused by Pathogens

Heterotrophic microorganisms have three principal ways of utilising plant biomass as a substrate. The majority are restricted to a saprophytic

Fig. 8.1 Symptoms of disease caused by plant pathogens. "Cherry spot hole disease" is a generic term used for bacterial leaf spot caused by the bacterium *Xanthomonas pruni* and cherry leaf spot caused by the fungus *Blumeriella jaapii*

lifestyle—that is, the degradation of dead plant material—because the plant defence system effectively prevents colonisation. Only a limited number of microorganisms have evolved the ability to either establish a **symbiosis** with a plant (Chap. 7, Sect. 7.4) or to overcome the plant immune system and thus gain access to the resources of a living plant. The latter group of microorganisms is collectively called **pathogens**. Their ability to complete at least part of their life cycle within a plant causes disease (Fig. 8.1). Pathogens other than viruses can be divided into biotrophic, hemibiotrophic and necrotrophic pathogens. **Biotrophic pathogens** keep their host alive while exploiting its resources for growth and reproduction, whereas **necrotrophic pathogens** kill their host before establishing themselves on it. **Hemibiotrophic pathogens** represent an intermediate form, as they eventually kill their host at later stages of the colonisation.

8.1.1 Types of Pathogens: Viruses, Bacteria, Fungi, Oomycetes and Nematodes

The specificity of plant pathogens can vary widely. Often the host range is restricted to only one species. This applies, in particular, to biotrophic pathogens. However, there are also examples of pathogens infecting multiple hosts. Several necrotrophic fungi (e.g. *Botrytis* species) cause disease in hundreds of plant species.

Viruses basically consist of a protein coat enclosing nucleic acids (DNA or RNA) that carry the information for the synthesis of only a handful of proteins. For their replication they have to force a host cell to produce these proteins, which then assemble and give rise to new virus particles. Unlike viruses infecting bacterial or animal cells, plant viruses do not have to destroy their host cell in order to release newly formed virus particles, which then attack neighbouring cells. Instead, they move through plasmodesmata from cell to cell and spread systemically via the phloem. Initial infection of a host plant mostly occurs through inoculation of the phloem via virus-carrying **phloem-feeding insects** such as aphids. Typical symptoms of virus-infected plants are yellowing or a mosaic-like colouration of leaves, stunted growth and sometimes the death of a plant.

Microbial pathogens typically infect only specific tissues or organs. **Phytopathogenic bacteria**, for example, can cause root rot, leaf chlorosis or stem dieback, depending on the pathogen and its infection strategy. Bacterial pathogens usually enter a plant through wounds or the stomata and multiply in the apoplast. Only a minute fraction of bacterial species have evolved the ability to infect plants. No more than a few hundred species have been described as pathogens of crop plants. Most disease-causing bacteria are gram positive and belong to a limited number of clades (e.g. *Xanthomonas*, *Pseudomonas*, *Erwinia* and *Dickeya*).

Economically the most important groups of plant pathogens are the oomycetes and **fungi**. **Oomycetes** were for a long time regarded as fungi, but phylogenetically they belong to the Chromalveolata and are thus very distant from fungi. Arguably the most famous plant pathogen is an oomycete. *Phytophthora infestans* is the causal agent of potato blight and was responsible for the Irish famine in the mid-nineteenth century, which left millions of people dead and triggered a mass emigration from Ireland to North America. Downy mildews are oomycetes too.

Among the possibly millions of fungal species living in association with plants, only a small fraction cause disease (Crous et al. 2015). Nonetheless, no other group of pathogens accounts for more yield loss than fungi. Important genera with phytopathogenic species include *Botrytis*, *Alternaria*, *Colletotrichum*, *Fusarium* and *Puccinia*.

A few taxa of **nematodes** are plant pathogens. Presumably because they almost exclusively attack the root system, they are less well studied. Phytopathogenic nematodes are obligate biotrophs—that is, they are absolutely dependent on a plant host for existence. Endo- and ectoparasites are differentiated according to whether they penetrate root tissue or not, respectively. Most of the considerable nematode damage to crop plants is due to infection by cyst and root-knot nematodes.

8.1.2 Pathogenicity Mechanisms

Pathogens have to gain access to the plant's resources and be able to grow and reproduce rapidly within plant tissues. Both processes require effective suppression of the plant's immune system. Invasion of plants is achieved through widely different strategies depending on the type of pathogen. As mentioned, viruses are transmitted by **insect vectors**. The same applies to some phytopathogenic bacteria such as **phytoplasma**. Most bacteria do not have the ability to actively penetrate plant surfaces. However, after entry through wounds or stomata into the apoplast they can degrade plant cell walls via the secretion of a suite of enzymes such as cellulases and pectinases. Cell wall degradation causes disease symptoms such as softening of tissues. For some *Erwinia* species it is known that the bacteria "wait" to secrete these enzymes only when a sufficiently large number of bacterial cells are present at the infection site to overwhelm the plant. Earlier release would only alert the plant immune system (as is discussed in Sect. 8.2.2). The "waiting" is mediated by **quorum-sensing** mechanisms, which bacteria use to monitor the density of a population.

Two other elements of bacterial virulence are common to both plant and animal pathogens—namely, **toxins** and **effectors**. The latter are molecules that bacteria transfer into host cells via secretion systems (e.g. **type III secretion system**; Fig. 8.2). Effectors influence host cells through specific interaction with target structures. They interfere with the plant immune system and render the plant environment more favourable for the bacteria. An example is the protein avrBs3 secreted by the tomato pathogen *Xanthomonas campestris*. Even though it is encoded by the bacterial genome, it has the features of a eukaryotic transcription factor. After release into the plant cell it enters the nucleus and interacts with specific promoter elements to activate a group of genes that collectively cause hypertrophy of cells and thereby disease (Kay and Bonas 2009) (Fig. 8.2). A particularly famous example of an effector molecule is the transfer DNA (T-DNA) of *Agrobacterium tumefaciens* that triggers tumour growth and the synthesis of organic nutrients for the bacteria (Box 8.1).

Like many effectors, toxins appear to often function as suppressors of plant defences. This is illustrated by coronatine, a molecule synthesised by *Pseudomonas syringae*. Coronatine mimics the **phytohormone jasmonate** and interacts with the **jasmonate receptor COI1**. Activation of the jasmonate pathway reverses the closure of stomata, which is an integral part of the plant's defence response (Melotto et al. 2006).

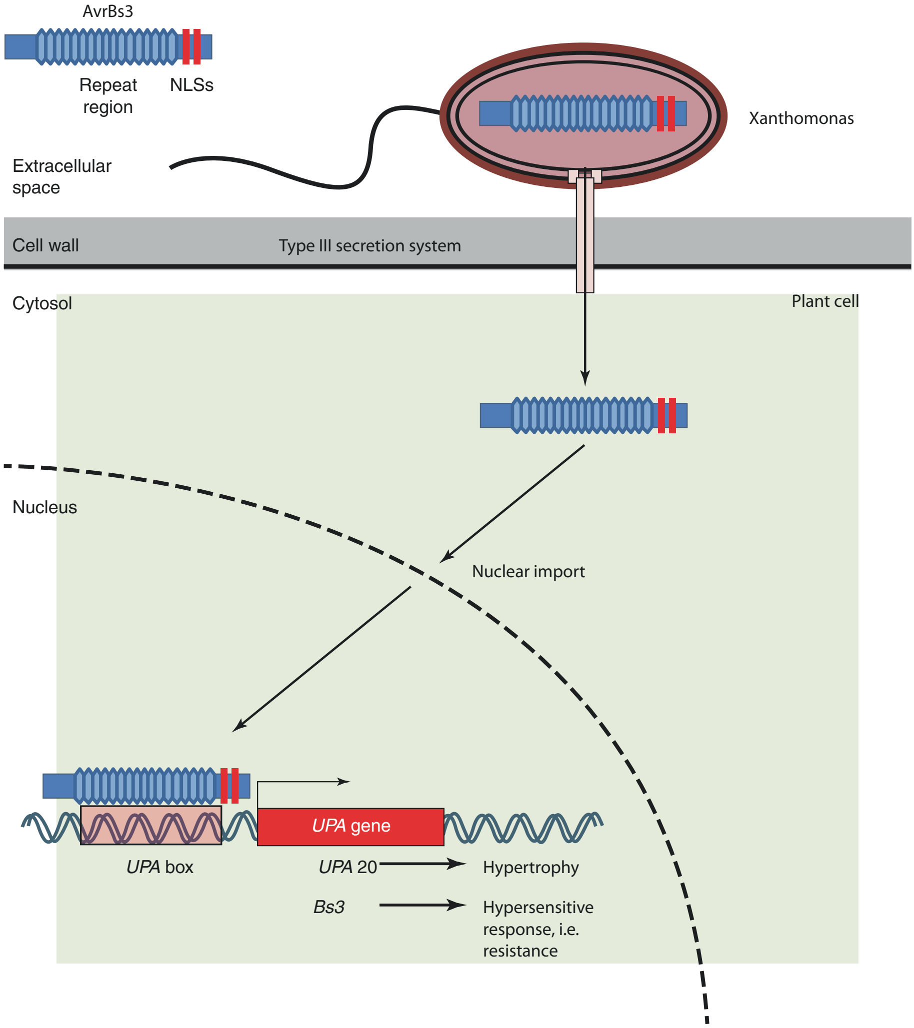


Fig. 8.2 Interaction between the avirulence gene *avrBs3* and the resistance gene *Bs3*. The bacterial pathogen *Xanthomonas* attacks tomato and pepper cells by injecting effector proteins through the type III secretion system. One of the effectors is avrBs3. It has features of a eukaryotic transcription factor—for example, nuclear localisation signals (NLSs). After entry into the nucleus it activates genes (*UPA* genes, upregulated by AvrBs3) whose activity causes disease. The matching tomato resistance gene, *Bs3*, which is present in some tomato cultivars, carries similar promoter elements (*UPA* box). However, *Bs3* activation triggers a cell death programme. The cell undergoes the hypersensitive response, and *Xanthomonas* cannot spread further. (Modified from Kay and Bonas (2009))

Box 8.1: *Agrobacterium tumefaciens*

The gram-negative soil bacterium *A. tumefaciens* is the causal agent of crown gall disease, which affects predominantly dicotyledonous species. Infection by *A. tumefaciens* leads to the formation of tumours—that is, the rapid proliferation of cells and the growth of undifferentiated tissue. Tumours are induced by **transfer DNA** (**T-DNA**), which the bacterium uses to transform the genome of a plant cell. The T-DNA carries genes encoding enzymes involved in the synthesis of the **phytohormones auxin and cytokinin**. Also, the T-DNA leads to the synthesis of opines, amino compounds that *A. tumefaciens* can use as sole carbon and nitrogen source. The emergence of such a favourable habitat for the bacteria requires the stable integration of the T-DNA into the host cell genome. The required machinery is encoded on the tumour-inducing plasmid (Ti plasmid) of *A. tumefaciens*. The *vir* (for *virulence*) genes on the Ti plasmid become activated when *Agrobacterium* senses the presence of plant metabolites such as acetosyringone. These and other phenolic compounds are released by damaged plant cells at a wound site. Products of the *vir* genes synthesise a copy of the T-DNA, transport it into the plant host cell and integrate it randomly into the host nuclear genome (Fig. 8.3).

When the molecular mechanisms underlying the *A. tumefaciens*–mediated gene transfer were elucidated in the 1980s, it was immediately realised that it could be utilised to genetically transform plants with other foreign DNA of interest (Caplan et al. 1983). The T-DNA localised between the so-called right border and left border sequences on the tumour-inducing plasmid (Ti plasmid) can be replaced by any DNA, using standard recombinant DNA techniques. Transformed plant cells do not give rise to tumours anymore but instead express genes encoded by the foreign DNA. A typical plant transformation employing *A. tumefaciens* encompasses the co-cultivation of *A. tumefaciens* cells carrying a modified Ti plasmid with wounded plant tissue (e.g. leaf discs), selection of transformed plant cells—for example, based on co-transformed antibiotic resistance—and regeneration of a whole plant, using tissue culture techniques.

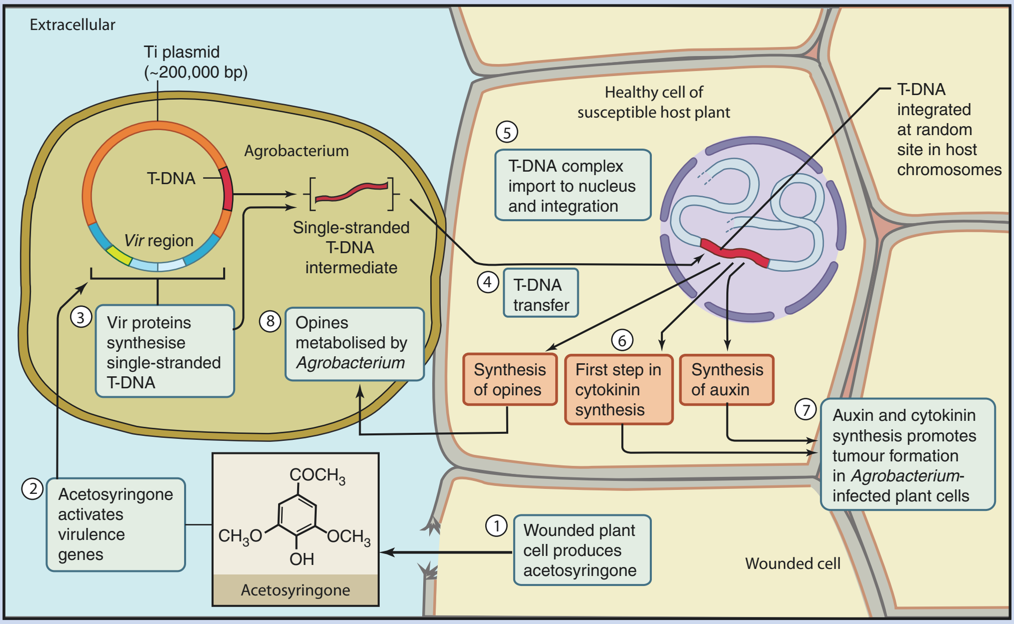


Fig. 8.3 Infection of a plant cell by *Agrobacterium tumefaciens*. (Buchanan et al. 2015)

Although **fungi** and **oomycetes** are unrelated, their infection strategies and growth forms as plant pathogens share several similarities, so they can be described together. An infection starts from a spore adhering to the surface of a plant and the germination of this spore. Biotrophic pathogens form an appressorium (Fig. 8.4). Within this appressorium, pressure builds up, exerting a mechanical force that, together with the activity of secreted enzymes (cutinases, cellulases and pectinases), disrupts the plant cuticle and cell wall. A feeding structure called a haustorium then develops behind an invagination of the plant cell plasma membrane (Fig. 8.4). The plant cell is kept alive but now supplies organic and inorganic nutrients to the invading fungus.

Necrotrophic fungi do not build haustoria. Instead they overpower a plant with non-specific or host-specific toxins and with cell wall–degrading enzymes. The plant cells die and the fungi utilise the dead organic material. An intensively studied potent toxin is fusicoccin, a diterpene synthesised by *Fusarium* species. It causes rapid wilting of exposed plants by constitutively activating the plasma membrane H$^+$-ATPase via the modulation of 14-3-3 proteins. In guard cells this activation prevents the closure of stomata because the cells remain hyperpolarised (Chap. 6, Sect. 6.3).

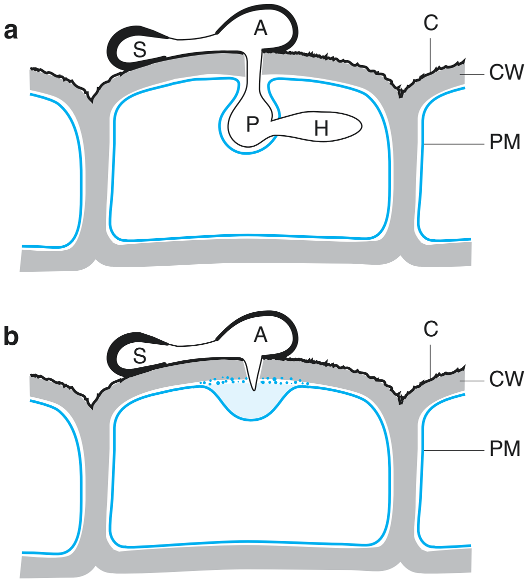


Fig. 8.4 Compatible **a** and incompatible **b** interactions during infection by a fungus. **a** A germinating spore (S) develops a germ tube from which an appressorium (A) is formed. Mechanical pressure building up in the appressorium, together with the secretion of cell wall–degrading enzymes, allows entry of a primary hypha (P) through the cuticle (C) and cell wall (CW). Later, secondary hyphae (H) grow into the host cell. **b** Defence against a fungal infection in a resistant plant. Pathogen recognition triggers rapid wall thickening under the appressorium. As a result the fungus is unable to penetrate the outer wall of the epidermal cell. (After Conrath and Kauss (2000))

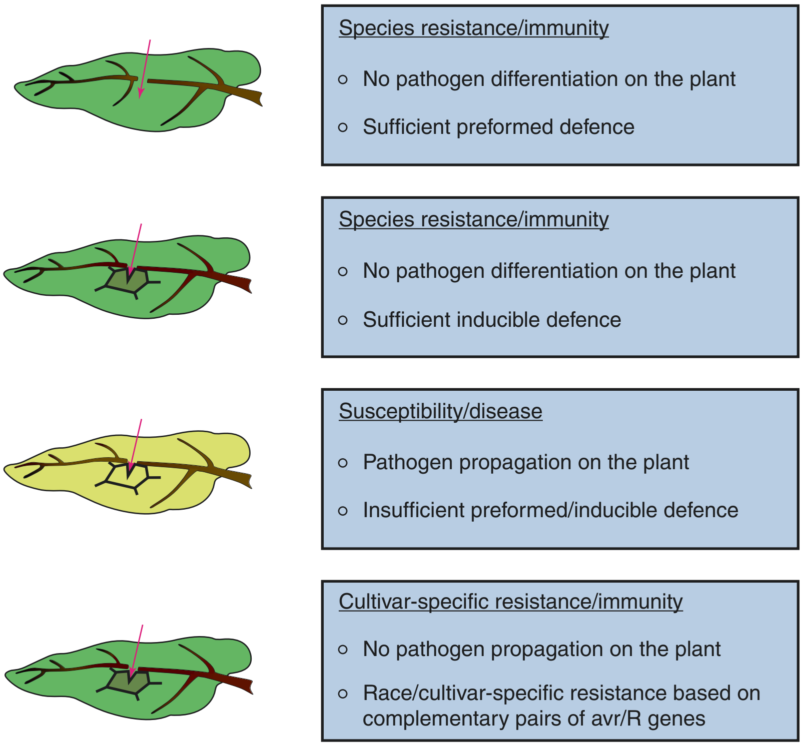
Like bacteria, fungi and oomycetes produce **effectors** to suppress the plant defence response and to disturb plant development or metabolism. The **phytohormone gibberellin** was discovered as a molecule the fungus *Gibberella fujikuroi* uses to trick rice seedlings into abnormal growth. This increases their risk of lodging and thereby falling victim to the fungus. *Ustilago maydis*, a biotrophic pathogen of maize (causing maize smut, characterised by large tumours), secretes more than 100 effector proteins during its attack. One of them is the enzyme chorismate mutase. Following uptake into plant cells it modulates the phenylpropanoid pathway in a way that synthesis of the defence hormone **salicylic acid** (Sect. 8.2.3) is disturbed (Djamei et al. 2011).

Nematodes penetrate plant cell walls with feeding stylets. Movement through root tissue is aided by the release of cell wall–degrading enzymes (Davis and Mitchum 2005). Inside plant cells, feeding tubes are formed that extract nutrients from the host. Molecules secreted by the nematode trigger dramatic changes in the regulation and metabolism of root cells, which eventually give rise to giant cells or symplastically connected cells that form syncytial feeding structures for the nematode.

8.2 Plant Defences Against Microbial Pathogens and Viruses

The interaction between a plant and a pathogen can have two principal outcomes. When no disease is caused, the interaction is **incompatible**. The pathogen is not able to differentiate and reproduce on the plant, because preformed and

Fig. 8.5 Types of plant immunity. (Modified from Nürnberger et al. (2004))



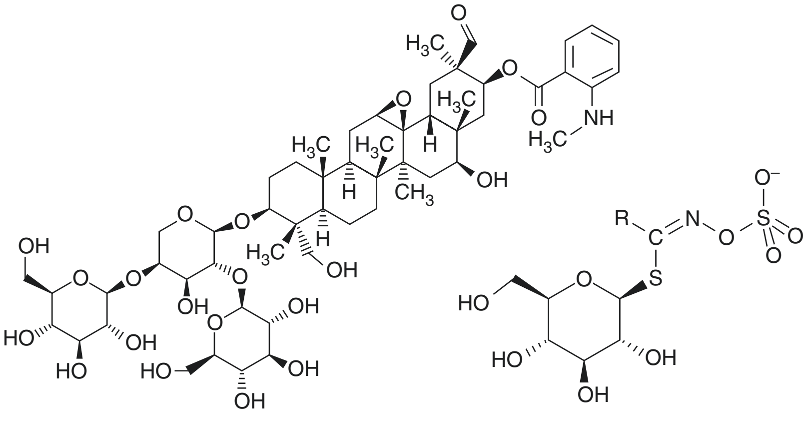
inducible defences prevent this. The plant is **resistant**. Successful colonisation, on the other hand, is referred to as **compatible interaction**. Pathogen propagation occurs at the expense of the host plant. Plant growth is slowed, tissues are damaged and a disease arises. The plant is **susceptible**, the pathogen **virulent**.

Three different scenarios for an incompatible interaction are distinguished (Fig. 8.5):

1. A pathogen cannot develop on a plant, because of efficient preformed defences.
2. None of the races (genotypes) of a pathogen is able to propagate on a particular plant species, because inducible defences restrict the invasion by the pathogen. This is called **non-host resistance**. The pathogens are non-adapted. Most pathogens are non-adapted to most plants. *P. infestans* can devastate potatoes, and barley powdery mildew can colonise barley leaves. Both are harmless to *Arabidopsis thaliana* or most other species, however, because they lack the specific means to overcome the defences of these plants.
3. The resistance is not species wide; it is restricted to certain genotypes (or cultivars in the agricultural context) of a plant species. Some genotypes (races) of a pathogen can propagate on a particular host genotype because they possess effectors that help overcome the plant's defences. Resistance to other races of a pathogen is based on the recognition of effectors and the induction of the hypersensitive reaction. The pathogen is **avirulent** because its effectors trigger rapid plant immune responses. The third scenario has long been recognised and described by the **gene-for-gene hypothesis** (Flor 1971). Genes encoding effectors (traditionally termed **avirulence genes** because their presence can induce defence in some host genotypes) interact with plant **resistance genes** (**R genes**). These encode proteins that recognise effector presence and activate cell death.

8.2.1 Preformed Defences Against Bacteria, Fungi and Oomycetes

Features of a plant's morphology and anatomy serve as a first line of defence against invasion by pathogens. The cuticle and cell walls form



Avenacin A-1

Glucosinolates

Fig. 8.6 Phytoanticipins. Saponins such as avenacin A-1 are found in *Avena sativa* but also in a wide range of other plant species. Glucosinolates are typical of Brassicaceae and other families in the Capparales

mechanical barriers against pathogen ingress. Many potential pathogens never gain access to plant cells and their resources, because they lack the means to overcome these barriers.

A characteristic of plant biology is the synthesis of thousands of **secondary metabolites**—that is, compounds that, in contrast to primary metabolites, are not found in every plant cell and species. Instead, different plants produce different spectra of secondary metabolites, which nonetheless serve important functions in the interaction of a plant with its environment (Bednarek and Osbourn 2009). Because "secondary" might be misunderstood as meaning "of lesser importance", "specialised metabolites" was proposed as an alternative and perhaps more meaningful term (Pichersky et al. 2006). Nonetheless, throughout this chapter the more common term "secondary metabolites" is used.

Another sensible distinction between primary and secondary metabolites is this: primary metabolites are involved in nutrition and essential metabolic processes; secondary metabolites are involved in the interaction of a plant with its environment (Buchanan et al. 2015). A prominent role is **preformed chemical defence** against pathogens. Plants produce a rich cocktail of compounds with antimicrobial activity, which are mostly stored in vacuoles or in specialised cells such as trichomes. Sometimes they are referred to as **phytoanticipins** (Fig. 8.6) and are distinguished from **phytoalexins**, which are synthesised de novo upon pathogen attack (Sect. 8.2.2).

Biotic interactions are regarded as an important driver of the evolution of an extremely rich diversity of secondary metabolites (Dixon 2001), a resource that provides important services to humans as a major source of pharmaceuticals. However, the spectrum of secondary metabolites produced by a given plant species is far from completely known even in the model systems. Also, because most compounds act as ingredients in a complex cocktail, few examples of a directly demonstrated antimicrobial effect exist. **Saponins** are widely distributed amphipathic triterpenoid or steroid glucosides with soap-like behaviour in aqueous solutions. One example is avenacin, found in oats (Fig. 8.6). Saponins provide broad-range protection against microbial pathogens. Mutant oat genotypes lacking saponin synthesis in root epidermal cells become susceptible to *Gaeumannomyces graminis* var. *tritici*, a pathogen that usually cannot infect oat but is able to colonise wheat and barley—two species that do not synthesise saponins. Conversely, successful pathogens have evolved the ability to metabolise saponins. The main tomato saponin, α-tomatine, is metabolised by the tomato pathogen *Septoria lycopersici* via secretion of a tomatinase. This enzyme is crucial for the pathogenicity of *S. lycopersici* (Bouarab et al. 2002). Another well-studied example of preformed chemical defence is the synthesis of glucosinolates (Fig. 8.6), which will be described in more detail as part of a plant's herbivory defence (Sect. 8.3.1).

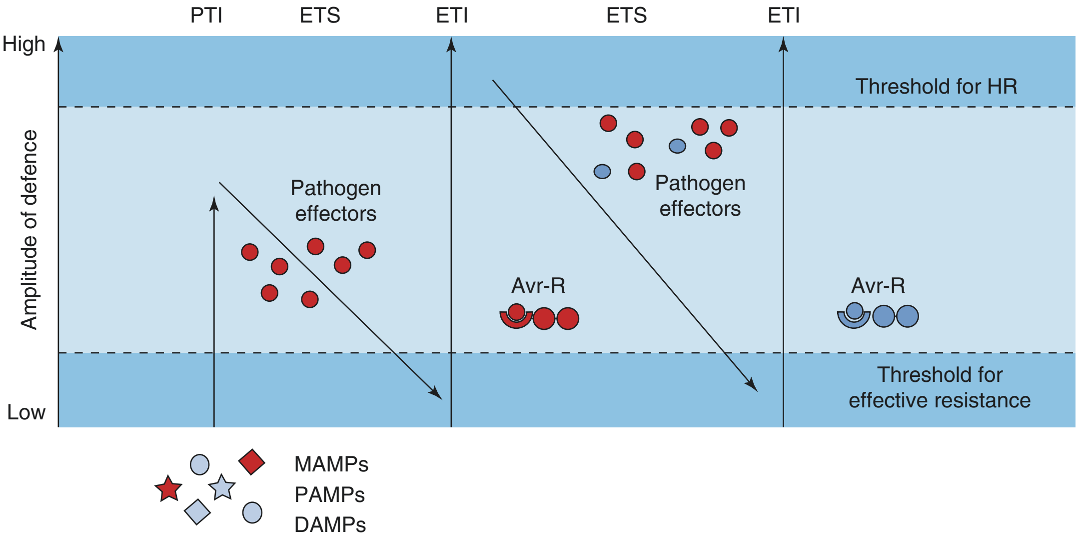


Fig. 8.7 Zig-zag scheme describing plant immunity. Two amplitudes of defence are activated by the recognition of two different types of molecules. The first line of defence depends on the perception of molecules typical of potential pathogens or their activities (microbe-associated molecular patterns (MAMPs), pathogen-associated molecular patterns (PAMPs) and danger-associated molecular patterns (DAMPs)) and is sufficient to prevent colonisation in most cases. The second line of defence recognises effector molecules or the activity of effector molecules produced by specialised pathogens trying to overcome host defences. Activation triggers the hypersensitive response (HR). *PTI* PAMP-triggered immunity, *ETS* Effector-triggered susceptibility, *ETI* Effector-triggered immunity. For more details, see the text. (Modified from Jones and Dangl (2006))

A rare alternative to chemical defence is so-called elemental defence. Metal hyperaccumulating plants apparently fend off pathogens and herbivores by accumulating metals such as Zn or Cd to toxic levels in their leaves (Chap. 7, Sect. 7.5.2).

8.2.2 Inducible Local Defences

Notwithstanding the presence of preformed defences, the outcome of an interaction between a plant and a potential pathogen (scenarios 2–4 in Fig. 8.5) is largely determined by the presence or absence and the activities of specific molecules on the host and pathogen sides. The major components are (1) molecules characteristic of potential pathogens (traditionally termed **elicitors**) and (2) plant receptors that detect such molecules, as well as (3) **pathogen effectors** (see above), and (4) plant proteins, encoded by **resistance genes**, which recognise the presence or activity of these effectors.

A characteristic feature of the plant immune system is **cell autonomy**. Practically every plant cell is capable of mounting defence responses. Thus, many interactions remain highly localised; this is apparent, for instance, as tiny necrotic lesions on leaves, stemming from cell death.

Depending on the severity of a pathogen attack, two principal amplitudes of defence based on two different recognition strategies can be distinguished. This is summarised in the zig-zag scheme of **plant immunity** (Jones and Dangl 2006) (Fig. 8.7), which provides a "unifying theory" integrating the multitude of plant defence responses and plant–pathogen interactions. The first layer fends off all potential foes that have not evolved specialised weapons to attack a particular plant. The respective pathogens are sometimes referred to as **non-adapted pathogens**, and the phenomenon is called **non-host resistance** (Sect. 8.2 and scenario 2 in Fig. 8.5).

The second, more intensive layer of defence becomes activated when a plant cell recognises an enemy equipped with effectors that could potentially overcome the plant's defence. The responses are stronger and faster, and can eventually lead to the hypersensitive reaction—that is, localised cell death (scenario 4 in Fig. 8.5). Inability to respond to the effectors results in susceptibility (scenario 3 in Fig. 8.5).

In cases where preformed defences are not sufficient to completely prevent the activity of a potential pathogen, the first layer of inducible defence, the **innate immunity**, becomes active. Plant cells respond to the presence of a potential foe with the induction of various defence mechanisms. Antimicrobial compounds (**phytoalexins**) are synthesised, cell walls are locally reinforced and defence proteins such as enzymes (e.g. chitinases) to attack microbial cell walls are produced.

Plants do not only constitutively store a wide range of secondary metabolites that are disadvantageous for potential pathogens coming in contact with these molecules (see preformed defence and phytoanticipins, Sect. 8.2.1 and Fig. 8.6). In addition, the recognition of a potential threat triggers the de novo synthesis of compounds with antimicrobial activity against a broad spectrum of fungi, oomycetes and bacteria. Collectively they are termed **phytoalexins** (Greek *alekein* = "to fend off") (Ahuja et al. 2012). The molecular mechanisms underlying their toxicity are largely unknown. Phytoalexins comprise a heterogeneous group of metabolites from different classes of secondary plant products. The predominant ones are **isoprenoids**, **flavonoids** and **stilbenes**. Examples include the stilbene resveratrol in grapevine and several isoflavonoids (e.g. medicarpin, pisatin) in legumes. Phytoalexin synthesis and exocytotic release are often highly localised at sites of pathogen attack. This is exemplified by vesicles filled with reddish defence compounds accumulating around a fungal penetration site on *Sorghum* leaves (Snyder and Nicholson 1990) (Fig. 8.8). Such localised response requires polarisation of the host cell, movement of particular organelles by the cytoskeleton and targeted secretion (Kwon et al. 2008).

Likewise, cell walls are strengthened locally—for instance, right underneath an attempted penetration site of a biotrophic fungus (Fig. 8.4b). Small papillae are formed by deposition of callose (a β-1,3-glucan) and lignin. Cross-linking of extracellular proteins with the cell wall matrix further reinforces the mechanical barrier to fungal ingress.

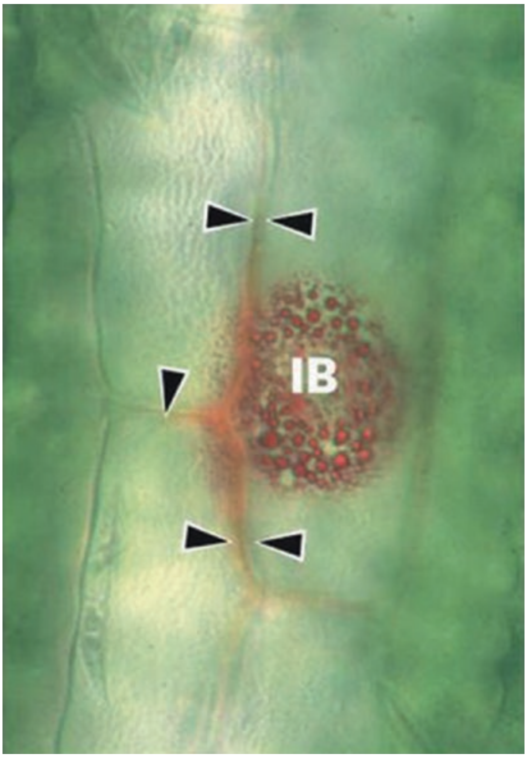


Fig. 8.8 A pathogen attack triggers highly localised defence responses. Phytoalexin accumulation (reddish inclusion bodies (IB)) and cell wall modification (*arrows*) are visible at an infection site on a *Sorghum* leaf. (Snyder and Nicholson 1990)

A third element of the defence response is the synthesis of many **pathogenesis-related proteins** (**PR proteins**) which, contrary to what the name suggests, are in fact proteins thought to have antimicrobial activity. As for a range of other stress-related proteins in plants (see dehydrins in Chap. 6), their actual biochemical function is poorly understood. Exceptions are chitinases and glucanases, which attack fungal cells walls.

Defence responses are dependent on changes in gene activity. Genes encoding PR proteins or enzymes involved in phytoalexin biosynthesis and in the deposition of callose are induced. The responses are mediated by **pattern recognition receptors** (**PRRs**) residing in the plasma membrane of plant cells (Fig. 8.9). PRRs bind **pathogen-associated molecular patterns** (**PAMPs**) or, more generally, **microbe-associated molecular patterns** (**MAMPs**). PAMPs/MAMPs correspond to elicitors

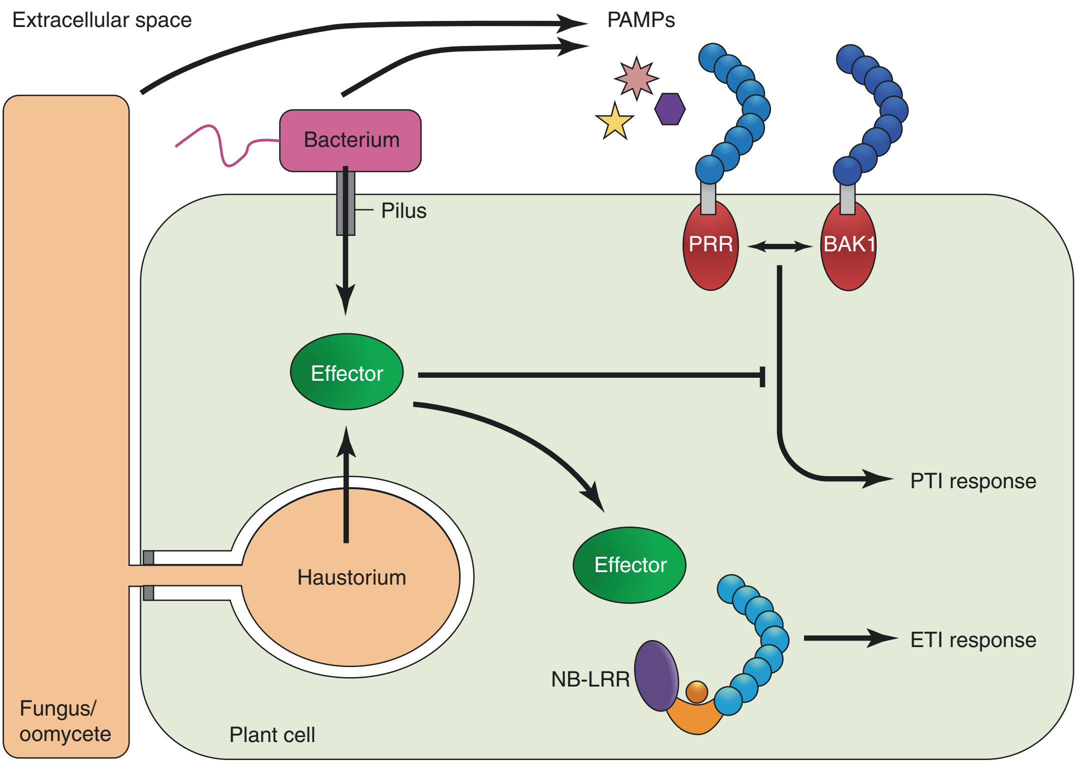


Fig. 8.9 Pathogen-associated molecular pattern (PAMP)–triggered immunity (PTI) and effector-triggered immunity (ETI). Perception of PAMPs (or microbe-associated molecular patterns (MAMPs) or danger-associated molecular patterns (DAMPs)) by pattern recognition receptors (PRRs) and their co-receptors (e.g. BAK1) triggers PTI responses. Specialised bacterial, fungal or oomycete pathogens release effector molecules to suppress PTI responses. Effectors or their activities are recognised by resistance gene products, typically nucleotide-binding domain leucine-rich repeat domain (NB-LRR) proteins. This event triggers ETI responses such as programmed cell death. For the sake of clarity, the plant cell wall is not shown. (Modified from Dodds and Rathjen (2010))

in the older literature. Defence responses elicited by PAMPs/MAMPs result in **PAMP-triggered immunity** (**PTI**) (Figs. 8.7 and 8.9). PAMPs/MAMPs represent molecules that are highly conserved in microbial species but absent from plants. A classic example is flagellin, the major protein of bacterial flagella. Receptor-mediated perception of flg22, a 22–amino acid peptide that is part of flagellin, reliably indicates the presence of flagellated bacteria. Similarly, chitin fragments give away fungal cells in the vicinity because chitin is a major polymer of the fungal cell wall and PRRs recognising chitin fragments are known. A third group of molecules perceived by PRRs are so-called **danger-associated molecular patterns** (**DAMPs**). These are characteristic structures not of microbes but, rather, of microbial activity. Examples are pectin fragments released by cell wall–degrading polygalacturonases of necrotrophic fungi (Boller and Felix 2009).

The number of PRRs per plant species is estimated at around 100–200. Together they constitute an effective **surveillance system** that enables plant cells to sense the extracellular presence of many different potential microbial pathogens. The **innate immunity** based on this surveillance system is mechanistically very similar to animal innate immunity. However, plant cells express far more PRRs than animal cells. This is regarded as one way to compensate for the absence of an adaptive immune system in plants (Dodds and Rathjen 2010).

Activation of PRRs triggers signal transduction events that (1) result in the production

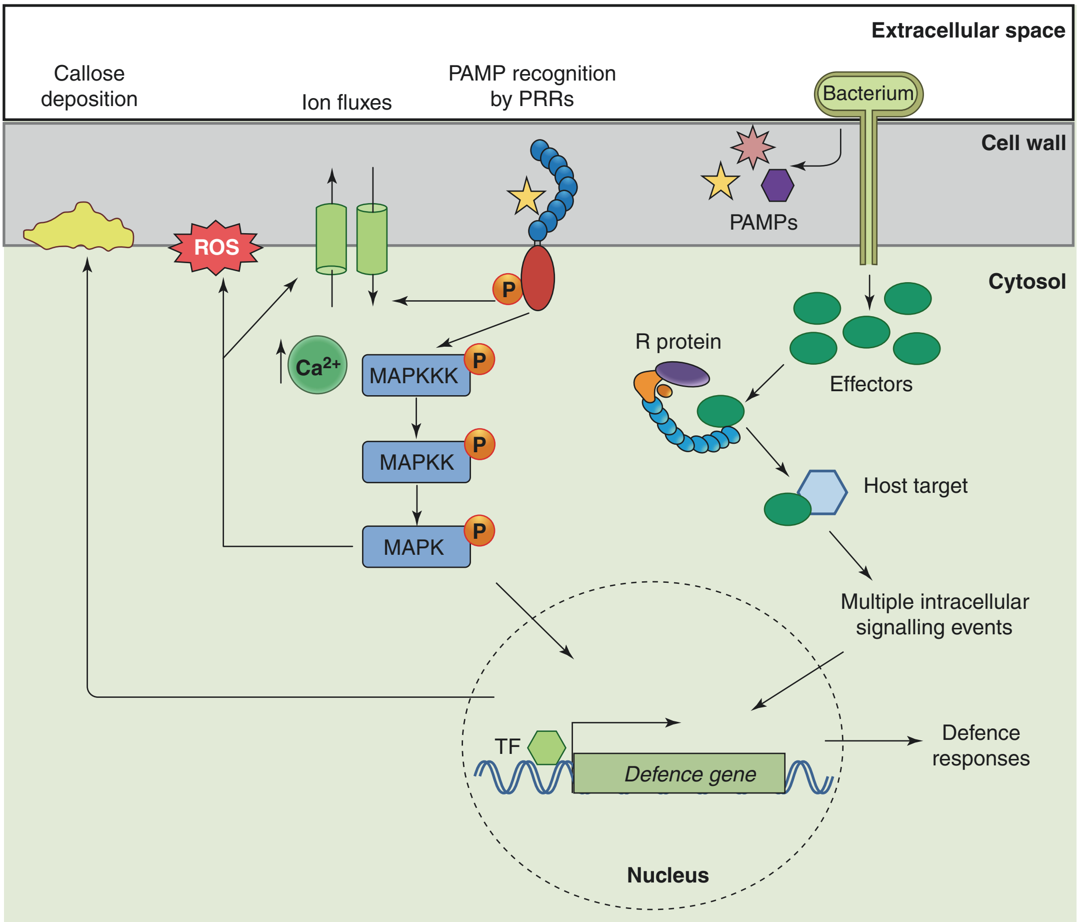


Fig. 8.10 Signal transduction in pathogen-associated molecular pattern (PAMP)–triggered immunity (PTI) and effector-triggered immunity (ETI). PAMP recognition triggers mitogen-activated protein (MAP) kinase phosphorylation cascades, Ca^{2+} spikes, modulation of ion fluxes (plasma membrane depolarisation) and an oxidative burst (reactive oxygen species (ROS) formation). Defence genes are activated and the cell wall is reinforced by callose deposition. Signalling downstream from effector recognition (shown on the *right side* in the scheme) is poorly understood. (Modified from Buchanan et al. (2015))

of reactive oxygen species (ROS) by plasma membrane-localised reduced nicotinamide adenine dinucleotide phosphate oxidases (**NADPH oxidases**) and extracellular peroxidases, causing an **oxidative burst**; and (2) result in altered gene regulation (Fig. 8.10). The oxidative burst has at least three different functions. ROS production in the apoplast supports local strengthening of the cell wall. H_2O_2 can be used as a substrate to cross-link molecules of the cell wall matrix. ROS can also directly damage pathogens. Finally, ROS may serve as signalling molecules and modulate the host cell response.

Transduction of the signal from activated PRRs to ROS-producing enzymes and to transcription factors proceeds via multiple phosphorylation steps. PRRs themselves are receptor kinases. Upon ligand binding they interact with co-receptors and become activated (Fig. 8.10). Ca^{2+} spikes and the activation of mitogen-activated protein kinase cascades (**MAP kinase cascades**) eventually modulate a complex network of transcriptional regulators that ensures an adequate response—that is, a reprogramming of the cellular metabolism, which is adjusted to the severity of the pathogen threat (Tsuda and

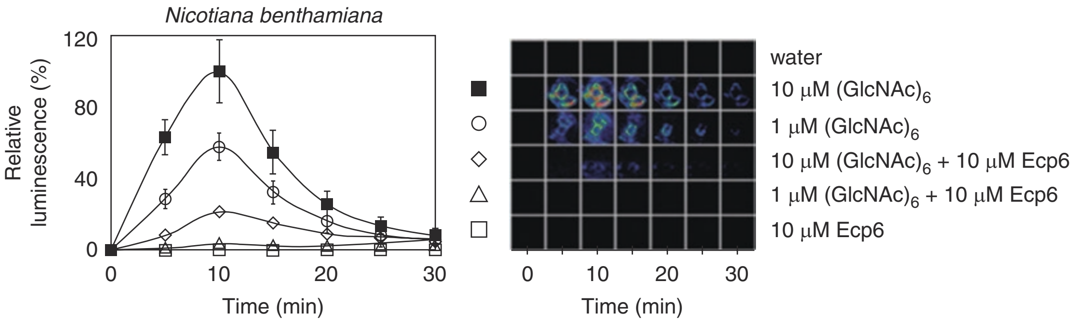


Fig. 8.11 Activity of a fungal effector. The fungal effector Ecp6 is produced by the fungal plant pathogen *Cladosporium fulvum*. It suppresses the recognition of danger-associated molecular patterns (DAMPs) by binding to chitin fragments. An oxidative burst of *Nicotiana benthamiana* cells, visualised as the chemiluminescence of oxidised luminol, upon treatment with fragments of chitin $(GlcNAc)_6$ is shown. (de Jonge et al. 2010)

Somssich 2015). Like all plant stress responses, PTI represents a balancing act to optimise resource allocation between defence and growth.

The second layer of defence is activated when pathogen effectors are recognised. At this level of immunity most of the co-evolutionary dynamics take place because unlike MAMPs/PAMPs/DAMPs, effectors are highly variable and also dispensable—that is, not essential for normal cell functioning (Dodds and Rathjen 2010). Therefore, effector recognition requires large sets of **resistance genes** (**R genes**), which are plant species specific and even genotype specific, while many PRRs are conserved across plant families because they perceive PAMPs, which are widely conserved as well. R gene products mediate the effector perception and the resulting **effector-triggered immunity** (**ETI**; see zig-zag scheme in Fig. 8.7).

As described in Sect. 8.1.2, during infection, plant pathogens synthesise and release up to several hundred effector molecules, which target a variety of sites in a host cell. Successful manipulation of the host defence system by well-documented examples such as avrBs3 (Fig. 8.2) and chorismate mutase results in **effector-triggered susceptibility** (**ETS**; see zig-zag scheme Fig. 8.7). A comparison across many different plant pathogen systems, which is now possible because of genome-wide studies, reveals that in spite of the huge diversity of effector molecules produced by bacteria, fungi, oomycetes or nematodes, the number of host processes that are predominantly targeted is rather small (Mukhtar et al. 2011; Dou and Zhou 2012). The list provides deep biological insight into key processes of defence and pathogenicity. It includes PRR-dependent immune responses, hormonal regulation, secretory processes and cell death programmes. Interference with PTI, for instance, is achieved either by effector proteins that inactivate PRRs directly or by proteins that reduce the concentration of DAMPs. The *Pseudomonas syringae* effector avrPto, for example, directly interacts with the flagellin receptor and other PPRs (Xiang et al. 2008). The *Cladosporium fulvum* effector Ecp6 binds chitin fragments in the apoplast and thereby inhibits activation of the respective PRRs sensing these DAMPs (de Jonge et al. 2010) (Fig. 8.11).

Upon recognition of an effector, a plant cell mounts a strong and rapid response that confers ETI. The most extreme manifestation of this response is the **hypersensitive reaction**, meaning **programmed cell death**, which effectively blocks further spread of an invading pathogen.

ETI is dependent on **R genes**. R genes can confer resistance to fungi, oomycetes, bacteria, nematodes and even viruses. They have been used extensively in crop breeding to achieve resistance against commercially important pathogens. Their molecular nature, however, was not known until 1995. Most R genes encode proteins that share certain structural domains—namely, leucine-rich repeats (LRRs), often involved in intermolecular interactions—and nucleotide-binding (NB) domains. There are, however, intriguing exceptions. The R gene

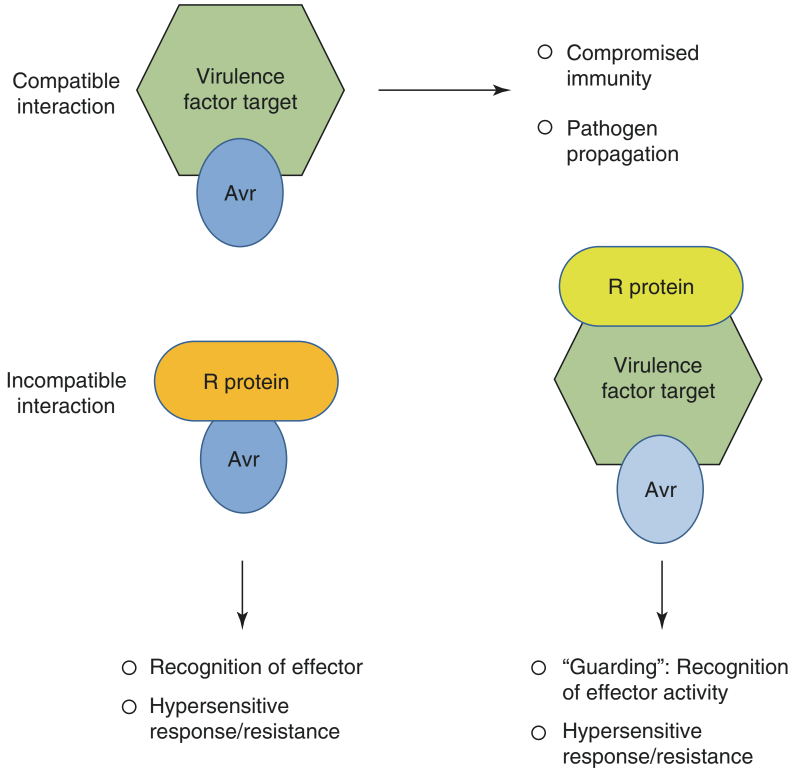


Fig. 8.12 The "guard hypothesis". Resistance proteins (R proteins) recognise either effectors (encoded by *avr* genes) or the modification of critical virulence targets by effectors. Both scenarios trigger a hypersensitive response and confer resistance; the interaction is incompatible. Successful attack on a virulence target compromises immunity and contributes to pathogen propagation (compatible interaction)

Bs3 in pepper "outsmarts" pathogens carrying the effector avrBs3 (Fig. 8.2). When activated, *Bs3* triggers a hypersensitive reaction (Römer et al. 2007). *Bs3* is activated by avrBs3 binding because the *Bs3* promoter carries the same *cis* element that is targeted by avrBs3 to cause disease. In other words, by attacking a plant cell with *Bs3* in its genome, *Xanthomonas campestris* terminates its own infection attempt.

R gene products have two principal functions: recognition of pathogen effectors and triggering of a cell death programme upon activation (Figs. 8.7, 8.9 and 8.10). The **gene-for-gene interaction** between pathogen effectors and host R genes raises the question: How do plants keep up with pathogens in the evolutionary race? Microbial pathogens can evolve new effectors much faster than plants can evolve R genes. Their mutation rate is higher and their generation time much shorter. In fact, in an agricultural context, resistance is often broken by the emergence of new pathogen races (Box 8.2). The adaptive immune system of animals generates a seemingly unlimited number of immune receptors and antibodies to cope with the genetic diversity and rapid evolution of pathogens. Part of the answer for plants lies in the way R gene products recognise effectors. Not all of them directly interact with effectors. As postulated by the "**guard hypothesis**" (Jones and Dangl 2006), many R gene products guard critical virulence targets and recognise not the effector itself but the abnormal modification of a host protein caused by an effector (Fig. 8.12). In this way a particular R gene can sense several different effectors, in some cases even from pathogens as diverse as fungi and nematodes. Structurally unrelated effectors of the fungal pathogen *C. fulvum* and the plant-parasitic nematode *Globodera rostochiensis* both perturb the function of an extracellular protease (Rcr3) that is important for resistance of tomato cells. The R gene Cf2 encodes an immune receptor that guards Rcr3—that is, it senses changes in Rcr3 and confers resistance against genotypes of the fungus and the nematode that express the respective effectors (Lozano-Torres et al. 2012).

Another reason why plants are not overwhelmed in the “arms race” with microbial pathogens is the diversity of R genes, which is driven by the continuous emergence of pathogen effectors. Plant genomes carry large numbers of R genes, many of them organised in clusters facilitating recombination events. R genes are consistently the most polymorphic class of genes in plant genomes. Thus, within a given plant population, hundreds or thousands of R gene variants exist that can sense effector-dependent pathogen attacks. **Genetic diversity** within a population reduces the vulnerability to pathogens.

The second function of R gene products, besides direct or indirect recognition of pathogen effectors (i.e. signalling to activate cell death programmes (Figs. 8.9 and 8.10)), is molecularly poorly understood.

Box 8.2: Ug99 Stem Rust on Wheat

Among the important traits of elite bread wheat varieties that made the dramatic yield increases of the “**Green Revolution**” possible was resistance against wheat stem rust, caused by the basidiomycete *Puccinia graminis*. Wheat stem rust can cause severe losses. Resistance was introduced into wheat cultivars by plant breeders around Norman Borlaug, who was awarded the Nobel Peace Prize in 1970 for his contributions to the Green Revolution. Because pathogens constantly evolve, new races can arise that escape the effects of prevailing resistance genes. In 1999 a highly virulent new race of *P. graminis* was discovered (named Ug99 because it was first detected in Uganda), which potentially threatens most of the currently cultivated wheat varieties in the world. Initially inspired and coordinated by the late Norman Borlaug, global efforts were launched to contain Ug99’s spread and to protect the world’s wheat cultivation against this threat. In 2013 the cloning of resistance genes against Ug99 was reported. These genes were found in the wild wheat relative *Aegilops tauschii* (Periyannan et al. 2013) and in *Triticum monococcum* (Saintenac et al. 2013). These genes—Sr33 and Sr35, respectively—can now be transferred into elite cultivars either via more time-consuming conventional breeding or via genetic engineering to confer Ug99 resistance (Fig. 8.13).

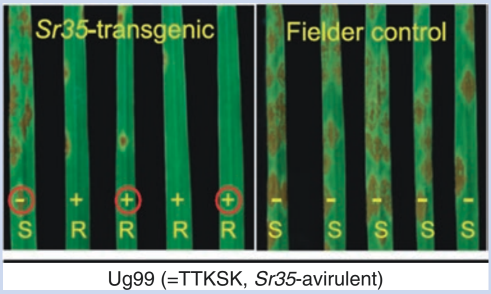


Fig. 8.13 Ug99 resistance conferred by transforming wheat with the resistance gene Sr35. Infection symptoms on seedlings of transgenic lines segregated for the resistance transgene. Plants carrying the transgene (+) were Ug99 resistant (R), plants without the transgene (−) were susceptible (S). (Saintenac et al. 2013)

8.2.3 Inducible Systemic Resistance

Besides the cell-autonomous plant immune system there is an additional layer of defence. Cells under attack do not only mount a local response; they also send out signals that activate defence in remote tissues and organs. This phenomenon is called **systemic acquired resistance** (**SAR**) (Fig. 8.14). SAR can last for weeks or months and protect a plant from secondary infection—that is, render an otherwise compatible interaction incompatible. SAR is non-specific in the sense that (1) any potential pathogen (avirulent or virulent) triggers SAR, and (2) protection is achieved against a wide range of pathogens. Furthermore, SAR prepares a plant to respond more rapidly and strongly to subsequent pathogen attack. The plant becomes primed for defence (**defence priming**).

Fig. 8.14 Systemic acquired resistance of cucumber plants to the anthracnose fungus *Colletotrichum lagenarium*. One cotyledon of the plant on the *left* was infected with spores of the fungus. It is suffering severely from necrosis. The plant on the *right* was left untreated. One week later, 20 drops of a spore suspension were placed on a main leaf of both plants. The leaf of the plant on the *left* remained fully healthy, as it had developed systemic resistance. The leaf of the plant on the *right*, which experienced no "immunisation", exhibited necrotic areas at the positions of every drop of spore suspension. (Conrath and Kauss 2000)

The main changes in systemic tissue involve the synthesis of **PR proteins** (Fig. 8.15). Unlike ETI, SAR does not involve cell death. Most of the PR proteins are either secreted into the apoplast (i.e. into the space colonised by potential pathogens) or stored in vacuoles. As mentioned above, the actual molecular mechanisms explaining PR protein–mediated protection are barely known. PR protein function is nearly impossible to dissect genetically, because many proteins act in concert and *PR* genes are often clustered in plant genomes, so multiple knockout mutants are practically impossible to obtain (Fu and Dong 2013).

The trigger for SAR is local ETI—that is, the response of cells under direct attack by a pathogen. ETI leads to an increase in the concentration of the defence hormone **salicylic acid**. This in turn elicits the generation of phloem-mobile signals, whose molecular nature has not been unequivocally shown (Fig. 8.16). Several compounds are candidates, among them azelaic acid (Jung et al. 2009) and pipecolic acid (Návarová et al. 2012).

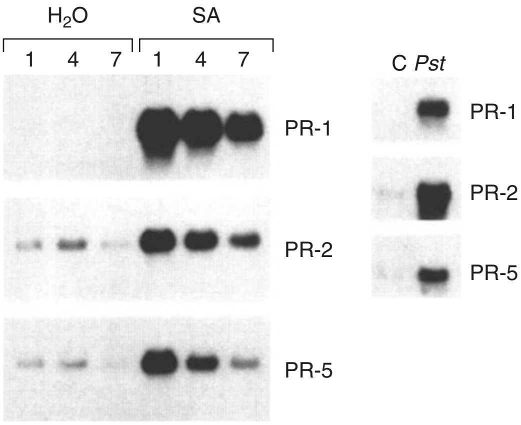


Fig. 8.15 Systemic induction of pathogenesis-related (PR) genes. Treatment of *Arabidopsis thaliana* leaves with the defence hormone salicylic acid (SA) or inoculation with *Pseudomonas syringae* strongly activates *PR* gene (PR-1, PR-2, PR-5) expression. Expression of *PR* genes was analysed by northern blot hybridisations. *C* control, *Pst Pseudomonas syringae*. (Uknes et al. 1992)

Arrival of the signals in the systemic tissue again results in an increase in the salicylic acid concentration, albeit smaller than that in the local tissue. Salicylic acid is perceived by different

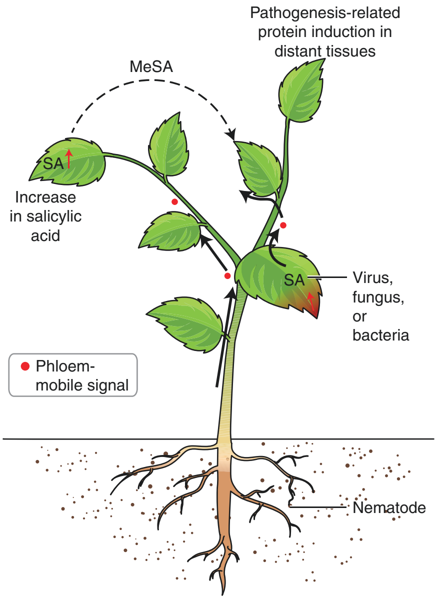


Fig. 8.16 Systemic acquired resistance. *MeSA* Methylsalicylate. (Buchanan et al. 2015)

receptors locally and systemically. In cells under direct pathogen attack, salicylic acid positively regulates cell death, while in systemic tissue it suppresses cell death and sets signalling cascades in motion that result in *PR* gene activation and SAR.

8.2.4 Defence Against Viruses via Gene Silencing

Defence against the systemic spread of viruses is conferred not only by the R gene–mediated **hypersensitive response** or by inducible systemic resistance; in fact, the main immune system against viruses in plants is based on **gene silencing**. For decades it has been observed in the field and under laboratory conditions that virus-infected plants develop resistance against a second infection by the same virus or a closely related virus. Weeks after an infection the newly developed leaves remain symptom-free even when inoculated with virus particles (Soosaar et al. 2005). This phenomenon, called "recovery", resembles the **immunisation** of humans or other mammals through treatment with an inactivated virus or a harmless related virus. We now know that a gene-silencing mechanism is behind the recovery from virus infection (Baulcombe 2004). This silencing targets virus-derived double-stranded RNA (dsRNA), which also explains why resistance covers not only the originally infecting virus but also viruses with a genome that is similar in sequence.

Most plant viruses are **RNA viruses**—that is, they carry genetic information as either single-stranded RNA (ssRNA) or double-stranded RNA instead of DNA. Different processes during the infection process give rise to the existence of dsRNA even when the genome is DNA or ssRNA. Replication catalysed by RNA-dependent RNA polymerases involves the formation of double-stranded intermediates. ssRNA can fold back and base pair into dsRNA. Bidirectional transcription of viral DNA can produce overlapping transcripts (Fig. 8.17). The presence of dsRNA triggers cleavage into **small interfering RNAs** (**siRNAs**) with a length of 21–24 nucleotides. The cleavage is catalysed by endonucleases called Dicer-like. Discovery of siRNAs in virus-infected plants was a major step in unravelling the existence of a complex world of regulatory small RNAs (Hamilton and Baulcombe 1999). One of the strands of the siRNA is then loaded onto another endonuclease, Argonaute (AGO), which is part of the so-called RNA-induced silencing complex (RISC). RISC targets RNA similar in sequence to the siRNAs and causes its degradation, thereby inhibiting replication or transcription of viral RNA. An alternative silencing mechanism is the sequence-specific **methylation of DNA** directed by siRNA. This mechanism is important for resistance against DNA viruses.

The protection of newly developed leaves requires the spreading of the RNA silencing throughout the plant. The action of RNA-dependent RNA polymerases on single-stranded viral RNA results in a strong amplification of the siRNAs. They can move through plasmodesmata and the phloem. In receiving cells they then trigger RNA-dependent RNA polymerases to produce siRNAs (Fig. 8.18). Viruses in turn have independently evolved a variety of proteins that suppress dsRNA-dependent virus resistance by interfering with components of the RNA silencing pathway. For example, suppressor protein p19, encoded in the genome of the tomato bushy stunt virus, binds to siRNA and prevents its integration into

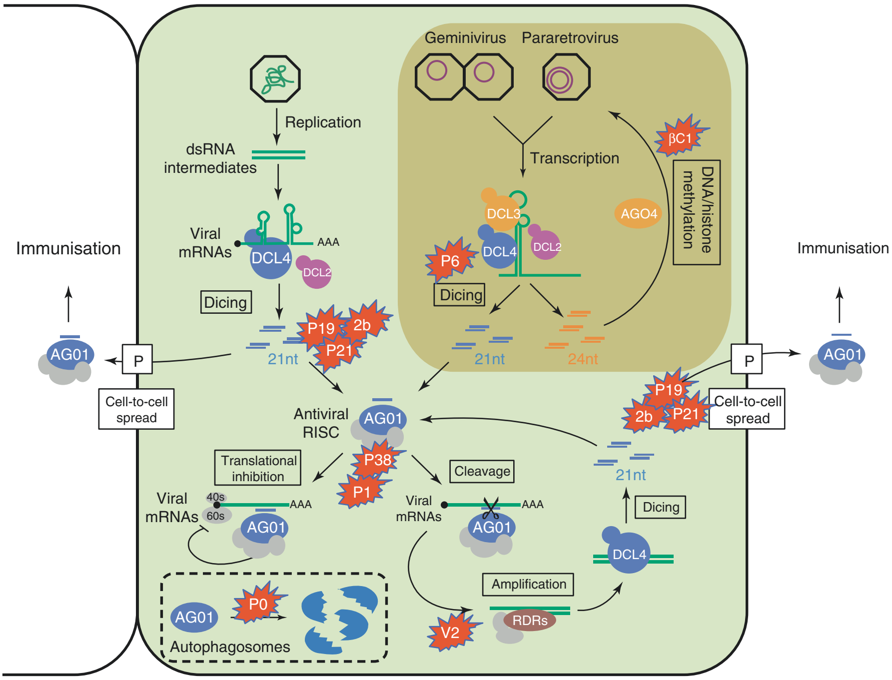


Fig. 8.17 Virus-induced gene silencing. The presence of double-stranded RNA (dsRNA) during the replication of viral genomes triggers processing by RNase-like plant enzymes (Dicer and Dicer-like (DCL)). The resulting small RNAs are loaded into Argonaute (AGO)-containing RNA-induced silencing complexes (RISCs) to guide translational inhibition and/or slicing of viral RNA. The virus-derived small RNAs have the potential to spread through plasmodesmata to neighbouring cells, thereby activating a systemic antiviral defence (= immunisation). On green background the RNA silencing triggered by RNA viruses is depicted. Brown background and yellow symbols indicate the additional defence against DNA viruses via the modification of their DNA genomes (methylation of DNA or histones) by small RNAs. *Red symbols* indicate viral suppressors of RNA silencing, produced by viruses to counteract the antiviral defence of the plant. *P* plasmodesmata. (Incarbone and Dunoyer 2013)

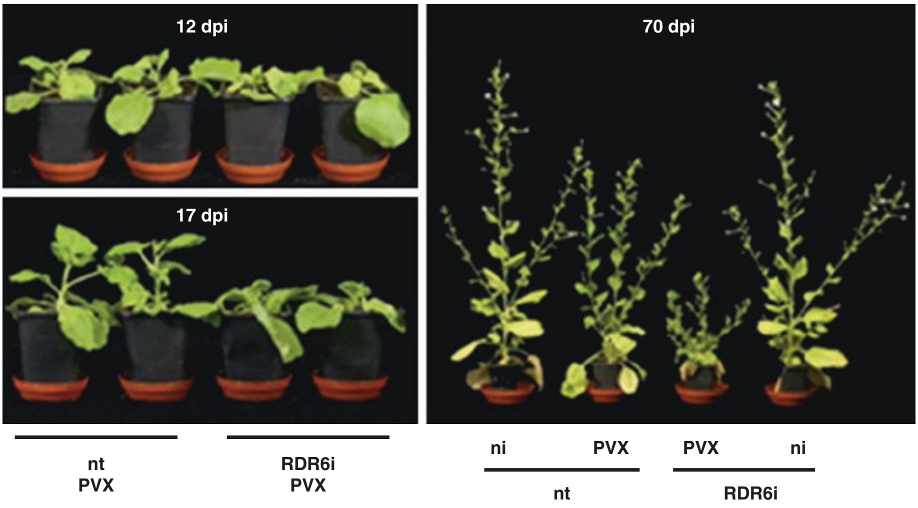


Fig. 8.18 Spreading of gene silencing confers resistance against viruses. Non-transformed *Nicotiana benthamiana* plants (nt) and plants with strongly reduced expression of the RNA-dependent RNA polymerase RDR6 (RDR6i) were inoculated with potato virus X (PVX). RDR6 is required for the response of cells to the systemic silencing signal. Stunting of RDR6i plants compared with nt and non-inoculated plants (ni) indicates loss of virus resistance. *dpi* days post infection. (Schwach et al. 2005)

RISC. Thus, the corresponding viral RNAs can no longer be targeted for degradation (Fig. 8.17).

8.3 Herbivory

Insects represent the most species-rich group of organisms, and a large number of them (an estimated one million species or more) are herbivorous. Collectively they are referred to as **plant pests**. Three categories of plant pests can be differentiated. Insects such as caterpillars and leaf beetles chew on leaves and other plant organs (Fig. 8.19). They cause the most significant physical damage and tissue loss. Piercing–sucking insects (e.g. thrips and mites) feed on plant cell content and cause comparatively little loss of plant biomass. Aphids and whiteflies are examples of phloem-feeding insects. They cause very little physical damage but can be dangerous to host plants as vectors for viruses (Sect. 8.2).

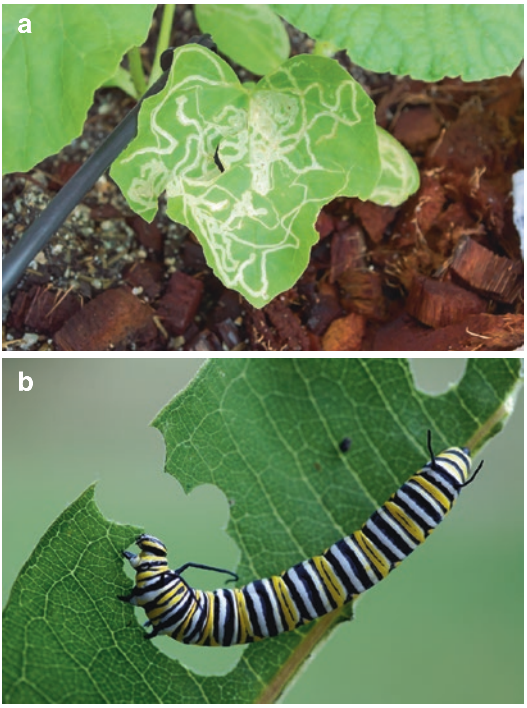


Fig. 8.19 Insect herbivores. **a** Feeding tunnels of leaf miners (Photo: copyright obtained from Shutterstock). **b** Monarch (*Danaus plexippus*) caterpillar feeding on a leaf of milkweed (*Asclepias syriaca*). (Photo courtesy of the National Science Foundation, USA)

A second fundamental distinction, in addition to the feeding style, is that between **generalist herbivores** (which do not show much preference for certain plant species) and **specialist herbivores** (which seek particular groups of plants as food source). Specialisation is a consequence of the ability these insects have evolved to overcome the defences typical of individual plant families such as the Brassicaceae (Sect. 8.3.1).

In spite of the abundance of herbivorous insects with their need to access the resources provided by photosynthesis, damage on plants is usually limited. Constitutive and inducible defences of plants act as effective barriers to the consumption of plant tissue by herbivores. While the discussion in this chapter focuses on insect herbivores, it should be noted that principally these defence mechanisms effectively restrict damage by vertebrate herbivores as well. Constitutive defences include morphological features such as thorns and trichomes. However, plant herbivore defence is predominantly chemical (Mithöfer and Boland 2012). Low molecular weight compounds and proteins act as feeding deterrents or as toxins with direct inhibitory effects on insect growth and fitness. Molecules of chemical defence either are preformed and stored or are synthesised in response to the presence of feeding insects. Similar to pathogen defence, the inducible defence can be local and systemic.

An additional layer of herbivore defence is indirect defence (Fig. 8.20) (Heil 2008). Many plant secondary metabolites or their respective breakdown products are volatile and influence a plethora of organisms in the ecological communities around a plant. It is now well documented that organisms from other trophic levels can be attracted by plant volatiles. For instance, parasitoids of attacking specialist herbivores find their hosts with the help of plant-derived cues. Thus, the emission of volatiles results in a plant's protection by the enemies of its enemies. A second mode of indirect defence relies on rewards (e.g. extrafloral nectar) provided by the plant for predators of herbivores.

8.3.1 Constitutive Defences

Plants rely heavily on chemical defences against herbivores. As discussed in Sect. 8.2.1, plants produce a plethora of **secondary metabolites**. More than 200,000 different chemical structures have been identified and presumably many more exist in nature. Per plant species, several thousand of these metabolites can be expected. A major biological role is protection against herbivore attack.

The major compound classes implicated in herbivore defence are **alkaloids**, **phenolic compounds**, **terpenoids** (including steroids), **cyanogenic glucosides** and **glucosinolates** (Mithöfer and Boland 2012) (Fig. 8.21). Their protective function can be due to toxicity, anti-digestive effects or the fact that they make a plant tissue unpalatable for herbivores. The modes of action or target sites in the herbivores, however, are barely understood at the molecular level. The few existing examples illustrate principal mechanisms such as interference with neurotransmission, inhibition of metabolic processes or disruption of signal transduction pathways. A negative effect of toxic compounds on the producing plant—that is, self-intoxication—is usually prevented by storage in vacuoles. Furthermore, many defence compounds are stored in an inactive form. It is only after mechanical damage has caused contact with processing enzymes localised elsewhere in the cell or in different cells that the active compounds are released (see cyanogenic glucosides and glucosinolates below, Fig. 8.25).

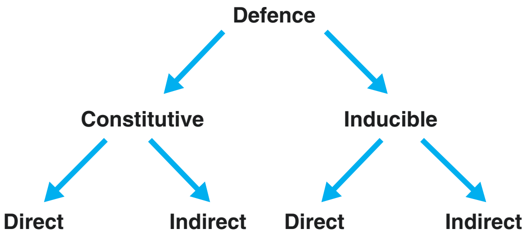


Fig. 8.20 Layers of herbivore defence

About 20% of all plant species produce **alkaloids**—N-containing metabolites synthesised from various amino acids. Many alkaloids are known as potent toxins, effective against both arthropods and vertebrates. Modes of toxicity vary. Some alkaloids affect the nervous system. For example, caffeine (an alkaloid of *Coffea arabica* and many other plant species) can have a paralysing effect on insects by inhibiting

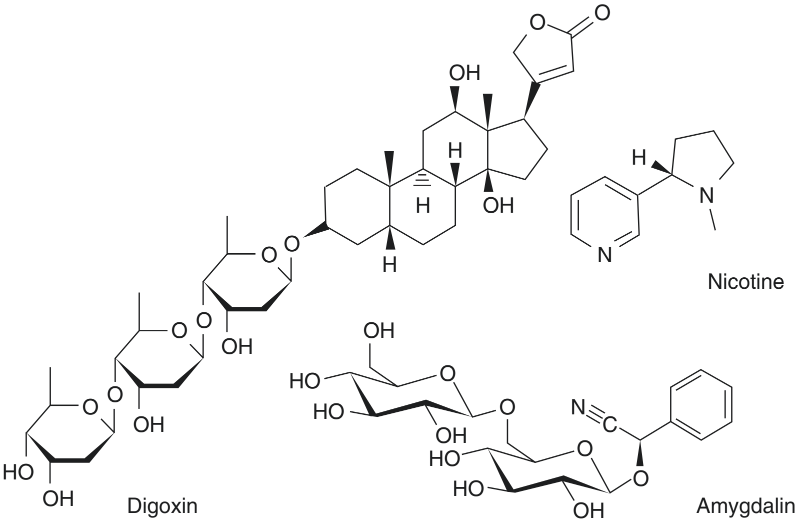


Fig. 8.21 Typical secondary metabolites with herbivore defence function. The steroid digoxin is a cardiac glycoside. It was isolated from the foxglove plant, *Digitalis lanata*, and is used as a treatment for various heart conditions because of its inhibitory effect on Na^+-/K^+-ATPases. Amygdalin is a cyanogenic glucoside that releases hydrogen cyanide. The alkaloid nicotine is synthesised in tobacco plants as a feeding deterrent and defence compound

phosphodiesterase activity at synapses. Another famous example of a toxic alkaloid with a defence function is nicotine (Fig. 8.21). Nicotine is produced in the roots of *Nicotiana tabacum* and transported via the xylem to leaf cells, where it is stored in vacuoles. In insects it inhibits abundant postsynaptic receptors, the nicotinic acetylcholine receptors, thereby affecting control over muscle movement. Nicotine can, in addition, act as a deterrent. Using transgenic *Nicotiana attenuata* plants with blocked nicotine biosynthesis, it was shown that nicotine in floral nectar reduces nectar robbery and at the same time modulates the behaviour of pollinators in a way that increases reproductive success. Hummingbirds feeding on nicotine-containing nectar are discouraged from staying too long at any one flower by the unpleasant taste of nicotine. This results in more cross-pollination of tobacco plants and thereby promotes **genetic diversity** (Kessler et al. 2008).

Phenolic compounds (or phenolics) comprise a huge and chemically diverse group of metabolites sharing an aromatic ring with at least one hydroxyl group. They are found in all plant groups and have a wide range of functions—for example, as major constituents of plant cell walls (lignin, suberin), as flower colours (anthocyanins) or as ultraviolet protectants (flavones, flavonols). Many phenolics act as toxins or antifeedants. **Tannins** are synthesised by the majority of plant species. In the leaves of many woody dicots they accumulate to concentrations of up to 10% of dry weight (Barbehenn and Constabel 2011). Two major types are distinguished: hydrolysable tannins are polymers of simple phenolics and sugars and are localised mainly in cell walls; condensed tannins are formed by the

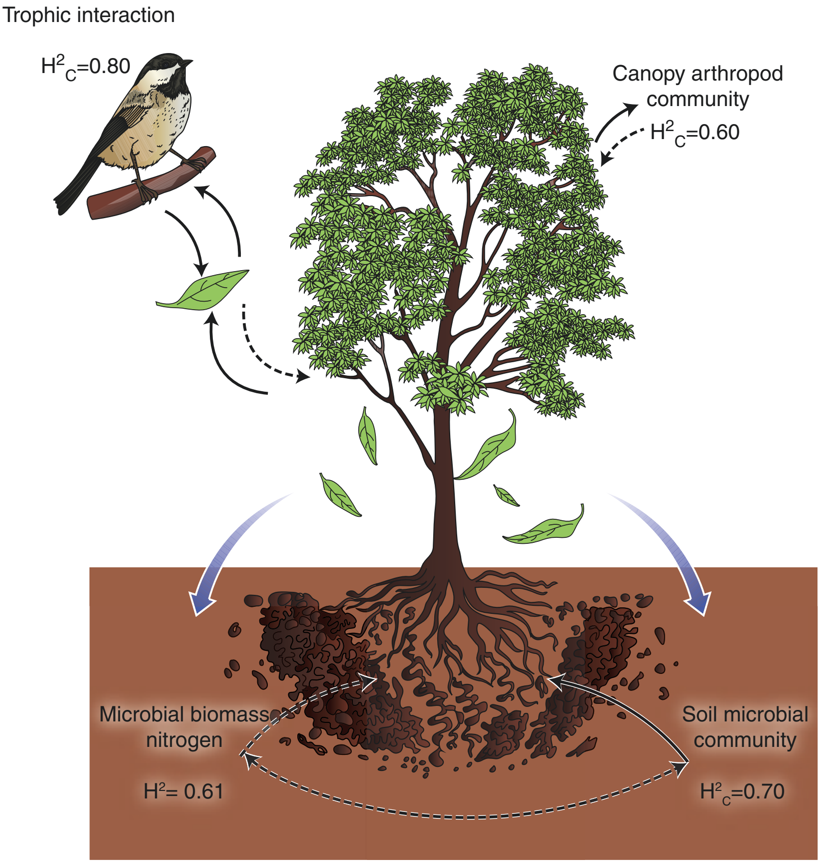


Fig. 8.22 Community phenotypes of poplar trees. The composition of communities living on and around a *Populus angustifolia* tree are strongly influenced by the genotype of the poplar individual, as determined in common garden experiments. This is apparent from the high degree of heritability (H^2 and H^2_c)—that is, the large proportion of phenotypic variance attributable to genetic variance. One of the genetically determined variable traits is the content of hydrolysable tannins. (Whitham et al. 2008)

polymerisation of flavonoids and are stored in vacuoles. Tannins can protect plants because they act as strong feeding deterrents for invertebrates and vertebrates. Beavers, for instance, prefer low-tannin poplars to high-tannin poplars. The toxic effects of tannins are not understood in molecular detail and are thought to be due either to non-specific interaction with proteins or to pro-oxidant activities that result in oxidative stress in the gut of herbivorous insects. Overall, tannins can serve as an example of the lack of direct evidence as to the exact activity and effects of compounds widely implicated in chemical defence. In the absence of clearly defined genotypes that differ only in the molecules in question, it is difficult to infer the actual consequences of these molecules for the interaction of a plant with its herbivores. Such ecological research greatly benefits from genetic modification, as demonstrated by the nicotine example described above (Kessler et al. 2008).

Nonetheless, studies on tannins in poplar were among the first to illustrate concepts of community or **ecosystem genetics** (Whitham et al. 2006). For poplars differing in a **quantitative trait locus** (**QTL**) controlling total condensed **tannin** concentrations, it was found in common garden and field experiments that a variation in one trait (tannin concentration) has far-reaching consequences for the communities living around such a **foundation species**. For instance, the composition of arthropod communities and soil microbial communities is associated with the variation in condensed tannins controlled by this one QTL. Thus, one can refer to “community phenotypes” of individual tree genotypes. These phenotypes show considerable heritability (Whitham et al. 2008) (Fig. 8.22).

Terpenoids represent another major class—with over 30,000 known structures in fact the largest class—of plant secondary metabolites. Terpenoids are derived from five carbon isoprene units. Besides the terpenoids that are essential players in plant biology as **phytohormones** (abscisic acid, gibberellins, brassinosteroids, cytokinins) or **pigments** (carotenoids), thousands of terpenoids are involved in plant–animal interactions, albeit with less defined functions for individual molecules. Terpenoids contribute to both direct and indirect defences. Many smaller terpenoids (monoterpenes, sesquiterpenes) such as linalool and α-farnesene are main components of **plant volatiles**. Plant volatiles are often released upon herbivore attack, differ in their composition from the blend emitted before herbivory and can therefore attract parasitoids and predators of plant pests. Since the first reports on the attraction of parasitic wasps to maize plants emitting terpenoids in 1990 (Turlings et al. 1990) (Fig. 8.23), many more corresponding examples have been documented. Even the transfer of the

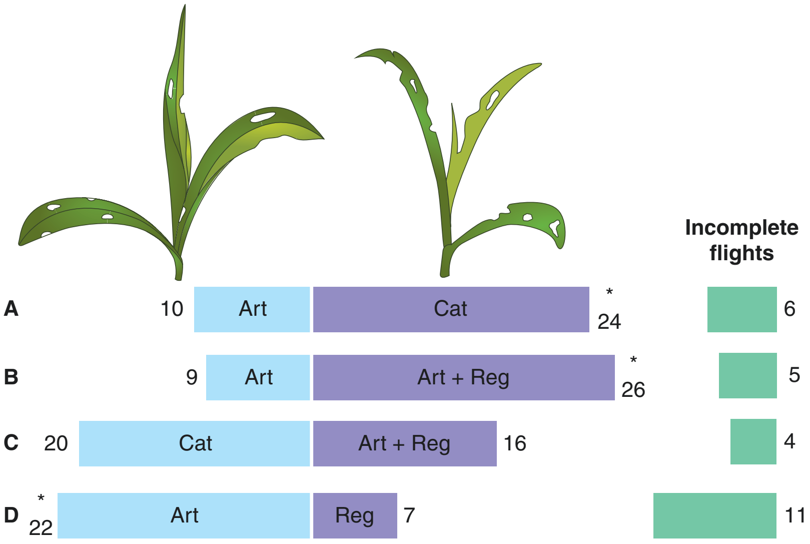


Fig. 8.23 Plant volatiles enable indirect herbivore defence. Choice experiments with parasitic wasps showed they prefer maize plants with caterpillar damage (Cat) over maize plants with artificial damage (Art) (A). Artificial damage treated with regurgitant (Art + Reg) (B, C) was nearly as attractive as caterpillar damage. Total numbers of flights are given with each bar. Asterisks indicate significant differences. (Turlings et al. 1990)

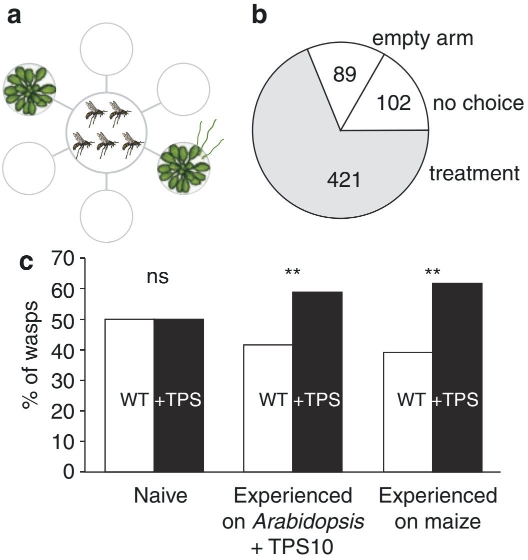


Fig. 8.24 Attraction of herbivore parasitoids by a volatile defence signal. *Arabidopsis thaliana* plants transformed with a terpene synthase (TPS10) produce volatile sesquiterpenes normally released by maize plants. Experienced individuals of the parasitic wasp *Cotesia marginiventris* prefer transgenic *A. thaliana* plants to wild-type plants. Transgenic TPS10 sesquiterpene–releasing *Arabidopsis* and wild-type plants were placed in two arms of a six-arm olfactometer **a** to test the attraction of parasitoid females **b**. Three groups of parasitoids were tested **c**: naive wasps, wasps with a previous oviposition experience in a host larva in the presence of transgenic *Arabidopsis* emitting TPS10 sesquiterpenes, and wasps with a previous oviposition experience in a host larva feeding on maize. **Significant preference ($p < 0.01$) for the odour of the transgenic *A. thaliana.* (Schnee et al. 2006)

ability to synthesise volatile terpenoids from one plant to another by transformation with a terpene synthase gene is sufficient to guide the choice of herbivore parasites (Fig. 8.24).

Direct defence is mediated, for instance, by the feeding deterrence of terpenoids in essential oils or resins, as well as the terpenoid volatiles emitted by some plants (Unsicker et al. 2009).

Steroids are triterpenes and thus are synthesised from isoprene units too. Among them are not only saponins (Fig. 8.6) but also cardenolides, the so-called cardiac glucosides (Sect. 8.2.1). They inhibit Na^+-/K^+-ATPase and thereby interfere with maintenance of the membrane potential in neurons. Related molecules with a likewise known mode of toxicity are phytoecdysons. They mimic insect hormones such as ecdysone and thereby interfere with developmental processes in insects.

Hydrogen cyanide (HCN) is a classic example of a compound that can be toxic to the producing plants themselves and therefore has to be stored in a conjugated, inactive form. HCN affects mitochondrial respiration by inhibiting the binding of oxygen to cytochrome c oxidase and is thus a non-specific toxin. Many plant species (cassava, almonds, apricots and more than 2500 others) store **cyanogenic glucosides** in their vacuoles. When tissue is damaged by herbivore feeding, the glucosides come into contact with cytosolic glucosidases, the sugar moiety is cleaved off and cyanohydrin is released, which spontaneously or enzymatically is converted to HCN (Fig. 8.25).

A second important class of conjugated defence compounds is the **glucosinolates**—sulphur-containing specialised metabolites typical of the order Capparales. Because Brassicaceae belong to this order and the model species *A. thaliana* belongs to the Brassicaceae, the mechanisms, evolution and diversity of glucosinolate biosynthesis are molecularly better understood than those of most other defence compounds (Box 8.3). Glucosinolates are sometimes referred to as the “mustard oil bomb”. They are synthesised from various amino acids (e.g. methionine, alanine, phenylalanine, tyrosine and tryptophane) and stored in a glycosylated form in vacuoles. Upon tissue damage, glucosinolates come in contact with myrosinases—thioglucosidases that remove the sugar. Myrosinases are present only in a few scattered cells (Fig. 8.25). The aglycones arising from the sugar cleavage are unstable and spontaneously rearrange into a variety of bioactive compounds, including isothiocyanates and nitriles. Isothiocyanates, in particular, are highly reactive and toxic to insects, mammals and many other herbivores. Volatile isothiocyanates are, in addition, known to attract organisms of the third trophic level (i.e. parasitoids of herbivores) and thus contribute to indirect defence (Hopkins et al. 2009). On the other hand, some herbivores specialising in Brassicaceae have evolved the ability to use isothiocyanates as cues for finding their host plant. These multiple roles of glucosinolates are major drivers of **genetic diversity** in the biosynthesis machinery (Box 8.3).

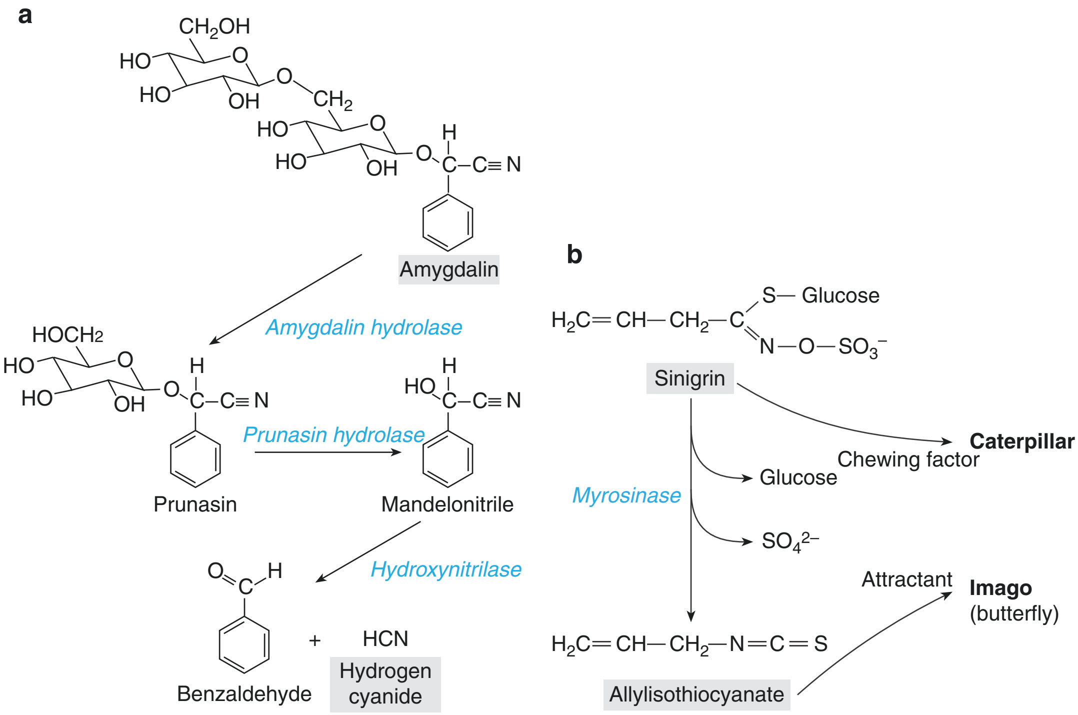


Fig. 8.25 Conjugated defence compounds and release of toxic compounds upon tissue damage. **a** The cyanogenic glucoside amygdalin occurs in seeds and leaves of many plant species. Upon wounding, the glucosidases amygdalin hydrolase and prunasin hydrolase become active. Following cleavage of the sugar moieties, hydroxynitrilases release hydrogen cyanide. **b** When cabbage leaves are damaged, the mustard oil glucoside sinigrin is released from the vacuole and comes into contact with a thioglucosidase (myrosinase). Removal of glucose by myrosinase results in a reactive intermediate, which is converted into volatile allyl isothiocyanate (allyl mustard oil). This compound, which has a pungent flavour to humans, is extremely toxic to many insects. For the specialist herbivore *Pieris brassicae* (the large cabbage white butterfly), the allyl mustard oil is, however, an attractant, which stimulates oviposition by the female butterfly

Besides the amino acids used for protein biosynthesis, plants produce numerous non-proteinogenic amino acids as important primary metabolites (e.g. S-adenosylmethionine) or as secondary metabolites. Most of the latter are specific to particular plant species. Fabaceae tend to produce more non-common amino acids than other plant families. Among the functions of these metabolites is herbivore defence. The best-documented example is canavanine, an important nitrogen storage compound in the seeds of jack beans and other legume species. Canavanine is an arginine analogue, can be incorporated into proteins in place of arginine and is therefore highly toxic to organisms ranging from bacteria to man (Huang et al. 2011).

Constitutively synthesised defence compounds are found in all plant organs. Concentrations can vary strongly depending on the developmental stage, the environmental conditions (see inducible defences in Sect. 8.3.2) and also the individual genotype (e.g. the tannin example discussed above). A substance particularly rich in defence compounds is latex, an emulsion exuded by about 10% of all plant species when mechanical damage occurs (Agrawal and Konno 2009). Probably the most famous example of a defence compound in latex is morphine in *Papaver* species. In fact, many of the compound classes discussed above can be present at higher concentrations in latex than in leaves. This is why plant latex is sometimes compared with animal venoms, a complex mixture of low molecular weight and proteinaceous defence molecules, which exert a multitude of effects on a range of species. To date, few of the effects have been resolved molecularly. Mulberry leaves are toxic to insects other than the silk-producing *Bombyx mori*. Part of the toxicity can be attributed to alkaloids in the latex that resemble sugar molecules and thereby inhibit glucosidases. They are present in high concentrations (>1.5%; about 100-fold higher than in leaves) and are toxic to caterpillars (Konno et al. 2006).

An alternative to chemical defence has evolved in a limited number of plant species: hyperaccumulation of potentially toxic elements in leaves (= **elemental defence**; Sect. 8.2.1). Selenium hyperaccumulation is the best-documented example; hyperaccumulation of Cd, Zn and Ni may serve similar functions (Cappa and Pilon-Smits 2013).

8.3.2 Inducible Defences Against Herbivores

The previous subchapter provided a glimpse of the huge variety of molecules synthesised by plants that influence the interaction with herbivores, as toxins, deterrents or attractants. While plants produce a complex cocktail of secondary metabolites constitutively, there is, in addition, the induced chemical defence, which comprises not only metabolites but also defence proteins and changes in the storage sites of carbohydrates to minimise the consequences of tissue loss. The advantage of induced defences is that the expenditure of resources is restricted to periods when defence is actually needed, thereby reducing the costs of defence, in favour of growth and reproduction. On the other hand, they have to be activated quickly in order to be effective.

Plant tissues respond locally to herbivore feeding—that is, the cells surrounding the damaged site reprogramme their metabolism and up-regulate the synthesis of defence molecules. In addition, such up-regulation of herbivore defence occurs in tissues distant from the site of attack. As in the case of pathogen attack, long-distance signalling passes the information on herbivore presence to sites not exposed to feeding. The incoming signal (Fig. 8.26) is then converted into changes in gene activities that turn the systemic tissue into a more hostile environment for herbivores. The **systemic response** to wounding was originally discovered in tomato (Green and Ryan 1972) and later found in a wide range of species.

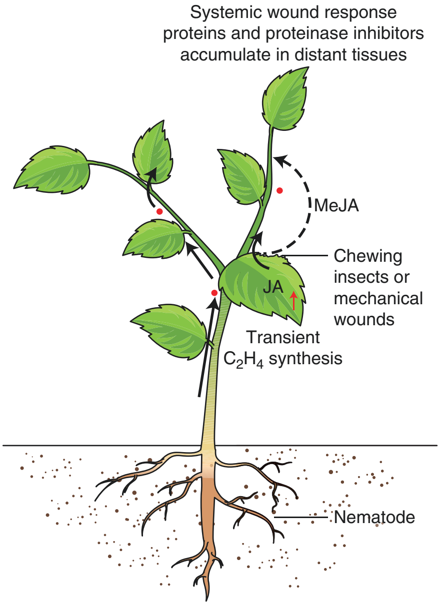


Fig. 8.26 The systemic wound response. *MeJA* Methyljasmonate. (Buchanan et al. 2015)

Induced herbivore defences—and, in particular, the systemic responses—add another layer of complexity to interactions within the communities of arthropods, etc., around a plant. Inducible defences connect organisms through space and time. Activities of root-feeding herbivores, for example, influence the chemical composition of above-ground tissues and, with that, the behaviour of organisms responsive to plant volatiles, etc. Similarly, herbivory early in the growing season has long-lasting systemic effects on a plant's biochemistry and, again, significantly impacts the interacting organisms later in the year.

Plant volatiles emitted by damaged plants can have yet another community consequence. They can result in the so-called **priming** of neighbouring plants. Perception of airborne signals indicating a herbivore attack on a plant leads to an up-regulation of defence in as yet uninfested plants or to more rapid and robust defence activation when those plants are attacked by herbivores (Fig. 8.27). This has been shown for lima beans (*Phaseolus lunatus*) exposed to spider mites (*Tetranychus urticae*). The bean plants released terpenoids, which triggered the activation of defence genes in plants exposed to the volatiles but not to the herbivores (Arimura et al. 2000). Similarly, the treatment

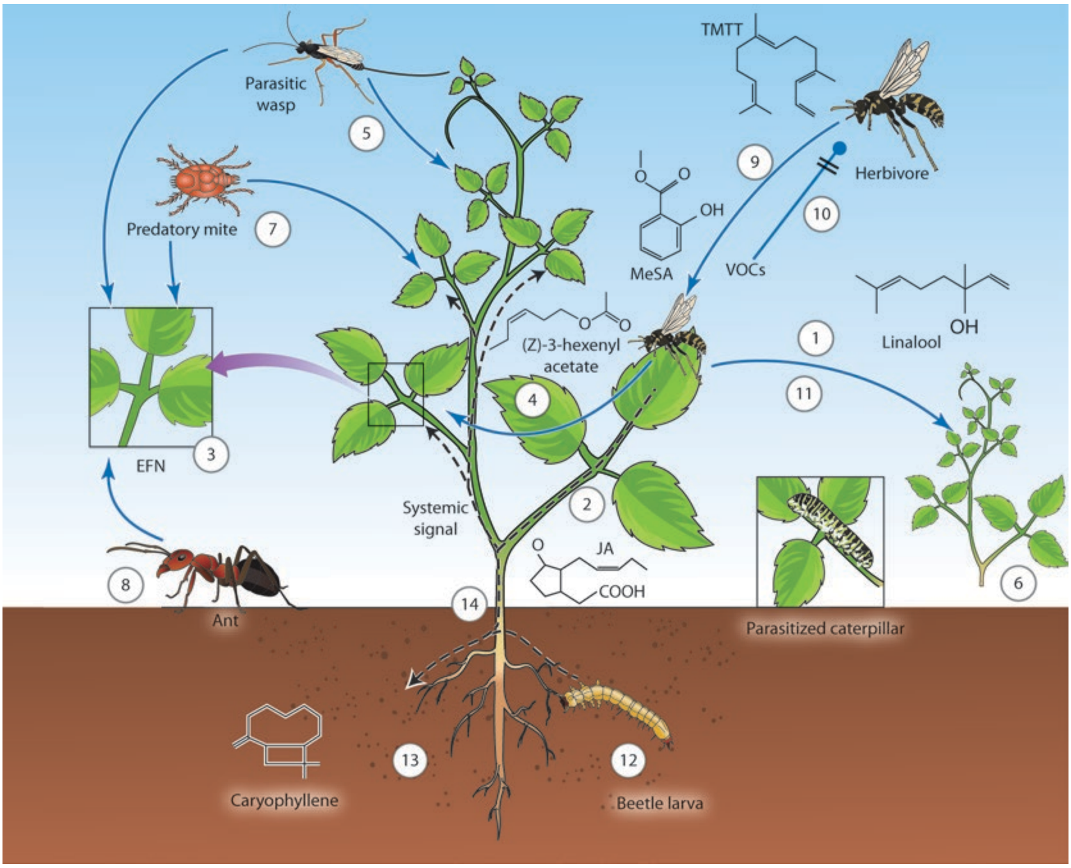


Fig. 8.27 Indirect herbivore defence via a multitude of tritrophic interactions. Biological effects and interactions of volatile organic compounds (VOCs) and extrafloral nectar (EFN). (1) Feeding by a herbivore. (2) Jasmonic acid (JA) synthesis. (3) Inducible release of VOCs and EFN from wounded and intact leaves. (4) Some VOCs can induce indirect defences systemically—that is, in as-yet-unattacked leaves. (5) and (6) VOCs attract parasitic wasps that parasitise herbivores. Attraction of predatory mites (7). Wasps and mites also feed on EFN, as do ants (8). (9) Both con- and heterospecific herbivores can be attracted by VOCs (9), as well as repelled (10). (11) VOCs can also be perceived by other plants of the same species or a different species. (12) Underground feeding by, for example, beetle larvae can induce release of VOCs from roots (13) and elicit a systemic signal triggering EFN production or VOC release from above-ground organs (14). *MeSA* Methyl salicylate, *TMTT* 4,8,12,-Trimethyl-1,3,7,11,-tridecatetraene. (Heil 2008)

of maize plants with volatiles typical of damaged leaves resulted in a much stronger defence response when these plants came in contact with caterpillars (Engelberth et al. 2004).

Most of the defence molecules described above are synthesised throughout the life cycle of a plant. Upon herbivore attack, production of some can be strongly up-regulated, so they are part of both the constitutive and the inducible defences. As a consequence, the attacked plant becomes more toxic and unpalatable. A further step towards this state is the synthesis of proteins that can affect the fitness and growth of herbivores. What is well documented is the production of protease inhibitors that interfere with an insect's digestive system. A range of different proteins complements the plant defence arsenal. Oxidative enzymes such as lipoxygenases and polyphenol oxidases have the potential to cause damage to insect tissues. Lectins and other carbohydrate-binding proteins can inhibit sugar-containing molecules in the insect gut. Cysteine proteases damage the peritrophic membrane that protects the gut epithelium. Arginine and threonine deaminases degrade essential amino acids. A feature that many of the plant defence proteins have in common is that they are comparatively resistant to gut proteases. This enables their biochemical identification via selective enrichment during gut passage (Howe and Jander 2008).

Indirect defences can be induced as well (Fig. 8.27). Changes in the blend of volatiles released by a plant upon herbivore feeding are either due to the processing of stored conjugated specialised metabolites (e.g. glucosinolates; Fig. 8.25) or attributable to newly synthesised volatile compounds. A different type of indirect defence relies on rewarding the enemies of herbivores. Secretion of **extrafloral nectar** attracts non-herbivorous ants and other predators of herbivores (Heil 2008) (Fig. 8.27). The exact chemical composition of such nectars is not known. In an analogy to floral nectaries the presence of sugars such as glucose and fructose, as well as secretion mediated by sugar transporters, can be assumed.

8.3.2.1 Recognition of Herbivore Attack

Rapid induction of direct and indirect herbivore defences is of course dependent on reliable cues perceived by the plant. Insect feeding causes mechanical damage, and plants indeed respond to this (**wounding response**). However, detailed comparative studies—for instance, of transcriptome changes—have clearly shown that a plant differentiates between the tissue loss due to mechanical wounding and the tissue loss caused by a feeding insect. The pattern of gene induction and repression is clearly distinct for the two conditions (Howe and Jander 2008). Thus, there are apparently signals associated with the insect's activity that provide information for the plant. Sources of such signals can be insect saliva, regurgitant (another form of oral secretions produced by lepidopteran larvae), oviposition fluids or faeces. In analogy to the term **MAMPs** used in the context of pathogen defence, these signals are now referred to as **HAMPs** (**herbivory associated molecular patterns**) or **insect elicitors**. In addition, the more general term **DAMPs** is used as well, summarising signals arising from the plant because of enemy activities (e.g. mechanical damage). In fact, the concept of **DAMP recognition** unifies induced plant immunity to pathogens and herbivores.

The first HAMP identified was volicitin, a fatty acid–amino acid conjugate isolated from oral secretions of beet army worm caterpillars (*Spodoptera exigua*) (Alborn et al. 1997). The conjugate is derived from a plant fatty acid, while the glutamine and the conjugation reaction stem from the insect. Treatment of artificially wounded maize plants with volicitin activates the production of volatiles typical of the herbivore response, while the wounding alone does not lead to production of the same volatile blend. Since the discovery of volicitin, several other HAMPs have been molecularly identified: a range of other fatty acid–amino acid conjugates, breakdown products of plant adenosine triphosphate (ATP) synthases called inceptins and sulphated fatty acids called caeliferins (Acevedo et al. 2015).

HAMP receptors are not known yet. Generally, recognition of HAMPs by plant cells is molecularly less well understood than MAMP recognition. The same is true of the early signal transduction events triggered by HAMP sensing, even though the existing knowledge shows extensive principal similarity to pathogen responses. The same basic modules are implicated: transient cytosolic Ca^{2+} spikes, membrane potential changes, ROS as signalling molecules, and mitogen-activated protein kinase cascades (Wu and Baldwin 2010).

As in the plant–pathogen interaction, there is evidence that herbivores produce **effectors** to overcome plant defences, and that plants have evolved the ability to sense such effectors or their activities. Again, the molecular understanding is far less advanced, at least partly because plant–herbivore interactions are less amenable to the type of genetic analysis that led to the **gene-for-gene concept**. An example of herbivore effectors are ATPases in insect saliva. Mechanical damage of plant cells causes a release of ATP into the extracellular space. This extracellular ATP can serve as a DAMP for the plant, and insect ATPases degrade this potential signal. Thus, a plant receptor for extracellular ATP presumably functions in DAMP recognition (Choi et al. 2014).

In contrast to the early events of herbivore sensing, the main regulators of plant herbivore responses have been known for a long time.

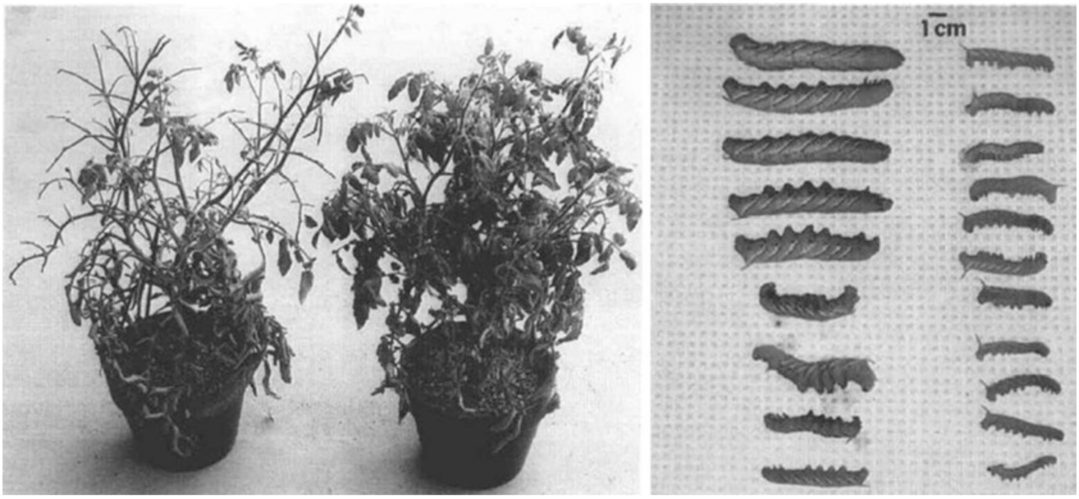


Fig. 8.28 Jasmonate biosynthesis is essential for effective herbivore defence. The tomato *defenceless* mutant (*left*)—which is deficient in jasmonate biosynthesis—and wild-type plants (*right*) were exposed to hornworm larvae for 13 days. The *right panel* shows the larval size after feeding on the mutant (*left*) and wild-type plants. (Howe et al. 1996)

Jasmonic acid (**JA**) and its derivatives are recognised as plant hormones that play a central role in balancing a plant's investments in growth versus defence in rapidly changing environments. JA generally inhibits growth, as well as assimilate export from vegetative tissues, and activates defensive and reproductive processes. Most prominent among the defensive roles of JA is protection from attack by insect herbivores and necrotrophic fungi. JA promotes the synthesis of practically all classes of chemical defence compounds, underpinning its universal role in the plant kingdom. For several plant species it has been shown that a loss of JA synthesis or JA perception severely compromises the ability to limit damage caused by all kinds of insect herbivores and even some vertebrates (Fig. 8.28). Field studies on transgenic *N. attenuata* plants with a defect in JA synthesis showed far-reaching consequences of JA signalling in the natural environment (Kessler et al. 2004). Not only were specialist herbivores more successful when the capacity of the plants to induce defences was compromised by the silencing of a lipoxygenase gene essential for **JA biosynthesis**, but also plants were chosen for oviposition and severely damaged by opportunistic herbivores (e.g. *Empoasca* sp. leafhoppers) that rarely attack *N. attenuata* plants in the wild. Also, JA-deficient plants were preferred to wild-type plants in choice experiments. Thus, plants fall victim to herbivores that they normally are able to fend off. Later field experiments revealed that leafhoppers probe plants during initial feeding, and those they select for extended feeding are the ones with the lowest level of JA-dependent activation of defence responses (Kallenbach et al. 2012).

The central position of JA in defence can be described in distinct steps. HAMP or DAMP recognition triggers the early signal transduction chains that activate the synthesis of JA and its derivatives, among them the actual receptor-active **JA–isoleucine** (**JA-Ile**) conjugate (Fig. 8.29). JA synthesis proceeds from the ubiquitous fatty acid linolenic acid via enzymatic reactions localised in plastids and peroxisomes (the **core JA module**). Perception of JA then activates the herbivore defence genes encoding enzymes and regulatory proteins involved in the synthesis of defence metabolites, or the antifeeding defence proteins such as protease inhibitors.

Upon pathogen or herbivore detection, the active signal JA-Ile, which is barely present in unstressed cells, can be synthesised rapidly (i.e. within minutes) in the cytosol from JA and isoleucine, and then sensed by a receptor in the nucleus (Fig. 8.30). Like several other phytohormone receptors, the **JA-Ile receptor COI1** (for "coronatine insensitive"; the name refers to the initial identification of

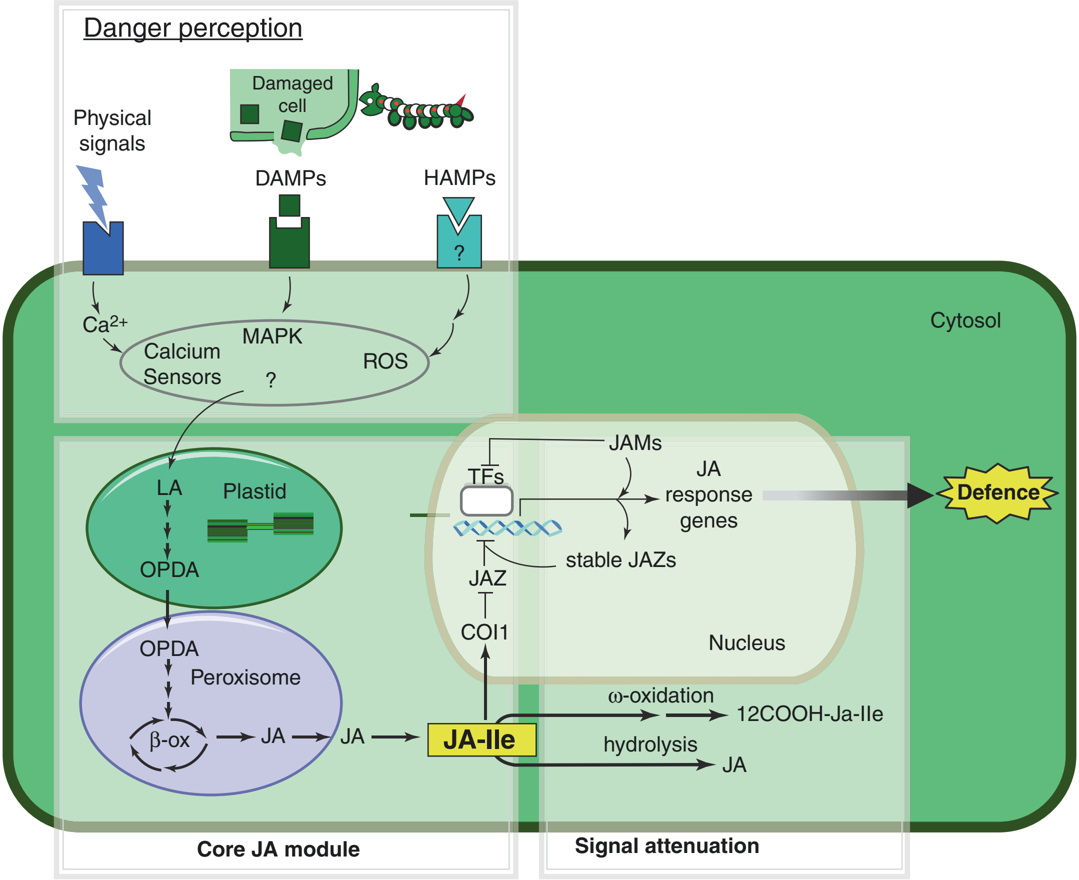


Fig. 8.29 Jasmonate-triggered herbivore defence. Danger signals derived from attacking herbivores (herbivory associated molecular patterns (HAMPs)) and damaged plant cells (danger-associated molecular patterns (DAMPs)) are recognised by pattern recognition receptors (PRRs) at the cell surface. PRR activation triggers intracellular signalling systems involving mitogen-activated protein (MAP) kinase pathways, Ca^{2+} spikes and reactive oxygen species (ROS) production. In a largely unknown fashion these signalling events activate jasmonic acid (JA) biosynthesis from its precursor, linolenic acid (LA), in plastids and peroxisomes. JA is the substrate for synthesis of the actual signal JA–isoleucine (JA-Ile) in the cytosol. In the nucleus, JA-Ile promotes JAZ-COI1 interaction and targets JAZ repressor proteins for proteolytic degradation by the ubiquitin-proteasome system (Fig. 8.30), thereby activating the expression of JA-responsive genes and the expression of defence traits. JA signalling is attenuated by catabolism of JA-Ile via ω-oxidation and hydrolysis, synthesis of JAZ repressors that are stable in the presence of JA-Ile, and transcription factors (JAMs) that negatively regulate JA response genes. *OPDA* 12-oxo-phytodienoic acid, *β-ox* β-oxidation, *JAM* JASMONATE-ASSOCIATED MYC2-LIKE, *JAZ* Jasmonate Associated Zinc-finger domain, *12-carboxy-JA-Ile* 12COOH-JA-Ile. (Modified from Campos et al. (2014))

a receptor mutant insensitive to the jasmonate analogue coronatine) is part of an E3 ligase complex that tags specific proteins for degradation in the 26S proteasome by adding ubiquitin chains. These proteins are the **JAZ repressors**. They prevent the activation of JA-Ile responsive genes by interaction with transcription factors (e.g. MYC2) that bind the promoters of early JA-Ile response genes. Degradation of the JAZ proteins relieves the repression and the JA response is activated (Fig. 8.30).

Herbivore defence responses are analogously switched on in tissues distant from the site of herbivore-inflicted damage. JA or JA conjugates are phloem-mobile signals, which may travel to as yet unaffected tissues. In addition, volatile methyljasmonate serves as an airborne long-distance signal (Fig. 8.26). The JA-dependent activation appears to be universal in the plant kingdom. Besides this central mechanism, there are other known signals and signalling modes. The

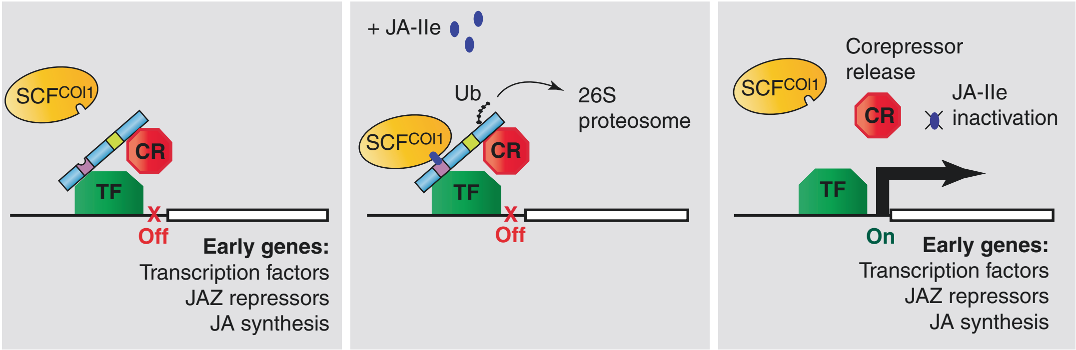


Fig. 8.30 Activation of defence genes upon jasmonic acid–isoleucine (JA-Ile) perception. JAZ proteins (*blue bar*), supported by co-repressors (CR), bind and repress transcription factors (TF) associated with the promoters of early genes in the JA response. JA-Ile binding to the receptor COI1 promotes interaction of the SC-COI1 E3 ligase complex and the tagging of JAZ for degradation in the proteasome. As a result, early JA response genes can now be transcribed. (Browse 2009)

systemic wound response was discovered and intensively investigated in tomato plants. An early breakthrough was the identification of **systemin**, a peptide signal derived from a pre-protein through proteolytic processing (Pearce et al. 1991). Systemin is produced in wounded tomato leaves and activates the JA pathway in neighbouring vascular tissues. It can thus be considered as a **DAMP** released by wounding. Orthologous peptides with comparable activity have never been found, suggesting that systemin and systemin-like peptides are restricted to a small group of plant species. Nonetheless, defence-activating peptides of a different molecular nature have in the meantime been identified, and they appear to be widespread in the plant kingdom (Bartels and Boller 2015).

A **systemic wound response** dependent on JA as the mobile signal takes a few hours to materialise. An alternative mode of long-distance signalling could be electrical. Indeed, the up-regulation of JA synthesis in distal tissues within minutes of wounding appears to depend on **electrical signalling** (Mousavi et al. 2013). Both insect feeding and wounding elicit surface potential changes in *A. thaliana* leaves, which travel through the rosette to distal leaves at an estimated speed of around 6 cm/min. The amplitude of the signal correlates with the strength of the JA response activation in these leaves. Conversely, the injection of current into leaves systemically triggers JA synthesis in the absence of wounding. Ion channels involved in the generation and propagation of the electrical signal are glutamate-receptor-like proteins.

8.3.3 How Plant–Herbivore Interactions Drive Genetic Diversity

The interaction of plants with the plethora of herbivorous animals surrounding them is generally regarded as a major driver of **biodiversity**. This has in a few cases been possible to demonstrate experimentally. In field experiments with a native plant, *Oenothera biennis*, it was shown that the suppression of insect herbivores in one half of the plants by insecticide treatment not only suppressed herbivore-inflicted damage but also resulted in **rapid evolutionary change**, apparent as genetic differentiation between the populations. Over five growing seasons, herbivore defence declined in the protected populations, for instance, because of lower elagitannin levels in fruits (Agrawal et al. 2012). Conversely, competitive ability increased. Such experiments document evolutionary consequences of a **trade-off** between defence and growth in real time.

Furthermore, plant–herbivore interactions are seen as a major reason for the rich diversity of plant secondary metabolism. As discussed, plant families or plant species synthesise a characteristic cocktail of secondary metabolites. Importantly, also, the spectrum of secondary metabolites produced by an individual plant is strongly influenced by its genotype—that is, the combination of allelic variants of genes encoding regulatory proteins, enzymes or other proteins controlling the spectrum and synthesis rate of secondary metabolites. The molecular dissection of chemical herbivore defence mechanisms provided the first detailed insights into how synthesis and diversity of secondary metabolites arose and which evolutionary forces maintain such diversity. A comparatively well-understood system is **glucosinolate biosynthesis** in Brassicaceae. Accessions of *A. thaliana* differ in the mixture of constitutively produced glucosinolates and of glucosinolate breakdown products released when glucosinolates come into contact with myrosinases (Fig. 8.25). The diversity arose through **gene duplications** and the **neofunctionalisation** of gene copies. The blend of breakdown products has various consequences for plant–herbivore interactions. The more volatile breakdown products are more likely to attract specialist herbivores or the parasitoids and predators of herbivores. Nitriles are less toxic than isothiocyanates but, at the same time, do not carry the risk of alerting specialists to the presence of a suitable host plant, because specialists use isothiocyanates as clues. Such contrasting consequences of defence molecules maintain the diversity of genotypes, since different habitats select for different genotypes. For example, variation in the polymorphic **GS-ELONG locus** controlling the side chain length of methionine-derived glucosinolates in *A. thaliana* (Box 8.3) is explained by the distribution of two specialised aphid species feeding on *A. thaliana* (Züst et al. 2012). Multigeneration selection experiments with artificial populations demonstrated that the herbivore pressure exerted by the two aphid species selects distinct **chemotypes**—that is, it causes rapid changes in the relative abundance of the alleles controlling these chemotypes (Fig. 8.31).

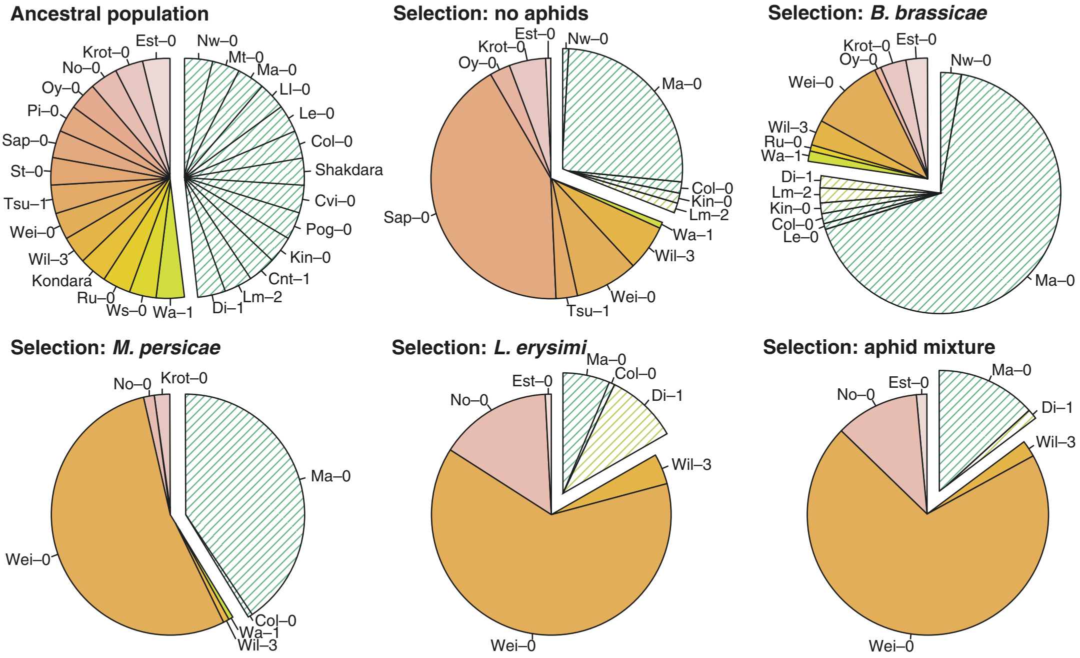


Fig. 8.31 Evolution in action: herbivores differentially select glucosinolate chemotypes. A multigeneration selection experiment was performed with an ancestral population consisting of 27 *Arabidopsis thaliana* accessions differing in the type of methionine-derived glucosinolates (*orange:* C3 chemotype, *green:* C4 chemotype). The populations were exposed to one aphid species (*Brevicoryne brassicae*, *Lipaphis erysimi* or *Myzus persicae*) or a combination of them. The pie charts illustrate the changes in the composition of *A. thaliana* accessions from equal proportions of 27 genotypes to treatment-specific compositions after five generations of selection. The mean genotype frequencies based on six replicate populations are shown. For example, the accession Sap-0, which produces much smaller amounts of glucosinolates than the other accessions, became dominant in the absence of herbivore pressure but was eliminated from the population in the presence of aphids. (Züst et al. 2012)

Box 8.3: The *GS-ELONG* Locus in *Arabidopsis thaliana*

The diversity of **glucosinolates** and glucosinolate breakdown products in *A. thaliana* is in part explained by allelic variation in four genetic loci. One of them is the *GS-ELONG* (or *MAM*) locus. The dominant glucosinolates in *A. thaliana* are methionine derived. They differ in the length of their side chain. This influences the volatility of the breakdown products and thus the interaction with insects of the second and third trophic levels. Most *A. thaliana* individuals carry either a *MAM* gene (*MAM2*) that results in the synthesis of a three-carbon side chain (C3) or a *MAM* gene (*MAM1*) that gives rise to a four-carbon side chain (C4). The gene enabling C4 synthesis arose by **gene duplication** and underwent **neo-functionalisation**. Sequence analysis revealed an over-representation of non-synonymous changes affecting the part of the MAM protein that controls substrate specificity. This suggested that changes in substrate specificity have been positively selected (Benderoth et al. 2009), meaning that a combination of gene duplication, neo-functionalisation and **positive selection** explains the generation of **metabolic diversity** (Fig. 8.32).

The logical next questions are: Which processes maintain the diversity? Why did the positively selected *MAM1* gene not completely replace the ancestral *MAM2* gene? Most likely, it was because under particular conditions it is advantageous for a plant to carry the *MAM2* gene instead of the *MAM1* gene. For example, *MAM2* provides an advantage against certain generalist herbivores because MAM2 activity is associated with larger quantities of glucosinolates. Thus, **balancing selection** maintains both

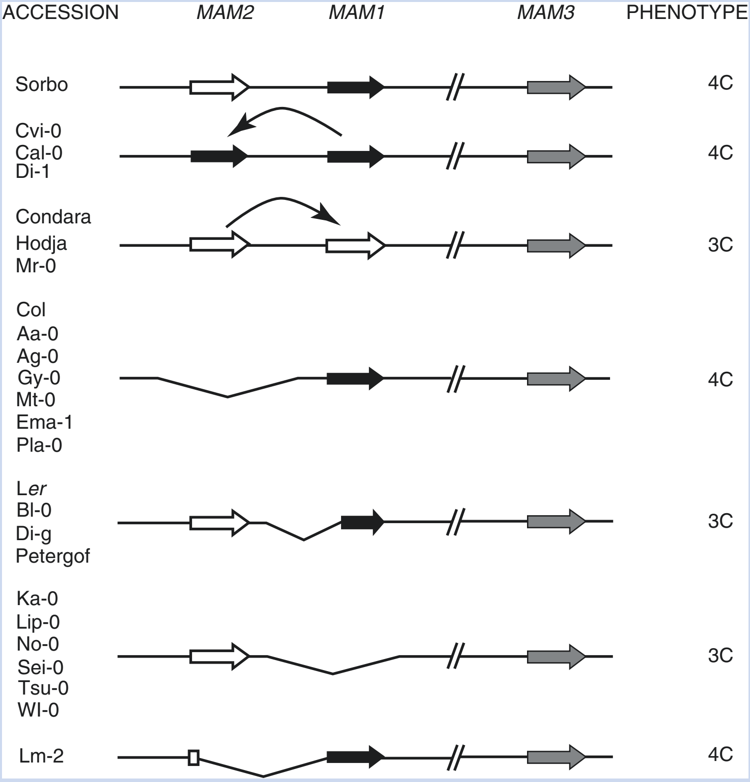


Fig. 8.32 Evolutionary dynamics of the MAM locus. The organisation of the *MAM* cluster in *Arabidopsis thaliana* accessions is highly variable. Partial or complete deletions of *MAM2* or *MAM1* have occurred frequently. Also, partial gene conversion has occurred between loci. The predominant aliphatic glucosinolate class phenotype resulting from the structure of the *MAM* locus is indicated in the right column (3C: homomethionine-derived, 4C: dihomomethionine-derived) (Benderoth et al. 2009)

variants. The composition of local herbivore communities varies considerably over time. The relative frequency of generalists, specialists, parasitoids, etc., temporally changes within a given habitat. With these changes, different glucosinolate cocktails are beneficial and therefore are selected by the herbivore pressure.

8.4 Parasitic Plants

About 1% of all dicot angiosperm species are parasitic. They show a heterotrophic lifestyle—that is, they utilise the photosynthetic products of a host plant by directly feeding on it. The degree of heterotrophy can vary widely and therefore two separate classes of parasitic plants are defined: **holoparasites** are completely dependent on host photosynthesis, while **hemiparasites** are photosynthetically active at least during some stages of their life cycle and sometimes take only water and mineral nutrients from the host (Fig. 8.33). Holoparasites are obligate parasites—that is, they absolutely require a host—while hemiparasites can be either obligate or facultative. The latter type opportunistically exploits neighbouring plants when the opportunity arises. Correspondingly, hemiparasites usually are morphologically indistinguishable from fully autotrophic plants, while some holoparasites lack typical plant structures such as leaves and roots altogether. Plant parasitism, as defined by direct feeding on host plants, is restricted to dicot angiosperms, where it evolved several times independently (Westwood et al. 2010). Commonly distinguished from parasitic plants are **myco-heterotrophic plants**. They exploit the mycorrhizal connection between another plant and a fungus. In this way they indirectly feed on a host plant. Several hundred plant species have evolved this lifestyle, among them many **orchids**.

Molecular insight regarding the interaction with host plants is largely restricted to parasitic plants sensu stricto and therefore only these will be discussed further. One reason for this bias is most likely the economic damage caused by parasitic plants such as **Orobanche** and **Striga** (Fig. 8.33), predominantly in Africa, where *Striga* infestation alone affects about 300 million farmers. Consequently, molecular understanding is mostly derived from studies involving species of these two genera.

Parasitic plants can be further divided into **root parasites** and **stem parasites**, depending on which host organ they invade. Root parasites, which include *Orobanche* and *Striga* species, are more common than shoot parasites (mistle-

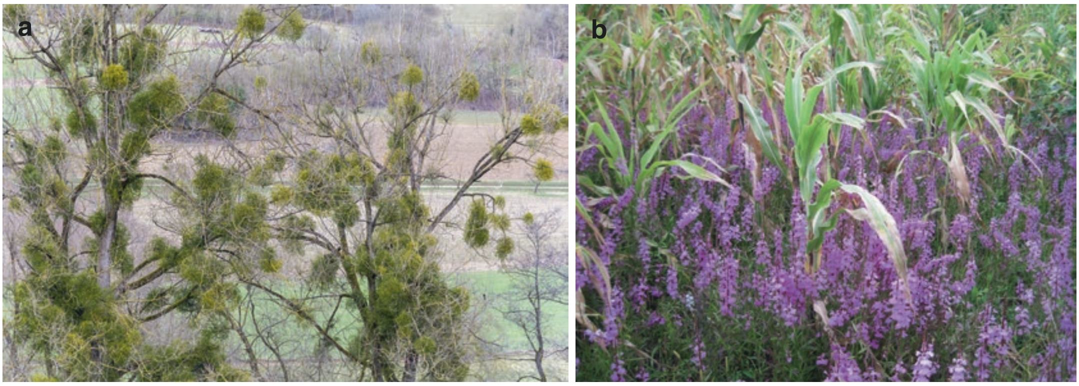


Fig. 8.33 Parasitic plants. **a** Hemiparasitic mistletoes on host trees (Photo: copyright obtained from Shutterstock). **b** The hemiparasite *Striga* flowering in a maize field

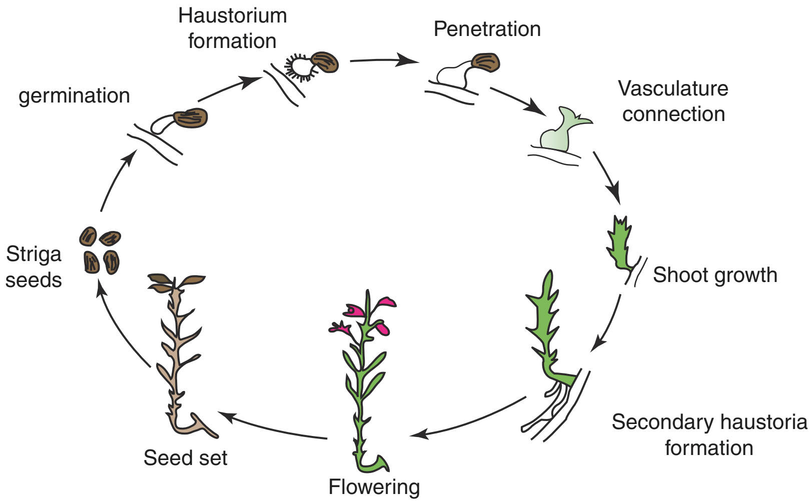


Fig. 8.34 Life cycle of *Striga*. (Yoshida and Shirasu 2012)

toes are one example). An essential element of parasitism is access to the vascular system of the host in order to draw water, minerals and assimilates. Parasitic plants penetrate host tissues with specialised structures called haustoria. These grow towards the vasculature and establish connections between the parasite and the host (Fig. 8.34). Haustoria are generally seen as the key innovation of parasitic plants and represent the core of the interaction with their hosts (Yoshida et al. 2016). Unlike haustoria of biotrophic fungal pathogens (Fig. 8.9), the haustoria of parasitic plants consist of many cells and remain intercellular in the host—that is, they do not enter host cells.

Other critical abilities of parasitic plants, besides haustoria-mediated penetration of host tissue, are the recognition of host plants and the establishment of nutrient transfer from the host. The first step is germination of seeds in response to signals that indicate the vicinity of a suitable host. The seeds of *Striga* and *Orobanche* are tiny and thus provide very little reserves for the developing seedlings. Early contact with a host is therefore essential. *Striga* and *Orobanche* locate hosts through highly sensitive detection of compounds exuded by the roots of such plants. Many structurally diverse molecules have, over the years, been shown to act as **germination stimulants**. Those best studied by far are the **strigolactones** (Fig. 8.35), a class of carotenoid-derived molecules found in small concentrations in **root exudates** (Fig. 8.35). They were isolated as germination stimulants for *Striga* seeds, hence the name strigolactones (Xie and Yoneyama 2010). For a long time it was not clear why a plant would exude compounds that compromise its performance by attracting enemies. This mystery was solved when strigolactones were first identified as indispensable signals for the interaction with mycorrhizal fungi (Chap. 7) and later as **plant hormones** that control shoot branching, root architecture and other developmental processes. Perception of strigolactones is thus an excellent example of how parasites or pathogens evolve the ability to use an essential molecule produced by potential hosts as a cue for the presence of such hosts.

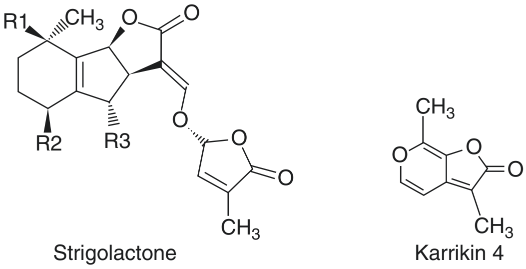


Fig. 8.35 Chemical structures of strigolactones and karrikins

Molecules structurally related to strigolactones, so-called **karrikins** (Fig. 8.35), promote seed germination in a wide range of plant species. Karrikins are found in smoke and serve as

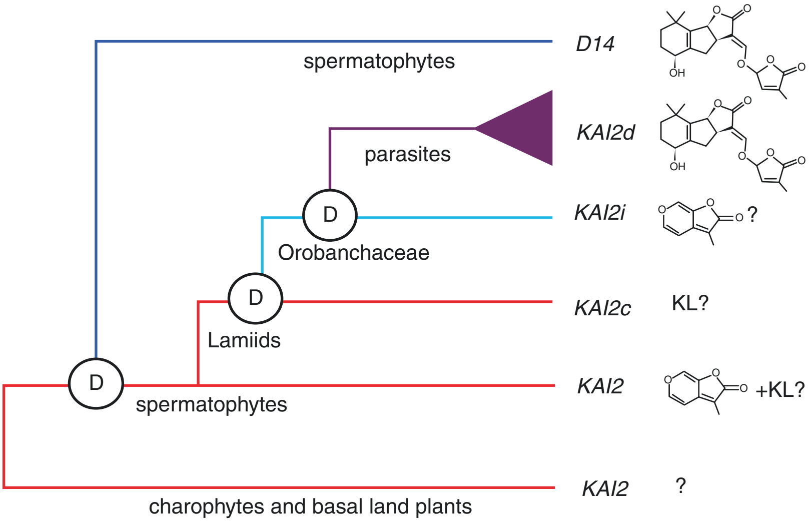


Fig. 8.36 Convergent evolution of strigolactone receptors. Homologues of the *KAI2* gene are found in basal lineages such as charophytes. The strigolactone receptor D14 probably arose from these ancestral genes before the evolution of spermatophytes. Additional duplications of related karrikin receptor genes gave rise to rapidly evolving variants in parasitic plants that acquired the ability to detect strigolactones. Thus, strigolactone receptors evolved twice from more ancient karrikin receptors. The second event represents one of the steps towards parasitism. *KL* KAI2 ligand, D gene duplication. Question marks indicate uncertainty about receptor ligands. (Conn et al. 2015)

fire cues. Vegetation fires provide favourable conditions for seedlings and in many plant species trigger seed germination (Chap. 2, Sect. 2.4.3). Recent findings on the **strigolactone receptors** of *Striga* indicate that they evolved independently from the strigolactone receptors ubiquitously present in plants (called D14 in rice and *A. thaliana*). Ancestral paralogues of *D14*, the *KAI2* genes, mediate the perception of karrikins in many plant species, including species not responsive to fires. In the parasitic Orobanchaceae lineage that *Striga* belongs to, the number of *KAI2* genes expanded and some of these paralogues represent a distinct clade of *KAI2* genes. They perceive strigolactones with very high sensitivity. Their ligand-binding pockets show structural changes when compared with related receptors in non-parasitic plants, meaning that these parasite-specific variants convergently evolved into strigolactone receptors and thus represent one of the molecular components enabling parasitism (Fig. 8.36).

Like germination, the next step—**haustoria formation**—is triggered by chemical signals originating from the prospective host. Again, a range of molecules has been found to show the respective bioactivity, among them flavonoids, quinones and phenolic acids. Perception mechanisms, however, have not been molecularly elucidated yet. Invasion of host tissue is then reliant on localised destruction of host cellular structures by secreted cell wall–degrading enzymes and proteases. Finally, haustoria develop further and connect either with the xylem and phloem (holoparasites) or only with the xylem (some hemiparasites such as *Striga*). Symplastic connections with host cells enable the acquisition of organic carbon and nitrogen, as well as the exchange of macromolecules (including DNA and RNA) between the parasitic plant and the host plant.

The host ranges of most parasitic plants are rather broad. For example, the majority of *Striga* species parasitise a variety of grasses. Still, there is some degree of specialisation, as a few *Striga* species parasitise dicots instead. Also, many other plant species are not colonised, demonstrating the existence of **non-host resistance** against parasitic plants. The underlying mechanisms, however, are not clear. Penetration of host tissue should elicit wound and defence responses. Whether parasitic plants—in a manner similar to fungal and bacterial pathogens—suppress host defences by effectors that would in turn be recognised by hosts is not clear.

8.5 Allelopathy

When one plant species inhibits the growth of another species through the production of chemicals, this is commonly referred to as allelopathy. The original definition dating back to Hans Molisch in 1937 has since been broadened to include also beneficial interactions (positive allelopathy). In accordance with the “molecular stress physiology” perspective, we will discuss only negative allelopathy—that is, a plant–plant interaction that is harmful to one of them.

Inhibition of the growth of a neighbouring plant can be beneficial because it reduces competition and increases the availability of resources. The inhibitory effect (Fig. 8.37) is achieved by the release of toxic compounds, referred to as **allelochemicals**, which can principally be found in leaf volatiles, in leachates from leaves, in root exudates or in decomposing tissue (Weir et al. 2004). It has, however, been notoriously difficult to ascertain that the concentrations of suspected phytotoxins are high enough in the soil to actually negatively affect the establishment or growth of neighbouring plants. Another principal challenge concerns the mode of action. What are the targets of toxicity, and how does the producing plant protect itself against the toxins? Molecularly these questions have not been answered yet.

For several invasive plant species it has been proposed that part of their success is attributable to toxins in root exudates. The effect of such toxins can be indirect. An example is the release of benzyl isothiocyanates by garlic mustard (*Alliaria petiolata*), an invasive plant in North American forests. The exudated allelochemicals suppress the establishment of ectomycorrhizal symbioses of several tree species and thereby reduce their growth (Fig. 8.38) (Stinson et al. 2006).

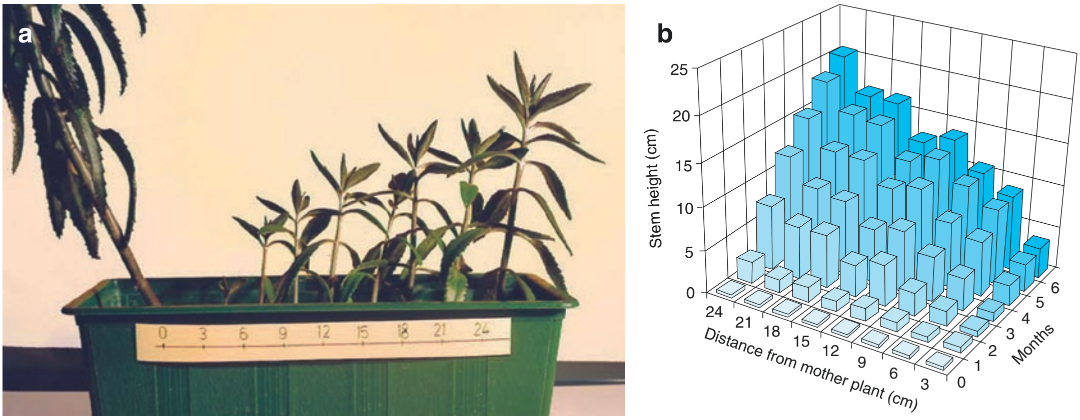


Fig. 8.37 Intraspecific allelopathy in *Kalanchoe daigremontiana*. **a** Same-age daughter plantlets were placed in sand soil at regular intervals from the mother plant. After 150 days the height of the daughter plants clearly shows the inhibitory effect of the mother plant on their growth. **b** Quantification shows that the inhibition of the young plants depends on the distance from the mother plant. (After Bär et al. (2000))

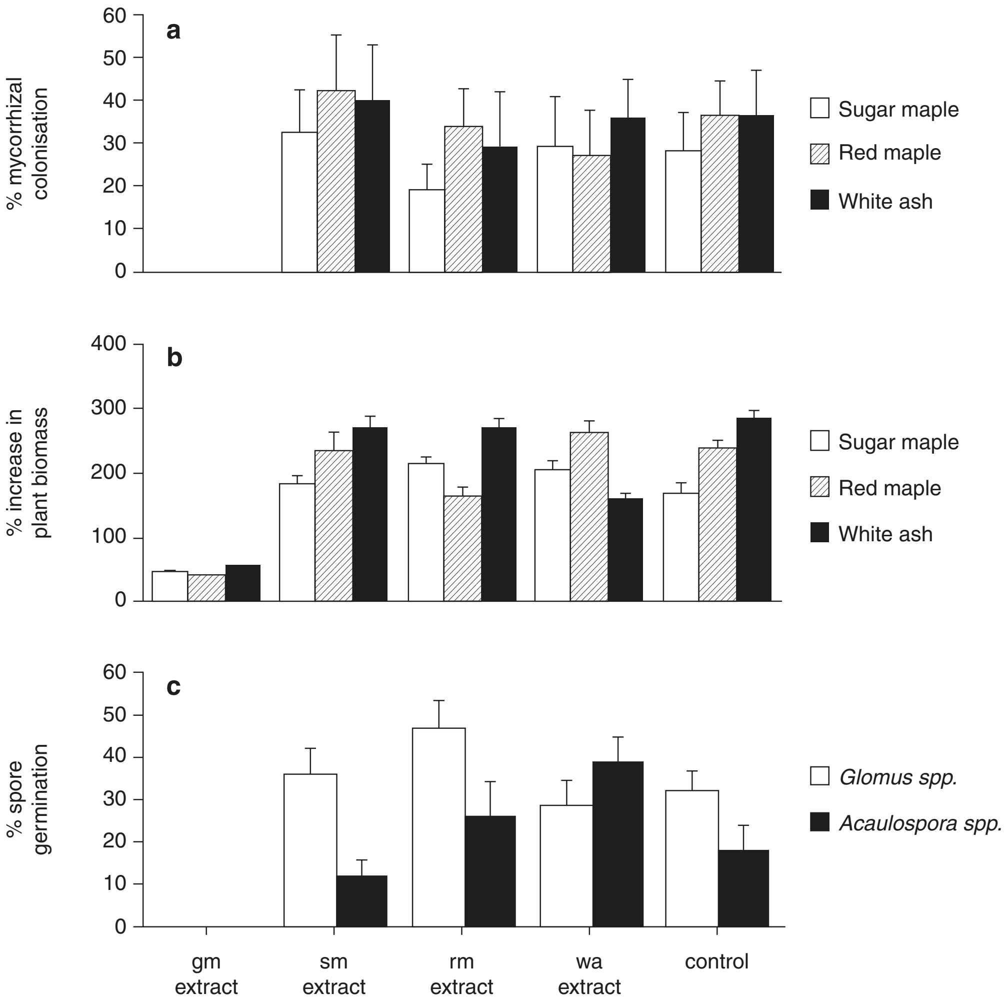


Fig. 8.38 The invasive plant *Alliaria petiolata* (garlic mustard) inhibits plant growth by disrupting symbiotic associations between native canopy tree seedlings and below-ground arbuscular mycorrhizal fungi. The extracts of garlic mustard (gm), sugar maple (sm), red maple (rm), white ash (wa) or a water control were tested for their effects on **a** mycorrhizal colonisation of native tree seedlings, **b** biomass gain of native tree seedlings and **c** percentage germination of native arbuscular mycorrhizal fungi spores. The *bars* represent the mean and standard error (Stinson et al. 2006)

Summary

- Plants are constantly under attack by a wide range of potential enemies—namely, pathogens and herbivores. Still, most plants remain healthy because they possess an array of constitutive and inducible defence mechanisms.
- Defences against pathogens and herbivores can both be divided into mechanical/physical and chemical defences. Also, both involve recognition events and signalling cascades that result in the induction of defence mechanisms upon the perception of a potential foe or the damage caused by it.
- Plant pathogens are found among viruses, bacteria, fungi, oomycetes and nematodes.
- Pathogens have to enter plant tissues, effectively suppress the plant's immune system, gain access to the plants resources and be able to grow and

reproduce rapidly within plant tissues.

- Viruses are transmitted by phloem-sucking insects and spread through plasmodesmata. Bacteria have to enter a plant passively through stomata or wounds. Fungi and oomycetes can actively penetrate a plant's surface.
- Phytopathogenic bacteria, fungi and oomycetes employ effectors and toxins to interfere with the plant's immune system and to disturb physiological or developmental processes.
- The interaction between a plant and a pathogen can have two principal outcomes: incompatible when no disease arises, or compatible when the pathogen is able to propagate. In the former case the plant is called resistant, in the latter case it is called susceptible. A disease-causing pathogen is called virulent.
- Constitutive defences are mechanical (e.g. cell walls, the cuticle) and chemical. Plants produce thousands of secondary metabolites with antimicrobial activity.
- Inducible defences are mounted upon recognition of a potential pathogen.
- Two principal amplitudes of defence based on two different recognition strategies can be differentiated. The first layer of inducible defence is referred to as innate immunity. Antimicrobial compounds (phytoalexins) are synthesised, cell walls are locally reinforced and various defence proteins are produced. These responses provide efficient protection against most potential pathogens.
- Innate immunity is activated by the perception of molecules characteristic of potential pathogens (e.g. highly conserved bacterial structures) or characteristic of the activities of potential pathogens (e.g. cell wall fragments). Plant cells express >100 different pattern recognition receptors mediating this perception. Together they constitute an effective surveillance system that enables plant cells to sense the extracellular presence of many different latent foes.
- Recognition triggers signal transduction cascades involving phosphorylation, Ca^{2+} signals and the production of reactive oxygen species in the oxidative burst.
- The second layer of inducible defence is activated when virulence factors (effectors) are detected by plants. A cell undergoes a programmed cell death programme (the hypersensitive response), which limits the spread of the pathogen. The underlying signal transduction is poorly understood. Effector recognition requires large sets of resistance genes (R genes) because effectors are not conserved and pathogens produce a wide variety of effector molecules. R genes are plant species-specific and even genotype-specific. The evolutionary relationship between effectors (encoded by so-called avirulence genes) and R genes is described by the gene-for-gene hypothesis. Matching genes lead to an incompatible interaction (hence avirulence genes).
- The ability of plants to keep pace with rapidly evolving pathogens in the evolutionary race is explained by the diversity of R genes in plant populations and the guard hypothesis. Many R gene products recognise not effector proteins but, rather, the modifications caused by effectors on sensitive virulence targets. Genetic diversity within a population reduces the vulnerability to pathogens.
- Plants mount not only a localised response to pathogen attack but also a systemic response resulting in systemic acquired resistance. Long-distance signalling conveys the information about a pathogen attack to uninfected organs. The defence hormone salicylic acid is a key player in the systemic activation of defence.
- The main immune system against viruses in plants is based on gene silencing mediated by small RNAs derived from double-stranded RNAs produced during virus replication. Immunisation against viruses is based on the systemic spread of gene silencing.
- Insect herbivores are often referred to as pests. Three categories can be differentiated: chewing insects, piercing–sucking insects and phloem-feeding insects. A second fundamental distinction in addition to the feeding style is that between generalist herbivores (which do not show much preference for certain plant species) and specialist herbivores. The latter find their hosts through chemical cues and have evolved the ability

to overcome the herbivore defences of their preferred hosts.

- Constitutive herbivore defences include mechanical barriers, morphological features such as thorns and, most importantly, a diverse cocktail of chemicals that render a plant toxic or unpalatable. Major compound classes implicated in herbivore defence are alkaloids, phenolic compounds, terpenoids, cyanogenic glucosides and glucosinolates. Many defence molecules are stored in a non-toxic form as glycosides and are degraded to toxic aglycones upon tissue damage. In addition, plants produce non-proteinogenic amino acids, protease inhibitors and other defence proteins such as carbohydrate-binding proteins.
- Inducible defences are both local at the site of herbivore-inflicted damage and systemic. Metabolism is reprogrammed and the synthesis of defence molecules is up-regulated.
- An additional layer of herbivore defence is indirect defence. Many of the plant secondary metabolites or their respective breakdown products are volatile and influence a plethora of organisms in the ecological communities around a plant. For example, they can attract predators or parasitoids of the herbivores. Another form of indirect defence is based on the provision of rewards (extrafloral nectar) for predators.
- Plant volatiles emitted by damaged plants can have yet another community consequence. They can result in the so-called priming of neighbouring plants. Perception of airborne signals indicating a herbivore attack on a plant leads to an up-regulation of defence in as yet uninfested plants or to more rapid and robust defence activation when these plants are attacked by herbivores.
- Induction of direct and indirect herbivore defences is dependent on reliable cues perceived by the plant. A plant responds not only to wounding but also distinctively to signals associated with the insect's activity. Sources of such signals can be insect saliva, regurgitant, oviposition fluids or faeces.
- Jasmonic acid (JA) and its derivatives are plant hormones with a central role in balancing a plant's investments in growth versus defence and specifically in protection from attack by insect herbivores and necrotrophic fungi. Loss of JA synthesis or JA perception severely compromises the ability of plants to limit damage caused by herbivores.
- JA-dependent induction of herbivore defence proceeds in several steps: recognition of signals derived from herbivore attack; signal transduction involving transient cytosolic Ca^{2+} spikes, membrane potential changes, reactive oxygen species as signalling molecules and mitogen-activated protein kinase cascades; activation of JA biosynthesis; JA perception; and expression of herbivore defence genes.
- JA synthesis proceeds from the ubiquitous fatty acid linolenic acid via enzymatic reactions localised in plastids and peroxisomes. The actual receptor-active JA–isoleucine (JA-Ile) conjugate is synthesised in the cytosol.
- JA-Ile interacts with the receptor COI1. Upon binding, the E3 ligase complex (which COI1 is part of) ubiquitinates JAZ repressor proteins for proteasomal degradation. Early JA response genes can then be transcribed.
- JA or JA conjugates are phloem-mobile signals that may travel to as yet unaffected tissues and activate the systemic wound response. In addition, volatile methyljasmonate serves as an airborne long-distance signal. An alternative mode of long-distance signalling could be electrical.
- The interaction of plants with herbivores is a major driver of biodiversity and specifically of the diversity of secondary metabolism. Indeed, selection experiments have demonstrated evolution in action—that is, rapid changes in the composition of populations, depending on the strengths and nature of herbivore pressure.
- About 1% of all dicot angiosperm species are parasitic. Two separate classes of parasitic plants have been defined: holoparasites are completely dependent on host photosynthesis, while hemiparasites are photosynthetically active at least during some stages of their life cycle and sometimes draw only water

and mineral nutrients from the host. Parasitic plants can be further divided into root parasites and stem parasites.

- An essential element of parasitism is access to the vascular system of the host. Parasitic plants penetrate host tissues with specialised structures called haustoria. These grow towards the vasculature and establish connections between the parasite and the host.
- Plant parasitism has evolved several times independently. One key innovation was the evolution of highly sensitive receptors for germination stimulants exuded by plant roots—for example, strigolactones.
- Allelopathy is the inhibition of one plant species by another plant species through the production and release of toxic chemicals. For several invasive plant species it has been proposed that part of their success is attributable to toxins in root exudates. However, few examples for clear molecular evidence of such interactions exist.

References

Acevedo FE, Rivera-Vega LJ, Chung SH et al (2015) Cues from chewing insects—the intersection of DAMPs, HAMPs, MAMPs and effectors. Curr Opin Plant Biol 26:80–86

Agrawal AA, Hastings AP, Johnson MTJ et al (2012) Insect herbivores drive real-time ecological and evolutionary change in plant populations. Science 338:113–116

Agrawal AA, Konno K (2009) Latex: a model for understanding mechanisms, ecology, and evolution of plant defence against herbivory. Annu Rev Ecol Evol Syst 40:311–331

Ahuja I, Kissen R, Bones AM (2012) Phytoalexins in defence against pathogens. Trends Plant Sci 17:73–90

Alborn HT, Turlings TCJ, Jones TH et al (1997) An elicitor of plant volatiles from beet armyworm oral secretion. Science 276:945–949

Arimura G, Ozawa R, Shimoda T et al (2000) Herbivory-induced volatiles elicit defence genes in lima bean leaves. Nature 406:512–515

Bär W, Pfeifer P, Dettner K (2000) Biochemische Interaktionen zwischen Kalanchoe-Pflanzen. Biologie in unserer Zeit 30:228–234

Barbehenn RV, Peter Constabel C (2011) Tannins in plant–herbivore interactions. Phytochemistry 72:1551–1565

Bartels S, Boller T (2015) Quo vadis, Pep? Plant elicitor peptides at the crossroads of immunity, stress, and development. J Exp Bot 66:5183–5193

Baulcombe D (2004) RNA silencing in plants. Nature 431:356–363

Bednarek P, Osbourn A (2009) Plant–microbe interactions: chemical diversity in plant defence. Science 324:746–748

Benderoth M, Pfalz M, Kroymann J (2009) Methylthioalkylmalate synthases: genetics, ecology and evolution. Phytochem Rev 8:255–268

Boller T, Felix G (2009) A renaissance of elicitors: perception of microbe-associated molecular patterns and danger signals by pattern-recognition receptors. Annu Rev Plant Biol 60:379–406

Bouarab K, Melton R, Peart J et al (2002) A saponin-detoxifying enzyme mediates suppression of plant defences. Nature 418:889–892

Browse J (2009) Jasmonate passes muster: a receptor and targets for the defence hormone. Annu Rev Plant Biol 60:183–205

Buchanan B, Gruissem W, Jones R (2015) Biochemistry and molecular biology of plants, 2nd edn. Wiley, Chichester

Campos ML, Kang J-H, Howe GA (2014) Jasmonate-triggered plant immunity. J Chem Ecol 40:657–675

Caplan A, Herrera-Estrella L, Inzé D et al (1983) Introduction of genetic material into plant cells. Science 222:815–821

Cappa JJ, Pilon-Smits EAH (2013) Evolutionary aspects of elemental hyperaccumulation. Planta 239(2):267–275

Choi J, Tanaka K, Cao Y et al (2014) Identification of a plant receptor for extracellular ATP. Science 343:290–294

Conn CE, Bythell-Douglas R, Neumann D et al (2015) Convergent evolution of strigolactone perception enabled host detection in parasitic plants. Science 349:540–543

Conrath U, Kauss H (2000) Das "Immunsystem" der Pflanze. Biologie in unserer Zeit 30:202–208

Crous PW, Hawksworth DL, Wingfield MJ (2015) Identifying and naming plant-pathogenic fungi: past, present, and future. Annu Rev Phytopathol 53: 247–267

Davis EL, Mitchum MG (2005) Nematodes. Sophisticated parasites of legumes. Plant Physiol 137:1182–1188

de Jonge R, van Esse H, Kombrink A et al (2010) Conserved fungal LysM effector Ecp6 prevents chitin-triggered immunity in plants. Science 329:953–955

Dixon RA (2001) Natural products and plant disease resistance. Nature 411:843–847

Djamei A, Schipper K, Rabe F et al (2011) Metabolic priming by a secreted fungal effector. Nature 478:395–398

Dodds PN, Rathjen JP (2010) Plant immunity: towards an integrated view of plant-pathogen interactions. Nat Rev Genet 11:539–548

Dou D, Zhou J-M (2012) Phytopathogen effectors subverting host immunity: different foes, similar battleground. Cell Host Microbe 12:484–495

Engelberth J, Alborn HT, Schmelz EA, Tumlinson JH (2004) Airborne signals prime plants against insect herbivore attack. Proc Natl Acad Sci U S A 101:1781–1785

Flor HH (1971) Current status of the gene-for-gene concept. Annu Rev Phytopathol 9:275–296. https://doi.org/10.1146/annurev.py.09.090171.001423

Fu ZQ, Dong X (2013) Systemic acquired resistance: turning local infection into global defence. Annu Rev Plant Biol 64:839–863

Green TR, Ryan CA (1972) Wound-induced proteinase inhibitor in plant leaves: a possible defence mechanism against insects. Science 175:776–777

Hamilton AJ, Baulcombe DC (1999) A species of small antisense RNA in posttranscriptional gene silencing in plants. Science 286:950–952

Heil M (2008) Indirect defence via tritrophic interactions. New Phytol 178:41–61

Hopkins RJ, Van Dam NM, Van Loon JJA (2009) Role of glucosinolates in insect-plant relationships and multitrophic interactions. Annu Rev Entomol 54:57–83

Howe GA, Jander G (2008) Plant immunity to insect herbivores. Annu Rev Plant Biol 59:41–66

Howe GA, Lightner J, Browse J, Ryan CA (1996) An octadecanoid pathway mutant (JL5) of tomato is compromised in signaling for defence against insect attack. Plant Cell 8:2067–2077

Huang T, Jander G, de Vos M (2011) Non-protein amino acids in plant defence against insect herbivores: representative cases and opportunities for further functional analysis. Phytochemistry 72:1531–1537

Incarbone M, Dunoyer P (2013) RNA silencing and its suppression: novel insights from in planta analyses. Trends Plant Sci 18:382–392

Jones JDG, Dangl JL (2006) The plant immune system. Nature 444:323–329

Jung HW, Tschaplinski TJ, Wang L et al (2009) Priming in systemic plant immunity. Science 324:89–91

Kallenbach M, Bonaventure G, Gilardoni PA et al (2012) Empoasca leafhoppers attack wild tobacco plants in a jasmonate-dependent manner and identify jasmonate mutants in natural populations. Proc Natl Acad Sci U S A 109:E1548–E1557

Kay S, Bonas U (2009) How Xanthomonas type III effectors manipulate the host plant. Curr Opin Microbiol 12:37–43

Kessler A, Halitschke R, Baldwin IT (2004) Silencing the jasmonate cascade: induced plant defences and insect populations. Science 305:665–668

Kessler D, Gase K, Baldwin IT (2008) Field experiments with transformed plants reveal the sense of floral scents. Science 321:1200–1202

Konno K, Ono H, Nakamura M et al (2006) Mulberry latex rich in antidiabetic sugar-mimic alkaloids forces dieting on caterpillars. Proc Natl Acad Sci U S A 103:1337–1341

Kwon C, Neu C, Pajonk S, Yun HS, Lipka U, Humphry M, Bau S, Straus M, Kwaaitaal M, Rampelt H, El Kasmi F, Jürgens G, Parker J, Panstruga R, Lipka V, Schulze-Lefert P (2008) Co-option of a default secretory pathway for plant immune responses. Nature 451(7180):835–840. https://doi.org/10.1038/nature06545

Lozano-Torres JL, Wilbers RHP, Gawronski P et al (2012) Dual disease resistance mediated by the immune receptor Cf-2 in tomato requires a common virulence target of a fungus and a nematode. Proc Natl Acad Sci U S A 109:10119–10124

Melotto M, Underwood W, Koczan J et al (2006) Plant stomata function in innate immunity against bacterial invasion. Cell 126:969–980

Mithöfer A, Boland W (2012) Plant defence against herbivores: chemical aspects. Annu Rev Plant Biol 63:431–450

Mousavi SAR, Chauvin A, Pascaud F et al (2013) GLUTAMATE RECEPTOR-LIKE genes mediate leaf-to-leaf wound signalling. Nature 500:422–426

Mukhtar MS, Carvunis A-R, Dreze M et al (2011) Independently evolved virulence effectors converge onto hubs in a plant immune system network. Science 333:596–601

Návarová H, Bernsdorff F, Döring A-C, Zeier J (2012) Pipecolic acid, an endogenous mediator of defence amplification and priming, is a critical regulator of inducible plant immunity. Plant Cell 24:5123–5141

Nürnberger T, Brunner F, Kemmerling B, Piater L (2004) Innate immunity in plants and animals: striking similarities and obvious differences. Immunol Rev 198:249–266

Pearce G, Strydom D, Johnson S, Ryan CA (1991) A polypeptide from tomato leaves induces wound-inducible proteinase inhibitor proteins. Science 253:895–897

Periyannan S, Moore J, Ayliffe M et al (2013) The gene Sr33, an ortholog of barley Mla genes, encodes resistance to wheat stem rust race Ug99. Science 341:786–788

Pichersky E, Noel JP, Dudareva N (2006) Biosynthesis of plant volatiles: nature's diversity and ingenuity. Science 311:808–811

Römer P, Hahn S, Jordan T et al (2007) Plant pathogen recognition mediated by promoter activation of the pepper Bs3 resistance gene. Science 318:645–648

Saintenac C, Zhang W, Salcedo A et al (2013) Identification of wheat gene Sr35 that confers resistance to Ug99 stem rust race group. Science 341:783–786

Schnee C, Köllner TG, Held M et al (2006) The products of a single maize sesquiterpene synthase form a volatile defence signal that attracts natural enemies of maize herbivores. Proc Natl Acad Sci U S A 103:1129–1134

Schwach F, Vaistij FE, Jones L, Baulcombe DC (2005) An RNA-dependent RNA polymerase prevents meristem invasion by potato virus X and is required for the activity but not the production of a systemic silencing signal. Plant Physiol 138:1842–1852

Snyder BA, Nicholson RL (1990) Synthesis of phytoalexins in Sorghum as a site-specific response to fungal ingress. Science 248:1637–1639

Soosaar JLM, Burch-Smith TM, Dinesh-Kumar SP (2005) Mechanisms of plant resistance to viruses. Nat Rev Micro 3:789–798

Stinson KA, Campbell SA, Powell JR et al (2006) Invasive plant suppresses the growth of native tree seedlings by disrupting belowground mutualisms. PLoS Biol 4:e140

Tsuda K, Somssich IE (2015) Transcriptional networks in plant immunity. New Phytol 206:932–947

Turlings TC, Tumlinson JH, Lewis WJ (1990) Exploitation of herbivore-induced plant odors by host-seeking parasitic wasps. Science 250:1251–1253

Uknes S, Mauch-Mani B, Moyer M et al (1992) Acquired resistance in Arabidopsis. Plant Cell 4:645–656

Unsicker SB, Kunert G, Gershenzon J (2009) Protective perfumes: the role of vegetative volatiles in plant defence against herbivores. Curr Opin Plant Biol 12:479–485

Weir TL, Park S-W, Vivanco JM (2004) Biochemical and physiological mechanisms mediated by allelochemicals. Curr Opin Plant Biol 7:472–479

Westwood JH, Yoder JI, Timko MP, dePamphilis CW (2010) The evolution of parasitism in plants. Trends Plant Sci 15:227–235

Whitham TG, Bailey JK, Schweitzer JA et al (2006) A framework for community and ecosystem genetics: from genes to ecosystems. Nat Rev Genet 7: 510–523

Whitham TG, Difazio SP, Schweitzer JA et al (2008) Perspective—extending genomics to natural communities and ecosystems. Science 320:492–495

Wu J, Baldwin I (2010) New insights into plant responses to the attack from insect herbivores. Annu Rev Genet 44(44):1–24

Xiang T, Zong N, Zou Y, Wu Y, Zhang J, Xing W, Li Y, Tang X, Zhu L, Chai J et al (2008) Pseudomonas syringae effector AvrPto blocks innate immunity by targeting receptor kinases. Curr Biol 18:74–80

Xie X, Yoneyama K, Yoneyama K (2010) The strigolactone story. Annu Rev Phytopathol 48:93–117

Yoshida S, Cui S, Ichihashi Y, Shirasu K (2016) The haustorium, a specialized invasive organ in parasitic plants. In: Merchant SS (ed) Annual review of plant biology, vol 67. Annual Reviews, Palo Alto, pp 643–667

Yoshida S, Shirasu K (2012) Plants that attack plants: molecular elucidation of plant parasitism. Curr Opin Plant Biol 15:708–713

Züst T, Heichinger C, Grossniklaus U et al (2012) Natural enemies drive geographic variation in plant defences. Science 338:116–119

Part II

Physiological and Biophysical Plant Ecology

Cocus nucifera, the coconut palm, a pantropical tree with nuts that are capable of floating, has long been used by humans for a wide variety of purposes. The trunk is used as timber for buildings, the leaves for roofing material, the fibrous mesocarp in ropes, and the nut shell is used as a drinking cup. The liquid endosperm provides vitamin-rich coconut milk, while the hard endosperm supplies the fat-containing copra. Worldwide the production of copra is two to four million tonnes per year. Coconut trees are pioneers along tropical coasts, especially on coral reefs, which are saline and receive high solar radiation. The picture shows a "desert" area on the Atlantic coast, Punta Cahuita, Costa Rica. (Photo: E.-D. Schulze)

Physiological and biophysical plant ecology investigates abiotic conditions, the responses of plant species to abiotic factors, and the transport of carbon, water and nutrients between plants and the surrounding soil or atmosphere. The range of possible responses of plants to the environment is wide and includes molecular, cellular and structural changes. The relationships between plants with soils and the atmosphere also include (bio)physical processes, for example the energy balance of plants. Plants have been very successful at adapting even to extreme environments. During the course of evolution, plants have occupied every terrestrial habitat, ranging from tropical climates to the eternal ice, from bogs to deserts, from extremely saline to nutrient-limited habitats. Plants have also developed manifold interactions with other organisms, ranging from mutualism with pollinators to antagonism with herbivores, and pathogen defence. These adjustments range from reversible **acclimations** (e.g. leaf movements) to non-reversible **modifications** (phenotypic plasticity) and long-term evolutionary **adaptations**. The latter occur as genetic changes in individuals of a population that may not even be phenotypically visible and that are not necessarily disadvantageous under the prevailing conditions of competition and stress in the habitat. However, if conditions change, for example, climate, supply of nutrients or competition, then individual plants with certain advantageous traits are able to compete better, have a better chance of survival, to maintain or enlarge the area they occupy, and to increase their fitness. This process is called **pre-adaptation**. Traits that are "advantageous" for certain habitats develop before the actual change of growth conditions and are the precondition for the colonisation of new habitats.

Plants occur in a wide variety of forms, from giant trees hundreds of years old, with a life cycle from germination to the flowering age of decades to centuries, to annual species in arid regions, with a life cycle from seed to seed of only a few days. Thus, plant responses to the environment not only occur at the biochemical level but also include structural changes and adjustments of the life span. The **physiological ecology** (also called **ecophysiology**) of plants considers the reactions at the level of individual organs (e.g. height of shoot, size of leaf, depth of root) or relationships between organs (e.g. distribution of resources between shoot and root, regulation of coordination between shoot and root). **Biophysical ecology** includes the laws of physics that control the fluxes of material between the plant individual and its environment. Thus, this section of the textbook provides the connection between Molecular Ecology (Part I) and Community Ecology (Part IV).

Part II on physiological and biophysical plant ecology is subdivided into the following chapters:

- Chap. 9: Thermal balance: Certain extreme temperatures must not be exceeded
- Chap. 10: Water relations: Active life requires cells maintaining a high water content
- Chap. 11: Nutrient relations: Growth is possible only with the supply of essential nutrient elements
- Chap. 12: Carbon relations: Life requires energy and carbon compounds to supply existing organs and resources for respiration, growth and reproduction

9

Thermal Balance of Plants and Plant Communities

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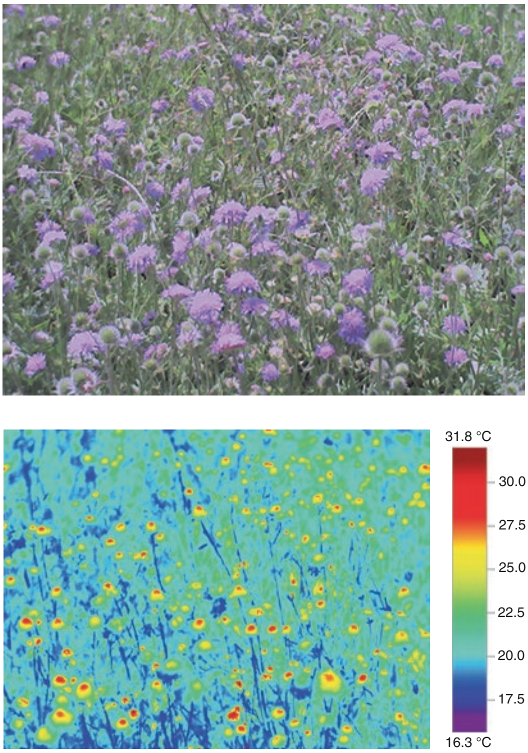


Infrared photo of a flowering meadow: The significance of the thermal balance becomes apparent from this image of a meadow with flowers of *Knautia arvensis* (common name: field scabious). The thermal infrared camera measures the emitted thermal radiation, based on the Stefan–Boltzmann law, using a fixed thermal emissivity factor (here: 0.95). The average temperature of the vegetation is 21.6 °C, almost 4 K above the ambient air temperature (18 °C), with the temperature of green leaves ranging between 16 and 22 °C. Only the flower heads reach temperatures above 30 °C, which is in fact close to the optimal temperature of foraging bees (35 °C). The high temperature of the flowers results from absorption of incoming solar radiation (960 W m^{-2} when the picture was taken), sensible heat exchange with the surrounding air and low transpiration rates of the flowers compared with their surrounding vegetation tissues. While all of these physiological and biophysical processes contribute to the thermal balance of plants and their coupling to the atmosphere, temperature variations of >10 K are easily possible in apparently homogenous meadow vegetation. The science of the thermal balance is aimed at understanding and explaining this temperature variation.
(Photos: T. Lanners)

E.-D. Schulze et al., *Plant Ecology*, https://doi.org/10.1007/978-3-662-56233-8_9

The thermal relations of plants are part of a plant's **energy balance**—that is, the sum of all radiative energy fluxes, the evaporation of water and sensible heat losses. Only about 1–2% of the incident solar energy is used for photosynthesis. The remainder of the energy (about 700–1000 W m^{-2} at full sunlight near the ground) has to be reflected or emitted again in order to keep the energy budget balanced. For example, plants can avoid the absorption of short-wave radiation by reflection, which depends on the reflectivity (the **albedo**) of their surface (e.g. waxes, hairs). Further ways to balance the incoming solar energy are the emission of long-wave radiation to the surrounding air (**sensible heat**) or the evaporation of water (i.e. transpiration, **latent heat**). The **temperature** of tissues results from the energy balance of incoming and outgoing radiation, heat and water fluxes, as well as from metabolic activity. Generally, the effect of metabolism on tissue temperatures (i.e. any process where energy is involved: photosynthesis, fluorescence, respiration, etc.; Chap. 4) is low in comparison with the magnitude of the sensible and latent heat fluxes (Oke and Christen 2015). To avoid damage, the temperature must be kept within certain physiological limits, even in an environment with variable incoming solar radiation. The energy balance must be regulated by the plant in such a way that damaging temperatures do not occur, even for short periods of time. Moreover, the temperature should be close to the range of the **physiological optimum** of metabolic processes or in a range that suits other purposes (e.g. pollination), which could be above or below the general temperature of the habitat. Some plants are able to influence their organ temperatures over a wide range, but they remain bound to biophysical processes such as reflection, absorption and transmission of radiation. For example, in the inflorescences of *Araceae*, temperatures of 20–40 K greater than in ambient air can be produced via cyanide-resistant electron transport in respiration in order to attract pollinators. In arid climates, leaf temperatures may be up to 17 K below the ambient temperature because of transpiration, thus reducing the risk of heat damage (Lange 1959). These examples nicely illustrate how the temperature of a plant or its tissues is the result of an energy balance and is regulated within certain limits by physiological processes.

In this book, the microclimatic environment of plants and communities is presented as well because the lower layers of the atmosphere—the so-called **atmospheric boundary layer**—are clearly part of a plant's habitat. First, the concepts of radiation and energy balances are introduced, followed by a biophysical analysis of the energy balance of a leaf and its effects on a plant's responses to the environment. The chapter finishes with a description of the adaptation of plants to extreme high and low temperatures. Molecular responses of plants at extreme temperatures are discussed in Chap. 4.

9.1 Energy Balance of the Atmospheric Boundary Layer

The **energy balance** of plants is closely connected to processes in the atmosphere, particularly to its radiation balance and to physical transport processes, which are typically studied in meteorology (see textbooks by Lutgens et al. (2013), Stull (1988) and Wallace and Hobbs (2006)). However, the absorption of solar energy used for metabolic processes, as well as the conversion into heat fluxes and the link to water vapour fluxes, take place close to the ground, where climate conditions may largely deviate from the conditions in the free troposphere. Gregor Kraus (1911) was the first scientist to describe this phenomenon quantitatively on limestone sites near Würzburg, Germany, and thus founded a new discipline of **micrometeorology** (see textbooks by Jones (2014), Monson and Baldocchi (2014) and Oke and Christen

(2015)). Thus, micrometeorology focuses on the boundary layer of the atmosphere—the zone near the Earth’s surface where the mean wind speed is reduced in comparison with the free airstream in the upper atmosphere.

The radiation balance of the atmosphere and the energy balance at the ground surface—the habitat of plants—are strongly dependent on the composition of the atmosphere and the optical properties of its constituents. While many trace gases and air pollutants (e.g. ozone, nitrous oxide, ammonia, methane) affect plant life, water vapour (Box 9.1), CO_2 and O_2 are the most important gases for a plant, highly relevant for its distribution, growth and fitness. Here, we will focus on the energy balance at ground level, linking radiation and sensible heat to water vapour and CO_2 in the atmosphere. Note: By definition, an **energy balance** is balanced (i.e. set to zero), while an **energy budget** can be out of balance (i.e. it can be positive or negative, or at zero).

Through the formation of clouds, **water vapour** influences:

- Absorption and reflection of short-wave radiation in the atmosphere, affecting the solar radiation reaching the Earth’s surface.
- Absorption and emission of long-wave radiation.
- Density of the atmosphere and atmospheric transport processes, including precipitation, depending on water vapour saturation.
- Evaporation from the Earth's surface, depending on saturation deficit and on plant cover.
- Transpiration of vegetation.

Carbon dioxide influences:

- The thermal budget of the lower atmosphere by absorption and emission of long-wave radiation.
- Photosynthesis, as one of the key ingredients in this process.

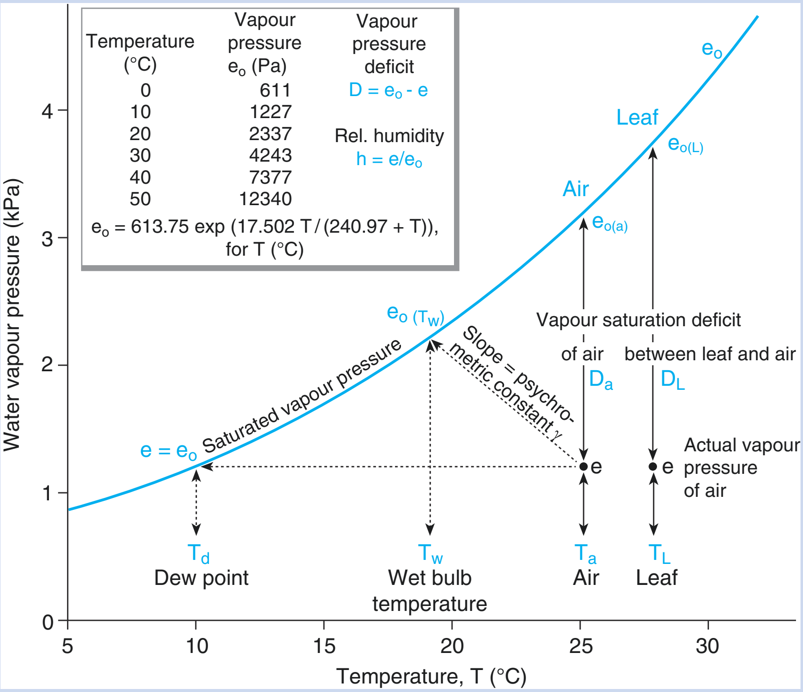
Box 9.1: Water Vapour in the Atmosphere

The chemical composition of the lower atmosphere consists of the following gases: about 78% N_2, 21% O_2, 1% Ar, 0.6–4% H_2O, 0.040% (= 400 parts per million (ppm)) CO_2, and further trace and noble gases of natural and anthropogenic origin. For exact data on the composition of air, see List (1971) and the Intergovernmental Panel on Climate Change (IPCC) 5th Assessment Report (2013). Here, we focus on water vapour as the most abundant greenhouse gas.

Water vapour pressure: The amount of water vapour that can be retained by the atmosphere, termed the saturation pressure (e_o), depends on air temperature and air pressure. The pressure of the atmosphere without water vapour, p_a, is derived from the measured pressure of the atmosphere, p, and the actual vapour pressure, e, as ($p_a = p - e$). At a constant air pressure, the vapour pressure rises almost exponentially with temperature.

Humid air is lighter than dry air, as determined by the relationship between the molecular weights of H_2O and the main constituent of air N_2, which is 0.64 (18/28). Thus, mixing of water vapour into dry air displaces some of the heavier constituents (when pressure is kept constant) and thus reduces the mass of this air volume. Hence, humid air in the lower atmosphere rises until water vapour condenses when cooling off, thus forming dew or fog at the ground or clouds in the atmosphere. For the same reason, condensation droplets form on the ceilings of humid rooms or on the lids of Petri dishes. This corresponds to dew formation in ecosystems.

The atmosphere is not always saturated with water vapour. The actual vapour pressure of the atmosphere (e) is mostly lower than the saturation value (e_o). There are a number of



Temperature (°C)	Vapour pressure e_o (Pa)	Vapour pressure deficit
0	611	$D = e_o - e$
10	1227	
20	2337	Rel. humidity
30	4243	$h = e/e_o$
40	7377	
50	12340	

$e_o = 613.75 \exp(17.502\, T/(240.97 + T))$, for T (°C)

Fig. 9.1 Dependence of saturation vapour pressure, e_o, on temperature, T. γ psychrometric constant, D_a saturation deficit of air, e actual vapour pressure of the atmosphere, $e_{o(a)}$ saturation vapour pressure at air temperature, $e_{o(L)}$ saturation vapour pressure at leaf temperature (where e_o (measured in pascals) can be approximated as $e_o = 613.75 \exp(17.502\ T/(240.97 + T))$ with T (in degrees Celsius)), T_a air temperature, T_d dew point temperature, T_L leaf temperature, T_w wet bulb temperature

terms that are used to describe the humidity of air (Fig. 9.1).

The following definitions hold in meteorology:

- **Absolute humidity**: $c_w = (2.17/T)\ e$, unit: grams per cubic metre. (Note: The volume of air is temperature and pressure dependent.)
- **Relative humidity**: $h = e/e_o$, normally given as a percentage. (Note: At constant vapour pressure, this is dependent on T.)
- **Water vapour saturation deficit of the atmosphere**: $D_a = (e_o - e)$, unit: kilopascals (often shortened to VPD (vapour pressure deficit)). (Note: The value is dependent on temperature, since e_o changes with T.)
- **Water vapour saturation deficit between leaf and atmosphere**: $D_L = e_{o(L)} - e$, where $e_{o(L)}$ is the saturation vapour pressure at leaf temperature and e is the actual vapour pressure in the atmosphere; this term is important as the modifying driving force for transpiration in plants (often also abbreviated as VPD or—better—WSD (water saturation deficit)).
- **Dew point temperature**: T_d for $e = e_o$ (the temperature, T, at which condensation temperature is reached and therefore condensation begins). This temperature is used for highly precise measurements of e.
- **Wet bulb temperature**: T_w. This temperature is measured to determine the actual vapour pressure (with a psychrometer): $e = e_{o(Tw)} - \gamma(T_a - T_w)$, where γ (the psychrometric constant) is 66.1 Pa K^{-1} for a ventilated thermometer at 100 kPa air pressure and 20 °C.

The radiation, as well as the energy balances at the ground, strongly depend on the optical properties of the atmosphere and its constituents, which interact via different biophysical processes (Mitchell 1989; IPCC 2013) and create rather complex interactions (Fig. 9.2a). The solar radiation (**incident radiation** on a horizontal surface) entering the Earth's atmosphere occurs in the short-wave range at about 6000 Kelvin (K), with maximum radiation at about a 0.6 μm wavelength (in the visible light). The mean radiant energy flux (measured in watts per square metre or joules per square metre per second) at the upper limit of the atmosphere is about 1361 W m^{-2} (**solar constant**, **solar irradiance**; measured in the stratosphere). Since the Earth is a sphere, the mean radiation flux during the day, averaged over the entire surface of the Earth, is about 340 W m^{-2} (±2 W m^{-2}) (Wild et al. 2013). This incoming short-wave radiation (I_s; extraterrestrial global radiation) is partially reflected, partially balanced by outgoing long-wave radiation (**thermal radiation**, I_l), which by itself is a balance between thermal radiation of the atmosphere and thermal radiation from the stratosphere at a temperature of 255 K.

Long-wave radiation follows the **Stefan–Boltzman law** (Eq. 9.1):

$$I_1 = \sigma T^4, \tag{9.1}$$

where $\sigma = 5.67 \times 10^{-8}$ (W m^{-2} K^{-4})—the Stefan–Boltzman constant—and T is the temperature in Kelvin. Without an atmosphere (with naturally occurring greenhouse gases), there would be no (downward, long-wave) back-radiation from the atmosphere. The average temperature on Earth would be about −18 °C (instead of about 16 °C), and thus no plant life would be possible on Earth.

However, atmospheric gases, particularly water vapour (H_2O) and CO_2, have the effect that part of the incoming solar radiation in the short-wave range is absorbed and reflected (Fig. 9.2b). Thus, the incoming short-wave radiation is limited to a narrow **radiation window**, with a maximum in the visible range (0.4–0.7 μm). In addition, ultraviolet (UV) radiation of the short-wave spectrum is absorbed particularly by ozone. The emitted, outgoing long-wave radiation (far-infrared) is strongly absorbed by H_2O vapour and CO_2, making the Earth hospitable for life. However, CO_2 and H_2O have an absorption minimum (**emission window**) between 8 and 14 μm in wavelength, in which the Earth's surface can lose thermal energy to space. However, with increasing greenhouse gas concentrations in the atmosphere, long-wave radiation is increasingly trapped in the Earth's atmosphere, and global temperatures are rising (Chap. 21).

A clear distinction is made between the radiation budget and the energy balance. The **radiation budget** comprises the sum of all short- and long-wave radiation fluxes, including their reflection, absorption or emission: incident short-wave solar radiation is absorbed and reflected by gas molecules, aerosol particles and clouds in the atmosphere (Table 9.1, Fig. 9.2c). A fraction of the incoming short-wave radiation, termed **albedo** (**α**), is reflected at the Earth's surface, depending on the type of land or vegetation cover. Long-wave radiation is emitted by the land surface and escapes into space. However, part of this emission is absorbed by clouds or trace gases, leading to back-radiation to the Earth's surface. Reflection, absorption and emission processes result in energy fluxes with different signs (representing the direction of the flux) and are additive in determining the energy balance of the Earth. On the other hand, the **energy balance** also includes—among short- and long-wave radiation fluxes—how radiation energy is dissipated into heat fluxes. These heat fluxes are the sum of thermal convection (**sensible heat flux**), latent heat of evapotranspiration from surfaces and of vegetation (**latent heat flux**), and the flux of heat into the soil (**soil heat flux**). While the radiation budget is normally not at equilibrium (i.e. it differs from zero), the energy budget must be zero since it is the sum of all processes (the **law of conservation of energy**). Thus,

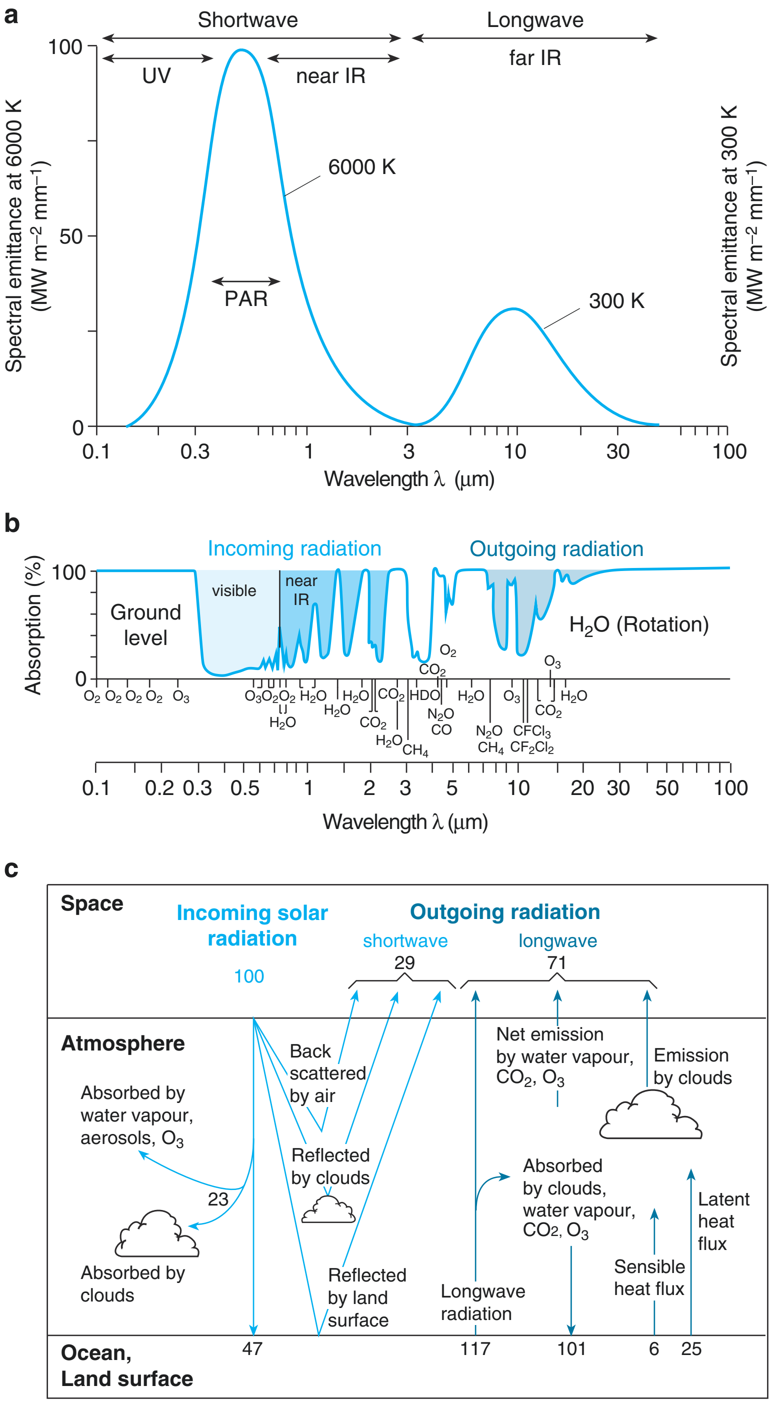


Fig. 9.2 Energy distribution and the incident radiation balance of the Earth. **a** Spectral distribution of short-wave incident solar radiation and long-wave thermal radiation of the Earth (Mitchell 1989). **b** Spectral absorption of incident radiation by gases in the atmosphere. Note that ozone absorbs short-wave radiation and ultraviolet light (UV), while CO_2 absorbs in the long-wave range. In addition, CO, N_2O and chlorofluorocarbons absorb emitted (outgoing) long-wave radiation (Mitchell 1989). **c** Energy balance of the Earth: transformation of incident radiation to thermal radiation at the ground surface and in the atmosphere. The percentages given are based on the average global solar incident radiation of 340 W m^{-2}. (Modified from Wild et al. (2013) and Hartmann et al. (2013))

the energy budget is balanced (Fig. 9.2c) (Wild et al. 2013; Hartmann et al. 2013).

The net **radiation budget** of the Earth (R_n; n = net) may be separated into a net radiation budget at the top of the atmosphere (R_{nA}) and a net radiation budget at the ground surface (R_{nG}) as expressed by the following equations:

$$R_{nA} = I_{sA} - \rho_{sA} I_{sA} - I_{lA} \tag{9.2}$$

Table 9.1 Energy balance[a] of the Earth (after Hartmann et al. 2013)

Input and processes contributing to radiation and energy balance		Radiation ($W\ m^{-2}$)	Relative contribution [rounded] (%)
Radiation budget at top of atmosphere			
Incident solar radiation (short-wave)	I_{sA}	+340	100
– Reflection (short-wave)	$\rho_{sA}I_{sA}$	−100	−29
– From aerosols and clouds		−76	22
– From land surface		−24	7
– Emission (long-wave)	I_{lA}	−240	−71
Net radiation budget at top of atmosphere	R_{nA}	0	0
Radiation budget at ground surface			
Incident solar radiation (short-wave)	I_{sA}	+340	100
– Reflection (short-wave)	$\rho_{sA}I_{sA}$	−100	−29
– From aerosols and clouds		−76	22
– From land surface		−24	7
– Absorption in the atmosphere (short-wave)		−79	−23
Net radiation input to ground (short-wave)	I_{sG}	*+161*	*+47*
Emission from land surface (long-wave)	I_{lG}	−398	−117
Radiation re-emitted to ground by clouds and atmosphere (long-wave)	I_{lAtoG}	+342	+101
Net radiation budget at ground surface	R_{nG}	105	31
Energy balance at ground surface			
Net radiation budget at ground surface	R_{nG}	105	31
Energy losses from ground surface			
– By sensible heat (long-wave)	H	−20	−6
– By latent heat (evapotranspiration)	λE	−85	−25
Energy balance at ground surface	Φ_{nG}	0	0

[a] The energy conversion with reflection, absorption and long-wave emission occurs in the atmosphere and at the ground surface. The solar constant (1361 $W\ m^{-2}$) is the amount of energy that arrives at a surface above the atmosphere vertical to the incident radiation from the sun. In contrast, the solar energy arriving at the top of the Earth's atmosphere (340 $W\ m^{-2}$) is the average amount of solar energy flux driving the Earth's climate system. The value for long-wave outgoing emissions takes the effect of a global energy imbalance into account (approximately 0.6 $W\ m^{-2}$), inferred from ocean heat content measurements. (Wild et al. 2013)

where R_{nA} is the budget of radiation fluxes at the top of the atmosphere (Eq. 9.2). I_{sA} is the short-wave incoming (incident) solar radiation at the upper boundary of the atmosphere (extraterrestrial global radiation), ρ_{sA} is the ability of the atmosphere (clouds, gases) and the land surface to reflect incoming short-wave radiation, and I_{lA} is the total long-wave emission from the atmosphere (clouds, gases) and the land surface. Thus, R_{nA} can be calculated as 340 $W\ m^{-2}$ minus 100 $W\ m^{-2}$ minus 240 $W\ m^{-2}$, resulting in 0 $W\ m^{-2}$ at the top of the atmosphere.

The radiation budget at the ground surface may be expressed analogously. The "ground surface" is considered as the Earth's surface, such as the soil surface or the top of a canopy. The net radiation budget at the Earth's ground surface (R_{nG}) is the sum of the net short-wave radiation input to the ground and the difference between outgoing long-wave emission from the land surface and **back-radiation**—that is, long-wave radiation re-emitted to the ground by clouds and the atmosphere (Eq. 9.3).

$$R_{nG} = I_{sG} - I_{lG} + I_{lA\,to\,G} \qquad (9.3)$$

where R_{nG} is the budget of the radiation fluxes at the ground surface. I_{sG} is the net incoming short-wave radiation at the ground level, calculated as the difference between incident short-wave solar radiation (I_{sA}), the short-wave radiation reflected by aerosols and clouds ($\rho_{sA}I_{sA}$), and the short-wave radiation absorbed in the atmosphere. This net short-wave radiation is also often just called **light**. I_{lG} is the long-wave radiation emitted from the land surface, and I_{lAtoG} is the long-wave radiation re-emitted to the ground by the clouds and the atmosphere, also called back-radiation. Thus, R_{nG} can be calculated as 161 W m^{-2} minus 398 W m^{-2} plus 342 W m^{-2}, resulting in 105 W m^{-2} at the ground surface. The net radiation budget, R_{nG}, is measured with a radiometer with a polyethylene dome, which is also transparent to long-wave radiation.

Moreover, the **energy balance** at the ground surface (i.e. at the soil or canopy surface) also includes the heat fluxes into which the net radiation at the ground is dissipated, thus balancing the energy budget (Eq. 9.4).

$$\Phi_{nG} = R_{nG} - H - \lambda E - G - M = 0 \qquad (9.4)$$

where Φ_{nG} is the energy balance at the ground surface (soil or canopy), and R_{nG} is the net radiation budget at the ground surface. The **sensible heat flux**, H, is proportional to the specific heat capacity of air (c_p = 1012 J kg^{-1} K^{-1}) and the temperature difference ΔT between the ground surface and the atmosphere, ρ is the density of air: (1.1884 kg m^{-3} at 20 °C and 100 kPa of air pressure). H, the upward flux of sensible heat, is dependent on the coupling of the exchange from the surface to the atmosphere. This coupling is expressed by the boundary resistance for heat transfer, r_b:

$$H = \frac{\rho c_p \Delta T}{r_b} \qquad (9.5)$$

In Eq. 9.4, λE is the **latent heat flux**, whereby λ expresses the energy required for evaporation of water (2.454 MJ kg^{-1} at 20 °C) and E is the evaporation from the soil and the transpiration of vegetation (kg m^{-2} s^{-1}). Furthermore, Φ_{nG} also includes the soil heat flux—that is, the downward-oriented sensible heat flux, G (omitted in Table 9.1 because of its negligible magnitude at global level). Energy used in metabolism (M) is very small in comparison with all other energy balance components and thus is most often ignored (as in Table 9.1).

The annual incoming short-wave solar radiation (Fig. 9.3) is unevenly distributed over the Earth's surface. Net radiation is highest over dry areas because there are fewer clouds, and it decreases towards the poles to about 40% and in the tropics to 70% of the radiation in the upper atmosphere. The global distribution of radiation is reflected in the global temperature and, in particular, low temperatures and **frosts**, and thus affects vegetation distribution, as well as plant performance (Chaps. 4 and 21).

About 342 W m^{-2} of the 398 W m^{-2} long-wave emissions from the Earth's ground surface (I_{lG} in Table 9.1) are re-emitted to the ground by clouds and the atmosphere (I_{lAtoG}). This effect, also called the **greenhouse effect**, is due to clouds and trace gases and their effect on the outgoing long-wave radiation from the Earth. Water vapour, CO_2, methane (CH_4), nitrous oxide (N_2O) and other trace gases such as ozone and anthropogenic **chlorofluorocarbons** (CFCs) absorb long-wave radiation (I_{lAtoG}) and re-emit it towards the ground, affecting the temperature of the atmosphere of the Earth—that is, its climate (Stott et al. 2001). These trace gases are therefore called **greenhouse gases**. In particular, ozone and CFCs absorb exactly at the wavelength of the maximum long-wave emission by the Earth and are thus more effective than trace gases such as CO_2, CH_4 and N_2O, which decrease the outgoing radiation at the edge of the absorption spectrum (Fig. 9.2b). Further details will be discussed in Part 5. Trace gases in the Earth's atmosphere are to a certain extent analogous to the window glass of a greenhouse. As window or greenhouse glass is more permeable to short-wave radiation than to long-wave radiation, short-wave radiation passes through the window glass without resistance and is absorbed by the atmosphere and ground surfaces inside the greenhouse, leading to heating of this volume. At the same time, long-wave radiation is emitted at the temperature of this absorbing volume, but this long-wave radiation cannot pass through the glass. It is thus “trapped” in the greenhouse. As a consequence, the temperature in the greenhouse further increases by heat conduction from the absorbing surfaces, since energy enters (as short-wave radiation) but does not exit (as long-wave radiation). However, the greenhouse effect in a greenhouse is intensified in comparison

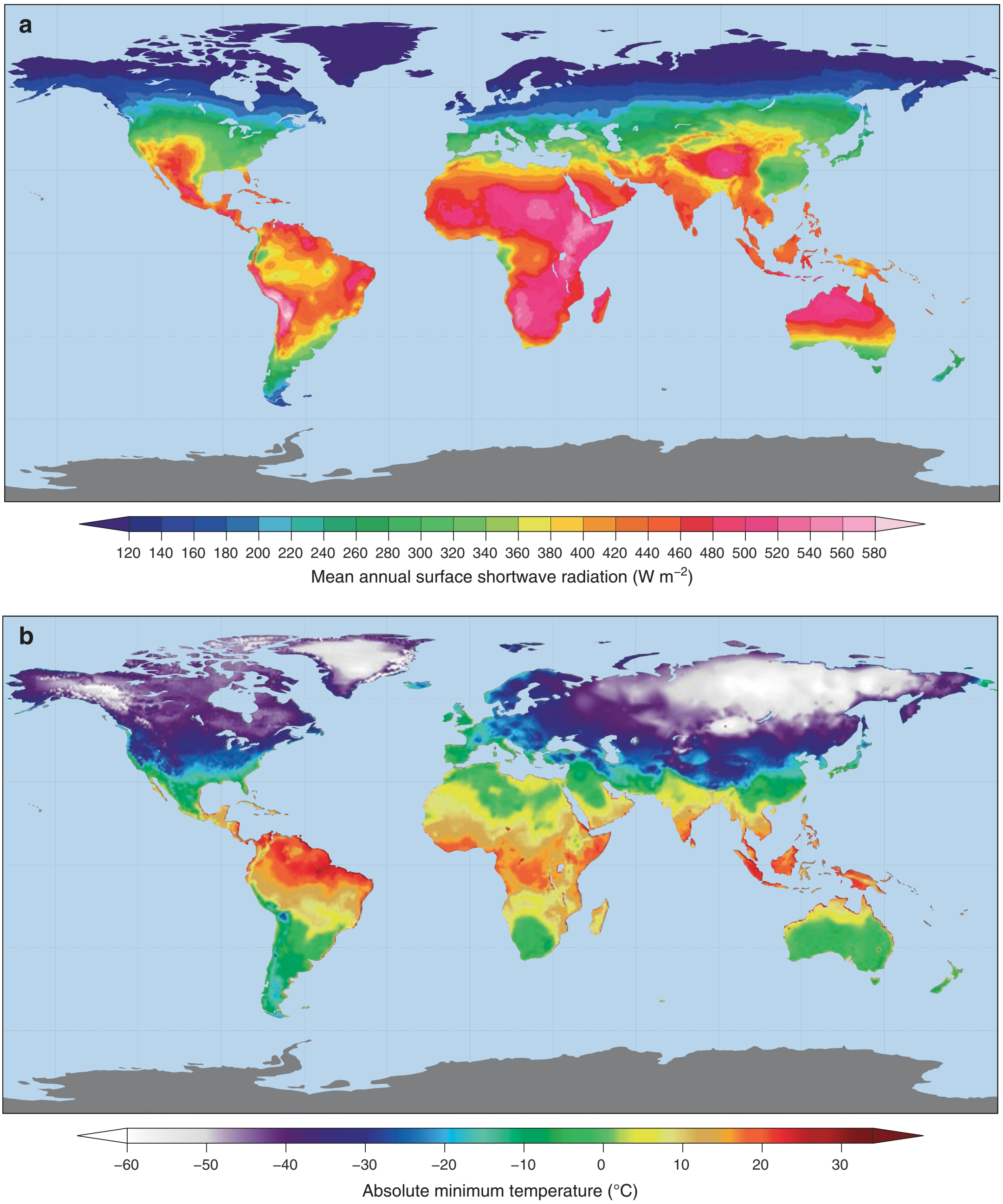


Fig. 9.3 Global distribution of solar radiation and occurrence of frosts. **a** Solar radiation is given as short-wave incident radiation of the sun at the Earth’s surface. **b** Frosts are given as absolute minimum temperatures recorded. (Images by J. Kaplan)

with the Earth's greenhouse gas effect, since convective transport of the heated air masses is prevented in a closed greenhouse but is possible in the environment outside confined buildings.

9.2 Microclimate Near the Ground Surface

9.2.1 Daily Changes in Temperature Near the Ground

As seen in Sect. 9.1, the **microclimate at ground level**—most relevant to plant life—is regulated by the same processes that are active in the atmosphere. However, larger extremes occur near the ground because of the exchange of energy with the ground, which could be bare soil or the canopy of a plant community (Fig. 9.4). The consequences of short-wave energy absorption and long-wave emission on temperature become most apparent during the **daily course of temperatures** of bare ground during a clear day (Walter 1960; Gates 1965).

At midnight: The long-wave radiation budget is characterised by high outgoing radiation and low incoming radiation fluxes, which substantially cool the Earth's surface. The negative radiation budget is partially compensated by heat conduction from the soil and by low heat exchange (via convection due to wind) with the air layers near the soil surface. Formation of dew and hoar frost may partially compensate this effect owing to heat released during condensation and freezing. During a cloud-free night, temperatures near the ground may fall more than 10 K below the temperature of the atmosphere 2 m above the ground. In the soil, the temperature increases with depth, reaching a time-lagged temperature minimum well after midnight, just before sunrise. At greater depths, the mean temperatures are almost constant (Scheffer 2002). This night-time cooling can limit the distribution of plant species, particularly at sites where diel temperature differences (i.e. over 24 h) can be very large—for example, at alpine elevations or in semi-deserts and deserts.

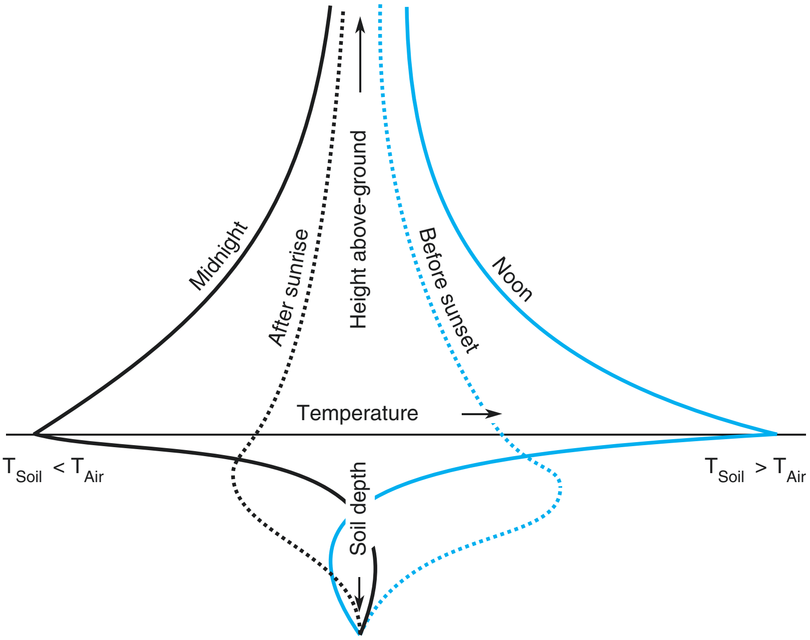


Fig. 9.4 Daily course of temperature. Above- and below-ground diurnal temperature profiles over bare ground during the course of a day. (After Gates (1965))

At sunrise: Incoming solar radiation quickly compensates outgoing net long-wave radiation from the soil surface. Because of the net emission to the atmosphere at night (see above) and the heat transfer into the soil, soil temperatures initially still decrease with depth during the early morning before they rise quickly at shallow depths, driven by air temperature changes, while they approach the mean temperatures of the season at greater soil depths.

At midday: Temperatures at the ground may rise up to 20 K above air temperatures measured 2 m above the ground. Heat transfer is via convection (heating of the atmosphere and development of turbulence) and heat conductance into the soil. The temperature decreases with soil depth and still shows a minimum dependent on the previous night, before reaching the mean temperature of the season at greater depth. These potentially very high temperatures during the day may impair plant regeneration at open sites—for example, after a clear-cut, in a natural forest gap or right after sowing at arable sites.

At sunset: The soil surface temperature decreases with the decreasing incoming radiation, but the temperature within the soil still rises because of the heatwave reaching the deeper soil with a time lag.

9.2.2 Modification of Environmental Radiation and Temperature by Abiotic Factors

Daily variations of temperature at the soil surface and average annual temperatures are affected by the soil conditions and site exposure (Chap. 18).

Heat conductivity and heat storage in soil: Dry soils have low heat conductivity and warm substantially faster at the surface during the day, because of incoming short-wave solar radiation, and cool greatly during the night, as the incoming (re-emitted) long-wave radiation is mainly balanced by the outgoing long-wave radiation from the soil. Moreover, in dry soils, heat exchange is limited to a small volume. On limestone near Würzburg, Germany, maximum surface temperatures of 60 °C have been measured (Kraus 1911). In contrast, wet soils have high heat conductivity and heat capacity, and thus lower daily amplitudes of temperature. Because of the higher evaporation and thus larger evaporative cooling effects on wet soils, their annual average temperatures are lower than those of dry soils.

Optical characteristics of surfaces: Absorption of incoming radiation is increased on black surfaces of rock or humus; reflection is increased on white mineral soils and with snow cover. With black organic cover, soil surface temperatures of more than 50 °C have been observed even in alpine climates. On organic soil exposed to the sun, the temperature tolerance of seedlings is often exceeded (e.g. beech seedlings are damaged at the soil surface and collapse).

Exposure and slopes: In the northern hemisphere, north slopes receive less radiation than south slopes—that is, they do not warm up as much at midday (Fig. 9.5a). South slopes receive radiation maxima according to the latitude of the site and the slope inclination. Slopes cool less during the night than the bottom of the valley, because cold air is heavier than warm air and flows downhill into the valley. The radiation budget of the slope is also more favourable during the night than in the valley, as re-radiation inputs from neighbouring slopes positively influence the radiation budget. Thus, vineyards at their northern growth limit are found on south-facing slopes, not in the valley. The climatic differences between north- and south-facing slopes in the northern and southern temperate climates may be large enough to cause differences in the local vegetation (Fig. 9.5b).

Depth and moisture of soil profile: Temperatures are much more constant within the soil than at the soil surface (see above). Depending on soil moisture, which determines the soil heat capacity, there is a clear seasonal shift of changes in soil temperature in comparison with air temperatures, with soils being generally cooler than the air during spring and early summer but warmer in autumn and early winter.

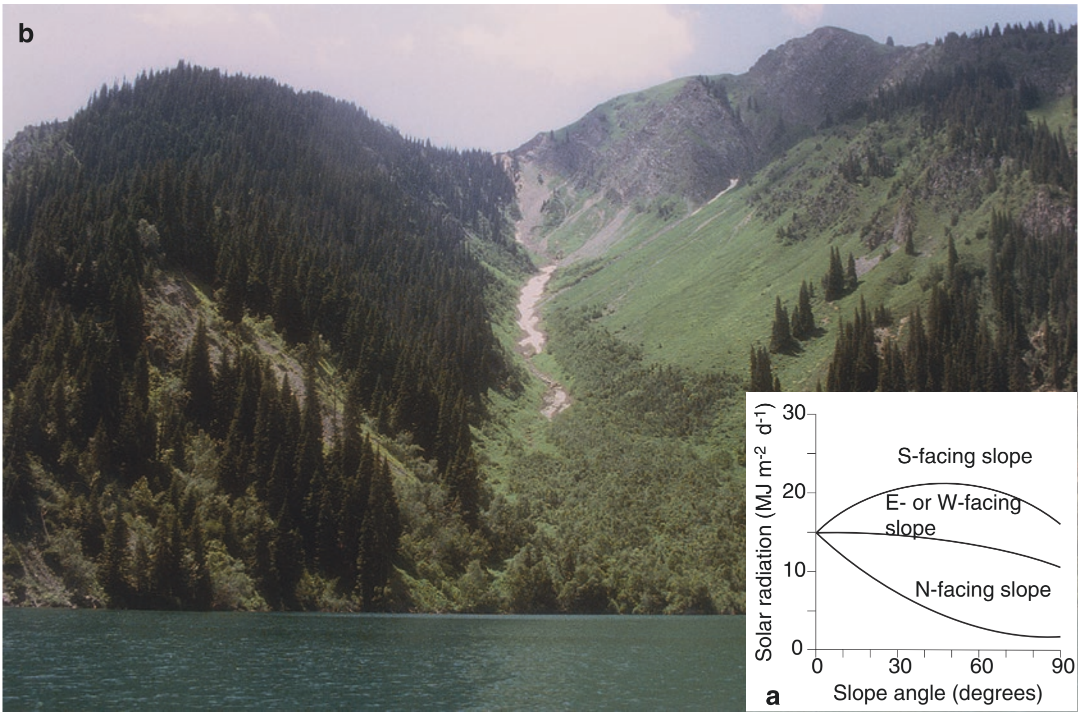


Fig. 9.5 Impact of slopes on incident solar radiation. **a** Influence of the orientation of a slope on the potential incident radiation (excluding clouds) at 55° latitude (after Jones (2014)). **b** Subalpine vegetation (2500–3000 m above standard zero) in the northerly Fergana mountain range (41°N in Sari Chilek, Kyrgyzstan) with a differentiation of the vegetation on the north- and south-facing slopes: *Picea schrenkiana* on the north slope, meadows on the south slope. The shrub vegetation (*Rosa*, *Lonicera*, *Berberis*) of the valley is a consequence of the increased snow and soil moisture. (Photo: E.-D. Schulze)

9.2.3 Modification of the Radiation Budget and Temperature by Biotic Factors

The radiation climate and temperature at the soil surface are highly affected by the vegetation cover.

Radiation reflection: The vegetation type determines its reflection. The reflection coefficient varies between 20% (e.g. for birch forests) and 12% for conifers. The low reflection of conifer forests affects the climate at the limit of boreal forests; more radiant energy is absorbed and thus more energy is kept as heat in the stand than in forest-free areas. The occurrence of evergreen conifers at high latitudes may thus accelerate a shift of the conifer treeline to the north. However, the effect is compensated by the shading of the forest floor by the evergreen canopy, which delays the snowmelt in spring and thus shortens the growing season.

Radiation absorption: The radiation budget changes with the leaf area and leaf orientation. The leaf area of vegetation cover is quantified by the **leaf area index** (**LAI**), which is defined as the sum of all leaf surfaces (one-sided leaf areas) per unit of soil area. The largest part of the incoming radiation is absorbed in the vegetation canopy, linearly scaling with LAI, modulated by the leaf arrangement in the canopy (Fig. 9.6a). Thus, light attenuation along a canopy profile in a forest follows patterns very similar to those in a cropland (see below). This can also be nicely observed in winter when snow around vegetation melts much faster than continuous snow cover without vegetation (Fig. 9.7).

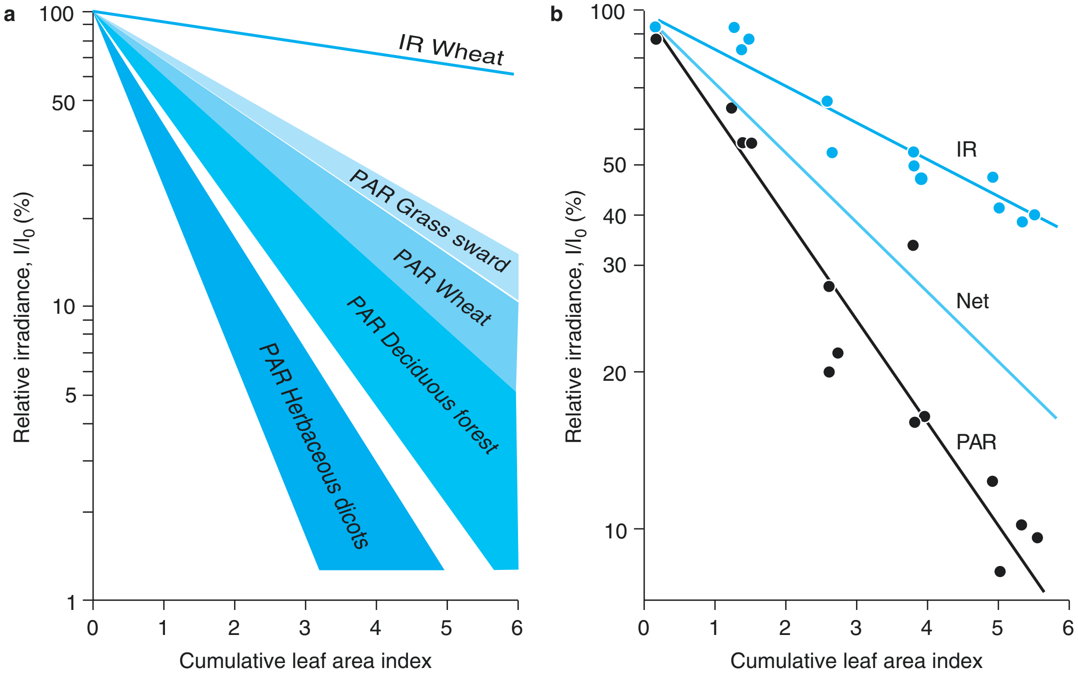


Fig. 9.6 Relationships of the stand leaf area index (LAI) and light attenuation. **a** Reduction of photosynthetically active radiation (PAR) with an increasing LAI for herbs (rather horizontal leaf position, extinction coefficient $k = 0.7$), deciduous forests, wheat field and grass meadows (vertical leaf position, extinction coefficient $k \leq 0.5$) (after Larcher (2003)). **b** Relative reduction of the light intensity of near-infrared light (near-IR), the net radiation budget (Eq. 9.2; incoming short-wave radiation minus short-wave reflection minus long-wave emission) and PAR (400–700 nm) with an increasing LAI in a wheat crop. (Jones 2014)

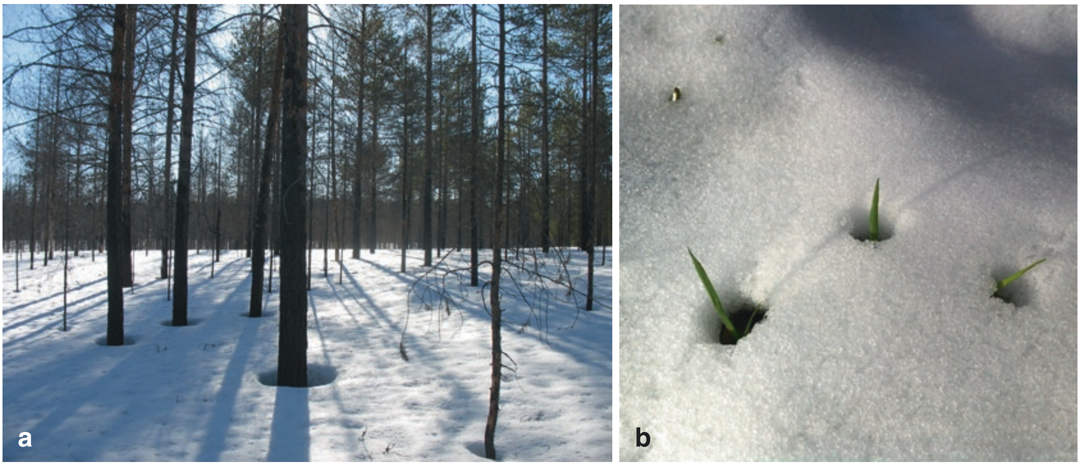


Fig. 9.7 Effect of vegetation on **snowmelt**. This is a typical phenomenon during winter when snow around vegetation—here, **a** pine trees in Siberia (Photo: E.-D. Schulze) and **b** grasses in Switzerland. (Photo: N. Buchmann)—melts much faster (because of radiation absorption by plant tissues and heat conductance along the stem) than the continuous snow cover

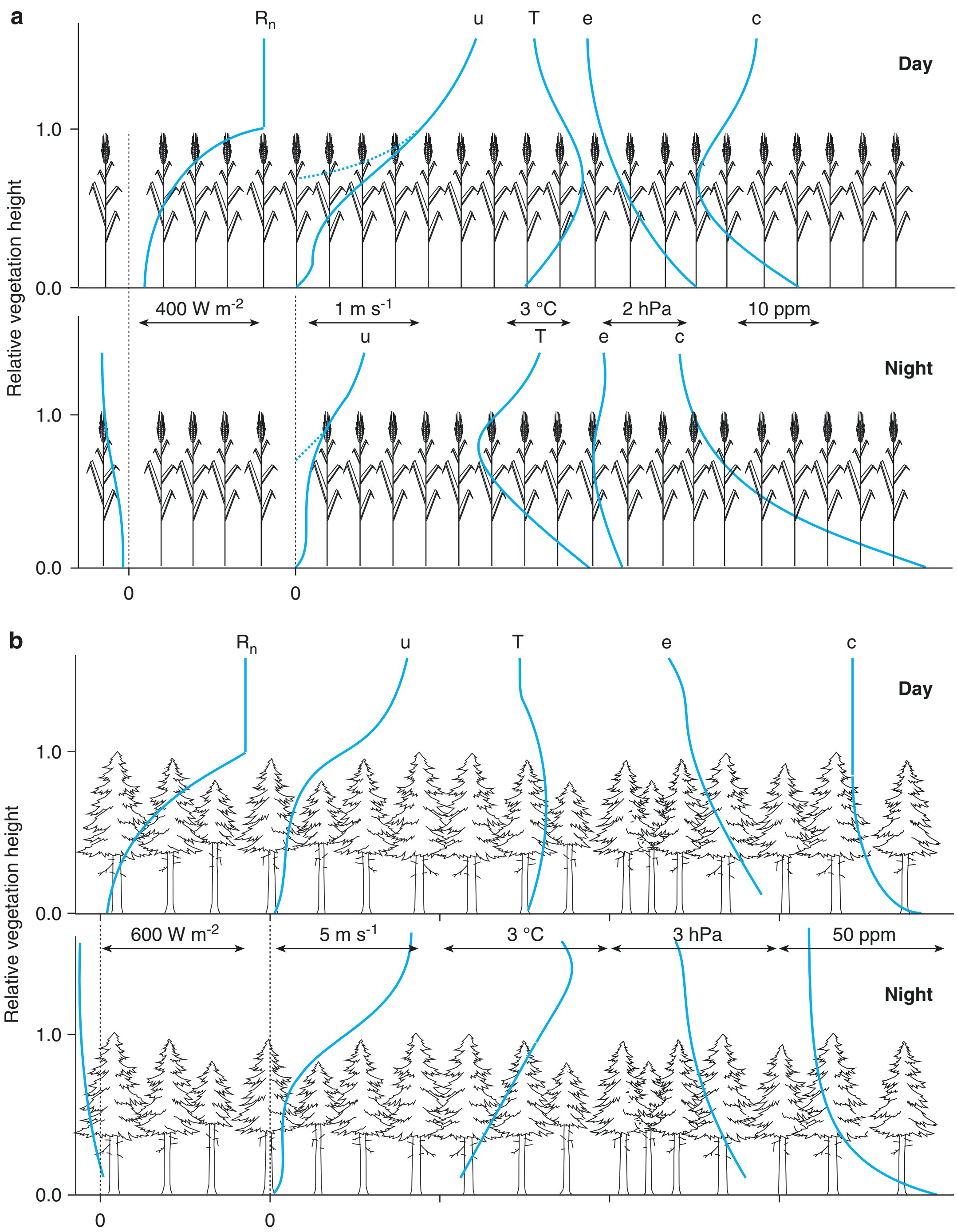


Fig. 9.8 Microclimate within vegetation stands. Energy transformation changes the meteorological variables during day and night **a** in a wheat field (Modified from Monteith and Unsworth (2013)) and **b** in a coniferous forest (measured by C. Rebmann). *c* CO_2 concentration, *e* actual water vapour pressure, R_n net radiation budget, *T* air temperature, *u* wind speed. During the day, absorbed radiation leads to a rise in temperature and an increase in water vapour pressure. The CO_2 concentration is minimal at the height of the assimilating layer of leaves, particularly when turbulence is impaired (in the wheat field). The wind speed inside the canopy is strongly reduced. During the night, there is a net loss of energy. This leads to the minimum temperature at leaf height. The CO_2 concentration is maximal at the soil surface because of high soil respiration fluxes and stable conditions (no wind). From the rise in the profile, the energy and mass balance can be calculated. Note the different absolute scales of the canopy profiles, presented here relative to the vegetation height

With the idealised assumption of a statistically random distribution of leaves and leaf orientation in the canopy, the decrease in radiation (**extinction** or **attenuation**) follows the **Lambert–Beer law** of absorption:

$$I = I_0 e^{-k\mathrm{LAI}}, \tag{9.6}$$

where I is the radiation flux at a defined height in the vegetation, I_0 is the incoming radiation above the canopy, LAI is the leaf area index above the measuring point and k is the extinction coefficient. k varies between 0.45 for vertical leaves (e.g. grasses) and close to 1.0 for horizontal leaves (e.g. clover). Thus, vegetation is able to increase its leaf area only until not enough light is available to maintain a positive carbon balance (Chap. 12), determined by incoming radiation (incident light, I_0) and the angle of the leaves (modulating k). Several species (particularly legumes) are able to move their leaves. Thus, leaf inclination is no longer random, but the LAI is actively regulated. Moreover, a clumped distribution of needles in conifers results in deeper penetration of sunlight (less attenuation of light) and thus in an increased LAI in conifer stands in comparison with grassland swards (Fig. 9.6). In contrast, the extinction of incoming diffuse near-infrared radiation (short-wave) in the canopy is less efficient (i.e. less complete) in comparison with visible light (Fig. 9.6b; Jones 2014). Near-infrared radiation penetrates much deeper into the canopy than photosynthetically active radiation, because leaves are relatively transparent in the near-infrared.

Microclimate within the vegetation: With changes of radiation along the canopy profile (Fig. 9.8; Monteith and Unsworth 2013), not only temperature but also all other climate variables change, particularly the vapour pressure saturation deficit and wind speed (i.e. turbulence). Since plants not only shape but also react to their environment, feedback mechanisms exist (Chap. 13). This means that microclimatic profiles develop because of the LAI and the distribution of foliage (e.g. clumping in coniferous forests) within the stand. Thus, attenuation of light is less steep in coniferous forests (relative to the height of the canopy) than in cereal crops. At the same time, assimilation, as well as transpiration, react to low light (due to self-shading) and high relative humidity (due to soil evaporation) deeper in the canopy, in turn affecting the CO_2 concentration and relative humidity profiles and, over time (because of growth), feedback on radiation profiles. As a result, daily variations of climate variables are less extreme inside a canopy than over a vegetation-free soil surface. For example, deep in a forest, daily fluctuations in the soil temperature are small.

Thus, the gradient of climate variables within the stand depends strongly on the physiological activity of the plants (and the soil organisms) but, in addition, the canopy structure determines the **roughness** of its surface and in turn its interactions with the overlying atmosphere, particularly in terms of wind speed. A surface is called very rough when it strongly decreases the wind speed of an air mass passing above this surface because of its high friction. For example, tall forests or cities exhibit higher roughness (due to their higher friction) than low crop fields or bare soil, which exhibit considerably lower roughness and are considered smoother. Consequently, the exchange between the vegetation and the atmosphere, the so-called **coupling**, is more direct at high roughness than at low roughness, which means that the higher the roughness of a vegetation canopy is, the more deeply the wind (but also trace gases or pollutants) can penetrate into it. Thus, wind profiles, but also profiles of other climatic variables, are affected. This can be nicely seen in deciduous stands in spring, when no new foliage is present yet (Fig. 9.9).

In addition, canopy profiles vary with time on both daily and seasonal time scales. During the night, the gradients of temperature, humidity and CO_2 concentration are reversed, reflecting different physiological processes at work (e.g. respiration instead of photosynthesis), as well as differences in the coupling of the vegetation to the overlying atmosphere (Fig. 9.8). Overall, differences in microclimate within canopies and among vegetation covers depend both on their physiological activity and on the roughness of their surfaces, and thus on the coupling to the atmosphere (Chap. 18).

In **deciduous temperate forests**, the intercepted solar radiation is seasonally highly variable (Fig. 9.10a). Before bud burst, 40% of the incident short-wave radiation reaches the soil (transmission; I_{sG}). The outgoing long-wave radiation during the night is lower than that of an area without any vegetation because of the radiation shielding of canopy branches. Thus, the organic layer at the ground warms up very quickly, and **spring geophytes** (Fig. 9.10b) (*Anemone, Corydalis, Primula* and others) develop faster than the leaves of the trees. With the emergence of leaves, >90% of the energy is intercepted above-ground in the canopy (transmission 9%). Thus, the floor of the forest remains relatively cool. The light received is often not even sufficient for herbaceous plants. Therefore, shade-tolerant plants use mainly diffuse light for photosynthesis (Schulze 1972). In **evergreen coniferous forests**, the short seasonal "window" in which direct radiation would reach the floor, as in deciduous forests, is absent. Thus, in evergreen forests, geophytes have little

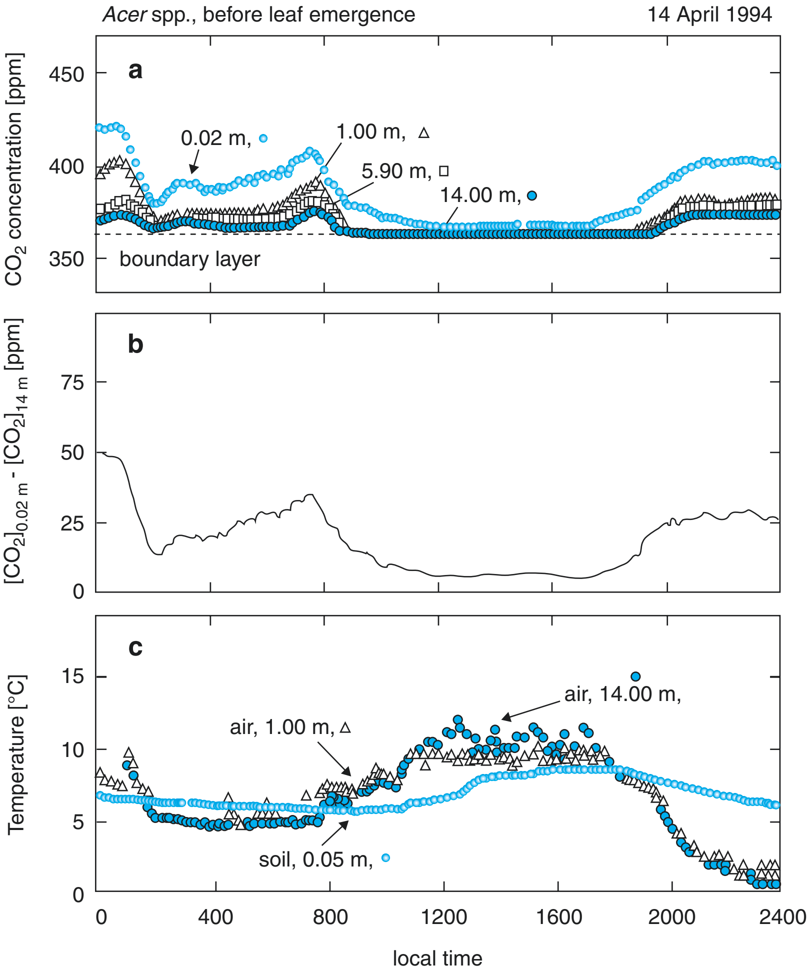


Fig. 9.9 Coupling of forests to the atmosphere. Diel course of **a** CO_2 concentrations at different canopy heights, **b** canopy CO_2 gradient and **c** soil and air temperatures within an open riparian maple stand before new deciduous foliage emerges (Buchmann et al. 1996). The decrease in CO_2 concentrations after sunrise, and particularly at midday, of up to 50 parts per million (ppm) CO_2 is due to turbulent exchange with the overlying atmospheric boundary layer, not due to photosynthesis (with no new foliage present). With the heating of the atmosphere after sunrise, atmospheric air with low CO_2 concentrations (around 365 ppm CO_2 in 1994) is mixed with canopy air with comparably higher CO_2 concentrations, which have built up during the night because of respiration of vegetation and the soil

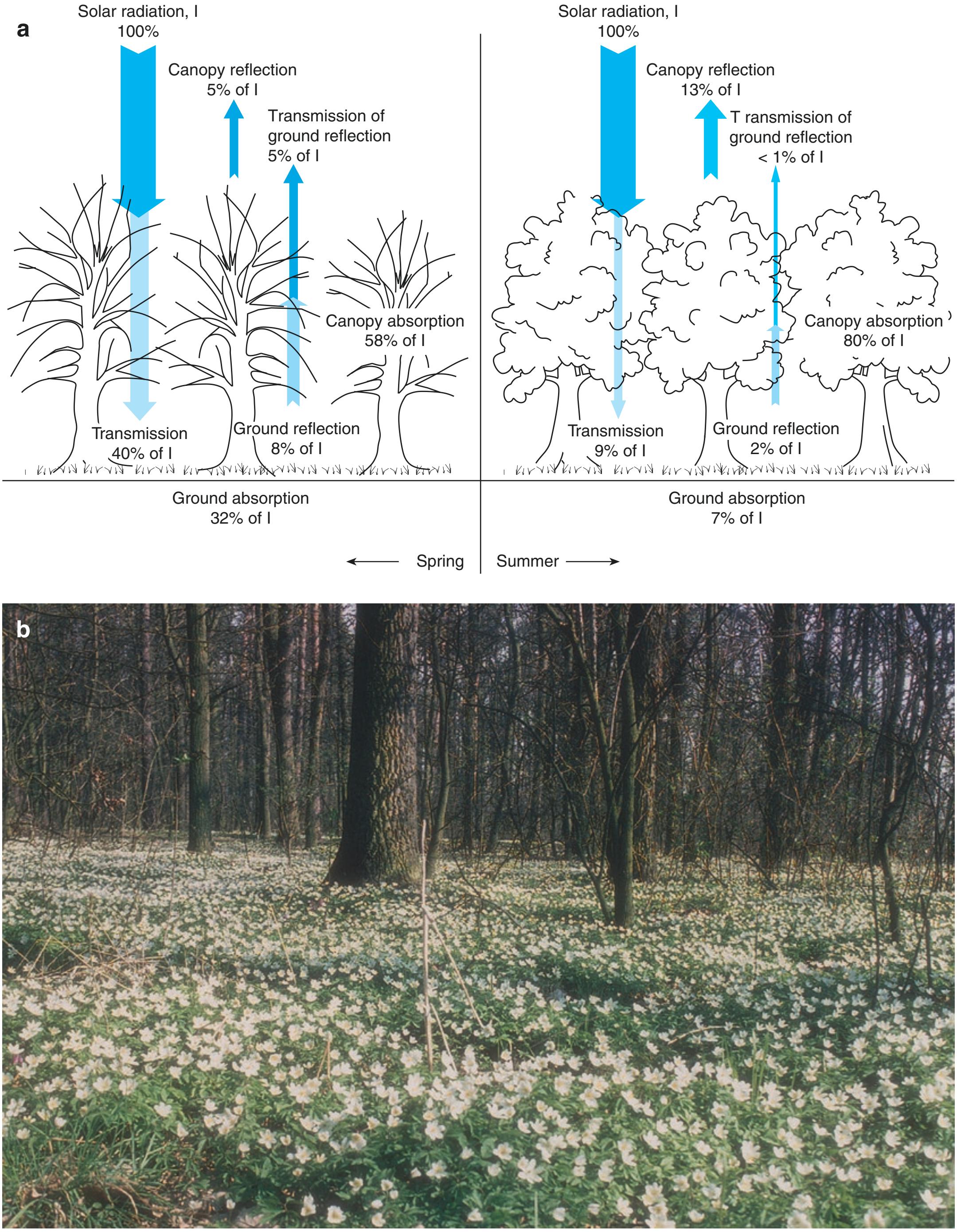


Fig. 9.10 Radiation budgets of a beech forest in spring and summer. **a** About 40% of the incident radiation reaches the forest floor in spring. About one third of the incident radiation is absorbed by the litter layer, which leads to a marked rise in temperature in the litter layer, thereby activating the spring geophytes and triggering organic matter mineralisation and thus nutrient supply. In summer, the leaf canopy absorbs about 80% of the incident radiation (for metabolic processes such as photosynthesis (1–2%), warming up, evapotranspiration, etc.) and less than 10% reaches the forest floor. Thus, the litter layer remains cool and damp (after Schulze (1982)). **b** Spring geophytes in a deciduous forest (close to Schweinfurt, Lower Franconia, Germany), with *Anemone nemorosa*. (Photo: E.-D. Schulze)

opportunity to grow. Shade in the forest also delays melting of snow on the forest floor and thus delays the beginning of the growing season, with negative effects on the water balance (Chap. 10). On the other hand, this slow warming of the forest floor in coniferous forests in spring, owing to the closed evergreen canopy, is linked at the same time to a fast heating up of the canopy, owing to the low albedo of the dark surface.

9.3 Energy Balance of Leaves

The **energy balance of a leaf** is discussed in this section as an example, representing any organ or surface of a plant. The thermodynamic laws applicable to a leaf are basically the same as those described for the atmosphere and ground surface. However, additional parameters need to be considered for a leaf—namely, the exchange resulting from reflection of short- and long-wave radiation on the upper and lower sides of the leaf, as well as reflection and re-radiation from the soil to the leaf (Fig. 9.11).

Since I_{sG} represents the net radiation flux to a horizontally oriented surface, but leaves have different angles, the **leaf orientation** has to be taken into account when describing the short-wave incoming radiation at leaf level I_{L} (Eq. 9.7):

$$I_{\mathrm{L}} = \sin\beta I_{\mathrm{sG}}, \tag{9.7}$$

where β is the angle between solar rays and the object—here, a leaf (note: This equation also describes the energy gain on slopes; Fig. 9.5).

The energy balance of a leaf, Φ_{nleaf}, can then be estimated, taking into account the net radiation budget at leaf height, R_{nL} (defining "ground surface" as the leaf surface; Eq. 9.3), as well as sensible and latent heat fluxes (H and λE, respectively), energy used in metabolism (M) and the change in heat storage in the leaf (S, often ignored; Eq. 9.8).

$$\Phi_{\mathrm{nleaf}} = R_{\mathrm{nL}} - H - \lambda E - M - S = 0 \tag{9.8}$$

The symbols and indexes are explained in Eqs. 9.1–9.3. The **sensible heat flux** for a leaf is:

$$H = \frac{\rho c_{\mathrm{p}}\left(T_{\mathrm{leaf}} - T_{\mathrm{atm}}\right)}{r_{\mathrm{b}}} \tag{9.9}$$

Here, the **boundary layer resistance**, r_{b}, is proportional to the length of the leaf (l) and inversely proportional to the wind speed (u):

$$r_{\mathrm{b}} = \sqrt{\frac{l}{u}} \tag{9.10}$$

Ignoring the boundary layer of the leaf and assuming the leaf is well coupled to the atmosphere (Chap. 16, Sect. 16.1), the **latent heat flux** is proportional to the vapour pressure deficit between the leaf and the atmosphere (D_{L}) and to **stomatal conductance** (g_{s}):

$$\lambda E = \left(\frac{\rho c_{\mathrm{p}}}{\gamma}\right) D_{\mathrm{L}} g_{\mathrm{s}}, \tag{9.11}$$

and, in addition, g_{s} is dependent on D_{L}.

The leaf energy balance shows that plants have various possibilities of changing the **leaf temperature** to avoid extremes and to keep it close to or within the optimal range for physiological activity. These possibilities are:

- Short-term (modulated) responses at the leaf level: changes of leaf angle, regulation of stomata and thus cooling by transpiration.
- Modified responses at the plant individual level: changes in leaf size (e.g. slitting of banana leaves with high irradiation) and the LAI.
- Evolutionary (genotypic) responses at the species level: changes in the spectral characteristics of the leaf—for example, hairs and pigment composition.

However, the leaf energy balance also shows that saving water (by reducing transpiration) leads to an increased heat flux, depending on the temperature difference between the exchanging leaf surface and the surrounding air. This in turn

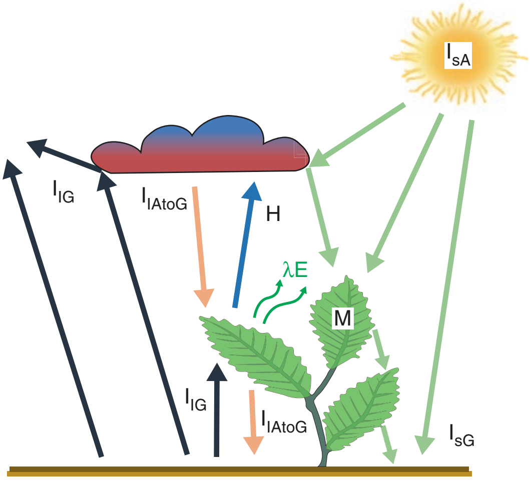


Fig. 9.11 Energy budget of a leaf. Incident short-wave radiation (I_{sA}) from the sun is reflected and absorbed in the atmosphere, resulting in a net short-wave radiation input to the ground and the leaf surfaces (I_{sG}). The long-wave radiation (I_{lAtoG}) re-emitted to the surfaces by clouds and the atmosphere, as well as long-wave radiation emitted from the ground (I_{lG}), comprise the thermal radiation fluxes to which a leaf is subjected. The net radiation at the leaf surface is then dissipated into the latent heat flux (λE) from the leaf via evapotranspiration, into the sensible heat flux from the leaf (H) and into the energy used in leaf metabolism (M). Any change in heat storage in the leaf is ignored here

will lead to increased leaf temperatures and might impose temperature stress (Sect. 9.4 and Chap. 4).

9.4 Acclimation and Adaptation to Temperature Extremes

The **temperature limit of plant resistance** to **temperature extremes** is generally beyond the maximum and minimum temperatures as measured in their organs under natural conditions (Chap. 4). This difference between "normal" conditions and the limits of resistance is important, as temperatures depend on incident radiation and may fluctuate rather quickly. Temperature ranges for metabolism and tolerance limits should not be exceeded, even for a short time, to avoid damage. Seedlings are particularly vulnerable to extreme temperatures, as are organs in direct contact with their surrounding boundary layer. The sequence of **life forms** according to Raunkiaer (trees, shrubs, herbaceous plants, annuals and geophytes; Chap. 20), with dominance of trees in the tropical regions but herbaceous plants in the cold regions of the Earth, can nevertheless not be interpreted as adaptation to temperature. There are many additional factors promoting or suppressing the growth of trees. The coldest place on Earth with vegetation (−70 °C: Oimikon, in eastern Siberia) is dominated by extensive forests of Siberian larch, and in hot climates, trees grow if water is available (e.g. palm trees in an oasis). At well-drained sites in Siberia (Chertskii), the forests extend almost up to the Arctic Ocean. The tree limit in alpine and boreal regions is caused by other factors (growing season length, frost drought, anaerobic conditions in the bogs of the tundra, fire).

Often, habitat limitation for plants is a consequence of temperature and water conditions. One example of such distribution limits is the deciduous beech (*Fagus sylvatica*). At the eastern borders, beech distribution is limited by the resistance of buds to the winter cold. The northern and western limits are caused by late frosts, which may damage young leaves, while the southern limit is due to drought. Moreover, "death from cold" or "death from heat" might often not be distinguishable from "death from drought" under field conditions (Chaps. 6 and 10). Nevertheless, there are many possible means of adaptation. The following examples may represent also many other species and situations.

9.4.1 Acclimation and Adaptation to High Temperatures

High temperatures combined with drought lead to many adaptations at the level of the leaf, ranging from molecular reactions (Chap. 4) to morphological changes at the levels of both acclimation and adaptation:

- **Changes of leaf surface** (wax, hair): The genus *Encelia* comprises several species characterised by variable densities of epidermal hairs (Fig. 9.12) (Jones 2014). These hairs reflect the incoming energy to different degrees (Ehleringer 1980), thus increasing survival, although at a large carbon cost (up to 70% of the annual C uptake).
- **Change in leaf size**: In habitats with high solar radiation, species often build smaller leaves (**microphylly**) (Fig. 9.13). In response to radiation stress, the same plant individual may produce small sun leaves and large shade leaves (Smith 1978). A famous exception to this rule, and therefore a clear example for adaptation, is *Welwitschia mirabilis* of the Namib Desert. It forms only two very large leaves, which may be up to 3 m long and 1 m wide, despite the high incoming radiation. Here, the leaf temperature is regulated by convection and long-wave radiation from the cooler soil (Schulze et al. 1980).
- **Changes in leaf angle**: For some plant species, particularly in the Fabaceae family, movement of the leaf plays an important role; the leaf blade moves either towards the sun to obtain maximum photon flux, or away from the incoming radiation to minimise absorption (Fig. 9.14). Classical examples are the cow pea (*Vigna unguiculata*) and the purple bush bean (*Macroptilium purpureum*). They turn their leaves to the sun or away from it, depending on the water supply. In extreme

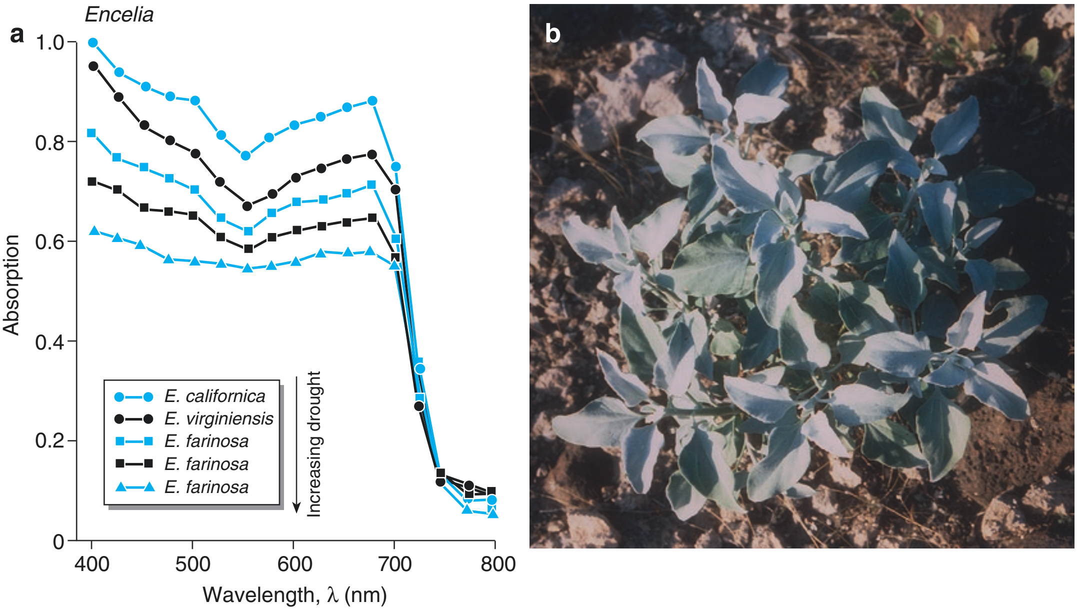


Fig. 9.12 Changes of leaf surfaces to adapt to high temperatures. **a** Effect of leaf hairs on radiation absorption of plants of three species of the genus *Encelia*. With increasing numbers of hairs on the surface, leaves absorb less and less radiation in the visible range. While green *Encelia californica* occurs in coastal regions or where there is a good water supply, *Encelia farinosa*, with white leaves, grows on dry slopes and in the Sonoran Desert (after Ehleringer (1980)). **b** *Encelia farinosa* in the Sonoran Desert, south Nevada. (Photo: E.-D. Schulze)

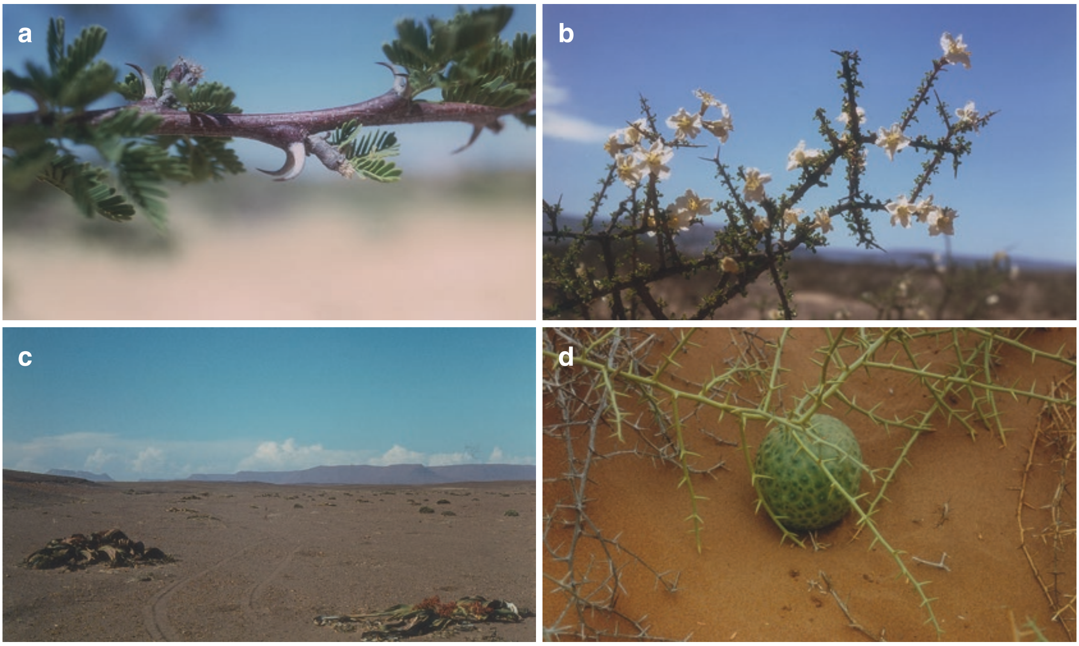


Fig. 9.13 Leaf morphology of plants growing in the Namib Desert: **a** Pinnate leaves: *Acacia detinens* (Mimosaceae); **b** Small leaves: *Boscia foetida* (Capparidaceae); **c** Large leaves: *Welwitschia mirabilis* (Welwitschiaceae); **d** Photosynthetically active shoots: *Acanthosicyos horrida* (Curcurbitaceae). (Photos: E.-D. Schulze)

cases, they turn their leaves so that the leaf does not cast a shadow (Shakel and Hall 1979). This leaf movement changes the leaf temperature and thus the vapour pressure gradient between the leaf and the surrounding atmosphere. This in turn affects transpiration (Eq. 9.11) and thus the water relations of the plant. However, even without leaf movement, the leaf angle is an important factor in the energy balance of vegetation (Chap. 3). The hanging leaves of *Eucalyptus* are well known, resulting in eucalypt forests hardly creating any shadow.

- **Changes of transpiration**. *Citrullus colocynthis* is a pumpkin, which grows near the ground in desert regions of North Africa (Lange 1959). The intact leaf transpires heavily and may have a temperature of about 40 °C when the surrounding temperature of the air layer near the ground is about 53 °C (Fig. 9.15) (Larcher 2003). This is the greatest transpirational cooling that has been measured in the field. If the leaf is cut off (abscised) and thus prevented from transpiring, its temperature rises to more than 60 °C and thus exceeds the upper limit for temperature tolerance, which is around 46 °C for this plant species (Chap. 4). However, transpirational cooling can result in leaf temperatures being lower than air temperatures only at rather high air temperatures and low relative humidities, rH (e.g. at an air temperature >22 °C and an rH value of about 30%, or at 33 °C and an rH of 60%) (Jones 2014). Irrespective of the special situation of transpirational cooling below air temperature, transpiration always reduces the temperature below the level of a non-transpiring surface.
- **Shading**: In a free-standing tree, branches and leaves protect the stem from direct radiation. This applies particularly to subtropical dry regions, where (e.g. in *Acacia reficiens*) the broad canopy shades the **base of the stem** (Fig. 9.16). Alternatively, there is also “**antenna growth**” (*Acacia mellifera*), where shoots extend high up, as far as possible, out of the hot air layer near the ground. However, in this case, the hypocotyl still requires

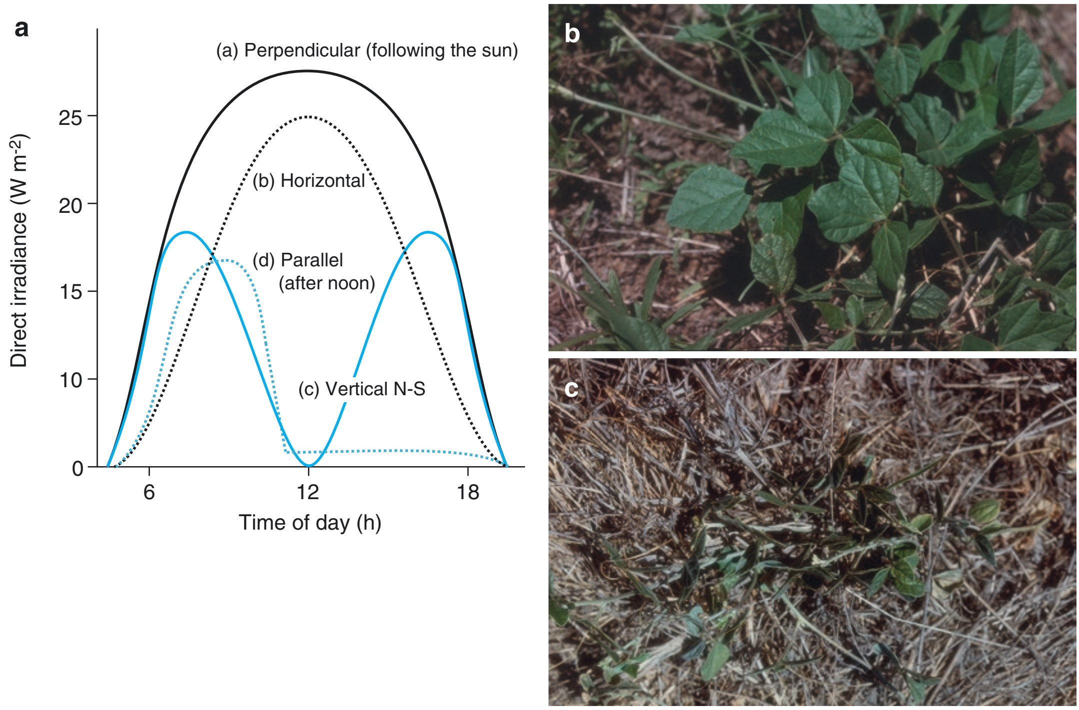


Fig. 9.14 Changes of leaf angles to acclimate to high temperatures. **a** Daily movement of a leaf with changes in the incident radiation (calculated for 50°N): **a** vertical to the incident radiation and tracking the sun during the day (e.g. beans); **b** fixed horizontal position (e.g. clover); **c** constant vertical position to the south or to the north (e.g. *Lactuca seriola*); **d** parallel to the incident radiation in the later afternoon (water-stressed *Vigna unguiculata* (from Jones (2014); *Vigna*: from Shakel and Hall (1979)). **b** *Macroptilium purpureum* (Leguminosae), a cultivar of Australian pastures, in a time of good water availability with leaves that follow the sun. **c** During drought, *Macroptilium* leaves are parallel to the sun and have no shadow (experimental farm, Narryen, Queensland, Australia). (Photo: E.-D. Schulze)

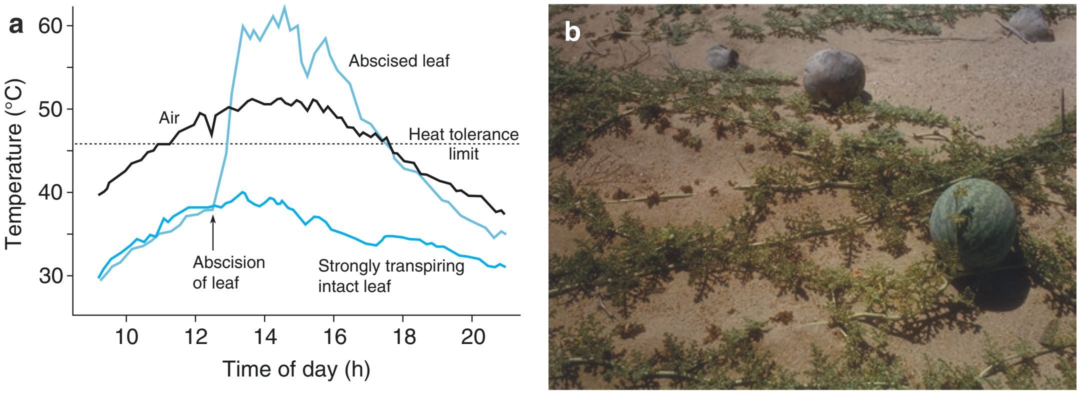


Fig. 9.15 Changes of leaf transpiration to acclimate to high temperatures. **a** Changes over 24 h in leaf temperature of *Citrullus colocynthis* in North Africa (Lange 1959). In natural conditions, a strongly transpiring leaf has a temperature about 12 °C below that of the air temperature. Cut the leaf off, and the temperature rises 10 °C above the air temperature because of the loss of the cooling effect of transpiration. The limit of heat tolerance for *Citrullus* is about 46 °C, so the cooling effect of transpiration prevents death by overheating. **b** Wild *Citrullus colocynthis*, Omaruru, Namibia. It can be clearly seen that the edges of the feathery leaves roll up at midday and also position themselves facing the sun, and so minimise the incident radiation absorbed—that is, they have reduced their shadow. (Photo: E.-D. Schulze)

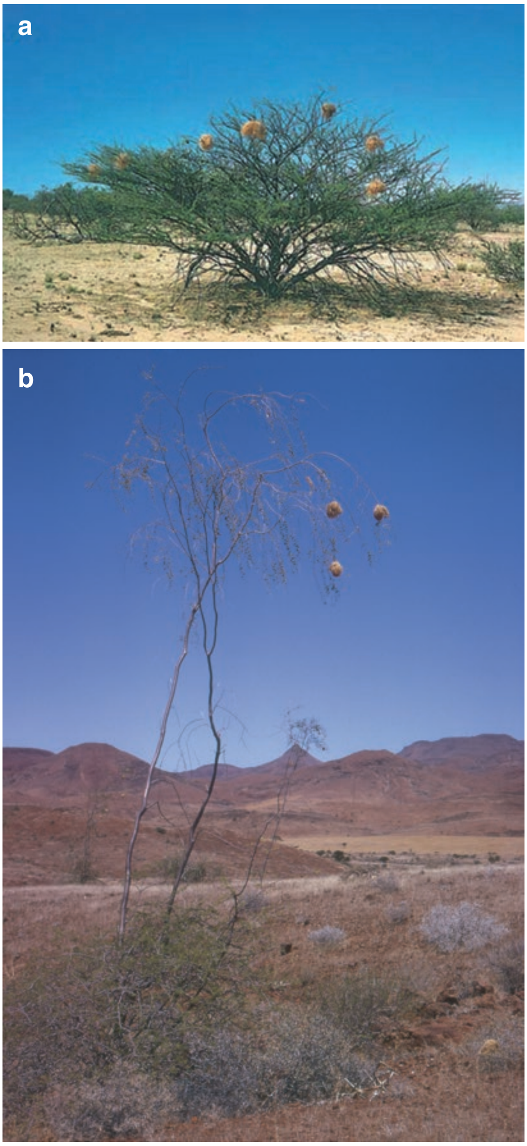


Fig. 9.16 Shading in habitats with high temperatures. **a** Shading of the trunk by the umbrella-like crown of *Acacia reficiens* (near Uis, Namibia). The protection of the base of the trunk is a common phenomenon in subtropical savannas. Light sensitive, shrubby dicotyledonous plants colonise the shade area surrounding the trunk, whereas the shrub-free area is colonised by C_4 grasses with vertical leaves. **b** "Antenna" growth of *Acacia mellifera* (near Khorixas, Namibia), which avoids high temperatures close to the ground by tall slender stems. The hypocotyl remains protected by dense, shrub-like sprouts close to the ground. In both cases, weaver birds nest only in the cooler upper layer of the tree crown. (Photos: E.-D. Schulze)

protection from radiation. Even in a temperate forest, gaps exist where high temperatures may occur around stems, causing damage (e.g. sunburn on beech stems in the leafless state). Thus, while having leaves or needles is a clear benefit in terms of shading (i.e. lowering temperatures within a stand), there is also a drawback of shading (i.e. preventing radiation from penetrating deep into a canopy and warming the ground, which is particularly disadvantageous in boreal and alpine climates) (Fig. 9.10).

9.4.2 Acclimation and Adaptation to Low Temperatures

There are few mechanisms to protect plants against lower temperatures and radiative cooling and thus against cooling below ambient. Therefore, molecular adaptations are particularly important (Chap. 4):

- **Rosette plants** in alpine climates use the warming of the soil below the rosette and the more favourable conditions on slopes. Similarly, cushion plants and so-called thorny cushions provide their own internal climates, temperature and humidity, because they minimise the surface area, and thus outgoing longwave radiation, due to their spherical form. Branches emerging from the surface experience less favourable conditions and thus stop growth (Chap. 10). This often leads to thorny short shoots at the surface.
- **Leaf inclination**: The angle of the leaf (or the angle of the bud) determines not only the reflection and absorption of short-wave radiation, but also the long-wave radiation flux of a leaf, particularly during the night.
- **Bud scales** are a morphological adaptation for changing the radiation balance. They raise the surface from which energy is re-radiated away from the bud meristem. Because of the low heat and water vapour conductances of the scales, this protects the bud not only against

cold but also against drying out (Chap. 6). In addition, the bud is a round surface, not a flat surface, thus minimizing the surface for heat loss to the atmosphere.

- **Heat storage**: In tropical alpine regions, the length of night frosts is limited and the days are warm. Species of *Lobelia* have a large store of free water, and this provides sufficient heat capacity so the growing point does not freeze (Chap. 4).

Summary

- The temperature of the Earth results from an equilibrium between short-wave solar radiation and long-wave emissions. The short-wave radiation reaching the Earth's surface is in the visible light range. Solar radiation is reduced by cloud cover and by biogenic or anthropogenic aerosols and gases in the atmosphere. Long-wave thermal emissions occur in a long-wave "window" where water vapour, CO_2 and other trace gases have an absorption minimum. This emission window is increasingly being closed by rising concentrations of anthropogenic trace gases (called greenhouse gases), especially chlorofluorocarbons, ozone, methane, nitrous oxide and CO_2. As a result, the Earth's temperature has increased with anthropogenic use of fossil fuels since industrialisation.
- Climate close to the ground differs by about −10 to +20 K from measurements 2 m above the ground, where climatic variables are measured to determine meteorological climate. At the ground, the radiation budget is closely linked to the energy balance, including latent and sensible fluxes. Thus, vegetation not only is affected by climate but also feeds back on climate. The microclimate the vegetation experiences is a result of gas exchange and canopy structure, interacting with the overlying atmosphere—for example, in terms of atmospheric turbulence and solar radiation. Vegetation can affect the amount of incident radiation that is absorbed through the leaf area index (LAI), depending on the available visible light and leaf inclination. The LAI changes with the season and determines the type of vegetation on the forest floor. Temporal variations of climate variables within canopies are much smaller than over bare ground.
- Temperature regulation of plants is possible within certain limits—for example, by changing the leaf inclination, leaf size, reflection, surface area, transpiration, and insulation. These aspects determine a leaf's energy balance and thus helping to avoid heat and cold stress. Structural modifications and regulation of transpiration via stomatal opening are usually sufficient to keep the temperature of the plant within the physiologically tolerable range. The critical period for a plant is germination and seedling establishment. Although global vegetation models use—to a large extent—temperature as the major factor determining plant distribution (Chap. 4), other factors (salt stress, drought, fire, length of vegetation periods, imbalance between temperatures in the soil and in the atmosphere, drought because of freezing) limit species distributions as well and should not be ignored (Part 5, Chap. 21).
- Temperature acclimation and adaptation of plants include changes in leaf position (direction of organs as energy-absorbing and energy-emitting surfaces) and the LAI (shading), leaf size and surface properties (avoidance of the laminar boundary layer and regulation of the sensible heat flux, waxes, hairs), insulation (bud scales, bark) and evapotranspiration (regulation of the latent heat flux). Heat dissipation and storage of heat have an additional function under particular climatic conditions (tropical alpine rosette plants, cacti). Similarly, warming by increased respiration is important under special conditions (flower spadices of Araceae).

References

Buchmann N, Kao WY, Ehleringer JR (1996) Carbon dioxide concentrations within forest canopies—variation with time, stand structure, and vegetation type. Glob Change Biol 2:421–432

Ehleringer JR (1980) Leaf morphology and reflectance in relation to water and temperature stress. In: Turner NC, Kramer PJ (eds) Adaptations of plants to water and high temperature stress. Wiley, New York

Gates DM (1965) Energy exchange in the biosphere. Harper and Row, New York

Hartmann DL, Klein Tank AMG, Rusticucci M, Alexander LV, Bronnimann S, Charabi Y, Dentener FJ, Dlugokencky EJ, Easterling DR, Kaplan A, Soden BJ, Thorne PW, Wild M, Zhai PM (2013) Observations: atmosphere and surface. In: Climate change 2013: the physical science basis. Contribution of Working Group I to the 5th assessment report. Cambridge University Press, Cambridge

IPCC—Intergovernmental Panel on Climate Change (2013) Climate change 2013: the physical science basis. Contribution of working group I to the 5th assessment report. Cambridge University Press, Cambridge

Jones HG (2014) Plants and microclimate; a quantitative approach to environmental plant physiology. Cambridge University Press, Cambridge

Kraus G (1911) Boden und Klima auf kleinstem Raum; Versuch einer exakten Behandlung des Standortes auf dem Wellenkalk. Gustav Fischer, Jena

Lange OL (1959) Untersuchungen über den Wärmehaushalt und Hitzeresistenz mauretanischer Wüsten- und Savannenpflanzen. Flora 147:595–651

Larcher W (2003) Physiological plant ecology, 4th edn. Springer, Berlin

List RJ (1971) Smithsonian meteorological tables. Smithsonian Institution Press, Washington, DC

Lutgens FK, Tarbuck EJ, Tasa D (2013) The atmosphere: an introduction to meteorology, 12th edn. Prentice Hall, Upper Saddle River

Mitchell JFB (1989) The greenhouse effect and climate change. Rev Geophys 27:115–139

Monteith JL, Unsworth MH (2013) Principles of environmental physics, 4th edn. Academic Press, Burlington

Monson R, Baldocchi D (2014) Terrestrial biosphere–atmosphere fluxes, 1st edn. Cambridge University Press, Cambridge

Oke T, Christen A (2015) Boundary layer climates, 1st edn. Chapman & Hall, Routledge

Scheffer F (2002) Lehrbuch der Bodenkunde. Scheffer/Schachtschabel, 15th edn. Spektrum Akademischer Verlag, Heidelberg

Schulze E-D (1972) Die Wirkung von Licht und Temperatur auf den CO_2-Gaswechsel verschiedener Lebensformen aus der Krautschicht eines montanen Buchenwaldes. Oecologia 9:235–258

Schulze E-D (1982) Plant life forms and their carbon, water and nutrient relations. Encycl Plant Physiol 128:616–676

Schulze E-D, Eller BM, Thomas DA, von Willert DJ, Brinckmann E (1980) Leaf temperatures and energy balance of *Welwitschia mirabilis* in its natural habitat. Oecologia 44:258–262

Shakel KA, Hall AE (1979) Reversible leaflet movements in relation to drought adaptation in cowpea, *Vigna unguiculata* (L.) Walp. Aust J Plant Physiol 6:265–276

Smith WK (1978) Temperatures in desert plants: another perspective on the ability of leaf size. Science 201:614–616

Stott PA, Tett SFB, Jones GS (2001) External control of 20th century temperature by natural and anthropogenic forcings. Science 290:2133–2137

Stull RB (1988) An introduction to boundary layer meteorology. Springer, Dordrecht

Wallace JM, Hobbs PV (2006) Atmospheric science: an introductory survey. Academic Press, San Diego

Walter H (1960) Grundlagen der Pflanzenverbreitung. Teil I Standortlehre. Ulmer, Stuttgart

Wild M, Folini D, Schar C, Loeb N, Dutton EG, Konig-Langlo G (2013) The global energy balance from a surface perspective. Clima Dyn 40:3107–3134

10 Water Relations

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A **"funnel" oasis** near El Qued, Algeria, northern Sahara: About 10 m of sand has been removed in sacks by donkeys. The limestone crust of an additional 10 m has been broken and excavated to reach a layer of sandy clay where typical oasis plants (*Phoenix dactylifera*: date palm; *Punica granatum*: pomegranate) and vegetables can be grown because water is found below the oasis floor at an additional depth of about 5–6 m, to be reached by hand-operated wells. The "funnel" is protected from refilling with sand by a series of concentric circles of dry date palm leaves, which trap windblown sand. The oasis has a total diameter of approximately 1 km. Thus, the donkeys have moved about seven million cubic metres per garden during construction. Permanent removal of windblown sand is still needed as maintenance. In the area of El Qued, Algeria, there are hundreds of such oasis constructions. (Photo: E.-D. Schulze)

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Life on Earth developed in water and, despite evolution over many millions of years, today—as then—all living processes, with their underlying biochemical reactions, are possible only in an aqueous milieu (Chap. 6).

10.1 Water as an Environmental Factor

10.1.1 Water Use by Plants and Animals

Organisms in their active state do not tolerate desiccation. This is illustrated by the **water concentration** of tissues: in the active state, the protoplasm of leaves and fleshy fruits contains 0.85–0.90 g H_2O $g^{-1}{}_{FW}$ (fresh weight). The water concentration of wood decreases to about 0.50 g H_2O $g^{-1}{}_{FW}$ due to the high contribution of structural carbohydrates and polymers in the xylem. The lowest values are reached in dormant seeds: 0.05–0.15 g H_2O $g^{-1}{}_{FW}$.

Land plants must keep the water concentration of their cells close to saturation or be fully saturated in an environment of relatively dry soil or air, and still maintain exchange of CO_2 with the atmosphere for photosynthesis (Chap. 12). Terrestrial life outside water brings benefits as well as dangers for plants, for the following reasons (Cowan 1977):

- The **diffusion coefficient of CO_2** in air is about 0.14×10^{-4} m^2 s^{-1} and decreases in water to 0.16×10^{-8} m^2 s^{-1}. Thus, CO_2 diffuses 10,000 times faster in air than in water (Sestak et al. 1971). In the Lower Devonian, when land plants evolved, the CO_2 concentration was significantly higher (about 4000 parts per million (ppm)) than it is today (about 400 ppm), which would have made the atmosphere even more attractive for plants in the past.
- During the evolution of plants, no membrane has been "invented" that is permeable to CO_2 but remains impermeable to H_2O vapour. Even in the future, there will not be a type of "GoreTex" for CO_2, because the molecular weight of CO_2 is larger than that of H_2O (44 versus 18). Of course, it was the availability of CO_2 in the atmosphere as a resource that made plants adapt from life in water (algae) to life on land. However, in order to use this carbon supply, mechanisms had to be developed to regulate the cellular water relations of land plants.
- Water relations are more important for the gas exchange of land plants than for animals because of the **chemical composition of air**. Photosynthesis creates a CO_2 gradient of about 100 ppm between the atmosphere and the mesophyll. At the same time, there is a gradient of water vapour of about 12,000 ppm between the water-saturated mesophyll walls and the ambient air. CO_2 diffuses 1.6 times more slowly than H_2O vapour, as the diffusion rate is related to the square root of the molecular weights $\left(CO_2\,44, H_2O\,18, \text{and} \sqrt{\frac{44}{18}} = 1.6\right)$. Thus, during uptake of 1 mole of CO_2, the plant loses about 200 moles of H_2O $\left(12{,}000 \times \frac{1.6}{100} = 192\right)$. Therefore, **water use** (here, water loss) by plants is very high relative to the photosynthetic gain.

Water use by animals differs from its use by plants. For **mammals** (warm-blooded animals with a body temperature of 37 °C), with 210,000 ppm O_2 in the atmosphere and 160,000 ppm O_2 in the breath, the O_2 gradient is about 50,000 ppm. The air that is breathed out is water saturated. Therefore, the water vapour gradient between the lung and the atmosphere is also about 50,000 ppm (at 20 °C, 50% rel. air humidity). Thus, a warm-blooded animal loses only about 1 mole of H_2O per mole of O_2 taken up. For cold-blooded animals the water loss related to O_2 uptake is even lower (about 0.2)—that is, water use related to O_2 gain is very low in animals. In addition, animals can move to a water source or protect themselves from adverse conditions, giving animals another advantage over plants under dry conditions.

As the loss of water from plants is so large, it is usually not cost effective for them to have **water storage**. During the course of a day, a sunflower leaf loses about ten times its own weight as water vapour. A 25 m high spruce loses about 100 – 1000 L of water per day, which is more than there

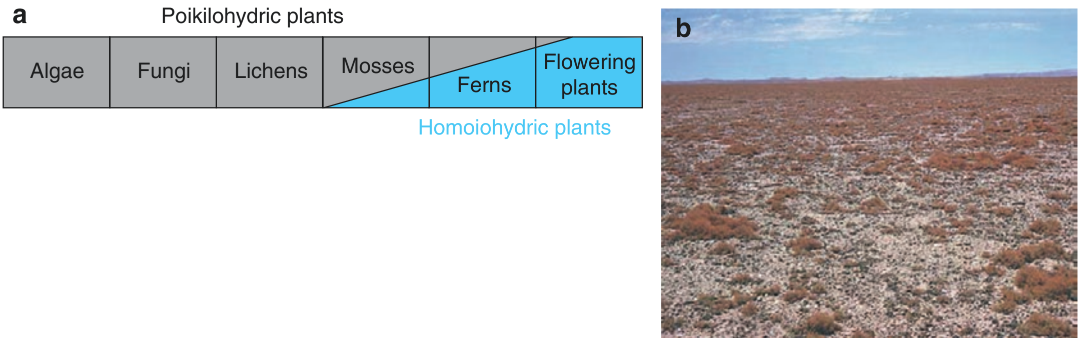

Fig. 10.1 Desiccation-tolerant and -intolerant plants. **a** Schematic presentation of the occurrence of desiccation-tolerant (poikilohydric) and desiccation-intolerant (homoiohydric) organisms. **b** Lichen growth dominated by *Teloschistes*, with almost no higher plants in the coastal region of the fog desert of Namibia. (Photo: E.-D. Schulze)

is in the stem. The available water stored in the stem and the crown of spruce is sufficient to maintain transpiration for only about 2 h in the humid morning hours (Schulze et al. 1985). This means that the costs of providing water from storage sufficient to safeguard the supply over days or months would be unreasonable: plants would have to construct enormous water stores. The aforementioned example of the daily water loss by a spruce tree shows that a 10-day drought period without water uptake from the soil would require a storage volume of up to 10,000 L to support normal transpiration. There are some species of cacti, euphorbias and Mesembryanthemaceae that live transiently on water stored in cell vacuoles (e.g. *Oppophyllum* spp. or *Prenia* spp.), but their biomass production is then very low. Even the baobab tree (*Adansonia digitata*) is hardly able to use the water stored in its stem (Schulze et al. 1998b). The wooden structure of baobab and other "bottle trees" is rigid and cannot shrink sufficiently to maintain transpiration. The function of the thickened stems of baobab trees is to store carbohydrates and amino acid reserves in sufficiently hydrated cells.

During plant evolution, two strategies of water use have developed (Fig. 10.1a):

1. **Desiccation-tolerant**, **poikilohydric plants** operate as a physical system of variable water content, which absorbs and loses water, depending on the humidity in the air (Chap. 6). When exposed to moisture from rain, dew or high humidity, these plants become fully active. They dry out with decreasing air humidity and become dormant during the time of desiccation. In this life cycle, there is an optimum water status. If the organism is too wet, diffusion of CO_2 from the atmosphere to the photosynthetically active cells is restricted and the rate of photosynthesis decreases with high water content (see Fig. 12.13). Thus, metabolism is restricted to the period when the tissue is wet, but not too wet, and diffusion of gases is possible. The most important representatives of this plant type of water use are algae, lichens and mosses (Fig. 10.1). Some mosses and lichens are able to obtain water from the ground by rhizoids and fungal hyphae via capillary forces but not via xylem vessels. Among flowering plants, there are also a few species that are desiccation tolerant—for example, *Myrothamnus flabelliformis* from the Namib Desert; *Borya* spp., native to Australia; and *Craterostigma plantagineum* in Africa, as described by Ziegler and Vieweg (1970) and Gaff (1971) (Chap. 6). These angiosperms, however, differ from non-vascular plants in that they cannot be activated by dew and high humidity as they have a cuticle, which restricts water uptake via the shoot (see also Burkhardt (2010)). These species are activated by water uptake through roots only.
2. **Desiccation-intolerant**, **homoiohydric plants** are able to maintain a high and almost constant tissue water content that is independent of the conditions in the surrounding environment.

There is a partitioning of labour between organs (Fig. 10.2): roots are specialised in uptake of water, the stem transports water and the green tissue (which may be leaves, phyllodes or phylloclades) assimilates CO_2 at the cost of evaporation. Homoiohydric plants have large vacuoles in their cells, which function, within a certain range, as short-term buffers for the cellular water status and thus stabilise the cell and plant water balance (Chap. 6). The leaf surface is covered with a cuticle composed of a lipophilic polymer, which is impermeable to CO_2 and H_2O but permeable to O_2. The leaf is connected to the free atmosphere via stomata, of which the aperture can be regulated. However, one developmental stage of intensive dehydration of cells also remains in these homoiohydric plants: the seed. In environments with high air humidity and low rainfall (e.g. the fog desert of the Namib, where there is no precipitation except for dew), higher plants are inferior—with respect to cover and growth—to lower plants (Fig. 10.1b).

In this chapter, our focus is on homoiohydric plants, as they form the largest fraction of the terrestrial flora. While Chap. 6 presents the molecular basis for the responses of plants to water stress, this chapter will focus on the biophysical links between plants and the environment.

10.1.2 Availability of Water on Earth

The **hydrological balance** provides the overall conditions for plant growth on the Earth (Ward and Robinson 2000). If changes of water storage in the soil are disregarded, the hydrological balance consists of **precipitation** (*P*), **evapotranspiration** (*E*) and **river discharge** (*F*: river flow) (Eq. 10.1), which is fed by surface run-off and seepage (groundwater recharge).

$$P - E - F = 0 \tag{10.1}$$

The global distribution of these variables, as shown in Fig. 10.3, indicates tropical and temperate regions with a high surplus of rainwater ($P > E + F$) and arid regions with a rainwater deficit ($P < E + F$).

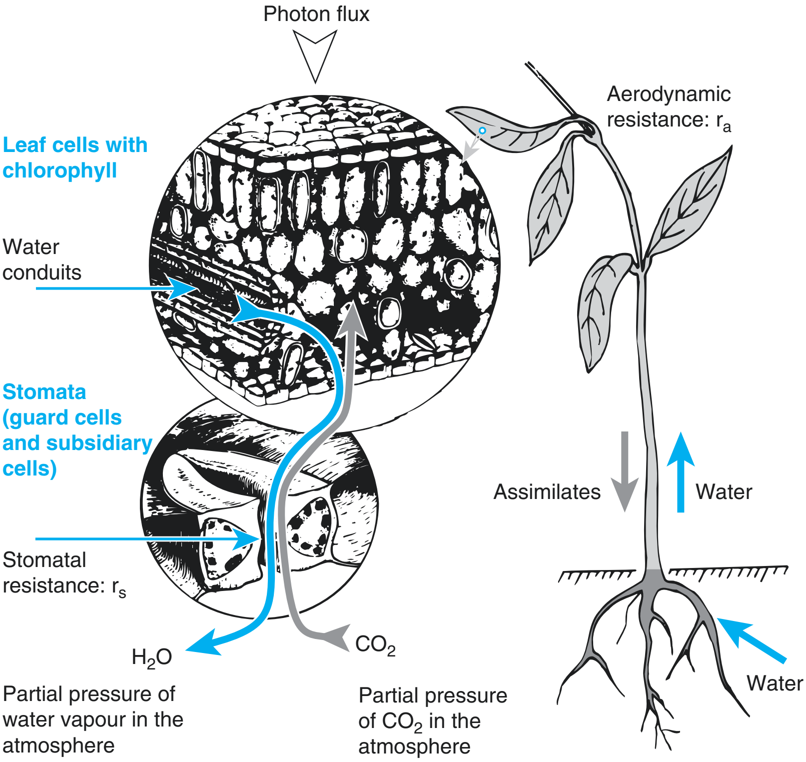

Fig. 10.2 Flow of water and assimilates in vascular plants. These are connected via the stem, which conducts the water and assimilate flows. In the stem, water and assimilates are transported by mass flow; in the leaf, there is a phase transition from liquid water to water vapour. At the same time, CO_2 is assimilated into soluble organic substances. Diffusion between the inside of the leaf and the atmosphere is controlled by the stomata. (Modified from Bonner and Galson (1952))

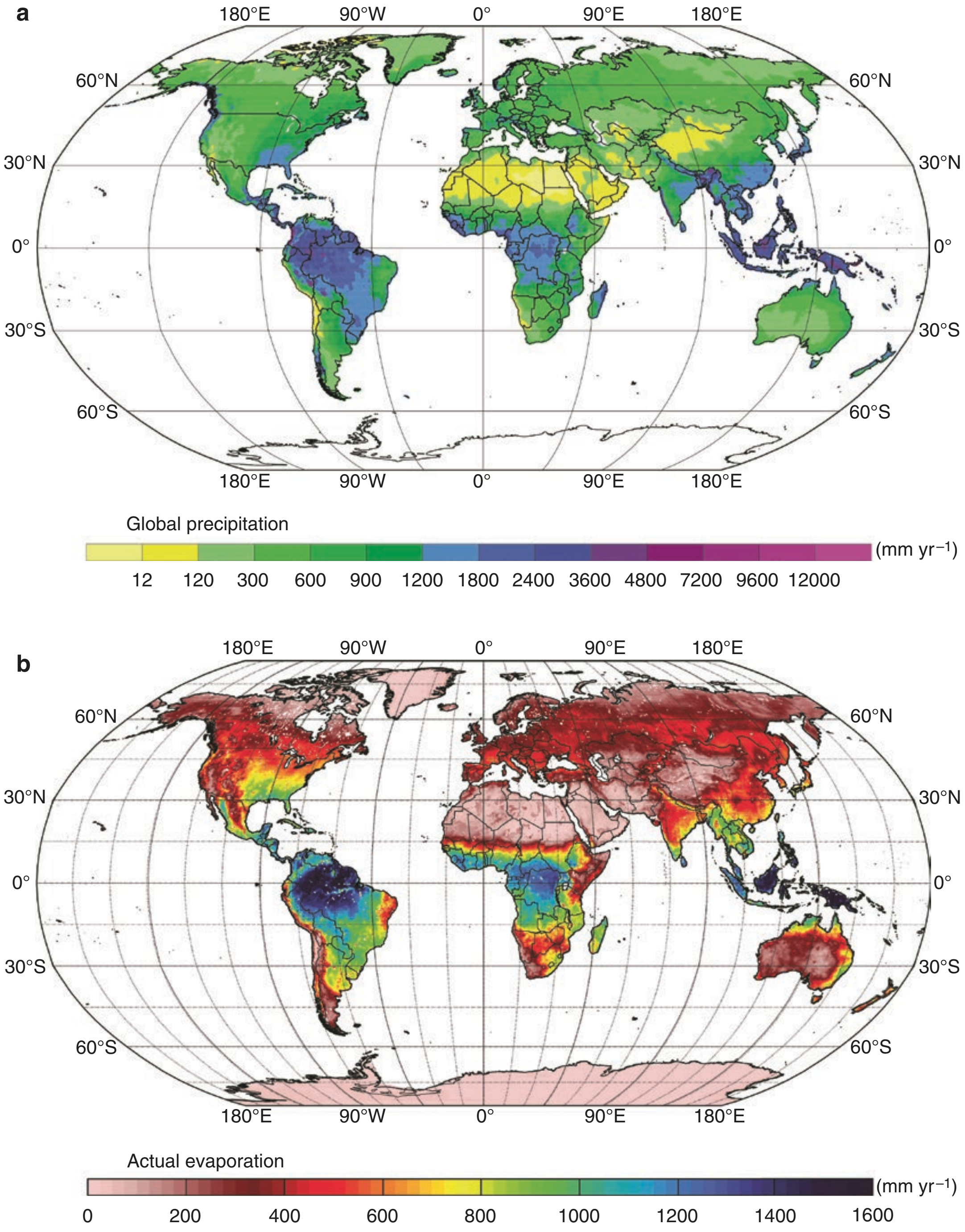

Fig. 10.3 Global distribution of components of the hydrological balance of the Earth. Global distribution of **a** precipitation (based on Schneider et al. (2014)), **b** actual evaporation (Miralles et al. 2011) and **c** groundwater recharge, equalling river flow (Döll 2009). **d** Climatic classification scheme, after Köppen and Geiger. (Kottek et al. 2006)

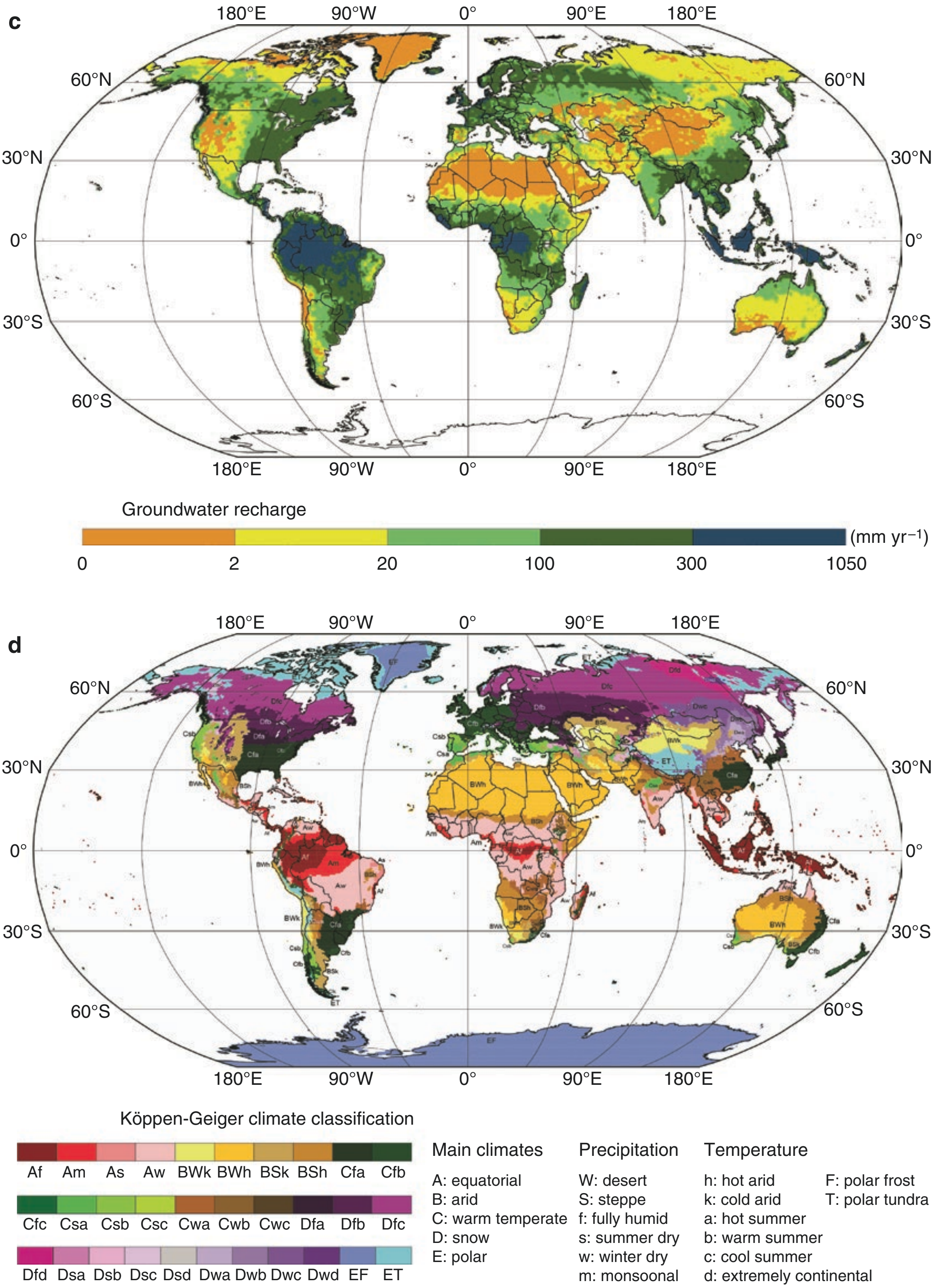

Fig. 10.3 (continued)

Precipitation is the main input into the natural water cycle (neglecting the use of fossil groundwater for irrigation (Fig. 10.3a; Chap. 21)). It is determined by the position of the sun, the global circulation of air masses and the recirculation of local evapotranspiration. All of these processes result in high precipitation over the tropics, a minimum of precipitation in the subtropics and increased precipitation at temperate latitudes. Precipitation over the continents is also determined by the distance from the oceans (**oceanity**) and the size of the continents (**continentality**). The Gulf Stream, with its northern extension towards Europe (the North Atlantic Drift), also provides exceptionally favourable conditions of temperature and rainfall for the eastern part of the Americas, as well as for Europe. Precipitation decreases in the Arctic and Antarctic.

Surface evaporation (*E*) includes evaporation from surfaces and transpiration of vegetation. If the ground surface is covered by plants, free evaporation occurs only after precipitation, when the **intercepted water** (the amount of precipitation captured by the canopy and not reaching the ground) evaporates. In spring, before plant cover is achieved, arable fields lose water similarly to a wet surface until the topsoil layer dries off. The rate of evaporation decreases as the crop grows (Greenwood et al. 1992). **Transpiration** describes the amount of water lost from the plant by evaporation, and it is thus subject to physiological control, in addition to energy-driven evaporation (Chaps. 9 and 16). In addition, evaporation from the ground occurs in any stand, depending on the leaf area index (LAI) (Schulze et al. 1995). The sum of free evaporation and transpiration is called **evapotranspiration** (Fig. 10.3b). One distinguishes between **potential evaporation**, which is a function of the meteorological conditions, and **actual evapotranspiration**, which is additionally regulated by the plant cover. The global distribution of actual evapotranspiration shows a maximum in the tropical regions and roughly follows the distribution of precipitation. However, evapotranspiration is additionally influenced by the available solar radiation and mean wind speed (Chaps. 9 and 16). Thus, evapotranspiration decreases with decreasing available solar energy in the higher latitudes (north and south).

Surface run-off, **water storage in the soil profile and river discharge** of water close the hydrological balance (Fig. 10.3c). Evapotranspiration does not increase with precipitation without limits. Fig. 10.4 shows a saturation curve, with **river discharge** making up a larger proportion of the total precipitation as precipitation increases. Even at low precipitation, vegetation does not consume the total amount of precipitation. In arid climates, precipitation occurs as heavy rainstorms, with sometimes massive surface run-off. This water is thus not available for plants at the site of rainfall but may be stored at greater soil depth (e.g. in the Kalahari sands), serve plant growth downhill (e.g. in dry valleys) or reach the ocean via rivers.

10.1.3 Drivers of Water Flow Between the Soil and the Atmosphere

In soils and in plants, water is not freely available but is bound mainly to molecules or surfaces. In soil science and ecology, the following distinctions are made:

- **Constituent water** comprises water that has been used in the plant metabolism.
- **Hydration water** describes the layer of water molecules that is arranged as dipoles around ions. The strength of the binding increases with the charge of the hydrated ion and decreases with its radius. Thus, Na^+ has a larger hydration layer than K^+ (Lüttge and Higinbotham 1979). All polar groups of organic molecules have a hydration layer. Of the total water in a leaf, 5–10% is therefore not freely available.
- **Capillary water** in cell walls and in the fine pores of soils is subject to capillary forces. The rise of the water column in a capillary (*h*,

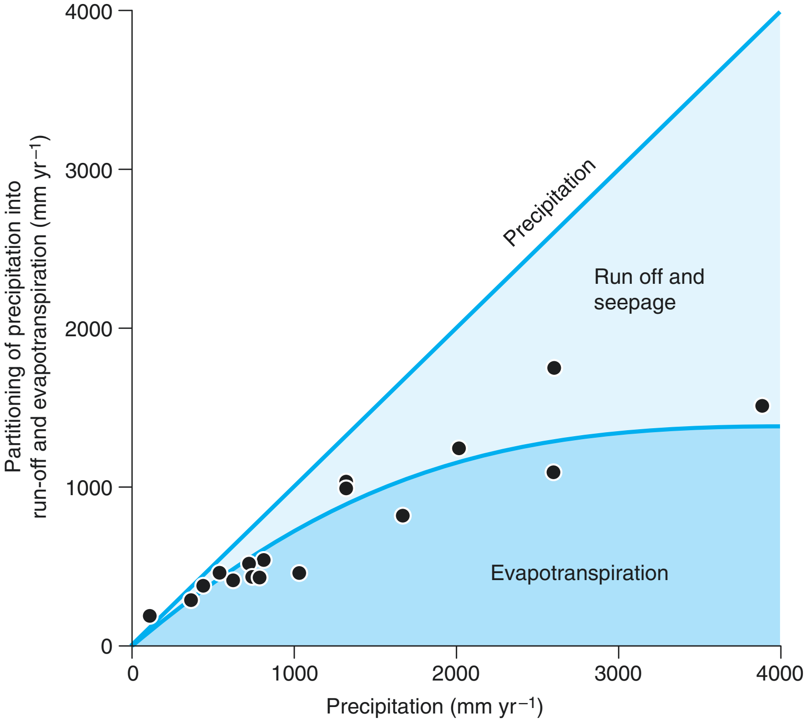

Fig. 10.4 Relations between river discharge, evapotranspiration and precipitation, based on river catchments. Evapotranspiration reaches a maximum that depends on the net radiation and surface conductance (for details, Chap. 16). Thus, the proportion of water that runs off or penetrates into the soil increases with increasing rainfall. (After Schulze and Heimann (1998))

measured in metres) is, as a first approximation, inversely proportional to the radius (r) of the capillary, because the water mass and the gravitational force affecting it ($\pi r^2 h\rho g$) must be balanced against the cohesive force produced by the surface tension ($2\pi r\sigma_w \cos\alpha$). Neglecting the contact angle, α ($\cos\alpha = 1$) for a 0° angle, the following equation applies (Nobel 2009):

$$r \cdot h \cdot \rho \cdot g = 2 \cdot \sigma_w \qquad (10.2)$$

where h is the height in metres to which the water column rises, ρ is the density of water (998 kg m^{-3} at 20 °C), g is the acceleration of the Earth (9.8 m s^{-2}), r is the radius of the capillary (metres) and σ_w is the surface tension of water (0.0728 N m^{-1} at 20 °C). Thus, the pressure (P) in a capillary, the so-called **capillary force** (as measured in Newtons) is:

$$P = h \cdot \rho \cdot g = \frac{2 \cdot \sigma_w}{r} \qquad (10.3)$$

and the height of the meniscus is calculated as:

$$h = \frac{2 \cdot \sigma_w}{(r \cdot \rho \cdot g)} = \frac{1.5 \times 10^{-5}\,\text{m}^2}{r} \qquad (10.4)$$

In a clean (lipid-free) glass capillary 3 μm in diameter (with a 1.5 μm radius), water rises 10 m. In a xylem vessel of 30 μm (typical for tracheids of conifers), water rises by capillary forces only 1 m, and in the 300 μm trachea of deciduous trees the water rises only 0.1 m via capillarity. Thus, the capillary force is not sufficient to lift water into the canopy of trees and therefore does not provide the lifting power required for the flow of water.

Cell water is osmotically bound (e.g. in the plant vacuole). The **osmotic pressure**, Π, depends on the number of particles per mole (n), the concentration (c_n), the gas constant, R (8.3144 Pa m^{-3} mol^{-1} K^{-1}) and the temperature, T (in Kelvins):

$$\Pi = n \cdot c_n \cdot T \cdot R \qquad (10.5)$$

In contrast to Chap. 6, the osmotic pressure is expressed here as positive pressure measured in Megapascals. This concept is based on an experiment that also demonstrates the phenomenon of **osmosis**: A closed chamber, called an **osmometer** (Pfeffer 1877), is divided by a semipermeable membrane into two compartments. The membrane allows passage of water molecules but is impermeable for ions. One compartment of the chamber is filled with distilled water, the other with a salt solution. In this case, free water is able to flow into the chamber with the salt solution, building up hydrostatic pressure. The level of water rises in the salty compartment, compared with the chamber containing free water, until the water column balances gravity. The height of the water column corresponds to the osmotic pressure. It is 2.48 MPa for a 1 molar solution.

To describe the flow of water between the very heterogeneous compartments of the plant and the environment, it is necessary to quantify the availability of water uniformly. This is possible by the definition of a common force for water transport, the **water potential** (Chap. 6):

$$\Psi = \frac{(\mu_w - \mu_o)}{V_w} = \left(\frac{V_w}{V_w^o}\right) \cdot \Pi \tag{10.6}$$

where μ_w is the chemical potential in the system (J mol^{-1}) and μ_o is the chemical potential of a reference system—that is, of pure liquid water at a given temperature and at normal pressure (atmospheric pressure). Dividing the difference of the chemical potentials ($\mu_w - \mu_o$) by the molar volume of liquid water (V_w) results in the water potential being defined in units of pressure (in Pascals) (Slatyer 1967; Walter and Kreeb 1970). Thus, the water potential describes the driving force for water movement in units that can be measured easily. V_w is slightly dependent on temperature and atmospheric pressure. V_w^o expresses the molar volume of pure water ($\Pi = 0$) in physical normal conditions.

In the gaseous phase the water potential is proportional to the relative humidity (Nobel 2009):

$$\Psi = \frac{T \cdot R \cdot \ln\left(\frac{e}{e_0}\right)}{V_w} \tag{10.7}$$

where e/e_0 expresses the vapour pressure of bound water (e.g. in solution or solid material) relative to that of free water. e/e_0 corresponds to the relative humidity. The proportion e/e_0 is also called **water activity**—describing, for example, the degree of swelling of colloids—and thus characterises the conditions for life of microorganisms or poikilohydric plants (Walter and Kreeb 1970).

As the chemical potential of bound water, μ_w, is more negative than that of free water, μ_o (energy has to be added to change, for example, bound water in a salt solution into the state of free water), the water potential has a negative sign. **Water movement** occurs from sites with high (more positive) potential to sites with low (more negative) potential. Thus, the water potential describes the state of water of the atmosphere, soils, plants or particles, and the water potential difference between compartments is the driving force for water flow.

Using the water potential, it is possible to describe water status and water flows in single-phase systems (e.g. in a plant), as well as in phase transitions (e.g. water uptake from soils; Chap. 6). In a cell with good water supply and without any water flow, the osmotic pressure is compensated by the counter-pressure of the cell wall—the **turgor pressure** (P_c)—which can be measured as a positive pressure in a cell (except for xylem cells where it is negative because of their special structure). With freely available water, the water potential of the cell or tissue is zero. With decreasing water content of the cell, the turgor pressure decreases and the osmotic pressure increases because of the increasing concentration of the residual solution in the cell. The difference, $P - \Pi$, corresponds to the water potential, Ψ, which becomes increasingly more negative when the cell dries out. In a tissue under such conditions, water flows, for example, from the cell wall into this cell until the water potential gradient equilibrates. If desiccation of the cell continues, the water potential may become equal to the osmotic pressure ($\Pi = -\Psi$). At this point of turgor loss, plants start to wilt and cells start plasmolysis.

The water potential of the living cell is described as:

$$\Psi = P_c - \Pi - \tau + \rho \cdot g \cdot h \qquad (10.8)$$

where τ represents an additional force describing the binding of water in the membrane-free matrix of the cell wall and their coating with water molecules (the so-called **matrix potential**; Sect. 10.2.1), which depends on surface forces and not on the number of particles in the solution, as in the case of Π. This is important under saline conditions (Kramer and Boyer 1995). $\rho\ g\ h$ is the water pressure, with ρ describing the density of water, g the gravitational force (9.807 m s^{-2} at 45° latitude) and h the height of the meniscus above-ground (in metres; see Eq. 10.3). Thus, the water potential is dependent on the turgor pressure, the osmotic pressure, the chemical binding of water, surface properties and gravity, which is particularly important for tall trees Eq. 10.8, where the water potential is different in the root and shoot, depending on the height. Many authors also use the expression:

$$\Psi_W = \Psi_P + \Psi_\Pi + \Psi_g \qquad (10.9)$$

where Ψ_W is the water potential in the cell, Ψ_P is the turgor, Ψ_Π is the osmotic potential and Ψ_g is the potential due to gravity (Chap. 6, Sect. 6.2).

If the water potential between the plant, soil and air is balanced, there is no net transpiration flux. In nature, this may occur at night or during early morning at high air humidity. Therefore, the early morning **predawn water potential** ($\Psi_{predawn}$) in a plant is used to characterise the water conditions of the soil in the zone from which the roots obtain their water, which is in equilibrium with the leaf under conditions of no transpiration. With transpiration, a gradient in water potentials develops between the soil and the atmosphere. The midday water potential (Ψ_{midday}) thus decreases far below the predawn level and may reach about 10 MPa.

In the continuum of water potentials between the soil and the atmosphere, water follows the water potential gradient (from high to lower potential, i.e. to increasingly more negative values), whereby the flow rate is limited by flow resistances depending on the characteristics of the soil and the types of tissue. In addition, there is a phase transition in the leaf from the liquid to the vapour phase at the site of evaporation in the leaf, with the rate of diffusion in the vapour phase being determined by the water vapour pressure of the atmosphere (e/e_0). In the **soil–plant–atmosphere continuum** (SPAC), the highest water potential gradient is between the cell walls of the leaf mesophyll where water evaporates and the atmospheric air, because of the extremely low water potential in the air (see Eq. 10.7 and Table 10.1). The physical description of leaf water status does not consider that the cellular water status might be additionally regulated by membrane-localised pores or valves—the **aquaporins** (Chap. 6)—which facilitate water transport across lipophilic membranes.

In a closed system, the water potential is related to the **relative humidity** of the surrounding air (see Eqs. 10.7 and 10.17). Thus, it is interesting to compare the relative air humidity with the water potential under equilibrium conditions, and various plant responses (Table 10.1). Most plants reach a

Table 10.1 Relationship between water potential and relative humidity. Following Eq. 10.7, air humidity can be measured in a closed vessel in which air equilibrates with salt solutions of different concentrations. Such an experiment can also be used to study particular processes—for example, moulds can establish at relative air humidity of >70%. (Walter and Kreeb 1970)

Relative humidity (%)	Water potential (MPa)	Condition in soil or plant
100	0	Field capacity of soil
99	−1.35	Matrix potential at permanent wilting point
98	−2.72	Strong water stress in a plant
90	−14.1	Lowest measured water potential in a desert plant
80	−30.1	Initiation of photosynthesis in lichens
70	−48.1	Initiation of respiration in moulds
50	−93.3	Ambient air in an office

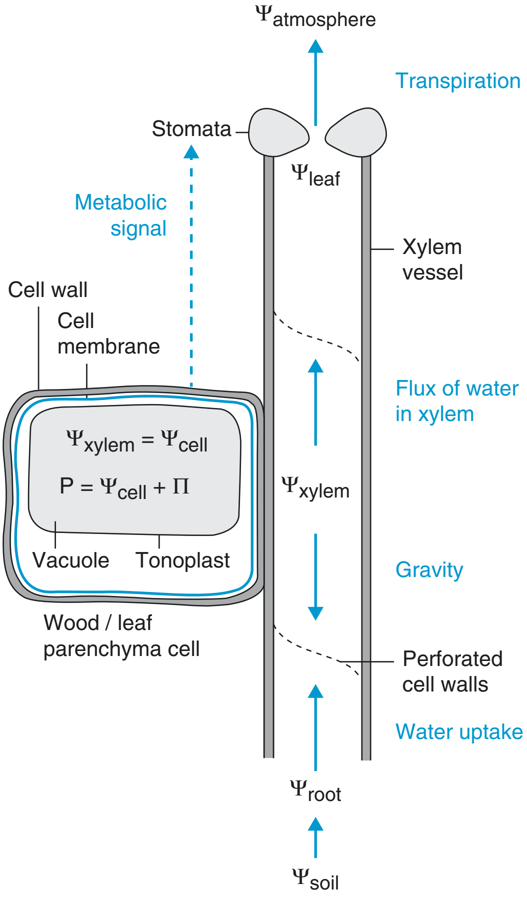

Fig. 10.5 Water status of a cell in a plant tissue

permanent wilting point (Fig. 10.6) already at −1.5 MPa soil water potential when the relative humidity decreases to 99% inside the mesophyll. Photosynthesis is initiated in lichens at 80% relative humidity, and respiration in fruit moulds is activated at 70% relative humidity. Thus, the atmosphere is too dry for active live under average conditions.

A cell in a plant tissue is embedded in a water potential gradient from the soil to the atmosphere as created by the water flow in the xylem, along a flow resistance (Fig. 10.5). The **cell water potential** equilibrates with the water potential in the xylem. Thus, the turgor pressure changes with the xylem water potential, and the cell may respond to these pressure changes by adjustment of the osmotic pressure in the vacuole. The water flow in the soil–plant–atmosphere continuum will be further discussed in Sect. 10.2.

10.2 Water Transport from the Soil to the Plant

10.2.1 Water Uptake

Precipitation seeps through the soil profile and may reach groundwater. The amount and rate of water movement in the soil depends on the soil type, the pore size and the water saturation. The **field capacity** describes the content of water, which is retained against gravity—that is, it is the amount of water that does not drip out of a flower pot after watering (field capacity is lower for sand than for loam). However, this water is only partially available for plants, because a proportion is bound as hydration water or by capillary forces—the **matrix potential** (Ψ_m) of the soil (see Eq. 10.4). In pores of 5 nm (e.g. pores in secondary cell walls of higher plants), the matrix potential reaches 3.0 MPa. It decreases in pores with a radius of 500 µm to only 30 Pa (Schachtschabel et al. 1998). Threshold values have been defined for the characterisation of soils on the basis of the relation between the water potential and the soil water content (Fig. 10.6a) (Or et al. 2012).

Loam and clay soils differ not only in the amount of available water (for loam it is almost ten times higher than for sandy soils), but also in the amount of water that is not available for plants in dry soils. This has consequences for the plant availability of water with decreasing precipitation (Fig. 10.6b). In areas with high precipitation, sandy soils are drier habitats than loamy or clay soils because sandy soils retain less water, owing to the larger pore sizes. At low precipitation the limit at which water can no longer be taken up by the plant is reached earlier in clay because the capillary and matrix forces are reached sooner than in sandy soils. In arid regions, sandy soils are therefore “moister” habitats for plants than clay soils. This is modified in nature by the frequency of precipitation (Fig. 10.6c).

Water transport from the soil to the root is determined not only by the water potential gradient but also by the hydraulic conductivity, which depends on the soil water content and soil texture. Roots may grow towards the water or “wait” until water flows from the soil to the root. In most plants, water transport to the roots is

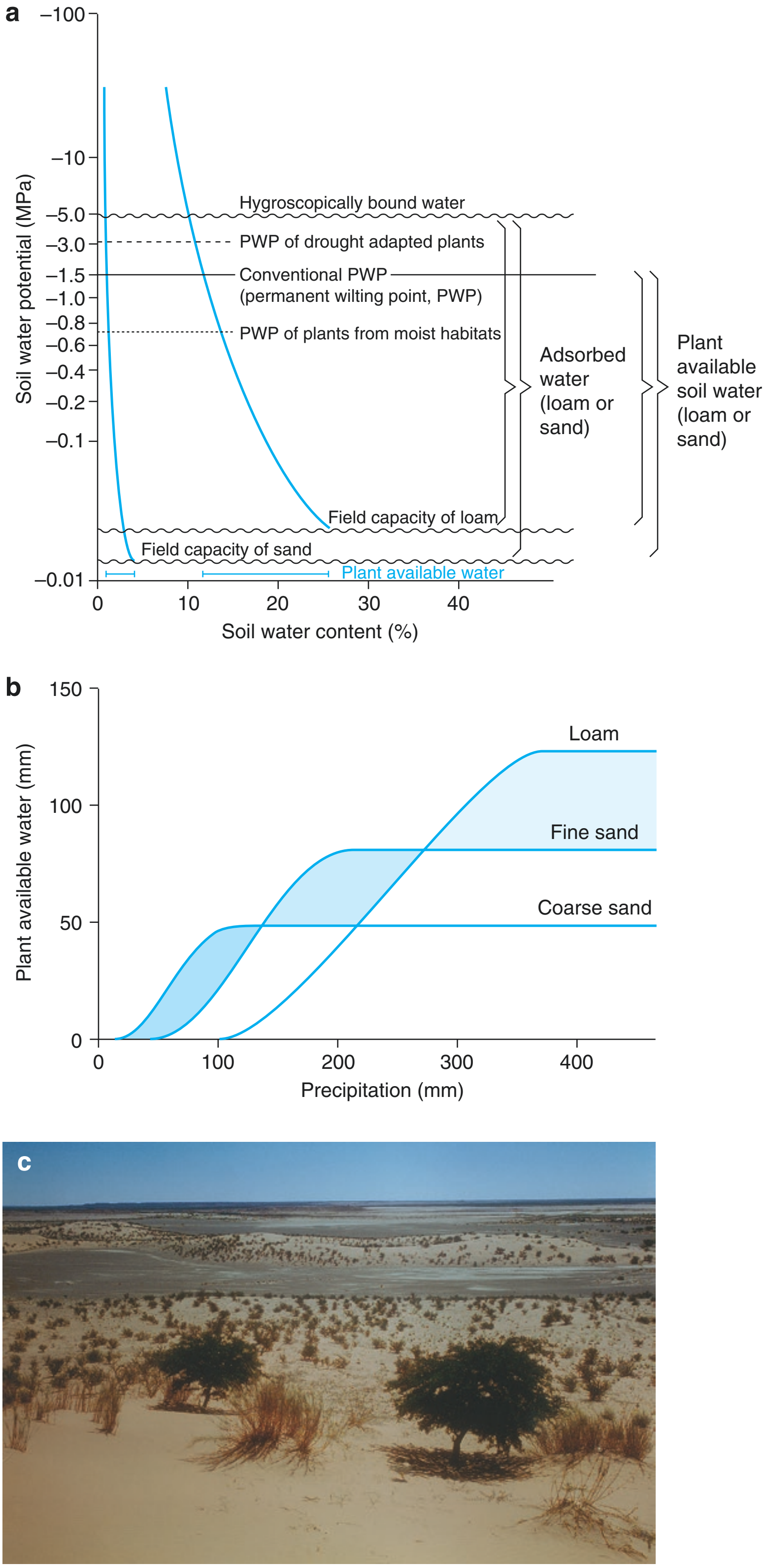

Fig. 10.6 Changes in water status and plant-available water in sandy and loamy soils. **a** Depending on the texture, the water potential at field capacity is −0.05 MPa (in sand) and −0.015 MPa (in loam). Convention sets the permanent wilting point (PWP) of agricultural systems at −1.5 MPa. Plants that live in wet or dry conditions may have wilting points at −0.7 MPa and −3 MPa, respectively, but the additional available water resulting from a shift in the wilting point is small. The limit of hygroscopically bound water is set at −5 MPa. The difference between field capacity and hygroscopically bound water is the exchangeable water, only a proportion of which is available for the plant (from Larcher (2003)). **b** Change in the amount of water available to a plant, depending on the soil texture. In arid areas, sandy soils contain more water that is available to a plant than in a loamy soil, as the water is not as strongly held by capillarity in sand as it is in loam. In contrast, in areas of high rainfall, the amount of water that can be stored by a sandy soil is less than that in a loamy soil (Modified from Walter (1960)). **c** Distribution of vegetation in the Namib Desert (Asab, Namibia) with *Acacia karroo*, *Aristida sabulicola* and *Acacia ciliata* growing on the sand dunes (with high water availability and low salt) and vegetation-free areas on the plain, where loam and clay soils have low water availability and higher salt concentrations. (Photo: E.-D. Schulze)

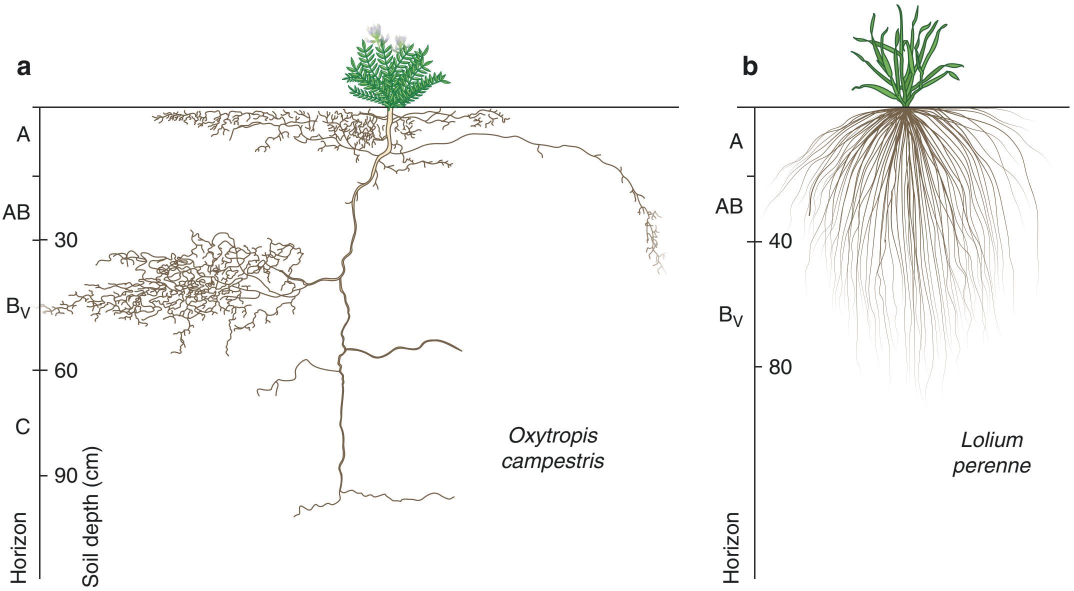

Fig. 10.7 Root architecture of dicotyledonous and monocotyledonous plants. Root distribution of **a** the dicotyledonous *Oxytropis campestris* and **b** the grass *Lolium perenne*. (redrawn from Kutschera and Lichtenegger (1992))

additionally facilitated by fungal hyphae forming the so-called **mycorrhizae** (Marjanovic and Nehls 2008) (Chap. 19), in which water is mainly transported towards the root by capillary forces. The availability of water in the soil determines the surface area of roots needed to provide leaves with a certain amount of water.

Water transport in soils is different in **saturated soils** (water content above field capacity) and **unsaturated soils** (water content below field capacity; water moves as vapour). In saturated soils, water flow follows **Darcy's law** (Darcy 1856). Darcy studied the water pressure in the wells of the city of Dijon, France. In this case the flux, or Darcy velocity (v, in volume per time and area, measured in cubic metres per hour per square metre or in metres per second), is proportional to the hydraulic gradient ($\mathrm{d}h/\mathrm{d}x$: change in height per change in the length of the flow path, which corresponds to the potential gradient) and the **saturated soil water conductivity** (k_s), which depends on soil texture, where soil texture describes the grain size of soil particles (stone, sand, silt, clay):

$$v = -k_s \left(\frac{\mathrm{d}h}{\mathrm{d}x} \right) \tag{10.10}$$

In stony soils k_s is $>10^{-3}$ m s^{-1}, in sand it is $>10^{-5}$ m s^{-1}, in silt it is 10^{-7} m s^{-1} and in clay it is 10^{-9} m s^{-1}.

In unsaturated soils, the rate of flux is much lower than that in saturated soils. It depends on the **unsaturated soil water conductivity**, k_Θ, which decreases with the soil water content, Θ, and is determined by the potential gradient, $\Delta\Psi$, over the distance, x.

$$v = k_\Theta \cdot \left(\frac{\Delta\Psi}{\Delta x} \right) \tag{10.11}$$

This equation is analogous to Eq. 10.10, but the water potential is the driving force, which in turn is related to the relative humidity in soil pores (Eq. 10.7). The values for k_Θ in silt soils range between 10^{-13} near saturation and 10^{-17} cm s^{-1} close to the wilting point. Soils are not homogeneous but structured in horizons and differentiated within the horizons in more or less dense aggregates. Thus, the hydraulic conductivity of soils varies over a very short distance with texture, aggregation and soil water content (Horn 1994). Thus, even within a single soil profile, water availability is highly variable, which results in high variability in the **root architecture** of plants. In dicots, the seminal root is long lived and, as a tap root, explores deeper soil horizons with an extensive root system. In horizons where nutrients and water are available, a dense adventitious root system is formed. In contrast, in grasses the seminal root is short lived. A dense adventitious root system develops near the soil surface (Fig. 10.7). There is an interaction between water and nutrient availability on the one hand and the hydraulic structure on the other (Ewers et al. 2000).

The soil layer from which plants gain their transpiration water may be determined with **stable isotopes** of hydrogen, D = deuterium, and oxygen, ^{18}O. The stable isotope values for hydrogen and oxygen (δD and $\delta^{18}O$) increase with the temperature of precipitation (Dawson 1993)—that is, winter rains have a lower stable isotope value than summer rains. In addition, isotopes

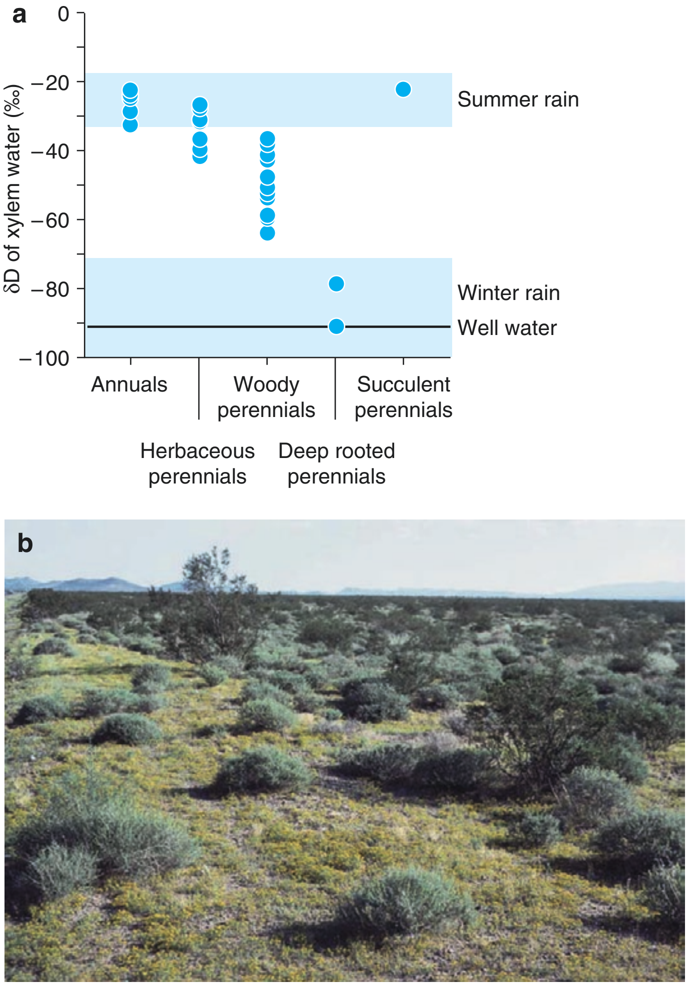

Fig. 10.8 Stable isotope values of hydrogen for plant types and groundwater in the Sonoran Desert. **a** Hydrogen isotope values in water from the xylem of different types of plants growing in the Sonoran Desert (*blue circles*), compared with the hydrogen isotope values in summer and winter rainfall (*blue bands*), as well as in groundwater (*black line*) (after Ehleringer (1993)). The δD value is calculated from the D/H ratio of the sample in comparison with a standard $[(D/H)_{sample}/(D/H)_{standard} - 1]$, where water from deep oceans is used as the standard (V-SMOW = Vienna standard mean ocean water). In the case of the Sonoran Desert, annuals use the summer rainwater, which has a high δD value depending on the temperature, almost exclusively. In contrast, deep-rooted perennials almost exclusively use water from winter rainfall, which has a low δD value due to the lower temperatures. The δD value of water from the xylem of plants shows from which soil level they obtain the water. **b** Vegetation in the Sonoran Desert close to Oatmans, South Nevada, with summer annual plants *Pectis papposa* (Asteridae, C_4 plants); perennial woody plants, *Ambrosia dumosa* (Asteridae, C_3 plants); and perennial deep-rooted *Larrea tridentata* (Zygophyllaceae). (Photo: E.-D. Schulze)

enrich at the soil surface, as water molecules containing heavier isotopes evaporate more slowly than molecules with lighter isotopes. Measuring the isotope ratios in (D/H or $^{18}O/^{16}O$) xylem water and in water along a soil profile provides information on the horizons from which species may take up their water.

Establishing the origin of transpired water (**water uptake**) with reference to the soil depth is most clear in regions with seasonal rainfall at different temperatures. An example is given in Fig. 10.8a for the Colorado Desert in the southwestern USA (Ehleringer 1993, 1995). Summer and winter rains show very different δD values, and groundwater is even more depleted in deuterium than winter rain because of isotope fractionation during seepage of water to a greater depth. Various plant species use water sources from different depths. In this subtropical "warm" desert (Fig. 10.8b), annuals and succulents use summer rains, which reach the Colorado Desert as sporadic subtropical fronts (note: in Mediterranean winter-rain regions, annuals use mainly winter rains). In contrast to the summer annuals, deeper-rooting perennials (usually, evergreen herbaceous plants and shrubs) utilise the water of winter rains or groundwater. In between these two contrasting types there is a group of moderately deep-rooting perennial plants, which use the water as it percolates through the soil profile. At times between these periods of precipitation, there are longer dry periods when these plants may even shed their leaves (i.e. they are deciduous). The differentiation of species according to their source of water applies not only to the Colorado Desert but also to other dry regions (e.g. the temperate semi-deserts in Argentina; Schulze et al. 1996b). Under arid conditions,

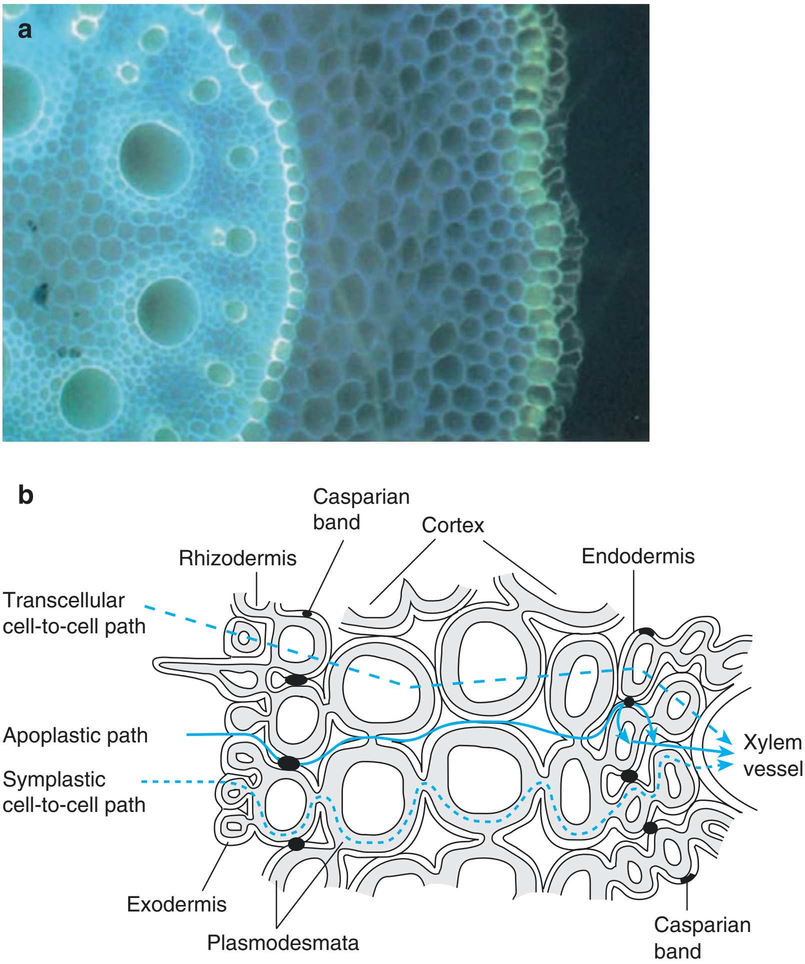

Fig. 10.9 Water flow through the root. **a** Cross-section through a maize root in which the lignin and lipids in the exodermis and endodermis are stained with berberin sulphate. **b** Schematic cross-section of a root showing routes of water and nutrient transport. The suberised Casparian bands appear as *black dots* in this cross-section, showing their position in the cell wall. *Blue arrows* mark clearly different paths that water can take. (After Steudle (1994))

water may also rise in the soil by capillary forces, but this will occur only above a water table. The hydraulic redistribution by plants is explained below (Fig. 10.11).

Water uptake by plants from the soil occurs in a zone behind the apex of the root tip where root hairs develop and the root cortex is not yet suberised (Steudle 1994, Steudle and Peterson 1998). In addition, water is taken up in meristematic regions of lateral roots. In older parts, the root is differentiated (Fig. 10.9a) into an epidermis below which a suberised layer called the **exodermis** exists in many species, followed by the **root cortex**, a heavily suberised or lignified endodermis (the **Casparian band**) and the central cylinder (the **stele**) with the xylem vessels and the phloem. Water follows (as a first approximation) the water potential gradients from the soil to the xylem, but along various pathways (Fig. 10.9b). In the region of the root cortex, water may (a) flow in the cell wall (**apoplast**), (b) move from cell to cell via the plasmodesmata (**symplast**) or (c) move across the cells (via the transcellular path). At the endodermis (and probably also at the exodermis), water must be moved through the symplast of specialised unsuberised **transmission cells**. In the undifferentiated root tip, where the endodermis does not yet exist, water may enter via the apoplast and the symplast of growing cells. Thus, water transport in the root may be described by a model with a series of parallel resistances connected by serial resistors. The **hydraulic conductivity** in each cell layer ($\mathrm{Lp_z}$, measured in metres per second per Megapascal; Eq. 10.12) may be described by:

$$\mathrm{Lp_z} = \gamma_\mathrm{c} \cdot \frac{\mathrm{Lp_c}}{2} + \gamma_\mathrm{cw} \cdot \frac{\mathrm{Lp_{cw}}}{\Delta x} \cdot \frac{\Delta x}{d} \qquad (10.12)$$

where $\mathrm{Lp_c}$ describes the hydraulic conductivity of cellular membranes and the factor 2 considers the fact that two membranes per cell must be crossed. $\mathrm{Lp_{cw}}$ is the hydraulic conductivity of the cell wall, γ_c and γ_cw are the amounts of cytosol and cell wall at the cross-section in the direction of the flux ($\gamma_\mathrm{cw} + \gamma_\mathrm{c} = 1$), Δx is the width of a cell layer and d is the thickness of the tissue. Equation 10.12 shows that the relevant fluxes may be distributed differently according to the structure of the root. The distribution of the pore size in the cell wall and the size of the hydrated ions determine the conductivity. Pores in the inter-micellar space of the cell wall are about 5 nm; the space between the cellulose fibrils is about 10 nm. In comparison, a water molecule diameter is about 0.3 nm, Na ions with their hydrated shell reach 0.5–0.7 nm, K ions measure 0.4–0.5 nm and a glucose molecule measures about 0.75 nm (Lüttge and Higinbotham 1979). Even though the cross-section available for apoplastic transport is much smaller than that for the cytosol, it depends on the conditions if the flux is hydraulic (following the water potential gradient of transpiration) or metabolically regulated following an osmotic gradient. Thus, the root is not a uniform structure (Steudle and Peterson 1998).

If the apoplast path is interrupted (e.g. by strong suberisation of roots), the cellular component dominates (Michael et al. 1997). The flow of water through the cell membrane in the cellular transport path is affected by **aquaporins** (proteins that act as valves in the hydrophobic membrane of the cell) (Tyerman et al. 1999) (Chap. 6).

Even though water transport through the endodermis is metabolically regulated, water flow can be inhibited by only about 50% by mercury, which binds to sulphur-containing amino acids in the aquaporins. Also, antisense-plants lacking aquaporins maintain 40% of the hydraulic conductivity of control plants (North and Peterson 2005).

The water transport across the Casparian band results in a positive pressure, which is visible on cut stems as emerging droplets. The **root pressure** is caused by an osmotic gradient of about 100 mM of inorganic ions, typically under conditions with high moisture or low/no transpiration. This results in a pressure in the order of 1–2.5 MPa and may lift water from the root to the leaves up to a height of 25 m (Nobel 2009; Lambers et al. 1998). However, for water transport in dry air, this process is not sufficient to carry enough water; it may however be important in healing cavitation of xylem elements (Fig. 10.15).

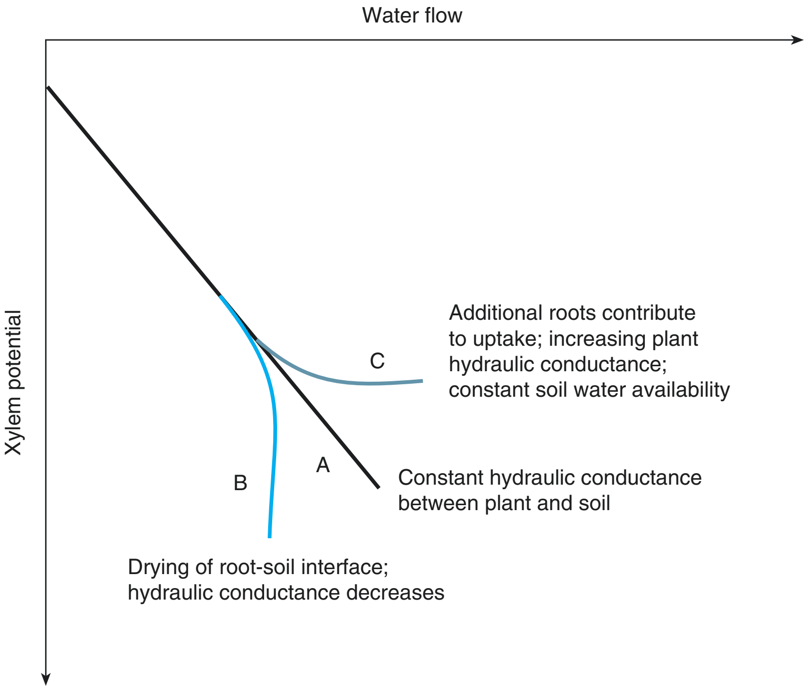

Fig. 10.10 Schematic diagram of changes in xylem water potential with increasing water flow. A The hydraulic conductance is constant. B The hydraulic conductance falls when the interface between root and soil dries out. C Additional roots contribute to the transport as the soil dries

The differentiation of root anatomy is, from an ecological point of view, a response to the conditions of water flow between the soil and root, and the uptake of nutrients. **Water uptake** normally does not limit the supply of water to the plant in moist soils. The water potential in the shoot is, of course, also determined by transpiration. Thus, in moist soils, the water potential in the xylem decreases (becomes more negative) with the amount of water that is transported through the system (Fig. 10.10, curve A), the slope representing the **hydrologic resistance** (gradient/flux) or **hydraulic conductance** (flux/gradient) of the root and the stem. In ecology, “conductance” is the preferred variable because it is proportional to the flux (Cowan 1977). In dry soils, corresponding to the low flux and the very low conductivity in the unsaturated soil, a dry zone may develop around the surface of the root—that is, further supply from the soil may, in this case, be the limiting factor (Michael et al. 1999). This state would be visible in the leaf by a strong reduction of water potential in the xylem without an associated increase in the flux through the vessels (Fig. 10.10, curve B). A corresponding turgor loss is expected to occur in the root tip under such conditions, leading either to osmotic adjustment or to production of the stress hormone abscisic acid (ABA) (Chap. 6). Conversely, there are situations where changes in water transport may occur without changes in water potential (Fig. 10.10, curve C), —for example, by water availability in specific horizons. Here, the water potential gradient between the soil and xylem reaches a magnitude that allows a flux via additional surfaces (i.e. other roots or root regions) that were not participating in water uptake because the potential gradient was too low. Thus, the hydraulic conductance of the root, and thus water uptake, is variable, and it is plant regulated through the root architecture (Ewers et al. 2000) and the molecular responses to drought in the root tip.

The site for water uptake also harbours a potential leak. The plant cannot seal itself against the soil. “Unprotected” regions are the root tips and the axial meristems of lateral roots (i.e. the regions of water uptake into the roots). Also, the transmission cells in the endodermis and in the exodermis may transport water in both directions—that is, roots not only are able to take up water from the soil but also may lose water to the soil. This is ecologically

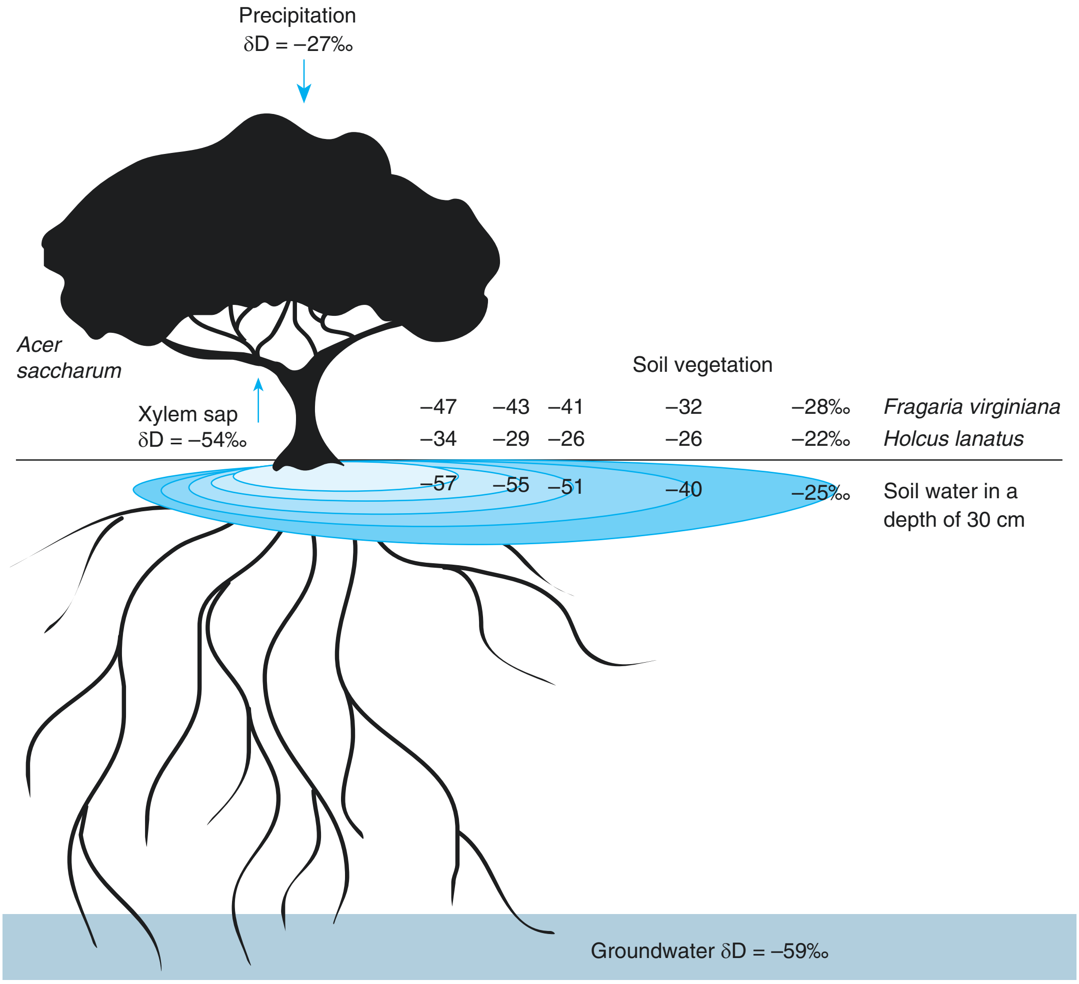

Fig. 10.11 Stable isotope values of hydrogen (δD values) as a marker of the source of water. The δD value is calculated from the D/H ratios of the sample in comparison with a standard $[(D/H)_{sample}/(D/H)_{standard} - 1)]$, where water from deep oceans is used as the standard (V-SMOW = Vienna standard mean ocean water). The δD value in vegetation is between the high value in rainfall and a significantly lower δD value in the groundwater. The lower δD value in the xylem water shows that *Acer saccharum* derives its water from the groundwater. The soil water (0–30 cm deep) shows a gradient in the δD value, from the low value near the trunk to a high δD value away from the trunk. The water with the lowest δD value can only have come from groundwater that is transported by the roots and is released into the soil, during the so-called hydraulic lift. The vegetation reacts differently to the water availability depending on how deeply the roots penetrate. While *Fragaria virginiana* is able to use the "lifted" water, the roots of *Holcus lanatus* do not go that deep. (After Dawson (1993))

important at low transpiration. During the **hydraulic lift** (also called hydraulic redistribution), water is taken up from wet soil (often in deep horizons) and moved by a water potential gradient to another (mainly the upper) soil horizon, where it is released into the dry soil (see reviews by Neumann and Cardon (2012) and Prieto et al. (2012)). Water release of plants to the soil was first observed in dry climates (Richards and Caldwell 1987), but it is also important in temperate climates. For *Acer saccharum* it was observed (Dawson 1993) that the isotopic composition of soil water in the region of the canopy corresponds not to the rainwater but to the much deeper groundwater (Fig. 10.11).

The smaller the distance to the root of the tree is, the more similar the isotopic composition of the xylem water of the herbaceous vegetation is to that of the tree xylem water.

Obviously, during the night, larger amounts of water are transported by tree roots from the moist subsoil above the water table into the dryer topsoil. The isotopic signature of the water of the topsoil changes correspondingly. The water is utilised during the day not only by the tree but also by the vegetation covering the ground in the shade of this tree ("**water parasitism**"). In this example, 30–60% of the water in the xylem of this ground flora originates from the hydraulic lift of the tree roots. This example may explain the often luxurious vegetation of herbaceous species in the shadow of trees in semi-arid regions.

The reverse process, the **inverse hydraulic lift** (Schulze et al. 1998a; Burgess et al. 2001), is ecologically just as important as the hydraulic lift. In arid regions the lower soil layers may very rarely be moistened as precipitation is sufficient only to wet the upper soil layers to field capacity. The "wave of water" produced in the soil by precipitation penetrates only a few decimetres (in silt) or metres (in sand). Lower soil layers remain permanently dry unless there is groundwater. Nevertheless, roots are able to penetrate such dry soil to a considerable depth by the inverse hydraulic lift (Fig. 10.12; Canadell et al. 1996).

The **maximum rooting depth** in deserts and savannas is more than 50 m. The absolute record for observed root depth is 68 m in the Kalahari, where the groundwater is more than 100 m deep, covered by dry sand, and it is expected that roots are able to penetrate to that depth. Roots up to 100 m deep have not yet been found. The deepest roots were found by chance during construction of a well. Penetration of roots to such a depth in dry soil is possible only by transport of water from the moist topsoil (i.e. the inverse hydraulic lift)—that is, the root must be kept wet in a very dry rhizosphere. Without additional transport of water, the root tip, which is protected only by mucilage, would desiccate in the dry soil.

Even though water uptake occurs predominantly in roots, liquid water may be taken up by shoots even from fog and dew via lenticels of the bark (Klemm 1989) and via water films of the stomata (Burkhardt 2010).

10.2.2 Xylem Water Transport

A **stem structure** distinction is made between **herbaceous and woody species**, but many transitions exist. In fact, the xylem elements of all herbaceous species contain lignin to achieve the needed rigidity of vessels, which operate under tension. Thus, Schweingruber and Büntgen (2013) concluded that the classification between woody and herbaceous species is not supported by wood anatomy. One may also distinguish between stems according to the structure of the vascular systems. In **closed vascular bundles**, the initial meristem between xylem and phloem cells, the cambium, terminates cell division. The xylem and phloem are surrounded by a vascular bundle, the bundle sheath, most conspicuously developed in grasses (Fig. 10.9). In contrast, **open vascular bundles** exist in most dicots where the cambium remains active and produces xylem cells towards the plant interior and phloem cells towards the outer periphery of the stem. An example is the herbaceous species *Arabidopsis thaliana*, which contains a stem anatomy identical to that of woody stems (Fig. 10.13a). Other herbaceous species (e.g. *Polygala alpestris*) even exhibit seasonal growth rings (Schweingruber et al. 2013). In trees and shrubs, a distinction is made according to the arrangement and size of vessels during the course of the growing season. In **diffuse porous wood** (Fig. 10.13b), vessels and tracheids of different diameter are formed according to the demand of water flow at any time of the season (e.g. in *Betula pendula*). The wood is very similar to that of *Arabidopsis thaliana*, except that large vessels exist only in trees and shrubs. In **ring-porous wood**, a ring of very large vessels is formed when growth is initiated after winter and new leaves develop (*Quercus robur*; Fig. 10.13c). With ongoing seasons, smaller vessels and even tracheids follow.

In all cases the xylem elements are formed by an open meristem where the cells die after elongation. The cambial activity is needed in long-lived species because phloem elements are relatively short lived. Since cell division of the cambium results in phloem and xylem elements, the dead xylem cells accumulate and remain functional for

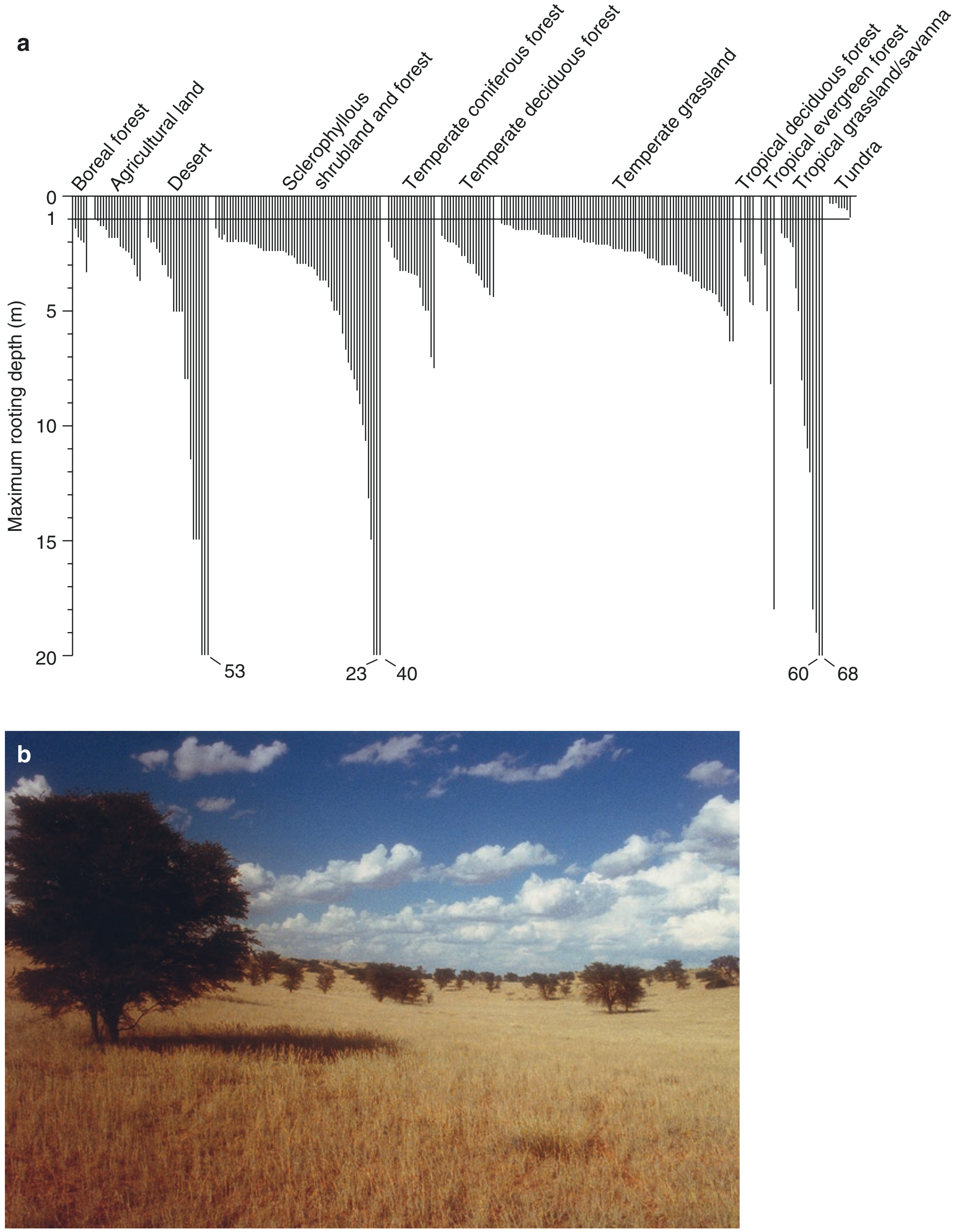

Fig. 10.12 Depth of roots in global vegetation types. **a** Maximum observed rooting depth of different types of vegetation. Each line represents a single measurement of a particular plant species. The numbers show the maximum depths that are beyond the y scale (from Canadell et al. (1996)). The deepest known root depth was measured in the Kalahari Desert from *Acacia erioloba* when bore holes were sunk to the water table. **b** *Acacia erioloba* savanna with perennial C_4 grasses *Aristida* and *Stipagrostis* (see Schulze et al. (1996a)) in the Kalahari Desert, north of Uppington, South Africa. (Photo: E.-D. Schulze)

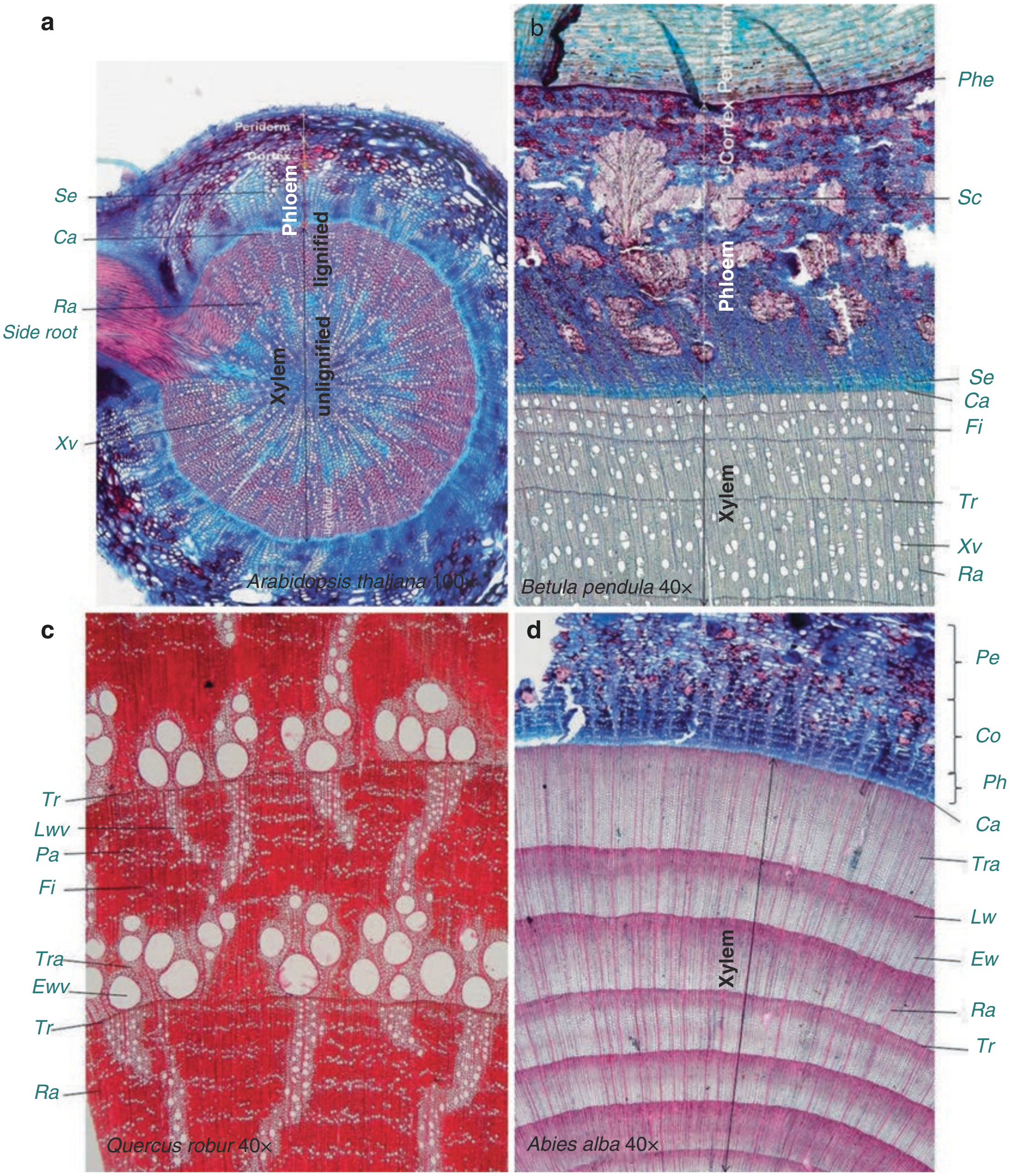

Fig. 10.13 Wood anatomy of plant types. Cross-sections of **a** the herbaceous stem of *Arabidopsis thaliana* with secondary xylem cells, **b** the diffuse porous wood stem of *Betula pendula* and **c** the ring-porous *Quercus robur*. **d** Coniferous wood of *Abies alba*. *Ca* cambium, *Co* cortex, *Ew* early wood, *Fi* fibre, *Lw* late wood, *Lwv* late wood vessel, *Pa* parenchyma, *Pe* phellogen, *Ped* periderm, *Ph* phloem, *Ra* ray, *Sc* sclerid cell, *Se* sieve elements, *Tr* tree ring, *Tra* tracheids, *Wwv* early wood vessel, *Xe* xylem element, *Xv* xylem vessel. (Anatomical sections by F. Schweingruber)

water transport, connecting the living root central cylinder with the living leaf mesophyll. The size of the **vessels** is determined by a plant-hormonal balance in the cambial layer (see Schweingruber et al. (2013)). Since there is also a balance between the **leaf area index** (**LAI**) of transpiring leaves and the total **xylem area** that transports water, the long-lived xylem elements become dysfunctional

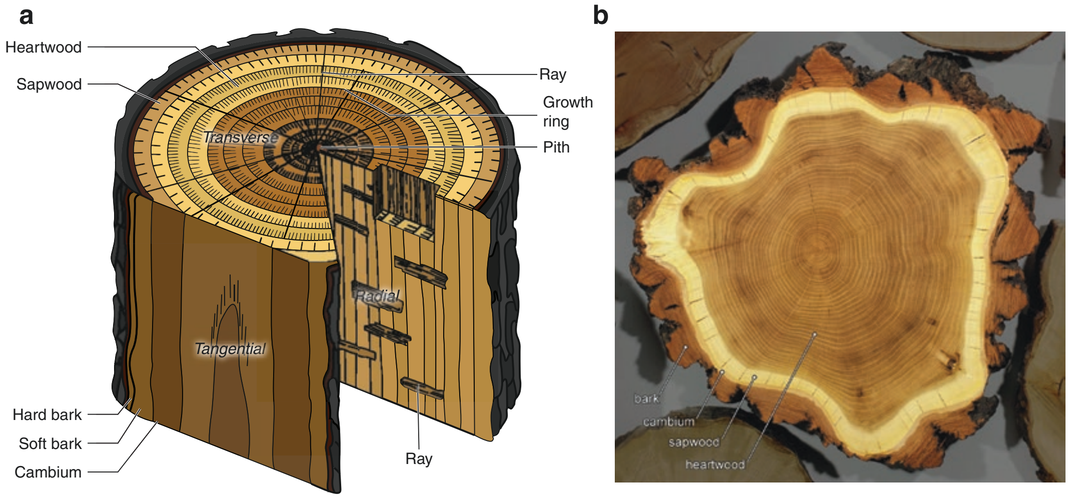

Fig. 10.14 Wood anatomy. **a** Section of a piece of wood with its main structures. **b** Cross-section of *Robinia pseudacacia*, with light-coloured sapwood and dark-coloured heartwood. (Photo: E.-D. Schulze)

if they do not participate any more in water transport. Under these conditions, the remaining meristematic cells of the wood seal the xylem elements mainly with tannins to make these elements resistant against fungal attack. Thus, we distinguish between an outer ring of xylem elements (the **sapwood**), which participates in the water flow, and an older inner part of the wood (the **heartwood**), which is not conducting water but stabilises the stem (Fig. 10.14). Because of the tannins, this wood is generally darker-coloured, but there are species where the heartwood is not clearly visible (e.g. *Picea abies*). It is the heartwood that gives a species the physical strength for larger structures. With heartwood formation, most meristematic cells also die, but some meristematic cells may remain alive for more than 100 years (in *Carpinus betulus*) (Fritzsche 1910). It should be noted that young trees contain only sapwood. Heartwood formation occurs when the stem area increases beyond a required sapwood area. Thus, the number of conducting elements in woody plants is regulated by the annual increase of new elements as well as by the transition of old elements from sapwood to heartwood (Fukuda 1997). Only the sapwood area conducts water.

The cambial activity is not constant but highly dependent on the growing conditions. Cambial activity ceases only during winter and during dry periods. This change in cambial activity results in growth rings (called **tree rings** in shrubs and trees) of variable activity. Since the anatomy of wood does not change any more after cambial division and elongation, tree rings are a “fossil” record of the growing conditions in the past and have been used to reconstruct the climate, on the basis of statistical models, explaining present-day ring width with climate conditions during the growing season (Vaganov et al. 2006). There are species that do not form a ring structure but terminate growth under conditions of drought without an obvious anatomical signal. Trees in humid tropical regions without any dry season also have no annual tree ring structure but exhibit visible changes in growth activity.

Xylem water transport follows the water potential gradient between the root and leaf during the day. The hydraulic conductivity of the xylem is relatively high. The question of the physical conditions in a capillary with negative pressure of more than 10 MPa has been a topic of research for many years. Böhm (1893) was probably the first to postulate that the cohesion between water molecules is sufficient to achieve a continuous water column in the xylem vessels under tension (**cohesion theory**). With the

Table 10.2 Anatomy, conductance and water flow in the xylem. Vessel radius and length, and maximum capillarity of vessels from different types of plants according to Zimmermann (1983), Carlquist (1991) and Nobel (2009)

Plant type	Specific conductance for water (m s^{-1} MPa^{-1})	Maximum rate (m h^{-1})	Vessel diameter (µm)	Vessel length (m)	Capillarity (kPa)
Conifers	$5–10 \times 10^{-4}$	1–2	10–40	0.002–0.005	29–7
Diffuse porous angiosperms	$5–50 \times 10^{-4}$	1–6	5–150	1–2	58–1.0
Ring-porous angiosperms	$50–300 \times 10^{-4}$	4–44	10–600	10	29–0.5
Herbaceous plants	$30–60 \times 10^{-4}$	10–60	10–500	1–2	29–0.6
Lianas	$300–500 \times 10^{-4}$	150	500	approx. 10	0.5

measurement of negative pressures of more than 1 MPa in xylem vessels (Wei et al. 1999) and the observation that the tension changes with the flux through the xylem vessels, the cohesion theory has also been confirmed by measurements.

Biophysically the **water flux** in a xylem vessel, J_x (in cubic metres per second), is described by the **Hagen–Poiseuille law** for laminar flows and depends on the radius, r, of the xylem vessel, the viscosity of the liquid ($\eta = 10^{-3}$ Pa s for water) and the hydrostatic gradient, dP/dx (in Pascals per metre):

$$J_x = \left(\frac{\pi r^4}{8\eta} \frac{dP}{dx} \right) \tag{10.13}$$

The flow is in the direction of the decreasing hydrostatic or water potential gradient (from less negative to more negative values). The flow must be sufficiently slow so that the conditions of laminar flow (in contrast to turbulent flow) are maintained, to avoid rupture of the water columns. The potential gradient required to transport a certain volume flow (e.g. 1 mm s^{-1}) across the cell wall is very high, about 3×10^5 MPa m^{-1}, according to Eq. 10.13 (Nobel 2009). Thus, major forces are required to move water through the cell wall of the leaf mesophyll, which leads to relatively slow movement of water in the xylem.

In addition to the regulation via the **vessel diameter**, the volume flux per time and unit area, I_x (measured in metres per second), in the xylem under a pressure gradient ($\Delta P/\Delta x$) is determined by the area of the cross-section per vessel and the number of xylem vessels, n, per organ:

$$I_x = \frac{r^2}{8\eta} \cdot \frac{\Delta P}{\Delta x} \cdot n = \mathrm{Lp}_x \cdot \Delta P \tag{10.14}$$

where I_x is measured in (square metres × Pascals)/(seconds × Pascals × metres) = (metre per second) and Lp_x corresponds to the hydraulic conductivity in the xylem (measured in metres per second per Pascal). The axial hydraulic conductivity is related to a 1 m length of xylem and thus has different dimensions from the Lp of the membrane.

Following Eqs. 10.13 and 10.14, plants have many possibilities to regulate the flux in the xylem and thus the water potential gradient, or the water potential gradient and the concomitant flux (Gartner 1995).

The **vessel radius** varies between 500 µm in lianas to approximately 100 µm in ring-porous woody plants (e.g. oak) and 10–40 µm in the tracheids of conifers (Table 10.2); a larger radius allows a considerably higher volume flux. In tropical lianas, in ring-porous woody plants and in dicotyledonous herbaceous plants, water taken up by the root reaches the transpiring leaf in less than 1 h. In contrast, it takes 2–3 months for the water taken up by the roots to reach the tip of a 100 m high *Sequoia gigantea*, because of the low average rate of flux during only part of the day.

At a constant volume flow, the water potential decreases (i.e. gets more negative) with increasing radius of the vessels. However, the advantage of wide vessels for rapid transport of large amounts of water is counteracted by the increased **risk of cavitation** (Tyree and Sperry 1989). The forces of cohesion, maintaining a continuous column of

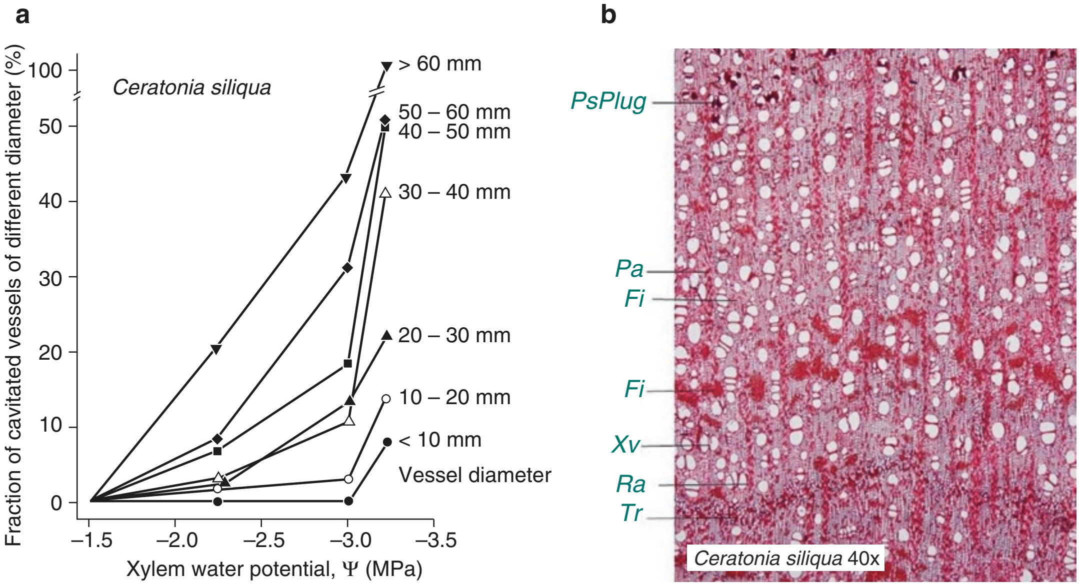

Fig. 10.15 Cavitation in xylem vessels. **a** Dependence of cavitation in xylem vessels of different size on the water potential in the xylem as the soil dries over several days. At a water potential of approximately −3.3 MPa, all large vessels of *Ceratonia siliqua* (>60 mm), but only 10% of the small vessels (<10 mm), are cavitated (Lo Gullo and Salleo 1991). **b** Cross-section of *C. siliqua*, consisting mainly of thick-walled fibres. Vessels with variable lumina are arranged in short radial rows. Large vessels in the older part of the wood are closed by thylosis, which are formed by cavitation during drought, whereby vessels that no longer participate in the water flow are sealed. The border of a growth ring is hardly visible, as indicated in the maritime climate of the island of Cyprus, where the investigated stem of *Ceratonia* grew. *Fi* fibre, *Pa* parenchyma, *PsPlug* phenolic substance plug, *Ra* ray, *Tr* tree ring boundary, *Xv* xylem vessel. (anatomical section by F. Schweingruber)

water in the xylem, decrease with increasing radius of the xylem vessels (Eq. 10.13) from about 1500 Pa in tracheids of conifers ($r = 10$–40 µm) to about 60 Pa in tracheids of ring-porous woods ($r = 500$ µm; Table 10.2). Thus, there is the danger that the cohesive force determining the continuity of the water column is exceeded. Cavitation describes the breakage of the water column in xylem cells. It is caused by small air bubbles, filled mainly with water vapour, forming in a thermodynamically unstable condition (Tyree 1997; Steudle 2000, 2001; Stroock et al. 2014). Once initiated, the bubble expands, causing an **embolism** in the xylem cell—for example, after injury. During the breakage of the water column, the flux in the vessel is interrupted. In wood, the pits of cell walls that separate xylem vessels seal cavitated vessels off. The water transport is redirected laterally (Grace 1993). Cavitation may be healed by various processes (Holbrook and Zwieniecki 2005). At high water potential, water vapour may condense again, restoring water column continuity. Cavitation and embolism may also be healed via root pressure if the plant is not too tall (Sperry et al. 1987; Gartner 1995). Plants may also be able to refill cavitated xylem vessels by phloem water because of the difference in the water potential in adjacent parenchyma (Hölttä et al. 2006; Nardini et al. 2011). However, if cavitation affects complete organs (leaves or branches), these parts dry and die.

Since the risk of **cavitation** increases with increasing size of xylem vessels (Fig. 10.15a) (Lo Gullo and Salleo 1991), cavitation occurs first in vessels with a large lumen, while the water column in vessels with a small lumen remains intact, even at high water tension. The structure of the conducting tissue determines the risk of cavitation at high rates of water transport into the shoot (Grace 1993). However, the plant is not unprotected in the face of this danger. With increasing drought, water transport in the soil and root changes, but the stomata will restrict the water flow (Sect. 10.3), and the relation of the leaf area to the xylem conducting area can be regulated by slowing of leaf formation or by shedding of leaves. Loss of productivity and plant mortality have been explained by hydraulic failure (Choat et al. 2012).

Obviously, species "adapted" to a habitat have generally evolved mechanisms to avoid lethal stress situations. Other species would not flourish in these habitats or would restrict their growth and reproductive phase to a short period in which this critical situation does not occur. For example, the Mediterranean *Bromus* spp. are successful invasive species in North American prairies and Australian semi-deserts, where the vegetative growth is restricted to the period with sufficient water supply. The invasive *Bromus* spp. gain this water with shallow roots from the top layers of soil at the cost of the water supply to indigenous perennial dwarf shrubs, particularly *Artemisia tridentata* in North America and *Atriplex* spp. in Australia (West and Young 2000) (Chaps. 13 and 20), which have deep-reaching root systems.

Generally, the diameter of vessels is larger in roots than in stems of the same species (Martínez-Vilalta et al. 2002), further decreases in peripheral organs like branches and twigs, and is particularly small in the petioles of leaves. While water potentials in the xylem decrease with increasing distance to the soil within the water conduits, the danger of cavitation is increasing. However, the small vessel diameters in the petioles reduce the risk of progressive cavitation.

At constant **hydraulic conductivity**, the water potential in the leaf decreases linearly with increasing transpiration. This can be used to demonstrate structural differences in the stem between species (Fig. 10.16a) (Schulze and Chapin 1987). Plants with lower xylem conductivity (i.e. with a steeper slope in volume per time and unit area and water potential gradient) have lower rates of transpiration and more negative water potentials. In contrast, plants with high xylem conductivity (i.e. with a flatter slope) also have high rates of transpiration; however, the water potential does not decrease to the same extent. In these species, the risk of cavitation is particularly great, leading to a substantial change in conductivity when the soil dries out (Fig. 10.16b) (Schulze and Hall 1982). In these latter species, the xylem water transport under moist conditions takes place in vessels with large lumina, while under dry conditions, xylem water transport is restricted to vessels with narrow lumina, which cavitate rather late (Fig. 10.15b). Regulation of water flux via structural characteristics of the shoot is thus possible and is dependent, to some degree, on the conditions under which a species grows.

The role of the **xylem structure** in water transport is demonstrated by measurements of water flow in the xylem of pines of different ages in the continental climate of central Siberia (Fig. 10.17) (Zimmermann et al. 2000), where the xylem flow increases linearly with the sapwood area. The greatest **sapwood area** is achieved at the age of 60 years. At this age the growth rate of trees is relatively high and the formation of heartwood has not yet started. In very old pines the sapwood area decreases, and thus the flow of water decreases. A certain plasticity in xylem development during radial growth according to the water supply has also been described (Eilmann et al. 2010; Plavcová and Hacke 2012; Bryukhanova and Fonti 2013).

10.2.3 Phloem Water Transport

The importance of water transport in the xylem and the danger of cavitation for the functioning of the whole plant are fully appreciated only when considering also the mass flow of material in the phloem (phloem water transport). In vascular bundles of plants, almost all neighbouring cells transport larger amounts of water in opposite directions, in the xylem from root to shoot, in the phloem from source to sink and laterally from the phloem to all heterotrophic living cells in the stem. Water transport occurs in the xylem along a water potential gradient, and in the phloem along an osmotic pressure gradient (the pressure gradient hypothesis; Fig. 10.18). An additional bidirectional flow of water exists within the meristem (Aloni 2004), the cell layers between the xylem

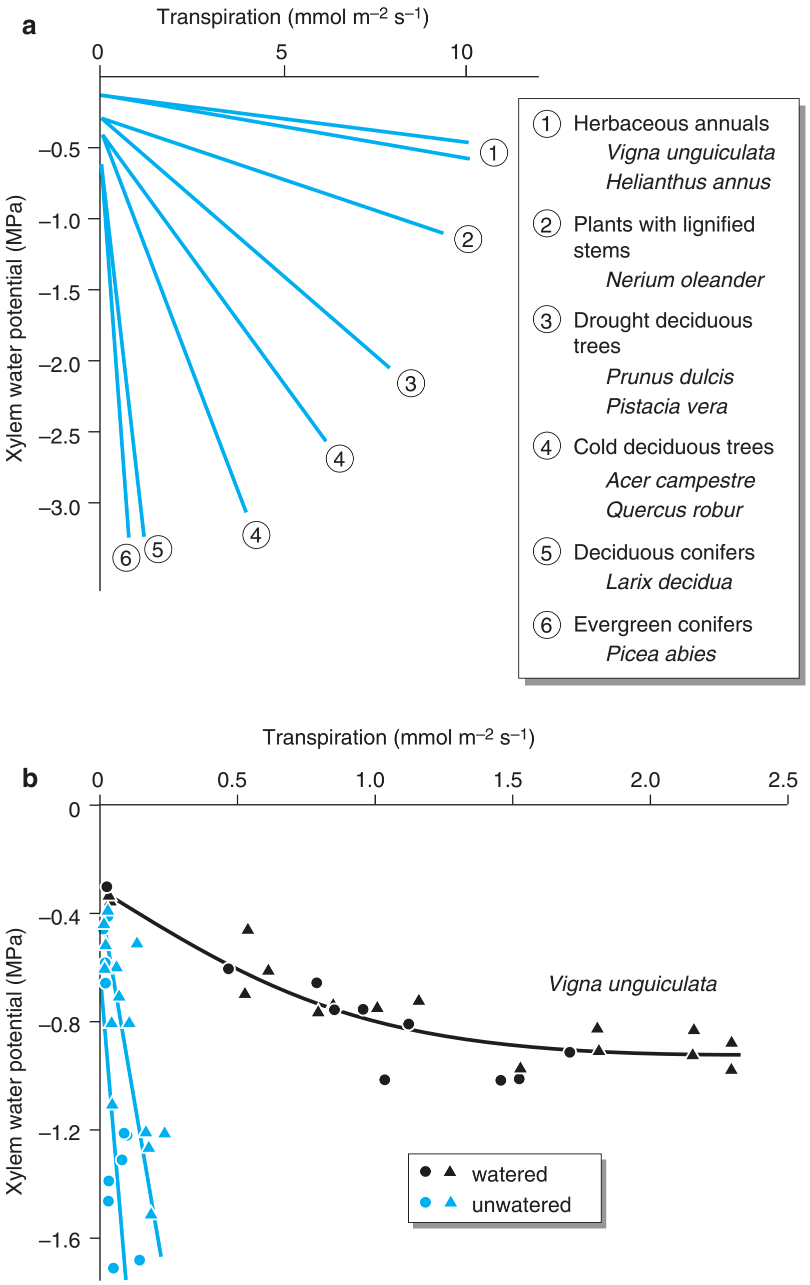

Fig. 10.16 Relationships between water potential in the xylem and transpiration **a** for different plant functional types (Schulze and Chapin 1987) and **b** for the crop plant *Vigna unguiculata* in drying soil (Schulze and Hall 1982). An increasing transpiration rate causes a lowering of the water potential. The slope of the graph is a measure of the hydraulic conductivity of the plant–soil system. *Circles* and *triangles* show the two groups of plants measured. (see also Fig. 10.10)

and phloem. The meristematic water flow is important in regulating growth.

Different gradients are maintained as follows. In moist soils, the water potential of roots is similar to that of the soil ($\Psi_{\text{root}} = 0$). With the uptake of ions, the osmotic pressure increases to about 0.1 MPa. Water transport starts because of the decrease of water potential in the leaf

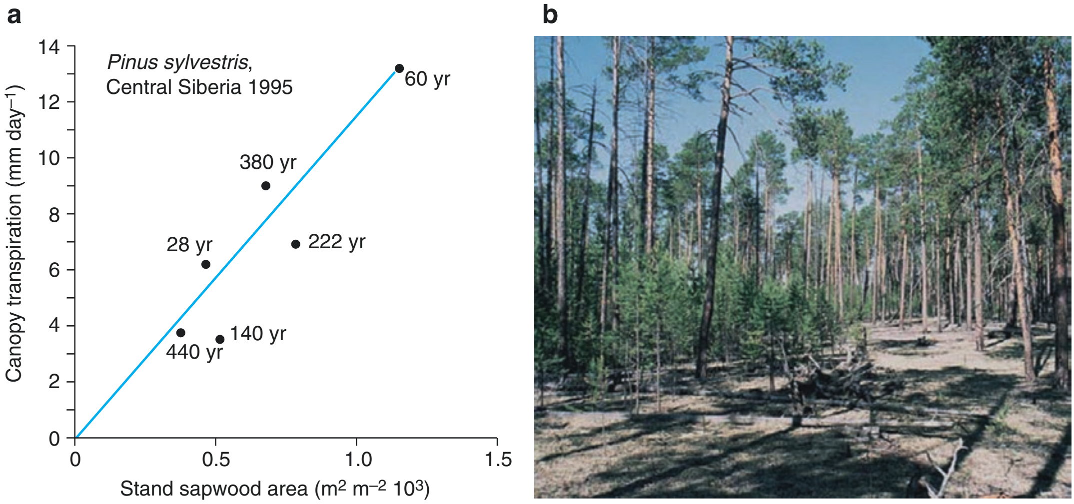

Fig. 10.17 Relation between canopy transpiration and stand sapwood area. **a** The rate of water flow rises linearly with the sapwood area; note that it is neither the youngest nor the oldest and largest trees that have the highest transpiration rates, but the 60-year-old pole stand. The small area of sapwood in the oldest stand is caused mainly by the low tree density in older stands (Modified from Zimmermann et al. (2000)). **b** *Pinus sylvestris* woods on Pleistocene sand dunes in central Siberia at 60°N on the west bank of the Jennesey. Here, cohorts of even-aged trees establish after fire (see Wirth et al. (1999)). The vegetation of the forest floor is *Cladonia*. (Photo: E.-D. Schulze)

($\Psi_{leaf} = -0.8$ MPa) as a consequence of evaporation and is dependent on the vapour pressure of the external air (e) and the net radiation (R_n). In the leaf, a smaller part of this water mass is redirected into the phloem where, because of the additional loading of the sieve elements with cations and sugars, an osmotic potential of 1.7 MPa at a water potential of −1.0 MPa and a turgor pressure of 0.6 MPa develops. This turgor pushes the phloem water from the leaf to the root as a sink. As the tissues along the sieve tubes remove sugar, the hydrostatic pressure

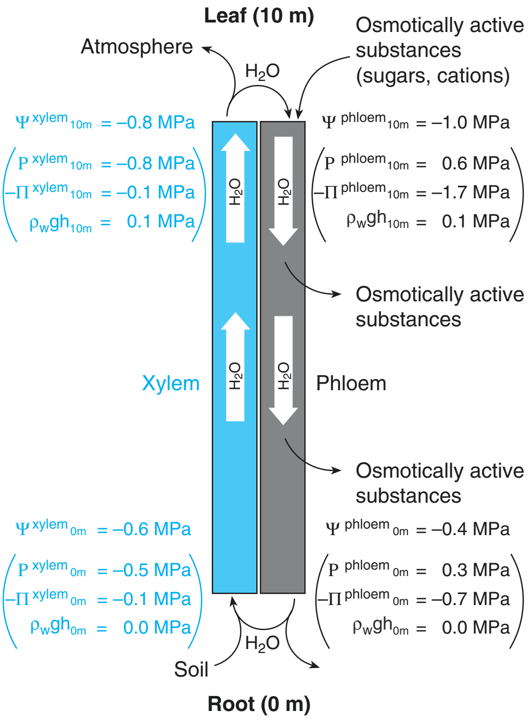

Fig. 10.18 Plant-internal water circulation. The driving force is the gradient of water potential, Ψ, which develops as a result of transpiration. In the phloem, the mass flow gradient is a result of the turgor (P), caused by loading and unloading of osmolytes (sugars and ions) in the phloem, and hence the osmotic pressure (Π) changes. In trees, there is the additional hydrostatic pressure ($\rho_w gh$) to be taken into account, where ρ_w is the density of water, g is gravity and h is tree height. Note: The turgor pressure in the xylem (P^{xylem}) is negative, unlike in most living cells, due to their different cell wall structure

decreases with decreasing osmotic pressure. This pressure-dependent transport occurs in an opposite direction to the longitudinal gradient of the water potential between shoot and root. In the root or along the stem, phloem water may re-enter the xylem. This **plant-internal water circulation** of water occurs even if the plant grows under extremely moist conditions (i.e. the water potential gradient = 0) (Tanner and Beevers 1990) or under very dry conditions. Under these extreme conditions, the circulation of water in the plant may be regarded as a "phloem-driven xylem flux" and may lead to "bleeding" of cut stems by root pressure (e.g. in sugar maple) (Cirelli et al. 2008). This transport would be interrupted only if the complete xylem were not functioning, because of cavitation during drying. In this case, the survival of the plant would no longer be possible. Consequently, all species with large xylem vessels also make small-xylem vessels so that redirection of water flows is possible in the case of cavitation, and special structures (pits) ensure that the damage is limited—that is, that cavitation does not continue in the stem. In the case of drying out, not only the water potential changes but also the osmotic pressure changes so the pressure gradient in the phloem is maintained (Schulze 1993).

10.3 Transpiration

Evaporation of water out of leaves (**transpiration**) starts at the surfaces of cell walls lining the intercellular spaces, from where the water vapour, as a consequence of the vapour pressure gradient, reaches the external air by diffusion via the stomata. The **stomata** are the valves limiting diffusion, regulated by processes in the leaf and in the roots, and by conditions in the environment (Fig. 10.2).

The **guard cells** of the stomata are a pair of cells, which stick together only at the ends, leaving a gap—the **stomatal pore**—in between (Fig. 10.19) (Meidner and Mansfield 1968).

The stomatal pore can open whenever the guard cells expand with increasing turgor. Because of the orientation of the micelles in the cell wall, the cell volume changes mainly by longitudinal expansion perpendicular to the orientation of the micelles. Thus, both cells form an opening of different widths (**stomatal aperture**), depending on the turgor pressure in these cells. The **stomatal density** (number of stomata per unit of epidermal area) and the size of the aperture depend on the species and site conditions, even though general relations do not emerge (Meidner and Mansfield 1968). Thus, the number of stomata (per square millimetres of leaf area) varies between 30 (in *Triticum* spp. and *Larix* spp.) to more than 5000 (in *Impatiens*). The size of the stomatal pore varies between 77 × 42 µm (in *Phyllitis* spp. and *Tradescantia* spp.) and 25 × 18 µm (e.g. in *Tilia* spp.).

The opening mechanism is based on a physiologically regulated change of turgor, where K^+ ions are taken up from the neighbouring cells (the so-called subsidiary cells). This ion uptake is regulated by the membrane potential (Chap. 6). The movement of the stomatal aperture is asymmetrical—that is, closing occurs much faster (1–10 min) than opening (30–60 min) (Lange et al. 1971).

Measurement of the stomatal apertures is possible in nature in some species with a microscope (Kappen et al. 1994). However, for most plant species, the aperture cannot be seen, as it is covered by protrusions of the cuticle or by waxy scales. Direct observations of the aperture are also difficult because disturbance of the leaf and the surrounding climatic conditions may affect the measurement. Therefore, rather than carrying out direct observations, in an analogy to **Ohm's law** the **leaf resistance** (R_L) or the **leaf conductance** (g_L) are calculated from the transpiration flux (E_L) and the gradient in the vapour pressure between the leaf and the air (D_L; where $_L$ refers to the leaf as a whole):

$$g_L = \frac{E_L}{D_L} = \frac{1}{R_L} \tag{10.15}$$

where the dimension (in mmol per square metre per second) has the same dimension as transpiration. At 15 °C, a conductance of 1 mmol m^{-2} s^{-1}

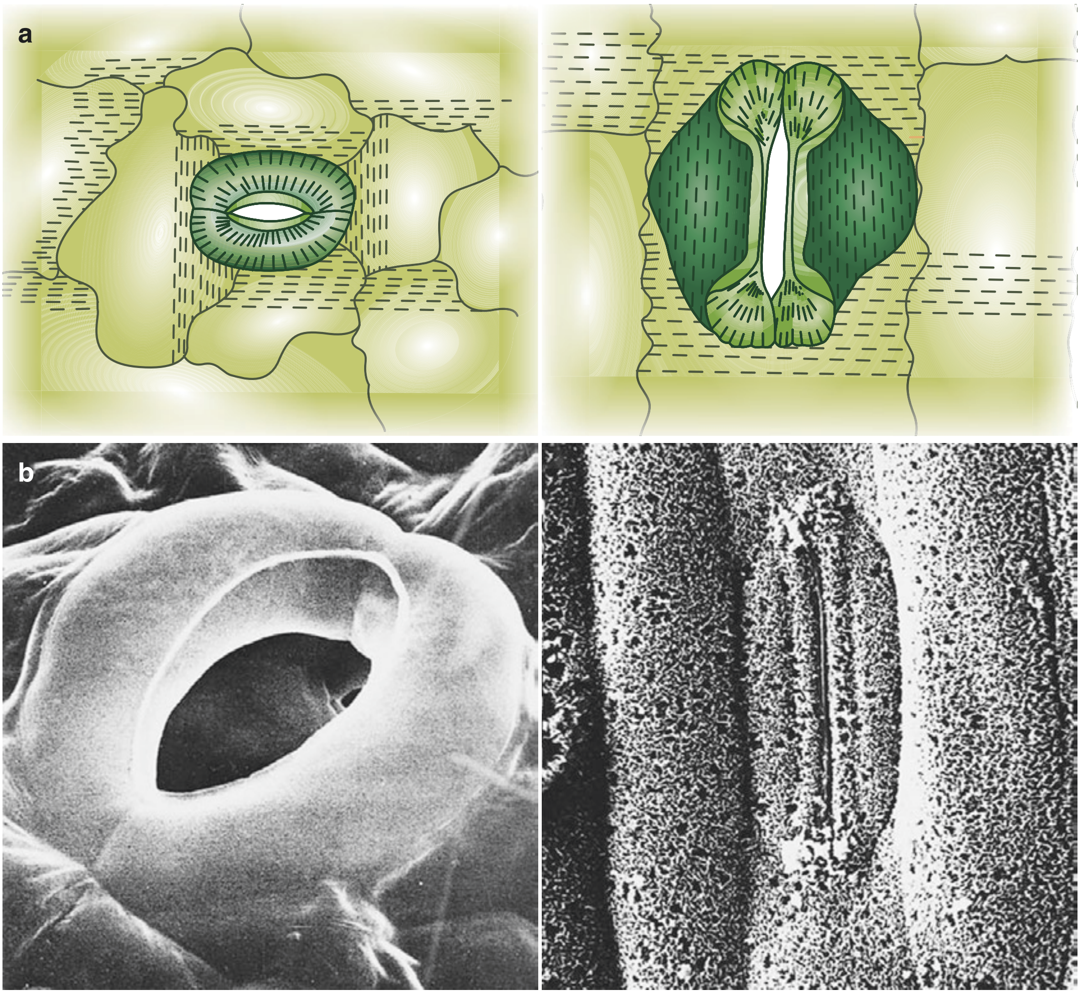

Fig. 10.19 Anatomy of guard cells. **a** Schematic structure of the cell wall of guard cells of dicotyledonous plants (*left*) and monocotyledonous plants (*right*). Micelles in the cell wall (*hatched lines*) are arranged so the expansion of the cell with increasing turgor can occur only perpendicularly to their orientation (from Meidner and Mansfield (1968)). **b** Scanning electron micrograph of a guard cell of grapevine (*left*) and of wheat (*right*). (Troughton and Donaldson 1972)

corresponds to a conductivity of 4.24 mm s^{-1} (3.83 mm s^{-1} at 45 °C). Equation 10.15 neglects cuticular transpiration, which is low for most plants. In general, stomatal conductance (Eq. 10.16) is preferred to resistance to estimate transpiration, as it changes in proportion to the flux (Cowan 1977):

$$E_L = D_L g_s \tag{10.16}$$

The volume flow (i.e. transpiration (E_L)) is determined by meteorological conditions in the atmosphere and by the stomatal aperture (Eq. 10.16). The vapour pressure of the air determines a directed diffusion of water molecules from the mesophyll via the stomata to the atmosphere. This transpirational water flow lowers the water potential in the leaf, which in turn results in a liquid flow of water in the xylem, which may feed back on stomatal opening. In this feedback loop, stomatal conductivity in plants is tuned to the hydraulic conductivity of the stem (see, for example, Hubbard et al. (2001)). Particular hydraulic barriers occur in

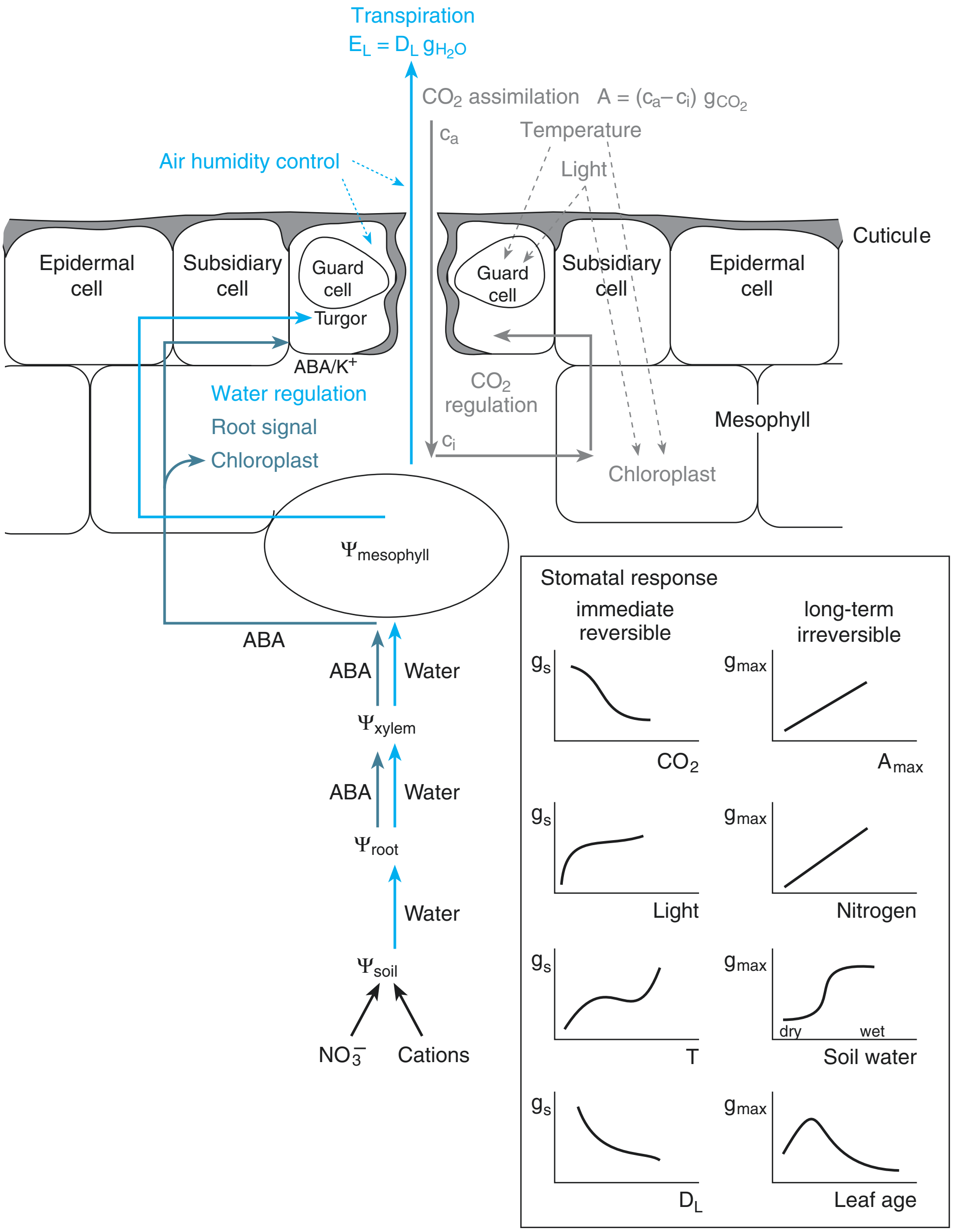

Fig. 10.20 Schematic model of the stomatal response to the environment and plant-internal factors. A "root signal" may be a change in water potential or a hormonal signal. ψ water potential, c_a atmospheric CO_2 concentration, c_i CO_2 concentration in the mesophyll, D_L water vapour pressure deficit between leaf and air, E_L transpiration, g_{CO_2} stomatal conductance of CO_2, g_{H_2O} stomatal conductance of H_2O, g_{max} maximum stomatal aperture (a measure of long-term responses to stress), g_s variable stomatal conductance

grasses, where water passes through parenchyma at the nodes.

The stomatal aperture is **regulated** by environmental conditions related to climatic factors (so-called **feed-forward regulation**) and by processes in the mesophyll (so-called **feedback regulation**). Feedback regulation is determined by water status and CO_2 assimilation. Fig. 10.20 illustrates the different responses, which are described in detail in Sects. 10.3.1 and 10.3.2.

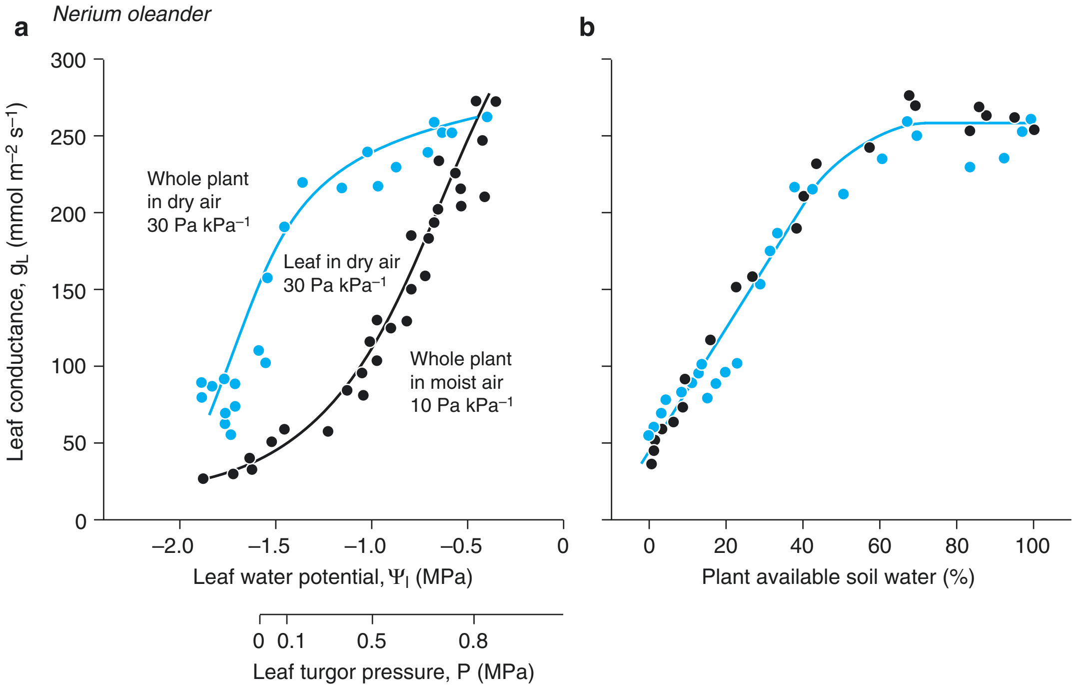

Fig. 10.21 Effect of leaf and soil water status on leaf conductance. **a** Relationship between conductance of the leaf and water potential in the xylem in *Nerium oleander* with increasing soil drying. The gradient of water vapour pressure between the leaf (on which the stomatal conductance was measured) and the air around the leaf was constant (10 Pa kPa^{-1}), but the plant itself was either in moist air (*black symbols*) or in dry air (*blue symbols*). The stomata closed (decreasing conductance) as the soil dried, but the humidity of the air around the whole plant altered the leaf water potential by almost 1 MPa in dry air compared with moist air, although the measured leaf was under constant conditions. **b** Leaf conductance in the same experiment, but related to soil water content (Modified from Gollan et al. (1985)). The results of this experiment imply that the stomata respond not to the leaf water potential but to the soil water content

10.3.1 Stomatal Responses to Plant-Internal Factors

Photosynthetic capacity: The maximum opening of stomata (g_{max}) correlates with the capacity for photosynthesis of leaves, depending on the nitrogen supply—which affects the carboxylation capacity (Schulze et al. 1994) (Chap. 12) and the specific leaf area (SLA, leaf area/leaf weight)—and on the species (greater in fast-growing species) (Reich et al. 1997). From the relation between conductance and leaf nitrogen concentration, global maps of maximum stomatal conductance are produced, from which also maximum rates of CO_2 assimilation can be derived (Chap. 12, Fig. 12.6c). The maximum capacity for the stomatal opening of a given plant has been described only empirically.

Soil water status: The availability of water in the soil is globally the most important environmental factor limiting stomatal conductance. During soil drying, a “root signal” regulates stomatal conductance. This root signal could be a hormonal signal (e.g. ABA) or a hydraulic signal (Heilmeier et al. 2007) (Chap. 6).

It has often been observed that stomata close with decreasing **water potential** in the leaf. However, the leaf water potential changes with transpiration as well as with the water supply from the soil (Fig. 10.21). This makes it difficult to separate atmospheric effects on transpiration from those of soil water status. Experimentally, both effects can be separated by compensating the matrix potential of the drying soil with a hydrostatic pressure applied to the soil. Thus, the effect of soil drying can be observed on fully turgid leaves. In this case, stomatal closure is dependent on the **soil water content** (Schulze 1994).

10.3.2 Stomatal Responses to Environmental Factors

Carbon dioxide: Stomata react to the gradient in the CO_2 concentration between the external air and the intercellular spaces of the leaves (Chap. 12). In a classical experiment, Raschke (1972, 1979) was able to open stomata by decreasing the CO_2 concentration down to a CO_2-free environment and close them by increasing the CO_2 concentration until saturation was reached. Neither light nor darkness influenced the observed CO_2 concentration effects. The CO_2 gradient between the leaf and the air, as expressed by the CO_2 concentration ratio, C_i/C_a, remains the main variable to model photosynthesis.

Epidermal water status: With decreasing turgor in the epidermis, the aperture of the stomata decreases (Nonami et al. 1990). In contrast to the reaction of the leaf to changes in the root water potential, this is a cellular imbalance in the epidermal turgor dependent on transpiration (Schulze 1993).

Light: Stomata open with increasing light intensity. In the morning, stomatal conductance increases earlier than photosynthesis. Therefore, stomata do not limit the uptake of CO_2 during the early morning when the humidity is high.

Temperature: At low temperatures (freezing point), stomata are closed, and they open as the temperature increases. This opening is exponential at temperatures above 40 °C, so the leaf temperature can decrease even below that of the air because of the strong cooling by transpiration if water is available and under low rH values (Chap. 9).

Air humidity and leaf water status: Stomata close with an increasing vapour pressure deficit between the leaf and the air, and this can also be observed with an isolated epidermis (Lange et al. 1971), where closing is faster than opening (Fig. 10.22a). This response can be so strong that transpiration decreases despite an increasing water vapour gradient between the leaf and the air (Fig. 10.22b; Schulze et al. 1972). It is still unclear how stomata "measure" humidity. From measurements with He-enriched air, Peak and Mott (2011) proposed that water vapour is the driving force for the stomatal response to humidity.

In tall trees the reaction to local deficits probably plays an important role in the regulation of stomata during the course of the day. In the canopy of a forest, turbulence of air movement occurs with fast exchanges of air packages with differing humidity. This correlates with fast changes in xylem flow. Neighbouring trees exposed to the same air masses show synchronous changes in xylem flow (Hollinger et al. 1994). Stomatal closure is induced by short-term changes in transpiration and the associated changes in the water state of the epidermis (Köstner et al. 1992). As closure is faster in dry air than opening is in moist air, a continuous decrease in stomatal conductance during the day is the consequence of fluctuating humidity in the atmosphere.

The **stomatal response to humidity** has been presumed to be a function of the driving force of transpiration, D_L, the gradient of water vapour concentration between the leaf and the air (Eq. 10.15), even though the response to D_L decreases with temperature. Also, with stomatal conductance as defined by D_L, no common relation with CO_2 assimilation can be observed. However, if the response of stomatal conductance to water vapour, g_{sw} (measured in moles per square metre per second), is scaled to relative humidity at the leaf surface (h_s) and to the mole fraction of CO_2 at the leaf surface (c_s), a linear relation emerges. This includes the response to CO_2 assimilation, A, and to air humidity at different temperatures, with k being an empirical coefficient, 9.31, which may depend on the species (Ball et al. 1987).

$$g_{sw} = k\,A\left(h_s / c_s\right) \tag{10.17}$$

Equation 10.17 is interesting in view of the biophysics of stomatal regulation, because the relative humidity at the leaf surface would express the water potential at the site of evaporation (see Eq. 10.7), and it would be an expression of the "hydration of the evaporating surfaces in the mesophyll", which could regulate stomata. Pieruschka et al. (2010) suggest that the driving force for all stomatal responses to the environment is radiation, which controls the water vapour production in the leaf interior.

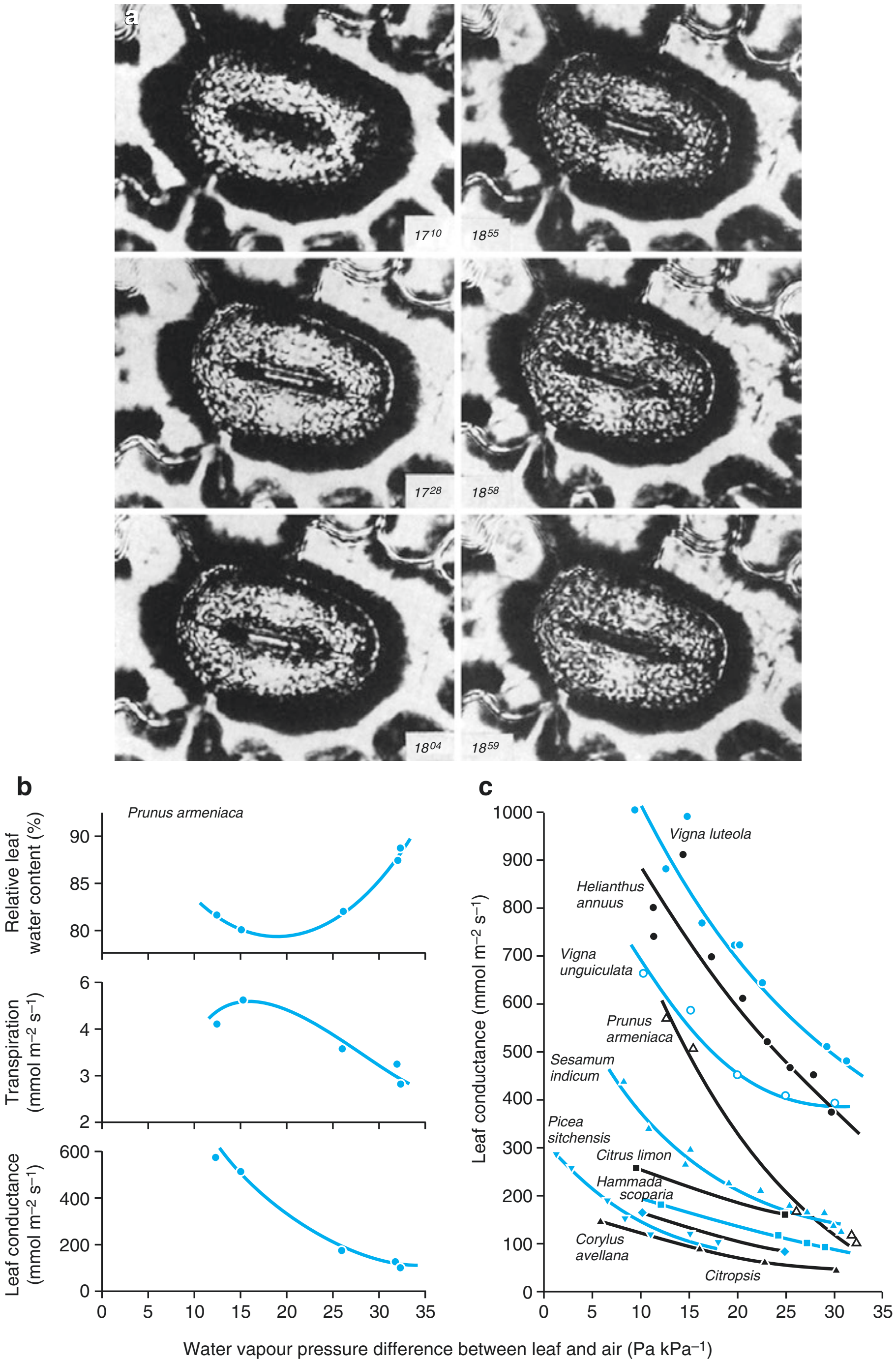

Fig. 10.22 Stomatal response to air humidity. **a** Stomata in isolated epidermis of *Polypodium vulgare*. The lower surface of the epidermis was in contact with water. Only a small air bubble simulated the sub-stomatal air space. On the upper surface, dry or moist air was blown over the stomata with a capillary. The experiment started with closed stomata in dry air. A change to moist air induced slow stomatal opening within 54 min. With constant moist conditions the stomata stayed open, but upon application of dry air they closed within 4 min (Lange et al. 1971). **b** Response of measured leaf conductance, transpiration and water content of a *Prunus armeniaca* leaf to dry air. The stomata closed, transpiration decreased and leaf water content increased (Modified from Schulze et al. (1972)). **c** Responses of different types of plant to dry air. (Schulze and Hall 1982)

Summary

- This chapter covers a wide range of plant organisation, starting from cellular water relations and ending with the regulation of water flow at the leaf level. (The responses of canopies and landscapes are discussed in Chap. 16.)
- Water vapour is the most abundant greenhouse gas in the atmosphere, which affects not only the climate via infrared absorption but also plant life via precipitation and humidity. The ratios of H_2O to CO_2 and H_2O to O_2 are the reasons why animals living on land have more favourable **water use** during oxygen exchange for respiration (about 1:1) than plants do during CO_2 exchange for photosynthesis (about 200:1).
- Plant water storage to support transpiration is not possible in the long-term for most species. Desiccation-tolerant (poikilohydric) plants and desiccation-intolerant (homoiohydric) plants represent different strategies to cope with dry atmospheres. Poikilohydrics are competitive at high dewfall and low precipitation (lichens in coastal deserts).
- Water is not freely available but bound by chemical, capillary and osmotic forces (the matrix and osmotic components of water potential), where the water potential describes the state of water in homogeneous and heterogeneous systems. It is a measure of the energy necessary to convert bound water to the state of free water. Water flows from a compartment with higher water potential to one with lower water potential. Cells regulate their water status by altering the osmotic pressure in the vacuole and thus maintain turgor in a quasi-steady state. Plant availability of water depends on the soil texture. Hygroscopically bound water is water that is bound by forces >5 MPa. The permanent wilting point is defined as a soil water status of −1.5 MPa when a sunflower plant is no longer able to replace the water that is lost through transpiration from the water in the soil, and thus wilts. The field capacity is defined as water bound at −0.05 MPa when water can no longer be retained by soil particles against gravity and therefore drains out of the soil. The amount of water in the soil available for plants corresponds to the water content between the field capacity and the wilting point.
- Plants exploit water with roots of very different anatomy and morphology. Water uptake is constrained to the unsuberised root and to meristematic tissue of lateral roots. By the hydraulic and inverse hydraulic lift, water may be redistributed in the soil profile.
- With water transport in the xylem, the flow of water increases with increasing size of vessels at increasing risk of cavitation, and by the number of vessels involved in transport, the functional xylem area increases. Xylem conductance is smallest in conifers and increases progressively in diffuse and ring-porous woods, herbaceous plants and lianas.
- Xylem transport occurs along a water potential gradient and is dependent on the vapour pressure deficit of the air, where the greatest change in potential occurs between the mesophyll and the atmosphere, where stomata regulate the water loss. Phloem transport occurs along a gradient of osmotic pressure, which depends on the loading and unloading of sugars. Circulation of water within the plant between the phloem and xylem is important for plant survival. Regulation of the xylem flux is achieved by stomatal closure, leaf abscission, partial senescence and hardwood formation.
- Stomata are the most important valves by which plants can regulate transpiration, which is a physically determined process that is under physiological regulation within certain limits. Since the stomatal aperture cannot be observed directly in most species, it is expressed and measured as “conductance” in an analogy to Ohms law. Stomata regulate the flux of CO_2 into the leaf for photosynthesis, they respond to root signals during drought, and they respond to environmental factors, particularly light, temperature and atmospheric humidity.

References

Aloni R (2004) The induction of vascular tissues by auxin. In: Davies PJ (ed) Plant hormones. Kluwer Academic Publisher, Dortrecht

Ball JT, Woodrow IE, Berry JA (1987) A model predicting stomatal conductance and its contribution to the control of photosynthesis under different environmental conditions. Progr Photosynth Res 4:221–224

Böhm J (1893) Capillarität und Saftsteigen. Ber Dtsch bot Ges 11:203–212

Bonner J, Galson AW (1952) Principles of plant physiology. Freeman, San Francisco

Bryukhanova M, Fonti P (2013) Xylem plasticity allows rapid hydraulic adjustment to annual climatic variability. Trees 27:485–496

Burgess SSO, Adams MA, Turner NC, White DA, Ong CK (2001) Tree roots: conduits for deep recharge of soil water. Oecologia 126:158–165

Burkhardt J (2010) Hygroscopic particles on leaves: nutrients or desiccants? Ecol Monogr 80:369–399

Canadell J, Jackson RB, Ehleringer JR, Mooney HA, Sala OE, Schulze E-D (1996) Maximum rooting depth of vegetation types at the global scale. Oecologia 108:583–595

Carlquist S (1991) Anatomy of vine and liana stems: a review and synthesis. In: Putz FE, Mooney HA (eds) The biology of vines. Cambridge University Press, Cambridge

Choat B, Jansen S, Brodribb TJ, Cochard H, Delzon S, Bhaskar R, Bucci SJ, Feild TS, Gleason SM, Hacke UG, Jacobsen AL, Lens F, Maherali H, Martínez-Vilalta J, Mayr S, Mencuccini M, Mitchell PJ, Nardini A, Pittermann J, Pratt RB, Sperry JS, Westoby M, Wright IJ, Zanne AE (2012) Global convergence in the vulnerability of forests to drought. Nature 491:752–755

Cirelli D, Jagels R, Tyree MT (2008) Towards an improved model of maple sap exudation: the location and role of osmotic barriers in sugar maple, butternut, and white birch. Tree Physiol 28:1145–1155

Cowan IR (1977) Stomatal behaviour and environment. Adv Bot Res 4:117–228

Darcy H (1856) Las Fontains Publiques de La Villa Dijon. Dalmont, Paris

Dawson TE (1993) Water sources as determined from xylem-water isotopic corn position: perspectives on plant competition, distribution, and water relations. In: Ehleringer JR, Hall AE, Farquhar GD (eds) Stable isotopes and plant carbon–water relations. Academic Press, San Diego

Döll P (2009) Vulnerability to the impact of climate change on renewable groundwater resources: a global-scale assessment. Environ Res Lett 4:035006

Ehleringer JR (1993) Carbon and water relations in desert plants: an isotopic perspective. In: Ehleringer JR, Hall AE, Farquar GD (eds) Stable isotopes and plant carbon-water relations. Academic Press, San Diego

Ehleringer JR (1995) Variation in gas exchange characteristics among desert plants. Ecophysiology of photosynthesis. Ecol Stud 100:361–392

Eilmann B, Buchmann N, Siegwolf R, Saurer M, Cherubini P, Rigling A (2010) Fast response of Scots pine to improved water availability reflected in tree-ring width and $\delta^{13}C$. Plant Cell Environ 33:1351–1360

Ewers BE, Oren R, Spery JS (2000) Influence of nutrients versus water supply on hydraulic architecture and water balance in *Pinus taeda*. Plant Cell Environ 23:1055–1066

Fritzsche A (1910) Untersuchungen über die Lebensdauer und das Absterben der Elemente des Holzkörpers. Dissertation, Leipzig

Fukuda H (1997) Tracheary element differentiation. Plant Cell 9:1147–1156

Gaff DF (1971) Desiccation-tolerant flowering plants in Southern Africa. Science 174:1033–1034

Gartner BL (1995) Plant stems: physiology and functional morphology. Academic Press, San Diego

Gollan T, Turner NC, Schulze E-D (1985) The responses of stomata and leaf gas exchange to vapour pressure deficits and soil water content. III. In the sclerophyllous woody species *Nerium oleander*. Oecologia 65:356–362

Grace J (1993) Consequences of xylem cavitation for plant water deficits. In: Smith JAC, Griffiths H (eds) Water deficits. Bios Scientific Publishers, Oxford, pp 109–128

Greenwood EAN, Turner NC, Schulze E-D, Waton GD, Venn NR (1992) Groundwater management through increased water use by lupine crops. J Hydrol 134:1–11

Heilmeier H, Schulze ED, Fan J, Hartung W (2007) General relations of stomatal responses to xylem sap abscisic acid under stress in the rooting zone—a global perspective. Flora 202:624–636

Holbrook NM, Zwieniecke MA (2005) Vascular transport in plants. Academic Press, San Diego

Hollinger DY, Kelliher FM, Schulze E-D, Köstner BM (1994) Coupling of tree transpiration to atmospheric turbulence. Nature 371:60–62

Hölttä T, Vesala T, Perämäki M, Nikinmaa E (2006) Refilling of embolised conduits as a consequence of “Münch water” circulation. Funct Plant Biol 33:949–959

Horn R (1994) The effect of aggregation of soils on water, gas and heat transport. In: Schulze E-D (ed) Flux control in biological systems. Academic Press, San Diego

Hubbard RM, Ryan MG, Stiller V, Sperry JS (2001) Stomatal conductance and photosynthesis vary linearly with plant hydraulic conductance in ponderosa pine. Plant Cell Environ 24:113–122

Kappen L, Schulz G, Vanselow R (1994) Direct observations of stomatal movements. Ecol Stud 100:231–246

Klemm O (1989) Leaching and uptake of ions through above-ground Norway spruce parts. Ecol Stud 77:210–234

Köstner BMM, Schulze E-D, Kelliher FM, Hollinger DY, Byers JN, Hunt JE, McSeveny TM, Meserth R, Weir PL (1992) Transpiration and canopy conductance in a pristine broad-leaf forest of *Nothofagus*: an analysis of xylem sap flow and eddy correlation measurements. Oecologia 92:236–241

Kottek M, Grieser J, Beck C, Rudolf B, Rubel F (2006) World map of the Köppen-Geiger climate classification update. Meteorol Z 15:259–263

Kramer PJ, Boyer JS (1995) Water relations of plants and soils. Academic Press, San Diego

Kutschera L, Lichtenegger E (1992) Wurzelatlas mitteleuropäischer Ackerunkräuter und Kulturpflanzen, vol 1. Fischer Verlag, Stuttgart

Lambers H, Chapin FS III, Pons TL (1998) Plant physiological ecology. Springer, Heidelberg

Lange OL, Lösch R, Schulze E-D, Kappen L (1971) Responses of stomata to changes in humidity. Planta 100:76–86

Larcher W (2003) Physiological plant ecology. Ecophysiology and stress physiology of functional groups, 4th edn. Springer, Berlin

Lo Gullo MA, Salleo S (1991) Three different methods for measuring xylem cavitation and embolism: a comparison. Ann Bot 67:417–424

Lüttge U, Higinbotham N (1979) Transport in plants. Springer, New York

Marjanovic Z, Nehls U (2008) Ectomycorrhiza and water transport. In: Varma A (ed) Mycorrhiza, vol 2. Springer, Heidelberg

Martínez-Vilalta J, Prat E, Oliveras I, Piñol J (2002) Xylem hydraulic properties of roots and stems of nine Mediterranean woody species. Oecologia 133:19–29

Meidner H, Mansfield TA (1968) Physiology of stomata. McGraw-Hill, London

Michael W, Schultz A, Meshcheryakov AB, Ehwald R (1997) Apoplasmatic and protoplasmatic water transport through the parenchyma of a potato storage organ. Plant Physiol 115:1089–1099

Michael W, Cholodova VP, Ehwald R (1999) Gas and liquids in intercellular spaces of maize roots. Ann Bot 84:665–673

Miralles DG, Holmes TRH, DeJeu RAM, Gash JH, Meesters AGCA, Dolman AJ (2011) Global landsuface evaporation estimated from satellite-based observations. Hydrol Earth Syst Sci 15:453–469

Nardini A, Lo Gullo M, Salleo S (2011) Refilling embolized xylem conduits: is it a matter of phloem unloading? Plant Sci 180:604–611

Neumann RB, Cardon ZG (2012) The magnitude of hydraulic redistribution by plant roots: a review and synthesis of empirical and modeling studies. New Phytol 194:337–352

Nobel PS (2009) Physicochemical and environmental plant physiology. Elsevier Academic Press, San Diego

Nonami H, Schulze E-D, Ziegler H (1990) Mechanisms of stomatal movement in response to air humidity, irradiance and xylem water potential. Planta 183:57–64

North GB, Peterson CA (2005) Water flow in roots: structural and regulatory features. In: Holbrook NM, Zwieniecki MA (eds) Vascular transport of water in plants. Academic Press, San Diego

Or D, Wraith JM, Robinson DA, Jones SB (2012) Soil water content and water potential relationships. In: Huang PM, Li Y, Sumner ME (eds) Handbook of soil sciences, Properties and processes, vol 1. CRC Press, Boca Raton

Peak D, Mott KA (2011) A new, vapour-phase mechanism for stomatal responses to humidity and temperature. Plant Cell Environ 34:162–178

Pfeffer W (1877) Osmotische Untersuchungen. Engelmann, Leipzig

Pieruschka R, Huber G, Berry JA (2010) Control of transpiration by radiation. Proc Natl Acad Sci 107:13372–13377

Plavcová L, Hacke UG (2012) Phenotypic and developmental plasticity of xylem in hybrid poplar saplings subjected to experimental drought, nitrogen fertilization, and shading. J Exp Bot 63:6481–6491

Prieto I, Armas C, Pugnaire FI (2012) Water release through plant roots: new insights into its consequences at the plant and ecosystem level. New Phytol 193:830–841

Raschke K (1972) Saturation kinetics of the velocity of stomatal closing response to CO_2. Plant Physiol 49:229–234

Raschke K (1979) Movements of stomata. In: Haupt W, Feinleib RE (eds) Physiology of movements. Springer, Berlin

Reich PB, Walters MB, Eldsworth DS (1997) From tropics to tundra: global convergence in plant functioning. Proc Natl Acad Sci 94:13730–13734

Richards JH, Caldwell MM (1987) Hydraulic lift: substantial nocturnal water transport between soil layers by *Artemisia tridentata* roots. Oecologia 73:486–494

Schachtschabel P, Blume HP, Brümmer G, Hartge KH, Schwertmann U (1998) Lehrbuch der Bodenkunde. Enke Verlag, Stuttgart

Schneider U, Becker A, Finger P, Meyer-Christoffer A, Ziese M, Rudolf B (2014) GPCC's new land surface precipitation climatology based on quality-controlled in situ data and its role in quantifying the global water cycle. Theor Appl Climatol 115:15–40

Schulze E-D (1993) Soil water deficits and atmospheric humidity as environmental signals. In: Smith JAC, Griffiths H (eds) Water deficits. Bios Scientific Publishers, Oxford

Schulze E-D (1994) The regulation of plant transpiration: interactions of feedforward, feedback, and futile cycles. In: Schulze E-D (ed) Flux control in biological systems. Academic Press, San Diego

Schulze E-D, Chapin FS III (1987) Plant specialization to environments of different resource availability. Ecol Stud 61:120–148

Schulze E-D, Hall AE (1982) Stomatal response, water loss and CO_2 assimilation rates of plants in contrasting environments. Encyclopaedia Plant Physiol 12B:181–230

Schulze E-D, Heimann M (1998) Carbon and water exchange of terrestrial systems. In: Galloway J, Mellilo J (eds) Asian change in the context of global climate change, IGBP Publ Series, vol 3. Cambridge University Press, Cambridge

Schulze E-D, Lange OL, Buschbom U, Kappen L, Evenari M (1972) Stomatal responses to changes in humidity in plants growing in the desert. Planta 108:259–270

Schulze E-D, Cermak J, Matyssek R, Penka M, Zimmermann R, Vasicek F, Gries W, Kucera J (1985) Canopy transpiration and water fluxes in the xylem of the trunk of *Larix* and *Picea* trees—a comparison of xylem flow, pyrometer and cuvette measurements. Oecologia 66:475–483

Schulze E-D, Kelliher FM, Körner C, Lloyd J, Leuning R (1994) Relationships among maximum stomatal conductance, carbon assimilation rate, and plant nitrogen nutrition: a global ecology scaling exercise. Annu Rev Ecol Syst 25:629–660

Schulze E-D, Leuning R, Kelliher FM (1995) Environmental regulation of surface conductance for evaporation from vegetation. Vegetatio 121:79–87

Schulze E-D, Ellis R, Schulze W, Trimborn P, Ziegler H (1996a) Diversity, metabolic types and $\delta^{13}C$ carbon isotope ratios in the grass flora of Namibia in relation to growth form, precipitation and habitat conditions. Oecologia 106:352–336

Schulze E-D, Mooney HA, Sala OE, Jobbagy E, Buchmann N, Bauer G, Canadell J, Jackson RB, Loreti J, Oesterheld M, Ehleringer JR (1996b) Rooting depth, water availability, and vegetation cover along an aridity gradient in Patagonia. Oecologia 108:503–511

Schulze E-D, Caldwell MM, Canadell J, Mooney HA, Jackson RB, Parson D, Scholes R, Sala O, Trimborn P (1998a) Downward flux of water through roots (i.e. inverse hydraulic lift) in dry Kalahari sands. Oecologia 115:460–462

Schulze E-D, Williams RJ, Farquhar GD, Schulze W, Langridge J, Miller JM, Walker BK (1998b) Carbon and nitrogen isotope discrimination and nitrogen nutrition of trees along a rainfall gradient in northern Australia. Aust J Plant Physiol 25:413–425

Schweingruber FH, Büntgen U (2013) What is "wood"—an anatomical re-definition. Dendrochronologia 31:187–191

Schweingruber FH, Boerner A, Schulze ED (2013) Atlas of stem anatomy on herbs, shrubs, and trees, vol 1 and 2. Springer, Heidelberg

Sestak Z, Catsky J, Jarvis PG (eds) (1971) Plant photosynthetic production. Manual of methods. Dr W Junk NV Publishers, Den Haag

Slatyer RO (1967) Plant–water relationships. Academic Press, London

Sperry JS, Holbrook NM, Zimmermann MH, Tyree MT (1987) Spring filling of xylem vessels in wild grapevine. Plant Physiol 83:414–417

Steudle E (1994) The regulation of plant water at the cell, tissue, and organ level: role of active processes and of compartmentation. In: Schulze E-D (ed) Flux control in biological systems. Academic Press, San Diego

Steudle E (2000) Water uptake by roots: effects of water deficits. J Exp Bot 51:1531–1542

Steudle E (2001) The cohesion–tension mechanism and the acquisition of water by plant roots. Annu Rev Plant Physiol Plant Mol Biol 52:847–875

Steudle E, Peterson CA (1998) How does water get through roots? J Exp Bot 49:775–788

Stroock AD, Pagay VV, Zwienicki MA, Holbrook MN (2014) The physicochemical hydrodynamics of vascular plants. Annu Rev Fluid Mech 46:615–642

Tanner W, Beevers H (1990) Does transpiration have essential function in long-distance ion transport in plants? Plant Cell Environ 13:745–750

Troughton J, Donaldson LA (1972) Probing plant structures. Chapman and Hall, London

Tyerman SD, Bohnert HJ, Maurel C, Steudle E, Smith JA (1999) Plant aquaporins: their molecular biology, biophysics and significance for plant water relations. J Exp Bot 50:1055–1072

Tyree MT (1997) The cohesion-tension theory of sap ascent. Current controversies. J Exp Bot 48:1753–1765

Tyree MT, Sperry JS (1989) Vulnerability of xylem to cavitation and embolism. Annu Rev Plant Physiol Plant Mol Biol 40:19–38

Vaganov EA, Hughes MK, Shashkin AV (2006) Growth dynamics of conifer tree rings. Ecological studies, vol 183. Springer, Heidelberg

Walter H (1960) Grundlagen der Pflanzenverbreitung. Teil I: Standortlehre. Verlag Eugen Ulmer, Stuttgart

Walter H, Kreeb K (1970) Die Hydratation und Hydratur des Protoplasmas der Pflanzen und ihre ökophysiologische Bedeutung. Springer, Wien

Ward RC, Robinson M (2000) Principles of hydrology, 4th edn. McGraw Hill, Berkshire

Wei C, Steudle E, Tyree MT (1999) Water ascent in plants: do ongoing controversies have a sound basis? Plant Sci 4:372–373

West NE, Young JA (2000) Intermountain valleys and lower mountain slopes. In: Barbour MG, Billings WD (eds) North American terrestrial vegetation. Cambridge University Press, Cambridge

Wirth C, Schulze E-D, Schulze W, von Stürzner-Karbe D, Ziegler W, Milukova I, Sogachev A, Varlagin A, Panfyorov M, Grigoriev S, Kusnetzova W, Siry M, Hardes G, Zimmermann R, Vygodskaya NN (1999) Aboveground biomass and structure of pristine Siberian Scots pine forests as controlled by competition and fire. Oecologia 121:66–80

Ziegler H, Vieweg GH (1970) Poikilohydre Spermatophyta. In: Walter H, Kreeb K (eds) Die Hydratation und Hydratur des Protoplasmas der Pflanzen und ihre ökophysiologische Bedeutung. Springer, Berlin

Zimmermann MH (1983) Xylem structure and the ascent of sap. Springer, Berlin

Zimmermann R, Schulze E-D, Wirth C, Schulze EF, McDonald KC, Vygodskaya NN, Ziegler W (2000) Canopy transpiration in a chronosequence of central Siberian pine forests. Glob Change Biol 6:25–37

11 Nutrient Relations

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Magnesium deficiency in spruce (Fichtelgebirge, Oberwarmensteinach, Germany): With insufficient Mg available in the soil, young needles obtain their Mg by re-translocation of Mg from the old needles via the phloem. Thus, the old needles become golden yellow at the time of bud break of new growth in spring. Excess of nitrogen enhances this process, especially when nitrogen is absorbed directly from the atmosphere. (Photo: E.-D. Schulze)

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11.1 Availability of Soil Nutrients and Ion Use

11.1.1 Plant Nutrients

Plants not only contain carbohydrates from carbon assimilation but also contain inorganic elements. This is apparent from the amount of **ash** that remains after burning biomass, when C, H, N and O are emitted as gases. For most plants, the ash content is 3–8% of dry weight; in halophytic plants the ash content reaches 20% because of the high NaCl content. In lichens, the ash content may reach 30% because of depositions of minerals on the surface of hyphae. The **element concentrations** of individual elements in plants span about six orders of magnitude (Table 11.1). The uptake of elements occurs in roots or in mycorrhiza from the soil solution and via above-ground plant parts after wetting by dew, fog or rain (Burkhardt et al. 2012).

Macro- and micronutrients are essential for the life of plants. Macroelements participate directly in metabolism (N, S and P) or indirectly support metabolism (K), and there are transitions to trace elements (Ca, Mg). Most micronutrients are metals, which are required for enzyme reactions (Chap. 7). **Facultative** or **beneficial elements** are required only in some plant groups (Si for grasses). Iodine and vanadium are not mentioned further here, as they are needed only in lower plants (Marschner 1988, 2012).

Concentrations of nutrient elements are often expressed in units of mass (grams per gram of dry weight). However, the physiological turnover and physico-chemical effects of these elements are usually measured not as mass but by the number of required molecules; therefore, the mole is a more relevant unit than the gram, but the gram remains as a measure of biomass. In contrast to the **element concentration** in biomass (moles or grams per gram of dry weight), in the field of plant ecology the **element content** quantifies the amount of nutrients per area (moles or grams per square metre of leaf or of ground area), which takes into account the bulk density and the profile depth in soils or the thickness of leaves (grams per square metre).

This chapter deals with the essential macronutrients. Molecular aspects of plant responses to nutrient scarcity and excess, transition metals as trace elements and stress caused by toxic elements are considered in Chap. 7.

Table 11.1 Typical concentration of nutrients in plant tissues (Marschner 1988)

Nutrient type	Element	Average concentration (μmol g^{-1})
Macronutrients	N	1000
	K	250
	Ca	125
	Mg	80
	P	60
	S	30
Micronutrients	Cl	3
	B	2
	Fe	2
	Mn	1
	Zn	0.3
	Cu	0.1
	Ni	0.001
	Mo	0.001
Beneficial elements	Si	11,000
	Na	200
	Co	0.1

11.1.2 Availability of Nutrients in Soil

Rocks are mixtures of different minerals and are classified according to their chemical composition and how they were formed. A distinction is made between **crystalline rocks** (formed from the cooling of molten magma in the Earth's crust (intrusive rock) or on the Earth's surface (igneous rock)), **sedimentary rocks** (originating from deposition of weathered material or of chemical degradation products by sedimentation and subsequent hardening) and **metamorphic rocks** (formed by partial re-melting and recrystallisation of crystalline and sedimentary rocks).

11.1.2.1 Primary Minerals

Minerals—for example, quartz, feldspar and mica—are created during the formation of rocks by crystallisation from molten magma (intrusive and igneous rocks) or by recrystallisation under conditions of high pressures and temperatures (metamorphic rocks) in the upper crust of the Earth. Depending on the chemical composition

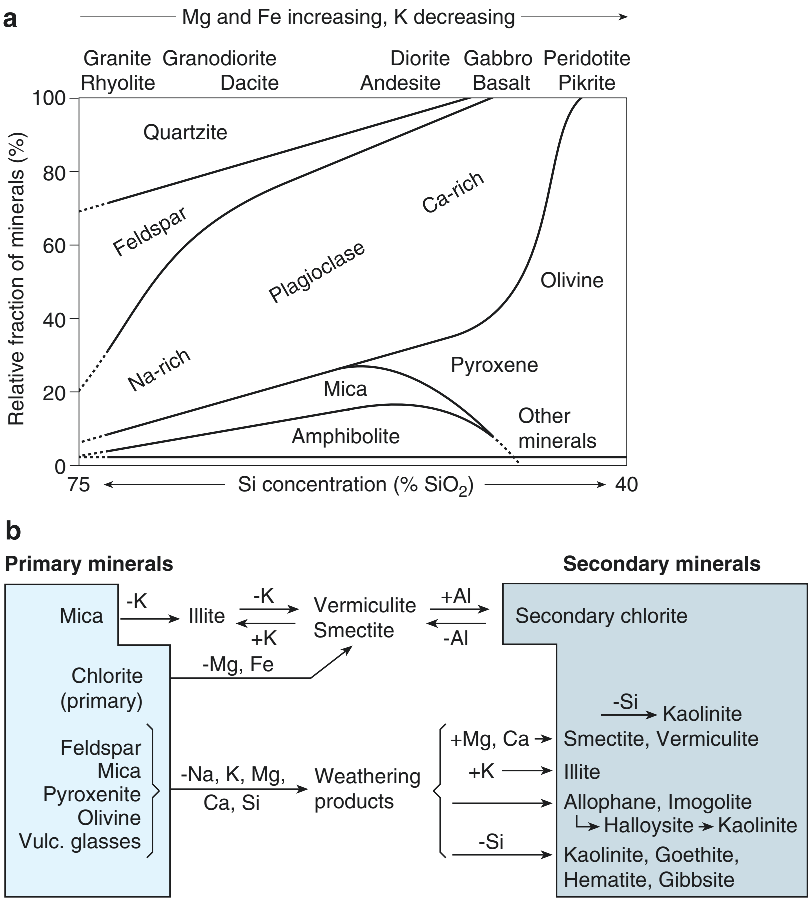

Fig. 11.1 Mineral composition of crystalline rocks and formation of clay minerals. **a** Composition of important rocks with respect to their base and Si content. **b** Conversion of primary minerals into secondary clay minerals. (Blume et al. 2010)

of the magma (acid to alkaline), and the temperature and pressure in the molten material, rocks of different mineral composition are formed (Fig. 11.1a). **Silicates** are made of silicon–oxygen tetrahedrons and occur with many different crystal structures, representing the largest proportion of primary minerals in the Earth's crust (see Blume et al. 2010). Different forms of silicates are distinguished (Table 11.2). In most silicates, Al^{3+} ions replace some of the Si^{4+} ions. In addition, Si is able to build Si–Si chains similar to C chains. The Si–Si bonds reduce the number of negative charges. Therefore, these minerals contain a reduced number of positively charged ions (cations) such as K^+, Na^+, Mg^{2+} and Ca^{2+}. During weathering, replacement of alkaline cations with H^+ takes place. Cations are released from the mineral matrix and then become available to plants, while the crystal structure loses its geometry and falls apart.

The free charges of various primary silicates, as listed in Table 11.2, are the basis for weathering and cation availability for roots. It is mainly the substitution of Si with Al that determines the actual cation content of the rock and the proportion of elements (Fe) that may be oxidised. A series of increasing stability with weathering (olivine → augite → tourmaline → feldspar → quartz) emerges. Basalt, for example, is much more alkaline than granite—that is, it contains more potassium, calcium and magnesium—and thus it weathers faster.

11.1.2.2 Secondary Minerals

Clay minerals: Weathering produces clay minerals directly from mica and chlorite, or clay minerals are newly formed from individual degradation products of silicate weathering. In this case, Si tetrahedrons and Al octahedrons are released. They bind by covalent bonds to form

Table 11.2 Tetrahedron structures of primary silicates

Primary silicate	Free charges per tetrahedron	Tetrahedra structure	Minerals
Nesosilicates SiO_4^{4-}	4	Tetrahedra are cation saturated	Olivine $(Mg, Fe)_2[SiO_4]$
Sorosilicates $Si_2O_7^{6-}$	3	Few tetrahedra covalently bound	Diopside $(Ca, Mg)[Si_2O_6]$
Inosilicates SiO_3^{2-}	2	Tetrahedra form a chain	Augite $(Ca, Mg, Fe, Al, Na)[Si_2O_6]_n$
Cyclosilicates$[Si_2O_6]^{1.5-}$	1.5	Tetrahedral chains form ribbons	Amphibolite $(Na, K, Ca, Mg, Fe, Al)(OH_4)[Al_{2-4}Si_{14-12}O_{44}]$ Tourmaline $NaMg_3Al_6[(OH)_1(BO_3)_3[Si_6O_{18}]$
Phyllosilicates $Si_2O_5^{2-}$	1	Tetrahedra form layers	Muscovite $(KAl_2)(OH_2)[Si_3AlO_{10}]$ Biotite $K(Mg, Fe, Mn)_3(OH, F)_2[AlSi_3O_{10}]$
Tectosilicates SiO_2	No free charges 1 free charge with Al replacing SiO_2		Quartz SiO_2 Orthoclase feldspar $K[AlSi_3O_8]$ Anorthite $Ca[Al_2Si_2O_8]$

secondary phyllosilicates, which contain alternate layers of Si tetrahedrons and Al octahedrons (Fig. 11.1b). Clay minerals are differentiated by the structure of the layers and the cations, which are bound between the layers.

- Two-layered minerals: 1 Si tetrahedral + 1 Al octahedral layer: Kaolinite, serpentine, with no cations in the intermediate layers.
- Three-layered minerals: 1 Si tetrahedral + 1 Al octahedral + 1 Si tetrahedral layer: Illite, chlorite, vermiculite, montmorillonite. Cations occur in the intermediate layers, and these cations can be reversibly exchanged against hydrogen ions.

The clay minerals allophane and imogolite are exceptions. They occur exclusively in soils derived from volcanic activity. They have a spherical or tubular structure, and they can adsorb anions in acid soils (e.g. phosphate) in such a tight manner that they are no longer available to plants.

Oxides and hydroxides: In parallel to the breakdown of the Si tetrahedrons during silicate weathering, oxidation of metals contributes to the breakdown of the primary crystal structure. The most important oxides and hydroxides are those of Fe (particularly those of Fe^{2+} to Fe^{3+} or Fe hydroxide) and of Mn and Al. Depending on climatic conditions, these oxides form different types of secondary minerals, which are often responsible for the characteristic colouring of soils. Tropical soils are often bright red as a consequence of haematite (α-Fe_2O_3), while the yellow-brown colour of many soils of the temperate zone is caused by goethite (α-FeOOH).

Sedimentary deposits are the consequence of transport and subsequent compaction of products of primary rocks. They differ from primary rocks mainly in Si and Ca content. A distinction is made according to the degree of compaction. There are rocks and loose sediments, which are characterised by decreasing Si content:

- Rocks: sandstone (70% Si), greywacke (67% Si), slate (59% Si), limestone (8% Si).
- Loose sediments: drifting sands (97% Si), loess (72% Si), marl (64% Si).

Depending on the original rock and its "weathering history", **sedimentary deposits** have different cation contents. Clay-rich soils possess a greater capacity for exchange of cations than sandy soils not only because of their much larger surface area for ion exchange but also because of the greater number of covalent bonds. Secondary minerals are included in sedimentary rocks; for example, limestone contains also aluminium oxide, iron oxide and manganese (hydr)oxide.

As soils develop from abiotic and biotic processes, it is not surprising that the soil map of the Earth reflects, in principle, the distribution

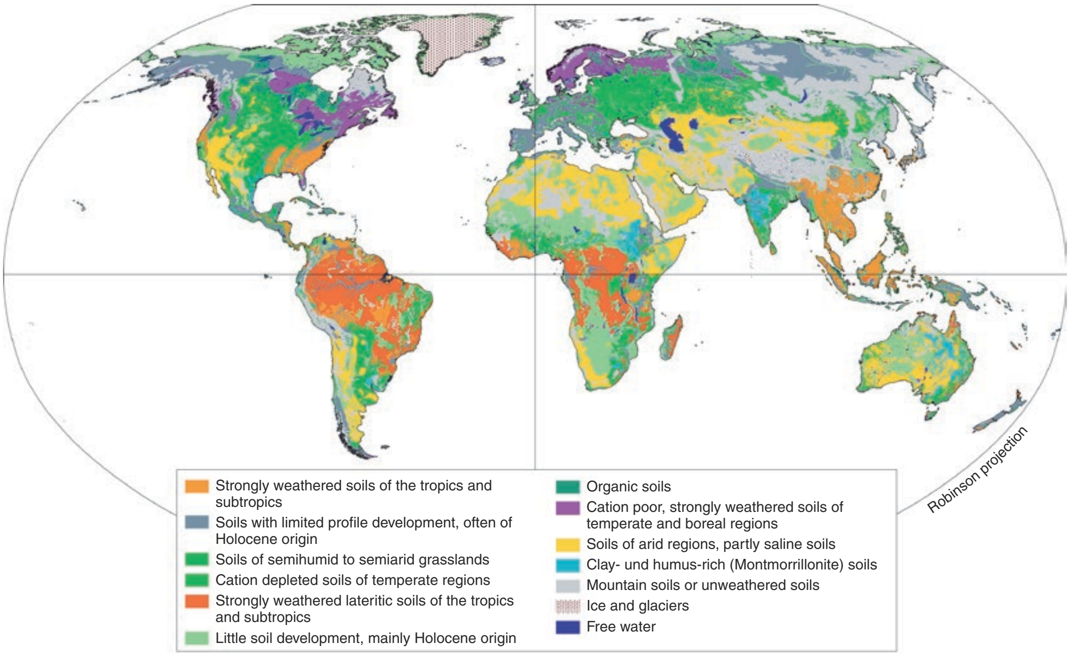

Fig. 11.2 Global distribution of important soil types (Compiled by G. Guggenberger)

of different types of vegetation on Earth (Fig. 11.2). Clay minerals are particularly important components of soils that are formed as new products of the Si–Al minerals during the course of weathering from silicates. According to the climatic conditions when these clay minerals were formed, these could be layer lattices in which the cations are embedded more or less tightly between the layers of Si tetrahedrons and Al octahedrons.

The **cation exchange capacity** (**CEC**) of a soil is a measure of the amount of cations that can be reversibly stored. It is large in clay minerals that swell (e.g. montmorillonite: 80–120 $\text{cmol}_c\ \text{kg}^{-1}$ (c = charge)) and small in non-swelling clay minerals (e.g. kaolinite: 1–10 $\text{cmol}_c\ \text{kg}^{-1}$) (see Box 11.1) (Osman 2013). The chemical composition of the original rock or of the sediments determines the availability of water and nutrients (**soil fertility**) and thus the type of vegetation. Plant cover may increase the CEC of soils by a factor of 10 by formation of “humus” as a product of incomplete decomposition of organic matter. But even at high humus contents in soil, the chemical composition of the original rock determines the type of humus formed and thus the availability of nutrients in the soil: humus has a potential CEC between 100 and 300 $\text{cmol}_c\ \text{kg}^{-1}$, where “c” expresses the fact that the number of charges is counted depending on the soil pH (Osman 2013). Thus, the availability of cations in the soil affects most ecosystem processes.

11.1.3 General Aspects of Plant Nutrition

11.1.3.1 Nutrient Supply in the Soil Solution

In mineral soils, chemically characterised by the content of alkaline cations (**base saturation**: e.g. K, Mg and Ca) and physically determined by the **texture** (particle size distribution), roots act as additional **ion exchangers**. While cations in the soil are in equilibrium between the exchanger (clay minerals, oxides, humus) and the free soil solution, roots cause chemical imbalances because of active transport processes, which enable plants to take up cations against the concentration gradient. This process is in most cases selective for certain ions. In exchange against cations from the soil, the root actively releases H^+, HCO_3^- or organic acids to the soil, which originated from the carbon cycle (Jones et al. 2004). The uptake of alkaline cations in exchange for protons results in acidification of soils. With uptake of anions, alkalinisation of soils may occur. If the vegetation is not managed or harvested, these minerals are returned in the dead biomass to the soil as litter. In agriculture and forestry, nutrients are removed from the soil by harvesting, grazing or use of litter, with the consequence that the chemical conditions in the soil change (**acidification of soil water**, **podzolisation**) if the depletion exceeds the resupply by weathering. Deposition into the soil of strong acids from the atmosphere, as a result of **air pollution** (SO_4^{2-}, NO_3^-), has an effect similar to that of harvesting of plant material, because the input of these anions is not balanced by cations. Fertilisation and liming of soils balance the loss of cations caused by harvesting or leaching.

Even though, energetically, uptake of anions and cations is fundamentally different, both ions

Box 11.1: Ion Exchange Capacity of Soils

Soils: Soils are the product of weathering and transportation of original materials of the Earth's continental land surface by physical and chemical processes and biological agents. They are mixed to different extents with dead organic matter, litter and humus.

Cation exchange capacity (**CEC**): The CEC is an important measure of the cation availability in soils, giving the number (in moles) of cations that can be adsorbed by a defined quantity of soil (expressed in centimoles of charge per kilogram). The magnitude of the CEC depends on the number of available exchange sites of clay minerals, humus, and (hydr)oxides. The carboxyl-, carbonyl- and enol-groups can adsorb cations only when deprotonated (variable charge), and this depends on the pH. In contrast, a proportion of the exchange sites in the crystal structure of clay minerals occurs by replacement of Si^{4+} with cations of lower valence (e.g. Al), which is independent of the soil pH (permanent charge). A distinction is drawn between the potential CEC, which includes all exchangeable cations (protons, Al and basic cations, measured at pH 8, for example) and the effective CEC, which includes the exchangeable basic cations and Al at soil pH (Fig. 11.3). In addition to the CEC, the anion exchange capacity (AEC) is important.

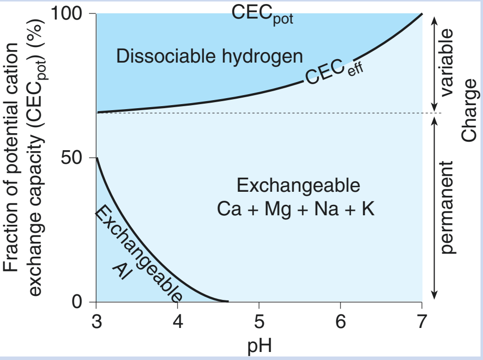

Fig. 11.3 Dependence of the effective cation exchange capacity (CEC_{eff}) on soil pH. The cation exchange capacity is shown for average conditions of a soil with 20–30% clay content and 2–3% humus content. The potential cation exchange capacity (CEC_{pot}) includes, in addition to the basic cations, the dissociable protons. (Blume et al. 2010)

According to their clay and humus contents, soils are distinguished by their potential CEC (Blume et al. 2010):

- Arable fields: marshland (37 $cmol_c\ kg^{-1}$), pelosol (22 $cmol_c\ kg^{-1}$), black earth (18 $cmol_c\ kg^{-1}$), para brown earth (17 $cmol_c\ kg^{-1}$)
- Forest: brown earth (60 $cmol_c\ kg^{-1}$), pseudogley (15 $cmol_c\ kg^{-1}$)

are taken up via transporters and ion channels (Chap. 7). There are specific interactions between cations and anions; for example, in the presence of Cl^-, uptake of K^+ decreases (see Marschner 2012).

11.1.3.2 Ion Uptake by Roots

Roots grow in soils as part of the **rhizosphere** (see Box 11.2), where decomposition of organic material interacts with ion and water uptake by roots. The root surface is covered by microbial and fungal communities. Water uptake and **ion uptake** (see Box 11.3) take place primarily through younger parts of the root and near the meristems of emerging adventitious roots. In addition, ions may be taken up or lost via leaves and shoots. Aboveground uptake of ions plays an important role during uptake of air pollutants (Burkhardt et al. 2012; Harrison et al. 2000). Along the root, uptake of nutrients changes with root development, as transport depends on the ion radius and chemical composition. Root uptake occurs either in the cell wall (the **apoplast**) or in the cytosol (the **symplast**) (Chap. 7). During radial transport from the soil to the central stele, the apoplast is composed of cell walls of cells outside the **endodermis**. At the endodermis, all ions must pass through the symplast of specialised **transmission cells**. Besides this radial transport pathway, uptake of ions may also take place through the meristems, where the endodermis is not yet formed. The partitioning of ion uptake between the symplast and apoplast remains under debate. For water it has been estimated that 10–70% of uptake occurs via the apoplasmatic pathway (White 2012); this flow of water may carry a major fraction of Ca, Na and Al through the apoplast into the xylem, and these ions may accumulate in leaves (White 2012). Nevertheless, for metabolic use, these ions must also enter the symplast. In contrast, uptake and transport of P, K, N and Mg occurs in the symplast. Ion transport decreases when the secondary root cortex is developed.

Plants require and consume nutrients for (Chap. 7):

- Growth (all nutrients).
- Catalysis (e.g. Fe in oxygenases, Zn in hydrogenases).
- Transport of electrons (Cu, Fe, Mn).
- Accumulation (Chap. 12 for definitions) of ions where supply exceeds demand.
- Storage and reserve (e.g. N, P).

Nutrient transport in plants and distribution of nutrients to sites of uptake, storage and consumption occur via the xylem and phloem (Chap. 10), with very different amounts and types of transported ions in both pathways. Thus, the concentrations in xylem and phloem sap are different (Table 11.3). It is obvious that the phloem sap contains not only large amounts of sucrose but also amino acids, and

Box 11.2: The Rhizosphere (Contribution by Else K. Bünemann)

The rhizosphere is defined as the volume of soil around living plant roots that is affected by root activities such as root growth, water and nutrient uptake, and exudation of organic anions. The efflux of carbon from roots via lysates from damaged cells and exudates from intact cells (**rhizodeposition**) is typically 10–20% of net photosynthetically fixed carbon. This carbon stimulates beneficial or pathogenic microorganisms around the roots; this was first observed by Lorenz Hiltner (1862–1923), who coined the term “rhizosphere effect”. The key players in the rhizosphere include the plant; saprophytic organisms such as bacteria, archaea, fungi and invertebrates; and symbiotic microorganisms such as rhizobia and arbuscular mycorrhizal fungi. The interaction of these key players with each other and with the soil environment is called **rhizosphere ecology**.

Nutrient uptake by plant roots occurs mainly in the root hair zone and leads to the depletion of nutrients close to the root. The extent of the depletion zone depends on the mobility of the nutrient in the soil. For example, the depletion zone of nitrate may extend 40 mm away from the root, while the depletion zone of phosphate typically extends only 2 mm. Phosphorus uptake in barley has been shown to be positively related to root hair length, indicating the importance of root hairs in nutrient uptake. In addition, arbuscular mycorrhizal fungi can transport phosphorus over a 10–15 cm distance. Root hairs and arbuscular mycorrhizal fungi can also increase the drought resistance of plants.

Changes in pH in the rhizosphere result from the secretion of protons or hydroxide ions by plants when they are taking up an excess of cations or anions, respectively, in order to keep their cytosolic pH constant and balance net charges. Mobilisation of iron by secretion of **phytosiderophores** can be beneficial not only to the secreting plant but also to a neighbouring plant that cannot produce phytosiderophores but can take up the iron–phytosiderophore complex. Secretion of carboxylates such as citrate and malate in order to solubilise phosphorus is sometimes accompanied by secretion of phenolics and cell wall degrading enzymes, which reduce the microbial degradation of the secreted carboxylate.

Fig. 11.4 Roots of a winter wheat plant pulled out of the ground in spring. The soil that sticks to the root is called the rhizosheath. This binding of soil to the root is largely due to root hairs. Note the root tips that are not yet covered with soil, because of the absence of root hairs in this root zone. In the field, rhizosphere soil can be obtained for further analysis by uprooting a plant, shaking off the non-adhering soil and collecting the adhering soil either by brushing it off or by immersion in a suitable liquid. (Photo: E.K. Bünemann)

Techniques to study the rhizosphere include (1) field approaches, as described in Fig. 11.4; (2) horizontal compartmental systems in which a root mat is typically formed on top of a mesh, allowing sampling of the soil just below the mesh; and (3) rhizoboxes with a transparent window allowing observation of root growth and sampling of soil in defined root zones.

this transport is associated with the transport of several nutrients (particularly K^+) (Herdel et al. 2001).

There are multiple interactions between **nutrient uptake** and the activity of various organs of plants (Fig. 11.5). Clearly, transport and retention of a nutrient do not occur independently of other nutrients and are almost always coupled to the transport of organic substances. Here we use nitrate and its turnover in a simplified model. One way of nitrate uptake starts with CO_2 assimilation in the leaf by the enzyme phosphoenolpyruvate (PEP) carboxylase, which carboxylates pyruvate to malate. Malate is transported with K^+ via the phloem to the root, and there it is decarboxylated to pyruvate and HCO_3^-. The proton may be excreted and exchanged with nitrate. Uptake of K^+ occurs simultaneously. Nitrate is transported, together with K^+ as a cation, via the xylem into the shoot. With the reduction of nitrate, K^+ is released again and balances the malate transport in the phloem. The ion transporters in the roots are regulated by photosynthesis; increased sucrose concentration in the phloem acts also as a signal for up-regulation of the expression of transporter genes involved in the uptake of nitrate, ammonium and other nutrients (see Lejay et al. (2003); Hammond and White (2008)). Independently of this cycle of potassium, malate may also be formed in the root from starch or via assimilation of CO_2 by PEP carboxylase. Anhydrases also form HCO_3^-, which may then be used to take up nitrate by an antiport (Moroney et al. 2001). As the plant requires more N than K, the soil is also made more alkaline by the nitrate uptake through the exchange with HCO_3^-. This is one pathway of nitrate uptake and, depending on the cation balance, nitrate may also be taken up by a symport of protons.

With respect to the **use of nutrients**, the following distinctions are made:

- Elements transformed in metabolism: They change the level of reduction (e.g. N and S).
- Elements that cannot be metabolised but support metabolism: These are freely moving

Table 11.3 Concentration of substances in the xylem and phloem of *Nicotiana glauca* (Schurr and Schulze 1995). The concentrations do not indicate the amount that is transported, because the mass flow is the result of the concentration and the flow rate. The flow in the phloem is slower than that in the xylem. Organic acids were not measured

pH and substances	Phloem ($\mu g\ ml^{-1}$)	Xylem ($\mu g\ ml^{-1}$)
pH	7.8–8.0	5.6–5.9
Sucrose	170–196	1.1–1.2
Amino substances	10,808	283
Potassium	3673	204
Phosphorus	435	68
Chlorine	486	64
Sulphur	139	43
Magnesium	104	34
Sodium	116	46
Calcium	83	189
Ammonium	45	10
Zinc	16	2
Iron	9	0.6
Copper	1	0.1
Manganese	0.9	0.2
Nitrate	<1	70

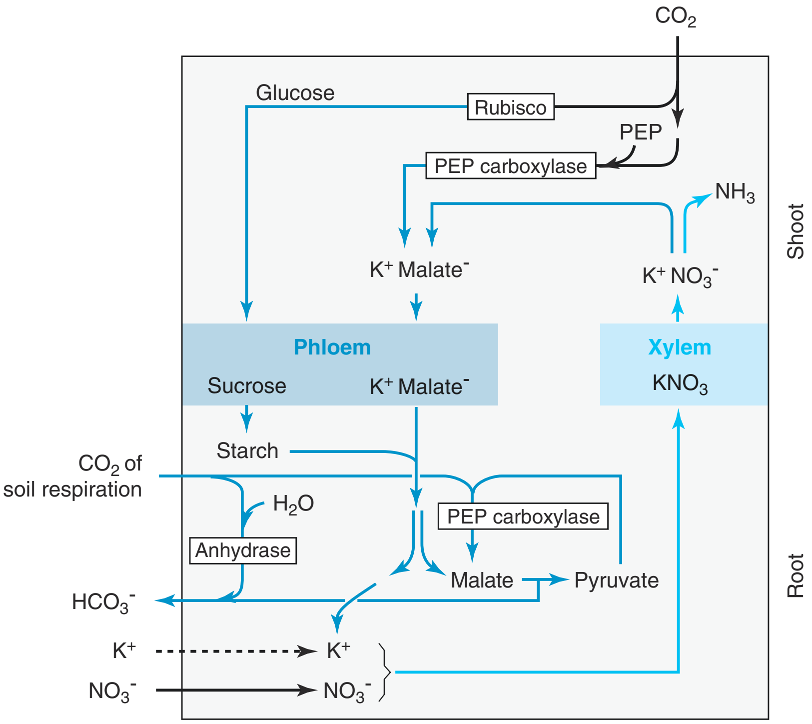

Fig. 11.5 Schematic model of the cycling of potassium and the uptake of nitrate in the xylem and phloem. In the phloem, K is the counter-ion for transport of malate and sugars. In the root, K is released from the phloem and transported into the xylem, where it is the counter-ion for nitrate. Nitrate uptake occurs both by co-transportation with potassium from the soil solution and by an exchange with HCO_3^-. (Marschner 1988)

Box 11.3: Ion Uptake (see White 2012)

The following processes lead to transport of ions in plants:

- **Diffusion**: Ion gradients lead to passive transport in soils and in the cell wall (Al^{3+})
- **Uniport**: An H^+ gradient leads to passive transport via ion channels (K^+)
- **Symport**: H^+ may be transported back with anions (Cl^-, SO_4^{2-})
- **Antiport**: H^+ efflux causes a cation influx (K^+, Ca^{2+}, NH_4^+)

In a plant cell, ion exchange occurs not only on the outer membrane surface but also at the membranes of plastids and vacuoles. Large differences in cation demand occur between organelles. Chloroplasts have high Mg concentrations, while mitochondria have high Ca concentrations. The vacuole serves as an ion reservoir. The pH of the cytosol is stabilised by the continuous exchange of cations and/or anions (a pH stabilisation mechanism, pH-stat). In this process, K^+ is important for balancing the exchange of H^+. Thus, K^+ and H^+ regulate the cellular proton concentration and proton gradients (Chap. 7)

Ion uptake occurs through ion channels or by carriers; these are proteins that span the lipid layers and have an internal passage through which ions can be passively or actively, but selectively, transported. The selectivity is largely due to the radius of the ion (i.e. K ions also pass through Ca channels) and amino acids lining the pore that forms the channel. Ion channels facilitate ion diffusion across membranes, and thus they are different from transporter proteins, which actively transport ions by using metabolic energy as pumps or in exchange of protons. Depending on the type of uptake, ion uptake:

- is oxygen-dependent
- can be inhibited by **mercury** if the ion channels or carriers are lined with S-containing amino acids
- is temperature dependent in the case of carriers, with an optimum generally at 30 °C
- is suited to the external concentration; that is, there are ion uptake systems that are most efficient at high or low external ion concentrations. Transporters with low efficiency for substrate ions can also have a function as sensors (Marschner 2012)
- is subject to competition in the presence of other ions; for example, the uptake of Mg^{2+} decreases in the presence of K^+ or Ca^{2+}

cations (K^+, Ca^{2+}, Mg^{2+}) and anions (PO_4^-) that store energy, or metals with catalytic functions that are bound firmly to proteins and act chemically, for example, because of changes in their oxidation state (Fe, Mn, Cu and others).

Analysis of the nutrient balance of the plant shows that a large part of nutrients is continuously exchanged within the plant; that is, ions circulate between the root and the shoot. This applies particularly to individual organs that have a limited **life-span**. Root tips and leaves are periodically or continuously formed newly, utilised transiently and disposed afterwards. Obviously, leaves are time-limited "machines". Old leaves are shed in response to decreasing physiological activity, for example, when shaded by new leaves. At the same time, formation and shedding of leaves are mechanisms for acclimation of the whole plant to changing environmental conditions (particularly light). Leaf shedding often also serves other functions, for example, detoxification following excessive uptake of salt (e.g. Na).

The expanding leaf is first a sink for carbohydrates and nutrients. Organic substances are required for the structure of the leaf. In the young state, leaves are thus a carbohydrate sink (Chap. 12); that is, **sink leaves** import carbohydrates for their growth. The leaf becomes a **source leaf** only after the development of about a third of the leaf area, exporting carbohydrates for maintenance or growth at other sites. Even before full development of the leaf area, a leaf's capacity for photosynthesis decreases and finally it becomes unproductive. This process of **leaf ageing** is modified by environmental conditions, including nutrition and light. In contrast to ageing, **senescence** is a genetically regulated process of the fully differentiated cell (Guarente and Kenyon 2000; Thomas et al. 2000). Ageing and senescence finally lead to shedding of leaves. However, before shedding, part of the invested resource of nutrients is remobilised and transported back into the plant. Large variations exist between species and between types of nutrients. Thus, the leaf is a "flow-through system" for nutrients, highly adjustable to environmental conditions and the internal requirements of the plant for nutrients. The turnover rate of nutrients in plants may change suddenly, depending on the ontogeny of the whole plant, particularly during the change from vegetative to reproductive growth.

11.1.4 Nutrient Deficiency and Excess

Nutrient deficiency and excess lead to **plant diseases**, recognisable by typical changes in the colour of needles or leaves (Fig. 11.6), and these are important indicators for the diagnosis of nutrient-dependent effects. Examples are leaf colour changes (browning and yellowing = **chlorosis**), progression of damage on individual leaves (e.g. dryness starting from the tip), progression of damage along the branch (damage starts in old organs) and the presence of pests as a consequence of lack or surplus of nutrients (e.g. by honey fungus (*Armillaria* spp.) attack). Nutrient analyses are required to confirm such observations. Tolerance of deficiency and excess, and development of symptoms, vary with the genotype and are species specific.

The development of symptoms by nutrient deficiency or excess is more marked in evergreen species than in deciduous species:

- **Nitrogen deficiency**: Evenly distributed chlorosis on the whole tree and for all needle ages; small needles, compressed sprouting, growth inhibition. Usually not limited to individual trees. On moor and heathland soils. Possibilities of misidentification: honey fungus (*Armillaria* spp.), but here individual trees or younger needles turn yellow.
- **Manganese deficiency**: Light yellow chlorosis of younger needles, starting in the lower canopy, particularly on limestone. Mn is not phloem mobile; that is, requirements for growth are met only by root uptake and influx in xylem water. Therefore, with increasing age, symptoms disappear.
- **Iron deficiency**: Whitish-yellow chlorosis of the youngest needles. Considerable deficiency causing needle tips to brown and die on limestone. Similar to Mn deficiency.
- **Potassium deficiency**: Pale yellow to violet-brown (reddish) colouration starting from needle tips, but at first predominantly on older needles, which are shed prematurely and lead to light canopies. K is phloem mobile and is thus first retransported to the youngest organs. K deficiency increases sensitivity to frost. Misidentification: Mg deficiency, but in this case the colouration is more intensely yellow or, rarely, red.
- **Magnesium deficiency**: Light yellow to golden-yellow chlorosis, starting in older needles from the tip. Shaded branches and the underside of needles are less decolourised. Mg is phloem mobile and therefore is remobilised from old to young needles. Occurs on silicate soils.
- **Air pollution (SO_2) damage**: Golden-brown to reddish-brown colouration, starting from the needle tip. Necrotic flecks or bands in the middle part of the needle. Buds often die off. Misidentification: damage from road salt, herbicides.
- **Road salt damage**: Needles of the previous year's growth are dark copper brown in spring, falling in early summer. Buds often fall. Damage along the edge of roads. Misidentification: frost-drought (but here, the needles are light reddish brown) or sulphur dioxide.
- **Phosphorus deficiency**: Starting with a dark blue-green colour (increased formation of chlorophyll), later violet-red to copper-brown

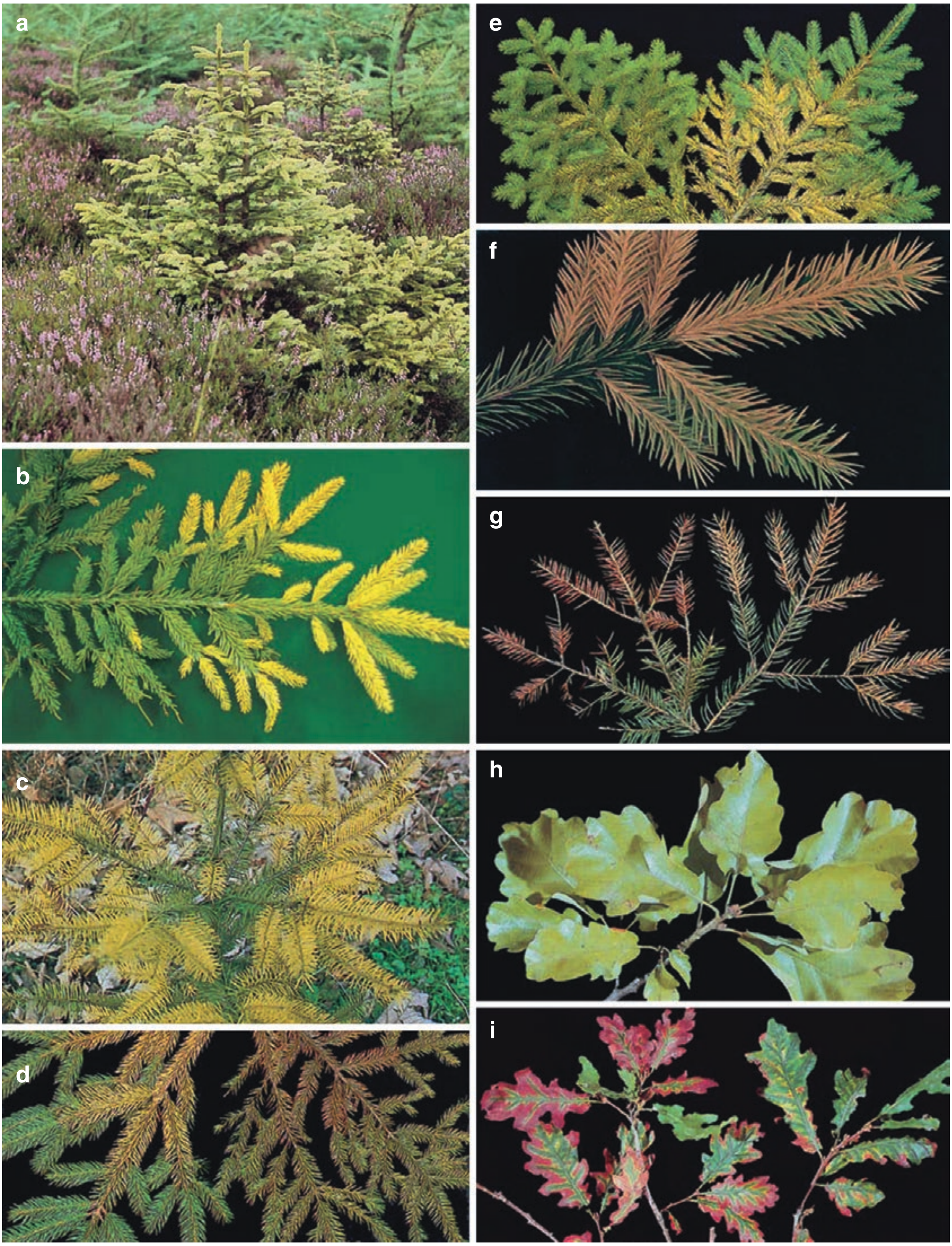

Fig. 11.6 Typical nutrient deficiencies and damage due to excess or deficits of nutrients. **a** Nitrogen deficiency. **b** Manganese deficiency. **c** Iron deficiency. **d** Potassium deficiency. **e** Magnesium deficiency. **f** SO_2 damage. **g** Road salt damage. **h** Mild phosphate deficiency. **i** Severe phosphate deficiency. (Hartmann et al. 1988)

and yellow colouration (anthocyanin), in parts spotty, starting from the edge of the leaf. Misidentification: K deficiency, drought, salt, but then without the violet-red colour.

11.2 Nitrogen Nutrition

11.2.1 Nitrogen in Plant Metabolism

Nitrogen is the nutrient required in the largest quantities. Plants require nitrogen for:

- Amino acids (free amino acids, proteins).
- Nucleic acid (DNA).
- Heterocyclic and azo-compounds (e.g. a pyrrole ring).

The huge amount of N_2 in the Earth's atmosphere is very inert and not directly available to plants. Nitrogen can be used only in its reduced or oxidised form (NH_4^+ or NO_3^-) or in its organic form ($-NH_2$). In nature, the transformation of gaseous N_2 into nitrogen available for plants occurs either in the atmosphere through lightning (10–40 mol N m^{-2} $year^{-1}$), by free-living bacteria in the soil, or in plant-associated nitrogen-fixing bacteria. Industrially reduced nitrogen for fertilisers is synthesised by the Haber–Bosch process from N_2 and H_2 at high temperatures and high pressures (Chap. 21).

The process of **N_2 fixation** occurs catalytically under anaerobic conditions in root nodules of legumes or in free-living cyanobacteria (blue-green algae; see Marschner 2012), where the microorganisms lower the oxygen concentration of the atmosphere via respiration. In the primary succession from open soil to vegetation with a closed nitrogen cycle, there is a stage at which N_2-fixing organisms dominate (Chap. 17). Because of the high energy demand for N_2 reduction (and the requirement for P associated with it), these organisms are unable to compete at the later stages of succession, when more nitrogen is available in oxidised and reduced forms (Read 1993). Here we concentrate on N uptake and turnover in plants.

11.2.2 Nitrogen Uptake and Nutrition

Plants gain nitrogen from litter and soil solution as amino acids, ammonium cations and nitrate anions. From the atmosphere, N is available as NH_3, NO or NO_2 gas. Leguminosae may gain nitrogen also by symbiosis with soil bacteria.

N and C metabolism are closely intertwined. Metabolism starts with photosystem I (PS I) when a surplus of electrons to ferredoxin not only reduces NADP to NADPH (which is used for CO_2 assimilation) but also is used for nitrate and sulphate reduction (Fig. 11.7a). The main processes involved in the interaction between the N and C cycles (Fig. 11.7b) are production of carbohydrates for root maintenance and growth; production of C skeletons for N assimilation; protein metabolism and effects of nitrate on the phytohormone balance (especially cytokinins); feedback coupling of protein availability and phytohormones for photosynthesis (30% of the N content of a leaf is in the CO_2-fixing enzyme RubisCO (ribulose-1,5-bisphosphate carboxylase/oxygenase); Chap. 7) and growth (principally of leaves); and regulation of C allocation by metabolites of the C cycle and nitrate.

11.2.2.1 Amino Acid Uptake and Nutrition

Amino acids are available from N_2 fixation by nitrogen-fixing bacteria, via the direct degradation of litter or from the soil solution (Wallenda et al. 2000). It is known from laboratory and field experiments that roots are able to take up a broad spectrum of amino acids (Näsholm et al. 2009).

Amino acid uptake by roots is very important, particularly in boreal forests at a low rate of nitrification (Persson et al. 2000). Under these conditions, amino acid uptake via the mycorrhiza supplies the plant with almost all of its N demand. Mycorrhizal fungi are able to excrete proteases and thereby break down proteins from litter and use the resulting amino acids directly (Näsholm et al. 1998; Wallenda et al. 2000). It has been shown (Nordin et al. 2001; Persson et al. 2006) that the uptake of amino acids also takes place in

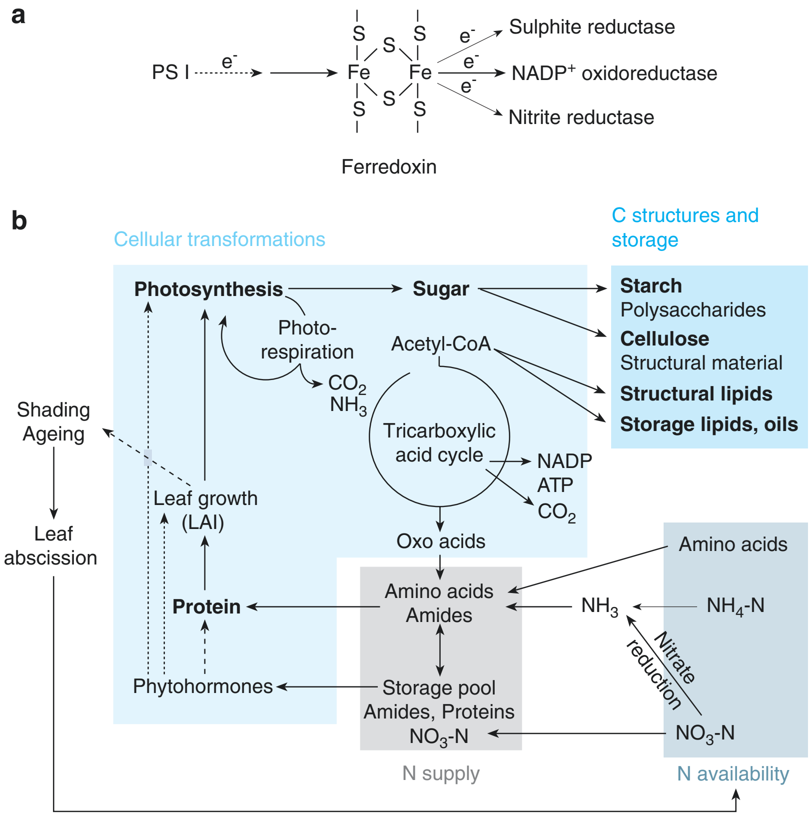

Fig. 11.7 Schematic model of the coupling of the photosystem and the cell metabolism of nitrogen. **a** Coupling of electron transport from photosystem I (PS I) to sulphite, nitrite and nicotinamide adenine dinucleotide phosphate (NADP) reduction via ferredoxin. **b** Diagram of the coupling of C and N metabolism in a plant. For a detailed description, see the text. (Marschner 1995)

the presence of ammonium and nitrate ions, and may reach the same level in fertile soils and at poor sites (Berthrong and Finzi 2006), even though the relative contribution to the N requirement is lower at fertile sites, as additional ammonium and nitrate are available and are utilised (Schulze et al. 1994; Michelsen et al. 1996).

11.2.2.2 Ammonium Uptake and Nutrition

Ammonium is taken up directly in the area of the root hairs or via mycorrhizae. NH_4^+ would be toxic as an ion because its ionic radius and strength are very similar to those of K^+. Thus, it could enter the cell instead of K^+, interfering with the pH regulation of the cell. Therefore, NH_4^+ taken up by the root is not stored or transported but rapidly converted into amino acids via the GOGAT (glutamine oxoglutarate aminotransferase) enzyme system. In this process, NH_4^+ is bound to glutamate, using adenosine triphosphate (ATP). The primary amino acid glutamine is formed, which donates the NH_2 group to oxoglutarate by transamination and thereby regenerates glutamate. GOGAT is the enzyme system that also traps free NH_4^+ ions in all other plant organs.

Ammonium uptake (Fig. 11.8; Marschner 1988) occurs generally as an antiport with protons that are excreted by roots. Uptake of ammonium thus leads to **soil acidification**. For NH_4^+ assimilation in the root, organic molecules are required to provide the C skeletons. They are derived from sucrose produced in the leaf and transported, via the phloem, into the root. Because free amino acids act osmotically and could interfere with the metabolism, amino acids and amides are transported via the xylem into the leaf or they are incorporated into proteins of growing tissues. Ammonium nutrition is important particularly in acidic soils, where nitrification is inhibited and particular cation deficiencies (e.g. Mg, K) may be triggered or increased because of ionic interactions of Mg^{2+} and NH_4^+.

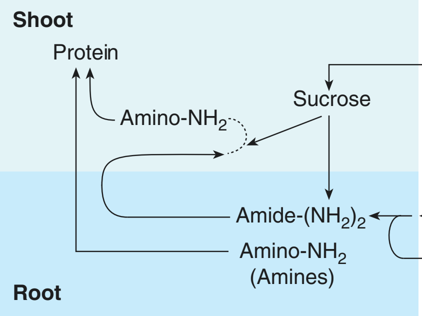

Fig. 11.8 Schematic model of the exchange and transport of ammonium. Protons are released to neutralise ionic charges when NH_4^+ is taken up; that is, the soil pH decreases (Fig. 11.9b). Ammonium is immediately assimilated into amino acids in the roots; for this reaction, C skeletons have to be transported from the shoot to the root. Ammonium-fed seedlings are deficient in soluble carbohydrates, as the C skeletons are used for assimilation of NH_4^+ in the roots and are thus not available for growth of shoots. Detoxification of ammonium leads to a surplus of amino acids, which are not used for protein synthesis, as the assimilates in the roots are required for the assimilation of ammonium ions. This effect is not apparent with nitrate, because nitrate can be stored in the vacuole in balance with growth. (Modified from Marschner (1988))

11.2.2.3 Nitrate Uptake and Nutrition

The same area of the root that assimilates ammonium also takes up nitrate and cations (Fig. 11.5). Some mycorrhiza species also take up nitrate. It is not possible to use nitrate directly in the metabolism. It must first be reduced to $–NH_2$. **Nitrate uptake** (Fig. 11.9; Marschner 2012) occurs either together with cations as a symport with protons or in exchange of OH^-. As the requirement for N is larger than that for alkaline cations, the symport with cations is not unlimited. In this case, nitrate uptake takes place in exchange with HCO_3^-, leading to increased soil pH in the rhizosphere. Conversely, with nitrate deficiency in the soil, nitrate is missing as an anion in the uptake of cations, resulting in uptake of Cl^- and SO_4^{2-} and leading to root injury.

Physiologically, nitrate is not toxic and thus it may be stored in the root or in the shoot. Nitrate storage in the leaf has a regulatory (signal) effect on C allocation (shoot–root growth) of plants (Scheible et al. 1997a, b; Klein et al. 2000). A high nitrate concentration in the leaf stimulates shoot growth and inhibits root growth by regulating the sugar transport to the root, whereas in the soil it stimulates root growth.

Generally, nitrate transport occurs via the xylem into the storage parenchyma of the stem, or into the leaf where nitrate is initially stored together with cations in the vacuole. This increases the osmotic concentration and the water content of leaves (e.g. in “crunchy” nitrate-fertilised vegetables—mainly salad vegetables). If required, nitrate may be transported back from the vacuole into the cytosol. This occurs in exchange with organic acids formed via PEP carboxylase in the leaf. For some plant species, oxalic acid is transported, in exchange for nitrate, into the vacuole. At high Ca supply, this leads to the formation of **Ca oxalate** in the vacuole. Because of the low solubility of Ca oxalate, crystals are formed in the vacuole, which may even damage the cell structure (rhaphides, giving the typical taste of rhubarb and banana peel). Nitrate is reduced to nitrite in the cytosol. Since nitrite is toxic, it must be reduced to NH_4^+ rapidly, which is then assimilated by the GOGAT system. The rate of turnover of nitrite reductase is faster than that of nitrate reductase. Some of the cations taken up with nitrate are transported back into the phloem; in particular, K^+ is relocated into the root, accompanied by associated organic acids. These acids are decarboxylated in the root (e.g. malate) and thus support nitrate uptake.

11.2.2.4 Ammonium Nitrate Nutrition

From the specific effects of ammonium and nitrate uptake, particularly with respect to the cation uptake, it becomes clear that the uptake of **ammonium nitrate** is most favourable for nutrition. Nutrition with ammonium nitrate:

- Maintains the balance of anions and cations in the plant and in the soil.
- Decouples the uptake of cations and anions from the N nutrition (the N requirement is larger than the requirement for cations).
- Maintains the C/N balance. The relation of nitrate and free amino acids (in the case of

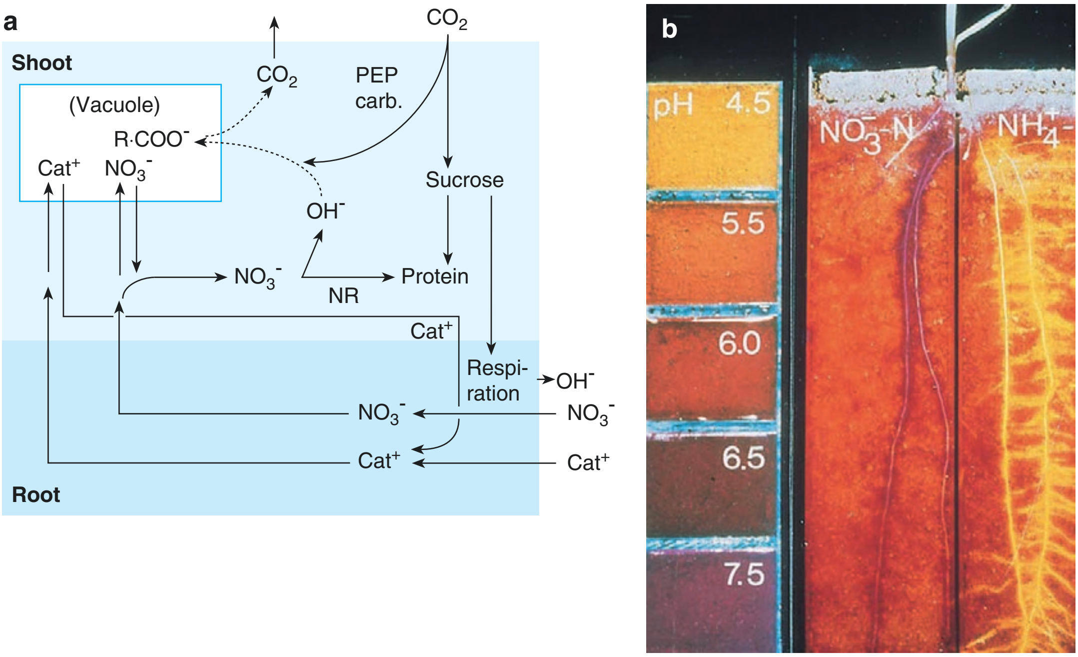

Fig. 11.9 Schematic model of the exchange and transport of nitrate. **a** Nitrate uptake and transport in the plant. To balance the charges, OH^- ions are released into the soil; that is, the soil pH rises. Nitrate can be stored in the vacuole until reduction (Marschner 1988). **b** Changes in soil pH after nitrate or ammonium uptake. Roots of plants were divided between two compartments: in one, the N source was nitrate and in the other it was ammonium. The *yellow colouration* shows the decrease in pH in proximity to the root during ammonium uptake. The *red colour* shows nitrate uptake and the corresponding pH increase. (Photo courtesy of E. George)

ammonium nutrition) to starch is a sensitive indicator of the state of nutrition in the leaf (Fig. 11.10). Large nitrate and amino acid concentrations are always connected and indicate excess fertilisation. In contrast, high starch concentrations in the morning correlate with small nitrate and amino acid concentrations and thus indicate N deficiency. Maximum growth rates are achieved under conditions where the nitrate and starch concentrations safeguard the supply for growth during the night, because growth and thus the N and C requirement continue during the night, although assimilation of N and C requires light.

11.2.2.5 Nitrogen Input from the Atmosphere

Nitrogen-containing **air pollutants** are taken up as gas (NH_3, NO, NO_2) by the plant via the stomata. NH_3 is more soluble than NO, which in turn is more soluble than NO_2. In the leaf, all gases are immediately assimilated into amino acids. Not only gases but also ions dissolved in rainwater and fog reach the inside of the bark via the medullary rays (Klemm 1989). Dust particles containing Mn are deposited on the outside of the cuticle, catalyse the oxidation of NO_2 and SO_2 to nitrate and sulphate in a surface reaction and thus increase N deposition. Uptake of nitrogen from the atmosphere contributes significantly to the N balance for growth in the canopy of trees (up to 20–40% of the N requirements) (Harrison et al. 2000; Burkhardt et al. 2012).

There is a basic difference between the N uptake via the shoot and that via the root. Uptake of nitrogen via the root is metabolically regulated; that is, the plant takes up nitrogen according to its requirements. In contrast, the plant has no "defence" mechanisms against uptake of NO_x, NO_2 or NH_4^+ via the shoot. In addition, uptake via the shoot occurs in exchange with cations (K, Mg); that is, it is

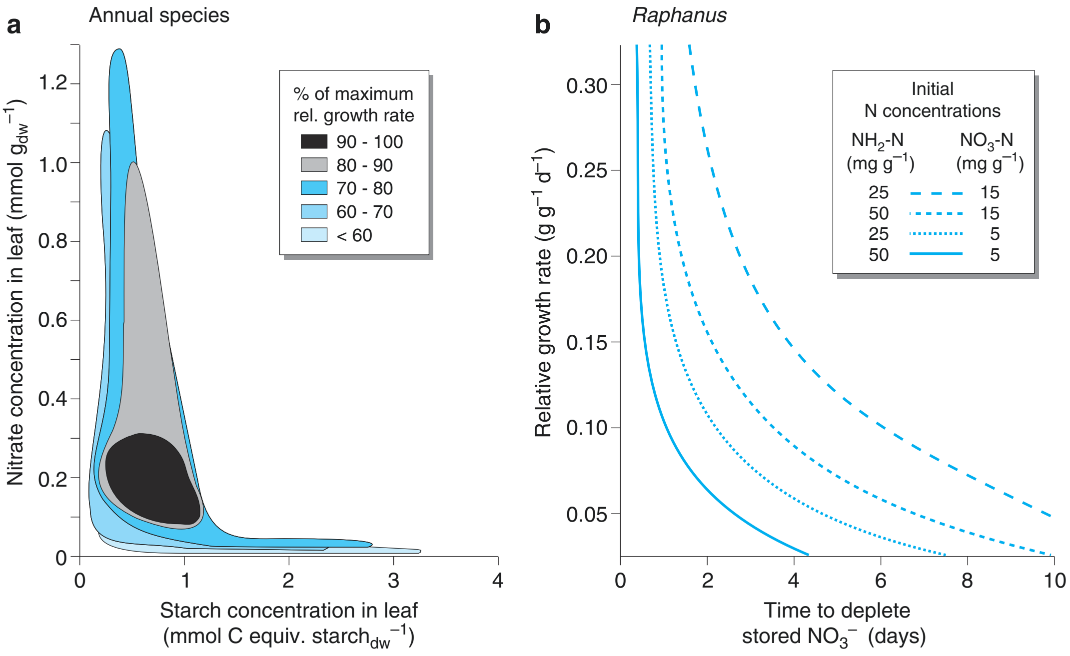

Fig. 11.10 Relations between nitrate, starch in leaves and plant growth. **a** Relative growth rate (RGR, shown as *isohypses*) in relation to nitrate and starch concentrations in the leaf. The highest growth rates occur at lower concentrations of the two substances. Starch accumulation is thus an indicator of N deficiency and nitrate accumulation is an indicator of C deficiency. **b** Consumption of nitrate reserves of plants grown in different nutrient conditions, following a sudden decrease in N availability. Even in plants that are well supplied with nitrate, the supply of nitrate from reserves lasts only a few days because of the high growth rate of *Raphanus*. (Stitt and Schulze 1994)

coupled with a loss of cations. **Nitrogen nutrition** from air pollutants thus may lead to an imbalance in cations, particularly if cation uptake is limited.

N_2 fixation by endosymbiosis enables species of particular plant families to make use of the atmospheric N_2. The Leguminosae family contains more than 12,000 species, the majority of which live in symbiosis with N_2-fixing soil bacteria called the Rhizobia. This rhizobia–legume symbiosis is estimated to be responsible for up to 60% of biologically fixed nitrogen on land (Chapin et al. 2002). A similar symbiosis between plants and bacteria exists in alder (*Alnus* sp.) and some Poaceae. Even though *Acacia* species (Leguminosae) are widely distributed in subtropical arid regions, their N_2 fixation is very low (Schulze et al. 2014). The main amount of biologically fixed nitrogen occurs globally in agricultural crops (soybean: *Glycine max*) (Fig. 11.11; Chap. 21).

11.2.3 Nitrogen Requirements for Growth

Nitrogen nutrition is important not only for plants growing under natural conditions but also for crops. The requirements and responses of woody plants are different in magnitude to those of herbaceous plants, because wood contains very little nitrogen. Not only the growth form but also the season determine the requirements for N.

Over a wide range, growth is linearly related to N supply. With ample N this response becomes saturated, but many other environmental factors determine at what level of nitrogen supply saturation is reached (Fig. 11.12). With an "optimal" supply of other nutrient elements, saturation occurs for agricultural crops at about 200 kg N ha^{-1} a^{-1}. Higher rates of fertilisation still result in a small increase in yield. The economic benefit of a marginally greater yield is determined by the prices of cereals and fertiliser. At the same time,

Fig. 11.11 Soybean field in Brazil (Photo courtesy of M. Hertel)

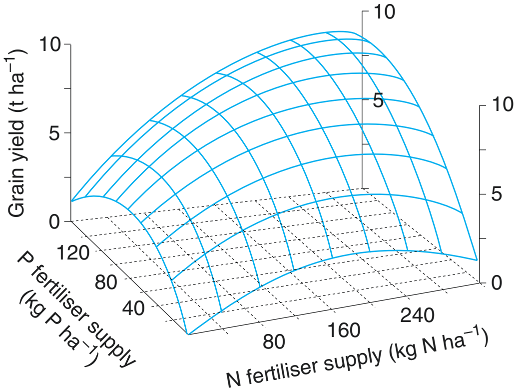

Fig. 11.12 Changes in the grain yield of maise with different N and P fertilisation. At high P availability (140 kg P ha^{-1}), 300 kg N ha^{-1} can lead to a high yield. If only 40 kg P ha^{-1} is available, then addition of only 160 kg N ha^{-1} leads to loss of yield. (Schopfer and Brennicke 1999)

high rates of fertiliser application affect the environment by nitrate leaching into groundwater if crops cannot use all of the fertiliser at that stage of development. In contrast to the high capacity for N utilisation of crops, consumption by trees is much smaller. When mineralisation exceeds N deposition of about 100 kg N ha^{-1} a^{-1}, deciduous trees and conifers are no longer able to use the N available. This is mainly because the N requirement for production of wood is much less than that for non-lignified tissues. Less than 10% of the nitrogen taken up is used for growth of a tree trunk (Nadelhoffer et al. 1999). This does not take into consideration that 90% of the nitrogen taken up and invested in leaf and branch growth creates the preconditions for the growth of wood by building up the photosynthetic apparatus. However, the biomass of leaves in the canopy may not be increased indefinitely. The maximum **leaf area index** (LAI) is dependent on the light supply and on structural characteristics of the canopy such as leaf inclination and leaf clustering (Chap. 9).

Herbaceous species are better equipped to utilise nitrate than woody species. Herbaceous species usually have smaller dry weights and greater water content per leaf area (Schulze et al. 1994), and they are better able to store nitrate because of their larger vacuoles. Because of greater N concentration in the mesophyll (and thus a greater concentration of the CO_2-reducing enzyme RubisCO), herbaceous plants usually have higher rates of photosynthesis and thus an greater capacity for nitrate reduction than woody plants (Fig. 11.7). A further basic difference between herbaceous and woody species is the association of herbaceous plant roots with **vesicular arbuscular mycorrhizae** (**VAMs**) and **ectomycorrhizae** (**EMs**) in woody plants. VAMs are more able to utilise mineralised P, while EMs are able to gain amino acids from litter (Smith and Read 1997). EM bypass mineralisation (Wallenda et al. 2000; Kähkölä et al. 2012). Ectomycorrhizae are also able to take up ammonium in acid soils, as they precipitate the toxic Al with phosphate. There are also mycorrhizae that reduce nitrate (Wallenda et al. 2000). Detection of whether plants utilise nitrate, ammonium or amino acids is partly possible via stable isotopes (Hobbie et al. 2000; Persson et al. 2006). The N requirement for growth (C/N relation) of fungi is higher than the N requirement of trees, as the cell wall of fungi consists of chitin (50 mg N g^{-1} dry matter for fungi and 1 mg N g^{-1} dry matter for wood). However, there are exceptions: *Fraxinus* spp. use large amounts of nitrate but do not possess any mycorrhizae. In trees, the nitrate is reduced in the mycorrhizae or in the roots, so nitrate can no longer be detected in the xylem water.

In ecology, a theory has been developed that species with a high material turnover are stress sensitive and those with a low turnover are stress tolerant concerning water supply (Orians and Solbrig 1977; Fig. 12.5). This could, however, not be supported for N supply and its interaction with growth by Fichtner and Schulze (1992). There was no difference in the response to reduced nitrogen between species that are adapted to high N supply (e.g. *Galeopsis tetrahit* (common hemp nettle (Labiatae) at eutrophicated sites)) and species adapted to poor N supply (e.g. *Teesdalia nudicaulis* (shepherd's cress (Cruciferae) on sandy lawns)). The important difference between the two species was that *Teesdalia* flowered at low N supply, when *Galeopsis* was able to set flowers only at high N supply (Chap. 12).

11.2.4 Nitrogen Storage

In all natural systems, nitrogen is a limiting nutrient. It is therefore to be expected that storage of nitrogen takes place in different organs and at different times. Nitrogen is stored in various forms:

- As **inorganic nitrogen** in the vacuole, only in the form of nitrate and together with cations. This storage balances the changing requirements during the diurnal rhythm of growth and during the changing seasonal nitrogen demand and supply.
- As **organically bound nitrogen** stored in the form of amino acids and proteins. Most of these substances have further functions; that is, storage is a by-product of metabolism and of an imbalance in production and consumption of certain materials. **Amino acids** serve as storage and transport forms for N even though amino acids act osmotically. Therefore, amino acids with several $–NH_2$ or –NH groups are stored (glutamine (2 N/4 C), asparagine (2 N/4 C), arginine (4 N/6 C), allantoin (4 N/4 C). Storage is short-term to seasonal and occurs in the phloem–xylem circulation or in the vacuoles of the storage parenchyma of stems. Some of the amino acids may not only have a storage function but also protect against frost and salt in winter (proline; Chaps. 6 and 7). The storage amino acids play an important ecological role in sprouting and growth of young leaves in spring. Thitithakanul et al. (2012) found that up to 45% of the total N stored during the previous year is mobilised before bud break in young poplars. **Polypeptides** and **proteins** are formed when the osmotic activity of amino acids may interfere with metabolism; for example, during the loading of phloem the number of molecules must be decreased and N must be concentrated in a few molecules (Schulze et al. 1999). Important storage proteins (e.g. prolamine, glutelin and albumin) accumulate in seeds and may also have protective functions. The CO_2-reducing enzyme RubisCO (ribulose-1,5-bisphosphate-carboxylase/oxygenase) forms about 30% of the N content of a leaf. Only a proportion of this protein is normally active—with the excess serving to safeguard the photosynthetic apparatus at high photon flux—or a proportion may be degraded during N deficiency and used for growth (Stitt and Schulze 1994). Before leaves are shed, part of this nitrogen is degraded and the amino acids are re-translocated back to the plant. This **remobilisation** of nitrogen from leaves may be as high as 20% of the leaf N (Chapin and Kedrovski 1983; Koch et al. 1988).

11.2.5 Insectivorous Plants

“Carnivorous” or **insectivorous** plant species are found in areas that are particularly deficient in nutrients. They have adapted by changing their leaves, in various ways, into organs that act as traps and are suitable for trapping insects, and at the same time they excrete proteases and chitinases that digest the insects (Fig. 11.13). They are differentiated into:

- Spring traps (e.g. *Dionaea*).
- Pitfall traps (e.g. *Nepenthes*).
- Sticky traps (e.g. *Drosera*).
- Suction traps (e.g. *Utricularia*).

These types have evolved in very different taxonomic groups (Fig. 11.13). Often the same trap types occur in geographically and taxonomically distinct regions (pitfall traps in *Nepenthes* in the Indonesian islands, *Sarracenia* in the eastern USA, *Darlingtonia* in the western USA and *Cephalotus* in southwest Australia). The effectiveness of insect capture can be measured using stable ^{15}N isotopes, as insects have a higher δ^{15}N value than soil N, depending on their trophic level (Table 11.4) (Schulze et al. 1991; Schulze et al. 1997).

Roridula gorgonias (from South Africa) is a special case, as it does not excrete proteases. The sticky leaves catch insects, which are then harvested by bugs (Hemiptera) that are adapted to

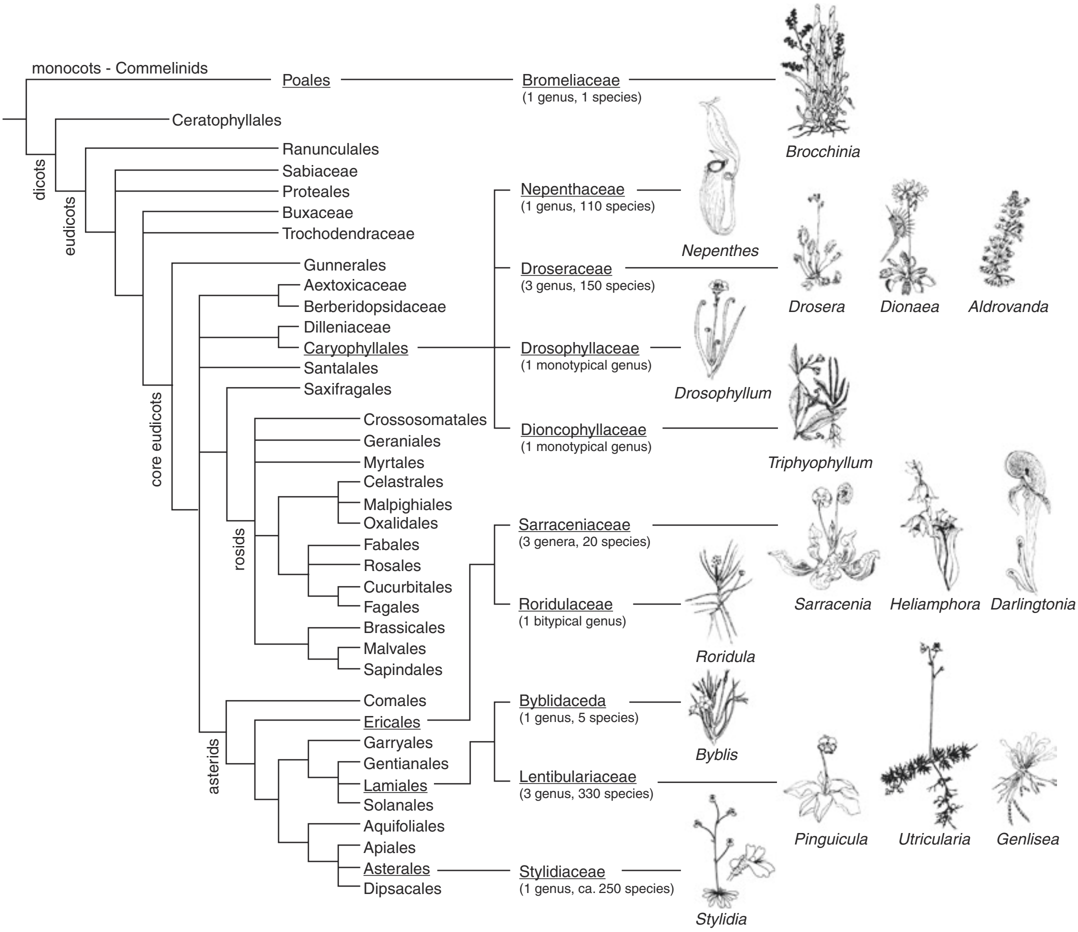

Fig. 11.13 Distribution of insectivorous plants in angiosperms. Different forms of leaf are used to capture insects. Spring traps: *Dionaea muscipula*; pitfall traps: *Darlingtonia californica* and *Nepenthes* spp.; sticky traps: *Drosera* spp.; suction traps: *Utricularia* spp. (Modified from Schulze (1991))

Table 11.4 Contribution of insect N to the N nutrition of insectivorous plants (Schulze et al. 2001)

Trap type	Genus	Growth form	Proportion of insect N in plant N (%)
Sticky trap	*Drosera*	Rosette	20 (e.g. *D. erythrorhiza*, Western Australia)
		Climber	53 (e.g. *D. macrantha*, Western Australia)
		Upright, low	48 (e.g. *D. stolonifera*, Western Australia)
		Upright, high	54 (e.g. *D. gigantea*, Western Australia)
	Roridula	Shrub	70
Pitfall trap	*Cephalotus*	Rosette	26
	Nepenthes	Climber	62 (100% in buds)
	Darlingtonia	Rhizome	76
	Heliamphora	Rhizome	79
	Brocchinia	Erect rosette	59
Spring trap	*Dionaea*	Rosette	80

life on the sticky trap and move slowly and carefully. *Roridula* uses the excrement of the bugs as a N source (Ellis and Midgley 1996).

Nepenthes takes nitrogen from the trapped insects in the form of ammonium, which is absorbed via glands (Schulze et al. 1997), where amino acids are formed before transport to the vascular bundle. There, polypeptides are formed (a N concentration mechanism) and then loaded into the phloem. In young *Nepenthes* shoots, 100% of the N content originates from trapped insects.

In the Venus flytrap (*Dionaea*), survival depends on the seedlings being able to trap insects (Schulze et al. 2001). Only after a significant catch can the larger spring traps develop that are suited to catching even larger insects; only the rosette is capable of flowering.

11.2.6 Nitrogen Deficiency and Excess

N deficiency and N excess are detectable by the following characteristics:

- **N deficiency**: Yellowing, reduction of growth of shoots and leaves, high dry weight/leaf area, starch accumulation, premature ageing and shedding of leaves. Yellowing of leaves is not very specific and is often also caused by deficiency of other nutrients and degradation of chlorophyll. The nitrogen–cation imbalance determines deficiency and excess.
- **N excess**: High chlorophyll content, high water content, low dry weight/area (shade leaf type), nitrate and amino acid storage, long internodes.

Because of the rapid and substantial alterations in N supply with changing conditions in time and location, it is very time and resource consuming to quantify the N supply. In contrast to nitrate, which is not bound to a soil exchanger and can thus be measured in the soil solution, quantifying the exchangeable ammonium in litter is difficult. In order to characterise the supply of nitrogen at a particular site, Ellenberg (1974) suggested deriving the supply from the presence of certain **indicator species** at a certain site. Each species was classified by a relative scale, with a range of 1–5 to 1–9 as **indicator values** (Ellenberg 2009) (see Box 11.4). Conversely, it is possible to draw conclusions from the occurrence of a certain species about the supply of resources at a certain site. The scaling of the indicator value is valid only in a limited region, as the interaction with other species changes the occurrence and thus the indicator value of a particular species (Chap. 19).

11.3 Sulphur Nutrition

11.3.1 Sulphur in Plant Metabolism

Sulphur is a macronutrient element, which can be metabolised and is available:

- in its oxidised form as **SO_4^{2-} ion** (sulpholipids are ester bindings of SO_4 to a sugar lipid; these occur in all membranes and as an **-S–S or -S–O group**, which occurs in species-specific

Box 11.4: Indicator Plants

Indicator plants are defined as follows (Ellenberg 2009; Chap. 19):

- About 2000 vascular plants in central Europe occur with varying frequency in different habitats and are classified into particular classes and locations. This classification is also applied to mosses and lichens
- The classification is based on three climatic factors (light, temperature and continentality) and four soil factors (N availability, soil pH, soil water content and salinity). Development of a classification of species in relation to P supply is in progress
- These values are the so-called indicator values and should allow general characterisation of a site, without additional analysis in a laboratory
- The values increase from 1 (small) to 9 (large)
- Indicator values are not a measured value but based on expert knowledge. They are extrapolated from the normal behaviour of a species in its natural environment; that is, they do not characterise the physiological requirements but the ecological niches they occupy. Thus, they apply only in areas where the initial floristic analysis was performed

As **nitrogen indicators**, they serve in the following way:

- N1 species only occur in N-poor environments (e.g. *Trifolium arvense*, *Erophila verna*, *Calluna vulgaris*)
- N2 and N3 species occur more often in N-poor locations than in N-rich locations (e.g. *Medicago sativa*, *Equisetum arvense*)
- N4 and N5 species occur in moderate to rich locations but only infrequently in N-poor locations (e.g. *Ribes nigrum*, *Primula vulgaris*)
- N6 and N7 species flourish only in N-rich locations (e.g. *Chenopodium album*)
- N8 species are special N indicators (e.g. *Mercurialis annua*, *Urtica urens*, *Epilobium angustifolium*, *Ballota nigra*)
- N9 species occur in extremely N-rich locations (e.g. *Chenopodium bonus-henricus*, *Lamium album*, *Sambucus nigra*)

secondary metabolites—for example, alliin in *Allium* and isothiocyanate R-N-C-S in Brassicaceae). These substances serve as S storage and protection against herbivory.

- in its reduced form as—**SH groups** in amino acids (cysteine, methionine), as a co-enzyme (acetyl-S-enzyme protein: acetyl-CoA), as a non-peptide unit making a functional protein (prosthetic group of ferredoxin, thiamine, biotin), in proteins to form the tertiary structure by oxidation of the disulphide, in cellular redox systems ($R1–SH + R2–SH \rightarrow R1–S–S–R2 + H_2$, particularly with participation of glutathione), in proteins to bind heavy metals (heavy metal resistance; Chap. 7, where cysteine participating in ion channels may bind to heavy metals (Hg)) and in the glutathione cycle to detoxify radicals.

11.3.1.1 Sulphur Metabolism

ATP activates sulphate (Fig. 11.14) and adenosine phosphosulphate (APS) is formed. This substance either is transformed by formation of phosphoadenine phosphosulphate (PAPS) into the sulphate ester metabolism—to give, for example, sulpholipids—or serves as a substrate for sulphur reduction. The reduced sulphur is deposited as thiol groups on C skeletons (usually an amino acid, e.g. glutathione), which are synthesised via a sulphotransferase. The S-reduction occurs in the chloroplast, where ferredoxin transfers the electrons to oxidised sulphur (Brychkova et al. 2012). The —SH group is transferred to O-acetylserine, which is split into acetate and cysteine. Cysteine is the starting point for the formation of all organic molecules with an —SH group and thus makes plants sensitive to heavy metals, particularly Hg (Chap. 7).

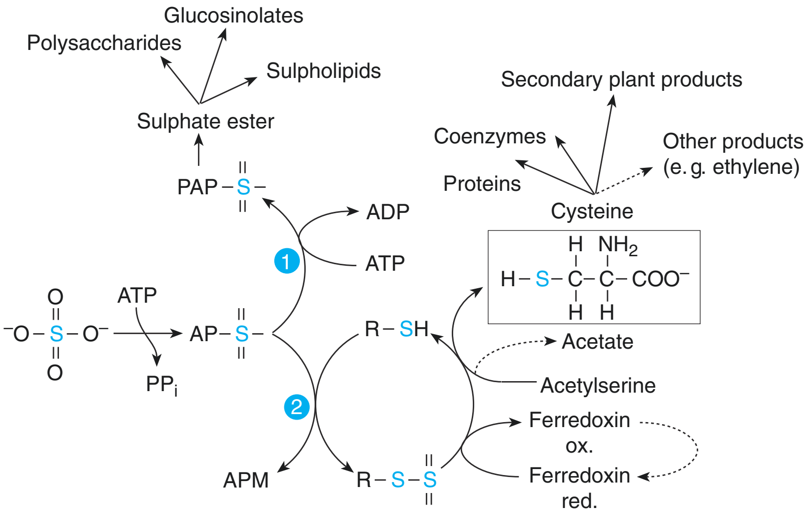

Fig. 11.14 Schematic model of the assimilation of sulphur into various plant metabolites. (1) sulphate esterase, (2) sulphate reductase, *APM* adenosine phosphomalate, *APS* adenosine phosphosulphate, *ATP* adenosine triphosphate, *PAPS* phosphoadenine phosphosulphate. (Marschner 1988)

11.3.2 Sulphur Uptake and Plant Requirements

Sulphur uptake as the SO_4^{2-} anion is a symport with protons. Sulphate is the most important additional anion, after nitrate and phosphate, in plant nutrition. Reduction of the sulphate anion to —SH occurs in the chloroplast, via sulphite utilizing the electron flow from PS I (Fig. 11.7). With calcium, sulphate forms crystals (**gypsum**). Thus, sulphate cannot be stored in its inorganic form in the vacuole.

Generally, the requirement for N also regulates the demand for S, as the N to S ratio in proteins is approximately constant (10:1). Only in some plant families does the S requirement increase because of secondary metabolism. This applies particularly to the Cruciferae, where mustard oil (glucosinolate) provides protection against herbivory but also serves as an S reserve. Rape seed belongs to those species that grow well at very high S supply. Since mustard oil is volatile, these plants are also able to remove S via stomata by emission of mustard oil (it can be smelled when rape seed is flowering). The S requirement is also large in Leguminosae, particularly because of the S-containing storage proteins in seeds.

Sulphur is taken up not only via the roots but also via the shoot. This particularly applies to **sulphur dioxide** (**SO_2**), which enters the intercellular spaces together with CO_2. SO_2 is soluble in the cell wall with formation of the toxic sulphite anion, which follows the pH gradient from the cytosol to the chloroplast, where it is assimilated. In general, SO_2 is oxidised to SO_4^{2-} by heavy metals in the cuticle and in the cell wall, particularly by Mn. Thus, airborne sulphate is assimilated in the mesophyll in the same way as sulphate that was taken up by the roots. Sulphate may react in the cell wall with Ca and form gypsum crystals. Because of its toxicity, the toxic sulphite formed from SO_2 after dissolution in cell wall water must be reduced and sequestered in amino acids rapidly.

In addition, the mass balance shows that most of the sulphur in coniferous needles originates not from SO_2 but from the uptake of **sulphate** from the soil solution (Köstner et al. 1998): 97% of S in the xylem of *Picea* originates from root uptake (Table 11.5). This demonstrates that the **forest damage** (**forest decline**) observed in the 1980s was not caused by atmospheric SO_2 but was indirectly caused by sulphate input and acidification of soils (Schulze et al. 1989; Ulrich 1995).

11.3.3 Indicators of Sulphur Deficiency and Excess

- **S deficiency**: The symptoms are similar to those of N deficiency (chlorosis), with accumulation of non-S-containing amino acids (arginine, aspartate) and inhibition of protein synthesis.
- **S excess**: High SO_2 stress leads to the well-known pollution (smog) damage. Lichens are

Table 11.5 Transport of S in the xylem of trees and from the atmosphere in healthy and damaged spruce trees (Köstner et al. 1998)

	Healthy stand (mmol m^{-2} soil $year^{-1}$)[a]	Damaged stand (mmol m^{-2} soil $year^{-1}$)[a]
Sulphate	25.9	34.7
Glutathione	0.52	0.47
Cysteine	0.14	0.14
Methionine	0.3	0.3
Uptake of SO_2	7.4	7.6
Total S load for the canopy	34.26	43.21

[a] The numbers indicate annual averages

particularly sensitive. The damage is caused by the formation of sulphite and accumulation in the chloroplast. The threshold for SO_2 damage is 5 µg m^{-3} as an average concentration in the air.

11.4 Phosphate Nutrition

11.4.1 Phosphorus in Plant Metabolism

Phosphorus is the central element in the **energy metabolism** of all living organisms. In this process, storage and transfer of chemical energy by formation and degradation of polyphosphate esters with adenosine take place. In contrast to nitrogen and sulphur, phosphorus is not reduced but remains in the highest oxidation state and it is esterified in this form. It is taken up as $H_2PO_4^-$. In the cell, phosphorus is available in this oxidised form (P_i) and binds as PO_4^{3+} to carbohydrates, forming simple phosphate esters (C–O–P, e.g. in sugar phosphate) or forming energy-rich pyrophosphate (P–P bonds) or di-ester bridges between carbohydrate groups (C–P–C).

- **Structural functions**: P participates in the formation of DNA and RNA as a bridge between the ribose-N bases, and in the formation of phospholipids of membranes.
- **Metabolic functions**: Energy is stored and transferred by polyphosphate esters with adenosine. Di- and tri-esters are involved in the actual energy storage in the cell (adenosine monophosphate (AMP), adenosine diphosphate (ADP), adenosine triphosphate (ATP)) and energizing of binding sites for metabolic turnover. Sugar phosphates (e.g. fructose-1,6-diphosphate) play a decisive role as substrates and, as substrates in the regulation of sugar metabolism and triosephosphates, are an important transport metabolite between the chloroplast and cytosol (Stitt 1994).

11.4.2 Phosphate Uptake and Plant Requirements

In many habitats, phosphate is a limiting factor for plants because of its low solubility in alkaline soil conditions (Ca phosphates, apatite) and acidic soil conditions (Al phosphates, goethite). In the sea, phosphorus accumulates in organisms of higher trophic levels. Sea birds bring this phosphorus to land: bird excrement (guano) is the primary source for P fertiliser (for a discussion on the import of nutrients from the sea to islands, see Erskine et al. 1998). Phosphate does not dissolve easily in soils and leaching hardly occurs, in contrast to nitrate, which dissolves easily. Root hairs or mycorrhizal hyphae provide good contact with soil particles, and the phosphate is dissolved by secretion of protons, organic acids and phosphatases. Mycorrhizae play an important role in dissolving phosphate from minerals and in primary **phosphate uptake**. After the uptake of phosphoric acid, this is directly bound to organic molecules. Despite this, transport in the xylem is in the form of P_i (inorganic **orthophosphate**). P_i occurs in the cell as a substrate, as well as a product, in all activations and enzyme reactions with ATP and ADP, and simultaneously regulates many enzyme reactions where phosphorylation has a central role in signal transduction. Because of its important physiological role, the concentration of P_i in the cytosol is regulated in a very narrow range (4–6 mmol l^{-1}). The vacuole serves as a storage site. The relative concentration of P_i in the cytosol and chloroplasts regulates (together with the concentration of sucrose in the cytosol) the formation of starch in the chloroplast (Fig. 11.15).

Phosphate is stored in plants in the form of polyphosphates or as sugar esters; in **phytate**, up

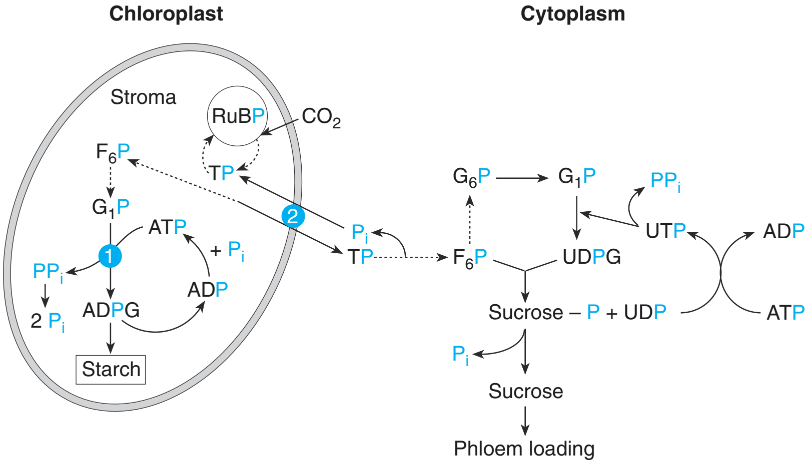

Fig. 11.15 Schematic model of the role of phosphate in the synthesis of starch and sucrose, and in regulating the metabolism of plants: adenosine diphosphate (ADP)–glucose pyrophosphorylase regulates starch synthesis: inhibition by inorganic orthophosphate (P_i) and stimulation by 3-phosphoglyceric acid (PGA) (1). Phosphate translocation regulates the export of photosynthetically produced substrates from the chloroplast: stimulation by P_i and triosephosphate (TP) (2). *F_6P* fructose-6-phosphate, *G_6P* glucose-6-phosphate. (Marschner 1988)

to six phosphate molecules may be deposited on one sugar (myoinositol). This form of storage is very important in seeds.

11.4.3 Indicators of Phosphorus Deficiency and Excess

- **P deficiency**: This causes interference in reproductive processes (delay in flowering), reduced longitudinal growth, dwarfing, smaller leaves because of reduced cell growth, increased root growth, dark green colouration of leaves and reddish colouring of needles, with chlorosis and premature ageing (Fig. 11.6).
- **P excess**: This does not occur naturally, because phosphate is not easily dissolved and may be regulated by polyphosphate formation.

11.5 Alkaline Cation Nutrition

The alkaline elements potassium, magnesium and calcium are essential macronutrients, which are not metabolised but are essential to provide the correct environment for particular reactions, to regulate pH and to regulate cellular water relations.

11.5.1 Magnesium

11.5.1.1 Function of Magnesium

Like other alkaline elements, **magnesium** is not metabolised.

- **Structural functions**: In the structure of chlorophyll (the central atom of four pyrrole rings) and in the ether connections of cellulose fibrils in cell wall pectins.
- **Metabolic functions**: In stabilizing enzymes, predominantly during the turnover of phosphates (nitrogenase, ATPase, phosphorylase and others). In these processes, Mg^{2+} binds to phosphate and, because of allosteric interactions, binding between the substrate and phosphate becomes possible. Mg^{2+} is involved in stabilizing energy-rich molecules—for example, phytate as phosphate storage. Mg^{2+} is a counter-ion for proton production during photosynthesis in the chloroplast (pH 7.6 in the dark and 8 with illumination). Mg^{2+} participates in the osmoregulation and pH regulation in the cell.

11.5.1.2 Uptake and Requirement for Magnesium

In the soil, magnesium is bound to the substrate predominantly as an exchangeable cation. Mg^{2+} is

Box 11.5: Interactions of Magnesium, Nitrogen and Aluminium During Forest Decline

Mg deficiency was found to be particularly prominent in combination with **forest dieback**—the so-called "mountain yellowing", diagnosed as magnesium deficiency (Zech and Popp 1983). Lange et al. (1989a, b) showed in a simple and impressive experiment that mountain yellowing was not caused by airborne pollutants (SO_2, ozone; Fig. 11.16). On spruce twigs with yellowed needles, buds were either left intact or removed so that no further growth could occur. On twigs on the opposite side of the same branch it was observed later that only the needles on twigs with buds yellowed. In contrast, needles on the twigs without buds were green. The experiment showed that magnesium availability from the xylem was sufficient to fulfil the requirement of a non-growing twig but was inadequate to supply growing twig. From this, the question arose as to what factors control growth. Oren and Schulze (1989) were able to show that there is an interaction with the N supply, with the unregulated uptake of nitrogen having a particular growth effect on the canopy. Uptake via the canopy not only leads to disequilibrium between the N supply and cation uptake but also has the effect of causing cation loss during the uptake of ammonium ions (Klemm 1989). The low supply of magnesium, which trees take up from the soil, is further reduced by an antagonism to ammonium, the main nitrogen form in sulphate-contaminated soils (Kaupenjohann et al. 1989). A high ammonium concentration in the soil solution leads to an exchange of ammonium against Al^{3+} on the clay particles, and to high Al concentrations in soil water, which may lead to root damage (Ulrich 1995).

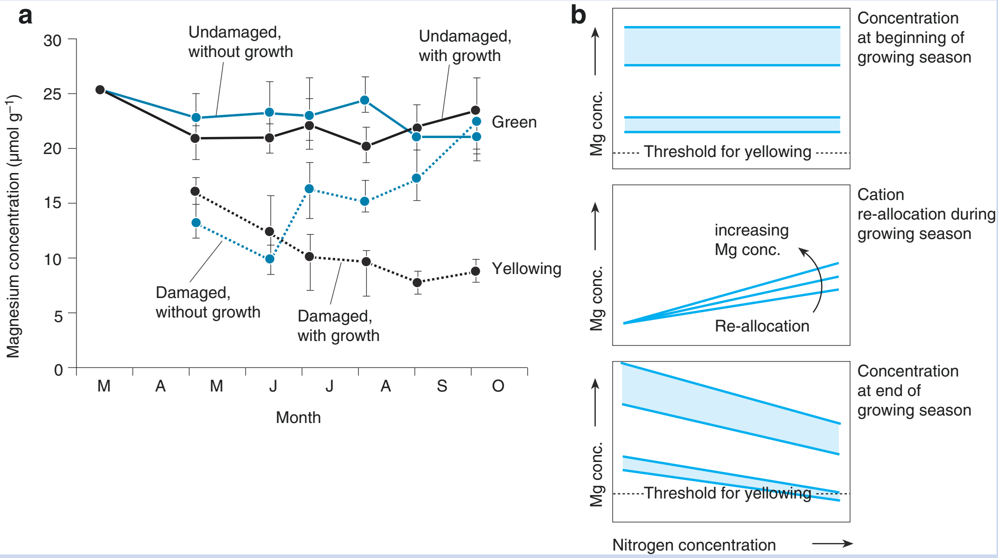

Fig. 11.16 Magnesium and N concentrations in healthy and damaged spruce. **a** Seasonal change (shown on the *x axis*) in the magnesium concentration of spruce twigs that, prior to treatment, had Mg deficiency symptoms, in comparison with healthy green twigs. In the damaged and undamaged twigs, either buds were removed and thus growth was halted, or buds were maintained unchanged. Damaged side shoots without buds showed an increase in the Mg concentration during the year and were green at the end of the growing season. This experiment was decisive in showing that yellowing of spruce grown in silicate soils was a direct consequence not of SO_2 but of the interaction between growth and Mg supply. Mg deficiency is also clearly visible on the spruce canopy on the title page of this chapter (Lange et al. 1989b). **b** Changes in magnesium concentration with N concentration in twigs of spruce before emergence (*top*); translocation of Mg from old to new needles (*centre*) and after emergence of young needles (*bottom*). The change is shown in twigs with high and low Mg supply. Only spruce grown in conditions of high N availability and low Mg supply cross the threshold that leads to yellowing. (Oren and Schulze 1989)

a component of primary and secondary minerals (serpentine), from which it is released by weathering. The most important antagonist for Mg^{2+} is Ca^{2+}, but also NH_4^+, K^+, Mn^{2+} and even H^+ influence the uptake of Mg^{2+}. In the plant, magnesium is transported in the xylem and phloem, and the ion is stored in chloroplasts. Remobilisation from ageing leaves occurs.

11.5.1.3 Magnesium Deficiency and Excess

- **Mg deficiency**: Yellowing of older leaves, yellow tips and early shedding of needles, chlorosis due to inadequate chlorophyll synthesis, starch accumulation because of the effect on phosphate metabolism, altered water relations due to poor osmoregulation, dwarf growth (Fig. 11.6).
- **Mg excess**: On Mg-rich substrates (serpentine) because of interactions with other nutrients, water stress may lead to increased concentrations of Mg.

11.5.2 Calcium

- **Structural function:** Stabilisation of the cell wall, together with Mg.
- **Metabolic functions:** Activator of membrane-bound enzymes (amylase) and ATPases, and osmoregulation (Ca oxalate). Ca^{2+} interacts with phytohormones (indole-3-acetic acid (IAA) and auxin) during elongation of cells (calmodulin) and with abscisic acid (ABA). Ca^{2+} is transported in the cytosol by linking to proteins. Ca^{2+} functions in the mitochondria, in contrast to Mg^{2+}, which regulates the proton gradient predominantly in chloroplasts.

11.5.2.1 Uptake and Requirement for Calcium

Ca occurs in the soil solution as Ca^{2+}. **Calcium-rich** soils are predominantly found on limestone (Box 11.6). The pH of these soils with almost unlimited $CaCO_3$ is stabilised by the dissolution of $CaCO_3$ at about pH 7. In Ca-poor soils, $CaCO_3$ is quickly consumed because it dissolves easily and is not stable against weathering, so the dissolved Ca^{2+} is bound to the ion exchangers in the soil only after the dissolution of the carbonate. The pH of Ca-poor soils is usually around 5 and may decrease on acidic rocks (shales containing pyrite) to 3.5. Below a pH of 5.5 the chemistry of the soil is increasingly determined by aluminium. Ca^{2+} uptake at the root is antagonistically influenced by other cations, particularly Al at low pH. If Al instead of Ca^{2+} is incorporated into the cell wall, elongation growth is inhibited.

Ca^{2+} uptake balances other anions, particularly nitrate and sulphate. It occurs predominantly at the root tip, where the endodermis is not yet formed. Transport into the xylem via the cell wall is possible. Ca^{2+} is transported in the xylem, but it is absent from the phloem. Because of the high pH in the phloem, Ca^{2+} would react with phosphate, forming insoluble apatite. But Ca^{2+} is transported in the phloem bound to a protein (e.g. calmodulin). Ca^{2+} is stored in cell walls and vacuoles together with malate, where Ca oxalate, Ca sulphate or Ca carbonate may be formed by precipitation. High Ca concentrations also occur in the endoplasmic reticulum.

Ca reaches the leaf in the xylem stream but may be transported out via the phloem only if bound to proteins, resulting in an excess and accumulation of Ca in the leaf over time. This becomes obvious from the Ca content of leaves, which rises with age and is particularly striking in conifers with needles of different ages (Oren et al. 1988).

The function of Ca as a stabiliser of the primary wall, by binding to pectin, becomes important in elongation growth, which essentially depends on the presence of Ca. However, Ca has further functions in growth, ranging from the formation of callose to the secretion of the calyptra and the regulation of geotropism. By forming bridges between phosphate and carboxyl groups of phospholipids, Ca maintains the membrane structure.

11.5.2.2 Calcium Deficiency and Excess

Ca deficiency and excess lead to the following responses:

- **Ca deficiency**: Disturbed growth by inhibition of cell division, desiccation of tips and

Box 11.6: Indicator Plants for Soil pH Conditions

The **reaction number** after Ellenberg (2009) is a qualitative indicator of soil pH:

- R1 + R2: Strong acidity indicators; they never occur on slightly acidic to alkaline soils (e.g. *Scleranthus annuus*, *Rumex acetosella*, *Spergula vernalis*)
- R3 + R4: Acidity indicators, mainly on acidic soils, but they also occupy soils of neutral pH (e.g. *Raphanus raphanistrum*, *Stachys arvense*, *Anthemis arvense*)
- R5 + R6: Moderate acidity indicators; they seldom occur on strongly acidic soils or on neutral to alkaline soils (e.g. *Sinapis arvensis*, *Veronica persica*, *Fumaria officinalis*)
- R7 + R8: Weak acidic to weak basic indicators; they never occur on strongly acid soils (e.g. *Aconitum napellus*, *Arctium lappa*, *Corydalis cava*)
- R9: Base and lime indicators; they only occur on alkaline soils (e.g. *Delphinium consolida*, *Adonis aestivalis*)
- For limestone- and silicate-indicating plants (Part 4, Chap. 18)

buds, death of root tips and chlorosis of needle tips. Ca deficiency is possible during ripening of fruits and in organs that grow fast but transpire little (bulbs, tubers, taproots, etc.), as Ca is not transported in the phloem. In fruits, Ca deficiency leads to increased susceptibility to fungal attack.

- **Ca excess**: Occurrence of Ca oxalate, Ca sulphate and Ca carbonate. Grasses generally require less Ca than dicotyledons. Low Ca requirements and adverse reactions to high Ca supply also occur in "calcifuge" plants, which are not able to maintain compartmentation of large amounts of Ca (Chap. 3).

11.5.3 Potassium

Potassium is the most required nutrient in plants (2–5% dry weight), after nitrogen, with the following metabolic functions (no direct involvement in chemical reactions): pH regulation, enzyme activation by changing the conformation of proteins (ATPase), influencing protein synthesis (translation, synthesis of ribulose-1,5-bisphosphate (RuBP) carboxylase), osmoregulation and elongation growth of cells, tropism and movement (stomata regulation), the main cation in phloem sap (Table 11.3).

These metabolic functions of potassium cannot be replaced by Na^+ (the most important cation in animals). However, the osmotic function of K^+ in the vacuole may be replaced by Na^+, Mg^{2+} and Ca^{2+}. The K concentration is high in the cytosol and low in the apoplast (except in movements and tropism: osmotically regulated movement—for example, of stomata). Transport through the membrane is via K channels.

Besides the general physiological importance of potassium in enzyme activation and protein synthesis, it is particularly important in the following processes:

- Regulation of photosynthesis (photophosphorylation) and drought resistance: K^+ determines the osmotic potential during drought and maintains growth with decreasing water potential (Fisher and Turner 1978). The effect of K^+ on osmoregulation also explains its importance in frost resistance
- Regulation of movements: Function of stomata (Chaps. 6 and 9). A corresponding mechanism affects other movements—for example, of the leaves of *Mimosa pudica* and *Dionaea muscipula* on touching, and the orientation of legumes to the sun
- Phloem transport: Potassium is the most important cation regulating the pH in the phloem and sucrose loading
- Regulation of fruit and tuber (potato) ripening

11.5.3.1 Uptake and Requirement for Potassium

Potassium occurs predominantly in silicate rocks and becomes reversibly bound to exchangers in the soil, particularly to clay minerals. Because of its ionic radius, potassium fits optimally into the intermediate layers of clay minerals and is therefore preferentially accumulated there (specific adsorption). In some soils, accumulation of K^+ in clay minerals that are able to swell results in contraction of these clays, which thus "fix" K^+ so strongly that it is no longer available for plants. The ionic radius and physical characteristics of K^+ are similar to those of ammonium, so these two ions are easily interchangeable. An excess of ammonium leads to a loss of K^+ (and other cations) and if these cations are leached, this stimulates acidification of soils. K^+ and ammonium are both used to determine the cation concentration of the exchanger.

11.5.3.2 Potassium Deficiency and Excess

With K deficiency and excess, the following symptoms occur:

- **K deficiency**: Reduced growth and increased remobilisation from ageing organs, disturbed water relations (drying of tips), wilting particularly at the edge of older leaves, yellowing and early shedding of needles (Fig. 11.6).
- **K excess**: With K excess (e.g. on granite containing muscovite), Ca and Mg uptake are competitively influenced, thus leading to increasing Mg deficiency at these sites.

11.5.3.3 Potassium Accumulation by Mistletoes

Mistletoes are heterotrophic phloem parasites (leaves without chlorophyll), as well as autotrophic xylem parasites (with green leaves). Xylem parasites have been known for their medicinal use since Hippocrates's time, and not just since Asterix and Getafix. Their alkaloids and lectins (carbohydrate-binding proteins) have major pharmaceutical relevance in the treatment of tumours (Lev et al. 2011). Mistletoes are of botanical interest (Calder and Bernhardt 1983) as they have a high potassium concentration in their leaves (40 mg g^{-1}). In hyperparasitic plants (mistletoe growing on mistletoe), additional accumulation of K and other cations may occur (157 mg g^{-1} Na in arid locations) (Ehleringer and Schulze 1985) because the mistletoe takes up the xylem water with the cations that accumulate in the shoot, as there is no connection and recirculation to the host's phloem. This accumulation of salt can lead to leaf damage and abscission. In mistletoes it is particularly significant that despite the high, almost toxic, ion concentrations, they maintain higher transpiration rates than their hosts (Ehleringer et al. 1985). Thus, mistletoes are not only significant sinks for cations but also water parasites (Glatzel and Geils 2009).

Under field conditions it is particularly interesting that even at high ion concentrations and even under arid conditions, mistletoes do not control transpiration despite high import of ABA entering with the xylem water. The controlling factor is their **nitrogen requirement**. Schulze et al. (1984) showed that N is the limiting factor for mistletoes and a high water requirement is needed to provide the N for substantial seed production. If mistletoe grows on a N_2-fixing plant, the transpiration rate is often not as high as that on a host plant that does not fix N_2 (Marshall et al. 1994). As trees predominantly transport amino acids in the xylem, their mistletoes gain additional carbon skeletons (i.e. they are not only cation, nitrogen and water parasites but also C parasites); 15% of the carbon for an "autotrophic" mistletoe originates from the host (Table 11.6) (Marshall et al. 1994). Photosynthesis is generally lower in the mistletoe than in the host plant.

An unusual botanical feature of Australian mistletoes (Fig. 11.17) is that their leaves mimic the shape and form of the host so closely that it is difficult to explain (Calder and Bernhardt 1983). Mistletoes have been identified as keystone species for their habitat (Watson 2009; Watson and Herring 2012). When mistletoes were removed from woodlands, species richness declined by over 20% within 3 years. Beside mistletoe fruits feeding birds directly, the nutrient-rich litter fall from the mistletoes, together with enhanced litter fall from the host trees, changes arthropod communities, extending and increasing their availability for insectivores.

Table 11.6 Characteristic nutrition of mistletoes and their hosts

	Mistletoe	Host	Source
K concentration (mg g^{-1})	28	11	(1)
P concentration (mg g^{-1})	2	1	(1)
N concentration (mg g^{-1})	28	25	(1)
	10	11	(2)
Transpiration (mmol m^{-2} s^{-1})	4	2	(2)
CO_2 assimilation (µmol m^{-2} s^{-1})	4	5	(2)

After Ehleringer and Schulze 1985 (1); Marshall et al. 1994 (2)

Fig. 11.17 Leaf mimicry of Australian mistletoe (see Calder and Bernhardt (1983)): *Acacia cambagei* with *Amyema maidenii*. (Photo: E.-D. Schulze)

Summary

- Plant nutrients are divided into (1) the macronutrients C, O, H, N, S, P, K, Mg and Ca; (2) the micronutrients Fe, Mn, Zn, Cu, B, Mo, Cl and Ni; and (3) the "beneficial" elements Na, Si, Co, I and V. The elements C, O, H, N and S are major constituents of organic matter. P esters are essential in energy transfer reactions. K, Na, Ca, Mg, Mn and Cl are involved in osmotic reactions, in enzyme reactions, in bridging reactions, and as balancing ions controlling membrane permeability. Fe, Cu, Zn and Mo occur as chelates in prosthetic groups of enzymes and enable electron transport by valency change.
- The availability of nutrients is variable and dependent on the type of the original rocks, which determines the texture and the chemical composition of soils; climate, which controls weathering; vegetation, which selectively removes or returns certain elements; and management of the nutrient supply.
- Nutrient uptake by plants occurs mainly via the roots but may also occur via shoots (leaves and bark), which is important in the presence of air pollutants.
- Depending on the availability of nutrients or biotic pests, specific deficiency diseases may occur, which are recognisable by specific symptoms in the leaves.
- Nitrogen is second to carbon in importance for plant life. N uptake occurs from the soil or from the air as ammonium, as nitrate, as amino acids, or as gaseous NH_3 or NO_x. A number of plant species can, together with symbiotic microorganisms, form nodules in which microorganisms assimilate N_2 from the air into ammonia. Ammonia and ammonium ions are toxic to cells and are rapidly assimilated into amino acids. Ammonium uptake leads to acidification of the soil, C imbalance and cation deficiency. The uptake of nitrate is coupled with cation uptake, which leads to increasing pH (alkalisation) in the soil. Excess nitrate leads to soil acidification due to leaching of nitrate and associated cations. Indicator plants allow an assessment of the average N availability in ecosystems. Nitrogen deficiency leads to selection of plants that capture mainly insects and use them as N sources. Nitrogen deficiency can be beneficial at low cation availability.
- Sulphur is required in plants in the oxidised form (sulphate ester), as well as in the reduced form (—SH groups of amino acids). Sulphate

reduction occurs in chloroplasts. Uptake occurs predominantly in the form of sulphate via the roots. Crucifers have particularly high S requirements.

- Phosphate serves as the carrier of chemical energy in the plant. Phosphate is not reduced in plants but is used in polyphosphate esters.
- Basic cations are not metabolised but are important in enzymatic reactions and in reaction centres of enzymes (Mg in chlorophyll). The requirement for K is higher than that for Ca and Mg. K regulates osmotic concentrations and the pH of the cell. Mg is involved in chlorophyll functions and in the transfer of phosphate from adenosine triphosphate to organic molecules. Ca acts as an osmotic dehydrating ion and as a signal in cell metabolism (calmodulin).

References

Berthrong ST, Finzi AC (2006) Amino acid cycling in three cold-temperate forests of the northeastern USA. Soil Biol Biochem 38:861–869

Blume HP, Brümmer GW, Horn R, Kandeler E, Kögel-Knabner I, Kretzschmar R, Stahr K, Wilke BM (2010) Scheffer/Schachtschabel: Lehrbuch der Bodenkunde, 16. Auflage edn. Springer Spektrum, Berlin

Brychkova G, Yarmolinsky D, Fluhr R, Sagi M (2012) The determination of sulfite levels and its oxidation in plant leaves. Plant Sci 190:123–130

Burkhardt J, Basi S, Pariyr S, Hunsche M (2012) Stomatal penetration by aqueous solutions—an update involving leaf surface particles. New Phytol 196:7774–7787

Calder M, Bernhardt P (1983) The biology of mistletoes. Academic Press, Sydney

Chapin FS III, Kedrovski RA (1983) Seasonal changes in nitrogen and phosphorous fractions and autumn retranslocation in evergreen and deciduous taiga trees. Ecology 64:376–391

Chapin FS, Matson PA, Mooney HA (2002) Principles of terrestrial ecosystem ecology. Springer, New York

Ehleringer JR, Schulze E-D (1985) Mineral concentrations in an autoparasitic *Phoradendron californicum* growing on a parasitic *P. californicum* and its host, *Cercidium floridum*. Am J Bot 72:568–571

Ehleringer JR, Schulze E-D, Ziegler H, Lange OL, Farquhar GD, Cowan IR (1985) Xylem tapping mistletoes: primarily water or nutrient parasites? Science 227:1479–1481

Ellenberg H (1974) Zeigerwerte der Gefässpflanzen Mitteleuropas. Scripta Geobotanica 9:97

Ellenberg H (2009) Vegetation ecology of Central Europe, 4th edn. Cambridge University Press, Cambridge

Ellis AG, Midgley JJ (1996) A new plant–animal mutualism involving a plant with sticky leaves and a resident hemipteran insect. Oecologia 106:478–481

Erskine PD, Bergstrom DM, Schmidt S, Stewart GR, Tweedie CE, Shaw JD (1998) Subarctic Macquarie Island—a model ecosystem for studying animal-derived nitrogen sources using ^{15}N natural abundance. Oecologia 117:187–193

Fichtner K, Schulze E-D (1992) The effect of nitrogen nutrition on growth and biomass partitioning of annuals originating from habitats of different nitrogen availability. Oecologia 92:236–241

Fisher RA, Turner NC (1978) Plant productivity in arid and semiarid zones. Annu Rev Plant Physiol 29:277–317

Glatzel G, Geils B (2009) Mistletoe ecophysiology: host–parasite interactions. Ann Bot 87:10–15

Guarente L, Kenyon C (2000) Genetic pathways that regulate ageing in model organisms. Nature 408:255–262

Hammond J, White PJ (2008) Sucrose transport in the phloem: integrating root responses to phosphorus starvation. J Exp Bot 59:93–109

Harrison AF, Schulze E-D, Gebauer G, Bruckner B (2000) Canopy uptake and utilization of atmospheric pollutant nitrogen. Ecol Studies 142:171–188

Hartmann G, Nienhaus F, Butin H (1988) Farbatlas Waldschaden; Diagnose von Baumkrankheiten. Eugen Ulmer Verlag, Stuttgart

Herdel K, Schmidt P, Feil R, Mohr A, Schurr U (2001) Dynamics of concentrations and nutrient fluxes in the xylem of *Rhizinus communis*—diurnal course, impact of nutrient availability and nutrient uptake. Plant Cell Environ 24:41–45

Hobbie EA, Macko SA, Williams M (2000) Correlation between foliar δ^{15}N and nitrogen concentrations may indicate plant–mycorrhizal interactions. Oecologia 122:273–283

Jones DL, Hodge A, Kuzyakov Y (2004) Plant and mycorrhizal regulation of rhizodeposition. Transley review. New Phytol 163:459–480

Kähkölä A-K, Nygren P, Leblanc HA, Pennanen T, Pietikäinen J (2012) Leaf and root litter of a legume tree as nitrogen sources for cacaos with different root colonisation by arbuscular mycorrhizae. Nutr Cycl Agroecosyst 92:51–65

Kaupenjohann M, Zech W, Hantschel B, Horn R (1989) Mineral nutrition of forest trees: a regional survey. Ecol Stud 77:282–296

Klein D, Morcuende R, Stitt M, Krapp A (2000) Regulation of nitrite reductase expression in leaves by nitrate and nitrogen metabolism is completely overridden when sugars fall below a critical level. Plant Cell Environ 23:863–872

Klemm O (1989) Leaching and uptake of ions through aboveground Norway spruce tree parts. Ecol Stud 77:210–237

Koch LW, Schulze E-D, Percival F, Mooney HA, Chu C (1988) The nitrogen balance of *Paphanus sativus* × *raphanistrum* plants. Growth, nitrogen redistribution and photosynthesis under NO_3-deprivation. Plant Cell Environ 11:755–767

Köstner B, Schupp R, Schulze E-D, Rennenberg H (1998) Organic and inorganic sulfur transport in the xylem sap and the sulfur budget of *Picea abies* trees. Tree Physiol 18:1–9

Lange OL, Heber U, Schulze E-D, Ziegler H (1989a) Atmospheric pollutants and plant metabolism. Ecol Stud 77:238–269

Lange OL, Weikert RM, Wedler M, Gebel J, Heber U (1989b) Photosynthese und Nährstoffversorgung von Fichten aus einem Waldschadensgebiet auf basenarmem Untergrund. Allg Forstzeitschrift 3:54

Lejay L, Gansel X, Cerezo M, Tillard P, Müller C, Krapp A, von Wirén N, Daniel-Vedelde F, Gojon A (2003) Regulation of root ion transporters by photosynthesis: functional importance and relation with hexokinase. Plant Cell 15:2218–2232

Lev E, Ephraim M, Ben-Arye E (2011) European and oriental mistletoe: from mythology to contemporary integrative cancer care. Eur J Integr Med 3:e133–e137

Marschner H (1988) Mineral nutrition of higher plants. Academic Press, San Diego

Marschner H (1995) Mineral nutrition of higher plants, 2nd edn. Academic Press, London

Marschner P (ed) (2012) Marschner's mineral nutrition of higher plants, 3rd edn. Academic Press. Elsevier, Amsterdam

Marshall JD, Ehleringer JR, Schulze E-D, Farquhar GD (1994) Carbon isotope composition, gas exchange and heterotrophy in Australian mistletoes. Funct Ecol 8:465–487

Michelsen AM, Schmidt IK, Jonasson S, Quarmby C, Sleep D (1996) Leaf ^{15}N abundance of subarctic plants provides field evidence that ericoid, ectomycorrhizal and non- and arbuscular mycorrhizal species access different sources of nitrogen. Oecologia 105:53–56

Moroney JV, Bartlett SG, Samuelsson G (2001) Carbonic anhydrase in plants and algae. Plant Cell Environ 24:141–154

Nadelhoffer KJ, Emmett BA, Gunderson P, Kjönaas OJ, Koopmans CJ, Schleppi P, Tietema A, Wright RF (1999) Nitrogen deposition makes minor contribution to carbon sequestration in temperate forests. Nature 398:145–147

Näsholm T, Ekblad A, Nordin A, Giesler R, Högberg M, Högberg P (1998) Boreal forest plants take up organic nitrogen. Nature 392:914–991

Näsholm T, Kielland K, Ganeteg U (2009) Uptake of organic nitrogen by plants. Transley review. New Phytol 182:31–48

Nordin A, Högberg P, Näsholm T (2001) Soil N from and plant N uptake along a boreal forest productivity gradient. Oecologia 129:125–132

Oren R, Schulze E-D (1989) Nutritional disharmony and forest decline: a conceptual model. Ecol Stud 77:425–443

Oren R, Werk KS, Schulze ED, Meyer J, Schneider BU, Schraml P (1988) Performance of two *Picea abies* (L.) Karst. stands at different stages of decline. VI. Nutrient concentrations. Oecologia 77:25–37

Orians GH, Solbrig OT (1977) A cost-income model of leaves and roofs with special reference to arid and semiarid areas. Am Nat 111:677–690

Osman KT (ed) (2013) Soils. Principles, properties and management. Springer, Dordrecht

Persson T, Rudebeck A, Jussy JH, Colin-Belgrand M, Priemé A, Dambrine E, Karlsson PS, Sjöberg RM (2000) Soil nitrogen turnover—mineralisation, nitrification and denitrification in European forest soils. Ecol Stud 142:297–331

Persson J, Gardeström P, Näsholm T (2006) Uptake, metabolism and distribution of organic and inorganic nitrogen sources by *Pinus sylvestris*. J Exp Bot 57:2651–2659

Read DJ (1993) Plant–microbe mutualism and community structure. Ecol Stud 99:181–210

Scheible WR, Gonzáles-Fontes A, Lauerer M, Müller-Röber B, Caboche M, Stitt M (1997a) Nitrate acts as a signal to induce organic acid metabolism and repress starch metabolism in tobacco. Plant Cell Environ 9:783–798

Scheible WR, Lauerer M, Schulze E-D, Caboche M, Stitt M (1997b) Accumulation of nitrate in the shoot acts as signal to regulate shoot–root allocation in tobacco. Plant J 11:671–691

Schopfer P, Brennicke A (1999) Pflanzenphysiologie. Springer, Berlin

Schulze W (1991) Versuche mit insektenfangenden Pflanzen. Biol Unserer Zeit 21:307–312

Schulze E-D, Turner NC, Glatzel G (1984) Carbon, water, and nutrient relations of two mistletoes and their hosts: a hypothesis. Plant Cell Environ 7:293–299

Schulze E-D, Lange OL, Oren R (1989) Forest decline and air pollution: a study of spruce on acid soils, Ecological studies, vol 77. Springer, Berlin

Schulze E-D, Gebauer G, Schulze W, Pate JS (1991) The utilization of nitrogen from insect capture by different growth forms of *Drosera* from southwest Australia. Oecologia 87:240–246

Schulze E-D, Kelliher FM, Körner C, Lloyd J, Leuning R (1994) Relationships among maximum stomatal conductance, ecosystem surface conductance, carbon assimilation and plant nitrogen nutrition: a global ecology scaling exercise. Annu Rev Ecol Syst 25:629–660

Schulze W, Schulze E-D, Pate JS, Gillison AN (1997) The nitrogen supply from soils and insects during growth of pitcher plants *Nepenthes mirabilis, Cephalotus follicularis* and *Darlingtonia californica*. Oecologia 112:464–471

Schulze W, Frommer WB, Ward JM (1999) Transporters for ammonium, amino acids and peptides are expressed in pitchers of the carnivorous plant *Nepenthes*. Plant J 17:637–646

Schulze W, Schulze E-D, Schulze I, Oren R (2001) Quantification of insect nitrogen utilization by the Venus fly trap *Dionaea* muscipula catching prey with highly variable isotope signatures. Exp Bot 52:1041–1049

Schulze ED, Nicolle D, Boerner A, Lauerer M, Aas G, Schulze I (2014) Stable carbon and isotope ratios of

Eucalyptus and *Acacia* species along a seasonl rainfall gradient in Western Australia. Trees 28:1125

Schurr U, Schulze E-D (1995) The concentrations of xylem sap constituents in root exudate, and in sap from intact, transpiring castor bean plants (*Ricinus communis*). Plant Cell Environ 18:409–420

Smith SE, Read DJ (1997) Mycorrhizal symbiosis. Academic Press, San Diego

Stitt M (1994) Flux control at the level of the pathway: studies with mutants and transgenic plants having decreased activity of enzymes involved in photosynthetic partitioning. In: Schulze E-D (ed) Flux control in biological systems. Academic Press, San Diego pp 13–36

Stitt M, Schulze E-D (1994) Plant growth, storage, and resource allocation: from flux control in a metabolic chain to the whole plant level. In: Schulze E-D (ed) Flux control in biological systems. Academic Press, San Diego pp 57–118

Thitithanakul S, Pételol G, Chalot M, Beaujard F (2012) Supplying nitrate before bud break induces pronounced changes in nitrogen nutrition and growth of young poplars. Funct Plant Biol 39:795–803

Thomas H, Thomas HM, Ougham H (2000) Annuality, perenniality and cell death. J Exp Bot 51:1781–1788

Ulrich B (1995) The history and possible causes of forest decline in central Europe, with particular attention to the German situation. Environ Rev 3:262–276

Wallenda T, Stober C, Högbom L, Schinkel H, George E, Högberg P, Read DJ (2000) Nitrogen up-take processes in roots and mycorrhizas. Ecol Stud 142:122–143

Watson DM (2009) Parasitic plants as facilitators: more dryad than Dracula? J Ecol 97:1151–1159

Watson DM, Herring M (2012) Mistletoe as a keystone resource: an experimental test. Proc R Soc B 279:3853–3860

White PJ (2012) Ion uptake mechanisms of individual cells and roots: short distance transport. In: Marschner P (ed) Marschner's mineral nutrion of higher plants. Academic Press, Amsterdam pp 7–47

Zech W, Popp E (1983) Magnesiummangel – einer der Gründe für das Fichten- und Tannensterben in NO-Bayern. Forstwissenschaftliches Centralblatt 102:50–55

Carbon Relations

12

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Nothofagus fusca in a temperate deciduous forest in New Zealand: The beech forests of New Zealand occur mainly on the South Island. They form approximately 36 m high stands of "red beech" (*N. fusca*) or of "silver beech" (*Nothofagus menziesii*). The stands grow at about 2000 mm rainfall and a yearly average temperature of about 9 °C. The stands are often very dense, with >1000 trunks per hectare and a basal area of >70 m^2 ha^{-1}, attaining a biomass of >600 m^3 ha^{-1}. The leaf area index reaches 7. There are about 20 very large trees per hectare, which are 300–400 years old, with a diameter at breast height of >5 m. Flux measurements of the carbon budget have shown for the first time that in an undisturbed primeval forest there is no steady-state. The forests are carbon sinks—that is, they accumulate (and have accumulated) carbon over thousands of years in the humus layer (Hollinger et al. 1994). (Photo: E.-D. Schulze)

E.-D. Schulze et al., *Plant Ecology*, https://doi.org/10.1007/978-3-662-56233-8_12

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Photosynthesis is not only the basis for growth of individual plants but also the most important process providing chemical energy and oxygen to ecosystems. From an ecological point of view, CO_2 fixation is only a part of the carbon balance, which consists of photosynthesis and respiration. Furthermore, the allocation of carbon to various structural components is decisive for understanding the growth and structure of plants. It is essential to consider the way by which plants, through their structure and phenology, regulate their carbon balance and thus keep their position in a plant community during competition with other species in a variable climate. Therefore, the carbon relations involve a broad spectrum of processes ranging from the biochemical assimilation of CO_2, via the responses to climate, to allocation and growth as the basis for competition in plant stands.

This chapter considers the carbon relations of individual plants and of different functional types. The carbon cycle of ecosystems is the focus of Chap. 16. Plant functional types are further explained in Chap. 20. The effects of climate change on the global carbon balance are discussed in Part V of the book.

12.1 Photosynthetic CO_2 Uptake: Physiological and Physical Basis

12.1.1 Photosynthesis as a Diffusion Process

Net photosynthesis, also called **CO_2 assimilation** (A), is the difference between biochemical **CO_2 fixation** (P) and **respiration** (R_L) of the leaf:

$$A = P - R_L \tag{12.1}$$

Respiration consists of a number of partial processes:

- **Mitochondrial respiration** of heterotrophic cells (R_{het}), which do not have chloroplasts but are indispensable for the functioning of the leaf (conducting tissues, epidermis).
- Respiration in mitochondria of photosynthetically active cells (R_{mit}), which depends on adenosine triphosphate (ATP) status in the cytosol.
- Light-induced respiration (**photorespiration** (**R_{phot}**)).

$$R_L = R_{het} + R_{mit} + R_{phot} \tag{12.2}$$

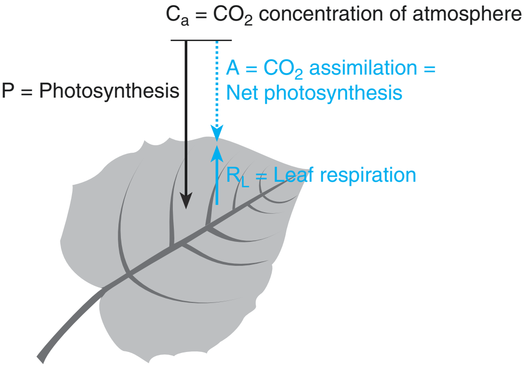


Fig. 12.1 CO_2 fluxes of a leaf. The net flux of CO_2 into a leaf A corresponds to the rate of photosynthesis (i.e., CO_2 fixation) minus the respiration R_L occurring at the same time

The sum of R_{het} and R_{mit} is also called **dark respiration** although it takes place during day and night (**R_{dark}**; Sect. 12.2). It is difficult to quantify these partial processes experimentally. Thus, net photosynthesis is used in ecology as an integrative variable to assess the plant carbon budget (Fig. 12.1). It is usually measured as the net CO_2 exchange of leaves. One could also measure the exchange of O_2. However, this would be technically demanding because of the high background concentration of O_2 in the atmosphere (Chap. 23).

CO_2 exchange is a **CO_2 diffusion process**. CO_2 in the atmosphere diffuses into the leaf through the stomatal pore, since the biochemical process of CO_2 fixation creates a carbon sink. Thus, the CO_2 concentration is lower in the intercellular spaces of the leaf than in the atmospheric (ambient) air.

The net influx rate of CO_2 (A) known as **net photosynthesis** rate per leaf area, is proportional to the gradient of CO_2 across the epidermis ($C_a - C_i$) and to **stomatal conductance** (**g_s**).

$$A = \left(C_a - C_i\right) \cdot g_s \tag{12.3}$$

where C_a is the CO_2 concentration in the atmosphere, C_i is the CO_2 concentration in the intercellular air space and g_s is the same conductance that regulates the water vapour flux (Chap. 10), corrected for the difference in the molecular weight of H_2O and CO_2 ($g_{H_2O} / g_{CO_2} = 1.605$) (Jarvis 1971). Equation 12.3 allows a non-destructive measurement of the net CO_2 flux of leaves. In Eq. 12.3 we use **stomatal conductance** (**g_s**) rather than leaf conductance (g_L; Chap. 10), because the stomata are the location of CO_2 exchange.

Also, the movement of CO_2 between the intercellular air space and the chloroplast can be described as analogous to a diffusion process even though it contains biochemical reactions (Eq. 12.1). Transport of CO_2 in the cell wall may partially also be in a dissolved form as HCO_3^-. Balancing all fluxes, a CO_2 concentration exists, where CO_2 fixation and respiration rates equilibrate, i.e., net photosynthesis becomes zero. This is the CO_2 **compensation point** (**Γ**). Making use of Γ, the following analogue equation applies:

$$A = \left(C_i - \Gamma\right) \cdot g_m \tag{12.4}$$

where A is the same CO_2 flux as in Eq. 12.3 and g_m is the conductance for CO_2 of the mesophyll and represents all leaf-internal transport processes (Sesták et al. 1971). If the CO_2 concentration in the atmosphere is decreased experimentally below the compensation point, increased or decreased respiration may be observed, depending on the experimental conditions.

The response of CO_2 assimilation to the CO_2 concentration in the atmosphere describes the physiological state of photosynthesis in the leaf. The response curve (Fig. 12.2) is characterised by three important ranges:

- A linear range above the CO_2 compensation point: In this range, CO_2 assimilation is limited by ribulose-1,5-bisphosphate carboxylase/oxygenase activity (**RubisCO activity**), which needs CO_2 as a substrate and for activation (Farquhar and von Caemmerer 1982; Lange et al. 1987). The slope ($\Delta A/\Delta c$) describes the **efficiency** of ribulose 1,5-bisphosphate (RuBP) carboxylase.
- A saturation range at high CO_2 concentration: With increasing supply of CO_2, RuBP carboxylase is fully activated, but CO_2 assimilation is limited by the **supply of the substrate RuBP**, to which the carbon of CO_2 is bound in the Calvin cycle. In this range, the turnover rate of RuBP carboxylase is saturated. It cannot use the supplied CO_2, because of the limited capacity of the Calvin cycle. Under natural conditions this will only rarely occur, because of the low concentration of CO_2 in the air, but it may be important for leaves growing close to the soil surface.
- The range below the compensation point: In CO_2-free air containing 20% O_2 the **oxygen-**

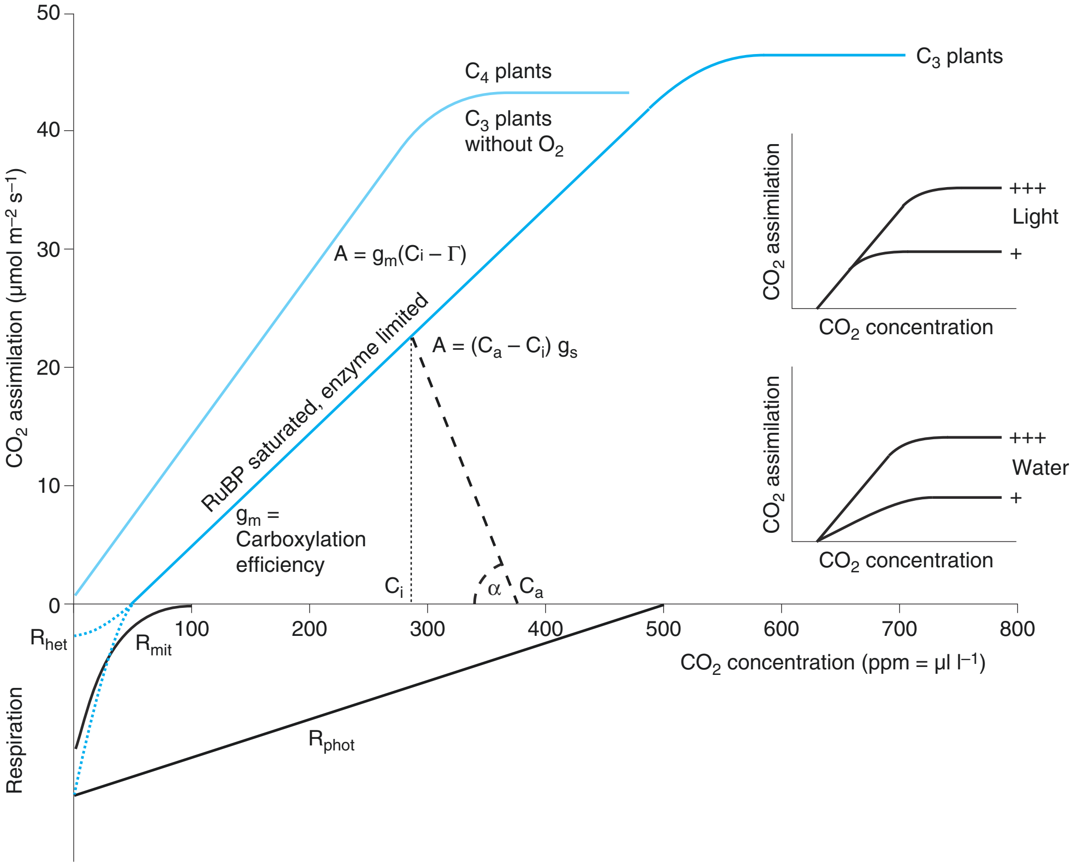


Fig. 12.2 Dependence of CO_2 gas exchange on the CO_2 concentration in the air. The *y axis* shows positive values for CO_2 assimilation and (increasing) respiration on the y axis pointing downward. The linear part of the curve shows enzyme limitation; the flat part shows saturation because of substrate limitation. The CO_2 compensation point is at about 50 ppm CO_2. The *insets* show that a change in light affects only the saturated region, whereas drought operates via enzyme limitation

ase function of RuBP carboxylase/oxygenase is fully active — that is, light-induced respiration (R_{phot}) reaches its highest value. At the same time, depending on ATP consumption in the cytosol, mitochondrial dark respiration (R_{mit}) is high. R_{mit} decreases with increasing rates of photosynthesis (Loreto et al. 2001). Also, light-induced respiration (R_{phot}) decreases depending on the CO_2 to O_2 ratio and is very low at CO_2 saturation.

The decrease in CO_2 concentrations along the diffusion path from ambient air (C_a) to the intercellular spaces of the leaf and into the mesophyll cells (C_i; Fig. 12.2) is driven by the efficiency of carboxylase (a function of demand) and the stomatal conductance (a function of supply; Raschke 1979). The concentration of CO_2 in the mesophyll (C_i; assuming CO_2 concentrations at carboxylation sites to be equal to C_i) is lower than in the ambient air (C_a), and lies between Γ and C_a. On average, $C_i/C_a = 0.7–0.8$.

$$A = (C_a - C_i)\,g_s = (C_i - \Gamma)\,g_m \qquad (12.5)$$

Therefore:

$$\frac{(C_\mathrm{a} - C_\mathrm{i})}{(C_\mathrm{i} - \Gamma)} = \frac{g_\mathrm{m}}{g_\mathrm{s}} \tag{12.6}$$

Stomatal conductance (g_s) can also be deducted graphically from the A-C_i curve described above, combining Eq. 12.3 and trigonometry:

$$\tan\alpha = \frac{\Delta y}{\Delta x} = \frac{\Delta A}{\Delta C} = \frac{A}{C_a - C_i} = g_s \tag{12.7}$$

since tan α represents the slope of a hypotenuse (dashed line in Fig. 12.2) in a right-angled triangle, calculated as the opposite (here: ΔA or simply A) over the adjacent (here: $\Delta c = C_\mathrm{a} - C_\mathrm{i}$)). The slope of this line thus represents stomatal conductance (g_s). Stomatal closure means a reduced conductance g_s (decrease in the **CO_2 supply function**), leading to a decrease in C_i at constant photosynthetic capacity (**CO_2 demand function**). Removing the epidermis experimentally would bypass the influence of stomata, and enable CO_2 assimilation to be measured at C_a and thus determine the RuBP-carboxylase activity. In this case, the measured rate (A_{Ca}) could reach the RubisCO limitation (Farquhar and von Caemmerer 1982).

A decrease in light intensity (Fig. 12.2, inset) results in a decrease of the saturated rate of photosynthesis at a constant CO_2 concentration, despite constant carboxylase activity. This need not necessarily affect C_i, since with decreasing light intensity the stomata also respond; they open and allow more atmospheric CO_2 to diffuse in, increasing C_i at constant carboxylase activity. Drought (Fig. 12.2, inset) or N deficiency reduce the efficiency of carboxylase — that is, at constant stomatal conductance, C_i increases because of lower synthesis of RubisCO. CO_2 assimilation increases more slowly and reaches saturation earlier than in plants with a sufficient water supply or N nutrition.

12.1.2 Evolution of C_3, C_4 and Crassulacean Acid Metabolism Plant Species

C_3 photosynthesis is the original pathway for carbon fixation. It remains the ultimate step for synthesizing carbohydrates, which store the energy originally coming from radiation. Succulence, crassulacean acid metabolism (CAM) and C_4 pathways appear to have evolved polyphyletically, independently of the taxonomy in the plant kingdom. This, however, does not imply that the evolution of these processes emerged synchronously.

During **evolution**, C_4 and CAM species emerged that were specifically adapted to low CO_2 concentrations in arid and saline environments exhibiting considerable changes in the process of CO_2 fixation, but not in the reactions of photosystems I and II (PS I and PS II) (Chap. 3). The variety of expressions of the C_3, C_4 and CAM pathways indicate a polyphyletic evolution (i.e. it emerged many times during evolution), even within the group of grasses that contain the largest number of C_4 species (Fig. 12.3) (Evans 1971; Clayton 1981; Gowik et al. 2011) (Chap. 6, Sect. 6.6).

12.1.2.1 C_3 Species

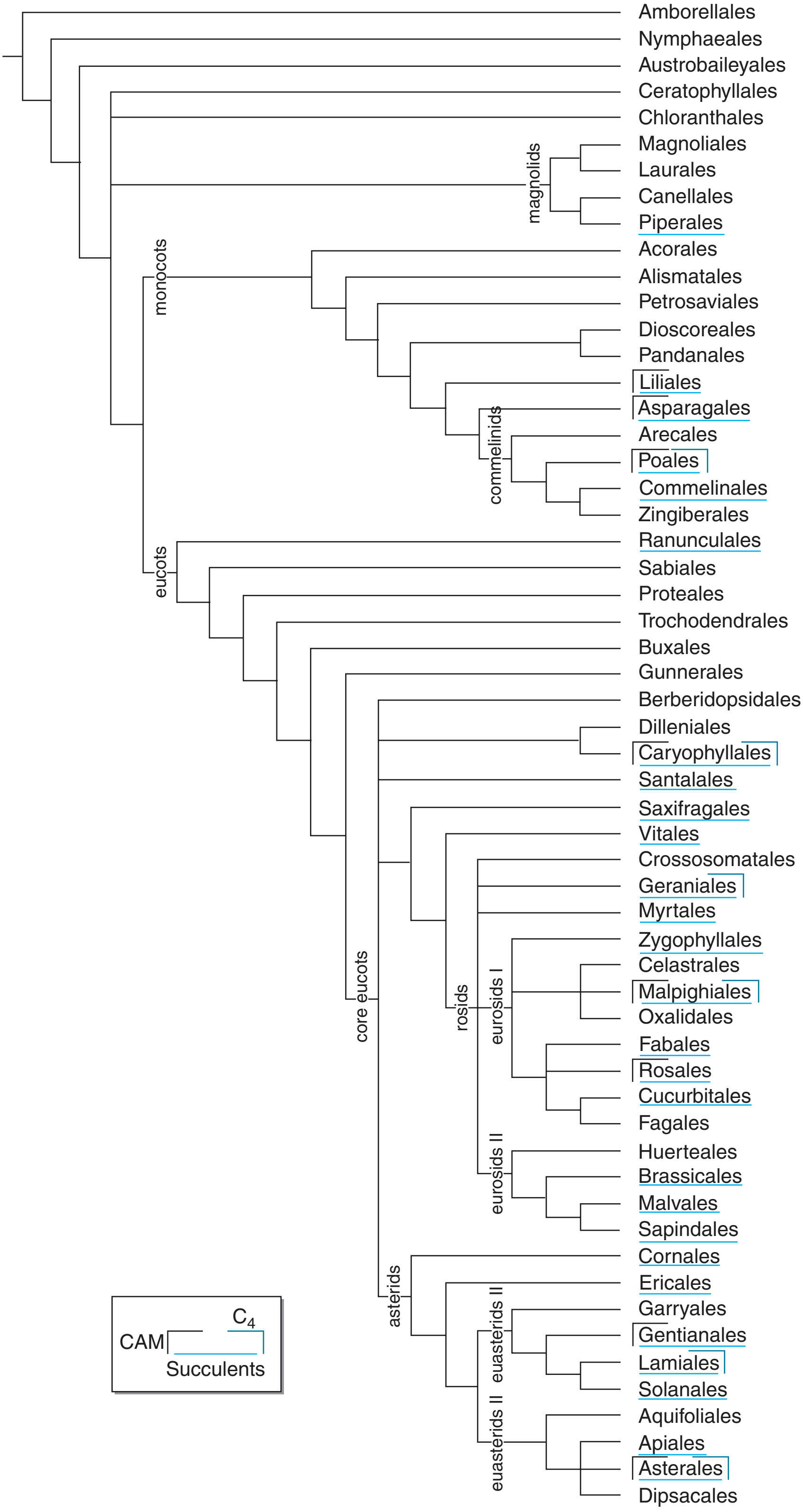
The metabolism of C_3 photosynthesis, as explained in Chap. 3, favours RubisCO for the CO_2 reduction and the formation of triose-phosphate over the O_2 reaction, in which O_2 forms phosphoglycolate with RuBP. The oxygenase reaction is enhanced by high temperatures (Chap. 6). Evolutionary the C_3 pathway evolved in an aquatic environment with low O_2.

C_3 photosynthesis is found in all plant species. About 95% of plant species operate along the A/C_i response curve described in Fig. 12.2. These **C_3 plants** include trees, shrubs, herbaceous dicots and grasses of all climatic regions, mainly at average daytime temperatures of 20–30 °C during the growing season. C_3 plants produce more than 75% of the terrestrial net primary production (Still and Berry 2003). The short-term oscillations of the **Mauna Loa** atmospheric CO_2 concentration measurements show the effects of plant activity in a seasonal cycle on average global atmospheric CO_2 concentrations.

12.1.2.2 C_4 Species

At low atmospheric CO_2 concentrations, the O_2 reaction gains dominance over the carboxylase reaction in C_3 plants. This became important during extreme geological events — for example, in

Fig. 12.3 Evolution of succulence in plants. Succulence is found in 14 orders of the plant kingdom. While the crassulacean acid metabolism (CAM) pathway is always associated with succulence but is found only in eight orders, C$_4$ metabolism, which can be expressed independently of succulence, is found in five plant orders, all of which also express succulence or CAM. (Evans et al. 2014; Lüttge 2004)



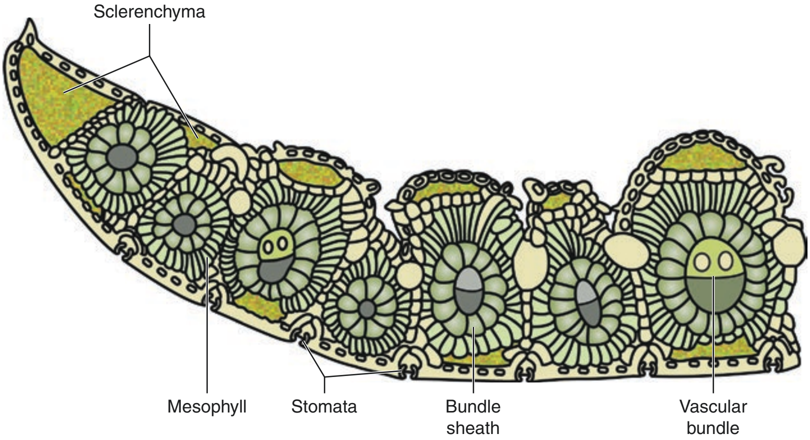


Fig. 12.4 Anatomical cross-section of *Sporobulus spicatus*. The cross-section was prepared by Volkens (1887), who was the first to recognise the specific anatomy of C_4 grasses in his flora of the deserts of Egypt. He coined the term "Kranz" anatomy

the Pleistocene, when atmospheric CO_2 concentrations dropped to below 250 parts per million (ppm) (Pagani et al. 2005; Edwards et al. 2010). Under those conditions, C_3 plants would have had a reduced ratio of carboxylase to oxygenase, with reduced growth and fitness. Thus, plants evolved with morphological and biochemical adaptations (Sage et al. 2012), including the large group of C_4 grasses. Since C_4 evolved polyphyletically, the **evolution of C_4** in grasses may have involved different steps. The earliest evolution dates back even to the Cretaceous and the Eocene in grasses (Jacobs et al. 1999), when atmospheric CO_2 was high (Edwards et al. 2010). **C_4 plants** became abundant in the early Oligocene (30–32 million years ago), when atmospheric CO_2 concentrations decreased with the onset of the Pleistocene (Pagani et al. 2005). Savanna-type vegetation and C_4-dominated grasslands expanded about 6–8 million years ago (Jacobs et al. 1999; Beerling and Osborne 2006).

In the Pleistocene atmosphere, which was a novel situation since the origin of angiosperms in the Cretaceous (about 100 million years ago; Chap. 17), plants evolved a mechanism to cope with low atmospheric CO_2 to O_2 ratios by fixing CO_2 as hydrogen carbonate via phosphoenolpyruvate (PEP) carboxylase. PEPC, fixing HCO_3^-, does not react with oxygen and, in addition, has a higher affinity for this ion than RubisCO has for CO_2 (Chap. 6). Binding HCO_3^- and PEP, it produces oxaloacetate, which can further react in different ways — for example, reduction to malate (malate dehydrogenase). These C_4 organic acids are formed in the mesophyll and then transported into specialised cells surrounding the vascular bundle, called **bundle sheath cells** (Fig. 12.4). In these cells, the organic acids are decarboxylated by malic enzyme and CO_2 is released. Since there are more mesophyll cells than bundle sheath cells (ratio 3:1) and the activity of the respective enzymes is higher than that of RubisCO, the decarboxylation results in a local increase in the internal tissue CO_2 concentration (up to about 1000 ppm). Thus, carbon fixation as hydrogen carbonate (i.e. HCO_3^-) by PEP carboxylase in combination with the transport of organic acids and the decarboxylation acts as a **CO_2-concentrating mechanism**. This overcame the unfavourable atmospheric condition of a low molar CO_2 to O_2 ratio in the atmosphere during the Pleistocene. In the bundle sheath cells of C_4 plants, RuBP carboxylation and oxygenation take place as in C_3 plants but at an elevated CO_2 to O_2 ratio. Most of the C_4 species that exist today are adapted to high temperatures where the oxygenase reaction of RubisCO in C_3 plants is enhanced.

On the basis of the type of organic acids formed, the anatomical structure of the bundle sheath and the assemblage of the chloroplast in the bundle sheath differ among different C_4 species. Different C_4 types exist (Fig. 12.4): species with or without **Kranz anatomy**. The term "Kranz" was coined by Volkens (1887). But, also, different physiological adaptations are present: species with the malate enzyme (ME) or with PEP carboxykinase (PCK), in combination with the proton acceptors nicotinamide adenine dinucleotide phosphate ($NADP^+$) or nicotinamide adenine dinucleotide (NAD^+), depending on malate reduction in the chloroplast or in the cytosol, respectively. Thus, three main C_4 types are differentiated: the **NAD-ME**, **NADP-ME** and **PCK types**.

Anatomy and physiology determine whether CO_2 may diffuse back out of the bundle sheath to be reassimilated in the mesophyll. This back-diffusion is called leakage (Brown and Byrd 1993; Dai et al. 1993). Leakage is highest in NAD-ME and lowest in NADP-ME types, particularly under stress (Buchmann et al. 1996). Thus, the NADP-ME type also achieves the highest rate of photosynthesis (Hattersley 1992). This type is not the most drought-tolerant type. While NADP-ME species dominate the herbaceous vegetation in savannas, the NAD-ME type dominates in deserts (Schulze et al. 1996).

The **advantages and limitations of C_4 photosynthesis** are more general than the original adaptation to low atmospheric CO_2 concentrations:

- PEP carboxylase has high affinity for bicarbonate.
- The CO_2 compensation point is close to zero because C_4 plants are able to reassimilate photorespiratory and mitochondrial respiratory CO_2.
- There is a cost: C_4 plants have a higher demand for ATP during PEP formation (Chap. 6). Thus, they require high solar radiation, which is not limiting in arid climates but may be a limitation in temperate or boreal climates, as well as in the shade of other species. Also, plants have evolved novel mechanisms to produce ATP in C_4 plants (Takabayashi et al. 2005). It is mainly the refixation of any CO_2 lost by RubisCO and respiration that result in higher photosynthesis rates and higher productivities than those in C_3 plants during the period of growth.
- Even though C_4 plants are found mainly in tropical and subtropical environments with high solar radiation, high temperatures and low rainfall, this does not mean that C_4 plants cannot exist in temperate and boreal regions with long hours of daylight. The success of *Zea mays* in agriculture illustrates the metabolic potential in a much broader climate envelope, even though the season may be too short to develop grains.
- Water use efficiency (WUE) is greater because stomata can be more closed and reduce transpiration at the same level of C_i as in C_3 plants.
- The N demand is lower, since C_4 species have lower RubisCO contents (per leaf area) than C_3 plants since a large amount of leaf N is used for RubisCO. However, with lower N, also forage quality is lower.

12.1.2.3 Crassulacean Acid Metabolism Species

Succulence and regulation of the water status of cells already existed in algae before land plants evolved, where the vacuole balances the salt concentration of single cell organisms (Walter and Kreeb 1970). There are succulent liverworts (*Marchantia* spp.), ferns (*Pyrrosia* spp.), gymnosperms (*Welwitschia mirabilis*) and an estimated 12,000 species of 70 flowering plant families in the entire phylogeny of flowering plants. Even within a confined group such as the Portulaccaceae, succulence emerged polyphyletically, forming leaf, stem, root and flower succulence (Nyffelder et al. 2008; Evans et al. 2014). Thus, succulence, as one prerequisite for the carbon dioxide concentration mechanism (vacuolar storage capacity for malate in CAM plants), is a ubiquitous feature in the plant kingdom as an adaptation to arid and saline environments.

The German poet Goethe (1749–1832) cultivated the crassulacean plant *Kalanchoe pinnata* (synonym *Bryophyllum calycinum*) in his house because it grew well even under dry conditions. The English botanist Heyne grew *Kalanchoe daigremontiana*, as suggested by Goethe, and in 1815 he discovered its acid metabolism by eating its leaves and realizing they tasted sour in the morning and bitter in the evening. Even though this metabolism occurs in many more plant families than the Crassulaceae (Fig. 12.3), the metabolic type was named **CAM** after this discovery in the crassulacean species *K. daigremontiana*.

CAM is expressed in succulents (plants with high water content per dry weight in leaves or stems) of arid or saline regions, and in epiphytes of tropical vegetation (Chap. 6). There are even trees that express CAM (*Clusia*, *Piper*). CAM enables plants to avoid transpiration in the daytime. Most CAM species are adapted to cool coastal deserts (the Atacama Desert, the Namib Desert, Baja California), because the air humidity at night-time is high in "**fog**" **deserts**. But the presence of CAM in tropical **epiphytic orchids** shows that it is not the low night temperature that limits CAM. Most likely it is the low leaf-internal CO_2 concentration at stomatal closure during daytime that has promoted the evolution of CAM. It is interesting to note that there are C_4–CAM intermediate species as well (Sage 2004).

12.2 Photosynthesis Models and Calculation of $^{13}C/^{12}C$ Fluxes (Contribution by A. Arneth)

Modelling of the fluxes of CO_2 is needed in order to make predictions of the global carbon cycle under conditions of global change. The processes taking place during CO_2 fixation in leaves of C_3 plants were originally described mathematically by Farquhar et al. (1980). This **photosynthesis model**, or some adaptation of it, is used in most state-of-the art vegetation models (Chap. 15). It is based on biochemical processes and the interactions of three metabolic pathways:

- Photosynthetic C reduction.
- Photorespiratory oxidation.
- Gain of chemical energy (reduction equivalents, ATP) by photosynthesis.

The model is based on the kinetics of carboxylation, specifically on the carboxylase–oxygenase reactions of RubisCO in the chloroplast. The model also combines RubisCO kinetics with the stoichiometry of electron transport and the requirements for NADPH and ATP. In the following discussion, only some of the most important points are summarised. For further reading, the derivation of the model is explained in detail in Farquhar et al. (1980), Farquhar and von Caemmerer (1982) and Farquhar and Lloyd (1993).

As mentioned before, the rate of CO_2 assimilation per leaf area (A) may be described as the minimum of two dependent processes: RubisCO limitation (A_v) or RuBP regeneration (A_j), which in turn is limited by the electron transport.

$$A = \min\left\{A_j, A_v\right\} \tag{12.8}$$

12.2.1 RubisCO-Limited or RuBP-Saturated Rate (A_v)

Because of photosynthetic C reduction and photorespiration, the rate of CO_2 assimilation in the stroma of the chloroplast is described as:

$$A_v = V_c\left(1 - 0.5\frac{V_o}{V_c}\right) - R_{dark} \tag{12.9}$$

where V_c is the rate of RuBP carboxylation, V_o is the rate of RuBP oxygenation and R_{dark} is (here) the rate of mitochondrial respiration in the light. This equation takes into account that photorespiratory oxidation loses 0.5 mol CO_2 per mol oxygenation and thus the rate of net C fixation is decreased. V_c and V_o depend on the maximum enzymatic rates (V_{cmax}, V_{omax}) and are limited by the presence of O_2 or CO_2, respectively, as follows:

$$V_c = V_{c\max}\frac{\mathrm{pC_c}}{\mathrm{pC_c} + K_c\left(1 + \frac{\mathrm{pO}}{K_o}\right)} \tag{12.10a}$$

and:

$$V_o = V_{o\max}\frac{\mathrm{pO}}{\mathrm{pO} + K_o\left(1 + \frac{\mathrm{pC_c}}{K_c}\right)} \tag{12.10b}$$

where K_c and K_o are the Michaelis–Menten constants for the **carboxylation** and **oxygenation**, respectively, and pO and $\mathrm{pC_c}$ are the partial pressures of oxygen and CO_2 in the chloroplast, respectively.

The ratio of the activities (ϕ) of the oxygenation and carboxylation of RubisCO is:

$$\text{Ø} = \frac{V_{\mathrm{o}}}{V_c} = \frac{V_{\mathrm{o\,max}} K_{\mathrm{c}} \mathrm{pO}}{V_{\mathrm{c\,max}} K_{\mathrm{o}} \mathrm{pC_c}} \qquad (12.11)$$

and this is reduced at $R_{\mathrm{dark}} = 0$ to:

$$\text{Ø} = \frac{2\Gamma^*}{\mathrm{pC_c}} \qquad (12.12)$$

where Γ^* is the **photosynthetic compensation point** in the absence of mitochondrial respiration.

On the basis of these general biochemical equations, the RubisCO-limiting rate of CO_2 assimilation, A_{v}, is calculated as:

$$A_{\mathrm{v}} = V_{\mathrm{c}} \left(1 - \frac{\Gamma^*}{\mathrm{pC_c}}\right) - R_{\mathrm{dark}} \qquad (12.13a)$$

$$A_{\mathrm{v}} = V_{\mathrm{c\,max}} \frac{\mathrm{pC_c} - \Gamma^*}{\mathrm{pC_c} + K_{\mathrm{c}}\left(1 + \frac{\mathrm{pO}}{K_{\mathrm{o}}}\right)} - R_{\mathrm{dark}} \qquad (12.13b)$$

K_{c}, K_{o} and Γ^* are temperature-dependent values (Harley et al. 1986; Kirschbaum and Farquhar 1984; von Caemmerer et al. 1994). At 20 °C the numerical value of $K_{\mathrm{c}} = 30.2$ Pa (CO_2), $K_{\mathrm{o}} = 25.6$ kPa (O_2) and $\Gamma^* = 3.46$ Pa.

12.2.2 RuBP Regeneration–Dependent and Electron Transport–Limiting Rate (A_{j})

A continuous rate of CO_2 reduction or oxygenation activity requires a continuous and equal rate of RuBP supply. RuBP is regenerated via the pentose phosphate cycle or the photorespiratory carbon oxidation cycle. Both processes consume ATP and NADPH, and there is a very complex stoichiometry — that is, PGA (phosphoglycerate) production, the rate of NADPH and ATP consumption, and the number of electrons required to produce the redox equivalents and ATP. This is in turn dependent on the linear rate of electron transport through PS I and PS II, as well as on cyclic electron transport. The sum of these processes is:

$$J' = \frac{J}{4.5 + \frac{10.5\Gamma^*}{\mathrm{pC_c}}} \qquad (12.14)$$

where J' is the maximum carboxylation rate maintaining the potential rate of electron transport and J is the potential rate of linear electron transport. It follows that the RubisCO-limiting rate of CO^2 assimilation, A_{j}, is:

$$A_{\mathrm{j}} = J \frac{\mathrm{pC_c} - \Gamma^*}{4\left(\mathrm{pC_c} + 2\Gamma^*\right)} - R_{\mathrm{d}} \qquad (12.15)$$

where J is the rate of electron transport. J increases hyperbolically with light (Q):

$$J = \frac{Q + J_{\mathrm{max}} - \sqrt{\left(Q + J_{\mathrm{max}}\right)^2 - 4\theta Q J_{\mathrm{max}}}}{2\theta} \qquad (12.16)$$

where θ describes the curvature of the hyperbolic function. J_{max} and V_{cmax} depend on the plant type and its growth environment, such as the temperature, but also the state of nutrition, light conditions and so forth. In practice, the temperature dependence of V_{cmax} and J_{max} is experimentally determined from a regression of the dependence of photosynthesis on conductance under the climatic conditions of interest.

12.2.3 Supply of CO_2 Through Stomata

The relationships described above may be applied only if the supply of CO_2 to the chloroplast (C_{c}) is known. The CO_2 supply in the leaf is a **diffusion process**, limited by stomatal conductance (g_{s}). Equation 12.8 may also be expressed as diffusion-limited CO_2 assimilation, A.

$$A = g_{\mathrm{s}} \frac{\left(\mathrm{pC_a} - \mathrm{pC_c}\right)}{P} \qquad (12.17)$$

where $\mathrm{pC_a}$ is the CO_2 partial pressure in the air that surrounds the leaf, and P is (here) the air pressure. It should be noted that the CO_2 concentration at the leaf surface also depends on the boundary layer conditions (Chap. 10).

The calculation of leaf photosynthesis rates requires simultaneous solution of Eqs. 12.8 and 12.17. In contrast to the processes related to carboxylation, no equally detailed biochemically based model for stomatal responses exists. To solve Eqs. 12.8 and 12.17, a set of equations is produced that determines the reaction of stomata empirically, and this is coupled to the photosynthesis model. In this model, g_s is a function of air humidity, temperature, light, soil water, atmospheric CO_2 and other growth factors insofar that they influence stomatal aperture (Jarvis 1976; Leuning 1995; Lloyd et al. 1995b; Arneth et al. 2002).

Although the original equations by Farquhar et al. (1980) were based solely on cellular processes, this model may also be applied to whole leaves, whole plants and whole ecosystems (Lloyd et al. 1995a; Leuning et al. 1998; Arneth et al. 1999; de Pury and Farquhar 1999). Depending on the question, the successful use of the model requires not only information on V_{max} and J_{max} but also knowledge of the state of nutrition and water supply from the soil.

12.2.4 $^{13}C/^{12}C$ Discrimination

The photosynthesis model developed by Farquhar et al. (1980) may also be used to model discrimination against ^{13}C in photosynthesis. The most important processes contributing to discrimination against ^{13}C compared with ^{12}C in leaves are the different rates of diffusion of $^{12}CO_2$ and $^{13}CO_2$ and the fractionation related to the carboxylation by RubisCO, while fractionation related to photorespiration and maintenance respiration are often neglected (but see Ghasghaie and Badeck (2014) for more details). According to Farquhar et al. (1989), the **carbon isotope flux rate** (**R_p**) in its simplified version is determined by:

$$R_p = \frac{^{13}A}{^{12}A} \qquad (12.18)$$

where ^{13}A and ^{12}A are the rates of assimilation fluxes of $^{13}CO_2$ and $^{12}CO_2$. According to the definition, the isotopic effect of carboxylation ($1 + b$) is:

$$\frac{R_i}{R_p} = 1 + b \qquad (12.19)$$

where R_i is the isotope ratio of the intercellular CO_2 and b is the net fractionation during carboxylation, which is primarily determined by RubisCO (27‰) in the case of C_3 plants (for C_4 plants, see below).

R_i may be calculated from Eq. 12.17, as the kinetic isotope effect for diffusion corresponds to the ratio of the diffusivities of $^{12}CO_2$ and $^{13}CO_2$ in air:

$$^{13}A = g_s \frac{R_a pC_a - R_i pC_c}{(1+a)P} \qquad (12.20)$$

where, corresponding to Eq. 12.19, $1 + a = g_s/^{13}gs$ and a describes the fractionation by diffusion in air (4.4‰).

These equations may be combined and expressed as:

$$\alpha = 1 + \Delta = \frac{R_a}{R_p} = (1+a)\frac{pC_a - pC_c}{pC_a} + (1+b)\frac{pC_c}{pC_a} \qquad (12.21a)$$

and:

$$\Delta = a\frac{pC_a - pC_c}{pC_a} + b\frac{pC_c}{pC_a} = a + (b-a)\frac{pC_c}{pC_a} \qquad (12.21b)$$

The above simplified equations for the **carbon isotope discrimination, Δ**, apply only to C_3 plants. Discrimination in C_4 plants is more complicated because of the higher affinity of PEP carboxylase for CO_2 and the transformation of CO_2 into HCO_3^-. In equilibrium conditions, there is more ^{13}C in HCO_3^-. Even though the effective discrimination of PEP carboxylase is about −5.7‰, a certain proportion of the CO_2 (φ) is lost by back-diffusion and the permeability of bundle sheath cells, also called **leakage**. This contributes to the discrimination by RubisCO in bundle sheath cells. The total effect of **discrimination in C_4 plants** is as follows:

$$\Delta = a + \left(b4 + b\varphi - a\right)\frac{pC_c}{pC_a} \qquad (12.22)$$

The numeric value of ($b4 + b\varphi$) is smaller than that of b. This value may be positive, zero or negative, depending on the permeability. In C_4 plants, Δ may therefore depend positively on pC_c/pC_a, be independent or depend negatively on pC_c/pC_a.

The equations shown here can be used to interpret measured ^{13}C to ^{12}C ratios in plant materials with respect to the effects of particular climatic and growth conditions. For example, from the measurements of the ^{13}C to ^{12}C ratio in plant dry matter, a time-integrated value of pC_c/pC_a may be calculated (Eqs. 12.21a, b). Alternatively, pC_c/pC_a can be derived from climatic conditions, the capacity of photosynthesis and electron transport (Eqs. 12.8–12.18). By comparing the calculated and measured values in annual rings of wood, the long-term effect of increasing CO_2 concentration on stomatal conductance may be deduced (Arneth et al. 2002). For further applications, Chap. 14, Sect. 14.2.

12.3 Specific Leaf Area, Nitrogen Concentrations and Photosynthetic Capacity

12.3.1 Specific Leaf Area

The **specific leaf area** (**SLA**) is defined as the ratio of projected leaf area and leaf weight (in square metres per kilogram). It is a sensitive indicator of several ecological processes and adaptations (Sect. 20.1 in Chap. 20). The SLA of organs for assimilation may differ by a factor of 5 among species. Annual crop plants reach 23.6 $m^2\ kg^{-1}$ SLA, in contrast to 4.1 $m^2\ kg^{-1}$ in evergreen conifers. These differences are species-specific and are determined by competition with other species. During the course of evolution, plants have developed ever greater leaf areas per unit of dry mass, thus increasing light capture. Competitive plants have supplied these thin leaves with optimal amounts of N (high N concentrations). The habitat, particularly the water and nitrogen supply together with changes in light conditions, results in modifications of the SLA.

An increase in the SLA has several ecologically important consequences:

- The **elasticity** of leaves decreases, while the ability to endure drought and other stresses increases.
- The packaging density (**concentrations**) **of nutrients**, particularly nitrogen (up to 40 mg N g^{-1} in crop plants but only about 10 mg N g^{-1} in conifers), increases with the SLA. The low N concentration in conifers is in part due to the large amount of sclerenchyma in evergreen needles.
- The relation of assimilating cells to the transpiring surface (**A/E ratio**) increases.

In general, species with a high SLA have higher metabolic activity than species with a low SLA. Species with a high SLA are opportunists (ruderal plants), settling at new sites with a high supply of resources. In contrast, plants with a low SLA occupy less favourable sites. Both groups occupy their respective sites not because they would not grow at more favourable sites (exceptions are, for example, obligate halophytes) but because they are generally outcompeted at favourable sites.

Orians and Solbrig (1977) formalised this observation in a **cost–benefit analysis** of the

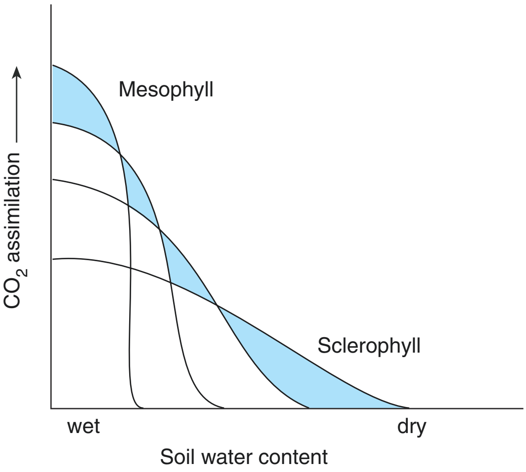


Fig. 12.5 Dependence of CO_2 assimilation on soil water content. Sensitive leaf types have a much higher rate of CO_2 assimilation than resistant leaf types when water is abundant. Sensitive types reduce CO_2 exchange early as the soil dries; under this condition, resistant types dominate. (After Orians and Solbrig 1977)

adaptation of plants to a gradient of increasing drought (Fig. 12.5). The model starts with the assumption that all species are able to live at a well-watered site. Species that assimilate large quantities of CO_2 are less stress tolerant. They have a large SLA and are sensitive to drought. CO_2 assimilation decreases with very little soil drying. In contrast, species with low rates of CO_2 assimilation usually possess leaves with a smaller SLA. These plants are able to endure drought stress to a greater degree. They are able to assimilate CO_2 when stress-intolerant species can no longer photosynthesise (Chap. 10).

Obviously, the specific leaf area is an important variable responding to habitat conditions. It is also a constitutive characteristic variable of species (herbaceous annuals in comparison with perennials), which affects the rate of CO_2

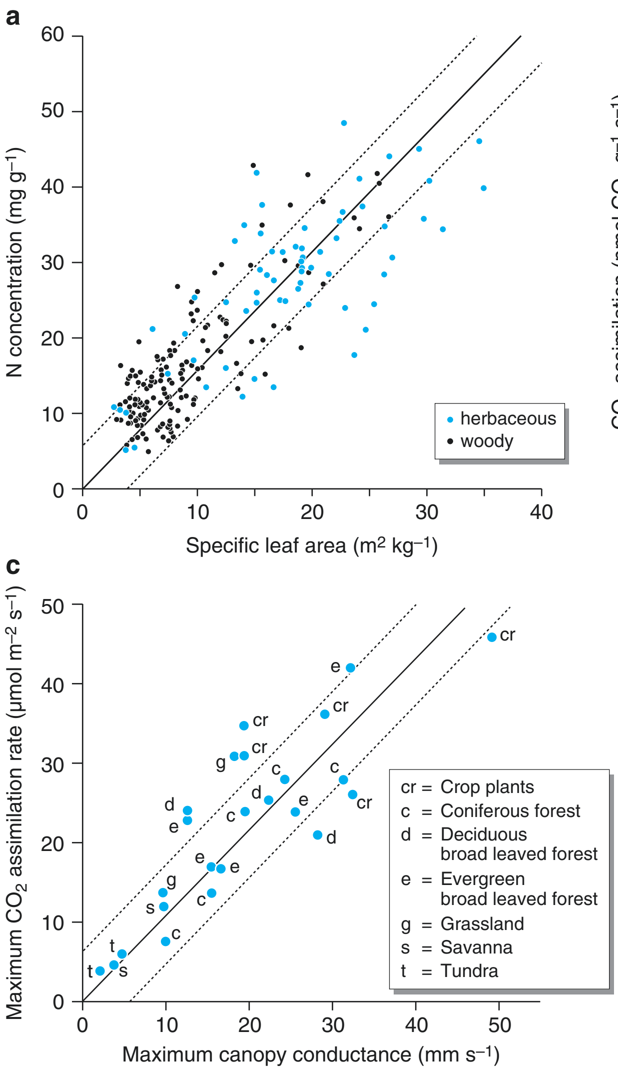


Fig. 12.6 Relations between N concentration, specific leaf area and CO_2 assimilation. **a** Correlation of N concentration (in milligrams per gram) in a leaf with specific leaf area (in square metres per kilogram) in herbaceous and woody species from all climatic regions of the Earth (Schulze et al. 1994). **b** Relation between maximum rate of light-saturated CO_2 assimilation and N concentration in the leaf (Field and Mooney 1986). **c** Relation between maximum CO_2 assimilation (A_{max}) and maximum conductance. In this case, the data represent measurements in single experimental plots in different vegetation zones of the globe. The lowest values occur in the tundra and the highest values occur in a wheat field. The second highest value is in a tree plantation of *Hevea brasiliensis*. (Schulze et al. 1994)

assimilation. The relation between the SLA (measured in square metres per kilogram) and nutrient (nitrogen) concentration in the leaf is linear over a wide range (Fig. 12.6a). There is also a close relationship between CO_2 assimilation and the N concentration (Fig. 12.6b), except for N_2-fixing plants (Adams et al. 2016). Species with a high maximum rate of CO_2 assimilation react more sensitively to N deficiency than species with less photosynthetic capacity. Corresponding to the model of Orians and Solbrig (1977), photosynthetic capacity is linearly related to maximum stomatal conductance (Fig. 12.6c).

12.3.2 Maximum Rates of CO_2 Assimilation

Loss of water and uptake of CO_2 occur via the stomatal aperture. Thus, there is a physical connection between the stomatal conductance and the rate of photosynthesis (Chap. 10, Sect. 10.3). It is therefore not surprising that the **maximum rate of CO_2 assimilation** (A_{max}) is linearly correlated with the maximum conductance of the surface for transport of water vapour (Fig. 12.6c). This function is important for global models of carbon budgets, as it allows an estimate of the maximum rate of CO_2 fixation. There is no corresponding correlation between E_{max} (the **maximum rate of transpiration**) and A_{max} (maximum assimilation), because transpiration depends on variable meteorological conditions (water vapour saturation deficit, irradiation; Chap. 10), while the maximum rate of photosynthesis is related to the CO_2 concentration in the atmosphere. Maximum rates of CO_2 assimilation are very different for different types of vegetation.

The physiological differentiation between C_3, C_4 and CAM plants becomes less important in the global perspective of CO_2 assimilation, where C_3 plants dominate. Gifford (1974) demonstrated that the differences between C_3 and C_4 photosynthesis, which are very distinct in the chloroplast, diminish under **agricultural field conditions**.

12.4 Response of Photosynthesis to Environmental Variables

Different conditions determine to what extent A_{max} may actually be achieved by plants. These factors are:

- **Climatic factors**: Primarily available light, which varies by two orders of magnitude (0.5 mol photons m^{-2} day^{-1} on the soil of a forest and 50 mol photons m^{-2} day^{-1} in a tropical grassland), and temperature and humidity.
- **Edaphic factors**: Mainly nutrition and the availability of water.
- **Time-dependent factors**: Particularly the duration of the growing season and the age of the leaf.

Climatic factors affect short-term, reversible responses as well as long-term, non-reversible changes, while edaphic factors are generally long-term and irreversible. The Sects. 12.4.1 to 12.4.7 consider how CO_2 assimilation depends on these conditions. Initially, the change of a single variable is considered with all other conditions remaining optimal and constant. In the natural environment there are, of course, different interactions between these conditions, which will be discussed in Section 12.4.8.

12.4.1 Light Response of CO_2 Assimilation

Photosynthesis increases with increasing irradiation (**light response of CO_2 assimilation**; Fig. 12.7a), while the energy demand of cells via mitochondrial respiration decreases and light-induced respiration increases (photorespiration increases with higher temperatures due to more light). As light further increases, a compensation point is reached at which CO_2 exchange is zero and above which net CO_2 assimilation takes place, eventually becoming saturated with increasing light. The immediate, short-term response of photosynthesis to the changing light is generally reversible. Diffuse light from a cloudy sky or scattering within a canopy results in higher rates of photosynthesis than direct sunlight (Brodersen et al. 2008).

In contrast to these short-term and reversible responses to radiation, acclimation can occur, involving structural modifications to the leaf (Chap. 3). **Sun** and **shade leaves** are responses to light. Leaves of shade plants acclimated to low-light conditions usually have a large SLA and a lower compensation point than those species acclimated to high light intensities (Fig. 12.7b). A shade leaf is damaged in strong light, shed and replaced by a new leaf acclimated to the new light conditions. Some but not all plant species are able to adapt to light conditions (Fig. 12.7c).

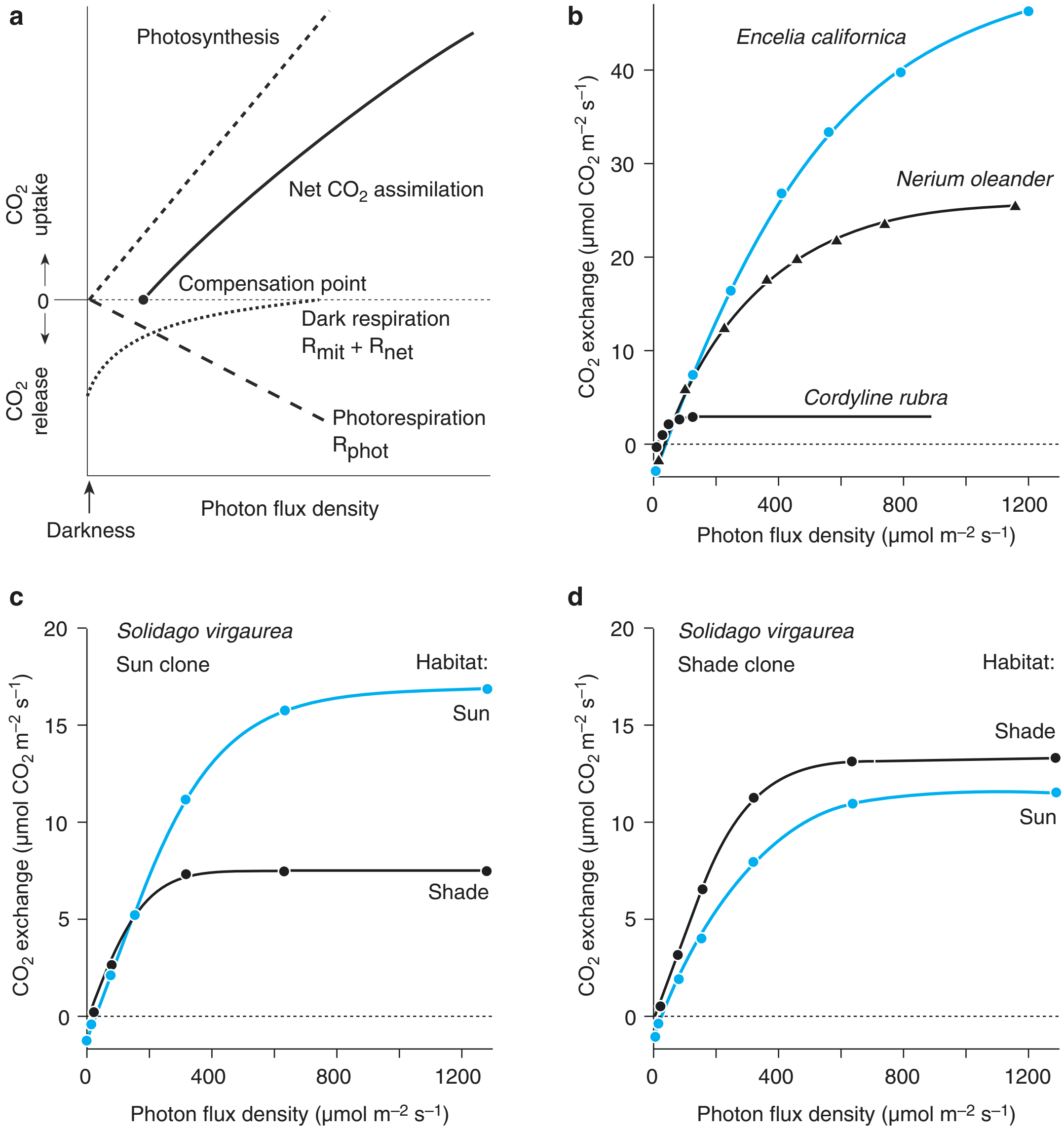


Fig. 12.7 CO_2 exchange related to photon flux density. **a** Dependence of CO_2 gas exchange on the light intensity measured as photon flux density (in micromoles of photons per square metre per second). The figure shows the processes that occur in the region below light saturation. **b** Dependence of CO_2 gas exchange on photon fluxes of species differently adapted to shade. **c** Change in CO_2 exchange with adaptation to the light climate in *Solidago virgaurea*. Clones that are preadapted to full light adapt their rate to the location (i.e. shade) in comparison with **d** clones that are adapted to the shaded location and do not change the rate of CO_2 exchange. (Fig. 12.7b–d: Björkman 1981)

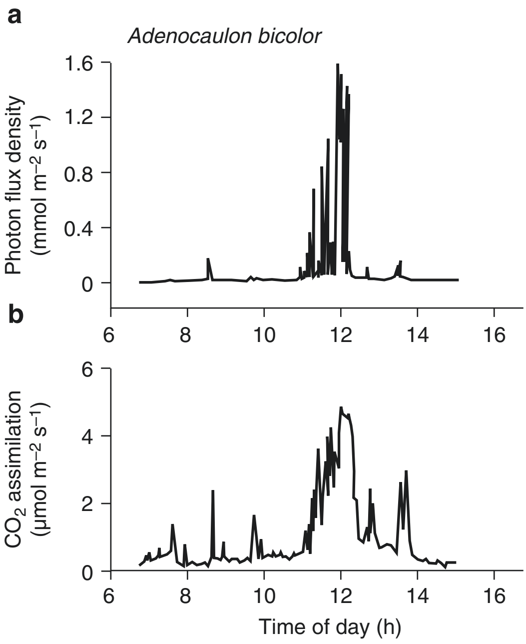


Fig. 12.8 Net CO_2 assimilation during sunflecks. **a** Occurrence of sunflecks in a shaded habitat and **b** delay in CO_2 fixation in *Adenocaulon bicolor*. The period of CO_2 uptake is longer than the duration of the sunfleck—that is, reduction equivalents are stored and, after the sunfleck has passed, these are used in dark reactions for CO_2 reduction. (Pearcy and Pfitsch 1994)

For obligate shade plants, the light dependency of photosynthesis does not change, even if the plant is grown at a sunny site. Specific adaptation to light may also be observed between different populations of a species (Fig. 12.7c, d).

There are ecologically important situations where specific adaptations to light are required, such as at extremely shady sites where sunflecks allow only a short time to assimilate CO_2 (Chap. 2, Sect. 2.1). Plants at shady sites may receive very high light intensities for short periods of time — so-called **"sunflecks"** (e.g. in the understorey or herbal layer of a forest; Fig. 12.8) (Pearcy and Pfitsch 1994). Photosynthesis responds to these sunflecks at higher rates than would be expected from the light response curve, as the acceptor for CO_2 is not limiting while the carboxylase may be fully activated. In addition, the pools of ATP and NADPH formed during the sunfleck may still be utilised for CO_2 fixation after the light has faded, so dark fixation of CO_2 continues at lower light intensity. As a result, a short sunfleck may cause a longer period of CO_2 uptake. With use of stable isotopes ($\delta^{13}C$) it was shown that about 50% of the dry matter production of these plants was assimilated in the extremely short periods of sunflecks (Pearcy and Pfitsch 1994).

A different situation exists in dry areas of the Earth where plants receive about 50 mol photons m^{-2} day^{-1} without having sufficient water to open their stomata for CO_2 uptake. A situation arises in the leaf in which PS I and PS II are not able to release electrons to NADP because no CO_2 enters the stomata and CO_2, as the substrate for reduction, is not available. The CO_2 concentration in the mesophyll is around the compensation point. In these situations, leaves may be photoinhibited.

12.4.2 Temperature Response of CO_2 Assimilation

Starting from temperatures below 0 °C where photosynthesis and respiration stall, respiration of leaf cells is generally activated earlier than photosynthesis with increasing temperatures. At low temperatures, a range exists at which only respiration is measurable. Photosynthesis, i.e. CO_2 uptake, starts at around −5 °C (**temperature response of CO_2 assimilation**: Fig. 12.9a), reaches an optimum and decreases at high temperatures. In contrast, respiration increases exponentially over a wide range of temperatures and decreases only at high temperatures. Net CO_2 assimilation (also called net photosynthesis) is the balance between these two processes, showing an optimum shift to slightly lower temperatures than photosynthesis. There is an interaction of light and temperature: at low light intensities, the temperature optimum is shifted to lower temperatures (Fig. 12.9b), with the consequence that plants operate in an optimum range of their net photosynthesis at low light intensity in the cool hours at dawn and at high temperatures and full light at midday.

The **temperature optimum** of CO_2 assimilation is not at all constant; for example, it changes with the season (Schwarz et al. 1997; Galvagno et al. 2013; Yamori et al. 2014). Similarly, the size of plant leaves is acclimated to the radiation

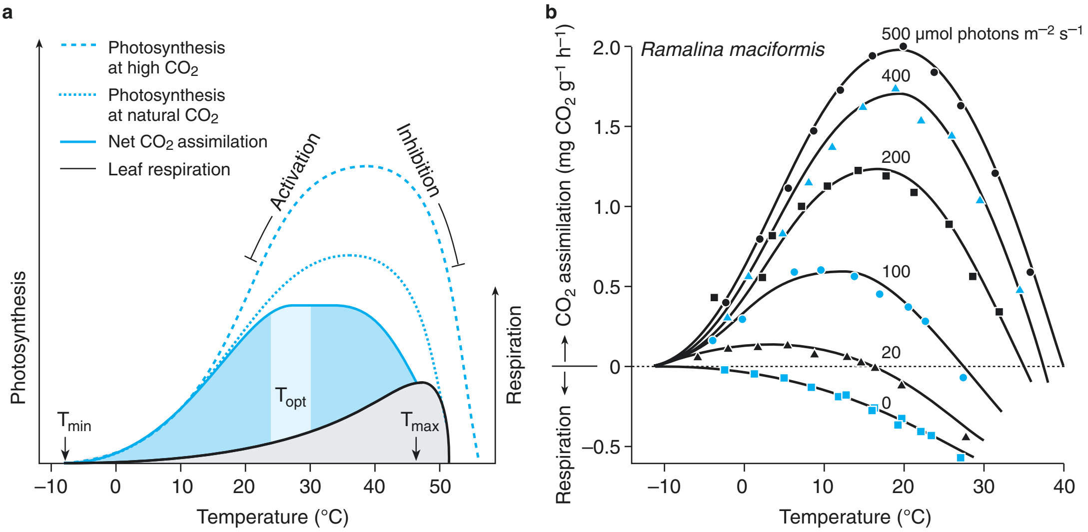


Fig. 12.9 Dependence of photosynthesis, respiration and net CO$_2$ assimilation on temperature. **a** Activation of photosynthesis leads to an exponential increase in CO$_2$ uptake. Increasing temperature also increasingly inhibits photosynthesis. Interaction between activation and inhibition leads to an apparent optimum of CO$_2$ uptake, which finally leads to a lower CO$_2$ uptake at high temperatures. The rate of net assimilation at increased temperature is balanced in part by the exponential rise in respiration. The temperature optimum for respiration is higher than that for photosynthesis (after Larcher 1994). **b** Interaction between light and temperature for photosynthesis (positive values on the *y axis*) and respiration (negative values on the *y axis*) leads to a decrease in the optimal temperature range at lower light intensities; for the lichen *Ramalina maciformis*, cool mornings with low light are the "optimum" for CO$_2$ uptake, as are high temperatures at full light. (Lange et al. 1977)

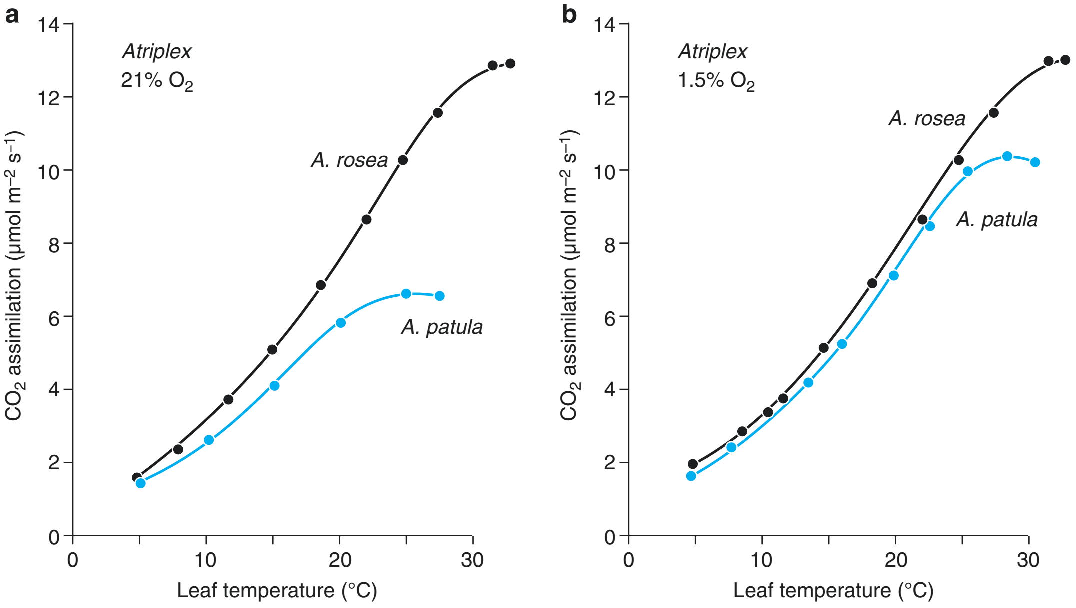


Fig. 12.10 Temperature dependence of CO$_2$ assimilation. **a** The C$_4$ plant *Atriplex rosea* and the C$_3$ plant *Atriplex patula* show clear differences in the maximum rate of CO$_2$ assimilation and in the temperature optimum. **b** The same experimental conditions as in **a** but with 1.5% O$_2$ and not 21% O$_2$ in the surrounding air. CO$_2$ assimilation by C$_3$ plants changes so it is like that of C$_4$ plants. Investigation at low partial pressure of O$_2$ experimentally demonstrates the existence and importance of photorespiration for CO$_2$ assimilation mediated by RubisCO. (Björkman 1971)

climate so the temperature remains in the physiologically optimal range (Chap. 9).

Even though plants operate for most of the day in a photosynthetically optimal range, there are two critical temperature ranges (Chap. 3):

- Low temperature is generally not a factor damaging photosynthesis (Chap. 4), but frost together with high light intensities leads to **photoinhibition**. This effect was first observed at alpine sites, which is not surprising as the CO_2 concentration decreases with increasing altitude and thus increases the imbalance between light flux and CO_2 fixation. After frost, net photosynthesis decreases and then recovers slowly but does not reach the same values as during the summer.
- High temperatures affect opening of stomata and result in a disproportional increase in transpiration. A leaf is more likely to dry out than be damaged by heat. On the physiological level, PS II (as the ATP-generating system) and carbon fixation by RubisCO are most sensitive to heat stress (Allakhverdiev et al. 2008).

C_4 plants have a higher temperature optimum for photosynthesis than C_3 plants. This effect may also be achieved by exposing C_3 plants to an atmosphere with little O_2 and thus reducing the oxygenase function of RubisCO (Fig. 12.10). The highest temperatures at which higher plants reached optimum rates of photosynthesis were observed in *Tidestromia oblongifolia* at 46 °C in Death Valley, California (Fig. 12.11). In contrast, CAM plants generally have a lower optimum temperature. Exceptions are tropical orchids (Yamori et al. 2014, Fig. 12.12).

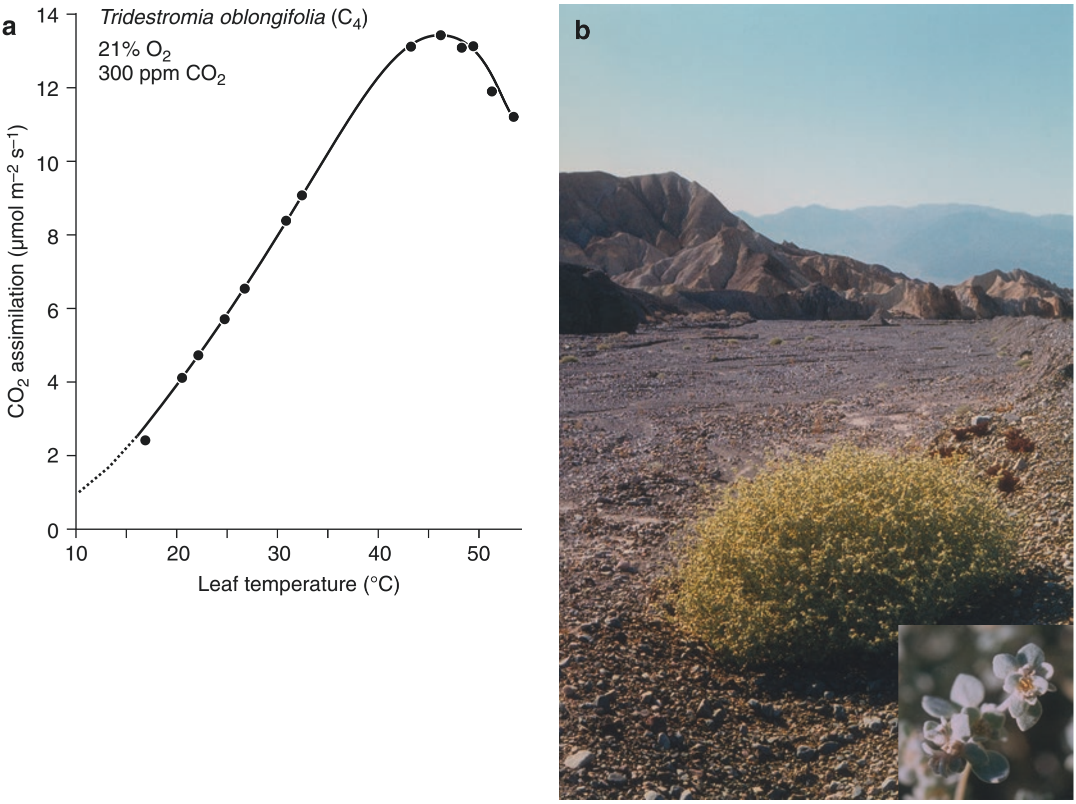


Fig. 12.11 **a** Temperature dependence of CO_2 assimilation of *Tidestromia oblongifolia* (Amaranthaceae) in Death Valley, California. This plant reaches a maximum rate of CO_2 assimilation at 48 °C. **b** *T. oblongifolia* grows in Death Valley as a summer annual in erosion gullies in which rainwater gathers and then percolates into the soil. (Photo: E.-D. Schulze)

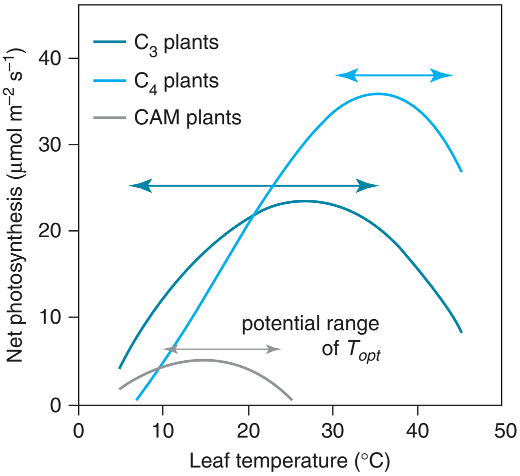


Fig. 12.12 Typical temperature responses of net photosynthesis in C_3, C_4 and crassulacean acid metabolism (CAM) plants. (Yamori et al. 2014)

12.4.3 Relative Air Humidity Response of CO_2 Assimilation

Net photosynthesis decreases with stomatal closure at low relative air humidity (**humidity response of CO_2 assimilation**). However, CO_2 assimilation generally does not decrease in proportion to stomatal conductance (Chap. 10). This is difficult to explain, because direct effects of humidity on photosynthesis have also been described (Mott and Parkhurst 1991). Obviously, stomata do not close synchronously, so some areas between the veins still have open stomata while others are closed. Thus, there is a higher CO_2 influx into the leaf in some small areas but a lower influx into other areas of the leaf. Consequently, the calculated average CO_2 concentration in the mesophyll remains constant, even though the total conductance of the leaf is decreased. The temperature distribution (Jones 1999) indicates that a leaf is not homogeneous, and so the heterogeneity — the so-called **patchiness of the leaf** — contributes to a partial decoupling of the flux of CO_2 and water vapour for the whole leaf (Mott et al. 1993).

12.4.4 Nutrient Response of CO_2 Assimilation

CO_2 assimilation and stomatal conductance change in proportion to the nutrition of the leaf, which also affects the SLA (**nutrient response of CO_2 assimilation**). This applies not only to changes in N nutrition (Sect. 12.5) but also to phosphorus. C_4 plants, despite a generally lower N concentration, have a potentially higher rate of assimilation than C_3 plants, as in C_4 plants RubisCO activity is concentrated in the bundle sheath. Under natural conditions, the higher photosynthetic capacity is not used in C_4 plants; rather, a lower stomatal conductance is reached, resulting in lower evaporation but assimilation similar to that in C_3 plants. Therefore, saving water appears more important than maximising photosynthesis. This leads to decreases in RuBP carboxylase and the N concentration in comparison with C_3 plants (see Penning de Vries and Djitèye 1982), with consequences for assimilate production and for distribution of plants exhibiting the two types of photosynthesis (Chap. 11).

12.4.5 Water Stress Response of CO_2 Assimilation

The **response of CO_2 assimilation to water stress** is easier to study in plants without an epidermis, such as **lichens**, which also do not have stomata. When dry lichens are moistened, respiration becomes measurable at a water content of 20% (per dry weight; Fig. 12.13). The equilibrium humidity for initiation of gas exchange corresponds to an air humidity of 80% and a water potential of −30 MPa (Chap. 10, Sect. 10.1). This water potential is much lower than is ever measured in higher plants (−11 MPa) (Kappen et al. 1972). Respiration and photosynthesis increase with water content. A water compensation point is reached at which photosynthesis equals respiration. Maximum CO_2 assimilation in lichens is reached at a water content of 80%. Increasing water content leads

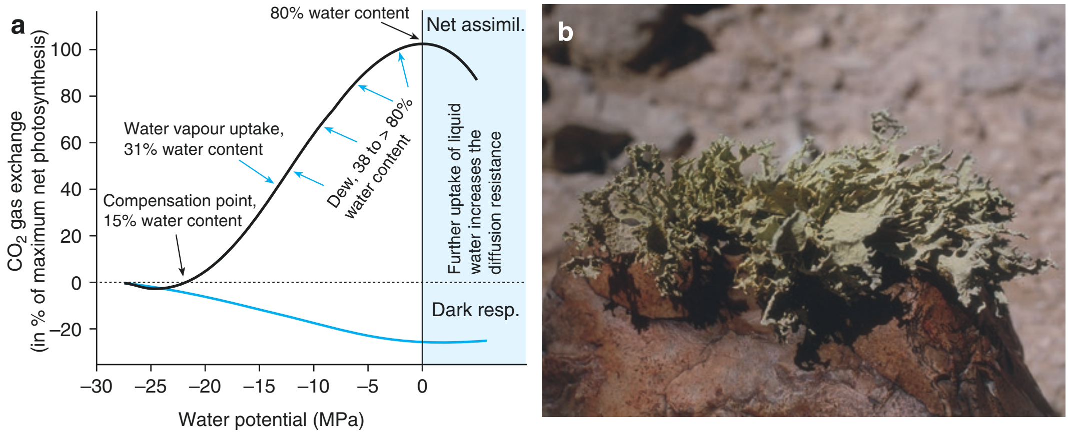


Fig. 12.13 Effect of water potential on net photosynthesis. **a** Dependence of CO_2 gas exchange (net assimilation and respiration) on net water potential of the thallus of the lichen *Ramalina maciformis* in the Negev Desert (temperature 15 °C, saturating light). On the *y axis* the positive values of CO_2 assimilation and the negative values of respiration are shown. For ecologically relevant conditions, the water content of the thallus is presented as a percentage of its dry weight. The *black arrows* indicate the maximum water content (given as a percentage of the dry weight of the thallus), which were measured after dew fall or with increased air humidity in the field (Modified from Lange (1965)). At low water potential, initially respiration is activated, followed by photosynthesis. This leads to a water compensation point for CO_2 uptake where respiration is equal to photosynthesis, which is considerably lower than the water potential so far measured in leaves of higher plants. **b** *R. maciformis* on flint in Avdat, Negev. (Photo: E.-D. Schulze)

to a swelling of fungal cells in the thallus and may restrict CO_2 diffusion (Cowan et al. 1992). Thus, high water content (which occurs after rain) may increase the diffusion resistance to CO_2 in many lichens such that CO_2 assimilation decreases and in extreme circumstances reaches the compensation point.

There are plants that have even lower water compensation points. An extreme example is the lichen *Dendrographa minor* (California), with activation of photosynthesis at −38 MPa. *D. minor* attains 50% of its net photosynthesis at −18 MPa (Lange 1988). There are also species that are not able to photosynthesise at low water potential. Cyanolichens (with cyanobacteria as symbionts rather than green algae) require fluid water (in contrast to water vapour) in order to activate photosynthesis.

In lower plants, photosynthesis starts in a range that is normally not reached in intact leaves of higher plants. However, photosynthesis responds to changes in **turgor** (Kaiser 1982). The changes in cell volume, and thus in turgor, depend on the rigidity of the cell wall ($\varepsilon = P/V$). Higher plants with a large SLA — the so-called mesophytes — are more sensitive to drying-out of the soil than plants with a small SLA (so-called **sclerophytes**; Fig. 12.5). Under field conditions, changes in the photosynthetic activity (this comprises not only photosynthesis) are best correlated with the **predawn water potential** ($\Psi_{predawn}$), which is an indicator of the water status of the soil (Chap. 10, Sect. 10.1). Photosynthesis decreases with $\Psi_{predawn}$ as the soil dries. At the same time, an increase in the **abscisic acid** (ABA) concentration in the xylem sap is observed, which originates from the roots (Chaps. 6 and 10 for stomatal closure). Under drought, ABA is also synthesised by the leaf.

12.4.6 CO_2 Response of CO_2 Assimilation

Elevated CO_2 concentrations increase the maximum rate of photosynthesis, while maximum stomatal conductance decreases (Hetherington and Woodward 2003). A long-term experiment over 10 years of exposing vegetation to enriched carbon dioxide concentration showed that an elevated concentration of 600 ppm led to a 43% higher rate of light-saturated leaf photosynthesis of fertilised perennial ryegrass (*Lolium perenne* L.) and effected a 37% increase in daily assimilation (Long et al. 2006). However, in unfertilised plots, a decrease in CO_2 assimilation was observed as N resources became limiting (Nösberger et al. 2006).

12.4.7 Developmental Responses of CO_2 Assimilation

During the course of **leaf development** from emergence to shedding, leaves undergo an ontogenetic change in activity (Chap. 11). Three phases may be distinguished. Leaves that are still developing, having formed less than about 30% of the leaf area, are carbohydrate sinks. They are often called **sink leaves**, as they consume or import more carbohydrates than they produce photosynthetically. In the next stage, fully grown leaves are **source leaves**, which produce an excess of carbohydrates and export these, via the phloem, for consumption by other organs. In the **ageing phase**, leaves yellow and there is degradation of structures, providing an additional source of carbohydrates and amino acids for the rest of the plant. However, not all resources can be reallocated, and some are lost as litter.

Herbaceous plant species: In herbaceous species, CO_2 assimilation reaches its maximum rate before complete leaf expansion (Fig. 12.14) and decreases continuously after complete expansion of the leaf until the leaf is shed. In the meantime the next leaf is developed, which reaches higher rates but ages according to the same pattern (Woodward 1976).

Deciduous trees: Sun leaves of beech emerge very quickly in May and reach maximum activity in mid-June (Fig. 12.15). As early as the beginning of August, ageing starts, with decreasing rates of CO_2 assimilation, and leaves are shed at the beginning of October. On the same tree, development of shade leaves is significantly slower. Maximum CO_2 assimilation is reached in August. Ageing then occurs faster and leaf shedding is only slightly delayed in comparison with that of sun leaves.

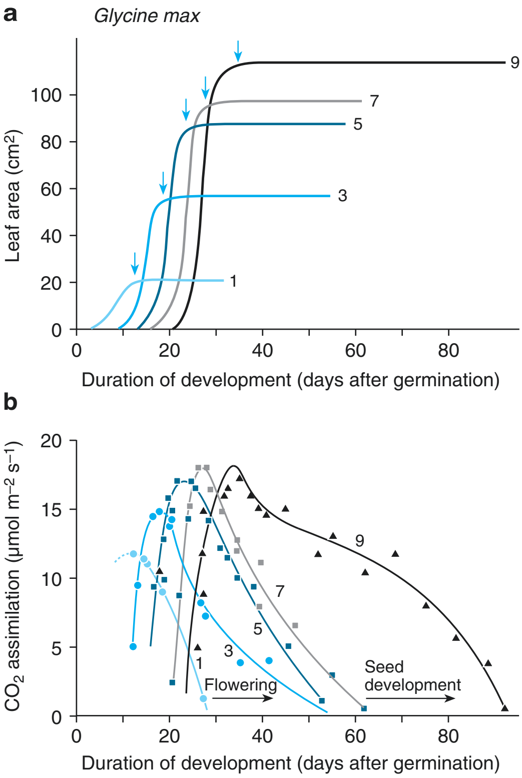


Fig. 12.14 Effect of leaf development on net photosynthesis. **a** Development of leaf area and **b** associated changes in net photosynthesis in *Glycine max* leaves of different ages. The *numbers* indicate the leaf numbers. The leaf starts to age before it has fully developed its leaf area. (Woodward 1976)

Conifers: Needles in conifers (Fig. 12.16) emerge later than leaves of deciduous trees. Maximum rates decrease only slightly in autumn, and the activity of needles remains constant in the following years. Ageing starts only after 3–5 years.

12.4.8 Daily Courses of CO_2 Assimilation and Water Use

CO_2 assimilation is obviously a variable process and may fluctuate considerably depending on the climate and soil, as well as on differences between species during the daily and seasonal course of CO_2 assimilation and transpiration. As long as the climatic conditions at the site are

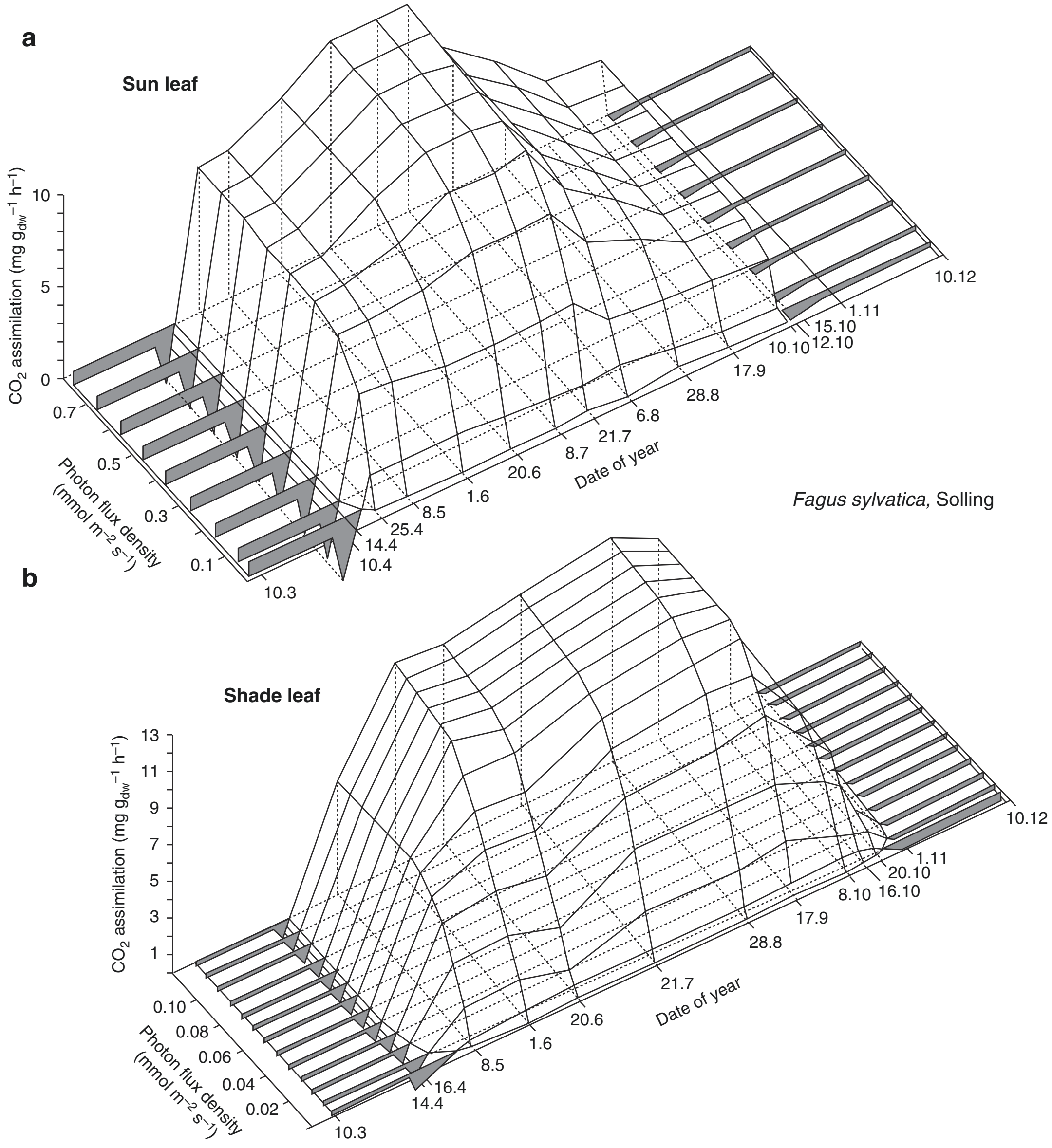


Fig. 12.15 Effects of the growing season on net photosynthesis of deciduous *Fagus sylvatica*. Light dependence of CO$_2$ assimilation related to leaf weight in **a** sun leaves and **b** shade leaves of beech throughout the year. Only in spring do buds show respiration, which rises sharply with bud break. With leaf emergence, CO$_2$ is assimilated. Also, in autumn, only respiration is measured in buds. Sun leaves develop faster but age faster than shade leaves. In sun leaves, full development takes almost 2 months (until mid-June); they are fully active for only 1 month and start to yellow in August. (Schulze 1970)

favourable for growth, the process is primarily determined by soil fertility and available light. As soon as conditions become colder or drier, several options in the plant kingdom exist for coping with these conditions. In the Negev Desert in Israel, lichens and CAM, C$_3$ and C$_4$ plants grow next to each other (Fig. 12.17) (Schulze and Hall 1982). During the course of the day, they behave differently regarding their CO$_2$ assimilation, transpiration and stomatal conductance. Lichens do

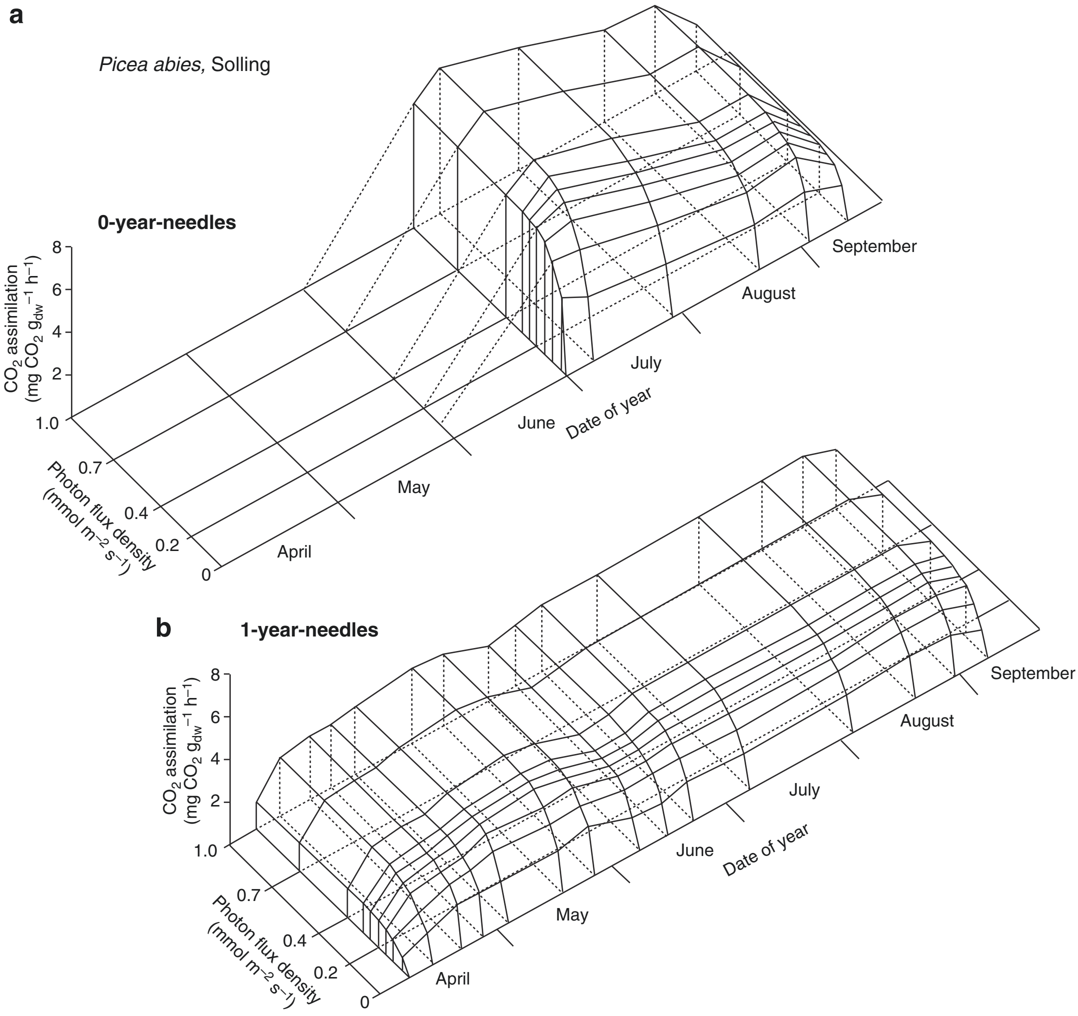


Fig. 12.16 Effects of the growing season on net photosynthesis of the conifer *Picea abies*. Light dependence of CO_2 assimilation based on leaf weight in **a** the current year's spruce needles and **b** 1 year old spruce needles throughout the year. Young needles develop later in the year than leaves of beech (Fig. 12.15). Development requires about 5 weeks before needles reach the highest rates of CO_2 assimilation. With the reinforcement of the cell walls in leaves, which continues until autumn of the current year, the rate of CO_2 uptake per dry weight decreases. In contrast, the rate of CO_2 assimilation is lower in the 1 year old needles than in the current year's needles but is constant for about 5 months. Ageing occurs after 3–5 years. (Fuchs et al. 1977)

not regulate water relations. Their CO_2 assimilation is restricted to a few hours in the morning after the falling of dew. Their growth is minimal. Nevertheless, lichens are among the most successful organisms in this desert. They settle on each stone and form extensive crusts on the loess soil. In contrast, the CAM plant *Opuntia* occurs in the Negev as an introduced plant, but *Caralluma negevensis* is an indigenous CAM plant, which behaves similarly (Lange et al. 1975). CAM plants assimilate during the night and at high soil moisture also during the day. Transpiration is substantially lower at night than for other species during the day. Despite the favourable relation of assimilation to transpiration, CAM plants in the Negev are rather rare, probably because of climatic conditions in the late Holocene, which limited invasion from other regions (Chap. 17).

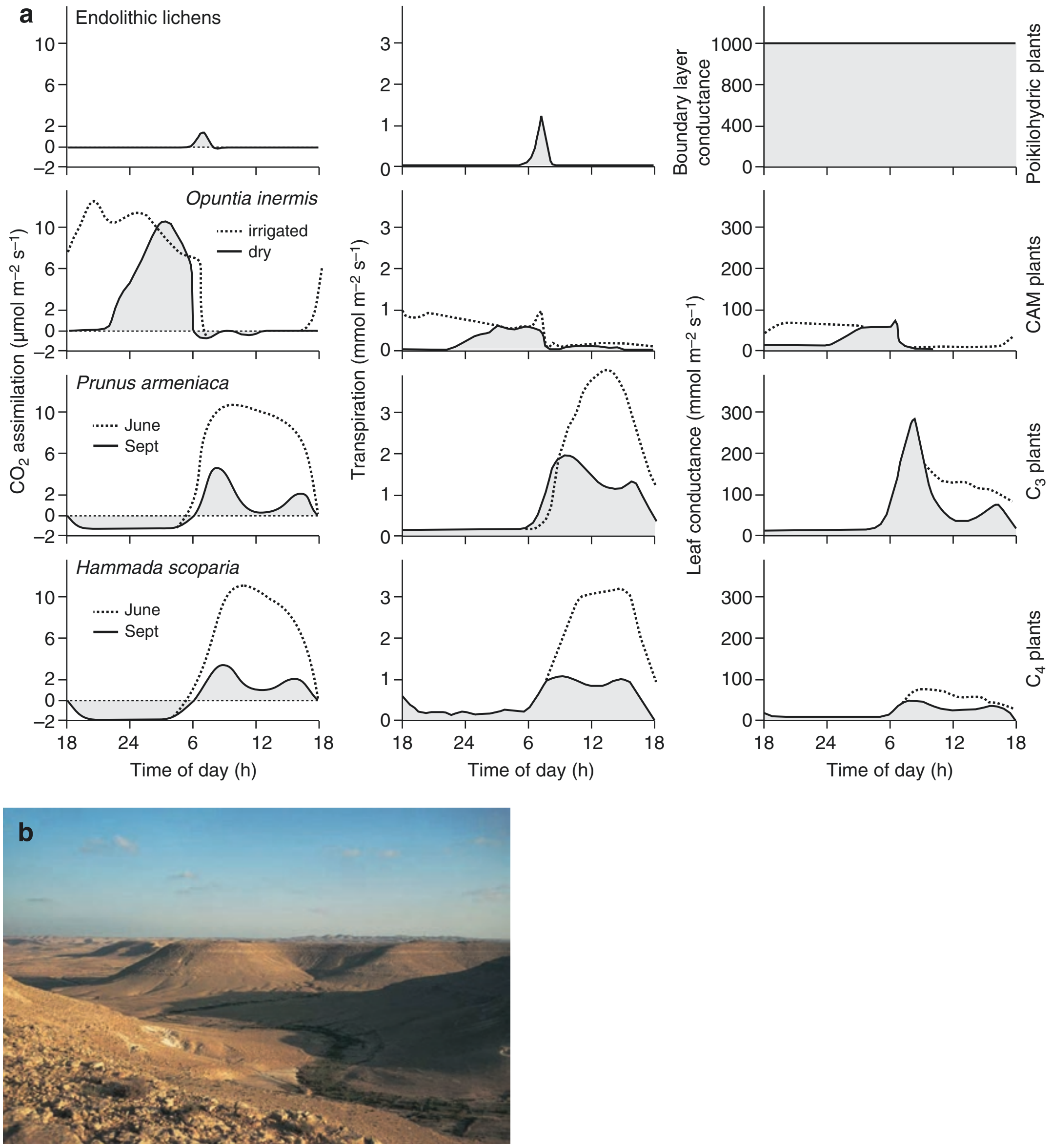


Fig. 12.17 Daily courses of leaf gas exchange of various plant types. **a** Daily changes in CO$_2$ exchange (CO$_2$ assimilation positive values; respiration negative values), evaporation and leaf conductance in various plant types in the Negev Desert: endolithic lichens, crassulacean acid metabolism (CAM) plants (*Opuntia inermis*), C$_3$ plants (*Prunus armeniaca*) and C$_4$ plants (*Hammada scoparia*). **b** The Negev Desert: slopes are occupied by dwarf bushes (*Artemisia herba alba*, *Zygophyllum dumosum*, *Reaumuria negevensis*), stones are covered with endolithic lichens and, *Caralluma negevensis* (a CAM succulent) may be found in the stone's shade. In the valley, remains of terracing from Nabatean farmers, currently used by Bedouins for wheat growing, are otherwise covered by the C$_4$ plant *H. scoparia*. (Photo: E.-D. Schulze)

C$_3$ and C$_4$ plants respond similarly to soil drought. Both attain similar rates of photosynthesis on dry soils; the rate decreases with soil drying. In summer, both species have a daily course with two peaks in CO$_2$ uptake and a "**midday depression**" caused by dry air. It is to be expected that the transpiration of C$_3$ plants is slightly higher than that of C$_4$ plants; this is related to the significantly lower stomatal conductance of C_4 plants. The potential advantage of a high assimilation capacity is not used by C_4 plants in nature; rather, it is used to avoid water stress. Despite this, C_4 plants settle not at extremely dry sites in the Negev but in the more favourable valley floors, which also have higher salinity. This does not mean that C_3 plants suffer maximum water stress at the dry sites. They regulate their water relations and physiological activity by leaf shedding. At the end of the dry period, the water status is more favourable for plants growing on a dry slope than for evergreen C_4 plants in the valley floors (Kappen et al. 1976).

With such a range of responses, the question remains as to whether there is a basic principle for the regulation of physiological activity. As the coupling of CO_2 assimilation to the atmosphere occurs via the stomata, through which in turn also water is lost, very different options exist for regulation, which balances photosynthesis and transpiration. It is striking that maximum photosynthetic rates are rarely attained at most sites. Most of the time, plants operate — in temperate woodlands as well as in desert regions — at an **average rate of CO_2 assimilation** that is about 50% of the maximum rate. This also applies to stomatal conductance. In temperate climates the actual rate of CO_2 assimilation is limited by light; in arid climates it is limited by light and air humidity.

Photosynthesis depends on the physiological activity of RubisCO and the CO_2 concentrations in the mesophyll and the atmosphere, but it is also regulated by stomata and dependent on the energy balance. It is basically not possible to write a simple equation to describe the relation between climate and assimilation, as the Penman–Monteith equation does for the dependence of evaporation on changes in leaf conductance ($\delta E/\delta g_L$; Chaps. 9 and 10). Cowan and Farquhar (1977) simplified the problem by assuming that photosynthetic activity remains constant. They came to the conclusion that there should be a balance between the response of assimilation ($\delta A/\delta g_L$) and transpiration ($\delta E/\delta g_L$) resulting from the change in leaf conductance. Neglecting the energy balance and possible changes in photosynthetic capacity, they concluded that "optimal" regulation, as expressed by λ, occurs when:

$$\frac{\delta A}{\delta E} = \lambda \qquad (12.23)$$

where A is a species-specific rate of CO_2 assimilation that is constant, at least over the course of a day. The ratio $\delta A/\delta E$ describes the slope of the relation between CO_2 assimilation and transpiration (A_L/E_L), which is also known as **leaf water use efficiency**. A/E differs from A/g, the **intrinsic water use efficiency** of stomatal regulation. Both terms differ again from the water use efficiency of canopies (A_{canopy}/E_{canopy}), which contain the effects of the atmospheric boundary layer and evaporation as well as respiration from soil surfaces (Chaps. 9 and 16), and they also differ from agricultural water use efficiency, which is based on plant growth (NPP/E) or on grain yield (grain/E) (see Schulze 1982).

The limits of this interpretation are at the next higher organisational level, the canopy of vegetation. It appears to be of limited use for an individual plant to behave optimally at the leaf level when the saved water remains in the soil and either seeps further into the soil profile, evaporates from the crust or is used by the plant's neighbours. With "non-cooperative behaviour" of neighbours (i.e. with excessive use of resources), the individual that is acting optimally might lose because the "neighbouring opportunist" has used almost all of the water. This is particularly relevant if the saved resource is required to maintain the life of the "optimiser" during drought conditions. This situation is observed under arid conditions as diversity of species and structures increases: equalisation of **opportunistic** (non-optimised) and **conservative** (optimised) CO_2 uptake and use of water does not occur. An opportunistic response is usually coupled to the ability of vegetation to complete development quickly (**annuals**), while conservative behaviour is coupled with slow development of vegetation and storage of resources over several growing seasons (**perennials**); an example of this is the invasion of *Bromus inermis* into the *Artemisia tridentata* steppe of North America, which was initiated by cattle grazing (Chap. 13, Sect. 13.5).

12.4.9 Distribution of C_3, C_4 and Crassulacean Acid Metabolism Species in the Course of Earth History

On the basis of the physiological characteristics of C_3 and C_4 plants, there is differentiation of these two photosynthetic types in the Earth's vegetation. Because of their high-temperature optima for photosynthesis and their ability to use high light intensities, C_4 plants (particularly perennials) are more prevalent than C_3 plants in subtropical **savannas and grasslands with summer rains** (Fig. 12.18a). In contrast, the main distribution area of C_3 grasses (often annuals) is in the **winter cold steppes** (Fig. 12.18b). The balance in the distribution of the two physiological types depends on the interactions of temperature, light and atmospheric CO_2 concentration.

The distribution of CAM plants in comparison with C_4 plants is botanically very interesting but is of rather secondary importance regarding the global C cycle. **Succulents** are mainly distributed in **coastal deserts with cool nights** (in South Africa and Namibia, Chile, Baja California and Tenerife) (Fig. 12.18c). The PEP carboxylase of these coastal succulents is adapted to low night temperatures. Independently of this, CAM plants can also be found in warm, humid, moist rain forests. These include epiphytic orchids and some tree species of the genus *Clusia* (Clusiaceae; Lüttge 1999). The PEP carboxylase of these genera is adapted, like C_4 plants, to high temperatures, showing that the distribution pattern of CAM succulents with their major distribution in cold coastal deserts does not depend on the temperature response of PEP carboxylase. It is probably caused by competition — that is, succulents grow too slowly to compete in the tropics, and in the tropical grasslands the humidity at night is too low, so stomata open during the night would also lose too much water.

With respect to the **geographic distribution of C_3 and C_4** plants, Ehleringer et al. (1997) showed — on the basis of the CO_2 concentration, light and temperature dependence of photosynthesis — that C_3 plants are competitively superior to C_4 plants at increasing CO_2 concentrations (Fig. 12.19a, b). During the Pleistocene, the atmospheric CO_2 concentration was at about 250 ppm; in that CO_2 climate, C_4 plants were superior to C_3 plants even at temperatures of 10 °C during the growing season. It is assumed that with increasing CO_2 concentrations, C_4 plants might be outcompeted in natural vegetation and have to move into climates with higher temperatures except under very dry conditions (Ward et al. 1999; Van der Kooi et al. 2016). The success of *Z. mays* in agriculture, with its expansion to the north with global climate change, may contradict this hypothesis, but in agriculture, competition between plant species is avoided. For current temperature and CO_2 distributions on Earth, C_3 plants dominate at latitudes greater than 45° north and south (Fig. 12.19b).

This observation is supported by the N requirement, which is higher for C_3 than for C_4 plants (Fig. 12.19d). Under **arid conditions**, the N concentration in leaves is high because of high N supply from soils after rains which triggered nitrification to increase. Also, growth of plants is limited by drought and the N concentration thus increases. In addition, nitrification in the soil is more drought resistant than the growth of plants. The N concentration decreases in the soil with increasing precipitation and increasing plant production. In subtropical arid climates, annual C_3 plants are superior to C_4 plants, while with high precipitation, C_4 perennial grasses dominate C_3 grasses. This has consequences for the use of land. The Sahara Bedouin move their herds to grazing sites with annuals that also have a high N concentration, while with higher precipitation, settled people pursue agriculture with C_4 grasses, which were perennials in their original forms (Penning de Vries and Djitèye 1982; MacFadden and Cerling 1996).

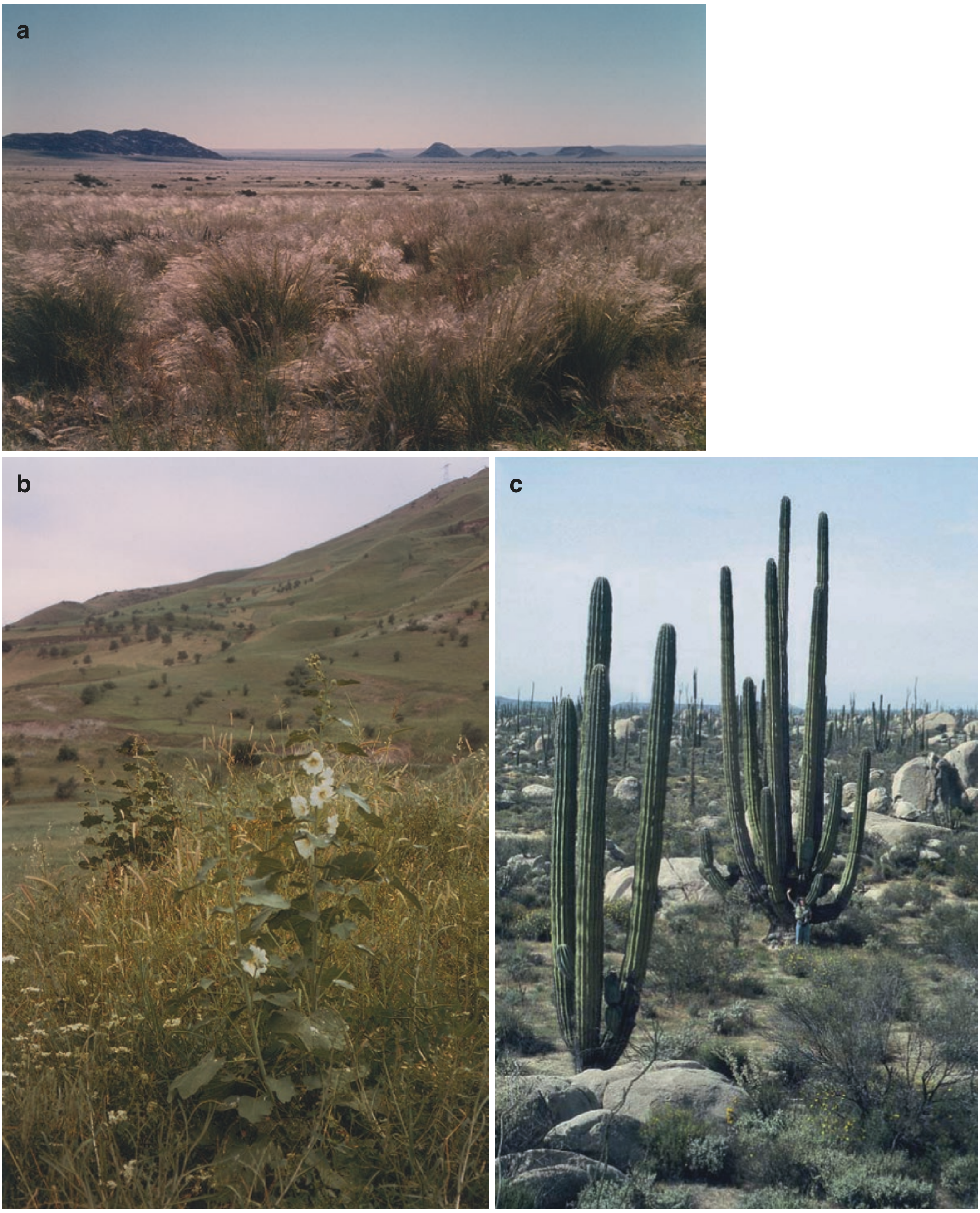


Fig. 12.18 Effect of soil on vegetation cover under arid conditions. **a** View of a tropical grassland in Namibia at about 200 mm rainfall of summer rains, when water is available at high temperatures. Thus, perennial C_4 grasses and single succulents of the genus *Euphorbia* are typical. **b** View of a continental steppe in Kazakhstan. Water is available after the snowmelt at a low temperature followed by a summer drought. The vegetation is characterised by annual and perennial C_3 grasses and shrubs (e.g. *Altaea* spp.), a higher proportion of annuals and Leguminosae (e.g. *Astragalu* spp.) and single shrubs (*Crataegus* spp.). **c** View of a succulent desert in Baja California, with *Pachycereus pringlei* as the dominant cactus species. In the undergrowth are shrubs of *Larrea tridentata*, *Encelia* spp. and *Ambrosia* spp., among others. (Photos: E.-D. Schulze)

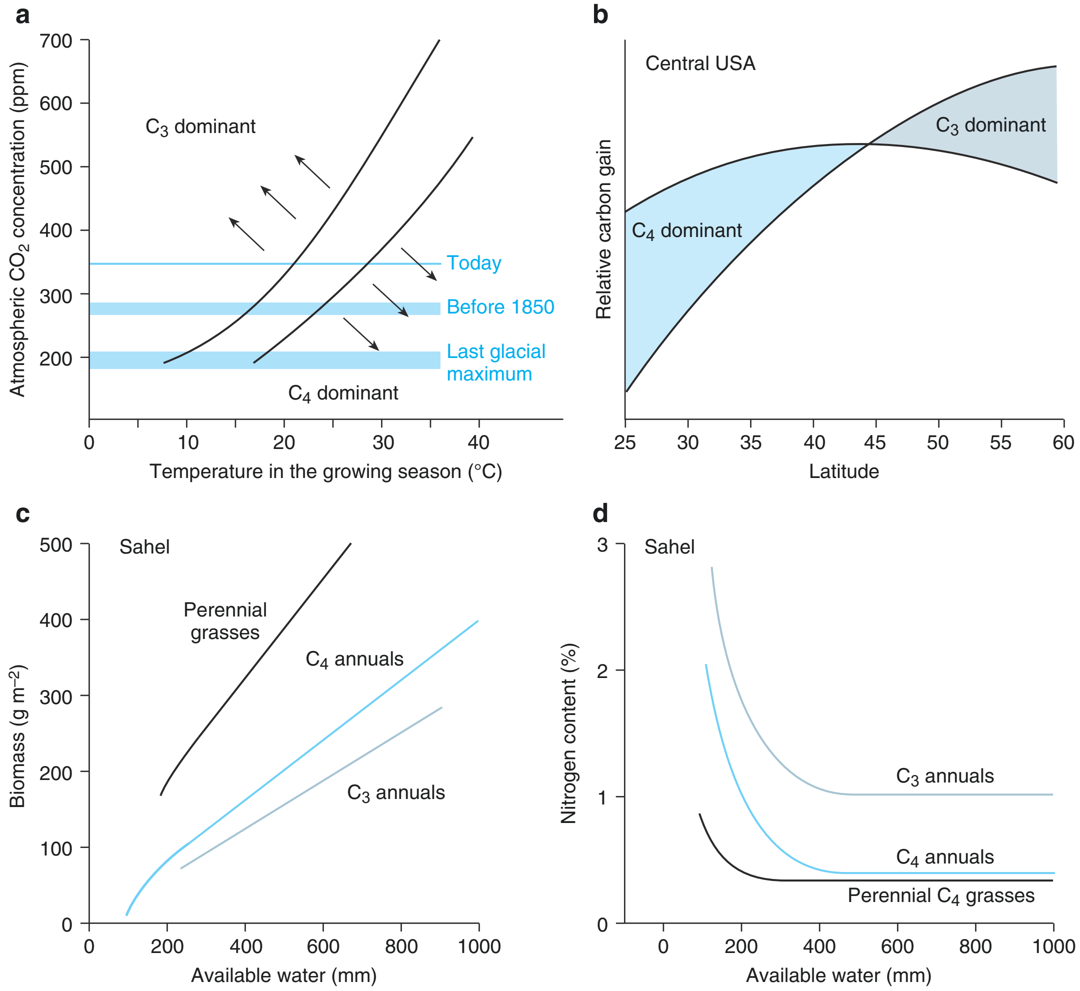


Fig. 12.19 Effects of drought and temperature on CO_2 assimilation, leaf N concentration, growth and biomass of C_3 and C_4 plants. **a** Distribution of C_3 and C_4 species in relation to temperature in the growing season and atmospheric CO_2 concentration. The *blue lines* indicate the shift of the temperature–CO_2 regime since glaciation (Ehleringer et al. 1997). **b** Relative carbon gain of C_3 and C_4 species in relation to latitude at the present CO_2 concentration (Ehleringer 1978). **c** Changes in biomass and **d** changes in nitrogen concentration of C_3 and C_4 plants with water availability from rainfall in the Sahel. C_4 plants have a lower N concentration than C_3 plants and therefore have a lower forage quality for grazing. (Penning de Vries and Djitèye 1982)

12.5 Growth and Storage

12.5.1 Whole-Plant Carbon Balance and Biomass Production

Ultimately, photosynthesis serves the plant to produce biomass and seeds. Assimilates supply the material for an increase in the size of the plant structure (which is important for competition with other plants) and for storage of resources (which are required for regrowth after disturbances, flowering and production of fruits). The production of viable seeds is the ultimate measure of performance and fitness. Thus, the **carbon balance** is of ecological importance.

For biomass production, additional energy is required for anabolic processes in plant cells and organs that have no chloroplasts. This is independent of the energy required to maintain the existing biomass. In both cases this energy is made available by the consumption of carbohydrates. Net primary production (NPP) results from actual net photosynthesis (A) of foliage and all carbon losses from the plant, mainly autotrophic respiration of the whole plant (R_a), but also root exudates or volatile organic carbon emissions, generally measured over an annual time scale:

$$\mathrm{NPP} = A - R_{\mathrm{a}} \tag{12.24}$$

Net photosynthesis (A) is often also called **gross primary production** (**GPP**), a term generally used in association with ecosystem flux measurements (Chaps. 14 and 16), where GPP is calculated from net ecosystem production (NEP) and ecosystem respiration (including soils).

Species with highest photosynthetic rates ($A_{\max}$) do not necessarily have the highest GPP per plant or per ground area. Spruce, for example, has a C gain about 80% higher than that of barley even though it has only about 25% of the photosynthetic rate of barley (Table 12.1). One reason for this difference is that spruce has double the leaf mass per hectare of barley, and the growing season of spruce is three times longer than that of barley. The deciduous beech is between these extremes. Costs for evergreen needle cover are paid, in spruce, by significantly higher respiration. Spruce invests relatively less carbon in the growth of branches than beech does. Therefore, the absolute stem growth of spruce that could eventually be harvested is almost a third higher than that of beech. For both tree species, the growth in stems is only a small fraction of the C gain (beech 15%, spruce 13%). The grain yield for barley would be comparable to the growth of stems, with a harvest index (grain yield/aboveground biomass) of 0.4, reaching about 1.8 t C ha^{-1}. This is about 20% of net photosynthesis and thus significantly higher than in trees.

Table 12.1 Carbon budget of *Fagus sylvatica* (beech), *Picea abies* (spruce) and *Hordeum vulgare* (barley)

	Beech	Spruce	Barley
Maximum CO_2 assimilation (mg CO_2 g^{-1} h^{-1})	10	5	20
Gross primary production (t C ha^{-1} year^{-1})	8.6 [100%]	14.9 [100%]	8.3 [100%]
Respiration	2.4 [28%]	7.8 [52%]	1.7 [20%]
Leaf	1.3	6.4	1.5
Shoot	0.4	1.0	0.0
Stem and root	0.7	0.4	0.2
Litter	3.2 [37%]	2.9 [20%]	6.6 [80%]
Leaves	1.8	1.2	4.4
Fine roots	1.4	1.7	2.2
Growth	3.0 [35%]	4.2 [28%]	0.0
Large roots	0.4	0.7	0.0
Branches	1.4	1.5	0.0
Trunk	1.3 [15%]	2.0 [13%]	0.0

The estimates are based on a beech forest (Schulze 1970; Scarascia-Mugnozza et al. 2000), a spruce forest (Fuchs et al. 1977; Scarascia-Mugnozza et al. 2000) and a barley crop (Biscoe et al. 1975; Jones 1994). Growth of leaves or needles is assumed to be equal to litter production

The example shows that **allocation** of carbohydrates is important for understanding of NPP and that the plant kingdom has many ways of regulating biomass production. These are, among others, the C budget over a growing season (mean rate of net photosynthesis × mean leaf area × length of growing season (Schulze 1982)), the distribution of assimilates to different organs (Stitt and Schulze 1994), the respiration in existing and growing biomass (Merino et al. 1982) and carbon storage (Chapin et al. 1990).

12.5.2 Respiration

Respiration of mitochondria is obviously an important component affecting the C budget (Amthor 1989). The amount of C required for the synthesis of certain products may differ by two orders of magnitude according to the product (Penning de Vries 1975, 1983) (Table 12.2).

It is possible to calculate the C requirements of growing organs from their products, but the

Table 12.2 **Respiratory CO_2 requirement for synthesis** of plant substrates required for growth and for respiration of organs. (After Penning de Vries (1975))

		Respiratory CO_2 requirement (mg CO_2 g^{-1})
Substrate	Organic acids	11
	Carbohydrates	170
	Proteins	544
	Lipids	1720
Plant organ	Leaves	333
	Stems	278
	Wood	426
	Rice grain	186
	Beans	420

requirement of existing organs is not quantified by this approach. McCree (1983) suggested separating two functions of respiration:

- **Growth respiration**, R_g (respiration serving growth).
- **Maintenance respiration**, R_m (respiration for maintenance of organs).

Dark respiration (respiration of autotrophic plants (R_d)) of a plant with weight W consists of the maintenance respiration and the growth respiration of the growing tissues *dW/dt* (all expressed in milligrams of CO_2 per plant per unit of time):

$$R_d = R_m + R_g \frac{dW}{dt} \tag{12.25}$$

Dividing by the weight results in respiration rates per unit of weight:

$$\frac{R_d}{W} = \frac{R_m}{W} + R_g \times \frac{dW}{dt} \times \frac{1}{W} \tag{12.26}$$

where *dW/dt* × 1/*W* is the **relative growth rate** (**RGR**). If R_d/W is plotted as a function of RGR for short periods of time, a straight line emerges. The slope of this relationship corresponds to the growth respiration (R_g) and the intercept (intersection with the *y* axis) equals the maintenance respiration per plant weight (R_m/W) (Fig. 12.20). The relation between R_m and R_g depends on the time during which individual organs are photosynthetically active. In herbaceous plants the root respires during 24 h, while the shoot shows net respiration only during the night. In woody plants, branch and sapwood respiration corresponds to the number of living cells during 24 h.

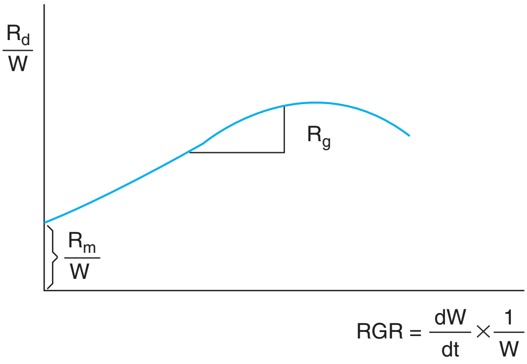


Fig. 12.20 Visual presentation of the definitions of growth respiration (R_g) and maintenance respiration (R_m). If dark respiration (R_d per unit of weight) is measured in relation to the relative growth rate (RGR = increase in weight over time per unit of total weight of the plant), the slope of the curve is a measure of growth respiration and the intercept on the *y axis* is a measure of maintenance respiration per unit of weight. (Modified from Amthor (1989))

12.5.3 Growth

Growth of plants and the processes of biomass accumulation can be shown as a conceptual model, as there is no satisfactory physiological model explaining the regulation of C allocation to various organs (Fig. 12.21). The term "growth" is often used to describe the process used to accumulate carbon over time, which is, more specifically, the **growth rate** (Lambers et al. 1998). "Growth" would thus be the integral over time. In woody plants, especially trees, the **increment** of volume or diameter is used as being equivalent to the "growth rate", and "growth" is the integrated **biomass** at a given time, which may be, in part, dead material (e.g. wood of trees).

CO_2 assimilation depends on the CO_2 gradient (Δc), the stomatal conductance (g) and the leaf area (LA). Assimilates thus form an assimilate pool as intermediary storage from which the distribution to growth of green and other supporting organs takes place. In both cases, growth is added to the existing biomass. Particularly with growth of leaves, self-shading may occur and old leaves are shed (Sect. 12.6.3: *Urtica dioica*). There is also root turnover. Growth of leaves has a positive feedback effect on CO_2 assimilation, which produces additional requirements for nutrients and water. Thus, transpiration (E) as a function of water vapour gradient (D_L), stomatal conductance and leaf area is also affected. Growth of non-green organs has a negative feedback effect on CO_2 assimilation but positively affects the uptake of nutrients and water. Regulation of assimilate distribution and rates of senescence determines the balance between assimilatory and respiratory organs, where the latter are responsible for the uptake of nutrients and

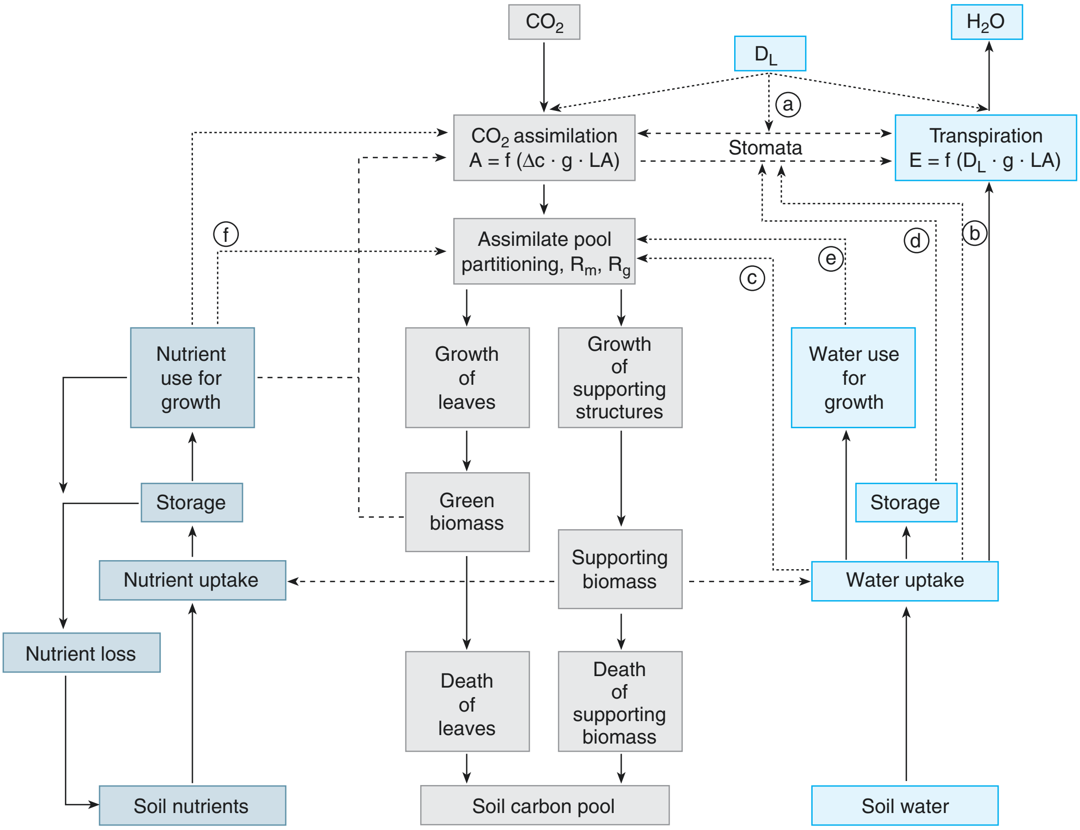


Fig. 12.21 Schematic model of plant-internal carbon, water and nutrient pools and fluxes. Fluxes are shown as continuous lines. Important feedbacks are depicted as broken lines. See text for details. The regulating factors are *a* the effects of climatic factors; *b*, *c*, *d* and *e* regulation of stomata and carbon partitioning by the water balance; and *f* regulation of assimilation and C partitioning by the nutrient relations. Storage of water is a small quantity. (Schulze and Chapin 1987)

water. A special situation occurs in woody plants because the biomass that dies remains in the stem (**heartwood**) and only a small ring of vessels (**sapwood**) is metabolically active (Chap. 10, Sect. 10.2). Thus, the heartwood does not respire but serves to increase the vegetative structure and is thus very important in competition with other species.

There are several regulatory mechanisms for the “communication” of the shoot and root. The carbohydrate supply is decisive for the growth of the root and stem. Roots regulate, via cytokinins, the partitioning and allocation of assimilates to the shoot and the roots. The supply of nutrients, particularly nitrate (Scheible et al. 1997; Beck 1999), and the availability of carbohydrates (Schulze et al. 1991) may also act as signals regulating carbon allocation.

The gain and consumption of resources need not be synchronous. This applies particularly to the uptake of nutrients and CO_2 assimilation. If plants were to only take up nutrients synchronously with their consumption, neighbouring plants would have the possibility of gaining these resources if they were available in the soil (Chap. 11). At the same time, light absorption must be controlled to maintain the existing photosynthetic apparatus when CO_2 uptake is low (e.g. in drought periods). Without the transfer of electrons to carbon, nitrogen or sulphur, chlorophyll would be damaged by irradiation. Therefore, assimilate and nutrient pools are important as “**storage**” from which various requirements of the plant are covered independently of CO_2 assimilation.

12.5.3.1 Relative Growth Rates

After germination, plant growth follows an exponentially increasing curve, which decreases in annual plants with flowering but may continue until death in trees. The basic rule is that larger plants grow faster because they have a larger available leaf area. The rate of carbon accumulation increases continuously with tree size (Stephenson et al. 2014) where the growth rate (G) is defined as the change of weight over time (Hunt 1982).

$$G = \frac{dW}{dt} \tag{12.27}$$

To compare the growth performance of different species, the **relative growth rate** is defined as G per weight of the growing plant (W):

$$\mathrm{RGR} = \frac{G}{W} \tag{12.28}$$

Since growth is determined by the carbon input from photosynthesis, RGR can also be defined by the available **leaf area** (**LA**) per plant mass and the rate of growth per leaf area (Lambers et al. 1998)

$$\mathrm{RGR} = \frac{\mathrm{LA}}{W} \times \frac{G}{\mathrm{LA}} \tag{12.29}$$

RGR may reach values of >2 g $\mathrm{g^{-1}}$ $\mathrm{week^{-1}}$ in fast-growing annuals (e.g. *Poa annua*) and decrease below 1 g $\mathrm{g^{-1}}$ $\mathrm{week^{-1}}$ in woody species of high biomass despite high absolute growth (Grime 2001).

12.5.4 Storage and Feedback

Plants use resources for growth, defence against herbivores and reserves/storage, and they accumulate these resources if their gain is greater than their consumption. Only part of these resources may be recovered later on, and only this fraction is considered a "store" (Fig. 12.22). Subdivision into accumulation and formation of reserves is thus difficult. **Formation of reserves** is the process in which stored products at the time of their production compete with growth processes. In contrast, **accumulation** is a process in which the acquisition of resources exceeds consumption by growth at the time of production.

The C, N, water and energy relations in the plant interact (Fig. 12.21). To understand the interactions between various plant parts, a model with several levels and feedbacks is required (Fig. 12.23). An excess of carbohydrates not only

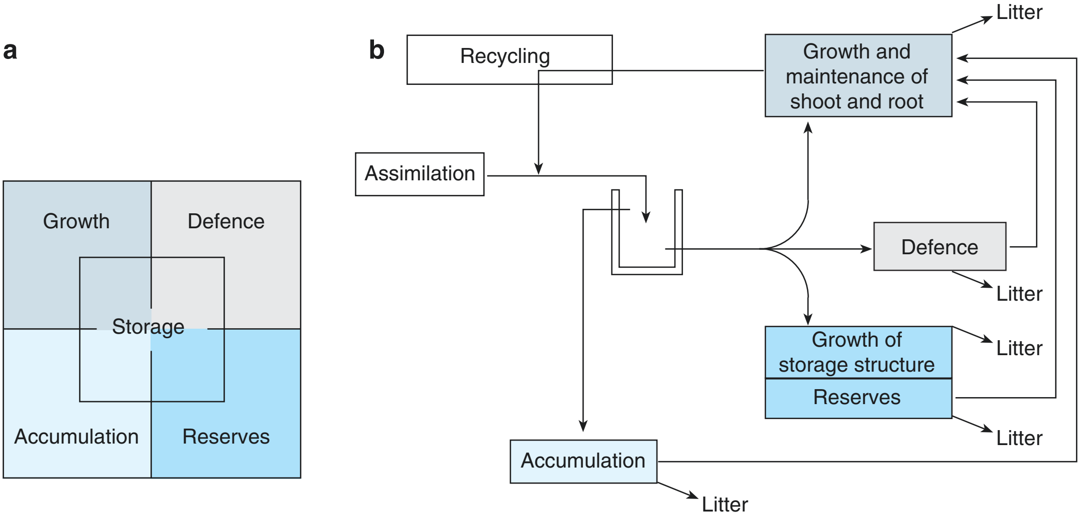


Fig. 12.22 Schematic presentation of partitioning of carbon in a plant for particular functions. **a** Growth, defence, formation and accumulation of reserves. Only part of this carbon can be reallocated and is thus a "store". **b** Flux of carbon assimilates from CO_2 assimilation to growth and reutilisation of C with death of plant parts (litter fall). Accumulation occurs when C production (assimilation plus reallocation) exceeds immediate requirements and consumption. Formation of reserves occurs when the conditions for formation of storage products (e.g. starch) compete with growth processes. Short-term assimilate pools, which act as physiological control, are shown as a "well". (Chapin et al. 1990)

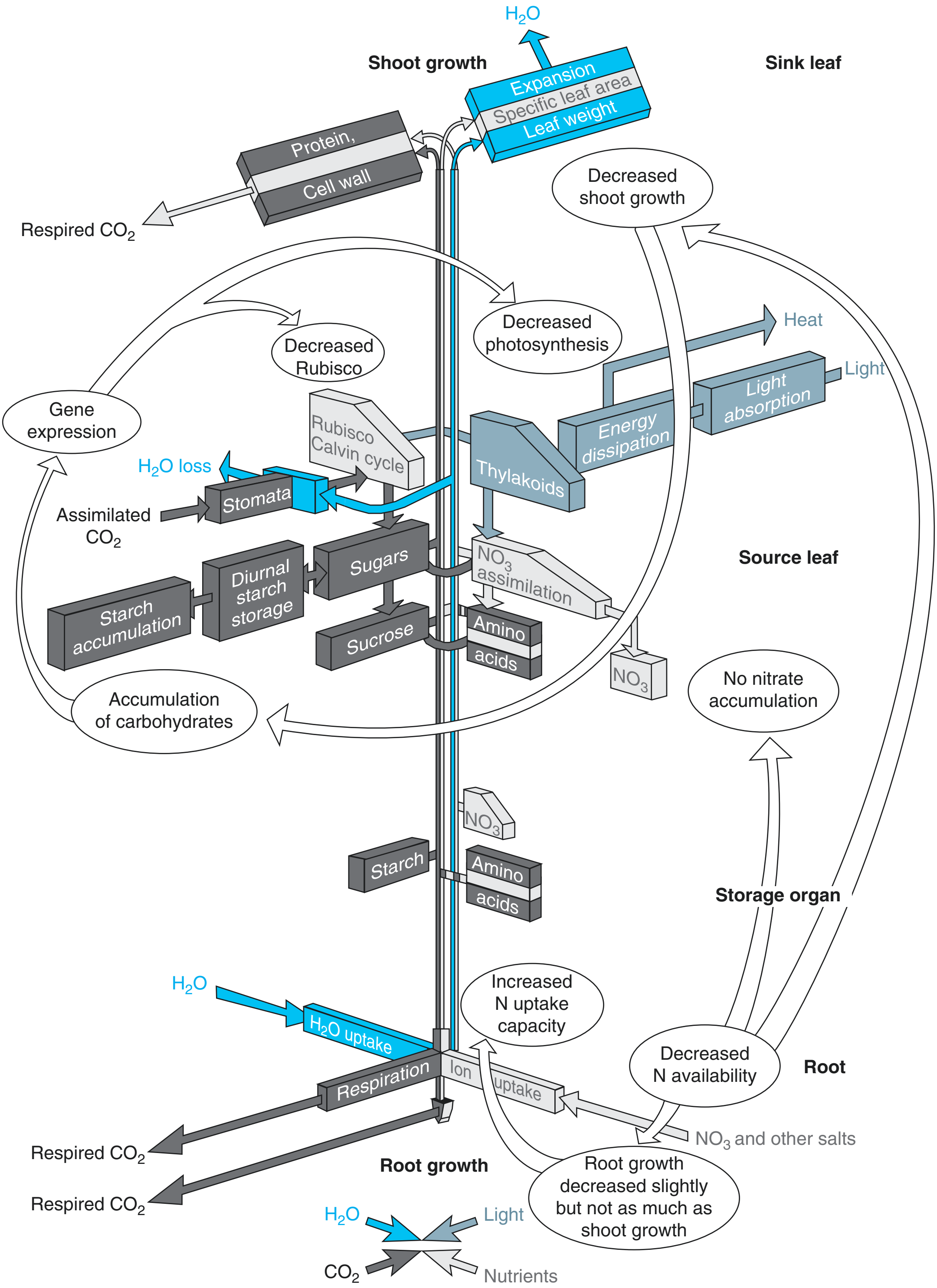


Fig. 12.23 Conceptual model showing the sequence of changes in metabolism resulting from changes in resource availability. Nutrient deficiency results in reduction of growth in sink organs. Consequently, carbohydrates accumulate in source leaves. This causes ribulose-1,5-bisphosphate carboxylase/oxygenase (RubisCO) and light-harvesting systems to decrease (yellowing of old leaves with N deficiency). Thus, nitrogen becomes initially available again for growth. (After Stitt and Schulze (1994))

affects the **sink activity** in the shoot and root but also stimulates nitrate reduction and may lead to inhibition of photosynthetic activity to produce amino acids. Conversely, lack of nitrogen leads to reduced growth and thus to accumulation of carbohydrates and a reduction in photosynthetic capacity.

12.6 Carbon and Nitrogen Balance in Different Plant Types

Plant species differ by more than one order of magnitude regarding the relation between green organs for assimilation (leaves, needles, phyllodes, phylloclades) and non-green biomass. In tropical rain forests, only 2% of the biomass is contained in leaves, while in a temperate meadow, leaves contribute about 50% to the total biomass (Table 12.3). Nevertheless, the material gain per year in the tropical forest is no different from that in tropical grasslands and is higher than that in temperate grasslands. The average monthly NPP calculated over a year is very similar (Fig. 12.24), showing that there are structural elements that not only differentiate the plant kingdom but also act compensatorily regarding biomass production. An analysis of plant structures that is independent of the taxonomic description of a species leads to the term **life form**.

In plant ecology, different classifications of **plant life forms** have been distinguished according to the authors who described them:

- Raunkiaer (1934): Trees, shrubs, perennial herbs, annuals, geophytes.
- Grime (1974): r-strategies, K-strategies, stress-tolerant species.
- Monsi (1960): Annuals versus perennials, herbaceous versus woody, evergreen versus deciduous.

The definition of life forms has had two goals. Geographers and botanists visiting "foreign" countries wanted to describe unknown vegetation. They also wanted to analyse those strategies with which plants survived in their environment. The term "life form" has been extended by the term "**functional groups**", which comprise not only structural characteristics but also physiological characteristics (C_3/C_4 plants, N_2 fixers,

Table 12.3 Change in biomass and net primary production in various types of global vegetation, and relative distribution of biomass to leaves, above-ground organs and roots (Schulze 1982)

Vegetation types	Biomass (kg m^{-2})	Primary production (kg m^{-2})	Mass of green material in photosynthetically active organs (%)	Mass of only respiring organs	
				Above-ground woody material (%)	Roots and underground shoots (%)
Evergreen trees of tropical and subtropical forests	41–65	6–17	approx. 2	80–90[a]	10–20[a]
Deciduous trees of temperate zones	18–60	0.4–2.5	1–2	approx. 80[a]	approx. 20[a]
Evergreen trees in taiga and mountain forests	20–90	0.2–1.5	4–5	approx. 75[a]	approx. 20[a]
Dwarf trees of the forest margins	5–10	0.1–0.5	approx. 25	approx. 30[a]	approx. 45[a]
Ericaceous dwarf shrubs of heaths and tundra	1–6	0.1–0.5	10–20	approx. 20[a]	60–70[a]
Meadow plants	–	0.1–1.3	approx. 50	–	approx. 50
Alpine grasslands	0.1–3	0.1–1	approx. 30	–	approx. 70
Steppe plants					
Wet years	–	0.1–1	approx. 30	–	approx. 70
Dry years	0.3–3	–	approx. 10	–	approx. 90
Plants at high altitude	0.1–4	0.1–0.5	10–20	–	80–90

[a] A large part of the mass is dead supporting material

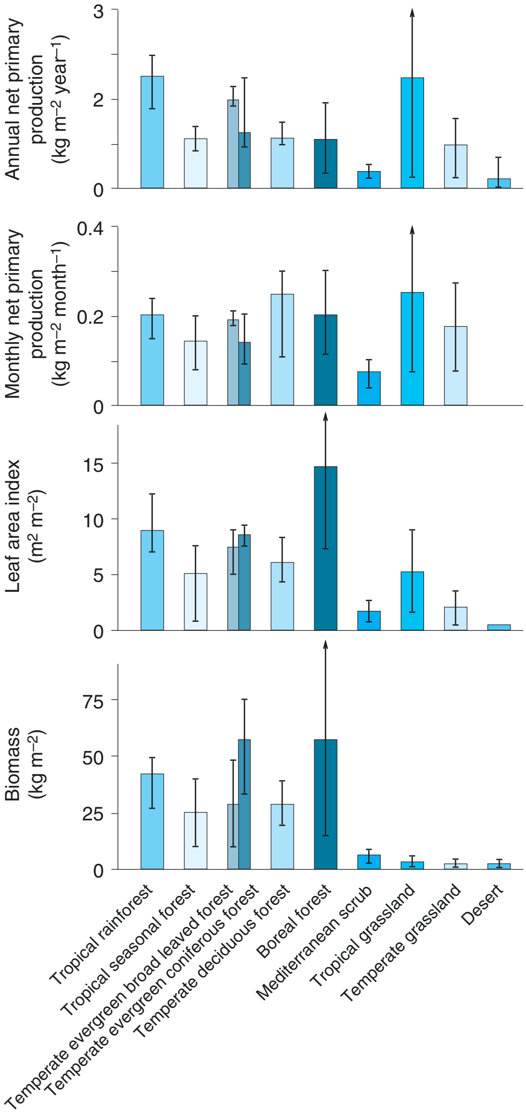


Fig. 12.24 Biomass, annual net primary production (NPP_a), leaf area index and monthly net primary production of different types of vegetation in different regions of the globe. Despite large differences in biomass and NPP_a, the monthly rate of NPP is very similar—that is, differences in NPP_a are mainly caused by differences in the duration of the growing season. (Schulze 1982)

deep roots and many others; Chap. 13, Sect. 13.2, and Chap. 20). To understand the distribution of resources in plants, the scheme by Monsi (1960) has proved particularly useful. With use of the Monsi system, the most important forms are explained in Sects. 12.6.1 to 12.6.4 on the basis of their C budget (Fig. 12.21).

12.6.1 Annual Species

Annual species are described by the following characteristics:

- They have a short life cycle (2–3 weeks from germination to formation of seeds — for example, in *Linaria haelava*, Plantaginaceae)
- All tissues are physiologically active (woody structures are exceptional — for example, in *Helianthus annuus*, Asteraceae)
- The shoot to root ratio is shifted towards the shoot (strong feedback coupling of leaf formation to the production process). There are hardly any subterranean storage organs (except after breeding for cultivation — for example, in radish (*Raphanus sativus*, Crucifereae))
- They have a high yield of seeds after a very short developmental phase. The harvest index (yield/above-ground biomass) may reach up to 60% (for example, in rice (*Oryza sativa*, Poaceae))

Within a very short time, multiplication of individuals in the population occurs as the number of seeds is large. Thus, annuals colonise wastelands very effectively (the r-strategy according to Grime (1974)). With a limited area there is soon intensive competition between individual plants, as the leaf area index (LAI) is determined by the available light.

Crop plants are the most important representatives of annuals. In wheat (Fig. 12.25), particularly in older varieties, the number of shoots increases after germination, as several flowering shoots form from the basal rosette. After about 40 days, this leads to competition between shoots and self-thinning (Chap. 13, Sect. 13.3), with some of the resources stored in the dying shoots being relocated into the remaining plant. One could consider the formation of such extra shoots a strategy to occupy space and to store resources from the soil temporarily. Only after stabilisation of the number of shoots and the development of a closed leaf cover with constant LAI does the biomass of the remaining shoot increase. Growth of new roots and leaves terminates with

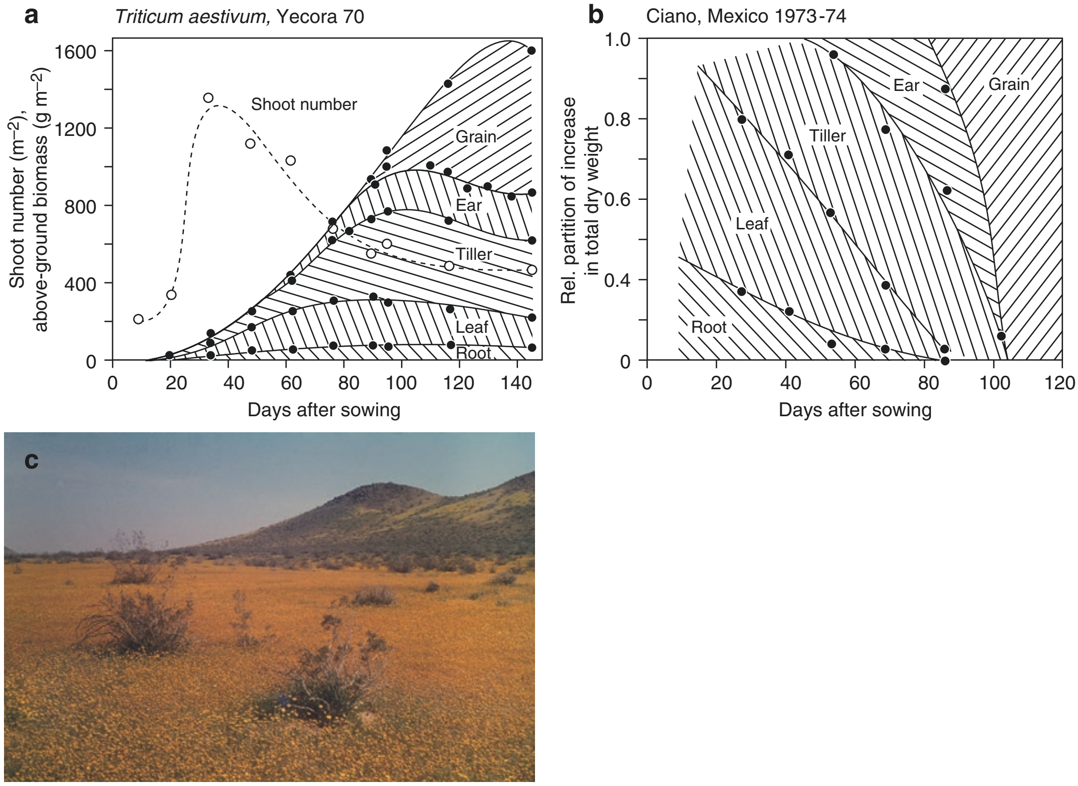


Fig. 12.25 Development of annuals. **a** Changes with time in above-ground biomass and numbers of shoots from germination to harvest in wheat, showing the cumulative biomass of individual organs. The *hatched areas* show the biomass per organ. **b** Relative distribution of growth in roots, leaves, stems, ears and grain, showing accumulated growth in the individual organs (Schulze 1982). **c** Flowering of the winter annual *Coreopsis bigelowii* in the Mojave Desert, which is dominated in the dry season by the perennial shrub *Larrea tridentata*. (Photo: E.-D. Schulze)

formation of the ear. At the end of the life cycle, all resources that can be relocated are deposited into the developing grains. Filling of grains with carbohydrates and amino acids is supported by awns, which do not possess functional stomata and thus can supply carbohydrates for the final ripening of seeds even at the beginning of a drought. The physiological achievement of these plants is enormous, if one considers that in a very short time (1–2 weeks), 60% of the above-ground dry weight is relocated from senescing leaves and stalks to grains in a regulated manner. The relation of grain yield/ above-ground biomass (the **harvest index**) in high-yielding crops is 0.5 (wheat) to 0.6 (rice) and is thus significantly higher than for natural annuals (0.3). In modern cultivars, only one flower stalk develops from the rosette and the distance between plants is set by seeding. The number of leaves along the stalk is reduced because competition with neighbours is avoided by seeding distance and application of herbicides.

Regarding the distribution of assimilates, annuals are a plant group with very high relocation from source leaves in the direction of new leaves from the time of germination. This is possible because these plants have a very effective transport system for water and an effective root system to take up nutrients. Most herbaceous species have **arbuscular mycorrhizae**, which are very effective in making phosphorus available from the soil (Chap. 11).

In comparison of annuals, which are native to soils of different fertility, species hardly differ regarding the vegetative phase with low N supply (Fig. 12.26; Fichtner and Schulze 1992).

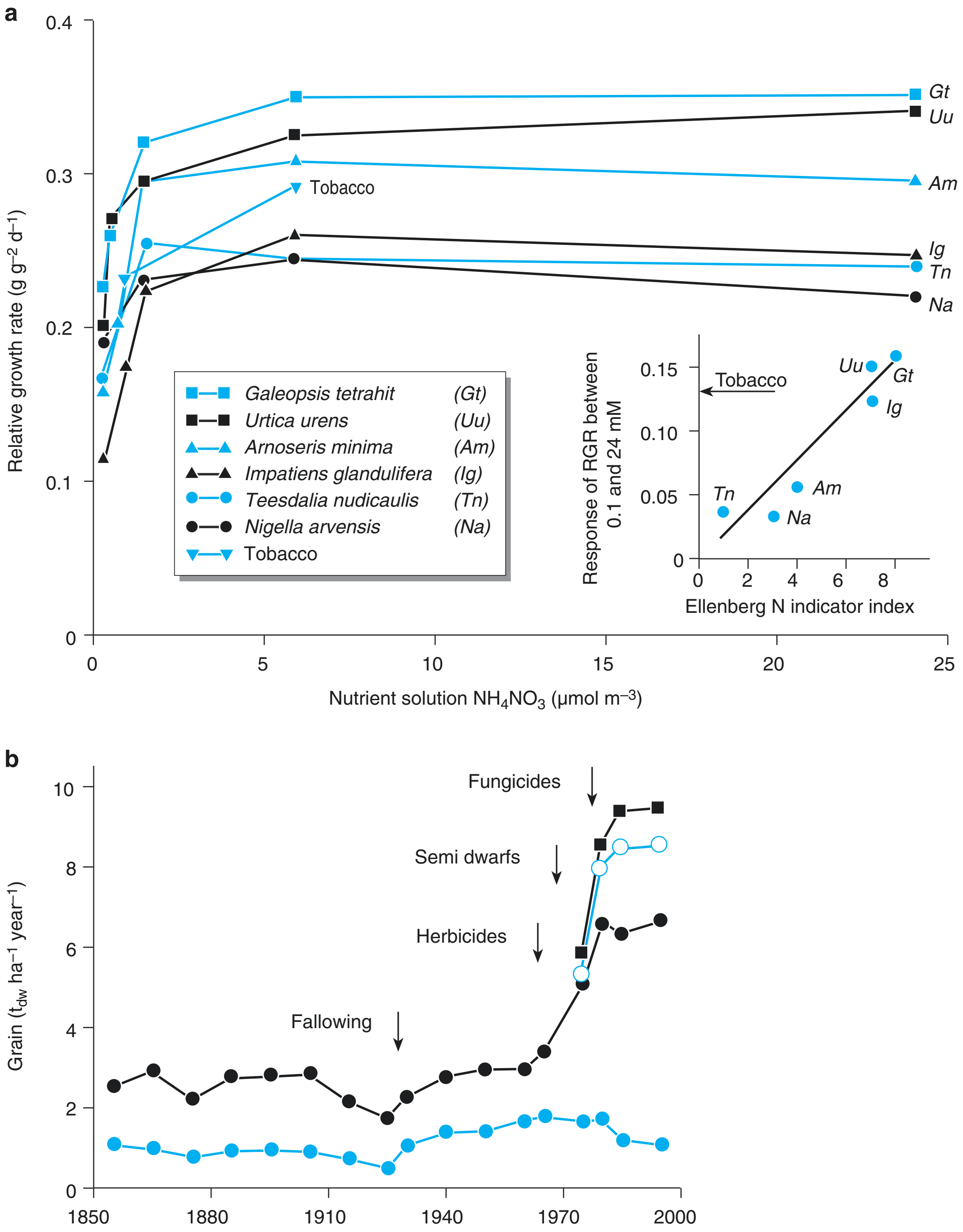


Fig. 12.26 Growth and grain production of annuals. **a** Alterations in biomass of native annuals in relation to the nitrogen concentration of the nutrient solution. As this is a physiological laboratory experiment, tobacco is used as a test plant. Tobacco has a particular function in ecophysiological laboratory studies, as it can be genetically transformed and single variables that influence growth can be regulated genetically. It is clear that some annuals of the native flora have faster growth rates than tobacco. The *inset* shows that the relative growth rate correlates with the Ellenberg indicator values for nitrogen (Fichtner and Schulze 1992); for tobacco studies, see Stitt and Schulze (1994). **b** Influence of particular crop management procedures on grain yield of wheat in the long-term experiment at Rothamsted Research, Harpenden, UK. Filled blue circles show wheat with no N fertilisation. (After Miflin (2000))

Growth rates of species adapted to nutrient-rich sites increase faster only with greater supply of resources. As shown in Chap. 11, the main difference between species is that only those species that are adapted to the lower N supply (*Teesdalia nudicaulis*, *Filago vulgaris*) flower with a low N supply. Species of nutrient-rich sites lack **flowering induction** at nutrient-poor sites, remain vegetative (*Galeopsis tetrahit*, *Urtica urens*) and die.

In natural vegetation, annuals are particularly successful on sites with a periodically abundant supply of resources (deserts, flooded meadows). The limits of the distribution of annuals are determined by the length of the growing season; therefore, they are missing in boreal climates. There are various adaptations to increase the duration of vegetative growth. This applies particularly to **winter annuals** (e.g. *Galium aparine*), which germinate in autumn and flower the next year. For these plants, as for all winter plants, including winter wheat, there is the danger of dying because of frost drought. A lengthening of the growing period to extend flowering occurs in facultative biennial species (e.g. *Daucus carota*) and true **biennials** (e.g. *Arctium tomentosum*).

With annuals it is possible to use a model to study the structural characteristics of a productive **crop plant**. This is independent of the potential physiological change possible through gene modifications (Miflin 2000). The structural characteristics include:

- **One stalk per seed**: Formation of fewer stalks has been achieved by breeding. Also, the distance between seeds when sowing the crop regulates competition, and the supply of resources should be controlled by fertiliser and herbicides.
- **Length of stem**: Stems with approximately three leaves are needed. It has been shown that the uppermost leaf (the flag leaf in cereals) is essentially responsible for grain filling. The lower leaves supply the stem and root. A tall stem is an advantage in competition with other species. However, if weeds are excluded by use of herbicides, long stalks are not needed. A short stem also stands better when carrying a large ear.
- **Many seeds per stem**: The yield of grain is proportional to the number of seeds and less to the weight per grain. An additional seed is thus a better C sink than a larger grain, which is important for the relocation of material during seed ripening.
- **Position of the leaf**: Erect leaves determine, at constant irradiation, the maximum leaf area index and thus regulate the C budget.
- **Depth of root**: Deeper-reaching, thin roots are desirable to increase root volume and exploit resources to as great a depth as possible. This is important for water relations at the time of seed ripening.
- **Awns**: Awns were bred out of crop plants because of their unpleasant characteristics during threshing. With machine threshing, the awn gains new significance as security at the time of seed ripening because stomata on awns are not functional; thus, awns continue to assimilate CO_2 even under severe water stress. Triticale — a crossing of *Triticum* (wheat) with *Secale* (rye) — is one of the very productive modern cereals with very long awns.
- **Control of diseases and competition**: Yields of cereals increase after regulation of nutrition (fertiliser application) and by (1) use of herbicides, (2) changes of crops, (3) introduction of dwarf varieties and (4) use of fungicides (Miflin 2000) (Fig. 12.26b).

12.6.2 Biennial Species

Biennial species have a transitional position between annual and perennial herbaceous species. They occur in the succession only for a short period between ruderal and perennial vegetation (Fig. 12.27) (Heilmeier et al. 1997). This is also expressed in the life cycle, which may be variable depending on resources. With a high supply of nutrients, biennials may flower in the first year after germination, but flowering may be delayed to a third year under poor nutrition.

Biennials are characterised by:

- Generally a life cycle analogous to that of annuals in the first year, but the formation of a

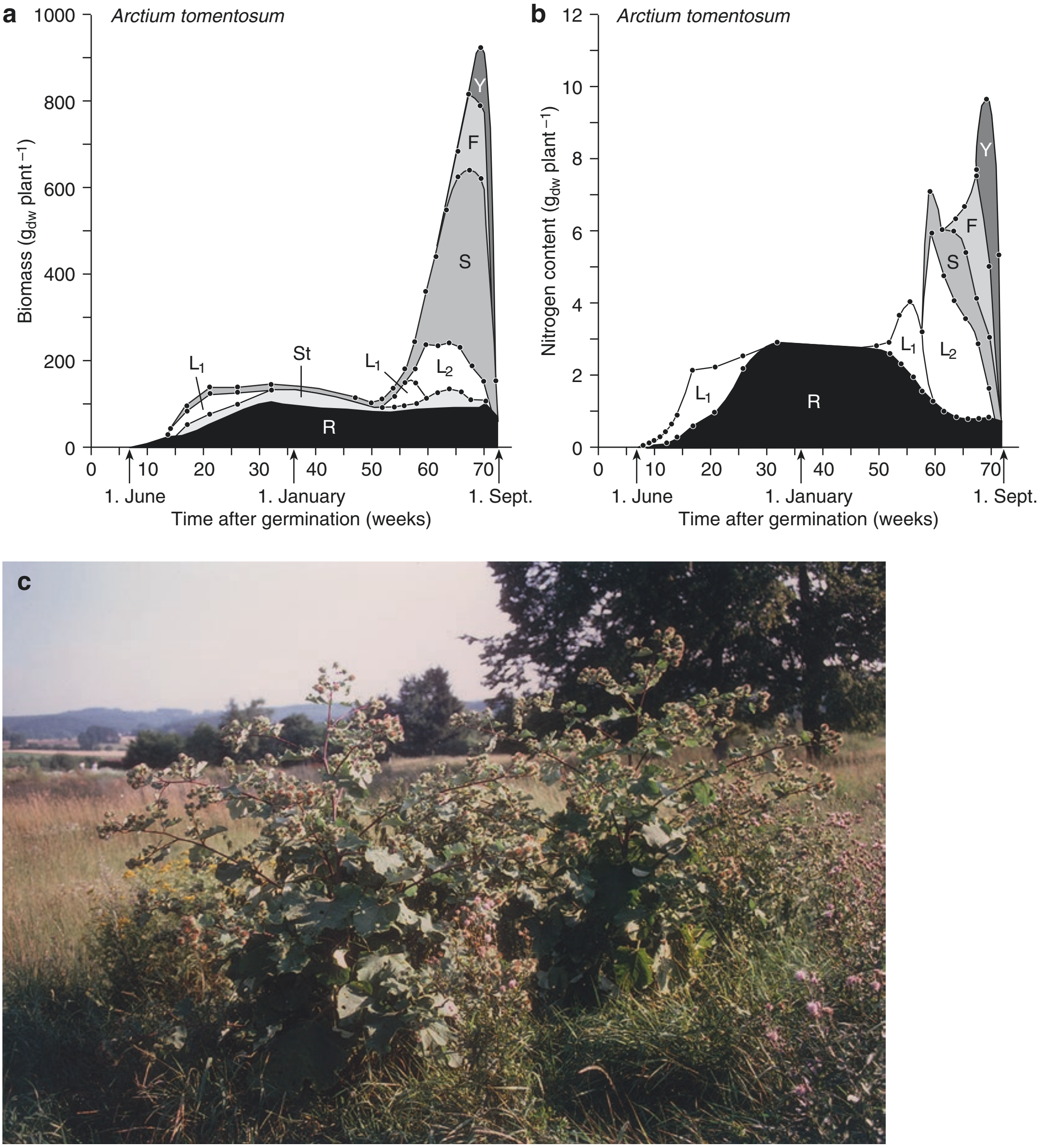


Fig. 12.27 Development of biennials. Changes with time in **a** dry mass and **b** amount of N in different organs of *Arctium tomentosum* during 2 years of growth from germination until death after seed production. Development of the storage roots (R) is particularly noteworthy for it supports early leaf emergence from the rosette in the second year. The large biomass production of *A. tomentosum* in its second year is mainly due to its "exploitation" of the habitat due to its rosette leaves (L_1) in its first year and the basal rosette in the second year (L_1 and L_2), making possible the harvest of nitrogen from an area of about 1 m^2. This nitrogen gain permits growth of large flowering shoots (S) and the leaves on the shoot (F), which assimilate CO_2 after L_1 and L_2 die. All resources are finally transferred to the fruits (Y). During flowering, when the rosette and the stem leaves are already dying, the plant receives some 15% of its total N from the root. Exploitation of the area in which the plant grows by the basal rosette is so complete that the seeds of this species can establish themselves in the area without significant competition from other species. Thus, the biannual *Arctium* occupies an area for many years (Heilmeier et al. 1986). **c** *Arctium lappa* in a ruderal situation in competition with couch grass and thistles at the Campus of the University of Bayreuth. (Photo: E.-D. Schulze)

storage organ (often the hypocotyl) occurs very early and is genetically fixed. This storage organ is formed during growth (formation of reserve) or is filled with resources only after the termination of growth (accumulation).
- Storage of free amino acids predominantly, sometimes lipids.
- Early emergence in the following year using stored N products at a time when the root is not yet active.
- Formation of the basal rosette, which reduces competition with other species, depending on the size of leaves, and which also enables exploitation of a larger ground area with reduced competition from neighbours. Thus, also the volume of soil and the availability of resources — in particular, N and water — increase.
- Formation of a flowering shoot in the second year, supplied with nitrogen by the dying leaves of the basal rosette.
- Relocation of all resources to the seed during a period of 1–2 weeks, with a harvest index corresponding to that of annuals.

Because of the formation of the basal rosette, biennials are often very successful in outcompeting other species, even in the long-term. After flowering, many seeds drop at the site where the basal rosette of the mother plants died, leaving space for establishment of the next generation. Seeds germinate and, because of high interspecies competition, only a few are left at the end of the new growing season and then flower again. Thus, large-leaved biennials are able to occupy habitats for decades.

Biennial species occur at a very wide range of sites. At nutrient-poor sites, these are often biennial legumes, which are able to fix N_2 (e.g. *Melilotus officinalis*); at nutrient-rich sites they are usually species with large leaves. Species from nutrient-poor sites often have many small seeds; those from nutrient-rich sites have a few large seeds.

Biennials are a suitable object to consider strategies and transitions between storage and accumulation. In *Arctium*, formation and filling of the **storage organ** occur after the development of the leaf so the store accumulates excess products. In contrast, for *Dipsacus sylvestris* or *Daucus carota* the development of the store occurs at the same time as the development of the leaf, so storage competes with growth (Steinlein et al. 1993).

12.6.3 Perennial Herbaceous Plants

Perennial herbaceous plants behave similarly to annuals after germination, forming storage organs, creeping shoots, tubers and other vegetative organs, which may also serve for vegetative multiplication but do not enter the reproductive phase. Thus, perennial species have the following characteristics:

- Individual plants live for many years.
- Storage of C and N dominates reproduction.
- Reserve material allows plants to start early and maintain a long period of growth.
- Many species are able to die back to very few vegetative apexes.

In contrast to annuals where the increase in the population is most important, in perennial species it is maintenance and growth of the individual plant. Seed production is delayed to a time with good resources and storage. In perennial **grasses**, carbohydrate transport occurs in the phloem of a rhizome predominantly in the direction of the vegetative apex, which is younger than the producing leaf. The vegetative growth is the main carbon sink (Chap. 11). There is very little transport into older organs. Thus, older shoots are more “insurance” for situations where the young shoot is damaged. In this case, older shoots regrow.

Different **storage products** may accumulate at different times in the same shoot during the season (Fig. 12.28). *U. dioica* stores starch in summer. This starch is required in autumn to produce new runners after the death of the above-ground shoots. Starch is also used as an energy source for the reduction of nitrate, which is mainly available in the soil in autumn and is taken up after above-ground parts have died. Storage of amino acids thus occurs in autumn and winter and is the

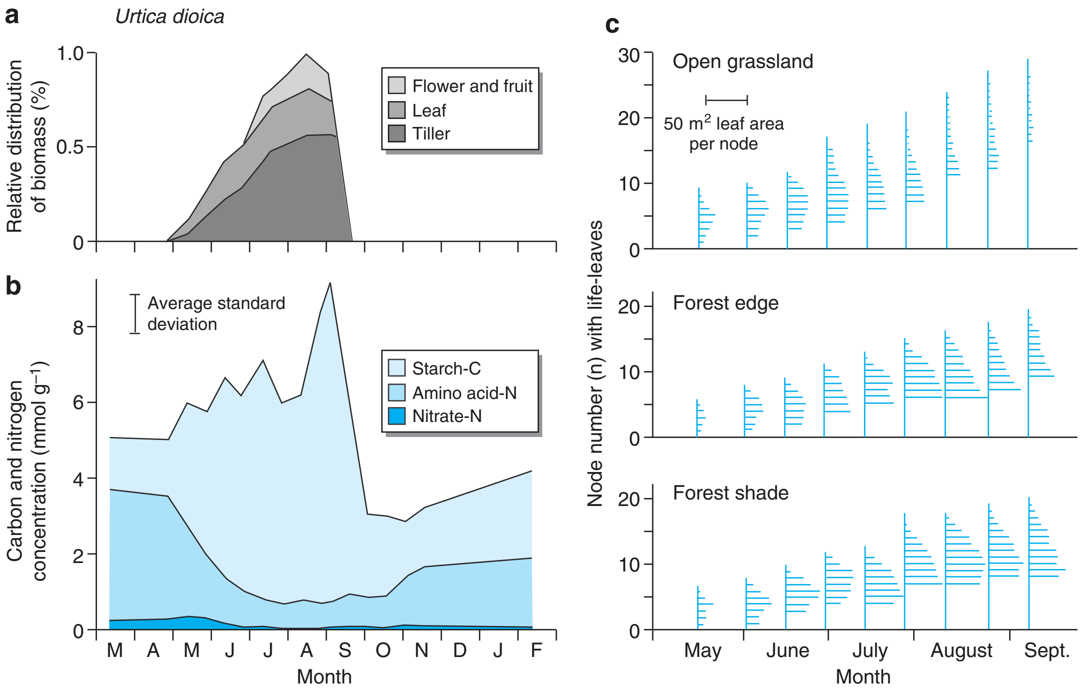


Fig. 12.28 Development of herbaceous perennials. Annual progression of **a** growth in biomass and **b** changes in the storage products starch, amino acids and nitrate in the rhizome of the stinging nettle, *Urtica dioica*. It is interesting that rhizomes of nettles function in summer as a starch store and in winter as an N store for amino acids. **c** Schematic of leaf development in *Urtica*. The height of the stems and the size of the leaves are shown. With growth of stems, new leaves are formed at their tips; at the same time, leaves at the base of the stem die, so the number of leaves per stem remains constant. In shaded areas, fewer but larger leaves are formed. In open areas there are more leaves of smaller area. In this way, more stems per unit of area can exist in brightly illuminated locations. (Stitt and Schulze 1994)

basis for early emergence in spring. Young leaves are very quickly self-sufficient with respect to carbon. In herbaceous perennial plants there is, as in the situation of annuals, very early strong competition between shoots. The LAI remains constant and individual shoots compete by continuous formation of new leaves, with the old leaves dying simultaneously. Thus, *U. dioica* leaves are exchanged about four times during the growing period. Formation of below-ground rhizomes also shows a variety of structures in nettles. On nutrient-poor sites, rhizomes (which may survive for up to 3 years) meander through the soil and new shoots are formed at their tip, while the old end of the rhizome dies off. On nutrient-rich sites, rhizomes (which may survive for more than 12 years) are probably destroyed only by burrowing animals. On dry sites, taproots with secondary growth in thickness are formed, supplying water to a whole cohort of shoots with short rhizomes. Therefore, it is not surprising that it is very difficult to eradicate nettles (*U. dioica*) or ground elder (*Aegopodium podagraria*) in a garden. Couch grass (*Agropyron repens*) and broadleaved dock (*Rumex obtusifolius*) are examples of successful perennial rhizomatous weeds in crops and grassland.

Besides their success under high nutrition, perennial herbaceous species are successful where there are **continuously poor growing conditions**. They occupy shady forest floors, salty sites, dry sites and cold habitats. Perennial herbs occur at greatest elevation in alpine regions (*Stellaria decumbens* in the Himalayas above 6000 m) and go furthest north in the Arctic (*Saxifraga oppositifolia*, 83° north). *Alocasia macrocarpa* is the species with the lowest measured light saturation of photosynthesis (80 µmol

m^{-2} s^{-1} photons). Some perennial herbaceous species flower only once and require several years to store sufficient resources for flowering. These “monocarpic” species include not only *Agave* spp. but also bamboo species and tropical alpine giant rosette plants, which have woody stems (*Lobelia* spp., *Senecio* spp.; Chap. 4).

For herbaceous perennial species, there appears to be a **maximum plant size** of the vegetative body, when respiration in non-photosynthetically active organs consumes the C gained by leaves. Bananas have to be cut back to maintain the development of flowers and fruits. Some species (e.g. sunflower) cope with this limitation of structure by secondary lignification of the shoot. Secondary thickening is rare in perennial herbaceous species but does occur, for example, in the root of nettles. Many herbaceous temperate species have close relatives in the woody flora of the tropics.

The balance of resources between respiring and assimilating biomass is most obvious in grasses where maximum production is reached with **grazing** or **mowing**. Grasses are most successful for such a use as they are able to regenerate new leaves quickly after grazing because of the intercalar growth of the leaf sheath and the meristems being close to the ground.

12.6.4 Woody Plants

Woody plants — trees and shrubs — are always perennial. They set flowers and fruits only after years. They differ from herbaceous species particularly by the fact that the growth of the woody body is balanced by the transformation of living **sapwood** into dead **heartwood**. This does not have to occur synchronously, but it is influenced by environmental conditions and species-specific characteristics. For the whole plant, the capacity of the xylem determines the leaf area, and the leaf area in turn determines the growth and area of sapwood. This was shown in the “**pipe model**” (Shinozaki et al. 1964), starting from a balance of growth processes in the stem, branches and leaves, regulated by the conductive area of the xylem. The ring-porous oak has only three to five functioning annual rings, in contrast to spruce, which has over 30, as spruce wood consists of tracheids with low hydraulic conductance and little ray parenchyma (Trendlenburg and Mayer-Wegelin 1955). It is important for the C budget that the respiring woody body remains in balance with the leaf mass. With use of non-respiring, dead biomass (heartwood) as the supporting apparatus, the functional limitation of the **size of the vegetative body** no longer applies, removing the limitation of growth for plants that do lignify. However, even in trees there is a functional maximum size which, however, is determined not only by the carbon but also by water and nutrient relations, even though the water relations are determined by the available sapwood. The tallest trees on Earth are found among *Eucalyptus marginata* (in southwest Australia; 140 m). The thickest trees are *Agathis australis* (in New Zealand; 7 m diameter, 50 m height; Fig. 12.29a). The species with the greatest volume is *Sequoiadendron giganteum* (in California; General Sherman tree: 96 m height, 6 m diameter at breast height, volume >1000 m^3). The death of big trees is set not by the C balance but by extreme events such as wind or by pathogens that destroy the heartwood, as shown for *Abies sibirica* in Siberia (Schulze et al. 2012).

The **maximum size** at which respiration of non-green parts is in balance with assimilation of green parts is achieved not only in large trees but also in shrubs. For *Calluna vulgaris*, for example, flowering depends on grazing, which regulates the ratio of green to non-green biomass. For un-grazed plants the non-green biomass increases, the number of shoots remains constant and the investment in flowers decreases with age. Similar effects have been shown for fruiting trees (apple), which need to be “cut back” to change the carbon and hormonal balance in order to increase the yield of fruits.

Storage of carbohydrates and nitrogen-containing substances is important in trees. Leaf emergence and early tree ring growth occur from the mobilisation of amino acids and carbohydrates from the woody parenchyma. In spruce, N concentration in the sap water increases to >5 mM in spring. Bottle trees (e.g. *Adansonia digitata*) do not store water but do store carbohydrates

Fig. 12.29 Tree structures. **a** Barrel-like trees: *Agathis australis* (kauri) in the subtropical forest of New Zealand's North Island. The base of the stem is branchless and may achieve 45 m in height with a 6–7 m diameter. The dimensions become clear with Waltraud Schulze, climbing a liana, in the picture. **b** *Eucalyptus pauciflora* as an example of sprouting plants—that is, tree species that regenerate from hypocotyl buds after fire. **c** An example of extreme longevity: *Pinus longaeva* in the Snake Mountains of Nevada at 3500 m above sea level. The trunks may be more than 4000 years old, resulting from death of the cambium which, except for a narrow strip, grows in balance with the resource supply from the shoot. Thus, an equilibrium is achieved between assimilation and respiration and between the shoot and root. The trunk grows only in width on the side with the living cambium—that is, the trunk develops in the shape of a plank over a long period. A trunk in its broad aspect (with E.-D. Schulze in the picture) and **d** in its side aspect (with Valmore LaMarche in the picture). **e** Aerial roots of *Ficus* growing through the canopy of a rain forest in Costa Rica. **f** After reaching the ground with its aerial root and thus securing water, *Ficus* (in Lamington, Queensland) enmeshes the host with a root net and thus kills the host. **g** *Ficus superba* (in Yakushima) with stilt roots, which grow from the canopy to the soil, supporting the canopy and supplying it with water and nutrients. **h** Central hole in the trunk of a *Ficus*, showing the position of the original host. (Photos: E.-D. Schulze)

Fig. 12.29 (continued)

and amino acids for the next wet period (Schulze et al. 1998). In vegetation that regenerates by fire (Mediterranean vegetation), there are so-called **seeders** — species with fruits that open only with fire, allowing seeds to fall into the fresh ash and germinate. These species do not have storage parenchyma in their roots, and the starch concentration in the root is low (1.9 ± 0.5 mg of starch per gram of root dry weight). This contrasts with so-called **sprouters**, which emerge from the root after fire (Fig. 12.29b); these have 14.1 ± 3.3 mg of starch per gram of root dry weight (Bell et al. 1996). Obviously, in cold winter climates, mostly N is stored (as the soil is still cold at the time of emergence), while in fire climates, predominantly carbohydrates are stored, as the ash contains sufficient nutrients for the new vegetation.

A particularly impressive C economy exists in trees that become very old, with high **longevity**. *Pinus longaeva* (commonly known as bristlecone pine) is one of the longest living tree species (Fig. 12.29c, d) (disregarding species with runners), living for up to 5000 years. This species occurs in the high alpine dry regions of the Sierra Nevada. In this climate, wood is only slowly degraded and conditions allow only very slow growth. Most of the cambium dies within the first 1000 years. Only a small strip of the living cambium remains, keeping the ratio of green biomass to respiring biomass almost constant. The trees grow like a board, 1–2 m wide and only 10–15 cm thick. Without external interference (lightning, storms), these trees may potentially live forever (LaMarche et al. 1984; Fritts et al. 1991).

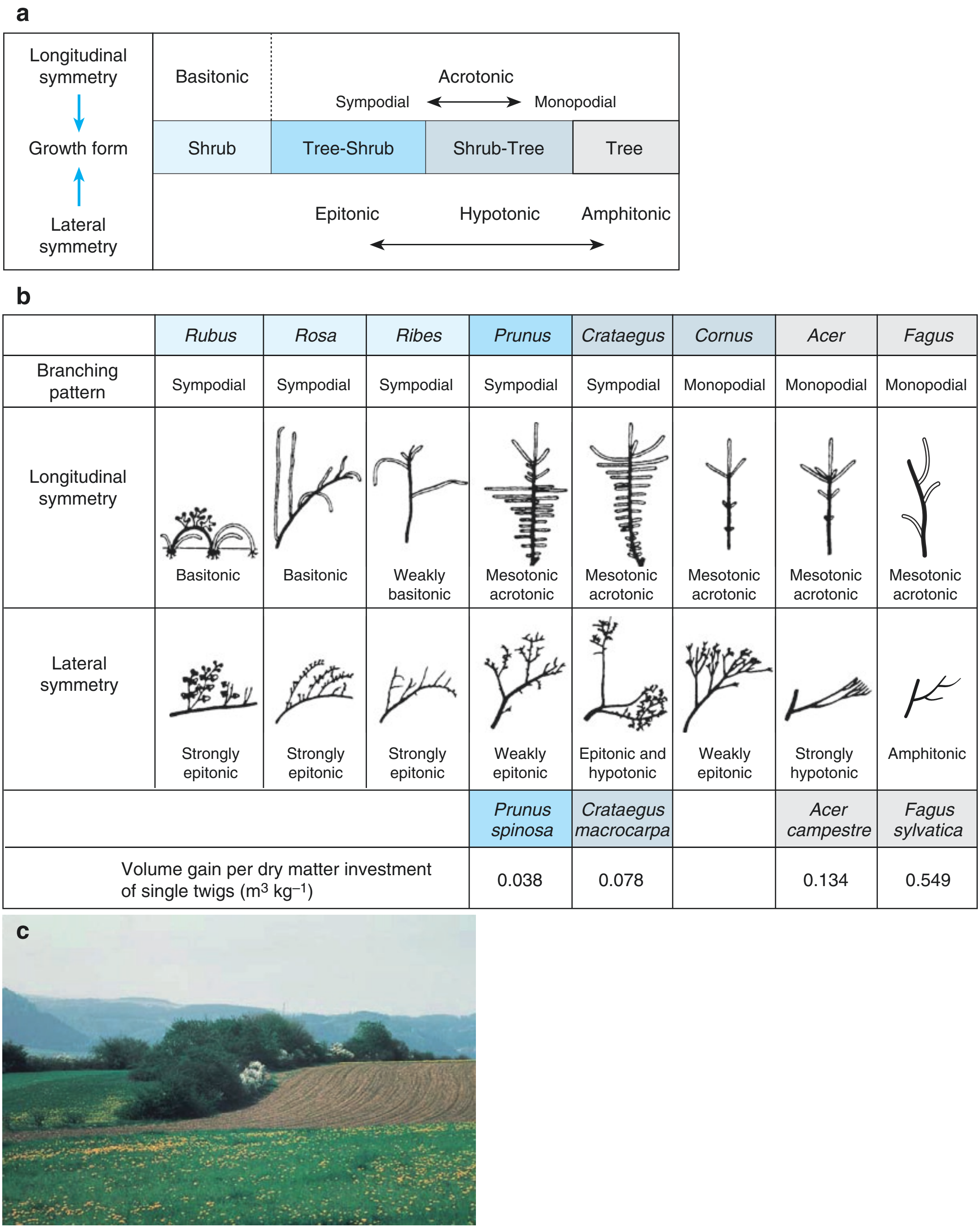
Among the many life forms termed “trees” (Vareschi 1980) are **figs**, which are masters of carbon resource economy. They germinate as epiphytes in the canopy of the rain forest and grow with a large aerial root through the canopy (Fig. 12.29e, f). As soon as the root reaches the soil and thus water, they enclose the host with a mesh of roots. The host dies as its phloem transport is interrupted by **strangulation** from the fig, which then uses nutrients released from the decomposing wood of the host. In the end, only a chimney-like structure remains of the host (Fig. 12.29h). The fig then increases in size by forming new aerial stilt-like supporting roots and conquers a new habitat for the tree. *Ficus benghalensis* (Fig. 12.29g) produces hundreds to thousands of stilt roots, which can cover an area of >20 ha and under which, according to Warburg (1913), “an army of 20,000 men could camp in the shade”. Similar areas are covered by *Populus deltoides*, developing underground runners, in the southern boreal forests of Canada.

Trees and **shrubs** are distinguished from each other by height (greater than or less than 2 m, respectively, according to Ellenberg (1978), or greater than or less than 5 m, respectively, according to the Food and Agriculture Organisation of the United Nations (FAO) (2000)) and are functionally distinguished by the dominance of regeneration buds (Fig. 12.30). In trees there is an apical dominance, also called **acrotony** (e.g. in spruce), in which the terminal bud remains dominant. The term **amphitony** is used if the terminal bud remains but one of the lateral buds gains dominance (e.g. in *Carpinus betulus*). In some trees the terminal bud dies off and the next bud on the upper side of twigs takes the lead, which is called **hypotony** (e.g. in *Acer pseudoplatanus* or *Tilia cordata*). Some deciduous trees (e.g. *A. pseudoplatanus*) have acrotonic growth in the juvenile period and hypotonous growth when older. In contrast, shrubs have renewal buds predominantly in the lower region of branches (e.g. in *Corylus avellana*, **basitonic dominance**) or on the underside of branches, also called **epitonic growth** (e.g. in *Rosa* spp. and *Rubus* spp.). Obviously, there are many transitions between these extremes, but it is usually possible to determine the tree form by the dominance of bud development along the main axis of the stem and along the branches. Thus, true trees are **monopodial** (one stem), while shrubs and tree-like shrubs are mostly **sympodial** (many stems). These different types of growth determine competition and succession in hedgerows (Küppers 1989).

In woody plants, the shoot–root communication depends on the species and is tuned so that shoot and root growth are tightly correlated (Fig. 12.31) (Heilmeier et al. 1997) even if, under extreme stress conditions, very different tree sizes are reached. For the almond (*Prunus dulcis*) there is a tight correlation between root and shoot biomass, as well as between the leaf area and the length of fine roots. Such regulation is also observed in basitonic shrubs. Evenari et al. (1982) called the phenomenon of root–shoot regulation “**survival through dieback**”, which is common in arid regions. In a dry year, part of the shrub dies back and only a few shoots survive, which are in balance with the roots.

In addition to the regulation of the respiring mass of their woody structure, trees have another means of regulation: the **life span of assimilatory organs**. A distinction is made between:

- **Deciduous** species (trees of temperate forests and rain-green savannas) with seasonal changes in leaves.



	Rubus	*Rosa*	*Ribes*	*Prunus*	*Crataegus*	*Cornus*	*Acer*	*Fagus*
Branching pattern	Sympodial	Sympodial	Sympodial	Sympodial	Sympodial	Monopodial	Monopodial	Monopodial
Longitudinal symmetry	Basitonic	Basitonic	Weakly basitonic	Mesotonic acrotonic	Mesotonic acrotonic	Mesotonic acrotonic	Mesotonic acrotonic	Mesotonic acrotonic
Lateral symmetry	Strongly epitonic	Strongly epitonic	Strongly epitonic	Weakly epitonic	Epitonic and hypotonic	Weakly epitonic	Strongly hypotonic	Amphitonic
				Prunus spinosa	*Crataegus macrocarpa*		*Acer campestre*	*Fagus sylvatica*
Volume gain per dry matter investment of single twigs ($m^3\ kg^{-1}$)				0.038	0.078		0.134	0.549

Fig. 12.30 Bud development and branching patterns in woody plants. **a** Definitions of terms according to the dominance of buds in the vertical (main stem) and horizontal (branches) axes of a woody plant. Shoot dominance ultimately determines the growth forms of woody plants. **b** Schematic of the important features of symmetry in native woody plants in a hedge (Troll 1939; Küppers 1985; Schulze et al. 1987) and quantification of the competitiveness of selective species on the basis of the volume of the living space occupied per unit of dry mass and per unit of photosynthetic carbon acquisition of the leaves. Species in the later succession have a greater capacity to exploit the space and also greater assimilate acquisition per unit of invested twig mass. **c** A hedge landscape on limestone near Stadtsteinach, Upper Frankonia, Germany. The hedge shows typical succession from the edge to the centre, with *Prunus spinosa* as the woody pioneer plant at the edge, followed by *Rubus* and *Rosa* species, then *Crataegus macrocarpa* and, finally, *Rhamnus cathartica* and *Acer campestre*. (Photo: E.-D. Schulze)

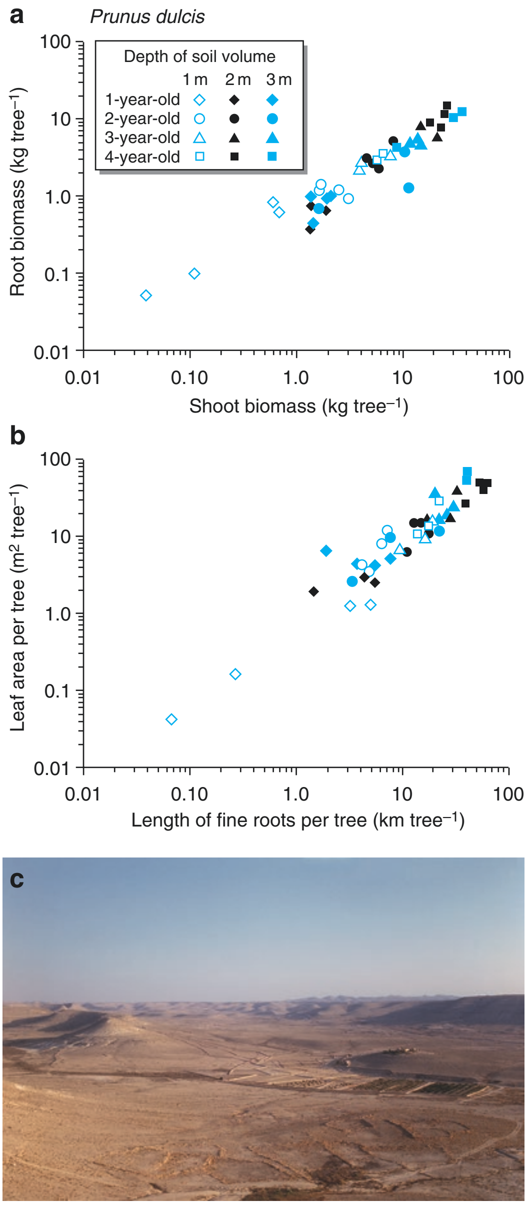


Fig. 12.31 Allocation of growth in a tree. Correlations between **a** root and shoot biomass and **b** leaf area and length of fine roots in *Prunus dulcis*. The plants were grown at the Avdat research station in the Negev Desert, in containers 3 m in diameter and 1, 2 or 3 m deep. The plants were watered only once in spring and had to regulate shoot and root growth in relation to the water stored in the soil. The strong correlation between the shoot and root is independent of the absolute water supply and the size of the plant; the allometry between the shoot and root is constant. Environmental factors determine the capacity for growth in this woody plant but not the partitioning of material. The plant is a grafted cultivated plant in which the shoot and root have their own genetic programmes, so the equilibrium is regulated by resource distribution within the plant (Heilmeier et al. 1997). **c** View of experiments on almonds at the run-off farm at Avdat (Evenari et al. 1982)

- **Semi-evergreen** species with an assimilatory organ life span of about 12–14 months, when the old leaves are shed with the emergence of new leaves (e.g. *Eucalyptus* spp. and many tropical species).
- **Evergreen** species with an assimilatory organ life span of up to 35 years (e.g. *Pinus longaeva*, California).

Deciduous and evergreen assimilatory organs show functional differences.

Evergreen species have a larger dry weight per area (specific leaf weight; Chap. 20) because they usually are forced to survive very unfavourable conditions (cold, drought).

A lower rate of CO_2 assimilation in evergreen species than in deciduous species correlates with the larger dry weight per area (Fig. 12.6). Short-lived leaves have greater CO_2 assimilation than long-lived leaves. The new investment in leaves balances a loss of physiological activity with lower investment in protection of cell walls. Evergreen species are able to use intermittently favourable weather conditions to assimilate (spruce is able to assimilate CO_2 on warm days during the European winter). Assimilation starts earlier in spring than for deciduous species and lasts longer in autumn. For deciduous species, the growing season is often limited by early or late frosts.

Deciduous species must form their assimilatory organs again each year, which leads to substantial consumption of carbohydrate reserves. In evergreen species the respiration of needles in winter is lower than the demand for resources required to completely build new assimilatory biomass. The material balance of both leaf types is surprisingly similar (Table 12.1), and the amount of usable wood mass depends again on the species-specific distribution to the stem and branches. The allocation scheme of C distribution is genetically fixed. Thus, material gain is dependent on the environment, but the shoot to root ratio remains almost constant (Heilmeier et al. 1997). Deciduous growth requires high nutrient uptake at the time of emergence. Thus, deciduous species are more frequently found in nutrient-rich soils than evergreen species.

It becomes obvious that there are several advantages and disadvantages of evergreen and deciduous assimilatory organs; therefore, it is not surprising that in many plant communities both leaf types (deciduous and evergreen) exist side by side. Analysis of the geographic distribution patterns of both types shows that all factors (shade, cold) that reduce the C gain of the plant (assimilation × leaf area) lead to longer life of the assimilatory organs (cold and shade habitats). Plants with high respiratory rates and low C gain must minimise investment in new assimilatory organs in order to safeguard the supply to the respiring organs. The plant manages this only by prolonging the life span of the assimilatory organs. For example, boreal pine forest succeeds temperate deciduous forest in alpine regions, as well as at higher latitudes where the growing period becomes shorter. With increased supply of nutrients (e.g. after a fire), these unfavourable climatic conditions are compensated for, so succession may occur at first via deciduous birch or poplar. In the central Asian continental climate, the evergreen boreal forest is replaced by deciduous larch forest, where investment in needles is particularly low (Schulze et al. 1995). Larch is therefore able to utilise the warm continental summer better than evergreen species. Additionally, in the continental climate with extremely cold winters, the investment in **protection** of evergreen needles increases, while a bud is less endangered than a fully developed assimilatory organ. Obviously, the functional causes of the change from evergreen to deciduous boreal conifers are diverse. Considering all factors, the time since the last major fire event appears to be one major factor determining the **succession** from larch to evergreen conifers in Siberia (Schulze et al. 2012). Larch is dominant in Asian but not in North American boreal forests. The difference in the dominance of larch between these two continents may be a reaction to drier periods in summer in continental Asia and an adaptation to fire. In the Siberian winter, on the other hand, temperatures are so cold (−50 to −70 °C) that damage to evergreen needles is possible; this would greatly affect the C budget. Besides the influence of climate, in Eastern Siberia the evergreen *Picea obovata* still occurs on riverbanks, so drought and related **fires** are probably also deciding factors responsible for the dominance of larch.

Nutrient-poor habitats lead to reduced photosynthesis; thus, greater investment in roots is required. This leads generally to evergreen growth (for example, tropical evergreen forests, Australian sclerophyllous woodlands).

Dry habitats stimulate evergreen growth of woody species (Mediterranean sclerophyllous woodlands). In the Mediterranean winter rain regions, occasional rains occur also in summer (thunderstorms) and thus evergreens are able to bridge the short dry periods with the help of deep roots and low stomatal conductance. In Southern California and Mexico, there are shrubs — the so-called **ombrophytes** (genus *Fouquieria*) — whose leaves emerge after each precipitation (i.e. many times per year) but are active only for a few days. As these plants are not able to store water, the duration of the **drought period** determines which species occur. Even in the Mediterranean vegetation there are deciduous species particularly at dry sites. The subtropical savanna is a further example of the change from evergreen tropical to deciduous vegetation. However, drought together with nutrient deficiency can, again, be advantageous for evergreen species, which often do not form leaves but form phyllodes or phylloclades similarly to, for example, *Acacia* in Australia. Very long drought periods are of advantage to evergreen species (e.g. Chenopodiaceae in North Africa), which are capable of reducing assimilating shoots if needed.

Summary

- Carbon relations of plants cover three major components — namely, CO_2 assimilation, respiration and growth. CO_2 assimilation comprises the diffusion of CO_2 through the stomata into the leaf mesophyll and photosynthesis of C_3, C_4 and crassulacean acid metabolism (CAM) plants. Respiration occurs during growth and for maintenance of all living tissues. Growth is the net result of these two main processes and comprises the allocation of carbon to different organs.
- Mathematical models are capable of describing the processes of photosynthesis. The model descriptions of the responses of stomata to environmental and plant-internal factors

and the modelling of plant growth are based on empirical evidence.
- At the leaf level, the rate of photosynthesis is determined by the specific leaf area and the leaf nitrogen concentration, which vary among plant species and with environmental stress.
- Environmental factors control stomatal conductance of CO_2 and water vapour. These environmental factors are mainly atmospheric CO_2, air humidity, air temperature, light, soil water status and soil nutrient availability.
- Plant growth is determined by the balance of CO_2 assimilation and whole-plant respiration. The relative growth rate describes the change in weight over time, related to total plant weight. Net primary production is possible only when net photsynthesis exceeds respiration. Storage of carbohydrates or lipids may equilibrate any imbalance of net photosynthesis and respiration. Metabolic energy is needed for maintenance and growth respiration of living plant tissues. Parts of the living tissues may die (e.g. wood) but remain as structural components (e.g. in trees).
- Different plant life forms have evolved, ranging from annual species, herbaceous biennial and perennial species to woody species, characterised by different patterns of carbon allocation among plant tissues.

References

Adams MA, Turnbull TL, Sprent JI, Buchmann N (2016) Legumes are different: leaf nitrogen, photosynthesis, and water use efficiency. Proceedings of the National Academy of Sciences 113:4098–4103

Allakhverdiev S, Kreslavski VD, Klimov VV, Los DA, Carpentier R, Mohanty P (2008) Heat stress: an overview of molecular responses in photosynthesis. Photosynth Res 98:541–550

Amthor JS (1989) Respiration and crop productivity. Springer, Berlin

Arneth A, Kelliher FM, McSeveny TM, Byers JN (1999) Assessment of annual carbon dioxide exchange in a water-stressed *Pinus radiata* plantation: an analysis based on eddy covariance measurements and an integrated biophysical model. Glob Change Biol 5:531–545

Arneth A, Lloyd J, Santrucova H, Bird M, Grigoriev S, Brand W, Werner R, Gleixner G, Schulze E-D (2002) Response of central Siberian Scots pine to soil water deficit and long-term trends in atmospheric CO_2 concentration. Global Biogeochem Cycles 16:5–13

Beck E (1999) Towards an understanding of plant growth regulation: cytokinins as major signals for biomass distribution. In: Strnad M, Péc P, Beck E (eds) Advances in plant growth and development. PERES Publishers, Prague. pp 97–110

Beerling DJ, Osborne CP (2006) The origin of the savanna biome. Glob Chang Biol 12:2023–2031

Bell TL, Pate JS, Dixon KW (1996) Relationship between fire response, morphology, root anatomy and starch distribution in south-west Australian Epacridaceae. Ann Bot 77:357–364

Biscoe PV, Scott RK, Monteith JL (1975) Barley and its environment. III. Carbon budget of the stand. J Appl Ecol 12:269–293

Björkman O (1971) Comparative photosynthetic CO_2 exchange in higher plants. In: Hatch MD, Osmond CB, Slatyer RO (eds) Photosynthesis and photorespiration. Wiley, New York. pp 18–34

Björkman O (1981) Responses to different quantum flux densities. Encycl Plant Physiol 12A:57–108

Brodersen CR, Vogelmann TC, Williams WE, Gorton HL (2008) A new paradigm in leaf-level photosynthesis: direct and diffuse lights are not equal. Plant Cell Environ 31:159–164

Brown RH, Byrd GT (1993) Estimation of bundle sheath cell conductance in C_4 species and O_2 sensitivity of photosynthesis. Plant Physiol 103:1183–1188

Buchmann N, Brooks R, Rapp KD, Ehleringer JR (1996) Carbon isotope composition of C_4 grasses is influenced by light and water supply. Plant Cell Environ 19:392–402

Caemmerer von S, Evans JR, Hudson GS, Andrews TJ (1994) The kinetics of ribulose-1,5-bisphosphate carboxylase/oxygenase in vivo interfered from measurements of photosynthesis in leaves of transgenic tobacco. Planta 195:88–97

Chapin FS III, Schulze ED, Mooney HA (1990) The ecology and economics of storage in plants. Annu Rev Ecol Syst 21:423–447

Clayton WD (1981) Evolution and distribution of grasses. Ann Mo Bot Gard 68:5–14

Cowan IR, Farquhar GD (1977) Stomatal function in relation to leaf metabolism and environment. In: Jennings JR (ed) Interaction of activity in the higher plant. Cambridge University Press, Cambridge. pp. 471–505.

Cowan IR, Lange OL, Green TGA (1992) Carbondioxide exchange in lichens—determination of transport and carboxylation characteristics. Planta 187:282–294

Dai Z, Ku MSB, Edwards GE (1993) C_4 photosynthesis. The CO_2-concentration mechanism and photorespiration. Plant Physiol 103:83–90

Edwards EJ, Osborne CP, Strömberg CAE, Smith SA, C_4 Grasses Consortium (2010) The origin of C_4 grasslands: integrating evolutionary and ecosystem services. Science 328:587–591

Ehleringer JR (1978) Implications of quantum yield differences on the distribution of C_3 and C_4 grasses. Oecologia 31:255–267

Ehleringer JR, Cerling TE, Helliker BR (1997) C_4 photosynthesis, atmospheric CO_2 and climate. Oecologia 112:285–299

Ellenberg H (1978) Vegetation Mitteleuropas mit den Alpen. Ulmer, Stuttgart

Evans LT (1971) Evolutionary, adaptive and environmental aspects of the photosynthetic pathway: assessment. In: Hatch MD, Osmond CB, Slatyer RO (eds) Photosynthesis and photorespiration. John Wiley, Sydney. pp 131–136

Evans M, Aubriot X, Hearn D, Lanciaux M, Lavergne S, Cruaud C, Lowry PP, Haevermans T (2014) Insights on the evolution of plant succulence from a remarkable radiation in Madagarscar (*Euphorbia*). Syst Biol 63:697–711

Evenari M, Shanan L, Tadmor N (1982) The Negev: the challenge of a desert. Harvard University Press, Cambridge

FAO (2000) Forest resources of Europe, CIS, North America, Australia, Japan and New Zealand. Main report. United Nations, New York

Farquhar G, Lloyd J (1993) Carbon and oxygen isotope effects in the exchange of carbon dioxide between terrestrial plants and the atmosphere. In: Ehleringer JR, Hall AE, Farquhar GD (eds) Stable isotopes and plant carbon–water relations. Academic Press, San Diego. pp 47–70

Farquhar GD, von Caemmerer S (1982) Modelling of photosynthetic response to environment. Encycl Plant Physiol 12B:549–587

Farquhar GD, von Caemmerer S, Berry JA (1980) A biochemical model of photosynthetic CO_2 assimilation in leaves of C_3 species. Planta 149:78–90

Farquhar GD, Ehleringer JR, Hubick KT (1989) Carbon isotope discrimination and photosynthesis. Annu Rev Plant Physiol Plant Mol Biol 40:503–537

Fichtner K, Schulze E-D (1992) The effect of nitrogen nutrition on growth and biomass partitioning of annual plants originating from habitats of different nitrogen availability. Oecologia 92:236–241

Field C, Mooney HA (1986) The photosynthesis–nitrogen relationship in wild plants. In: Givnish TJ (ed) On the economy of plant form and function. Cambridge University Press, Cambridge. pp 25–56

Fritts HC, Vaganov EA, Sviderskaya IV, Shashkin AV (1991) Climatic variation and tree-ring structure in conifers: empirical and mechanistic models of tree-ring width, number of cells, cell size, cell-wall thickness and wood density. Climate Res 1:97–116

Fuchs M, Schulze E-D, Fuchs MI (1977) Spacial distribution of photosynthetic capacity and performance in a mountain spruce forest of northern Germany. II. Climatic control of carbon dioxide uptake. Oecologia 29:329–340

Galvagno M, Rossini M, Migliavacca M, Cremonese E, Colombo R, Morra di Cella U (2013) Seasonal course of photosynthetic efficiency in *Larix decidua* Mill. in response to temperature and change in pigment composition during senescence. Int J Biometeorol 57:871–880

Ghasghaie J, Badeck FW (2014) Opposite isotope discrimination during dark respiration in leaves versus roots—a review. New Phytol 201:751–769

Gifford RM (1974) A comparison of potential photosynthesis, productivity and yield of plant species with differing photosynthetic metabolism. Aust J Plant Physiol 1:107–117

Gowik U, Bräutigam A, Weber KL, Weber AMP, Westhoff P (2011) Evolution of C_4 plants in the genus *Flaveria*—how many and which genes does it take to make C_4? Plant Cell 23:2087–2105

Grime JP (1974) Vegetation classification by reference to strategies. Nature 250:26–31

Grime JP (2001) Plant strategies, vegetation processes, and ecosystem properties. Wiley, Chichester

Harley PC, Tenhunen JD, Lange OL (1986) Use of an analytical model to study limitations on net photosynthesis in *Arbutus unedo* under field conditions. Oecologia 70:393–401

Hattersley PW (1992) C_4 photosynthetic pathway variation in grasses (Poaceae): its significance for arid and semi-arid lands. In: Chapman G (ed) Desertified grasslands: their biology and management. Academic Press, London. pp 181–212

Heilmeier H, Schulze E-D, Whale DM (1986) Carbon and nitrogen partitioning in the biennial macrocarp *Arctium tomentosum* Mill. Oecologia 70:466–474

Heilmeier H, Erhart M, Schulze E-D (1997) Biomass allocation and water use under arid conditions. In: Bazzaz F, Grace J (eds) Plant resource allocation. Academic Press, San Diego. pp 93–112

Hetherington AM, Woodward FI (2003) The role of stomata in sensing and driving environmental change. Nature 424:901–908

Hollinger DY, Kelliher FM, Byers JN, Hunt JE, McSeveny TM, Weir PL (1994) Carbon dioxide exchange between an undisturbed old-growth temperate forest and the atmosphere. Ecology 75:134–150

Hunt R (1982) Plant growth curves. Edward Arnold, London

Jacobs BF, Kingston JD, Jacobs LL (1999) The origin of grass-dominated ecosystems. Ann Mo Bot Gard 86:590–643

Jarvis PG (1971) The estimation of resistances to carbon dioxide transfer. In: Sesták Z, Catsky J, Jarvis PG (eds) Plant photosynthetic production: manual of methods. Junk, Den Haag. pp 566–631

Jarvis PG (1976) The interpretation of the variations in leaf water potential and stomatal conductance found in canopies in the field. Philos Trans R Soc Lond B 273:593–610

Jones HG (1994) Plants and microclimate, 2nd edn. Cambridge University Press, Cambridge

Jones HG (1999) Use of thermography for quantitative studies of spatial and temporal variation of stomatal conductance over leaf surfaces. Plant Cell Environ 22:1043–1055

Kaiser WM (1982) Correlation between changes in photosynthetic activity and changes in total protoplast volume in leaf tissue from hygro-, meso- and xerophytes under osmotic stress. Planta 154:538–545

Kappen L, Lange OL, Schulze E-D, Evenari M, Buschbom U (1972) Extreme water stress and photosynthetic activity of the desert plant *Arteminsia herba-alba*, asso. Oecologia 10:177–182

Kappen L, Lange OL, Schulze E-D, Evenari M, Buschbom U (1976) Distributional pattern of water relations of *Hammada scoparia* (Pomel) Iljin in a desert environment. Oecologia 23:323–334

Kirschbaum MUF, Farquhar GD (1984) Temperature dependence of whole-leaf photosynthesis in *Eucalyptus pauciflora* Sieb. Ex Spreng. Aust J Plant Physiol 11:519–538

van der Kooi CJ, Reich M, Löw M, DeKok LJ, Tausz M (2016) Growth and yield stimulation under elevated CO_2 and drought: a meta-analysis on crops. Envion Exp Bot 122:150–157

Küppers M (1985) Carbon relations and competition between woody species in a central European hedgerow. IV. Growth form and partitioning. Oecologia 66:343–352

Küppers M (1989) Ecological significance of aboveground architectural patterns in woody plants: a question of cost–benefit relationships. Trends Ecol Evol 4:375–379

LaMarche VC Jr, Graybill DA, Fritts HC, Rose MR (1984) Increasing atmospheric carbon dioxide: tree ring evidence for growth enhancement in natural vegetation. Science 252:1019–1021

Lambers H, Chapin FS III, Pons TL (1998) Plant physiological ecololgy. Springer, Heidelberg

Lange OL (1965) Experimentell-ökologische Untersuchungen an Flechten der Negev-Wüste. I. CO_2-Gaswechsel von *Ramalina maciformis* (Del.) Bory unter kontrollierten Bedingungen im Laboratorium. Flora 158:324–359

Lange OL (1988) Ecophysiology of photosynthesis: performance of poikilohydric lichens and homoiohydric Mediterranean sclerophylls. J Ecol 76:914–937

Lange OL, Schulze E-D, Kappen L, Evenari M, Buschbom U (1975) CO_2-exchange patterns under natural conditions of *Caralluma negevensis*, a CAM plant of the Negev Desert. Photosynthetica 9:318–326

Lange OL, Geiger IL, Schulze E-D (1977) Ecophysiological investigations on lichens of the Negev Desert. V. A model to simulate net photosynthesis and respiration of *Ramalina maciformis*. Oecologia 28:247–259

Lange OL, Beyschlag W, Tenhunen JD (1987) Control of leaf carbon assimilation—input of chemical energy into ecosystems. Ecol Stud 61:148–163

Larcher W (1994) Ökophysiologie der Pflanzen. UTB, Eugen Ulmer, Stuttgart

Leuning R (1995) A critical appraisal of a combined stomatal–photosynthesis model for C_3 plants. Plant Cell Environ 18:339–355

Leuning R, Dunin FX, Wang YP (1998) A two-leaf model for canopy conductance, photosynthesis and partitioning of available energy. II. Comparison with measurements. Agric For Meteorol 91:113–125

Lloyd J, Grace J, Miranda AC, Meir P, Wong SC, Miranda BS, Wright IR, Gash JHC, McIntyre J (1995a) A simple calibrated model of Amazon rainforest productivity based on leaf biochemical properties. Plant Cell Environ 18:1129–1145

Lloyd J, Wong SC, Styles JM, Batten D, Priddle R, Turnbull C, McConchie CA (1995b) Measuring and modelling whole-tree gas exchange. Aust J Plant Physiol 22:987–1000

Long SP, Ainsworth EA, Bernacchi CJ, Davey PA, Hymus GJ, Leakey ADB, Morgan PB, Osborne CP (2006) Long-term responses of photosynthesis to elevated [CO_2] in managed systems. Ecol Stud 187:254–270

Loreto F, Velikova V, Di Marco G (2001) Respiration in the light measured by $^{12}CO_2$ emission in $^{13}CO_2$ atmosphere in maize leaves. Aust J Plant Physiol 28:1103–1108

Lüttge U (1999) One morphotype, three physiotypes: sympatric species of *Clusia* with obligate C_3 photosynthesis, obligate CAM and C_3-CAM intermediate behaviour. Plant Biol 1:138–148

Lüttge U (2004) Ecophysiology of crassulacean acid metabolism (CAM). Ann Bot 93:629–652

MacFadden BJ, Cerling TE (1996) Mammalian herbivore communities, ancient feeding ecology and carboisotopes: a 10-million-year sequence from the Neogene of Florida. J Vertebrate Paleontol 16:103–115

McCree KJ (1983) Carbon balance as a function of plant size in *Sorghum* plants. Crop Sci 20:82–93

Merino J, Field C, Mooney HA (1982) Construction and maintenance costs of Mediterranean-climate evergreen and deciduous leaves. I. Growth and CO_2 exchange analysis. Oecologia 53:208–213

Miflin B (2000) Crop improvement in the 21st century. J Exp Bot 51:1–8

Monsi M (1960) Dry-matter reproduction in plants. I. Schemata of dry-matter reproduction. Bot Mag 73:82–90

Mott KA, Parkhust DF (1991) Stomatal response to humidity in air and helox. Plant Cell Environ 14:509–515

Mott KA, Gordon ZG, Berry JA (1993) Asymmetric stomatal closure for the two surfaces of *Xynthium strumarium* L. leaves at low humidity. Plant Cell Environ 16:25–34

Nösberger J, Long SP, Norby RJ, Stitt M, Hendrey GR, Blum H (2006) Managed ecosystems and CO_2, Ecological Studies, vol 187. Springer, Heidelberg

Nyffelder R, Eggli U, Ogburn M, Edwards E (2008) Variations on a theme: repeated evolution of succulent life forms in the Portulacinae (Caryophyllales). Haseltonia 14:26–36

Orians GH, Solbrig OT (1977) A cost–income model of leaves and roots with special reference to arid and semiarid areas. Am Nat 111:677–690

Pagani M, Zachos JC, Freeman KH, Tipple B, Bohaty S (2005) Marked decline in atmospheric carbon dioxide concentrations during the Paleogene. Science 309:600–603

Pearcy RW, Pfitsch WA (1994) The consequences of sunflecks for photosynthesis and growth of forest understory plants. Ecol Stud 100:343–357

Penning de Vries FWT (1975) Use of assimilates in higher plants. In: Cooper JP (ed) JGP 3: photosynthesis and productivity in different environments. Cambridge University Press, Cambridge. pp 459–480

Penning de Vries FWT (1983) Modelling of growth and productivity. Encycl Plant Physiol 12D:117–150

Penning de Vries FWT, Djitèye MA (1982) La productivité des pâturages sahéliens: Une étude des sols, des végétations et de l'exploitation de cette ressource naturelle. PUDOC, Wageningen

de Pury DGG, Farquhar GD (1999) A commentary on the use of a sun/shade model to scale from the leaf to a canopy. Agric For Meteorol 95:257–260

Raschke K (1979) Movements of stomata. Encycl Plant Physiol 7:383–441

Raunkiaer C (1934) The life forms of plants and statistical plant geography: being the collected papers of C. Raunkiaer. Clarendon Press, Oxford

Sage RF (2004) The evolution of C_4 photosynthesis. New Phytol 161:341–370

Sage RF, Sage TL, Kocacinar F (2012) Photorespiration and the evolution of C_4 photosynthesis. Annu Rev Plant Physiol 63:19–47

Scarascia-Mugnozza G, Bauer GA, Persson H, Mateucci G, Marci A (2000) Tree biomass, growth and nitrogen pools. Ecol Stud 142:49–62

Scheible WR, Gonzáles-Fortes A, Lauerer M, Müller-Röber B, Caboche M, Stitt M (1997) Nitrate acts as a signal to induce organic acid metabolism and repress starch metabolism in tobacco. Plant Cell 9:783–798

Schulze E-D (1970) Der CO_2-Gaswechsel der Buche (*Fagus silvatica* L.) in Ahhängigkeit von den Klimafaktoren im Freiland. Flora 159:177–232

Schulze E-D (1982) Plant life forms and their carbon, water and nutrient relations. Encycl Plant Physiol 12B:616–676

Schulze E-D, Chapin FS III (1987) Plant specialisation to environments of different resource availability. Ecol Stud 61:120–148

Schulze E-D, Hall AL (1982) Stomatal responses, water loss and CO_2 assimilation rates of plants in contrasting environments. Encycl Plant Physiol 12B: 181–230

Schulze E-D, Küppers M, Matyssek R (1987) The role of carbon balance and branching pattern in the growth of woody species. In: Givnish TJ (ed) On the economy of the plant form and function. Cambridge University Press, Cambridges. pp 585–602

Schulze W, Stitt M, Schulze E-D, Neuhaus HE, Fichtner K (1991) A quantification of the significance of assimilatory starch for growth of *Arabidopsis thaliana* L. Heynh. Plant Physiol 95:890–895

Schulze E-D, Kelliher FM, Körner C, Lloyd J, Lenning P (1994) Relationships among maximum stomatal conductance, ecosystem surface conductance, carbon assimilation and plant nitrogen nutrition: a global ecology scaling exercise. Annu Rev Ecol Syst 25:629–660

Schulze E-D, Schulze W, Kelliher FM, Vygodskaya NN, Ziegler W, Kobak KI, Koch H, Arneth A, Ksnetsova WA, Sogachev A, Issajev A, Bauer G, Hollinger DY (1995) Aboveground biomass and nitrogen nutrition in a chronosequence of pristine Dahurian *Larix* stands in eastern Siberia. Can J For Res 25:943–960

Schulze E-D, Ellis R, Schulze W, Trimborn P, Ziegler H (1996) Diversity, metabolic types and $\delta^{13}C$ carbon isotope ratios in the grass flora of Namibia in relation to growth form, precipitation and habitat conditions. Oecologia 106:352–369

Schulze E-D, Williams RJ, Farquhar GD, Schulze W, Langridge J, Miller JM, Walker BH (1998) Carbon and nitrogen isotope discrimination and nitrogen nutrition of trees along a rainfall gradient in northern Australia. Aust J Plant Physiol 25:413–425

Schulze E-D, Wirth C, Mollicone D, von Lüpke N, Ziegler W, Achard F, Mund M, Prokushkin A, Scherbina S (2012) Factors promoting larch dominance in central Siberia: fire versus growth performance and implications for carbon dynamics at the boundary of evergreen and deciduous conifers. Biogeosciences 9:1405–1421

Schwarz PA, Fahey TH, Dawson TE (1997) Seasonal air and soil temperature effects on photosynthesis in red spruce (*Picea rubens*) saplings. Tree Physiol 17: 187–194

Sesták Z, Catsky J, Jarvis PG (eds) (1971) Plant photosynthetic production: manual of methods. Junk, Den Haag

Shinozaki K, Yoda K, Hozumi K, Kira T (1964) A quantitative analysis of plant form—the pipe model theory. II. Further evidence of the theory and its application in forest ecology. Jpn J Ecol 14:133–139

Steinlein T, Heilmeier H, Schulze E-D (1993) Nitrogen and carbohydrate storage in biennials originating from habitats of different resource availability. Oecologia 93:374–382

Stephenson NL, Das AJ, Condit R, Russo SE, Baker PJ, Beckman NG, Coomes DA, Lines ER, Morris WK, Rüger N, Álvarez E, Blundo C, Bunyavejchewin S, Chuyong G, Davies SJ, Duque Á, Ewango CN, Flores O, Franklin JF, Grau HR, Hao Z, Harmon ME, Hubbell SP, Kenfack D, Lin Y, Makan J-R, Malizia A, Malizia LR, Pabst RJ, Pongpattananurak N, Su S-H, Sun I-F, Tan S, Thomas D, van Mantgem PJ, Wang X, Wiser SK, Zavala MA (2014) Rate of tree carbon accumulation increases continuously with tree size. Nature 507:90–93

Still CJ, Berry JA (2003) Global distribution of C_3 and C_4 vegetation: carbon cycle implications. Global Biogeochem Cycles 17:1006

Stitt M, Schulze E-D (1994) Plant growth, storage, and resource allocation: from flux control in a metabolic chain to the whole plant level. In: Schulze E-D (ed) Flux control in biological systems. Academic Press, San Diego. pp 57–118

Takabayashi A, Kishine M, Asada K, Endo T, Sato F (2005) Differential use of two cyclic electron flows around photosystem I for driving CO_2-concentration mechanism in

C_4 photosynthesis. Proceedings of the National Academy of Sciences 102:16898–16903

Trendlenburg R, Mayer-Wegelin H (1955) Das Holz als Rohstoff. Carl Hanser Verlag, Munich

Troll W (1939) Vergleichende Morphologie der höheren Pflanzen. Bd. 1: Vegetationsorgane. Verlag Gebrüder Bornträger, Berlin

Vareschi V (1980) Vegetationsökologie der Tropen. Ulmer, Stuttgart

Volkens G (1887) Die Flora der ägyptisch-arabischen Wüste auf Grundlage anatomisch-physiologischer Forschung. Gebrüder Bornträger, Berlin

Walter H, Kreeb K (1970) Die Hydration und Hydratur des Protoplasmas der Pflanzen und ihre ökophysiologische Bedeutung, Protoplasmologia, vol IIC6. Springer, Wien

Warburg O (1913) Die Pflanzenwelt, Bd 1. Bibliographisches Institut, Leipzig

Ward JK, Tissue DT, Thomas RB, Strain BR (1999) Comparative responses of model C_3 and C_4 plants to drought in low and elevated CO_2. Glob Change Biol 5:857–867

Woodward GR (1976) Photosynthesis and expansion of leaves of soybean grown in two environments. Photosynthetica 10:274–279

Yamori W, Hikosaka K, Way DA (2014) Temperature response of photosynthesis in C_3, C_4, and CAM plants: temperature acclimation and temperature adaptation. Photosynth Res 119:101–117

Part III

Ecosystem Ecology

Mixed temperate forest at the Lägeren, Switzerland. This forest ecosystem is located at 682 m above sea-level on a south-facing slope and is characterised by a relatively high species diversity and a complex canopy structure. It is dominated by European beech (*Fagus sylvatica*), but also includes species like Norway spruce (*Picea abies*), European ash (*Fraxinus excelsior*), silver fir (*Abies alba*) and sycamore maple (*Acer pseudoplatanus*). This diverse forest grows on rendzic leptosols (or rendzinas) and haplic cambisols which have developed on limestone and marl and already start less than one metre below the soil surface. In spring, a lush understory of wild garlic (*Allium ursinum*) is present. (Photo courtesy of N. Brinkmann)

The previous chapters focused on plants (Part I: Molecular Ecology) and their reactions to (mainly) the environment (Part II: Physiological and Biophysical Plant Ecology), but plants do not grow in isolation. They interact with each other as well as with microorganisms and animals, they rely on carbon dioxide, water and nutrients, and they are affected by climatic conditions, disturbances and by land management. Plants can even shape their environment. Supporting Lovelock's original Gaia hypothesis (1979), which in parts has been adopted in Ecology and Earth System Science, the biosphere affects certain properties of the abiotic environment, for example the Earth's temperature and oxygen concentrations. All these interactions take place at the site (or habitat) where plants grow, where they reproduce and where they die: in an ecosystem. A **terrestrial ecosystem** includes the soil, microorganisms (both in the soil and aboveground), vegetation and animals as well as the lower level of the atmosphere, all interacting with each other. Terrestrial ecosystems are **functional units** in a given heterogeneous landscape and are present in all climatic zones, ranging from tropical forests to arctic tundra. Their size ranges from a couple of square metres, for example a dwarf heather ecosystem at alpine elevations, to a couple of square kilometres, for example a uniform agricultural field or a boreal coniferous forest. In any case, terrestrial ecosystems are the functional unit where biogeochemical processes happen, such as nitrogen mineralisation, where these processes provide the necessary inputs, such as plant available nitrogen forms, to ensure plant performance, such as growth, and where organisms compete with each other and interact with their environment. In addition, terrestrial ecosystems must also be considered thermodynamically "**open**" ecosystems, where water and nutrients get lost, for example as emissions to the atmosphere or via leaching and run-off, thereby also affecting the environment. Terrestrial ecosystems are also the management unit that agriculture and forestry use (Part V: Global Ecology). Thus, terrestrial ecosystems are the organisational unit where processes such as primary productivity and water use need to be understood to predict the impacts of natural and anthropogenic disturbances on the provisioning of services, such as food and timber production.

The science of (terrestrial) ecosystem ecology has grown considerably over the last several decades. Various scientific **approaches** are being used, ranging from classical observations to manipulation experiments, from plot to continental scales, from empirical or statistical modelling to dynamic vegetation models combined with biogeochemistry models. Over the last several decades, measurement techniques used in ecosystem ecology have been developed and improved tremendously, adding techniques from formerly neighbouring disciplines as well, nowadays for example including high-tech systems to measure biospheric-atmospheric greenhouse gas fluxes and their isotopic signatures as well as remote sensing techniques used on airborne platforms or at tall towers. Terrestrial ecosystem ecology draws on many disciplines, from soil science and hydrology, microbiology, animal and plant sciences to meteorology and atmospheric sciences. However, the link between community ecology (Part IV; mainly focusing on environmental effects on communities and community dynamics) and ecosystem ecology (mainly focusing on pools and fluxes) has only developed over the last decade, triggered by the wish to understand how species and communities, affected by environmental change, in turn affect ecosystem processes and services. Thus, ecosystem ecology is truly **interdisciplinary**, that is scientists from different disciplines work together to jointly address their research objectives. Sometimes ecosystem scientists even reach out to stakeholders, such as farmers, foresters, nature conservationists or politicians, and therefore ecosystem ecology has become **transdisciplinary**.

Here we will focus on terrestrial ecosystems, neglecting aquatic ecosystems on land, such as rivers or lakes (i.e. freshwater systems). We will consider managed and unmanaged ecosystems, the latter sometimes erroneously called "natural" ecosystems, although most ecosystems on Earth are managed in one way or another, from agricultural production to protection for nature conservation. Furthermore, all ecosystems are affected by environmental and human **drivers**, independent of management. Thus, we must realise that all global ecosystems are affected by **human activities**, even very remote ones (Part V). We will first explain the concept of an ecosystem and describe the characteristics of a terrestrial ecosystem as functional, not as hierarchical unit (Chap. 13: Ecosystem Characteristics). Then different approaches will be illustrated that are used to study terrestrial ecosystems, and insights into representative ecosystem studies will be given (Chap. 14: Approaches to Study Terrestrial Ecosystems). We will then give an overview about ecosystem modelling (Chap. 15: Approaches to Model Processes at the Ecosystem Level). Finally, a process-oriented view will be adopted, and selected biogeochemical fluxes into, within and out of terrestrial ecosystems will be discussed, such as those of water, carbon and nitrogen, as well as nutrients (Chap. 16: Biogeochemical Fluxes in Terrestrial Ecosystems).

Reference

Lovelock JE (1979) Gaia: a new look at life on earth. Oxford University Press, Oxford

Ecosystem Characteristics

13

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An experimental stand of beech trees in Solling, Germany. This experimental site was important for the development of the International Biological Program (IBP). Methods developed in the years 1965–1975 at the Solling site have served as a model for the global work of the IBP (Ellenberg 1971; Ellenberg et al. 1986). For the first time, many relevant processes were investigated in the same forest ecosystem at the same time so the results could be related to each other. (Photo: E.-D. Schulze)

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As early as 1866, Ernst Haeckel defined "**ecology**" as the science addressing the interactions of organisms with their organic and inorganic environment. Many different terms have been used since then to describe and define systems where individual species interact with the environment, where soil chemical and physical properties affect plant and animal communities, where plants compete and facilitate each other, and where vegetation can create microclimatic conditions very different from the large-scale climatic conditions. In 1935, Tansley proposed his definition of such a system and argued:

> I have already given my reasons for rejecting the terms "complex organism" and "biotic community". Clements' earlier term "biome" for the whole complex of organisms inhabiting a given region is unobjectable, and for some purposes convenient. But the more fundamental conception is, as it seems to me, the whole system (in the sense of physics), including not only the organism-complex, but also the whole complex of physical factors forming what we call the environment of the biome—the habitat factors in the widest sense. Though the organisms may claim our primary interest, when we are trying to think fundamentally we cannot separate them from their special environment, with which they form one physical system.
>
> It is the systems so formed which, from the point of view of the ecologist, are the basic units of nature on the face of the earth. Our natural human prejudices force us to consider organisms (in the sense of the biologist) as the most important parts of these systems, but certainly the inorganic "factors" are also parts—there could be no systems without them, and there is constant interchange of the most various kinds within each system, not only between the organisms but between the organic and the inorganic. These ecosystems, as we may call them, are of the most various kinds and sizes. They form one category of the multitudinous physical systems of the universe, which range from the universe as a whole down to the atom. (Tansley 1935)

Thus, Tansley defined the ecosystem not just as a symbiosis or as part of a superorganism but as a system that is characterised by the interaction of plants and animals with their physico-chemical environment. This scientific concept has its origin in thermodynamics and systems theory. Today, we use the term "**ecosystem**" when we consider the entire system of soil, microorganisms, vegetation and animals, as well as the lower level of the atmosphere, with all components interacting with each other. Thus, an ecosystem is the **functional unit** where biogeochemical processes happen, such as the decomposition of organic matter, providing the necessary nutrients to ensure plant life, and where plant, animal and microbial species interact with each other, changing and shaping their environment. An ecosystem is also a thermodynamically **open system**, where energy and matter also get lost to the atmosphere or the hydrosphere, such as N losses during denitrification and nitrification, or nutrient losses via leaching and run-off. Through such processes, but also through their biospheric–atmospheric exchange and surface albedo, ecosystems feed back on their environment, affecting, for example, the local to regional climate (Chap. 9, Sect. 9.2; Chap. 16). But ecosystems are also the organisational unit where ecosystem processes, such as primary productivity and evapotranspiration, translate into ecosystem services, such as food and timber production, when used by humankind (Part V: Global Ecology). Thus, it becomes clear that ecosystems are more than an assembly of species and that ecosystems have a range of spatial, temporal and functional characteristics that are system specific, showing system-level phenomena—so-called **emergent properties**. Emergent properties develop only in the system as a whole and are not present with/in any of its components; examples are the ecosystem structure, biogeochemical cycling within ecosystems, species and process interactions, and time lags in ecosystem responses. Some of these ecosystem characteristics are well defined—for example, the reference system (the unit of ground area), the presence of interactions among organisms, the existence of biogeochemical cycles (although not the exact nature of these interactions, their dynamics and magnitudes) and the irreversibility of some ecosystem processes. Other characteristics are not clearly defined and depend on the research questions asked, such as the boundaries or size of ecosystems, compartmentalisation of ecosystems, complexity of species and process interactions, ecosystem structure and temporal time lags after certain impacts on ecosystems (such as drought, fire, harvest or insect outbreaks).

13.1 Boundaries and Size of Ecosystems

The **boundaries** and the size of an ecosystem are not well defined. Some researchers even consider ecosystems as "large and individualistic" (Currie 2011). In contrast to a catchment, which is defined by the hydrological flow of water above the bedrock into the same downstream creek or river, the **horizontal boundaries** of an ecosystem are generally set by another adjacent ecosystem type to start with—for example, a boreal wetland neighbouring a boreal coniferous forest or a managed grassland adjacent to a temperate deciduous forest. The upper **vertical boundary** of an ecosystem is typically restricted to the height of the vegetation or to the canopy height interacting with the atmosphere (generally up to about one third of the total canopy height above the canopy). The lower vertical boundary can be set by the rooting depth, although it is most often set by experimental constraints—often a 30 cm or 1 m soil depth—and not by the actual deepest root present.

The area and thus the **spatial extent** of an ecosystem are typically defined by the similarity of species composition and/or biogeochemical processes, but are also often a subset of another larger area—for example, foraging areas of animals covering more than one ecosystem type. The spatial extent should contain all **fluxes** above and below the ground area under consideration. Bormann and Likens (1967) considered river **catchment** areas as basic units for ecosystems within landscapes, as the element or substance budgets may be completely quantified only within this range. However, a river catchment is a mosaic of different ecosystem types. The riparian zone near creeks and ecosystems relying on rain and groundwater have very different process rates per ground area from those of peaty river valleys or dry woodlands, for example. Thus, river catchments integrate over very heterogeneous components in a given region and would thus be too large to be valid as a basic unit of an ecosystem. The opposite extreme, a rotting tree in a mixed forest, would be considered too small to define the forest ecosystem. Overall, the **limits** of an ecosystem must extend so far that the relevant fractions of all substance flux rates per ground area (e.g. carbon assimilation, nitrogen mineralisation and formation of groundwater) of this particular ecosystem are taken into account. From this point of view, the rotting tree trunk is considered only a partial system or a component of a forest. Thus, if one studies any given forest ecosystem, only the total flux rate per ground area describes the characteristics and limits of this ecosystem, requiring a scientific approach and methodology adequate to represent the area under study (Chap. 14). For example, in ecosystem process studies, the fetch (i.e. the upwind area until another ecosystem is present) of a flux tower to measure biosphere–atmosphere exchange of greenhouse gases is often considered the appropriate area of an ecosystem (Chap. 14, Sect. 14.1). In the field of **landscape** ecology, larger and more heterogeneous areas or regions are studied to understand large-scale patterns and spatial variability, which is due to smaller-scale interactions. The term **biome** is used for even larger scales and for subcontinental systems characterised by one major vegetation type, such as the grassland biome in North America or the temperate deciduous forest across Europe. The definition of an ecosystem is independent of the facts that some organisms (e.g. migrating birds) also have an influence on the ecosystem under study beyond its limits and that components of the ecosystem possess their own dynamics (such as a rotting tree trunk in a forest ecosystem).

Given these considerations regarding the spatial characteristics of an ecosystem, the **reference**

system of any ecosystem study is the **unit of ground area**, typically measured in square metres or hectares. Element or substance flux rates or turnover are no longer expressed as concentrations (in grams per gram or in moles per gram) of the element or substance in certain organs or individual plants; **processes** are expressed per unit of ground or surface area (in grams per square metre or in moles per square metre) above or below which these fluxes occur. Similarly, substance **pools** are no longer constrained to single plants or tissues but also relate to the unit of ground—for example, carbon pools in soils and vegetation. For soil pools, information on the soil depth that is considered might also be important and is therefore often given as well (in grams per square metre per 30 cm depth). At the same time, stand or stocking densities (i.e. the number of trees per hectare or the number of grass tillers per square metre) and individual plant-specific ecophysiology (e.g. the sap flow rate) relate to the element or substance flux rates per unit of ground but can be highly variable within the ecosystem under study. In addition, partial systems might have flux rates different from those of the system as a whole. These partial systems can include living plants, different species, standing dead trees, leftover stubble on a field, litter layer, below-ground, etc. If the partitioning into the origin of these component fluxes is of interest, an appropriate sampling design (e.g. stratified sampling, transects, grid points; Chap. 14) or the application of new techniques (e.g. stable isotopes, eddy covariance, remote sensing) needs to be implemented.

13.2 Components of an Ecosystem

Different actors, components and compartments make up an ecosystem. These partial systems or **system components** interact with each other, with strong or weak **interactions**, with linear or nonlinear interactions, with direct or indirect interactions, and with positive or negative interactions. Depending on the research question asked, the following criteria to separate different components of an ecosystem are the ones most frequently used:

- Above-ground versus below-ground: This approach roughly separates autotrophic from heterotrophic processes (exception: below-ground root (i.e. autotrophic) respiration). In addition, it is possible to separate the ecosystem into soil versus vegetation compartments
- Trophic levels: Separation of organisms present in an ecosystem into producers, consumers and decomposers describes the energy (and matter) flux within an ecosystem
- Functional groups: Many species that have similar characteristics are often considered a functional group or functional type (e.g. nitrogen-fixing plants, trees, invasive species, phloem-sucking insects and parasites; Chap. 20, Sect. 20.2). Species can belong to many different functional groups—for example, *Robinia pseudoacacia*, a nitrogen-fixing tree species, is also considered invasive in Europe
- Overstorey and understorey: The vertical structure of vegetation is important for the coupling of ecosystems to the atmosphere, particularly for energy, trace gas fluxes, atmospheric deposition or rain interception. In forests, the separation into trees, shrubs, lianas/vines and herbaceous plants (understorey vegetation) is often used. For grasslands, but also forests and woodlands, separation into the upper and lower canopy, as well as in understorey or suppressed plant species is frequent

Often, multiple **components** and actors, as well as their interactions, are investigated in the same study; then a so-called **systems approach** is used, which also provides the conceptual framework to connect all components and actors mechanistically—for example, in a mathematical model (Chap. 15). In contrast, studies focusing on single species—for example, dominant species (dominating in abundance) or keystone species (being a major driver of change or of certain processes)—or on species interactions within a plant community, are often carried out within the context of evolutionary biology, community ecology and biodiversity research (Part IV, particularly Chaps. 19 and 20).

These different components of an ecosystem are not equally distributed in space. They often form a **mosaic** of different components (e.g. in a riparian zone); they might create patterns and thus **patchiness** (e.g. the hummocks and hollows in a bog). These patterns might be vertical (facilitated by different height growth, resulting in a canopy structure) and/or horizontal (facilitated by plant density and species composition). The origins of these patterns are manifold. Patterns might be the consequence of soil conditions, topography, disturbance, competition or management. In any case, research in such a patchy ecosystem must pay special care to capture this **spatial variability** in order to represent the entire ecosystem and not only one or several components (Chap. 14).

13.3 Ecosystem Complexity and Interactions of Processes and Drivers

Ecosystems are, by definition, a **complex network of relationships and processes**—that is, they are determined by a multitude of factors and interactions. The **complexity** of an ecosystem develops very slowly **over time**, starting from a few actors—often mosses and lichens, such as on bare rock in glacier fore-fields when the ice retreats or after major disturbances such as eruptions of volcanoes—and eventually reaching the highly diverse ecosystems, such as temperate grasslands or tropical forests, that we know and use. Thus, the **age** of ecosystems is difficult to determine, since many generations of plants, animals and microorganisms have shaped the ecosystems that we study. Furthermore, ecosystem development over time is not linear, but rates can change at varying stages over time, triggered both internally and externally. Sudden events or disturbances, occurring in minutes and hours, change ecosystems as fundamentally as slow continuous changes in environmental conditions, occurring over decades. Internal drivers of **ecosystem change** can be species competition and thus vegetation succession, but also accumulation and/or consumption of resources, which change basic life conditions. External drivers can be natural disturbances such as landslides or insect outbreaks, or anthropogenic impacts such as land use, climate change or introduction of invasive species. Moreover, the components of an ecosystem are able to adapt, self-organise and interact with each other, but they also show emergent properties, making ecosystems prime examples of complex, **adaptive systems**, according to complexity theory (Currie 2011). Here, we will give an overview of ecosystem complexity. More process-oriented examples can be found in Chaps. 14 and 16.

13.3.1 Unpredicted Existence of Neighbours

One of the most important emergent properties, from the point of view of an individual plant, is the unpredictable existence of **neighbours**, which can possess a multitude of different competitive traits. Thus, the success or failure of an individual plant or a species in an ecosystem is no longer solely determined by the physiological characteristics (as described in Part I) and responses of the species to the environment (as described in Part II), but is suddenly co-determined by random effects such as the presence or absence of competitive neighbours (Chap. 19, Sect. 19.3). Particularly at the early stage of stand development, the composition of vegetation is determined by germination rates, establishment and survival during the seedling stage. In the medium term, interactions among plant species become decisive (Chap. 20). In the longer term, mainly abiotic disturbance processes, sometimes also called interferences, become more important; plant responses to processes such as invasion, extreme events or management practices may drastically change ecosystems within a very short time, sometimes as short as minutes or hours (e.g. hailstorm, flooding). Element or substance pools that have accumulated over centuries and millennia may disappear or degrade within a very short period, in turn also affecting the presence or absence of certain neighbours.

13.3.2 Scaling up of Processes

Processes within ecosystems occur at different spatio-temporal levels (sometimes also named **scales**), i.e. from foliage to landscapes or from seconds to millennia from small to large scales, respectively, also differing among components of the ecosystem. Often processes differ profoundly on different scales. For example, while small and fast scales are often dominated by chemical and biophysical processes, larger and slower scales are rather controlled by interspecies competition, species composition and community ecology. On very large scales, environmental boundary conditions affect ecosystem structures and dynamics over centuries and millennia. Nevertheless, even if these processes are identical (for example, photosynthetic CO_2 fixation) the response of the process to the same driver (in this case, light intensity) will differ with the organisational level or scale—that is, from leaves to fully leaved branches to the entire ecosystem. Thus, processes cannot simply be scaled from the leaf to the ecosystem level because additional constraints, such as spatial structure—an emergent property of an ecosystem—come into play. One classical example of such an **upscaling** issue is net assimilation. While leaf photosynthesis follows a saturation function driven by the availability of light and CO_2, as well as vapour pressure deficit (Sect. 12.4 in Chap. 12), photosynthesis at the ecosystem level is rather linearly related to incoming light. Moreover, it reaches much higher assimilation rates, in comparison with the leaf or branch levels, at higher light intensities—not reaching saturation—because more light can be used by more leaves within the entire ecosystem. Moreover, the light compensation point is higher at the ecosystem level than at the leaf or branch levels because more light is needed to overcome auto- and heterotrophic respiratory losses of CO_2 in low-light conditions within the entire ecosystem, in comparison with the leaf or branch levels (Fig. 13.1). The **leaf area index** (**LAI**) and thus light attenuation (i.e. the decrease of incoming light supply deeper in the canopy), as well as the nutrient supply, determine the actual magnitude of net assimilation at the ecosystem level.

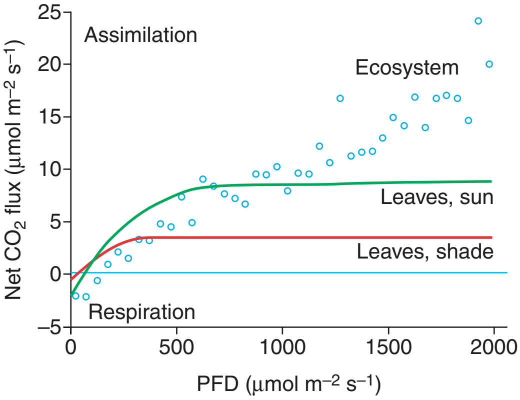

Fig. 13.1 Upscaling of CO_2 exchange from leaves to the ecosystem. Differences in net CO_2 fluxes—that is, assimilation and respiration—in response to light intensity (PFD, photon flux density) between foliage (beech leaves) and the entire ecosystem. (Leaves: after Larcher (2003); ecosystem: data from E. Paul-Limoges)

Thus, the emergent property of an ecosystem (here, ecosystem structure) can change the response to the same driver (here, light intensity) of an ecosystem in comparison with its components. These new characteristics can be related to resource use at the ecosystem level but can also be linked to the interactions of different species (Part IV).

13.3.3 Response Functions to Interacting Drivers

Each process has a typical **response function** to its major **driver**—for example, net assimilation to light, or respiration to temperature. These response functions can be linear (Fig. 13.1) but also curvilinear or even exponential. However, typically, processes are driven by multiple factors. In this case, nonlinear and irregular behaviour might set in. One example of such **interacting drivers** is the response of **soil respiration** to soil temperature and soil water availability. As long as soil moisture is abundant, soil respiration increases exponentially with temperature (Lloyd and Taylor 1994). However, as soon as soil water availability

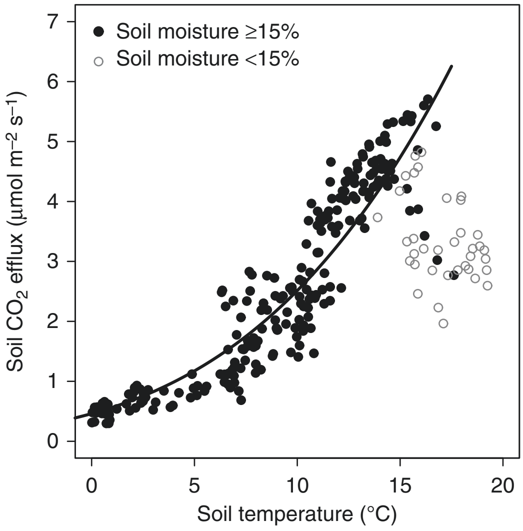

Fig. 13.2 The dependence of soil respiration (daily averages) in a mixed temperate forest on soil temperature differs depending on soil water availability. Data are given for 2006. The Lloyd and Taylor model ($R^2 = 0.83$) is given only if soil moisture ≥15%, depicted with *filled symbols*. *Open symbols* stand for soil moisture <15%. Soil respiration (SR) = 2.58 $e^{419.6((1/56.02)-1/(T-46.02))}$. (Data from N. Ruehr)

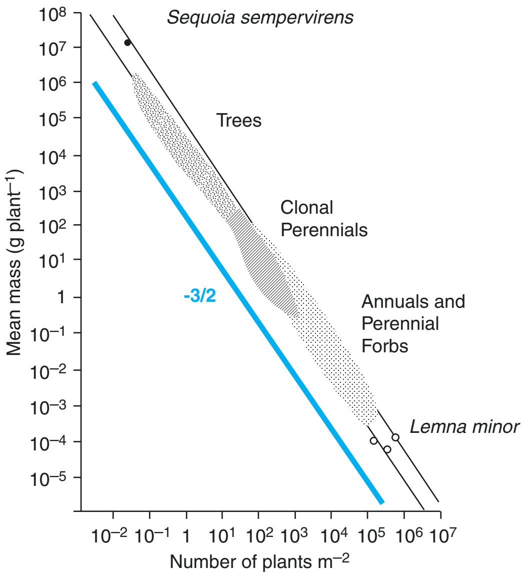

Fig. 13.3 Self-thinning in different communities. When the logarithm of the average plant weight is plotted as a function of the logarithm of the stand density, the data generate a line with a slope of −3/2. (After Silvertown and Lovett Doust (1993))

becomes limiting, soil respiration rates are much lower than those modelled by an exponential temperature response function (Ruehr et al. 2010; Fig. 13.2). Often one can determine **threshold** values below which soil water availability becomes the dominant driver. However, such thresholds are generally site specific; that is, they depend on soil and vegetation characteristics, and vary temporally—for example, with the time of the year and thus vegetation phenology.

13.3.4 Self-Thinning

Some processes, such as the production of plant biomass in a stand, are driven not only by interacting environmental drivers but also by **density-dependent effects**. For example, intra- and interspecies competition (Chap. 19, Sect. 19.3), but also the occurrence and severity of pathogen and parasite damage affect a stand's productivity. **Self-thinning** occurs when plants in dense plant populations or communities compete vigorously with each other for resources and some die, in turn decreasing the density of the survivors. The increasing growth rate of the survivors leads to continuous competition, increasing **mortality**, thus decreasing the number of survivors even further. Yoda et al. (1963) formalised this relationship and expressed the biomass of individual plants (W) as a function of the density of individual plants (n) in a stand, where c is a proportionality factor depending on light and nutrient supply:

$$W = cn^{-3/2} \tag{13.1}$$

This equation states that the biomass of an individual plant declines when plant density in this stand is increasing. Since this relationship holds for many different plant communities (Fig. 13.3), this relationship is also called the **−3/2 power law**, with −3/2 being the self-thinning constant. This constant can be explained by the spatial expansion of the biomass (three-dimensional volume, exponent 3) and the expansion of this biomass per unit of ground (two-dimensional area, exponent 2; Osawa and Allen 1993).

Expressing this self-thinning law based on plant biomass per ground area (B), thus multiplying the individual plant biomass (W) with the number of plants per unit of ground (n), results in:

$$B = cn^{-1/2} \tag{13.2}$$

Taking the logarithm of this equation yields the linear equation:

$$\log B = \log c - \frac{1}{2}\log n \tag{13.3}$$

This equation shows that the maximum biomass of a monospecific stand that can be achieved in an area depends on the number of individual plants. The slope (−1/2) applies to a broad range of growth forms (herbaceous plants, shrubs, trees) (Westoby 1984), while the parameter c describes the productivity, which is determined by many factors such as the site conditions and growth characteristics of the species.

Thus, in a managed forest stand, density-dependent effects mean that after an exponential growth phase up to canopy closure, a phase of self-thinning follows, during which **mortality** occurs. The growth rate of the stand decreases (in comparison with the exponential growth rate in the early stages) and the standing biomass reaches a certain level (Fig. 13.4a). The maximum attainable biomass then depends on the climate, vegetation structure, nutrient supply and management, as a result of plant plasticity to increased competition and of mortality. Climate conditions lead to **regional differentiation**—for example, the yield of forests in southern Germany is higher than that in northern Germany because of higher annual irradiance in the south.

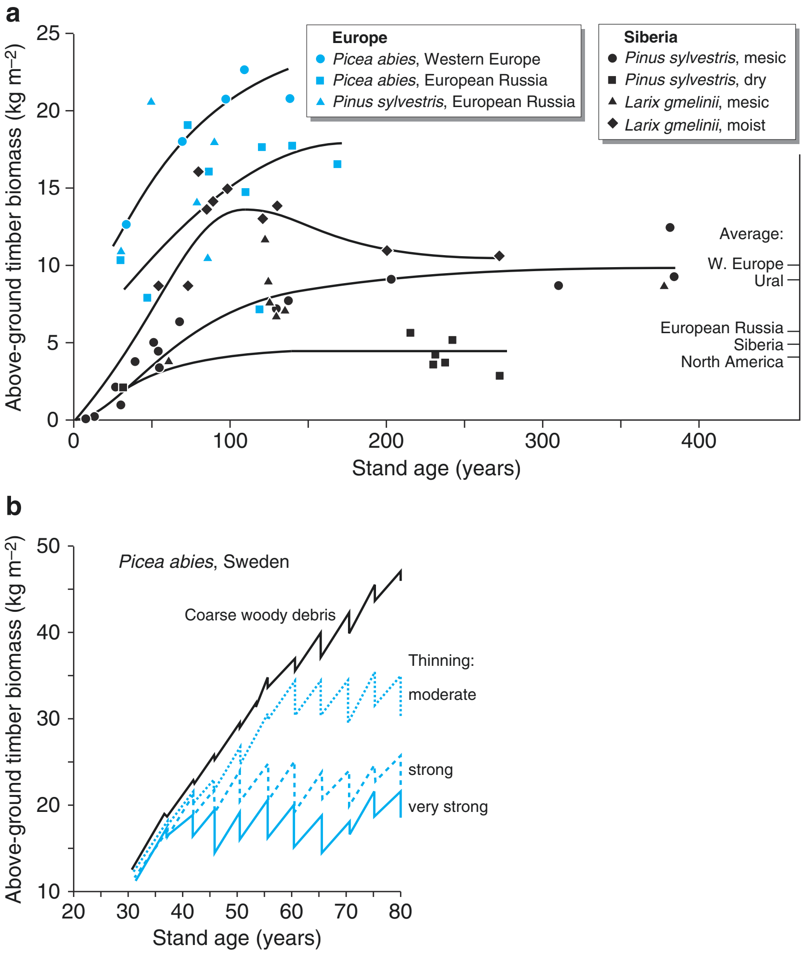

Fig. 13.4 Relationships between standing biomass and stand age. **a** Increase in biomass with age of trees in managed spruce forests in Germany compared with unmanaged forests of spruce, pine and larch in eastern Europe and Siberia (Schulze et al. 1999). It is shown that even unmanaged forests reach maximum biomass. This is not the result of an equilibrium between assimilation and respiration; it is the result of different stress impacts (fire, wind). **b** Influence of forest management—that is, thinning—on the development of a spruce stand in southern Sweden. The zig-zag path in the development of the stand is due to the removal of biomass in forest management and the subsequent recovery of the stand. (After Kramer (1988))

In managed systems, the biomass (and thus the competition among trees) is additionally controlled by different management practices such as thinning in forestry (Fig. 13.4b). Overall, the development over time of many processes resembles a **saturation function** (Schulze 1982), both for forests and for agricultural systems. However, in some systems—for example, intensively managed grasslands—the saturation plateau is rarely reached because mowing of such grasslands typically takes place during the exponential growth phase, when forage quality is very high, well before the biomass reaches the saturation plateau. Thus, the managed grassland is permanently kept at a juvenile stage, when regeneration growth of new foliage replaces the cut biomass.

13.4 Concepts of Equilibrium, Resistance and Resilience, Susceptibility and Vulnerability

The idea that ecosystems are in **equilibrium** with their environment (Gleason 1926) has been proven incorrect. Short- and long-term variability of the environment and the occurrence of **disturbances** not only constantly change the environment but also cause continuous adjustments of biogeochemical and ecophysiological processes and changes in species composition (Chap. 17). Thus, also **steady-state** conditions—that is, the state when processes or characteristics are not changing over time—are rare on longer time scales. Although an ecosystem is constantly subjected to sudden disturbances and slow-changing drivers, not all of these events trigger a response at the ecosystem level. The number of events or reoccurrence of events per time unit, i.e. the **frequency**, but also the strength of an event, i.e. the **intensity**, or the **dose**, i.e. intensity × time duration, are decisive and, together with certain ecosystem properties (see below), determine if an ecosystem is changing in response to an event or not. In the current literature, the terms "shock" and "extreme event" are also used to describe a (sudden) event or disturbance (Reichstein et al. 2013; Frank et al. 2015). In order to decide if an unusual or statistically rare disturbance or an extreme event has happened, it is necessary to know the typical/normal variability of the occurrence of disturbances or weather events. Sometimes also a combination of events is of interest, such as a combined heatwave and drought, as occurred in Central Europe in 2003, or a combined drought and insect outbreak. This means that long-term data sets of many variables are necessary, although sometimes not available. Furthermore, **lagged** versus non-lagged (also called **concurrent**) responses of an ecosystem to an event are differentiated, depending on when the ecosystem responds to a disturbance or change (Smith 2011). Additional terms used for lagged responses are **legacy effects** and memory effects, the latter of which should be avoided because of its human connotation.

The concept of **stability** includes a variety of aspects, all describing how an ecosystem reacts to or withstands internal or external perturbations. Although there are many definitions of stability (163 according to Grimm and Wissel (1997)), the response to and recovery after a perturbation are decisive in describing stability (Fig. 13.5). If an ecosystem is not reacting to a disturbance or environmental change and stays at its current state, this ecosystem is **resistant** to the disturbance or change. It retains its structure, and the current processes and species composition of the ecosystem will also continue in the future. This typically happens only when the event is not very strong in terms of either frequency, intensity or dose. If the event is stronger, more frequent or lasts longer, the **resistance** must increase to maintain the ecosystem's current state. On the other hand, if the ecosystem is able to adapt to these perturbations (e.g. to changes in the environment), recovers over time and thus does not lose species or the capacity to carry out certain processes permanently, this ecosystem is **resilient** to change. It reacts to the disturbance but persists within its boundaries and thus is rather robust. If a perturbation event is even more severe, occurs in combination with other(s) or is of a new type that the ecosystem has not experienced yet, the ecosystem might not have the **adaptive capacity** (also called

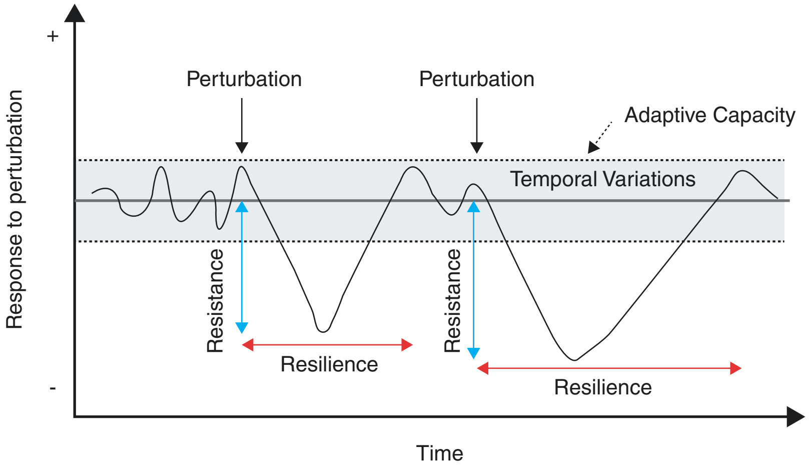

Fig. 13.5 Different aspects of stability. The resistance and resilience of the ecosystem to the first perturbation are higher than those to the second perturbation. In the second case, the ecosystem needs much longer to recover from the perturbation than in the first case. Resistance and resilience are two aspects of stability that are widely used today (sometimes also called resistance and resilience stability, respectively). However, many more definitions and special cases do exist (Chap. 17)

buffering capacity) to withstand or dampen such an event and might thus be transformed into another state. Thus, under these conditions, the ecosystem loses its capacity to function, changes its species composition or both. Nevertheless, one has to keep in mind that resistance or resilience are not inherently beneficial characteristics of an ecosystem. For example, restoration of a degraded ecosystem would likely benefit from less resistance or resilience in the system.

To describe the potential or the probability of this change in state, additional concepts have been developed: **susceptibility** and **vulnerability**. Both terms are often used as synonyms, although there is a difference. While susceptibility only considers the impact on (in our case) an ecosystem, vulnerability also takes into account the probability of the disturbance or change happening. Thus, an ecosystem is called susceptible or vulnerable to a disturbance or change if its resilience is small or already impaired, or if one expects this ecosystem to change soon and lose its current species composition and/or function. Climate change is often mentioned in this respect because of the projected change in the frequency of extreme weather and climate events.

13.5 Impacts of Slow Continuous Forcing and Sudden Disturbances

Because of their age and complexity, the responses of ecosystems to **slow continuous forcing** by the environment—such as global warming, the spread and establishment of invasive plants or the consequences of the presence or absence of ecosystem engineers such as beavers and elephants, but also moles and earthworms (Chap. 20)—are difficult to predict (Part V). Often the underlying mechanisms are not fully understood and thus their consequences at the ecosystem level are difficult to model. Similarly, although at first ecosystem responses to **sudden disturbances** are obvious—for example, damage after flooding or eradication of entire ecosystems after a volcanic eruption—the long-term responses and the recovery of the affected ecosystems are less clear. Both types of event—slow continuous **forcing** and sudden disturbances—have impacts on individuals, species, populations and ecosystems, and thus they change the boundary conditions for all actors and components present in ecosystems, as well as all processes taking place. Such impacts range from small adjustments—for example, the physiological acclimation to changing environmental conditions (Part II)—to changes in species composition and species mortality, or loss of entire ecosystems (Chap. 17), with impacts at different **levels of organisation**:

- Individuals: transient damage (e.g. by late frosts), weakening by pests and parasites, failing reproduction because of weather events, death by windthrow
- Populations: changes in the structure of populations and gene pools (e.g. by reduction of the number of individual plants or by the presence of new spatial barriers to pollination), extinction by events occurring over large areas (e.g. volcanic eruption)
- Ecosystems: changes in species composition by arrival of **non-native species** (which might become invasive), loss of ecosystem components (e.g. by land use), changes or loss of nutrient cycling (e.g. after fire or due to leaching)

Slow continuous forcing, as well as disturbances, are thus events changing the species composition, as well as the continuous element or substance turnover, either slowly or suddenly, often in unexpected directions. At the level of the ecosystem, it is important whether the system loses resources or whether these resources are only relocated within the system but stay in the system. This can be nicely shown for carbon (C) cycling within ecosystems, where the following drivers can be distinguished (Schulze et al. 1999):

- Drivers exerting a continuous forcing (e.g. temperature, precipitation, radiation, CO_2)
- Drivers reallocating pools, but organic matter and therefore nutrient resources bound to it stay in the ecosystem (e.g. herbivory by insects, browsing by animals, grazing in extensive land use systems, C inputs into soils after windthrow)
- Drivers removing species and pools such as organic matter and thus resources from the system (e.g. pathogens, pests, fire, harvest)

13.5.1 Slow Continuous Forcing

Factors such as temperature and precipitation directly control many processes of the C cycle in an ecosystem (as discussed for soil respiration in Sect. 13.3). Similar controls are also present for biomass production by plants, thus affecting the entire carbon budget of the ecosystem. These factors typically show a large temporal variability, resulting in years with large and small carbon gains and losses and highly variable process rates of substance turnover. Recently, new factors driving the C cycle in ecosystems have gained relevance—that is, the increase in the atmospheric CO_2 concentration, atmospheric N deposition, fertilisation and global warming (Part V). These slow but continuous changes in the **growth conditions**, particularly of plants as the primary producers in ecosystems, exert a strong forcing on many C-related processes, from leaf gas exchange to organic matter decomposition. In the long-term, this forcing disturbs the delicate balance of interacting ecophysiological and biogeochemical processes, often with pronounced consequences for ecosystem functions and the original species composition. For example, continuously increasing **CO_2 concentrations** affect growth of plants but also increase their nutrient requirements. Since nutrient availability stays constant (or even decreases because of drier soils), these nutrient requirements, particularly for nitrogen (N), are not easily met, leading to larger C to N ratios in plant tissues, which in turn decompose much more slowly than tissues produced under lower CO_2 concentrations (Chap. 16, Sect. 16.2). Thus, the feedback to the atmosphere in terms of respired CO_2 from decomposition is also influenced, not only the assimilation of atmospheric CO_2.

13.5.2 Sudden Disturbances and Reallocation of Pools

These continuously changing drivers and their impacts are quite different from **sudden disturbances** which, for example, interrupt production and decomposition of organic matter. "**Catastrophes**" such as hurricanes, snow damage and herbivory by insects are examples of these sudden disturbances, as are smaller disturbances such as those caused by moles or wild boars, as well as grazing in extensive (land use) systems, as long as the organic matter is only relocated among different pools but not exported out of the system. Such disturbances can directly accelerate decomposition of plant and soil organic matter by increased litter production in response to the disturbance, or they can change the aggregate structure of the soil—one of the factors controlling the activities of soil biology. This type of disturbance may lead to temporary accumulation of organic matter in certain compartments (e.g. as litter or woody debris) and to reallocation of pools and thus resources. However, these disturbances generally do not change the ecosystem, since most ecosystems are quite resilient to natural disturbances—that is, they can adapt and buffer their impacts. Sometimes, combined disturbances happen—for example, drought plus the occurrence of a pathogen. Then, the second disturbance, often only occurring after the first one, can have devastating effects, even leading to species loss and ecosystem change (Box 13.1).

Box 13.1: Impacts of Combined Disturbances

A well-known example from western North America is the combination of unusually hot and dry summers and mild winters over the recent years, followed by an outbreak of the **mountain pine beetle** (*Dendroctonus ponderosae*) (Fig. 13.6a) carrying the **blue stain fungus**, which blocks the xylem and thus the water and nutrient transport in the tree. Millions of hectares of **conifer forests** have been killed over the last decade. Normally, the beetle attacks only weak and old trees. However, because of the drought, many trees were already water-stressed when they got infected with the fungus and became a breeding ground for the larvae of the beetle. Climate change also favoured the beetle populations, which typically die back in cold winters, restricting their range. Nowadays, even two life cycles of the beetle are possible within 1 year, increasing the beetle population, which in turn also infests healthy, mature trees in larger areas. These trees die within 3–4 years (Fig. 13.6b), turning the forest from a carbon sink (sequestering C in biomass and soils) into a carbon source. This is when trees can become natural hazards themselves, as fuel for fires or by damaging power lines when they fall. In addition, loss of CO_2 assimilation and loss of transpiration but also a larger snowpack with a faster snowmelt negatively affect annual carbon sequestration while increasing water run-off out of these forests in spring.

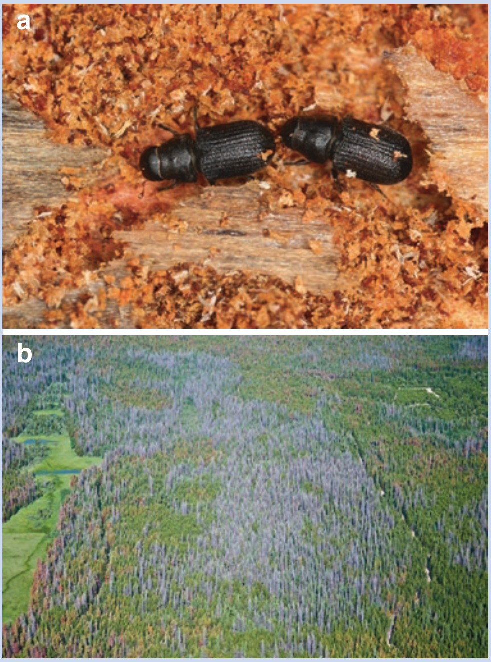

Fig. 13.6 **a** Mountain bark beetle *Dendroctonus ponderosae* (Photo courtesy of B. Wermelinger). **b** Landscape with infested trees in Wyoming, USA, in 2009 (Photo courtesy of J. King, enabled by Light Hawk)

13.5.3 Sudden Disturbances and Loss of Pools

Disturbances that result in removal of biomass and resources from the ecosystem (**export of resources**) have impacts rather different from those disturbances after which pools and thus resources remain in the ecosystem. Loss of organic matter primarily occurs through harvests and fires, but also after large pest and pathogen infestations, by animals browsing and grazing in intensive land use systems where animal faeces are not returned to the pastures. In all of these disturbances, biomass and associated nutrients are lost or exported from the ecosystem and/or decomposed somewhere else—for example, in human-dominated systems, in sewage works or by burning of waste. The heterotrophic organisms of the ecosystem in which the organic matter was once produced are no longer involved in the decomposition process.

Harvests and **intensive grazing** remove not only carbon as plant organic matter but also nutrients with the export of biomass. This export of nutrients can quickly lead to soil degradation if nutrients are not resupplied by fertilisation. Historically, **litter raking** in forests was an important forest use. Newly fallen leaves were collected and used during the winter as bedding for animals in stables and taken to the fields in spring as fertiliser. As leaves and needles have considerably higher nutrient contents than wood, this form of forest use drastically decreased forest soil fertility and led to reallocation of nutrients from forests to fields over large areas of land. The effect of this type of forest use is still visible after decades as shallow humus layers in the affected forests (Schulze (2000), a site at Aubure in France). The impacts of intensive grazing strongly depend on the **stocking rate** of the livestock, which must be in accordance with the vegetative growth to be sustainable. If these sustainable stocking rates are exceeded, **overgrazing** occurs, which results first in a change of vegetation composition, then in a decrease of vegetation cover, then open (bare) soil and, finally, soil erosion—visible, for example, as tracks of grazing on steep slopes in alpine meadows. Measurement of net ecosystem CO_2 fluxes over a pasture in Panama clearly demonstrated how overgrazing can lead to large CO_2 losses, turning the pasture into a carbon source for the 2 years of the study (Wolf et al. 2011).

Another globally very important disturbance is **fire**, which can destroy standing biomass or deep peat soils over large areas in a short time. The intensity of the fire depends mainly on the available biomass but also on the wind speed, the moisture content of the fuel and oxygen concentrations (relevant for below-ground **smouldering peat fires**). Therefore, rare fires—in which plant biomass and soil organic matter that have accumulated in the long interval between the fires are consumed (**stand-replacing fires**)—can have more drastic effects than frequent and thus less intense ground fires. A famous example of such a fire is the one in Yellowstone National Park in 1988, which destroyed 320,000 ha over a couple of weeks because of special weather conditions and wildfire suppression for more than 50 years. Low-intensity fires (**surface fires**) are frequent in savanna systems, where temperatures at ground level usually remain below 100 °C and 40 °C is rarely reached at a 10 cm soil depth (Bradstock and Auld 1995). The often very short duration (only minutes) of the fire at the same site, owing to the low fuel load (i.e. biomass), is the reason for these fire characteristics.

Fire releases large amounts of carbon and nitrogen from the system in the form of different gaseous oxidation products (Konovalov et al. 2014), while base cations mostly remain in the ash in the ecosystem. A fraction of the remaining organically bound nitrogen is readily transformed into ammonium and nitrate in the warm soils covered with dark ash. Thus, seeds, young plants and surviving rhizomes experience good growth conditions, sometimes even better than those before the fire. Therefore, fire is used worldwide as an **agricultural practice** to burn off plant residues that would otherwise not decompose easily (e.g. in dry and hot areas) and to support new growth by increasing nutrient availability right after the

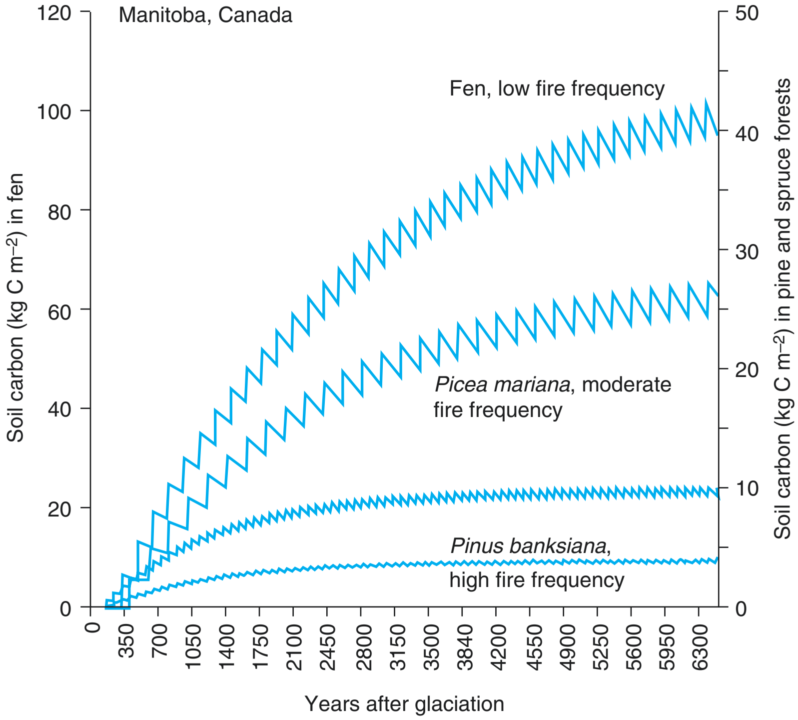

Fig. 13.7 Modelled changes in soil carbon in a wetland fen with a low frequency of fires and in *Picea mariana* and *Pinus banksiana* stands experiencing increased fire frequencies. The zig-zags of the curves reflect the frequency with which fires occurred. The figure illustrates the cumulative amount of C that is removed from these ecosystems directly or indirectly by fires (Harden et al. 2000)

fire. However, in the long-term, fire will lead to a reduction of soil fertility, particularly for the N supply, if this resource loss is not counteracted either by legumes or by fertilisation.

In boreal coniferous forests, the fire sequence determines the amount of carbon that may be stored in the soil (Fig. 13.7). Calculated over a period of 6000 years (since the retreat of the Laurentide Ice Sheet in North America), the frequently burned *Pinus banksiana* stands contain only half as much C in the soil as the less frequently burned *Picea mariana* stands. These amounts, in turn, are significantly smaller than those in very rarely burned blanket bogs where, independently of the fire frequency, the high water table conserves the carbon in the soil, indicating this ecosystem's potential to accumulate organic matter. Saturation occurs in all cases—that is, there is a balance between the formation of organic matter in the soil and its consumption by respiration and fires—but this balance is also affected by the high frequency of fires and the low productivity of the vegetation (Harden et al. 2000).

13.5.4 Impacts on Species Composition

Disturbances not only change the element or substance pools and associated fluxes, but also affect the **composition of species** within the ecosystem. Areas suitable for growth are opened that were previously occupied by other species now weakened or killed by the disturbance. The remaining, surviving organisms may spread or new species may appear because seedlings can establish without competitors, for example, after a stand-replacing fire. The greatest number of species is found with average disturbance intensities (the **intermediate disturbance hypothesis**; Fig. 13.8) (Connell 1978) (Chap. 20, Sect. 20.2). If the frequency of disturbance increases, only a few specialists remain.

At sites where fires occur regularly, vegetation has adapted to fires, with thick bark (e.g. *Sequoia* in North America), capacity to resprout (e.g. many Mediterranean shrubs), the presence of lignotubers (i.e. thick swelling of the root crown, filled with starch, lots of meristems to resprout,

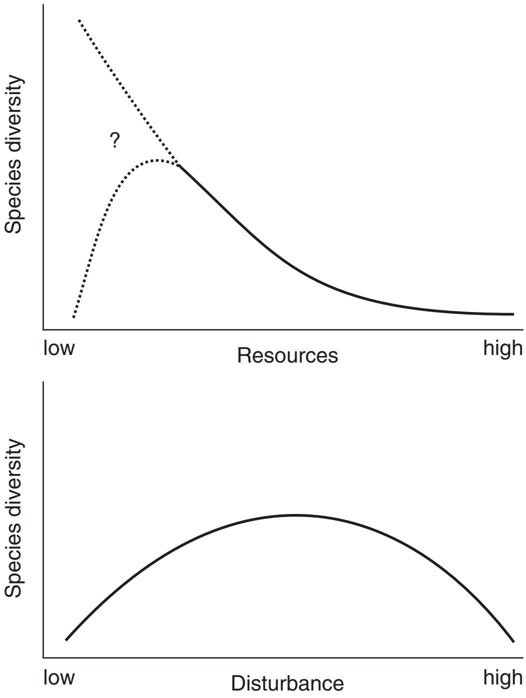

Fig. 13.8 Conceptual model of the relationship between species diversity and resource availability, and between species diversity and habitat disturbance. Species diversity reaches a maximum with average ecosystem disturbance. (After Hobbie et al. (1994))

e.g. *Eucalyptus* in Australia), or cones that need high temperatures to open and release seeds (e.g. *Banksia* in Australia). Sometimes, only the outer layer of the woody stems is burned and turns to charcoal, so regeneration from living tissues at the base of the stem is still possible. The Australian grass tree (*Xanthorrhoea*) even contains a resin that is difficult to burn and protects the stem from fire. In savanna systems, the sparse trees (between 10% and 50% cover) can typically survive (Fig. 13.9a, b); the grasses present in these systems can regrow from meristems close to the ground or below the ground, and herbaceous vegetation can germinate from the seeds below the ground (**seed bank**) and establish very quickly. Lush growth of herbaceous species is thus often a consequence of surface fires, as many nutrients become readily available in the ash (Fig. 13.9c) and shortly afterward because of high mineralisation rates in dark soils (the albedo effect), despite large fractions of C and N being lost from the system. Some plants—the so-called **pyrophytes**—even need fire to stimulate flowering or open their fruits (Fig. 13.9d).

Often, continuous slow forcing and sudden disturbances create new growth conditions that favour different plant species from those prior to these events. But the new species might also feed back on other organisms and organism groups in the ecosystem (Chap. 19, positive and negative feedbacks), as well as on the environmental growth conditions. Thus, they create an environment that favours their own species, at the expense of its native competitor. Some of the underlying mechanisms at the molecular and plant levels have been already discussed in Parts I and II (e.g. Chap. 12), but new (feedback) processes come into play when we are considering the ecosystem level (Sect. 13.3, emergent properties; Chap. 19, positive and negative feedbacks). An example from North America illustrates this situation very nicely:

The Mediterranean grasses *Bromus tectorum* and *Bromus rubens* successfully invaded the North American *Artemisia tridentata* **shrubland** since the end of the nineteenth century, which led to a marked reduction of *Artemisia* (West and Young 2000) and a pronounced change in the fire frequency. *Bromus* is a winter annual, which germinates in the autumn, establishes and grows over winter and completes its life cycle in late spring/summer, avoiding most of the hot and dry summers as seed. *Artemisia* is a long-lived shrub, which grows throughout the summer and flowers in late summer/early autumn. It contains terpenoid compounds against herbivory and can resprout after a fire. When *Bromus* was introduced accidentally to this perennial ecosystem, a plant with not only a very different life cycle but also very different ecophysiology was introduced (Germino et al. 2016). *Bromus* has very high water use early in the growing season before seed set, when water availability in the soil is still high. However, this means that the soil water pool is depleted faster and *Artemisia*, which must survive the dry summer period, does not have enough water later in the season. Thus, *Artemisia* dies, often without having formed seeds. In addition,

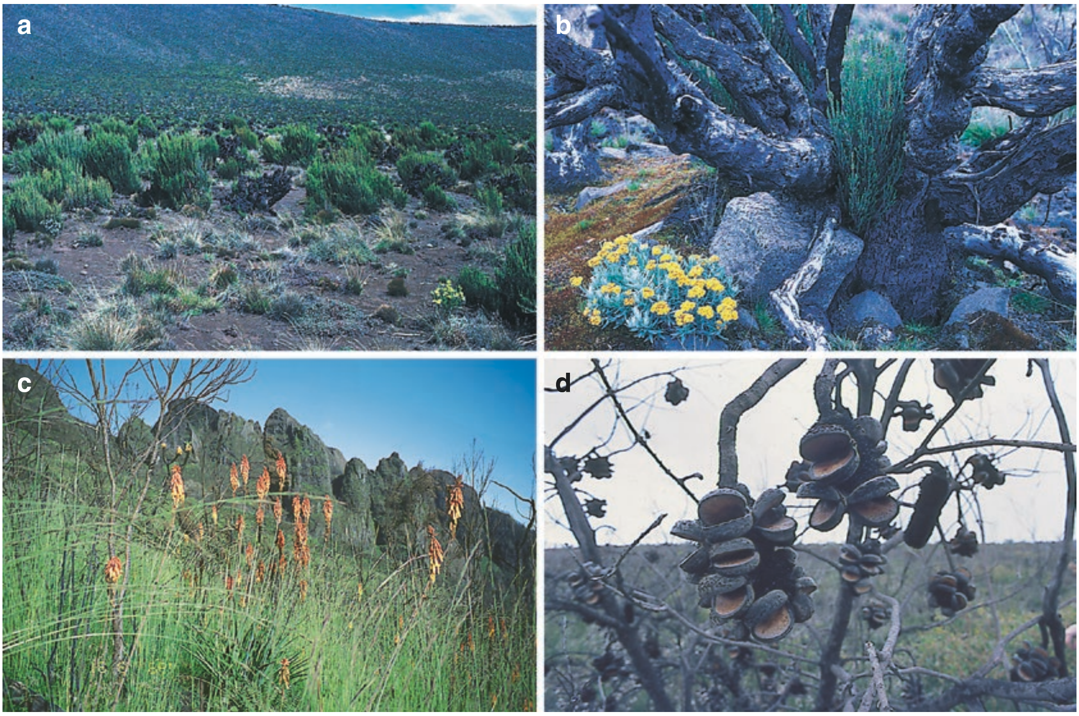

Fig. 13.9 Examples of vegetation adapted to fire. **a**, **b** Fire vegetation on Mount Kilimanjaro (Shira Plateau). **a** *Erica arborea* as stunted vegetation that regenerates from charred branches. On average, there is a fire every 3–5 years. **b** Charred *E. arborea* at a site with less frequent fires. The bifurcated twigs show that the plant had survived at least one fire. Between the last and the most recent fire a substantial trunk had developed, and the intensity of the fire was therefore high. Both pictures were taken 2 years after the fire. Rejuvenation of the bushes had occurred, with bushy growth on the frequently burned site, where little biomass had accumulated between fires. In contrast, growth from the charred thick trunk was comparatively sparse. In the foreground is *Helichrysum splendidum*, a typical fire indicator. **c** Vigorous germination of *Festuca obturbans* and *Kniphofia thomsonii* after an intense fire in the alpine zone of Mount Kilimanjaro. In the foreground are charred twigs of *Erica arborea* and *Erica trimera*. **d** Fruits of the Australian *Hakea* (Proteaceae) open only after a fire. (Photos: E. Beck)

the effect of differential water use is enhanced by fire. Because of the high fuel load with dead *Bromus* biomass during summer, the fire frequency has increased from 60–110 years to only 3–4 years (D'Antonio and Vitousek 1992). This again favours *Bromus*, which germinates from seeds in the autumn, when its own standing biomass has been burned and its competitor, *Artemisia*, has been weakened or killed. Moreover, *Artemisia* cannot regenerate as fast as *Bromus*, and *Artemisia* seedlings are not able to compete with *Bromus* when competing directly. This example demonstrates that the consequences of resource use are quite different at the plant level versus the community level—that is, when competition for the same resource sets in and "saving" water might just provide water for a competitor. Therefore, many successful **invasive species** have relatively high resource demands, not being very resource efficient (Fig. 13.10). This example also shows how changes in the native species composition owing to slow changes and disturbances can in turn affect the ecosystem's environment. Fire frequencies have changed because *Bromus* produces a lot of standing biomass that burns easily and, as a grass, it can withstand fires easily and either germinate from the seed bank or regrow from root collar meristems. Thus, shortened fire intervals have favoured the invasive grass over the native perennial shrub.

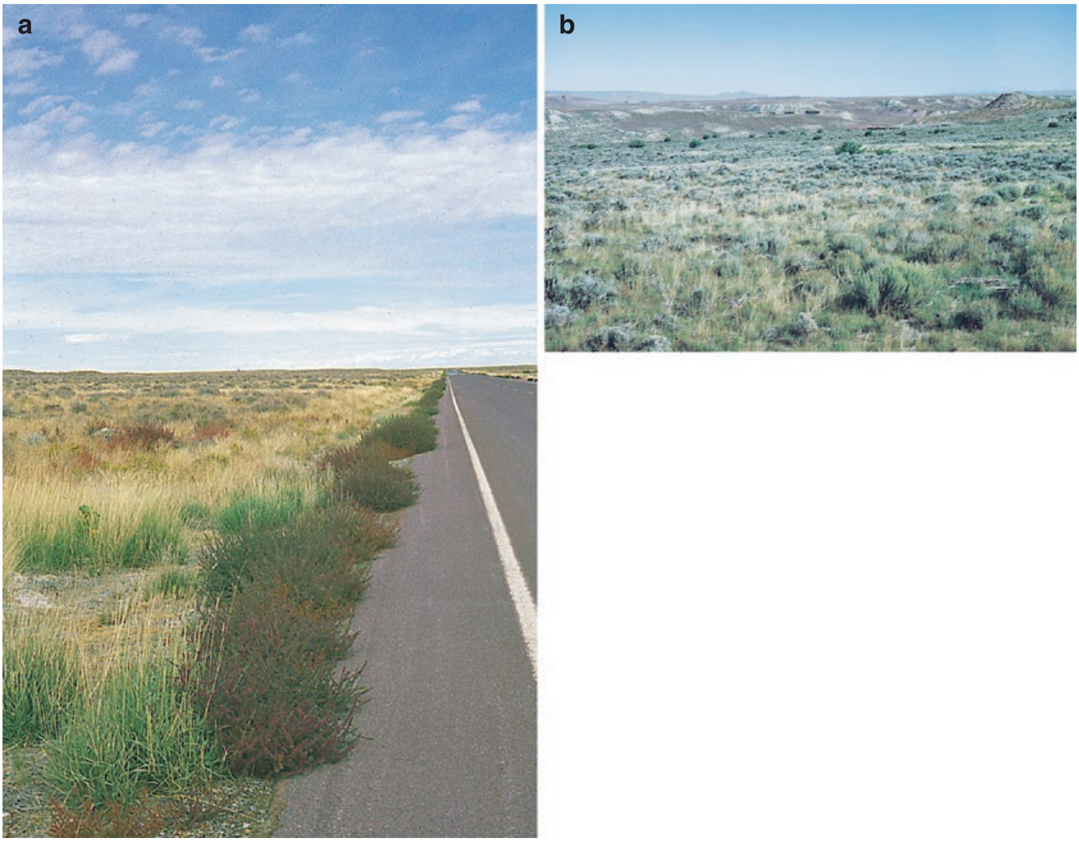

Fig. 13.10 Invasive plant species. **a** Invasive species often spread along roads. *Salsola kali* (Chenopodiaceae) can be found close to roads in the semi-deserts of Utah in western North America. *Salsola* is a salt-tolerant species from Asian deserts. Away from the kerb of the road, the Mediterranean *Bromus* dominates. **b** Mediterranean *Bromus* in the *Artemisia* shrubland of Wyoming. *Artemisia* cover is already broken. (Photos: E.-D. Schulze)

13.6 Ecosystem Budget Approach

Biogeochemical processes that take place in terrestrial ecosystems can be described as fluxes into, out of or within ecosystem components and compartments, but also as size changes of element or water pools present in ecosystems. Often element or nutrient pools are also called **stocks**—for example, soil carbon stocks. **Pools** or stocks can be compared with the amount of money in a bank account, while fluxes in this analogy would be all transfers—that is, deposits and withdrawals from this bank account. Thus, if the withdrawals exceed the deposits, the pool is decreasing in size or even disappears; if the deposits exceed the withdrawals, the pool is increasing in size. One can also calculate the **net budget** of all gains (deposits) and losses (withdrawals). This net budget (the sum of all transfers) can be either positive (gains > losses) or negative (gains < losses), depending on the fluxes (transfers). If one considers the CO_2 budget of an ecosystem, a positive net budget represents the condition when assimilation exceeds respiration; a negative net budget represents the condition when assimilation is lesser than respiration. If one considers the C budget, additional fluxes need to be considered—for example, methane uptake and loss, volatile organic carbon losses, dissolved organic and inorganic losses, etc. Often these fluxes have a special **sign convention**, depending on the discipline in which they are used. So plant ecophysiological calculate with positive numbers when assimilation is studied, while micrometeorologists calculate with negative numbers when they consider assimilation, since CO_2 taken up by plants is lost from the atmosphere. In all disciplines, the following units are used to describe biogeochemical processes:

- Pool or stock size (amount of an element or substance): grams per square metre
- Unidirectional element or substance flux rate: grams per square metre per unit of time
- Net element or substance budget: grams per square metre per unit of time, often partitioned into losses and gains, also called sources and sinks

Ecosystem budget studies have become increasingly frequent in recent decades, although tracing and measuring all processes within an ecosystem will hardly be possible, despite the application of sophisticated new methods. Mechanisms regulating the size of the flux include regulation by the substrate (i.e. **feed-forward regulation**), regulation by the products (i.e. **feedback regulation**), branching, modulation and co-limitation (Parts I and II). The details of selected biogeochemical fluxes are described in Chap. 16.

13.6.1 Stand Growth

Growth of plant stands depends not only on assimilation of CO_2 and the availability of water but also on the **turnover** and availability of nutrients (Chap. 12, Sect. 12.4). This means that to describe stand growth, the net budgets of carbon, water and nutrients need to be quantified. Water and CO_2 may be regarded in ecosystems as renewable resources from an indefinitely large atmospheric pool (with certain exceptions, such as deserts). This is different for nutrients. Generally, nutrients are released during decomposition of organic matter or during weathering of primary minerals or bedrock, and they are then reversibly absorbed to the soil ion exchange system or to soil organic matter (SOM). The ash content of biomass shows the amount of nutrients taken up by plants from the soil (neglecting above-ground uptake from deposition). These nutrients become available by decomposition of organic biomass when it is not exported (for example, by harvesting) but remains as dead biomass (litter, debris) in the system (Chap. 16). Ulrich (1987) has formalised the connection between the availability of CO_2, water and nutrients, and their incorporation into organic substances, with an equation of substance and energy balance for organic matter in ecosystems:

$$\begin{aligned} a\mathrm{CO_2} + x\mathrm{M^+} + y\mathrm{A^-} + (y-x)\mathrm{H^+} + z\mathrm{H_2O} + \text{energy} \\ \leftrightarrow \left(\mathrm{C}_a\mathrm{H}_{2z}\mathrm{O}_z\mathrm{M}_x\mathrm{A}_y\right)\text{org. matter} + (a+\ldots)\mathrm{O_2} \end{aligned} \tag{13.4}$$

where M^+, A^- and H^+ are cations, anions and hydrogen ions, and the coefficients a, x, y and z are stoichiometric coefficients in the soil solution. To maintain high production rates (of organic matter containing these substances) in managed systems, the use of elements from the environment owing to harvesting must be replaced by fertilisation.

13.6.2 Mean Residence Times

In a well-balanced system, formation of biomass and mineralisation of organic matter would occur simultaneously and be in equilibrium. However, this equilibrium does not occur in the real world, as there are considerable time lags between use (for biomass formation) and release (via mineralisation) of resources, described by the **mean residence time** (MRT; Eq. 13.5) in the respective compartment.

$$\mathrm{MRT} = \frac{\text{Pool}}{\text{Flux rate}} \tag{13.5}$$

where Pool is given in mass per area and Flux rate is given in mass per area and time. Thus, the unit of MRT is time.

For example, leaves are synthesised within one year, but the foliage stays on a plant maybe for years and the litter is decomposed over many months to years—that is, nutrients bound in leaves will, on average, become available for further uptake and growth only after 2–8 years (Persson et al. 2000). The mean residence time of these nutrients in the foliage is thus 2–8 years. In wood, nutrients may be bound for more than 100 years. The decomposition of a tree trunk takes decades, and thus the delay between uptake of resources and return of the same resources is a lot longer for wood than for leaf litter (Chap. 16, Sect. 16.2.2).

The accumulation of litter is thus a sign that the shedding of leaves or needles exceeds the capacity of soil organisms to decompose this litter. Fast **decomposition** is limited either by lack of the organisms capable of mineralisation this litter, by plant compounds that are difficult to metabolise, by unfavourable climatic conditions, by stabilisation in the soil, or by a combination thereof. An open stand typically provides better conditions for mineralisation (higher soil temperature and moisture, affecting soil organisms) than a closed stand. Evergreen needles are less decomposable than deciduous leaves. Woody material decomposes more slowly than foliage. Depending on the decomposability of organic matter, different fractions of soil organic matter have very different ages, ranging from very young (recent soil carbon, up to 30 years old) to soil organic matter, which might be older than 1000 years (Townsend et al. 1995; Schulze et al. 2000; Schlesinger and Bernhardt 2013).

13.6.3 Loss of Resources

Terrestrial ecosystems are thermodynamically **open systems**—that is, energy and matter get lost. Some of these losses are unavoidable, since they occur naturally either as part of the energy budget (Chap. 9), during background soil biogeochemical and plant ecophysiological or defence processes (Chaps. 11 and 12), while some of these losses have natural agents such as wind, water and fire. But also anthropogenic activities play a major role—for example, human-induced fires, forest and agricultural management (Sect. 13.5.3), and environmental pollution. The resources that are lost include:

- Water: owing to the energy budget, run-off and infiltration into deeper soil horizons
- Mineral particulate matter: during dust storms and owing to water erosion
- Organic particulate matter: owing to erosion and during fires
- Carbon and nutrients (natural): via decomposition and nitrification, respiration and volatile organic carbon (VOC) production, infiltration into deeper soil horizons, run-off, erosion after natural disturbances
- Carbon and nutrients (anthropogenic): during fires and owing to management of terrestrial ecosystems
- Increased nutrient losses: owing to soil acidification after environmental pollution (N deposition)

Some of these **resources** lost from one ecosystem can be **beneficial** to other ecosystems. For example, mineral dust transported across the Atlantic Ocean fertilises the Amazonian forest with basic cations (Bristow et al. 2010). On the one hand, some losses are core for closing biogeochemical cycles. Denitrification (the release of N_2) is the only natural process capable of closing the global N cycle. On the other hand, some losses from terrestrial ecosystems have **detrimental** effects on **ecosystem health**—of the ecosystem losing the resource and of the ecosystem(s) receiving it. For example, accelerated nitrate and cation losses occurred because of soil acidification after environmental pollution (N deposition) and resulted in decreased forest health and tree growth across Europe in the 1980s and 1990s.

Chemical conditions in the soil are primarily dependent on the constitution of the original bedrock (Chap. 11). However, these conditions are changed as a consequence of the mobilisation and uptake of nutrients by microorganisms and plants—for example, when seasonality of plant growth, and thus demand, is decoupled from supply via microbial decomposition and nitrification processes. Since nitrate in the soil is not bound to minerals or organic matter, it can be leached into deeper soil horizons and/or the groundwater, taking along cations. For example, if nitrate is formed in autumn, when most plants stop growing, large nitrate and cation losses occur during winter. In summer, however, the nitrogen requirement of the vegetation can even exceed the supply from the soil. This asynchronous pattern of supply and demand leads, in the end, to changes in habitat conditions, with local overexploitation (loss of cations in the upper mineral layer—that is, podzolisation and acidification of soils; Chap. 11, Sect. 11.1) or accumulation of intermediary products, given that degradation is impeded by decreasing pH (e.g. raw humus).

But also anthropogenic activities, such as **acid deposition** with strong acids (H_2SO_4, HNO_3), affect chemical conditions in the soil. The rate of soil **acidification** depends on the mineral constitution of the bedrock and the cumulative acid inputs. On limestone soils with a high $CaCO_3$ content, incoming acid deposition is at first balanced by weathering of carbonate (Eqs. 13.6 and 13.7; Fig. 13.11a):

$$CaCO_3 + H_2CO_3 \leftrightarrow Ca^{2+} + 2HCO_3^- \quad (13.6)$$

and:

$$H_2CO_3 \leftrightarrow H^+ + HCO_3^- \leftrightarrow CO_2 + H_2O \quad (13.7)$$

The Ca^{2+} ions that are released occupy the charges that are freed at the soil exchange sites (Chap. 11, Sect. 11.1). With time, $CaCO_3$ will be continuously consumed, the soil pH will further decrease and a reversible exchange of **cations** will occur with clay minerals and organic matter. Under continuing acid inputs and thus loss of cations from the exchange buffer, the H^+ buffering will be achieved by metal oxides and hydroxides, leading to a pH-dependent increase in the availability of certain metal ions. For example, Mn^{2+} becomes mobile at a pH between 5 and 4.2. At a pH of 4.2, the soil reaches another stable buffer system, the one buffered by Al hydroxides (Chap. 7, Sect. 7.5). The iron buffer range (with Fe^{3+}) is reached below pH 3.8. The availability of ions is very variable during the course of this process, and each element is specifically dependent on the pH of the soil solution (Fig. 13.11b).

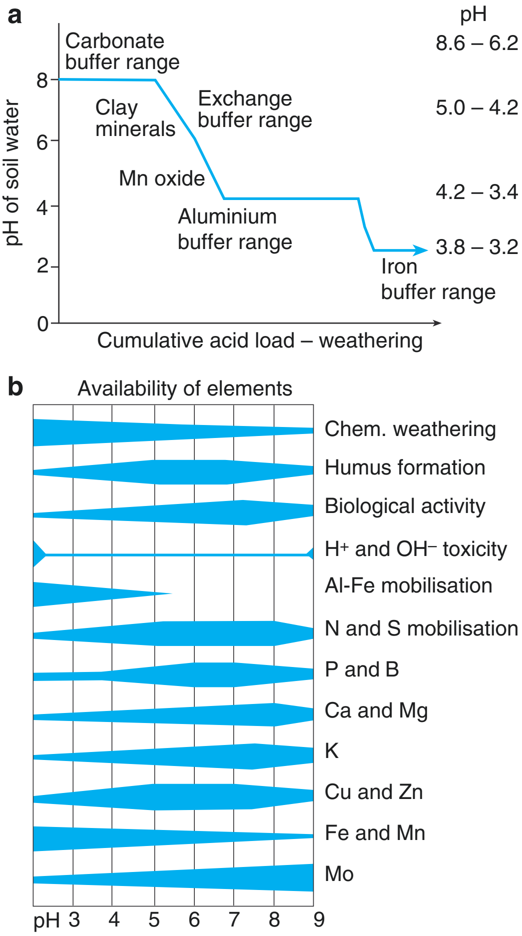

Fig. 13.11 Change of nutrient availability with soil pH. **a** Changes in the pH of the soil solution with continuing weathering as a consequence of the cumulative proton stress—that is, acid deposition (after Schulze and Ulrich (1991)). **b** Availability of nutrients depends on the pH of the soil solution (Larcher 2003)

The chemical changes in the soil are reversible—that is, by fertilisation or liming, provided that the clay minerals are not restructured. As soon as the crystalline structure of silicates and clay minerals is changed (e.g. by dissolving the Al lattice in a replacement of alkaline cations with protons; Chap. 11), a reversal into the original state is no longer possible, not even by abundant supply of cations. The ecosystem's health is damaged irreversibly.

Summary

- Terrestrial ecosystems are functional units in a given heterogeneous landscape and include soil, microorganisms, vegetation and animals, as well as the lower level of the atmosphere.
- Ecosystems are complex networks of relationships and processes. Here, biogeochemical processes happen and plant, animal and microbial species interact with each other.
- All ecosystems, managed and unmanaged, are affected by environmental and human drivers, even very remote ones. There are no "natural" ecosystems.
- An ecosystem is a thermodynamically open system, where energy and matter can also get lost to the atmosphere or the hydrosphere. Thus, to study ecosystems, a systems approach is used. Pools and fluxes of energy and matter must be measured per unit of ground area.
- Ecosystems exhibit emergent properties, such as ecosystem structure, biogeochemical cycling within ecosystems, species and process interactions, or time lags in ecosystem responses.
- Ecosystems are characterised by nonlinear response functions for processes with interacting drivers. These include saturation in production of organic matter with increasing biomass and exponentially increasing respiration with temperature, counteracted by low soil moisture.
- The availability of resources (especially water and nutrients) determines the turnover rates in an ecosystem. Internal cycling and resource losses can be major factors. Uptake of nutrients by plants and their remineralisation usually do not occur simultaneously; hence in ecosystems, carbon is accumulated and losses of nitrogen and nutrients may occur. Harvesting and grazing are important factors removing resources from an ecosystem.
- Ecosystems are generally not at equilibrium or at steady-state with respect to the various biogeochemical processes or species composition. Disturbances constantly change these dynamics. Depending on the resistance and the resilience of ecosystems, slow continuous forcing, as well as sudden disturbances, affect their processes and species composition.

References

Bormann FH, Likens GE (1967) Nutrient cycling. Science 155:424–429

Bradstock RA, Auld TD (1995) Soil temperatures during experimental bushfires in relation to fire intensity: consequences for legume germination and fire management in south-eastern Australia. J Appl Ecol 32:76–84

Bristow CS, Hudson-Edwards KA, Chappell A (2010) Fertilizing the Amazon and equatorial Atlantic with West African dust. Geophys Res Lett 37:L14807

Connell JH (1978) Diversity in tropical rain forests and coral reefs. Science 199:1302–1310

Currie WS (2011) Units of nature or processes across scales? The ecosystem concept at age 75. New Phytol 190:21–34

D'Antonio CM, Vitousek PM (1992) Biological invasions by exotic grasses, the grass/fire cycle, and global change. Annu Rev Ecol Syst 23:63–87

Ellenberg H (ed) (1971) Integrated experimental ecology. Methods and results of ecosystem research in the German Solling project, Ecological Studies, vol 2. Springer, Berlin

Ellenberg H, Mayer R, Schauermann J (1986) Ökosystemforschung. Ergebnisse des Sollingprojektes 1966–1986. Eugen Ulmer Verlag, Stuttgart

Frank D, Reichstein M, Bahn M, Thonicke K, Frank D, Mahecha MD, Smith P, van der Velde M, Vicca S, Babst F, Beer C, Buchmann N, Canadell JG, Ciais P, Cramer W, Ibrom A, Miglietta F, Poultier B, Rammig A, Seneviratne SI, Walz A, Wattenbach M, Zavala MA, Zeischler J (2015) Effects of climate extremes on the terrestrial carbon cycle: concepts, processes and potential future impacts. Glob Change Biol 21:2861–2880

Germino MJ, Chambers JC, Brown CS (eds) (2016) Exotic brome-grasses in arid and semiarid ecosystems of the Western US, Springer Series on Environmental Management. Springer, New York

Gleason HA (1926) The individualistic concept of the plant association. Bull Torrey Bot Club 53:7–26

Grimm V, Wissel C (1997) Babel, or the ecological stability discussions: an inventory and analysis of terminology and a guide for avoiding confusion. Oecologia 109:323–334

Haeckel E (1866) Generelle Morphologie der Organismen: Allgemeine Grundzüge der organischen Formen-Wissenschaft, mechanisch begründet durch die von Charles Darwin reformirte Descendenz-Theorie. G. Reimer, Berlin

Harden JW, Trumbore SE, Stocks BJ, Hirsch A, Cower ST, O'Neill KP, Kasischke ES (2000) The role of fire in the boreal carbon budget. Glob Change Biol 6:174–184

Hobbie SE, Jensen DB, Chapin FSIII (1994) Resource supply and disturbance as control over present and future plant diversity. Ecol Stud 99:385–408

Konovalov IB, Berezin EV, Ciais P, Broquet G, Beekmann M, Hadji-Lazaro J, Clerbaux C, Andreae MO, Kaiser JW, Schulze E-D (2014) Constraining CO_2 emissions from open biomass burning by satellite observations of co-emitted species: a method and its application to wildfires in Siberia. Atmos Chem Phys 14:10383–10410

Kramer H (1988) Waldwachstumslehre. Parey, Hamburg

Larcher W (2003) Physiological plant ecology: ecophysiology and stress physiology of functional groups, 4th edn. Springer, Berlin

Lloyd J, Taylor JA (1994) On the temperature dependence of soil respiration. Funct Ecol 8:315–323

Osawa A, Allen RB (1993) Allometric theory explains self-thinning relationships of mountain beech and red pine. Ecology 74:1020–1032

Persson T, Rudebeck A, Jussy JH, Clin-Belgrand M, Prieme A, Dambrine E, Karlsson PS, Sjöberg M (2000) Soil nitrogen turnover—mineralisation, nitrification and denitrification in European forest stands. Ecol Stud 142:297–331

Reichstein M, Bahn M, Ciais P, Frank D, Mahecha MD, Seneviratne SI, Zscheischler J, Beer C, Buchmann N, Frank D, Papale D, Rammig A, Smith P, Thonicke K, van der Velde M, Vicca S, Walz A, Wattenbach M (2013) Climate extremes and the carbon cycle. Nature 500:287–295

Ruehr NK, Knohl A, Buchmann N (2010) Environmental variables controlling soil respiration on diurnal, seasonal and annual time-scales in a mixed mountain forest in Switzerland. Biogeochemistry 98:153–170

Schlesinger WH, Bernhardt ES (2013) Biogeochemistry: an analysis of global change, 3rd edn. Academic Press, Amsterdam

Schulze E-D (1982) Plant life forms and their carbon, water and nutrient relations. In: Lange O, Nobel PS, Osmond CB, Ziegler H (eds) Physiological plant ecology II. Water relations and carbon assimilation, Encyclopedia of plant physiology, new series, vol 12B. Springer, Berlin, pp 616–676

Schulze E-D (ed) (2000) Carbon and nutrient cycling in European forest ecosystems, Ecological Studies, vol 142. Springer, Berlin

Schulze E-D, Ulrich B (1991) Acid rain—a large-scale, unwanted experiment in forest ecosystems. Scope 45:89–106

Schulze E-D, Lloyd J, Kelliher FM, Wirth C, Rebmann C, Lühker B, Mund M, Knohl A, Milyokova IM, Schulze W, Ziegler W, Varlagin A, Sogachev AF, Valentini R, Dore S, Grigoriev S, Kolle O, Panfyorov MI, Tchebakova N, Vygodskaya NN (1999) Productivity of forests in the Eurosiberian boreal region and their potential to act as a carbon sink—a synthesis. Glob Change Biol 5:703–722

Schulze E-D, Högberg P, van Oene H, Persson T, Harrison AF, Read D, Kjöller A, Matteucci G (2000) Interactions between the carbon and nitrogen cycle and the role of biodiversity: a synopsis of a study along a north-south transect through Europe. Ecol Stud 142:468–492

Silvertown JW, Lovett Doust J (1993) Introduction to plant population biology, 3rd edn. Blackwell Scientific Publications, Oxford

Smith MD (2011) An ecological perspective on extreme climatic events: a synthetic definition and framework to guide future research. J Ecol 99:656–663

Tansley AG (1935) The use and abuse of vegetational concepts and terms. Ecology 42:237–245

Townsend AR, Vitousek PM, Trumbore SE (1995) Soil organic matter dynamics along gradients in temperature and land use on the island of Hawaii. Ecology 76:721–733

Ulrich B (1987) Stability, elasticity, and resilience of terrestrial ecosystems with respect to matter balance. Ecol Stud 61:11–49

West NE, Young JA (2000) Intermountain valleys and lower mountain slopes. In: Barbour MG, Billings WD (eds) North American terrestrial vegetation, 2nd edn. Cambridge University Press, Cambridge, pp 255–284

Westoby M (1984) The self-thinning rule. Adv Ecol Res 14:167–225

Wolf S, Eugster W, Potvin C, Turner BL, Buchmann N (2011) Carbon sequestration potential of tropical pasture compared with afforestation in Panama. Glob Change Biol 17:2763–2780

Yoda K, Kira T, Ogawa H, Hozami K (1963) Self thinning in overcrowded pure stands under cultivated and natural conditions. J Biol Osaka City Univ 14:107–129

Approaches to Study Terrestrial Ecosystems

14

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14.2 **Experiments** 494
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Rain-out shelters to study the impact of extreme summer drought (*to the left in the background*), close to an eddy covariance flux station to measure biospheric–atmospheric gas exchange of intensively managed grassland (*to the right in the foreground*). The site, Chamau, is located at an elevation of about 400 m, close to the city of Zug, Switzerland. The shelters are 3 × 3.5 m in area, 2.1 m tall at the highest point and open on all sides; the shelters’ large openings are directed towards the main wind direction to ensure sufficient air circulation inside the shelters. Instrumentation at the flux station to measure CO_2 and H_2O vapour fluxes—that is, infrared (IR) gas analysers and a three-dimensional sonic anemometer—is installed on a 2 m mast, complemented by further sensors for microclimate and soil heat fluxes. (Photo courtesy of S. Burri)

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One can study terrestrial ecosystems in many ways: as an attentive observer, as an experimentalist designing hypothesis-driven experiments, or as a modeller. Depending on the research questions asked and where the focus of this system-oriented and often also process-oriented research is, one not only carries out measurements of biogeochemical pools and fluxes but also quantifies responses of individual species and plant communities to changes in environmental conditions, plant diversity or ecosystem management. Studies can be short-term or long-term; they can be carried out at a single site or can rely on multiple sites. However, all of these different approaches, measurements and/or models need to account for the ecosystem characteristics mentioned in Chap. 13. Thus, the methodology used to study terrestrial ecosystems is often based on many different disciplines (e.g. biology, soil science, hydrology and micrometeorology) and is typically used in combination (e.g. measurements of biospheric–atmospheric gas exchange of entire ecosystems). This leads to **interdisciplinary** research, which demands solid disciplinary background knowledge but also interest and skills in interacting with neighbouring disciplines.

Which measurements are taken when, where and how often depends on the research question:

- If one is interested in the effect of drought on water use in a grassland, then different water supplies to this grassland need to be taken into account—that is, precipitation, soil water storage, groundwater and maybe even irrigation. Thus, measurements of climatic variables such as precipitation and temperature, but also soil moisture, evapotranspiration and stand biomass and architecture, will have to be taken close to the field site (climate) and at the field site (all other variables), including soil profile measurements down to a certain depth, either continuously or in campaign mode before, during and after the drought.
- However, if one is interested in the effects of drought on competition for water in a grassland, then the vegetation composition needs to be taken into account as well (Chaps. 19 and 20), in addition to the variables mentioned above. Thus, measurements of growth and ecophysiology (Chaps. 9 and 10) will have to be added at species or functional group levels and carried out in campaign mode in the field or in the greenhouse.

Overall, good knowledge of **experimental design** and **statistics** is crucial for the study of ecosystems, whether one focuses on observations or experiments.

Furthermore, **long-term** studies are necessary to separate short-term responses of ecosystems to environmental factors from long-term trends. If one is interested in the impacts of global warming on forest productivity, then short-term responses to a summer heatwave causing water stress in a particular year might counteract a long-term trend of increased productivity. Long **time series** of multiple decades are needed to separate these short-term signals (sometimes also called **noise**) from the long-term **signal** of global warming, particularly when the driver (air temperature) increases only slowly. However, such long-term data are rarely available. On the other hand, **short-term** studies, often carried out as campaigns of several days to weeks or as 3-year experiments (the typical funding period), need to take **transient effects** into account. Such effects occur when environmental conditions have been changed very suddenly in an experiment (e.g. by changing fertilisation or by establishing a new species composition) while the processes under study (e.g. plant growth or soil microbial processes) respond much more slowly in comparison with the change in the driver. For example, plant growth will be related not only to the new fertilisation regime but also to the large pool of nutrients already present in the soil. Thus, changes in plant growth in response to the new fertilisation regime might not become apparent until much later, when the old pool of soil nutrients is really affected by the new fertilisation. Using chronosequences (i.e. multiple sites subjected to the same driver but at different times) might be the way to go. For the example discussed above, a **chronosequence** with multiple sites (typically unreplicated) at which fertilistion was changed 1, 3, 6, 9 and 12 years

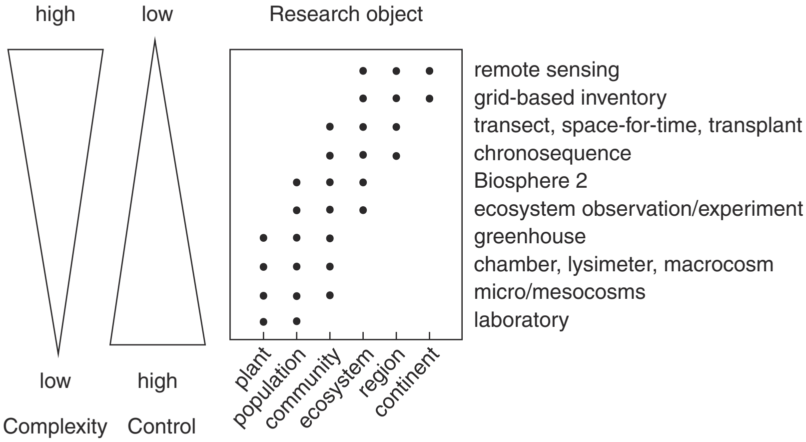

Fig. 14.1 Different approaches to study terrestrial ecosystems. The approaches described in this chapter differ in complexity and possibility to control for environmental conditions, as well as in their spatial applications

ago might be better suited to study the responses to a change in the fertilisation regime. However, replacing time for space is based on the assumption that conditions were constant over time, which is not always the case (Sect. 14.1.2 for further details).

Spatially distributed studies are necessary for generalisation of the findings from otherwise individual case studies. Thus, single sites are part of gradients (typically along environmental drivers or management intensities) or transects (typically across the landscape or across continents), networks or grid-based inventories (Fig. 14.1). Definition of the variables and criteria on which these spatially distributed studies are based is relatively easy (e.g. annual temperature, across Australia, grid size 500 × 500 km). However, quantification of the abiotic and biotic factors that covary with these criteria (e.g. annual precipitation, soil type, elevation and management), and identifying these interactions, is very difficult and thus often limits the applicability of such spatial approaches (Sect. 14.1.3).

14.1 Observations

Observations are often used to investigate processes and patterns in terrestrial ecosystems; that is, no additional manipulations of the natural conditions are carried out, but the actual environmental conditions the ecosystem is experiencing are studied. Typical research questions addressed with this type of approach are: How does forest productivity react to changes in climate? How does the native species composition change in response to a non-native organism invading the system? Sometimes observations are distinguished from **monitoring**. Although this distinction is not very well defined, one could argue that measurements done for a legal purpose—for example, for pollution control or for habitat assessment required for national or international treaties—become a monitoring effort. In contrast, measurements driven by scientific objectives are often called observations.

Nevertheless, ecosystems under natural conditions can also be subjected to “treatments” or “experiments”. Comparison of different management intensities of agricultural systems might qualify, for some researchers, as comparison of different treatment levels of an experiment. Climate change has been called an “inadvertent global experiment” affecting the Earth system in an unprecedented way (Ramanathan 1988). Thus, the study of ecosystems over very long time periods might allow assessments of their responses to global change or to natural hazards. Ideally, such time series should be replicated at different locations, although unique time series exist for single locations (e.g. the CO_2 concentration record at Mauna Loa, Hawaii, USA).

14.1.1 Whole-Ecosystem Observations

Whole-ecosystem observations started with the onset of **plant geography**, when scientists and explorers such as Willdenow, von Humboldt, de Candolle and Grisebach described vegetation composition and plant distribution around the world in the eighteenth and nineteenth centuries. Later, experimental studies were added by Stahl, Kerner von Marilaun, Warming and Schimper, along with physiological, histological and climatological aspects in the twentieth century (Buchmann 2002; Sect. 14.2). Whole-ecosystem observations gained new momentum with the **International Biological Program** (**IBP**; 1964–1974) from the United Nations Educational, Scientific and Cultural Organisation (UNESCO), originating in Europe and inspired by the major scientific success of the International Geophysical Year (IGY; 1957–1958). The IBP was followed by the **Man and the Biosphere Programme** (**MAB**; still running), launched in 1971 also by UNESCO, extending the scope of the science to include humans. Ecosystem ecology entered a new era, also called "**big ecology**" (Coleman 2010). Large-scale studies were complemented by regional to global networks, employment of new technology and new approaches to access, for example, tall canopies allowed completely new research questions to be addressed. For example, the **World Climate Research Programme** (**WCRP**) was established in 1980 to develop our scientific understanding of the physical climate system. Many studies on global environmental change were brought together within the **International Geosphere–Biosphere Programme** (**IGBP**), launched in 1986. In parallel, the **International Human Dimensions Programme** (**IHDP**) was initiated in 1990 to address the human and societal aspects of global change, and **Diversitas** was established in 1991 to study the loss and change of global biodiversity (Greenaway 1996). All four programmes were brought together in 2001 under the umbrella of the **Earth System Science Partnership** (**ESSP**) to foster better cooperation among them and to support greater integration across disciplines, particularly between natural and social sciences. All of these efforts continued until the end of 2015 and have now been brought together in **Future Earth** (http://www.futureearth.org) to provide scientific knowledge to support the transition of global societies towards global sustainability (Part V of this book).

14.1.1.1 Large-Scale Case Studies

Many large-scale observational studies of ecosystems had their origin during the IBP, such as the German Solling Project (Ellenberg 1971) or the Grassland Biome Studies (French 1979). In the **Solling Project**, questions about the effects of acid rain on soils and forest ecosystems were the main focus, later followed by experimental manipulations of incoming precipitation. The time series of soil nutrient fluxes started at this time (Brumme and Khanna 2009), in its duration comparable to the atmospheric CO_2 concentration measurements at Mauna Loa. Some of the most prominent achievements were recognition of the relevance of below-ground processes for nutrient cycling, identification of atmospheric deposition as a nutrient source for vegetation, greater understanding of the year-round activity in/of ecosystems and confirmation of the usefulness of models to describe ecosystem processes. The Ulrich **canopy** budget model (1983) is a prime example of interdisciplinary work on the ecosystem scale (Chap. 13, Sect. 13.6), allowing interception deposition and canopy exchange to be estimated on the basis of meteorological input variables, physical surface characteristics, leaf area and stand structure information. At about the same time, the **Hubbard Brook Ecosystem Study** (**HBES**) started (Sect. 14.2), investigating the effects of forests on watershed hydrology and flood control, later followed by whole-watershed biogeochemistry and modelling. All of these ecosystem studies relied on measurements of many different components of and actors in a single ecosystem (e.g. soil, water, microorganisms, vegetation, fauna and atmosphere; Sect. 13.2), always carried out by many different research groups working at the same site and often embedded in national or international networks.

14.1.1.2 Regional to Global Networks

Whole-ecosystem observational studies started out as single-site studies, sometimes already with the intention to be run long-term, but it became obvious that such studies were inherently limited in terms of spatial representativeness and replication (Chap. 13). Thus, the scientific community realised during the IBP in the early 1970s that **networks of sites** help to overcome this limitation, providing the necessary statistical rigour and a wide range of further benefits: exchange of ideas and methodologies; upscaling to larger regions, biomes, continents or even the globe; and identification of global trends in environmental conditions and the respective response of the terrestrial biosphere, to name just a few. Thus, national networks evolved, such as the US Long-Term Ecological Research network (LTER; since 1980; http://www.lternet.edu/), which in 1993 was expanded into the **International Long-Term Ecological Research network** (**ILTER**; https://www.ilter.network//), a global **network of networks** aiming to understand the response of ecosystems to global change. Similar networks were created within the framework of international conventions, such as the International Co-operative Programme on Assessment and Monitoring of Air Pollution Effects on Forests (**ICP Forests**; http://icp-forests.net/), monitoring forest conditions at 6000 plots in 42 countries in 2016. Taking on monitoring tasks and also responding to the increasing demand for easier access to and greater usability of data, the European research infrastructure project **Integrated Carbon Observation System** (**ICOS RI**; https://www.icos-ri.eu) was created in 2015. This pan-European network of long-term measurement stations for greenhouse gas emissions and their regional dynamics includes not only terrestrial but also atmospheric and marine stations. Within these networks, a high level of standardised sensor specifications (e.g. sensor drift due to sensor ageing or ambient temperatures), harmonised protocols (e.g. sampling details and calibrations) and experimental set-ups (e.g. placement of measurement devices) enable comparable measurements to be taken. This in turn is a fundamental prerequisite for spatial and temporal upscaling for reliable identification of ecosystem responses to environmental change.

14.1.1.3 New Technologies

With the development of instruments to measure CO_2 and H_2O vapour exchange at very high temporal resolution (at 20 Hz, i.e. 20 times per second), a new type of ecosystem-scale study became possible in the early 1990s. By use of these new instruments for the so-called **eddy covariance** (**EC**) **method**, ecosystem CO_2 and H_2O vapour exchange with the atmosphere could be quantified. The EC method is based on measurements of a turbulent flux in the air above an ecosystem (the measurement height is about one third higher than the stand height). The vertical wind speed and the gas concentrations in air parcels moving past the respective sensors are measured with high temporal resolution (among other meteorological variables). Assuming that advection is negligible, the covariance of the vertical wind speed and gas concentration (i.e. the product of the deviations of both variables from the mean, typically over 30 min) is a direct measure of the net flux. The ability to measure the **biospheric–atmospheric gas exchange** of an ecosystem continuously—that is, 24 h a day, 7 days a week, 365 days a year—for several years, instead of upscaling manual chamber measurements of soil respiration and evaporation combined with leaf-level gas exchange taken during weekly or monthly campaigns, suddenly allowed a much deeper insight into temporal changes of ecosystem processes than ever before. On the basis of micrometeorological theory (Aubinet et al. 2012), the physical origin of whole-ecosystem fluxes could be determined (e.g. **footprint** analysis) and fluxes could be partitioned into component fluxes, such as gross primary production (GPP; i.e. CO_2 uptake) and total ecosystem respiration. Nowadays, **Fluxnet** (http://fluxnet.fluxdata.org/about/), a global network of micrometeorological flux sites, consists of >850 flux tower sites located on five continents, providing more than 6600 site-years of measurements (Fig. 14.2).

On the basis of such measurements, carbon sequestration of terrestrial ecosystems can be


a
20+ yr
16-20 yr
11-15 yr
6-10 yr
1-5 yr
b
c

directly estimated by summing up fluxes over a growing season or 1 year. It has turned out that forests, after reaching canopy closure, are typically a **carbon sink**, even at very great age (several hundreds of years), while very young and open forests are typically a carbon source (despite the trees growing) due to high respiratory CO_2 losses from the soil (Buchmann and Schulze 1999; Kolari et al. 2004; Magnani et al. 2007). Thus, these flux measurements challenge the long-standing theory of Odum (1971) that old forests are at **carbon equilibrium** (i.e. with a ratio of gross production to community respiration approaching 1) and thus respire almost as much as they assimilate, resulting in a carbon budget of zero at mature stand stages, being neither a sink nor a source. However, this theory, prominently presented in Odum's textbooks *Fundamental Ecology* (Odum 1971, 2005) and *Basic Ecology* (Odum 1983), was based on a hypothetical model of a 100-year age series of dense forest stands by Kira and Shidei (1967), who rather focused on the fact that net forest productivity is the balance between gross production and respiration. Ecosystem flux measurements with this new technology clearly proved that old forests are not at carbon equilibrium. Further technological progress (e.g. the newest developments in laser spectrometry) nowadays allows not only measurement of concentrations of **trace gases** such as CH_4 and N_2O but also measurement of stable isotopic signatures of all highly relevant gases such as CO_2, H_2O_{vapour}, N_2O and CH_4, at high temporal resolution (e.g. 10 Hz for CH_4 and N_2O; 1–5 Hz for ^{13}C and ^{18}O in CO_2). This now offers the unique opportunity to investigate the biological origin of these molecules (Wolf et al. 2015).

14.1.1.4 New Approaches to Access Tall Canopies

Not only networks of sites but also the development of new approaches to access and to observe previously inaccessible compartments of terrestrial ecosystems have enabled new insights into ecosystems. These new approaches to **forest canopies** are:

- Canopy rafts linked to blimps—the "Radeau de Cimes", first employed in French Guiana in 1986 (Hallé et al. 2000), then later on also in Cameroon, Gabon and Panama.
- Canopy walkways—first employed in Hopkins Forest (MA, USA) in 1991, then refined and replicated globally (Lowman 1999).
- Canopy cranes—first employed in Panama in 1990, then replicated globally and also organised within a network—the International Canopy Crane Network (ICAN) (Stork et al. 1997; Sutton 2001).

All of these have allowed access to 30 to 50 m tall canopies, formerly accessible only via tree climbing. New insights into biological diversity present in tropical tree canopies, canopy structure and plant ecophysiology were the results. Currently, a new tool is emerging: the rapidly increasing employment of **drones** (or unmanned airborne (or aerial) vehicles (UAVs)). They can be used for observation of ecosystems from above, including spatial assessment of species composition, foliage phenology and biochemistry, as well as stand structure and spatial extent of certain systems or disturbances, depending on the sensor type flown (Anderson and Gaston 2013). Thus, drones can close the gap to remote sensing

Fig. 14.2 Flux sites where biospheric–atmospheric gas exchange is measured using the eddy covariance technique. **a** Global map of Fluxnet, showing the locations of sites as of October 2015 (image courtesy of D. Baldocchi; http://fluxnet.fluxdata.org/sites/site-summary/). **b** 35 m tower at the Davos evergreen forest site (Graubünden, Switzerland). The instrumentation for eddy covariance is installed on the top beams visible above to highest platform (Photo courtesy of L. Hörtnagl). **c** 2 m mast at the Chamau lowland meadow site (Zug, Switzerland) (Photo courtesy of L. Merbold). Both sites are part of the Swiss Fluxnet, the network of flux sites in Switzerland (http://www.gl.ethz.ch/research/bage/fluxnet-ch.html) techniques (Sect. 14.1.4). UAVs also allow revisitation of field sites at frequent intervals and flights at low altitudes for fine spatial resolution, at relatively low operating costs, but special permits might be needed.

14.1.1.5 Observations of Biodiversity

Questions as to how biodiversity affects ecosystem functioning has led to various approaches being used. Certainly the first approach that comes to mind is observation of natural communities that differ in one aspect of **biodiversity** (e.g. the number of species present or the abundance of a certain functional group; Chap. 20) and comparison of them in terms of a variety of ecosystem processes. Thus, several forest stands would be sampled with a random or grid-based selection of plots across a specific area, ecosystem functions (e.g. biomass production) measured and then related to the observed biodiversity (e.g. the number of tree species). Such **monitoring** or **sample surveys** reflect natural conditions with respect to the age structure, canopy and root architecture, food webs or biogeochemical cycles of well-established sites (Leuschner et al. 2009), thus, transient effects do not occur. In addition, such an approach capitalises on the large number of permanent forest inventory plots existing in many countries (national inventories, ICP Forests; see above). However, usually, not every level of biodiversity is equally represented; often plots have biodiversity levels close to the mean or even close to the low end of diversity in managed forest ecosystems (Vilà et al. 2007). In addition, unless site conditions are almost identical, such cross-habitat or cross-site comparisons may hide effects that biodiversity exhibits within a site, because environmental differences between sites introduce "noise" into the diversity–function relationship (Sect. 14.1.2). Moreover, these **environmental covariables** might determine the diversity of an ecosystem and hence ecosystem properties and processes, and plotting biodiversity orthogonally to ecosystem function has thus been considered a "strange thing to do" (Naeem et al. 2009). For example, an asymptotic increase in biomass production with increasing tree species richness could be due to functional differences among species, leading to niche differentiation, higher resource exploitation and hence higher productivity. However, more productive stands may simply permit the coexistence of more species (Chap. 20). Thus, monitoring or sample surveys can be used to document correlations between biodiversity and ecological processes; however, causal relationships can only be approximated by accounting for measured (!) environmental covariables, using suitable statistical procedures such as structural equation modelling (e.g. path analyses). To avoid some of these confounding effects, **comparative studies** have been designed, where a similar number of plots per diversity level are deliberately chosen along gradients of biodiversity, ideally coupled with maximum standardisation of environmental conditions, including stand age or management history (e.g. Baeten et al. 2013). Nevertheless, there are many environmental variables influencing biodiversity, so the selection of study sites remains subjective.

14.1.2 Transects and Chronosequences

Transects (i.e. a collection of sites along an imaginary line, most often along an environmental **gradient**) and chronosequences (i.e. a collection of sites subjected to the same driver but at different times) are additional approaches used to address research questions in ecosystem ecology. Typical research questions are: How does increasing precipitation/temperature/soil fertility affect stand productivity? How does carbon allocation above-ground versus below-ground change with increasing altitude? Does soil carbon sequestration reach saturation eventually? What are the effects of fire on species composition?

14.1.2.1 Transects

Assembly of a **transect** requires a strong gradient in the environment (e.g. climate, soil fertility, elevation) while other potential environmental drivers of ecosystem processes are kept either relatively constant or can be measured. For example, the elevational and thus the climatic transect on the island of **Hawaii** offers unique conditions. Ranging from sea level up to >2400 m in elevation the precipitation gradient ranges from 500 to >5800 mm annual precipitation and the air temperature gradient ranges from about 10 to >20 °C mean annual temperature. At the same time, all sites are located on the same bedrock—that is, recent volcanic substrates (Vitousek et al. 1992; Allison and Vitousek 2004). Along these environmental gradients, nutrient cycling, decomposition and vegetation composition have been shown to be intricately linked. Even invasion by six exotic invasive species has been shown to be related to the nutrient status of the native vegetation.

Many very long transects (>1000 km in length) were established in the early 1990s by the international Global Change and Terrestrial Ecosystems (GCTE) core project within the **IGBP** to study large-scale responses to global change (Walker et al. 1999; Canadell et al. 2002). These long transects have proven ideal to provide data for large-scale synthesis and integration efforts and thus the necessary large-scale information for global models. Some transects have been used over more than a decade, such as the sub-Saharan and Kalahari transects, ranging from the arid subtropics to the moist tropics (Shugart et al. 2004), while others have been used less frequently, such as the Patagonian transect (Schulze et al. 1996). There also exist networks of transects—for example, the Australian Transect Network (ATN), which consists of seven transects spanning across different biomes and across large rainfall, temperature and land use gradients from the coast to inland areas (http://www.tern.org.au/). Overall, the lengths of transects vary substantially, ranging from several thousand kilometres (such as in sub-Saharan Africa) to less than 100 m in Sweden (Högberg 2001). This illustrates that environmental gradients can act on very different scales, across individual slopes to across continents, creating a mosaic of ecosystems across the landscape.

14.1.2.2 Chronosequences

Chronosequences are often used when the impacts of drivers are studied that trigger rather slow reactions of the ecosystem over long time periods (e.g. responses to slow continuous forcing) or when transient responses of ecosystems are expected (e.g. responses to sudden disturbances; Sect. 14.1.5 and Chap. 17). Preferentially, only the time since the driver changed should differ between the sites forming a chronosequence. In reality, this is extremely difficult to achieve, since other **state variables** might have changed over time as well—that is, variables that describe the ecosystem well enough to predict its future behaviour in the absence of any external driver affecting the system (Jenny 1941). Such state variables can be climate, soil properties, previous management practices, vegetation composition or microbial communities. If changes in state variables are expected, in addition to the main driver studied, the experimental set-up and measurement portfolio need to be adjusted accordingly—that is, by adding actual measurements of these variables.

Studying the long-term response of tree growth to atmospheric nitrogen (N) deposition can be done only using a chronosequence approach, since experimental manipulations would simply take too long. While spruce trees grew until the 1940s according to well-established growth isolines based on site quality and yield tables (Fig. 14.3), stem growth rates increased strongly between 1940 and 1970. In turn, trees of all age classes “crossed” growth isolines, concomitantly with increased **atmospheric N deposition**, thus growing better than traditional forestry knowledge (collected before the 1960s) would have suggested. However, between the 1970s and the mid-1980s, growth rates ceased to increase, at a time when strong forest decline symptoms were observed throughout central Europe, linked to high S and N deposition. Since the late 1980s, growth rates have increased again, related to a decrease in atmospheric S pollution but continued high N deposition (Fig. 14.3) (Mund et al. 2002).

Although this example nicely illustrates the power of a chronosequence approach, this study relied on certain assumptions regarding other state variables, as discussed above: all trees should have had the same genetic origin, and all stands should have had comparable soil and

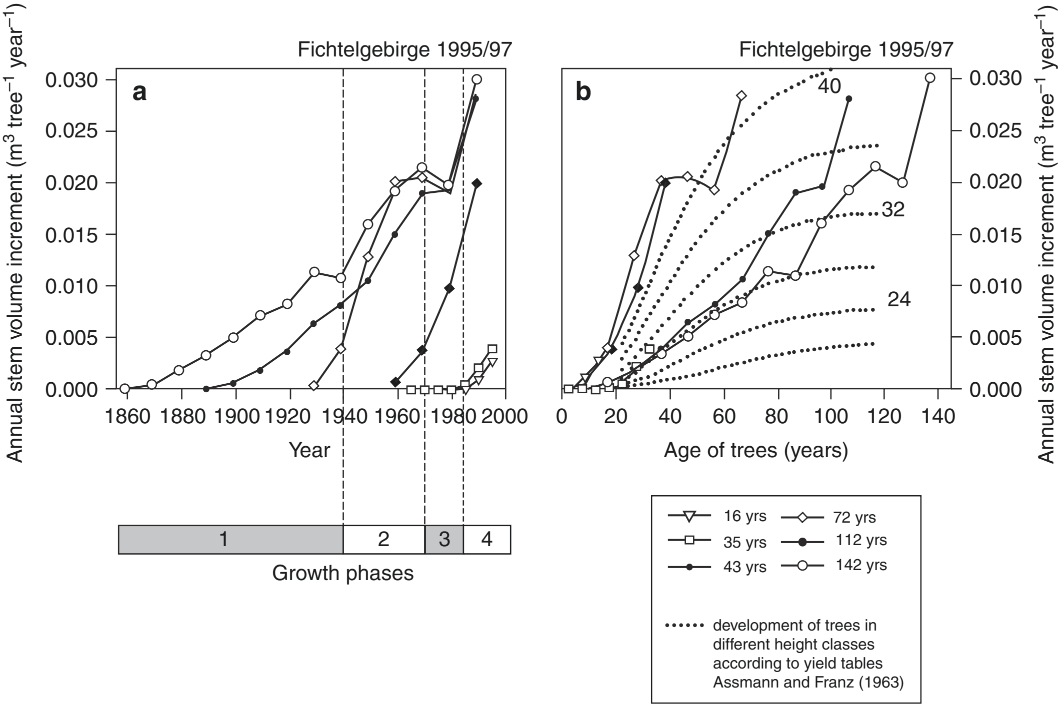

Fig. 14.3 Long-term growth patterns of spruce trees. **a** Average annual stem volume increment of trees growing in different aged spruce stands (*Picea abies*) over 142 years. **b** Annual stem volume increment as a function of tree age. (Mund et al. 2002)

climate conditions, as well as comparable management practices (e.g. thinning). Most of these assumptions were explicitly tested in this study; thus, the general interpretation is rather robust.

Overall, both approaches have their advantages and disadvantages; thus, awareness of their shortcomings is a necessary first step to avoid erroneous data interpretation. Nevertheless, use of transects and chronosequences has resulted in unprecedented and detailed insights into spatial patterns and ecosystem adaptations across space and time.

14.1.3 Grid-Based Inventories

Grid-based **inventories** are often used in monitoring studies to increase spatial representativeness, to avoid experimental bias (e.g. due to subjective plot selection) or to provide inputs into geographical information systems (GIS). Typical research questions are: How severe is the effect of insect outbreaks/fire/flooding across the country? Is there a relationship between species diversity across a landscape and land cover fragmentation? How has soil fertility management affected agricultural productivity across a region?

The location where information is available or measurements are taken is determined on a regular grid. **Grid sizes** can vary depending on the research questions and data availability, from small grid sizes of 0.5 × 0.5 m for small field studies (e.g. on vegetation cover or soil properties) to medium grid sizes of between 500 × 500 m and 10 × 10 km in regional or national studies to large grid sizes of 0.5°× 0.5° in global model runs. Aggregation (or disaggregation) questions come into play when data are available at different grid sizes but need to be combined. Spatial uncertainty needs to be considered if the data are valid for scales smaller than the final grid size used—for example, by calculating error correlation lengths or semi-variograms (see spatial statistics textbooks for details). Often information about many different variables is gathered at the

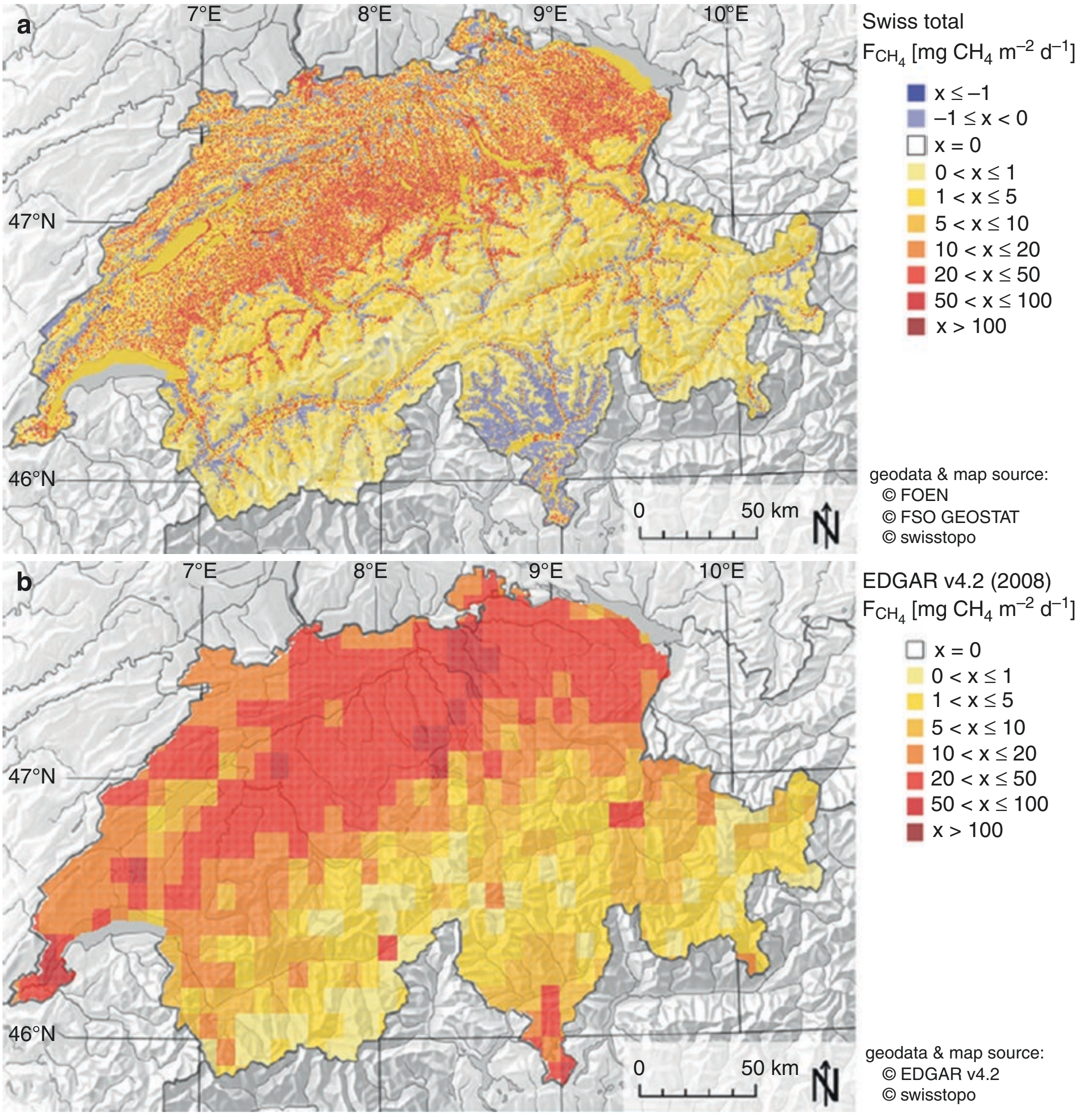

Fig. 14.4 Role of grid sizes in spatial analyses. Spatially explicit CH_4 emission inventory at grid sizes of **a** 500 × 500 m and **b** 0.1° × 0.1° equivalent to 10 × 10 km (Hiller et al. 2014). The emissions depicted in panel **a** include both natural and anthropogenic sources (which made up >95% of total emissions), while panel **b** depicts anthropogenic CH_4 emissions according to the EDGAR v4.2 inventory only. Note the coarse resolution in panel **b** compared with that in panel **a**, reducing the information content tremendously

same grid size to overlay this information to gain new insights. For instance, to construct the first spatially explicit Swiss **CH_4 emission** inventory (Hiller et al. 2014), information about the spatial distribution of livestock and agricultural farms, and also terrestrial ecosystems such as forests, grasslands, wetlands and lakes (and reservoirs) as well as population density, urban areas and waste facilities was used (Fig. 14.4).

14.1.4 Remote Sensing

On even larger scales—that is, on continental or global scales—only **remote sensing** approaches can provide the necessary information on terrestrial ecosystems. Today, the term “remote sensing” typically refers to airborne sensors (e.g. on satellites, aircrafts, drones), which either emit a signal (**active remote sensing**) or simply record a signal (**passive remote sensing**). Often, multispectral platforms (i.e. multiple wavelengths of electromagnetic radiation) are used, such as Earth observation satellites (e.g. Landsat and IKONOS). Landsat data are available since the 1970s, with spatial resolutions between 15 and 100 m and pass-over times every 16 days, while IKONOS data are available since 1999, with spatial resolutions between <1 m and 3.2 m and pass-over times every 3 days. Typical research questions are: Where are the hotspots of land degradation/productivity/species diversity/deforestation across a continent? How do multispectral signals relate to plant and stand performance across large regions?

Depending on the research question, different remote sensing products can be obtained, often available at almost daily to biweekly intervals, sometimes even free of charge (e.g. Landsat, Moderate Resolution Imaging Spectroradiometer (MODIS) and Advanced Very High Resolution Radiometer (AVHRR)). Many of these products from passive remote sensing are based on the spectral properties of surfaces—that is, **reflectance** (or **absorbance**) of light at different wavelengths: from visible light (0.38–0.72 μm) to near-infrared (0.72–1.3 μm), short-wave infrared (1.3–3 μm), mid-wave infrared (3–5 μm) and long-wave infrared (8–15 μm). Note that the subdivisions for infrared light are not precise and depend on their applications. Reflecting surfaces can be those of plant tissues, soil, water or man-made structures. For plant foliage, the leaf biochemistry, leaf structure and foliage distribution within a canopy, but also the leaf colour and leaf water content, are important factors affecting the reflectance of light at different wavelengths (Chap. 9). While moist green foliage mainly absorbs blue and red light but reflects green light (because of **chlorophyll**) and shows low reflectance in near-infrared and short-wave infrared wavelengths, dry brown or senescent foliage reflects more in the red wavelengths (because of carotenes and other pigments) than in the green wavelengths and shows high reflectance in short-wave infrared wavelengths.

These differences in the reflectance of different wavelengths are then used to calculate **vegetation indexes** such as the **Normalised Difference Vegetation Index** (**NDVI**), the Photochemical Reflectance Index (PRI) and the Enhanced Vegetation Index (EVI), to name just a few important ones. While the NDVI scales positively with biomass and the leaf area index (LAI; until about an LAI of 6), the PRI provides seasonal information about the ratio of chlorophyll to carotenes. Both indexes have been successfully used to assess terrestrial productivity and its changes, particularly over continental areas or globally (Myneni et al. 1997; Running et al. 2004). The EVI is more sensitive to high biomass and thus high-LAI areas than the NDVI, also better reflecting stand architecture. More recently, **sun-induced fluorescence (SIF)** has been used to estimate GPP of terrestrial vegetation (Guanter et al. 2014). All of these indexes and proxies, when they relate to plant activities, can also be used to upscale point measurements to larger areas on the basis of data acquisition from airborne sensors (UAVs, aircrafts, satellites). However, such indexes need to be checked with adequate ground truthing before they can be used as a basis for modelling (Chap. 22).

Active remote sensing—that is, the employment of RADAR (RAdio Detection And Ranging) and LiDAR (Light Detection And Ranging)—is based on the time delay between the emission and return of a signal. **RADAR** is based on the emission of radio waves, which are reflected or scattered by objects, and is used for purposes such as large-scale digital elevation models. The advantage of RADAR (using radio waves) over LiDAR (using visible, infrared or ultraviolet light) is the low absorption of radio waves by the medium they pass through—for ecological applications, mainly the medium of air. Thus, clouds, fog or rain limit RADAR applications much less than LiDAR applications. For the use of airborne or terrestrial **LiDAR**, a laser beam is emitted, which is back-scattered by surfaces or molecules. On the basis of the recording of the return, the height and structure of vegetation or land surfaces can be determined/scanned. Coupling of both airborne and terrestrial LiDAR gives the best results.

Overall, remote sensing approaches have been widely used and have provided unprecedented insights. However, they also have drawbacks, and one needs to pay attention to their limitations. For example:

- Remote sensing products are often proxies for a biological process or ecosystem characteristic. As such, they introduce uncertainty, since the proxy is never identical to the variable under study because their relationship is typically not 1:1.
- Certain variables such as land use intensity (fertilisation levels, harvesting frequencies) cannot easily be seen from above or would need many images of the same scene.
- Ground-truthing might still be necessary, particularly if new products are employed on scales smaller than the globe.
- Depending on the approach chosen and the region under study, clouds might obscure the view from above. Then composite images are used—for example, over 10–30 days. One has to pay attention to whether this temporal resolution is then still adequate for the process under study.

14.1.5 “Natural Experiments”

Yet another approach to observation of terrestrial ecosystems is to use “**natural experiments**” or “**accidental experiments**”, such as sudden disturbances or slow continuous forcing (Chap. 13). Typical research questions are: How does a landscape recover after a large disturbance event? What is the fate of a pollutant within ecosystems and along food chains? What are the effects of global warming on ecosystem processes and the provisioning of ecosystem services?

Obviously, one cannot wait for such natural or man-made hazards to suddenly happen, but one can be attentive to make use of them once they do occur—for example, volcanic eruptions, strong storms, flooding, devastating insect outbreaks, large-scale fires or radioactive fallout/spills. Thus, **long-term research** efforts are needed, preferentially starting before but clearly after such sudden disturbances. Nevertheless, excellent examples are available—for example, the research following the Mt. St. Helens (WA, USA) outbreak in 1980, the large fires in **Yellowstone National Park** (YNP; USA) in 1988, the extensive bushfires in Australia between 2003 and 2009, and the devastating mountain pine beetle outbreak in North America in 2008. Sometimes research after such sudden disturbances leads to conceptual changes in science or even ecosystem management (e.g. fire management in YNP (Franke 2000; Barker 2005)) and might challenge long-standing theories (e.g. the diversity–stability relationship after flooding (Wright et al. 2015)).

These “natural” or “accidental” experiments have also been shown to provide great insight into ecosystem ecology, particularly when one is dealing with anthropogenic impacts on the environment—for example, when studying the effects of climate change or invasive species, or when determining the transport of particular substances in ecosystems (Table 14.1). However, such studies can also have drawbacks because information about the starting point of the “experiment” or defined boundary conditions might not be available (Diamond 1983; HilleRisLambers et al. 2013). Nevertheless, such “experiments” can be particularly important when scientifically planned experiments in ecosystems are not acceptable to the public (e.g. involving increased radioactivity or chemical concentrations in the environment after nuclear fallout or chemical spills, respectively) or when such experiments are not practicable (e.g. increasing atmospheric temperatures over Europe). Depending on the background information prior to the “accidental” experiment, valid conclusions might be drawn about the effects and ecosystem responses to the accidental driver. A further option to exploit “natural experiments” of **slow continuous forcing**—for example, acid atmospheric deposition, climate change or species invasions—is to combine observations with monitoring and dedicated experiments (Sect. 14.2). Then, also such slow changes in the environment can be used to learn about the mechanistic underpinning of ecosystem processes and species interactions (e.g. increasing frequency of drought events and tree mortality (Allen et al.

Table 14.1 Characteristics of different approaches to study ecosystems: observations and monitoring, experiments, and natural and accidental experiments. (Modified from HilleRisLambers et al. (2013))

Characteristics	Observations and monitoring	Experiments	Natural and accidental experiments
Control over natural perturbation	None	None to low (if counteracting measures are taken)	None
Control over treatment	None to low (land use)	High	Intermediate
Appropriate control	None to low (time series, chronosequence)	High	None to low (time series, chronosequence)
Spatial scale	Small to large	Typically small	Small to large
Temporal scale	Short-to long-term	Typically short-term	Short- to long-term
Difficulty of imposing treatments	Easy (no treatments)	Difficult	Easy (treatment already imposed)
Relative costs (investment, supplies, labour)	Low to intermediate	High (treatments have to be imposed)	Low to intermediate
Main advantages	Large spatio-temporal scales, ecosystem dynamics, high representativeness in networks, study of remote sites	Control over treatments, cause–effect relationships	Large spatio-temporal scales, opportunity for treatments not otherwise possible
Main disadvantages	Correlations and covariates limit cause–effect interpretation	Small spatio-temporal scales, treatment strengths subjective, treatments can fail, costs, logistics	Treatments unpredictable and infrequent, representativeness of treatment, correlations and covariates limit cause–effect interpretation

2010, 2015)), making a well-designed monitoring network even more important.

In general, all approaches described in Sect. 14.1 have their advantages and disadvantages, based on their diverse characteristics (Table 14.1). Whether there is control over naturally occurring perturbations in addition to potential treatment effects; whether a control exists (either a zero treatment or use of time series analysis or chronosequences); what spatio-temporal scales one can study; what difficulties and costs might arise—all of these aspects depend on the study approach that is taken. No one approach is better than the other; its selection is simply based on the research questions that are asked, as outlined above.

14.2 Experiments

When the study of terrestrial ecosystems under natural conditions is not sufficient to address the research questions asked or does not provide enough explanatory power, **experiments** need to be carried out in which the natural setting is altered (i.e. the **treatment**) and then compared with the natural condition, also called the **ambient condition** (i.e. the **control**). Experiments addressing ecosystem ecology are typically carried out in the field but are sometimes also done with "artificial" ecosystems under more controlled conditions (Sect. 14.2.5). A semi-artificial setting is the **common garden** approach, where plants from different locations are planted together in one location (i.e. the common garden) to study, for example, their plasticity in response to environmental factors.

14.2.1 Manipulations of Pools and Processes

Experiments focusing on processes, without changing the natural environmental setting, are often very close to observations. **Treatments** typically manipulate a selected pool (e.g. litter) or process (e.g. carbon allocation), and one observes this pool or process, as well as its interactions with other pools, processes and organisms in the ecosystem under study. Typical research questions are: Does soil respiration depend on canopy photosynthesis? How fast is the coupling between above-ground and below-ground? What determines litter decomposition under field conditions?

Such experiments are often carried out over one or multiple growing seasons, but not necessarily over decades or longer. The **duration** of such experiments is determined by the time needed to observe a response reliably and also to separate the treatment effect from intra- and inter-annual variations in the pool or process under study. Experiments sometimes include multiple levels or qualities of treatment. Litter decomposition studies, for instance, can be set up by changing the frequency (e.g. multiple harvest times of litter bags), the intensity (e.g. different litter amounts or mesh sizes in litter bags) or the quality (e.g. different litter types) of the treatment. They may also include multiple treatment combinations (e.g. litter quality × litter placement × litter amount). Thus, the **experimental design** becomes very important when one is setting up such uni- or multifactorial experiments, particularly in terms of (pseudo-)replication (for details, see statistics textbooks). It was on the basis of such litter decomposition studies that the relevance of the plant growth form was shown, which was even more important than direct climatic effects (Bardgett and Wardle 2010).

Experiments most often start with a clear **research question** (e.g. How are above-ground and below-ground processes linked?), a clearly formulated **hypothesis** (e.g. Carbon allocation below-ground is linked to canopy photosynthesis.) or an **objective** (e.g. to assess above-ground and below-ground interactions). Thus, the experimental treatment is aimed at manipulating the setting under which the process under study occurs (e.g. transfer of carbohydrates from the canopy to below-ground). The **treatment** can be designed to either (1) limit or prevent the transfer of carbohydrates (e.g. by girdling the tree stems—that is, cutting parts of the phloem away while leaving the xylem intact) when working in a forest (Högberg et al. 2001); or (2) to trace the freshly fixed carbohydrates below-ground (e.g. by labelling the carbohydrates with (stable or radioactive) carbon isotopes (^{13}C or ^{14}C, respectively)) by providing labelled CO_2 as a source for photosynthesis (forest: Högberg et al. 2008; grassland: Burri et al. 2014; artificial ecosystem: Ruehr et al. 2009). **Measurements** are taken according to the research question and the experimental set-up, and also need to assess the environmental conditions during which the experiment is taking place. In the example on allocation, ambient climate and soil conditions need to be measured (e.g. temperature, light, vapour pressure deficit (VPD), soil water content, soil texture) to explain any physiological process rate; above-ground and below-ground processes need to be assessed (e.g. photosynthesis, soil respiration, root exudation, microbial activity) to describe above-ground and below-ground activities; and samples need to be taken for isotope analyses (e.g. bulk tissues, foliage, phloem and root samples for carbohydrate extractions) to assess transfer rates of labelled photosynthates from CO_2 fixation in the canopy to arrival of labelled carbohydrates below-ground or loss of labelled CO_2 due to root or soil respiration. On the basis of such a measurement portfolio, soil respiration in a forest was shown to be clearly coupled to canopy photosynthesis, with about a 54% contribution of **root respiration** to total respiration during the growing season (Högberg et al. 2001). On the other hand, above-ground coupling slowed down under drought conditions in grassland (Burri et al. 2014) and artificial ecosystems with beech saplings (Ruehr et al. 2009). Thus, the duration of the experiment needs to be adjusted to plant and soil activities (e.g. the photosynthesis rate as the source process; and root or soil respiration, carbohydrate storage in roots and root growth rate as the sink processes) and also to canopy height, since transfer rates scale with canopy height (Kuzyakov and Gavrichkova 2006). Such an allocation experiment in a forest might take days to weeks to accomplish, but only hours to days in a grassland. The number of **replicates** (here, replicated plots) needs to be determined as a function of biological variability and also of time and financial constraints. Because of the latter, the average number of replicates is often three to five per treatment level or control in field ecology, although greater numbers are desirable.

14.2.2 Manipulations of Environmental Conditions

Experiments manipulating environmental conditions for entire ecosystems can be—and have been—done in various ways. One can manipulate the resources for terrestrial ecosystems, the climatic conditions under which all processes take place, the biogeochemical cycling (Sect. 14.2.1), as well as the organisms present in an ecosystem (Sect. 14.2.3). Focusing on the environmental factors, such **manipulation** experiments have a long tradition in ecosystem ecology to answer the following research questions: What are the effects of drought/high CO_2 concentrations/fertilisation on water and nutrient uptake/turnover in a given ecosystem? Do different species react differently to changing environmental conditions? How resistant/resilient is a given ecosystem to changes in climate? Thus, the following manipulations have been carried out:

- Resources (i.e. water, nutrients or light): Drought and irrigation; N/atmospheric deposition exclusion and addition; elevated CO_2 or O_3 concentrations; liming, fertilisation; shading; root trenching.
- Climate: Soil warming with heating cables, ecosystem heating with IR lamps, increased ultraviolet (UV)-B.
- Various combinations of the above.

14.2.2.1 Transplant Experiments and Space-for-Time Experiments

One can set up quite an elaborate infrastructure to manipulate environmental conditions in a given ecosystem (see below) or use natural environmental gradients and move entire ecosystems into a new environment. Such **transplant experiments** thus use natural spatial variations, such as elevational gradients in climate, to study the response of ecosystems to changes in climate over time (**space-for-time substitution**). Transplanting alpine plants to lower elevations in the Swiss Alps, Alexander et al. (2015) were able to show the strong impacts of changing competitor identities on target plants' performance: competitive pressure at the warmer, new site was more detrimental than the related climatic benefits. Likewise, gradients in soil development and fertility in glacier fore-fields can be used to study the temporal development and succession of emerging high alpine ecosystems. Transplant experiments obviously work only with small-statured ecosystems such as grasslands and/or small units of "ecosystems" (e.g. small monoliths of soil plus vegetation), which are transferred to the new location with great care (using means ranging from human power to helicopters) to avoid disturbances of the "ecosystem" (Ineson et al. 1998; Bassin et al. 2007). Such an approach has clear advantages, such as relatively easy logistics, fast set-up, small expense, and no need for manipulation infrastructure. However, this approach also bears great risks—such as disturbance of the soil profile, damage to root systems, large edge effects and different trophic interactions at the new location—and cannot be done for ecosystems with tall vegetation. The risks need to be known and either controlled or accounted for in the statistical analyses of the data. In addition, some research questions simply cannot be asked—for example, questions about trophic interactions or pest and pathogen pressures under the "future" climate (i.e. transplantation of vegetation to lower elevations where it is warmer), since the higher trophic levels, pests and pathogens have not been transplanted as well. The choice of treatments is also restricted by the existence of natural gradients, since environmental conditions must match the scientific objectives, as discussed by Beier et al. (2012).

14.2.2.2 Fertilisation and Irrigation Trials

One approach to manipulate the environmental conditions of whole ecosystems is to use experimental trials to increase resource supply.

Originally employed in agricultural sciences (Sect. 14.2.4), the approach of fertilisation trials was adopted in the forest sciences only in the 1970s, often focusing on the expectedly most limiting resource, usually nitrogen or water. For example, trials on 30 × 30 m^2 *Pinus sylvestris* plots were established in northern Sweden by Olaf Tamm and co-workers, supplying the boreal forest with 34, 68 or 120 kg N ha^{-1} $year^{-1}$ (compared with a low atmospheric background N deposition of about 3 kg N ha^{-1} $year^{-1}$). These plots were followed over 30 years and yielded valuable insights into dose-related responses of tree growth to **N additions**, and also into tree recovery when treatments were stopped (Högberg et al. 2006). The larger the N additions were, the smaller the increase in tree productivity was in the long-term, despite increases in tree growth in the early years. Moreover, large N additions resulted in lower soil pH values, with base cations being lost and increasing Al^{3+} concentrations in the soil solution, clearly showing the relationships among biogeochemical processes and the need for long-term studies of them.

An interesting **twin approach** was used in the early 1980s, when trials started in central Sweden (with *Pinus sylvestris*; 30 × 30 m^2) and Australia (*Pinus radiata*; 50 × 50 m^2*),* manipulating water and nitrogen supply. Using comparable designs with control, irrigation, and solid or liquid nitrogen addition plots, as well as their respective combination of nitrogen × irrigation plots (Linder 1987), both trials supplied nitrogen related to the daily N demand (in Sweden) or weekly N demand (in Australia) of the trees. Although the trials' main focus was on the primary production of trees and understorey, soil, tree water use and nutrient dynamics, as well as plant traits (e.g. foliage characteristics) were also measured. Both experiments showed the same general patterns, despite very different environmental settings and actual magnitudes of response rates. The major results included increased tree growth (but only when nitrogen and water were both added to support the larger basal and leaf areas), increased water use efficiency and substantial internal nutrient retranslocation prior to dormancy. Because of the increased tree growth, the canopy microclimate also changed, affecting the understorey and lichen composition, as well as litter decomposition. Thus, emergent properties (Chap. 13, Sect. 13.3) became apparent, resulting in feedbacks and interactions among different traits and processes within these forest stands.

14.2.2.3 Roof Experiments

Another approach to manipulate environmental conditions in ecosystems is the reduction of resource supply—for example, the supply of N or water. By use of large **roofs** (static or mobile), precipitation and/or **atmospheric deposition** have been excluded in forest studies since the 1980s (Wright 1989; Gunderson et al. 1998). Questions about the impacts and the reversibility of soil acidification due to S and N deposition could thereby be answered. For example, it was shown that nitrate leaching was reduced rather fast after roof establishment—that is, when N inputs via throughfall were reduced. In addition, nitrogen concentrations in spruce needles decreased in comparison with controls. Although much was learned about the effect of N deposition, questions about nitrogen saturation and critical levels of N deposition for terrestrial ecosystems are still debated today (Binkley and Högberg 2016). Since the 2000s and 2010s, the research focus has shifted and rain-out shelters have been increasingly used to simulate **drought conditions** in grasslands, arable croplands and forests (Vicca et al. 2014). The results were generally less clear for this resource, since experimental levels established for soil water availability differed more than those, for example, for nitrogen deposition (typically reduced to zero under the roofs). Nevertheless, reduced soil moisture and thus water availability often led to reduced vegetation growth and soil activity, and sometimes also to a change in vegetation composition. Also multifactor climate change manipulations (typically with two- or three-factor combinations of enriched CO_2, increased temperatures and reduced precipitation) have been carried out (Kreyling and Beier 2013; Frank et al. 2015).

14.2.2.4 Free-Air Carbon Dioxide Enrichment Experiments

Triggered by increasing atmospheric CO_2 concentrations measured globally, and interest in their impacts on terrestrial ecosystems, **Free-Air Carbon Dioxide Enrichment** (**FACE**) experiments have been carried out since the 1990s in many different ecosystem types, ranging from agroecosystems (arable land and grassland) (Nösberger et al. 2006) to wetlands, deciduous and evergreen forests, and even a desert site (Norby and Zak 2011). However, the overall number of active FACE experiments is currently decreasing because of financial constraints. Some notable exceptions are the recent set-up of EucFACE in Australia (operational since 2013 in a native eucalypt forest) and the plans to set up a FACE experiment in the Amazon (AmazonFACE). These **FACE experiments** have allowed a new type of ecosystem-scale climate impact study to be performed, enabling scientists to test *in situ* how ecosystems would respond to elevated atmospheric CO_2 concentrations, going beyond climate chamber, open-top chamber (OTC) and greenhouse studies (Fig. 14.5).

The circular plots in most FACE experiments have a diameter of up to 30 m (Hendrey and Miglietta 2006) and are surrounded by pipes that release either pure CO_2 or air enriched with CO_2. The release depends on the wind direction and wind speed, and is thus controlled by a computer system. Flow rates are adjusted to achieve the set target CO_2 concentration (often between 550 and 700 parts per million (ppm)) within the vegetation of each plot, but only during the day (when photosynthesis is taking place) and not at night nor during the leafless period of the year. This set-up allows tall vegetation stands to be studied and avoids many confounding effects of climate chambers, OTCs or greenhouse settings (i.e. size, light intensity, soil conditions). In forest FACE experiments, particularly, mainly young plantations have been studied. At most FACE sites, net primary production (NPP) increased in the first years of operation because of the so-called fertilisation effect, but the growth response to elevated CO_2 concentrations diminished over time, most probably because of physiological down-regulation at the leaf level (Chap. 12), as well as development of nutrient deficiencies (limited soil nitrogen and phosphorus supply), thus interactions at ecosystem level. Therefore, the postulated (short-term) fertilisation effect is not supported by long-term measurements. The Swiss Web-FACE, which released high CO_2 from thin tubes hanging in the tree crowns instead of from tall pipes, overcame the age problem (Körner et al. 2005) but provided information on individual mature deciduous trees (n = 11) rather than on a mature forest stand. After 8 years of operation, this experiment showed no elevated CO_2 effect on the stem growth, litter production or leaf traits of the deciduous trees studied (Bader et al. 2013). However, tree–water relations were affected: the trees transpired less, leading to higher soil moisture levels. Overall, so far, FACE experiments have shown no carbon limitation of the ecosystems under study. Also the new EucFACE supports this conclusion: unexpectedly, the growth and LAI of the eucalypt forest did not respond to elevated CO_2 concentrations in the first 3 years after operation started; it responded only to natural water limitations (Duursma et al. 2016).

The same set-up used for elevated CO_2 research has also been used for **ozone** (O_3). In Swiss grassland, O_3 concentrations were increased 1.2–1.6 times over ambient levels using circular plots (Volk et al. 2006); in a 60-year-old mixed beech/spruce forest in southern Germany, O_3 concentrations in canopy air were increased by a factor of 2 during the growing season using tubes hanging in the canopy (Matyssek et al. 2010). In both ecosystem types, growth was significantly decreased (by 25% in grassland and by about 44% in mixed forest) because of O_3-induced stomatal closure and thus lower photosynthesis rates in comparison with the ambient controls. In addition, species composition changed in the grassland (with strong reductions in legume abundance) and water run-off increased in the forest, clearly illustrating how important a **systems approach** is to understand environmental impacts on terrestrial ecosystems.

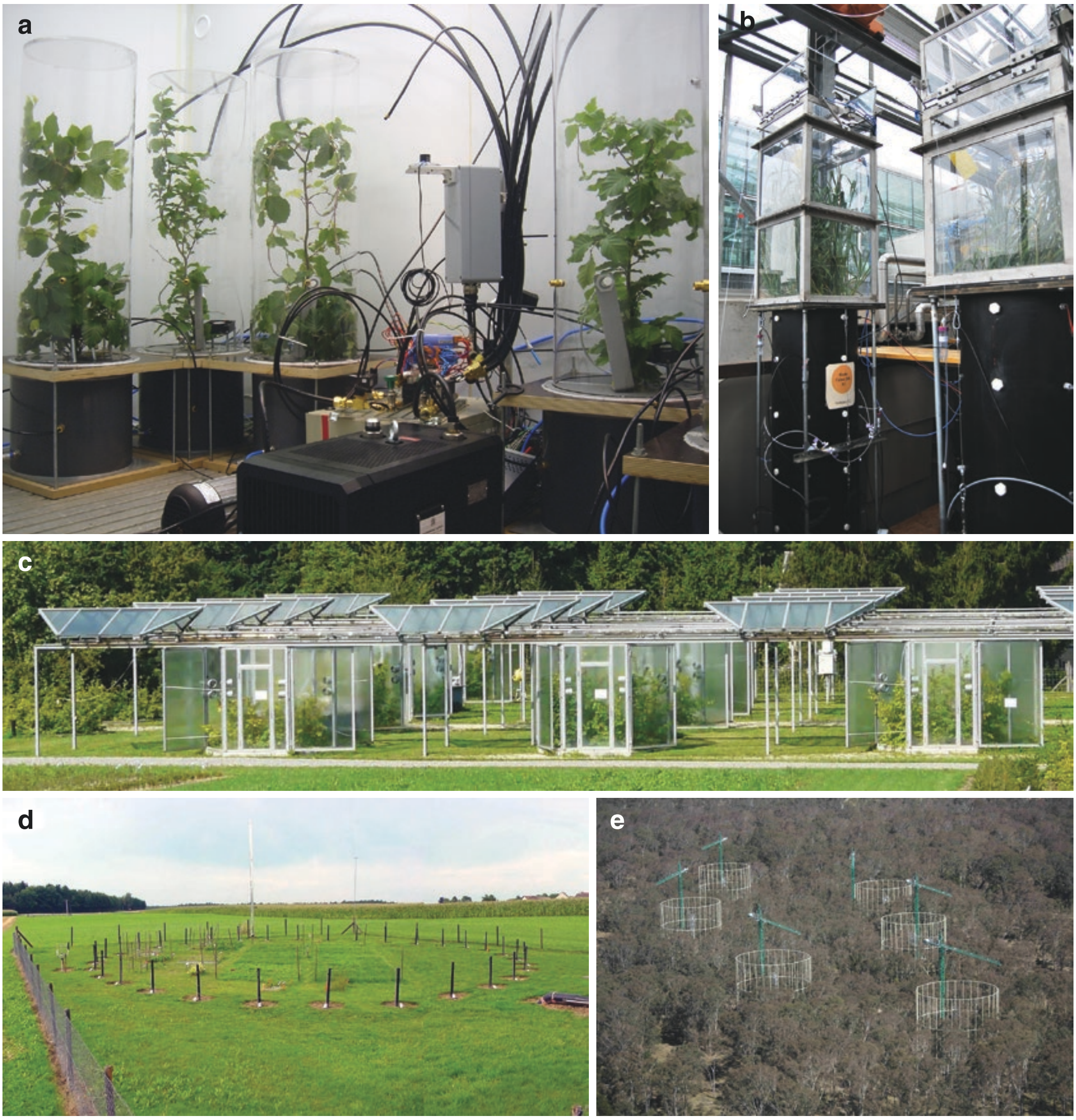

Fig. 14.5 Different experimental set-ups to simulate enriched atmospheric CO_2 concentrations. **a** and **b** Installations in climate chambers and in the greenhouse (Photos courtesy of M. Barthel). **c** Open-top chambers at the Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Switzerland (Photo courtesy of M. Arend). **d** and **e** Free-Air Carbon Dioxide Enrichment (FACE) experiments in Eschikon, Switzerland (Photo courtesy of J. Nösberger) and EucFACE. (Photo courtesy of D. Ellsworth)

14.2.2.5 Controls

In each of these manipulation experiments, a new "environment" is created for the ecosystem under study, which is then compared with either ambient conditions or yet another treatment. Preferentially, the plot set-up should thus be similar for all treatments. This means that the **control plots** in a drought experiment should also have roofs or rain-out shelter structures to keep the canopy microclimate similar; the controls in a soil-warming experiment should also have heating cables installed to create similar soil disturbances for roots and microorganisms in all plots. However, such a set-up will require some additional efforts, since the control plots in a drought experiment need to be supplied with (collected) rainwater in a manner as similar to the natural precipitation patterns as possible. This requires not only a collection facility for precipitation water close by but also pipes and pumps so that water can be supplied to the control plots. The timing and the amount need to be controlled and triggered by the signals of a nearby weather station in near-real time. One can imagine that such additional efforts to create a manipulation infrastructure are often not made; instead, environmental variables in the control and treatment plots are closely followed—for example, by dedicated measurements of the soil water content and VPD.

14.2.2.6 Hidden Treatments

Furthermore, any manipulation of an environmental factor might trigger further changes in the ecosystem, which are most often unintended and sometimes even unknown until much later. A typical example are **unintended changes** (albeit well known) in light conditions—in terms of both the absolute amount and also the spectral composition—when any kind of roof, foil or shelter material is used. Such changes are due to the material itself and also to shading by the structure carrying the roof or foil or shading by deposits on the roof, foil or shelter surfaces (e.g. dust, pollen). Another example of previously unknown or unexpected interactions comes from a forest FACE experiment. It was recognised only after some years into the experiment that trees growing in the enriched-CO_2 plots depleted the soil nitrogen pool much faster than the control trees and thus experienced slight nitrogen deficiency, counteracting the growth stimulation of higher CO_2 concentrations (Oren et al. 2001). Supplemental N fertilisation triggered the growth of trees growing in the enriched-CO_2 plots to the level of the early years in this FACE experiment. Yet another example from large-roof experiments showed that the sprinkler system could not reproduce the natural variability of rain—in particular, for small rain events—resulting in unintended drying of the litter layer with consequences for organic matter decomposition and mineralisation below the roofs (Gunderson et al. 1998). It is clear that such additional effects cannot be fully avoided, since ecosystems are complex (Mikkelsen et al. 2008). However, an appropriate experimental set-up must be in place to eventually detect these "**hidden treatments**" and to either experimentally counteract them or take them into account during data analyses and interpretation.

14.2.3 Manipulations of Biodiversity

Studies experimentally manipulating **biodiversity** have been advocated to overcome the potentially confounding effects described in Sect. 14.1.1. Such experiments allow decoupling of diversity effects from environmental conditions and might enable quantification of causality (for modelling, Chap. 15). Experimental manipulation of diversity also allows isolation of different aspects of biodiversity—for example, the effects of plant species richness, functional diversity or phylogenetic diversity. Two main types of manipulation experiments in biodiversity research have been carried out: removal experiments and synthetic assemblage experiments. Typical research questions asked are: What is the effect of decreased species richness on water/nutrient/carbon dynamics in the ecosystem? Is there a "legacy effect" on plant performance via the soil? Do top-down or bottom-up processes drive biodiversity–ecosystem functioning relationships? Is the diversity of other organisms in the ecosystem linked to the diversity of plants? How are ecosystem processes related to functional diversity?

14.2.3.1 Removal Experiments

In **removal experiments**, a gradient in diversity levels is created, ranging from natural to depauperate communities, by removing selected components from these ecosystems (e.g. species, functional groups) (Fig. 14.6). These types of experiments mimic the loss of species—for example, as a result of specific pests or pathogens in the past. They reflect natural abiotic and biotic filtering of the regional species pool, represent non-random extinction scenarios (due to the order of species removal as a treatment) and usually involve a large variety of organismic and

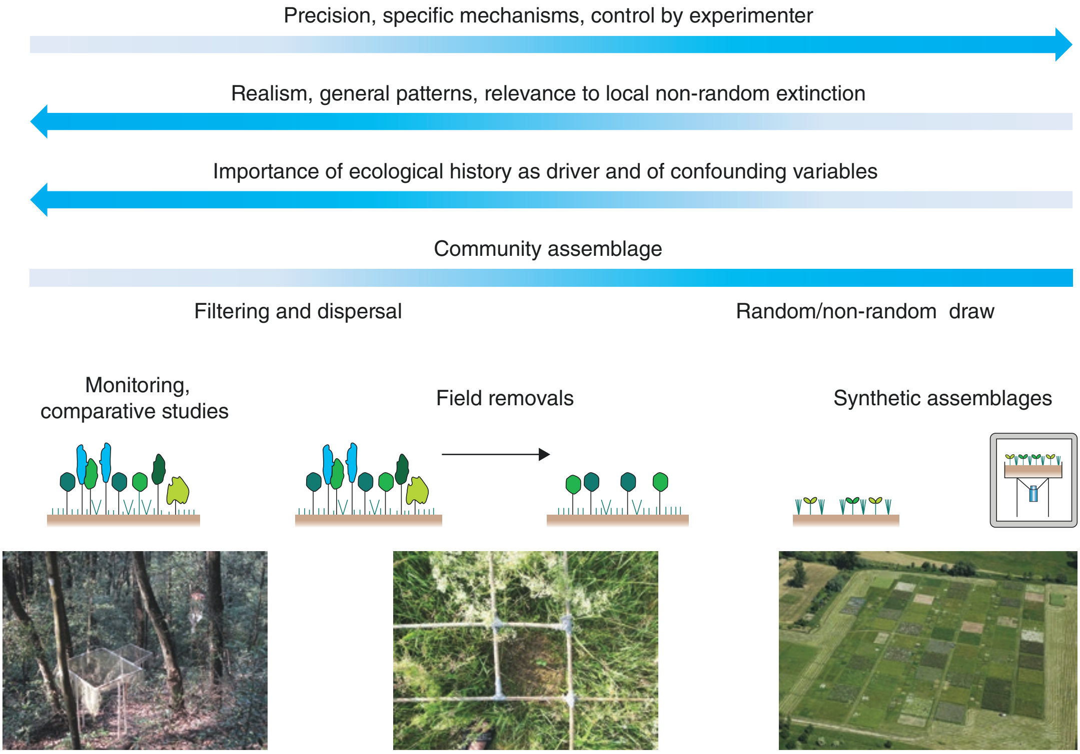

Fig. 14.6 Comparison of complementary scientific approaches to the study of biodiversity–ecosystem functioning relationships (based on Díaz (2013)). Modelling studies are not included. The examples shown in the photographs are from a comparative study in subtropical China (*left*) (Bruelheide et al. 2011; Photo: M. Scherer-Lorenzen), a species removal experiment (Photo courtesy of C. Dorman) and the Jena Experiment in Germany (*right*). (Roscher et al. 2004; Photo courtesy of the Jena Experiment)

functional groups (Díaz et al. 2003). However, they face the problem of proper control treatments and often induce large disturbance effects (when above-ground or below-ground tissues are removed), changes in density, spatial segregation of species or increased biogeochemical cycling (when increased root litter is left to decompose). On the other hand, important lessons can be learned. For example, removal of selected plant functional groups and plant species on forested Swedish islands of different sizes (used as a proxy for fire disturbance) affected many ecosystem processes and also clearly demonstrated that the results were ecosystem specific and thus context specific (Wardle and Zackrissen 2005). This means that relationships observed in one ecosystem cannot necessarily be transferred to and used in other ecosystems, unless they are properly tested.

14.2.3.2 Synthetic Assemblage Experiments

Establishing new communities, according to self-set rules, such **synthetic assemblage experiments** have been increasingly used over the last two decades to study biodiversity–ecosystem functioning relationships, particularly for plant and microbial diversity studies. For plant diversity studies, a biodiversity gradient is created by sowing or planting, keeping environmental conditions (e.g. climate, fertility and land use history) as constant as possible (Fig. 14.6). Such experiments are conducted in the field and also in controlled environmental facilities (Sect. 14.2.5). For very practical reasons, fast-growing, small-sized, mainly early-successional model systems are used, often with grassland species. Nevertheless, also tree diversity is being studied. Probably the largest research facility for ecosystem science is the global network for tree diversity experiments, TreeDivNet (www.treedivnet.ugent.be), with one million trees planted for science at 36 sites totalling 800 ha and 4000 plots (Verheyen et al. 2016). The first experiments in the Ecotron facility at Imperial College/Silwood Park, UK (a multitrophic study) (Naeem et al. 1994) in North American prairie systems at Cedar Creek, MN, USA (Tilman et al. 1996) and in serpentine grasslands in California, USA (Hooper and Vitousek 1997), as well as in European grasslands in the BIODEPTH project (Hector et al. 1999) paved the road for even larger and more sophisticated designs. The second generation of biodiversity experiments included larger plot sizes (up to 20 × 20 m in grassland) (Roscher et al. 2004) and greater replication of diversity treatments (e.g. Tilman et al. 1997). They were designed to allow separation of sampling from complementarity effects (Chap. 20) and study of multitrophic interactions, as well as interactions with land use intensity and drought (e.g. the Jena Experiment) (Roscher et al. 2004; Weigelt et al. 2009; Vogel et al. 2012). The most prominent result was probably the positive relationship between **species richness** and productivity, which was highly consistent across all experiments (for details, Chap. 20). Some diversity experiments also allow the study of interactions with other global change drivers, such as nitrogen deposition and increasing CO_2 levels (e.g. Reich et al. 2001). The drawbacks of these synthetic assemblage experiments have been discussed intensively—for example, artefacts introduced by certain experimental procedures (e.g. the need to continuously weed unsown species), often unrealistic **random draw diversity loss** scenarios or the occurrence of transient effects (Díaz et al. 2003; Lepš 2004). Nevertheless, these experiments resulted in a profound knowledge gain about the way ecosystems work (Chap. 20).

14.2.4 Manipulations of Management and Changes in Land Cover

Terrestrial ecosystems are often managed ecosystems, as introduced in Chap. 13. Thus, it does not come as a surprise that some of the oldest whole-ecosystem experiments focus on agricultural systems and study the relationships of the management regime (e.g. different fertilisation schemes) and land use change (e.g. comparison of mature forest stands and clear-cuts).

The **Park Grass Experiment** (about 2.8 ha in area) (Fig. 14.7) at Rothamsted Experimental Station (now Rothamsted Research), Harpenden, UK, started in 1856 to study how different fertilisers affect the biomass yield from grasslands. It is the oldest permanent grassland experiment worldwide (https://www.rothamsted.ac.uk/long-term-experiments). After previous use of the site as a pasture for at least a century, different treatments with inorganic fertilisers were established at the very start (nitrate-N, ammonium-N, P, K, Mg, Na and Si) while treatments with organic fertilisers were added 50 years later (in 1905, farmyard manure (FYM) and fishmeal). Since the start of the experiment in the nineteenth century, the plots have been decreased in size twice (in 1903 and 1965) to accommodate different liming treatments (control and set pH values of 5, 6 and 7). The extensive agricultural management has stayed the same over the last 160 years, with plots being mown and cut plant tissues being removed in summer (typically in June) and autumn.

Early on, it became clear that management practices and soil pH were closely related to biomass production and also to plant species richness. Over time, evidence arose that community composition and also soil chemistry and biology responded negatively to atmospheric N deposition. The experiment provided clear evidence for small-scale adaptation (at the plot level) and reproductive isolation among plots by natural selection. Higher trophic levels were also studied and showed treatment-specific distribution among the different plots (for a review of results for 1856–2006, see Silvertown et al. 2006). Thus, this grassland experiment clearly illustrates the value **long-term experiments** have, and also their ever increasing value the longer they run. It has also become clear over the last 160 years that experiments set up originally for a very different purpose (here, to study the response to management) might be used over time to answer completely dif-

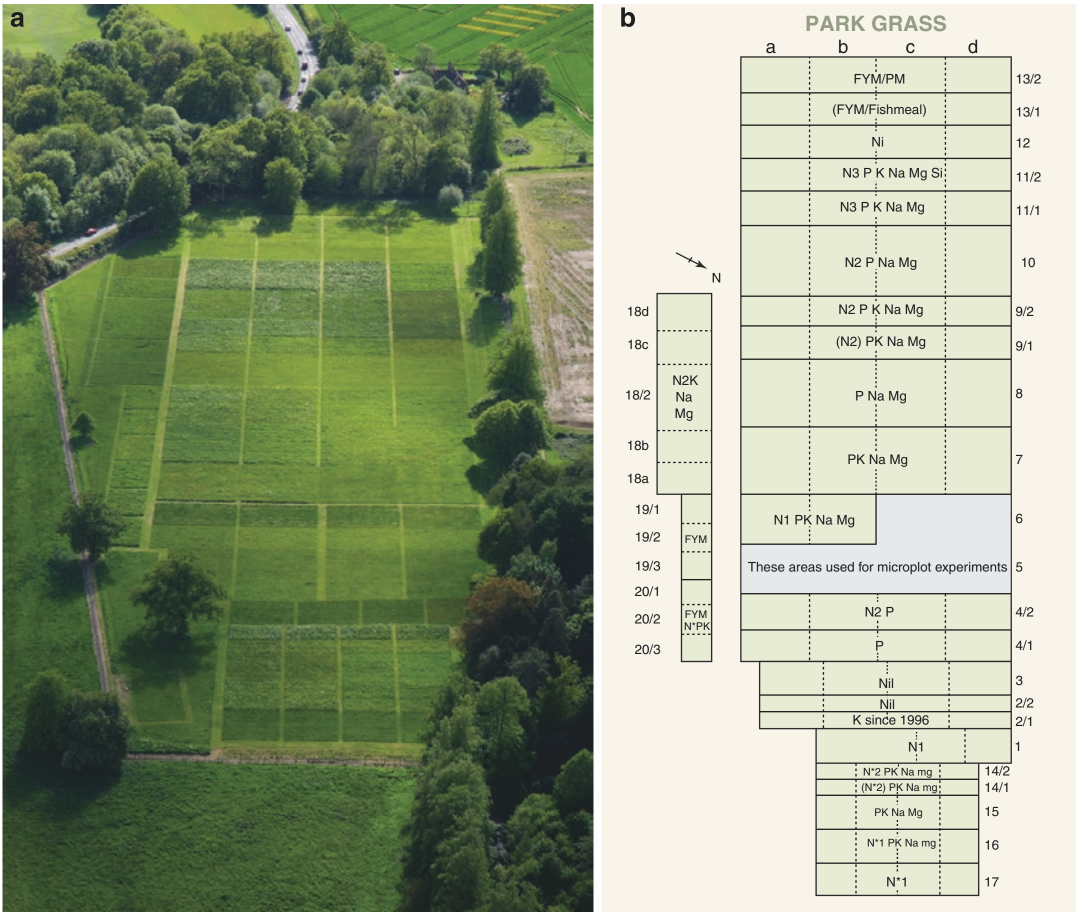

Fig. 14.7 The Park Grass Experiment, the oldest permanent grassland experiment on Earth, established in 1856. **a** Aerial view. **b** Plot layout. (Photo courtesy of Rothamsted Research)

ferent research questions from those originally posed, particularly when new technology becomes available (Chap. 13).

Manipulations in management are typically not followed over such long periods. However, the **resampling** of older experiments can also yield highly valuable results. One fine example is a study by Spiegelberger et al. (2006). In 2002, they resampled a large-scale fertilisation experiment in a subalpine grassland near Interlaken in Switzerland, which had been set up in the 1930s (1932–1935) as a multifactorial experiment with 340 plots to study the effects of liming and NPK fertilisation. Although these treatments had been applied for only 2–4 years, the plant community composition and also the soil microbial community showed clear effects of the liming treatments, though not the NPK treatments, after almost 70 years! The authors concluded that even such short-term changes in management can have profound and long-lasting impacts—here, on soil pH—indicating very low resilience of these mountain grasslands.

The oldest experiment manipulating entire forest ecosystems is the Hubbard Brook Ecosystem Study (HBES) (Fig. 14.8) (Holmes and Likens 2016). Established in 1955 to investigate management of watersheds in New England, experiments in the **Hubbard Brook Experimental Forest** (**HBEF**) started in 1963. Neighbouring small watersheds with northern hardwood forest were assigned to different treatments: control (watershed 6), clear-cut in winter 1965 followed by herbicide treatment (1965–1968; watershed 2) and further logging

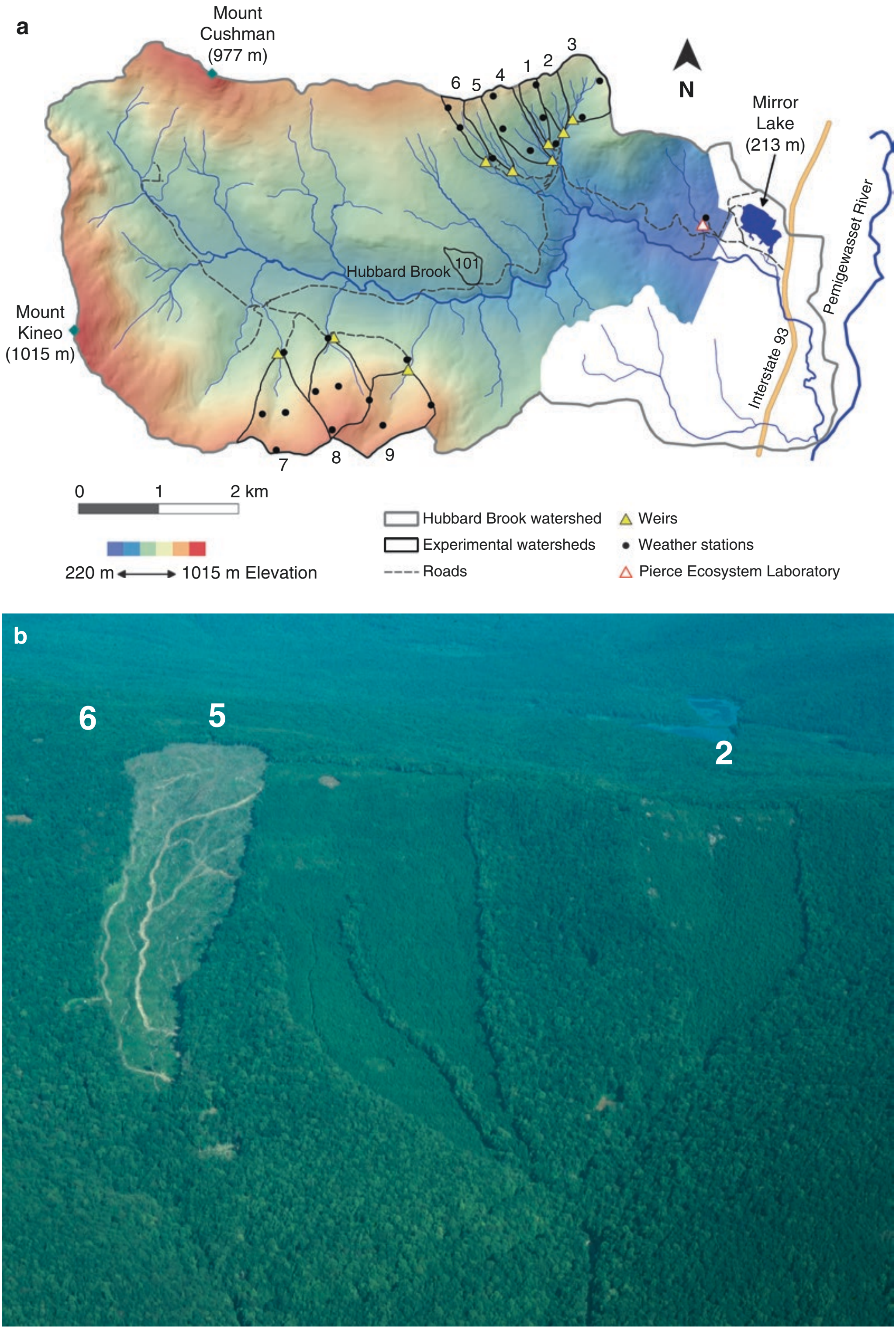

Fig. 14.8 Hubbard Brook Experimental Forest. **a** Map of the watershed (Holmes and Likens 2016; copyright granted by Yale University Press). **b** Map of experimental watersheds (watershed 2: clear-cut; watershed 5: whole-tree harvest; watershed 6: control). (Photo courtesy of Hubbard Brook Experimental Forest)

experiments (watershed 5; whole-tree harvest). Use of a "small **watershed** technique" (Likens et al. 1977) allowed measurements of both the volume and the chemistry of precipitation inputs and stream water outputs of a spatially clearly defined unit—that is, a small watershed (Chap. 13)—and to study the effects of changing land cover on ecosystem nutrient budgets. Since then, many more experiments and observations have been carried out within the watershed of the Hubbard Brook (www.hubbardbrook.org). Of the original experiments, in particular, the clear-cut of an entire forested watershed and the subsequent herbicide treatment to prevent regrowth for 3 years provided unprecedented insight into the responses of watershed hydrology and biogeochemistry to land cover changes. Streamflow increased by a factor of 5 in the following year (hydrological year 1965–1966), and evapotranspiration decreased by a factor of 4. Even more spectacular, nitrate concentrations in stream water increased from close to zero to values of about 50 mg/L and stayed high, similar to cation concentrations, until regrowth of vegetation started in 1969. These changes in water and nutrient pools and fluxes, related to vegetation cover, were later shown to also affect other ecosystem characteristics and processes, such as surface albedo, C sink strengths, erosion and biological diversity, to name a few (see Holmes and Likens (2016) for the latest synthesis).

14.2.5 Artificial Ecosystems

A very different approach to the study of entire ecosystems from the ones mentioned above is to "create" entire ecosystems artificially under controlled or semi-controlled environments. Different facilities of various sizes are available (micro-, meso- and macrocosms) and have been used in recent decades to answer research questions such as: How do changes in environmental conditions affect the root exudation in diverse grasslands? How do nutrient and water fluxes interact and affect the NPP of different community members in a given ecosystem?

- **Open-top chambers** (**OTCs**) **and whole-tree chambers** (**WTCs**): These mesocosms are typically round enclosures of varying heights (from <1 m to about 10 m) and diameters (from <1 m to about 3 m), depending on the ecosystem type under study (Fig. 14.9; OTC). They are covered by a transparent dome made of plastic, foils or films with high transmission of UV and visible light. Often they are open to the top/side to allow natural precipitation to enter and, to prevent heating up, sometimes they are temperature controlled. Typically, OTCs have a confined below-ground compartment as well, either with walls extending into the native soil or with more sophisticated instrumentation such as weighing devices or lysimeters filled with soil (see below). Depending on the set-up, OTCs contain either local vegetation on grown soil or planted/seeded communities in lysimeters filled with soil. For example, OTCs treated with single and combinations of global change drivers (elevated CO_2, increased soil and air temperatures, increased N deposition, increased precipitation) were used in the 1990s in the **Jasper Ridge Global Change Experiment** (http://globalecology.stanford.edu/DGE/Dukes/JRGCE/home.html) to study the responses of Californian grassland to global environmental change (Shaw et al. 2002).
- **Lysimeters**: These are cylinders, open at the top and closed at the bottom, with diameters and heights of up to about 3 m. Typically put into the ground so they form an even surface with the surrounding vegetation, they are filled with (in the best case) undisturbed soil and covered by sown/planted vegetation. To study soil water dynamics and soil leaching, the drainage water in the cylinder is collected at the bottom and used for further chemical analyses. Lysimeters can be combined with other facilities, such as OTCs or WTCs, or put onto balances. Then they require underground walk-in facilities for maintenance and sampling. One prime example for such a combined set-up is the Montpellier European Ecotron in Montferrier-sur-Lez, France (www.ecotron.cnrs.fr). Here, 30 m^3

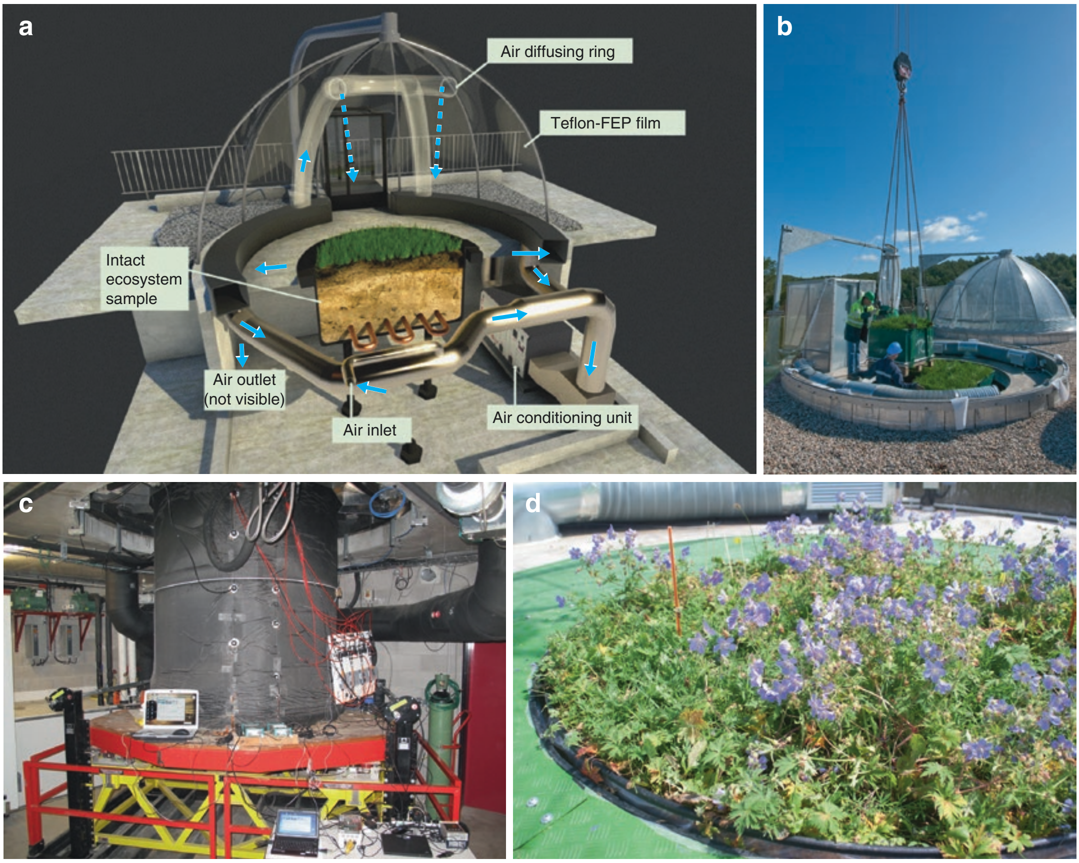

Fig. 14.9 Macrocosm facility at the Montpellier European Ecotron. **a** Scheme of the set-up: an intact ecosystem is placed below a dome made of Teflon-FEP (fluorinated ethylene propylene) film. The soil monolith is placed in a lysimeter, which is located in an underground, walk-in, air-conditioned room. The air is circulated through the soil and air-diffusing rings into the dome, and it leaves the dome through circular pipes at the soil surface. **b** Setting up a new experiment with soil monoliths. **c** View of the lysimeter room, with the weighing system and many soil sensors for measurements in the soil monolith. **d** View of a sown grassland situated in the lysimeter. The size of the ecosystem can be adjusted in diameter and soil depth, here seen by the green metal ring. (Photos courtesy of Montpellier European Ecotron)

transparent domes are situated directly on top of lysimeters that are 1.6 m in diameter and 2 m in depth (Fig. 14.9).

- **Biosphere 2**: A well-known example of an artificial ecosystem is Biosphere 2 (named after "Biosphere 1"—the Earth), which was established close to Tucson, AZ, USA, in 1991 to test whether human life would be possible in a closed, self-sufficient ecological system; if successful it was to be used as a role model for longer space missions. The facility (1.3 ha in area and about 204000 m^3 in volume) included about 3800 species in several ecosystems (ocean, mangrove, tropical rainforest, savanna, desert, intensive agriculture) and living quarters for eight persons, who stayed in Biosphere 2 for about 2 years. However, the first experiment (1991–1993) failed because of decreases (to about 14%) in the concentrations of oxygen (which was slowly consumed by microbial respiration in soils, while respiratory CO_2 was captured by the concrete structures) (Severinghaus et al. 1994) and large changes in species abundance (e.g. loss of pollinators versus dominance of cockroaches and greenhouse ants), nicely demonstrating the complexity of ecological interactions. The second experiment (in 1994) was terminated after 6 months because of a management controversy. The facility has subsequently been used for ecological and biogeochemical research by the University of Columbia (1996–2003) and the University of Arizona, which has owned the Biosphere 2 Laboratory (B2L) since 2011. The facility has been used to carry out global change experiments—for example, with increasing CO_2 concentrations, air and soil temperature manipulations and drought simulations—as well as to test new technological approaches (Gonzalez-Meler et al. 2014). B2L closes the methodological gap between small enclosures (such as OTCs, WTCs and small growth chambers) and mature ecosystems (such as forest stands) and, for example, has enabled the study of isoprene emissions in ecosystems under controlled conditions and provided data to improve the representation of soil respiration in ecosystem models. Today, B2L is still used for research, and also for education and outreach (http://biosphere2.org/). Although not the first artificial "Biosphere" (Box 14.1), B2L is clearly the most famous one.

Box 14.1: Bios-1 to Bios-3

Bios-1 to Bios-3 (sometimes also called CELSS (for Controlled/Closed Ecological/Environment Life-Support System)), designed for the Soviet space programme and employed until 1984 in experiments involving humans, had a mission very similar to that of Biosphere 2. Using highly artificial and strongly simplified ecosystems, Biosphere 3 was employed to find a way to sustain human life in outer space for a long period of time. Although now named **Biosphere 3**, it was designed and used by the Institute for Biophysics in Krasnojarsk, Siberia, much earlier (1965 and 1972) than Biosphere 2 but became known only much later because of the Cold War. Biosphere 3 was smaller than Biosphere 2 (only 315 m^3 in volume) and was made to accommodate a maximum of three persons at a time. The longest experiment ran for 180 days. Waste recycling using green algae (*Chlorella vulgaris*) or higher green plants (wheat, sedge nuts and vegetables) allowed removal of carbon dioxide in the system while producing oxygen and food. Three experiments, always with three persons in the facility, were carried out with different setups (algae versus higher plants, differences in duration, differences in crew composition), all providing great insights into the theory of closed systems and how to model them. Important aspects discovered during these experiments were a certain lack of self-regulation, the challenge of balancing food production and food consumption, the role of trophic levels in human diets, the need to avoid "deadlock substances" (i.e. elements and molecules, particularly micronutrients, being permanently removed from the system) and changes in microbial populations both in the soils and on human skin (Salisbury et al. 1997). Ensuring "stability" in any of these artificial systems was a difficult task in both these small systems and the larger Biosphere 2, demonstrating that stability or resilience can maybe only be achieved in rather complex, diverse ecosystems.

Summary

- Many different approaches to study terrestrial ecosystems are available.
- Observations include whole-ecosystem studies, transects, chronosequences, grid-based inventories, remote sensing applications and natural experiments.
- Experiments include manipulations of pools and fluxes, of environmental conditions and biodiversity, and also of management and land cover. Artificial ecosystems can be designed in open-top chambers, whole-tree chambers or macrocosms such as Biosphere 2. Selection of appropriate controls is essential—for example, to account for hidden treatment effects.
- Whole-ecosystem studies are often part of larger networks, increasing spatial representativeness and also enabling standardisation of measurements and data processing.

- Development of new technologies—for example, for canopy access or measurements of trace gas fluxes—has increased our understanding of ecosystems dramatically.
- Long-term studies avoid the problem of transient effects. They become more valuable the longer they run.

References

Alexander JM, Diez JM, Levin JM (2015) Novel competitors shape species' responses to climate change. Nature 525:515–520

Allen CD, Macalady AK, Chenchouni H, Bachelet D, McDowell N, Vennetier M, Kitzberger T, Rigling A, Breshears DD, Hogg EH, Gonzalez P, Fensham R, Zhangm Z, Castro J, Demidova N, Lim JH, Allard G, Running SW, Semerci A, Cobb N (2010) A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. For Ecol Manag 259:660–684

Allen CD, Breshears DD, McDowell NG (2015) On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. Ecosphere 6:129

Allison SD, Vitousek PM (2004) Rapid nutrient cycling in leaf litter from invasive plants in Hawai'i. Oecologia 141:612–619

Anderson K, Gaston KJ (2013) Lightweight unmanned aerial vehicles will revolutionise spatial ecology. Front Ecol 11:138–146

Assmann E, Franz F (1963) Voriaufige Fichtenertragstafeln fur Bayem. Mittleres Ertragsniveau. In: Bayerisches Staatsministerium fiir Emahrung, Landwirtschaft und Forsten (eds) Hilfstafeln fur die Forsteinrichtung. Bayerisches Staatsministerium fur Emahrung, Landwirtschaft und Forsten, Munich

Aubinet M, Vesala T, Papale D (eds) (2012) Eddy covariance: a practical guide to measurement and data analysis. Springer Atmospheric Sciences, Springer Verlag, Dordrecht

Bader MKF, Leuzinger S, Keel SG, Siegwolf RTW, Hagedorn F, Schleppi P, Körner C (2013) Central European hardwood trees in a high-CO_2 future: synthesis of an 8-year forest canopy CO_2 enrichment project. J Ecol 101:1509–1519

Baeten L, Verheyen K, Wirth C, Bruelheide H, Bussotti F, Finér L, Jaroszewicz B, Selvi F, Valladares F, Allan E, Ampoorter E, Auge H, Avăcăriței D, Barbaro L, Bărnoaiea I, Bauhus J, Beinhoff C, Benavides R, Benneter A, Berger S, Berthold F, Boberg J, Bonal D, Brüggemann W, Carnol M, Castagneyrol B, Charbonnier Y, Chećko E, Coomes D, Coppi A, Crespo BC, Dalmaris E, Dănilă G, Dawud SM, de Vries W, De Wandeler H, Deconchat M, Domisch T, Duduman G, Fischer M, Fotelli M, Gessler A, Gimeno TE, Granier A, Grossiord C, Guyot V, Hantsch L, Hättenschwiler S, Hector A, Hermy M, Holland V, Jactel H, Joly FX, Jucker T, Kolb S, Koricheva J, Lexer MJ, Liebergesell M, Milligan H, Müller S, Muys B, Nguyen D, Nichiforel L, Pollastrini M, Proulx R, Rabasa S, Radoglou K, Ratcliffe S, Raulund-Rasmussen K, Seiferling I, Stenlid J, Vesterdal L, von Wilpert K, Zavala MA, Zielinski D, Scherer-Lorenzen M (2013) A novel comparative research platform designed to determine the functional significance of tree species diversity in European forests. Perspect Plant Ecol Evol Syst 15:281–291

Bardgett RD, Wardle DA (2010) Aboveground–belowground linkages, Series in ecology and evolution. Oxford University Press, Oxford

Barker R (2005) Scorched earth: how the fires of Yellowstone changed America. Island Press, Washington, DC

Bassin S, Volk M, Suter M, Buchmann N, Fuhrer J (2007) Nitrogen deposition but not ozone affects productivity and community composition of sub-alpine grassland after three years of treatment. New Phytol 175:523–534

Beier C, Beierkuhnlein C, Wohlgemuth T, Penuelas J, Emmett B, Körner C, de Boeck H, Hesselbjerg Christensen J, Leuzinger S, Janssens IA, Hansen K (2012) Precipitation manipulation experiments—challenges and recommendations for the future. Ecol Lett 15:899–911

Binkley D, Högberg P (2016) Tamm review: revisiting the influence of nitrogen deposition on Swedish forests. For Ecol Manag 368:222–239

Bruelheide H, Böhnke M, Both S, Fang T, Assmann T, Baruffol M, Bauhus J, Buscot F, Chen X, Ding BY, Durka W, Erfmeier A, Fischer M, Geißler C, Guo D, Guo LD, Härdtle W, He JS, Hector A, Kröber W, Kühn P, Lang AC, Nadrowski K, Pei KQ, Scherer-Lorenzen M, Shi XZ, Scholten T, Schuldt A, Trogisch S, von Oheimb G, Welk E, Wirth C, Wu YT, Yang XF, Yu MJ, Zeng XQ, Zhang SR, Zhou HZ, Ma KP, Schmid B (2011) Community assembly during secondary forest succession in a Chinese subtropical forest. Ecol Monogr 81:25–41

Brumme R, Khanna PK (2009) Functioning and management of European beech ecosystems, Ecological Studies, Vol 208. Springer, Berlin

Buchmann N (2002) Plant ecophysiology and forest response to global change. Tree Physiol 22:1177–1184

Buchmann N, Schulze ED (1999) Net CO_2 and H_2O fluxes of terrestrial ecosystems. Glob Biogeochem Cycles 13:751–760

Burri S, Sturm P, Prechsl UE, Knohl A, Buchmann N (2014) The impact of extreme summer drought on the short-term carbon coupling of photosynthesis to soil CO_2 efflux in a temperate grassland. Biogeosciences 11:961–975

Canadell JG, Steffen WL, White PS (2002) IGBP/GCTE terrestrial transects: dynamics of terrestrial ecosystems under environmental change. J Veg Sci 13:297–450

Coleman DC (2010) Big ecology: the emergence of ecosystem science. University of California Press, Berkeley

Diamond JM (1983) Laboratory, field and natural experiments. Nature 304:586–587

Díaz S (2013) Ecosystem function measurement, terrestrial communities. In: Simon AL (ed) Encyclopedia of biodiversity, 2nd edn. Academic Press, Waltham, pp 72–89.

Díaz S, Symstad AJ, Stuart Chapin IF, Wardle DA, Huenneke LF (2003) Functional diversity revealed by removal experiments. Trends Ecol Evol 18:140–146

Duursma RA, Gimeno TE, Boer MM, Crous KY, Tjoelker MG, Ellsworth DS (2016) Canopy leaf area of a mature evergreen Eucalyptus woodland does not respond to elevated atmospheric [CO_2] but tracks water availability. Glob Change Biol 22:1666–1676

Ellenberg J (1971) Integrated experimental ecology, Ecological Studies, Vol 2. Springer, Berlin

Frank D, Reichstein M, Bahn M, Thonicke K, Frank D, Mahecha M, Smith P, van der Velde M, Vicca S, Babst F, Beer C, Buchmann N, Canadell JG, Ciais P, Cramer W, Ibrom A, Miglietta F, Poulter B, Rammig A, Seneviratne SI, Walz A, Wattenbach M, Zavala MA, Zeischler J (2015) Effects of climate extremes on the terrestrial carbon cycle: concepts, processes and potential future impacts. Glob Change Biol 21:2861–2880

Franke MA (2000) Yellowstone in the afterglow: lessons from the fires. National Park Service, Mammoth Hot Springs

French NR (1979) Perspectives in grassland ecology: results and applications of the US/IBP grassland biome study. Ecological Studies: analysis and synthesis, Vol 32. Springer, New York

Gonzalez-Meler MA, Rucks JS, Aubanell G (2014) Mechanistic insights on the responses of plant and ecosystem gas exchange to global environmental change: lessons from Biosphere 2. Plant Sci 226:14–21

Greenaway F (1996) Science international: a history of the International Council of Scientific Unions. Cambridge University Press, Cambridge

Guanter L, Zhang Y, Jung M, Joiner J, Voigt M, Berry JA, Frankenberg C, Huete A, Zarco-Tejada P, Lee J-E, Moran S, Ponce-Campos G, Beer C, Camps-Valls G, Buchmann N, Gianelle D, Klumpp K, Cescatti A, Baker JM, Griffis TJ (2014) Global and time-resolved monitoring of crop photosynthesis with chlorophyll fluorescence. Proceedings of the National Academy of Sciences 111:E1327–E1333

Gunderson P, Boxman AW, Lamersdrof N, Moldan F, Andersen BR (1998) Experimental manipulation of forest ecosystems: lessons from large roof experiments. For Ecol Manag 101:339–352

Hallé F, Cleyet-Marrel D, Ebersolt G (2000) Le Radeau des Cimes: l'exploration des canopées forestières. JC Lattès, Paris

Hector A, Schmid B, Beierkuhnlein C, Caldeira MC, Diemer M, Dimitrakopoulos PG, Finn J, Freitas H, Giller PS, Good J, Harris R, Högberg P, Huss-Danell K, Joshi J, Jumpponen A, Körner C, Leadley PW, Loreau M, Minns A, Mulder CPH, O'Donovan G, Otway SJ, Pereira JS, Prinz A, Read DJ, Scherer-Lorenzen M, Schulze ED, Siamantziouras ASD, Spehn E, Terry AC, Troumbis AY, Woodward FI, Yachi S, Lawton JH (1999) Plant diversity and productivity experiments in European grasslands. Science 286:1123–1127

Hendrey GR, Miglietta F (2006) FACE technology: past, present, and future. Ecol Stud 187:15–45

Hiller RV, Bretscher D, DelSontro T, Diem T, Eugster W, Henneberger R, Hobi S, Hodson E, Imer D, Kreuzer M, Künzle T, Merbold L, Niklaus PA, Rihm B, Schellenberger A, Schroth MH, Schubert CJ, Siegrist H, Stieger J, Buchmann N, Brunner D (2014) Anthropogenic and natural methane fluxes in Switzerland synthesised within a spatially-explicit inventory. Biogeosciences 11:1941–1960

HiIleRisLambers J, Ettinger AK, Ford KR, Haak DC, Horwith M, Miner BE, Rogers HS, Sheldon KS, Tewksbury JJ, Waters SM, Yang S (2013) Accidental experiments: ecological and evolutionary insights and opportunities derived from global change. Oikos 122:1649–1661

Högberg P (2001) Interactions between hillslope hydrochemistry, nitrogen dynamics and plants in Fennoscandian boreal forest. In: Schulze E-D, Heimann M, Harrison S, Holland E, Lloyd J, Prenice IC, Schimel D (eds) Global biogeochemical cycles in the climate system. Academic Press, San Diego, pp 227–233

Högberg P, Nordgren A, Buchmann N, Taylor AFS, Ekblad A, Högberg MN, Nyberg G, Ottosson-Löfvenius M, Read DJ (2001) Large-scale forest girdling shows that current photosynthesis drives soil respiration. Nature 411:789–792

Högberg P, Fan H, Quis M, Binkley D, Tamm CO (2006) Tree growth and soil acidification in response to 30 years of experimental nitrogen loading on boreal forest. Glob Change Biol 12:489–499

Högberg P, Högberg MN, Göttlicher SG, Betson NR, Keel SG, Metcalfe DB, Campbell C, Schindlbacher A, Hurry V, Lundmark T, Linder S, Näsholm T (2008) High temporal resolution tracing of photosynthate carbon from the tree canopy to forest soil microorganisms. New Phytol 177:220–228

Holmes R, Likens GE (2016) Hubbard Brook: the story of a forest ecosystem. Yale University Press, New Haven

Hooper DU, Vitousek PM (1997) The effects of plant composition and diversity on ecosystem processes. Science 277:1302–1305

Ineson P, Taylor K, Harrison AF, Poskitt J, Benham DG, Tipping E, Woof C (1998) Effects of climate change on nitrogen dynamics in upland soils. 1. A transplant approach. Glob Change Biol 4:143–152

Jenny H (1941) Factors of soil formation. A system of quantitative pedology. McGraw-Hill, New York

Kira T, Shidei T (1967) Primary production and turnover of organic matter in different forest ecosystems of the western Pacific. Jpn J Ecol 17:70–87

Kolari P, Pumpanen J, Rannik U, Ilvesniemi H, Hari P, Berninger F (2004) Carbon balance of different aged scots pine forests in southern Finland. Glob Change Biol 10:1106–1119

Körner C, Asshoff R, Bignucolo O, Hättenschwiler S, Keel SG, Pelaez-Riedl S, Pepin S, Siegwolf RTW, Zotz G (2005) Carbon flux and growth in mature deciduous forest trees exposed to elevated CO_2. Science 309:1360–1362

Kreyling J, Beier C (2013) Complexity in climate change manipulation experiments. Bioscience 63:763–767

Kuzyakov Y, Gavrichkova O (2006) Time lag between photosynthesis and carbon dioxide efflux from soil: a review of mechanisms and controls. Glob Change Biol 16:3386–3406

Lepš J (2004) What do the biodiversity experiments tell us about consequences of plant species loss in the real world? Basic Appl Ecol 5:529–534

Leuschner C, Jungkunst HF, Fleck S (2009) Functional role of forest diversity: pros and cons of synthetic stands and across-site comparisons in established forests. Basic Appl Ecol 10:1–9

Likens GE, Bormann FH, Pierce RS, Eaton JS, Johnson NM (1977) Biogeochemistry of a forested ecosystem. Springer, New York

Linder S (1987) Responses to water and nutrients in coniferous ecosystems. Ecol Stud 61:180–200

Lowman MD (1999) Life in the treetops—adventures of a woman in field biology. Yale University Press, New Haven

Magnani F, Mencuccini M, Borghetti M, Berbigier P, Berninger F, Delzon S, Grelle A, Hari P, Jarvis PG, Kolari P, Kowalski AS, Lankreijer H, Law BE, Lindroth A, Loustau D, Manca G, Moncrieff JB, Rayment M, Tedeschi V, Valentini R, Grace J (2007) The human footprint in the carbon cycle of temperate and boreal forests. Nature 447:848–852

Matyssek R, Wieser G, Ceulemans R, Rennenberg H, Pretzsch K, Häberle KH, Löw M, Nunn AJ, Werner H, Wipfler P, Oßwald W, Nikolova P, Hanke DE, Kraigher H, Tausz M, Bahnweg G, Kitao M, Dieler J, Sandermann H, Herbinger K, Grebenc T, Blumenröther M, Deckmyn G, Grams TEE, Heerdt C, Leuchner M, Fabian P, Häberle KH (2010) Enhanced ozone strongly reduces carbon sink strength of adult beech (*Fagus sylvatica*)—resume from the free-air fumigation study at Kranzberg Forest. Environ Pollut 158:2527–2532

Mikkelsen TN, Beier C, Jonasson S, Holmstrup M, Schmidt IK, Ambus P, Pilegaard K, Michelsen A, Albert K, Andresen LC, Arndal MF, Bruun N, Christensen S, Danbæk S, Gundersen P, Jørgensen P, Kongstad J, Maraldo K, Priemé A, Riis-Nielsen T, Ro-Poulsen H, Stevnbak K, Selsted MB, Sørensen P, Larsen KS, Carter MS, Martinussen T, Miglietta F, Sverdrup H (2008) Experimental design of multifactor climate change experiments with elevated CO_2, warming and drought—the CLIMAITE project. Funct Ecol 22:185–195

Mund M, Kummetz E, Hein M, Bauer GA, Schulze E-D (2002) Growth and carbon stocks of a spruce forest chronosequence in central Europe. For Ecol Manag 171:275–296

Myneni RB, Keeling CD, Tucker CJ, Asrar G, Nemani RR (1997) Increased plant growth in the northern high latitudes from 1981 to 1991. Nature 386:698–702

Naeem S, Bunker DE, Hector A, Loreau M, Perrings C (eds) (2009) Biodiversity, ecosystem functioning, & human wellbeing: an ecological and economic perspective. Oxford University Press, Oxford

Naeem S, Thompson LJ, Lawler SP, Lawton JH, Woodfin RM (1994) Declining biodiversity can alter the performance of ecosystems. Nature 368:734–737

Norby RJ, Zak DR (2011) Ecological lessons from free-air CO_2 enrichment FACE experiments. Annu Rev Ecol Evol Syst 42:181–203

Nösberger J, Long SP, Norby RJ, Stitt M, Hendrey GM, Blum H (2006) Managed ecosystems and CO_2: case studies, processes, and perspectives, Ecological Studies, Vol 187. Springer, Berlin

Odum E (1971) Fundamentals of ecology. WB Saunders, Co., Philadelphia

Odum E (1983) Basic ecology. Harcourt Brace College Publishers, New York

Odum E (2005) Fundamentals of ecology. Thomson Brooks/Cole, Belmont

Oren R, Ellsworth DS, Johnsen KH, Phillips N, Ewers BE, Maier C, Schäfer KVR, McCarthy H, Hendrey G, McNulty SG, Katul GG (2001) Soil fertility limits carbon sequestration by forest ecosystems in a CO_2-enriched atmosphere. Nature 411:469–472

Ramanathan V (1988) The greenhouse theory of climate change: a test by an inadvertent global experiment. Science 240:293–299

Reich PB, Knops J, Tilman D, Craine J, Ellsworth D, Tjoekler M, Lee T, Wedin D, Naeem S, Bahauddin D, Hendrey G, Jose S, Wrage K, Goth J, Bengtson W (2001) Plant diversity enhances ecosystem responses to elevated CO_2 and nitrogen deposition. Nature 410:809–812

Roscher C, Schumacher J, Baade J, Wilcke W, Gleixner G, Weisser WW, Schmid B, Schulze ED (2004) The role of biodiversity for element cycling and trophic interactions: an experimental approach in a grassland community. Basic Appl Ecol 5:107–121

Ruehr NK, Offermann CA, Gessler A, Winkler BJ, Ferrio JP, Buchmann N, Barnard RL (2009) Drought effects on allocation of recent carbon: from beech leaves to soil CO_2 efflux. New Phytol 184:950–961

Running SW, Nemani RR Heinsch FA, Zhao M, Reeves M, Hashimoto H (2004) A continuous satellite-derived measure of global terrestrial primary production. Bioscience 54:547–560

Salisbury FB, Gitelson JI, Lisovsky GM (1997) Bios-3: Siberian experiments in bioregenerative life support. BioScience 47:575–585

Schulze ED, Mooney HA, Sala OE, Jobbagy E, Buchmann N, Bauer G, Canadell J, Jackson RB, Loreti J, Oesterheld M, Ehleringer JR (1996) Rooting depth, water availability, and vegetation cover along an aridity gradient in Patagonia. Oecologia 108:503–551

Severinghaus JP, Broecker W, Dempster W, MacCallum T, Wahlen M (1994) Oxygen loss in Biosphere 2. Eos Trans AGU 75:35–37

Shaw MB, Zavaleta ES, Chiariello NR, Cleland EE, Mooney HA, Field CB (2002) Grassland responses to global environmental changes suppressed by elevated CO_2. Science 298:1987–1990

Shugart HH, Macko SA, Lesolle P, Szuba TA, Mukelabai MM, Dowty P, Swap RJ (2004) The SAFARI 2000—Kalahari transect wet season campaign of year 2000. Glob Change Biol 10:273–280

Silvertown J, Poulton P, Johnston E, Edwards G, Heard M, Biss PM (2006) The Park Grass Experiment 1856–2006: its contribution to ecology. J Ecol 94:801–814

Spiegelberger T, Hegg O, Matthies D, Hedlund K, Schaffner U (2006) Long-term effects of short-term perturbation in a subalpine grassland. Ecology 87:1939–1944

Stork NE, Wright SJ, Mulkey SS (1997) Craning for a better view: the Canopy Crane Network. Trends Ecol Evolut 12:415–420

Sutton SL (2001) Alice grows up: canopy science in transition from Wonderland to reality. Plant Ecol 153:13–21

Tilman D, Wedin D, Knops J (1996) Productivity and sustainability influenced by biodiversity in grassland ecosystems. Nature 379:718–720

Tilman D, Knops J, Wedin D, Reich P, Ritchie M, Siemann E (1997) The influence of functional diversity and composition on ecosystem processes. Science 277:1300–1302

Ulrich B (1983) Interaction of forest canopies with atmospheric constituents: SO_2, alkali and earth alkali cations and chloride. In: Ulrich B, Pankrath J (eds) Effects of accumulation of air pollutants in forest ecosystems. D Reidel Publishing Company, Dordrecht, pp 33–45

Verheyen K, Vanhellemont M, Auge H, Baeten L, Baraloto C, Barsoum N, Bilodeau-Gauthier S, Bruelheide H, Castagneyrol B, Godbold D, Haase J, Hector A, Jactel H, Koricheva J, Loreau M, Mereu S, Messier C, Muys B, Nolet P, Paquette A, Parker J, Perring M, Ponette Q, Potvin C, Reich P, Smith A, Weih M, Scherer-Lorenzen M (2016) Contributions of a global network of tree diversity experiments to sustainable forest plantations. Ambio 45:29–41

Vicca S, Bahn M, Estiarte M, Alberti G, Ambus P, Arain A, Beier C, Bentley LP, Borken W, Buchmann N, Collins SL, Costa ACL, de Dato G, Dukes JS, Escolar C, Fay P, Guidolotti G, Hanson PJ, Kahmen A, Kröel-Dulay G, Ladreiter-Knauss T, Larsen KS, Lellei-Kovacs E, Lebrija-Trejos E, Maestre FT, Marhan S, Marshall M, Meir P, Miao Y, Muhr J, Niklaus PA, Ogaya R, Peñuelas J, Poll C, Rustad LE, Savage K, Schindlbacher A, Schmidt IK, Smith AR, Sotta ED, Suseela V, Tietema A, van Gestel N, van Loon EE, van Straaten O, Vargas R, Wan S, Weber U, Janssens IA (2014) Can current moisture responses predict soil respiration under altered precipitation regimes? A synthesis of manipulation experiments. Biogeosciences 11:2991–3013

Vilà M, Vayreda J, Comas L, Ibáñez J, Mata T, Obón B (2007) Species richness and wood production: a positive association in Mediterranean forests. Ecol Lett 10:241–250

Vitousek PM, Aplet G, Turner D, Lockwood JJ (1992) The Mauna Loa environmental matrix: foliar and soil nutrients. Oecologia 89:372–382

Vogel A, Scherer-Lorenzen M, Weigelt A (2012) Grassland resistance and resilience after drought depends on management intensity and species richness. PLoS One 7:e36992

Volk M, Bungener P, Contat F, Montani M, Fuhrer J (2006) Grassland yield declined by a quarter in 5 years of free-air ozone fumigation. Glob Change Biol 12:74–83

Walker BH, Steffen WL, Canadell J, Ingram JSI (1999) The terrestrial biosphere and global change: implications for natural and managed ecosystems, Synthesis volume. Cambridge University Press, Cambridge

Wardle DA, Zackrissen O (2005) Effects of species and functional group loss on island ecosystem properties. Nature 435:806–810

Weigelt A, Weisser WW, Buchmann N, Scherer-Lorenzen M (2009) Biodiversity for multifunctional grasslands: equal productivity in high-diversity low-input and low-diversity high-input systems. Biogeosciences 6:1695–1706

Wolf B, Merbold L, Decock C, Tuzson B, Harris E, Six J, Emmenegger L, Mohn J (2015) First on-line isotopic characterization of N_2O emitted from intensively managed grassland. Biogeosciences 12:2517–2531

Wright RF (1989) RAIN project—role of organic-acids in moderating pH change following reduction in acid deposition. Water Air Soil Pollut 46:251–259

Wright AJ, Ebeling A, de Kroon H, Roscher C, Weigelt A, Buchmann N, Buchmann T, Fischer C, Hacker N, Hildebrandt A, Leimer S, Mommer L, Oelmann Y, Scheu S, Steinauer K, Strecker T, Weisser W, Wilcke W, Eisenhauer N (2015) Flooding disturbances increase resource availability and productivity, but reduce stability in diverse plant communities. Nat Commun 6:6092

Approaches to Model Processes at the Ecosystem Level

15

Contribution by C. Sierra

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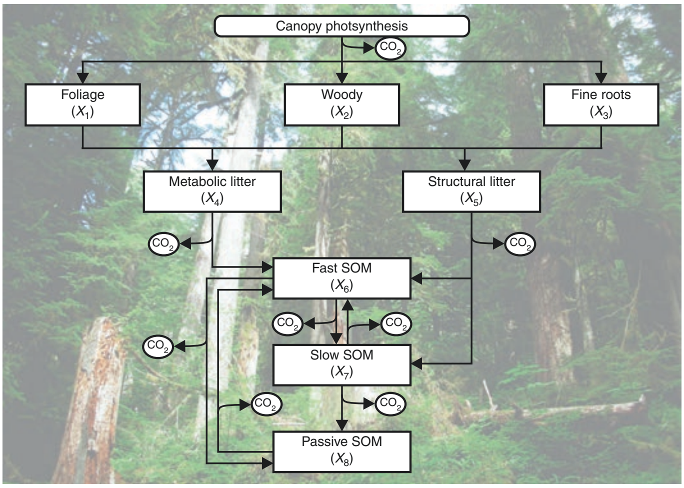

Ecosystems, with all their pools and fluxes, as well as biotic and abiotic interactions, are often described using mathematical models. In biogeochemical models, the various ecosystem compartments and their associated fluxes are represented to the best of our knowledge (depicted here: structure of the Terrestrial Ecosystem Carbon Model, TECO; see text for details). Models are then used, for example, to test certain underlying assumptions or to predict their responses to changing environmental conditions. (Photo: E.-D. Schulze)

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Owing to the complexity of ecosystems (Chap. 13), the many interactions that take place and the diversity of ecosystems globally, we cannot study or experimentally manipulate ecosystems everywhere all the time. Thus, mathematical models are a fundamental tool in the study of plant ecology and ecosystem dynamics. They can be used to formalise our conceptual understanding of physiological and ecological processes in the form of mathematical relations, which can serve to facilitate the development of testable hypotheses. Models also serve as tools for integrating different sources of information and for predicting the consequences of changes in the future behaviour of a system by changing the assumptions the models are based on (Canham et al. 2003; Soetaert and Herman 2009).

Models at the ecosystem level are generally focused on describing **processes** related to the water, carbon, nutrient and energy budgets of ecosystems (Ågren and Andersson 2012). They generally describe the physiology of plant processes in terms of carbon, water and nutrient uptake and the transfers of these materials to the soil system. Other ecological processes are also often included, such as competition among individuals for light and nutrients, age-related mortality or the dispersal and reproduction of species (Botkin et al. 1972; Ågren et al. 1991; Bugmann 2001; Sierra and Harmon 2008).

In this chapter, different classifications of models will be explored and the basic building blocks of ecosystem and biogeochemical models reviewed from a mathematical point of view. A **holistic approach** will be adopted, in which the most general mathematical aspects of models will be considered while ignoring specific details of each process for the sake of a general understanding.

15.1 Classification of Ecosystem Models

15.1.1 Model Dichotomies

There exists a large variety of mathematical models to represent terrestrial ecosystems and their biogeochemistry. They can be classified into different categories, which are often ambiguous or can apply equally to very dissimilar models. It is common for models to be presented in dichotomies, such as empirical versus mechanistic or deterministic versus stochastic, depending on a main attribute of the model being highlighted (Jones 1992).

A model is generally classified as **empirical** when a mathematical relation (e.g. a linear regression of species richness vs. area) only captures a trend observed in a given data set and when there is no explicit representation of underlying processes. These types of models are generally contrasted with **mechanistic** models (e.g. an exponential relationship of temperature vs. respiration), in which a basic understanding of underlying processes is used to set the mathematical structure of the model. Compared to empirical models, mechanistic models usually contain a higher level of detail and descriptions of interactions of ecosystem components. However, empirical models can more easily accommodate **measurement uncertainty** (e.g. due to plant phenology or interannual variability in the environment) and produce **predictions** within a given confidence interval (e.g. within the coming decade). In addition, empirical models are usually the starting point for the development of more detailed mechanistic models and serve to guide our intuition in the development of more complex theories.

Another important model dichotomy is deterministic versus stochastic. **Deterministic models** produce exact and invariable predictions when all inputs to the model are known (e.g. energy budget of a leaf) (Chap. 9). This contrasts with **stochastic models**, in which random elements are included (e.g. tree mortality or disturbances) and predictions are always different, even if all model parameters are fixed. A large number of **simulations** are used in stochastic models to determine the plausible interval of model predictions. A very important group of stochastic models are the so-called **gap models** (Bugmann 2001). They represent the dynamics of individual trees growing on a patch of forest (a forest gap), and the emergent dynamic of the system is the result of the interactions among individuals. These types of models have been very important in predicting

Table 15.1 Common characteristics of main classes of vegetation and ecosystem models

Class	Scale	Characteristics	Examples
Physiological	Hours to days; single plant	Detailed calculation of photosynthesis, respiration, transpiration, and nutrient and carbon allocation; usually high level of detail for leaf processes.	SIB, BATS, LSM, Canveg, SPA
Biogeochemical	Days to decades; ecosystem patch to globe	Soil–plant–atmosphere interactions; includes photosynthesis, respiration, growth, allocation, nutrient uptake, and water and energy budgets.	Century, TEM, CASA, BIOME-BGC, PnET
Gap	Seasons to decades; forest patch to biomes	Population and community dynamics; represents competition among different individuals and random processes such as mortality, fire or insect outbreaks.	Jabowa, SORTIE, FORET, ED, StandCarb, FORCLIM
Biogeographical	Years to centuries; regions to globe	Species distributions and climate control on vegetation; potential distribution of vegetation types and biomes across the Earth.	Miami, DOLY, MAPSS, BIOME
Dynamic global vegetation	Hours to centuries; globe	Representation of carbon, water, energy and nutrient budgets on global scale; vegetation–climate interactions as well as disturbances and human impacts.	LPJ, ORCHIDEE, CLM, JSBACH

the effects of climate change on species distributions (Huston and Smith 1987; Bugmann 2001; Shugart 2002).

Other dichotomies, such as static versus dynamic (also known as time invariant) or numeric versus analytic, are common in the classification of models. **Static** models are very useful for studying the main characteristics of an ecosystem under steady-state conditions, while **dynamic** models are useful for studying the transient behaviour of an ecosystem as it is altered by external factors such as climate. When models are solved using computers, they are classified as **numerical**, whereas when solutions are derived mathematically, they are classified as **analytical**. There are many other dichotomies in the classification of models, such as theoretical vs. applied, qualitative vs. quantitative, mathematical vs. statistical, discrete vs. continuous, population-based vs. individual-based, spatial vs. point-based, or global vs. regional.

15.1.2 Model Classes

In addition to model dichotomies, it is possible to classify models in general classes associated with the scale or the main processes represented in the model. Five main classes of models are commonly distinguished in the scientific literature; these are physiological, biogeochemical, gap, biogeographical and dynamic global vegetation models (Table 15.1). However, it should be noted that the boundary between these classes is not very clear in many cases, and some of these models could be easily classified in different categories.

15.2 Basic Approach to Model Development

The large majority of ecosystem and biogeochemical models are special cases of **linear dynamical systems** (Ågren and Bosatta 1996; Pastor 2008; Luo and Weng 2011; Ågren and Andersson 2012). This is a group of mathematical equations, systems of ordinary differential equations, that have very similar properties. They are widely used for many applications in science and engineering and can reproduce complex dynamics such as those produced by the cycling of biogeochemical elements and their interactions with the environment.

The main principle behind all ecosystem models is **mass balance** (Rodhe 2000; Ågren and Andersson 2012). Therefore, the differential equations that inform models are all based on the idea that changes in matter and energy are the result of inputs and outputs to and from the system. For example, the changes over time in mass of a reservoir X can be expressed as

$$\frac{dX(t)}{dt} = \text{Inputs} - \text{Outputs} = I(t) - O(t). \qquad (15.1)$$

A particular characteristic of linear dynamical systems is that the outputs O from a reservoir can be expressed as a proportion k of the existing mass in that reservoir. If this proportion changes over time, we can express this proportion as $k(t)$. Each component of the ecosystem (reservoir) can then be expressed as

$$\frac{dX(t)}{dt} = I(t) - k(t) \cdot X(t). \qquad (15.2)$$

An ecosystem model is a collection of differential equations of this type. The number of conceptual pools or reservoirs in a model determines the number of differential equations in the model. This is sometimes called the **dimension** of the model. For example, a model that explicitly represents the dynamic behaviour of five pools (canopy, woody biomass, roots, litter and soil) is represented by five differential equations, and therefore it has dimension five.

Using these concepts, we can now build a very simple carbon model with two reservoirs, vegetation and soil (Fig. 15.1). In this model, carbon is fixed by the vegetation V and transferred to the soil S. From both pools, a fraction is also lost to the atmosphere as CO_2 by the process of respiration. We can represent the conceptual model of Fig. 15.1 mathematically by the following linear system of differential equations:

$$\frac{dV(t)}{dt} = P - c_1 V(t), \qquad (15.3)$$

$$\frac{dS(t)}{dt} = \alpha c_1 V(t) - c_2 S(t), \qquad (15.4)$$

where P represents the annual amount of photosynthetically fixed carbon that enters the ecosystem, c_1 is the proportion of carbon that leaves the vegetation every year, both as respired CO_2 and transferred to the soil pool, α is the proportion of the carbon that leaves the vegetation and is transferred to the soil, and c_2 is the proportion of carbon stored in the soil that is lost every year by heterotrophic respiration.

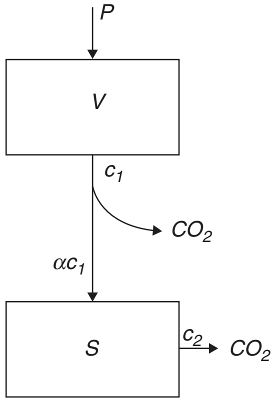


Fig. 15.1 Simple two-pool model of carbon transfers between vegetation (V), soil (S) and the atmosphere. P represents inputs from gross primary production; c_1 and c_2 are coefficients of carbon flow out of each reservoir. Fluxes out of the system are represented as respiration losses in the form of CO_2. The atmosphere is not explicitly represented

Although Eqs. (15.3) and (15.4) do not explicitly show a calculation of respiration, the amount of respired carbon from each pool can be calculated easily as

$$r_1(t) = (1-\alpha) c_1 V(t), \qquad (15.5)$$

$$r_2(t) = c_2 S(t), \qquad (15.6)$$

where r_1 and r_2 represent the amount of respiration from the vegetation and the soil pools, respectively. Notice that only a fraction $(1 - \alpha)$ of the carbon leaving the vegetation pool is respired, while all carbon that leaves the soil pool is respired.

A lot of the complexity that is present in real ecosystems is not included in Eqs. (15.3) and (15.4). For example, this model does not explicitly represent plant hydrological processes, the uptake and use of nutrients, or the allocation of carbon to different plant parts. To explicitly represent these processes, it would be necessary to partition the vegetation and soil pools into many more compartments and include many more differential equations. In fact, most ecosystem models are structured and interrelated collections of a large number of equations that describe particular processes in vegetation and soils.

To analyse the mathematical properties of an ecosystem model, it is much easier to represent them in terms of **vectors** and **matrices** than writing a long list of differential equations. In vector and matrix notation, the model of Eqs. (15.3) and (15.4) can be expressed as

$$\begin{pmatrix} \frac{dV(t)}{dt(t)} \\ \frac{dS(t)}{dt(t)} \end{pmatrix} = \begin{pmatrix} P \\ 0 \end{pmatrix} + \begin{pmatrix} -c_1 & 0 \\ \alpha c_1 & -c_2 \end{pmatrix} \cdot \begin{pmatrix} V(t) \\ S(t) \end{pmatrix}, \tag{15.7}$$

which by matrix multiplication and summation yields the exact system of equations as Eqs. (15.3) and (15.4). Even more compactly, this model can be written as

$$\frac{d\boldsymbol{x}}{dt} = \boldsymbol{p} + \mathbf{C} \cdot \boldsymbol{x}, \tag{15.8}$$

where the italic boldface characters correspond to vectors and uppercase boldface correspond to matrices. We will use this notation to present a general model of ecosystem carbon cycling and analyse its parts and general properties.

15.3 General Ecosystem Carbon Model

Using vector and matrix notation, Luo and Weng (2011) proposed a model that generalises a large majority of models of carbon cycling in terrestrial ecosystems. The model is given by

$$\frac{d\boldsymbol{x}(t)}{dt} = U(t) \cdot \boldsymbol{b} + \xi(t) \cdot \mathbf{A} \cdot \mathbf{C} \cdot \boldsymbol{x}(t), \tag{15.9}$$

where $\boldsymbol{x}(t)$ is a vector of carbon pool sizes, $U(t)$ represents photosynthetically fixed carbon, $\boldsymbol{b}$ is a vector of allocation coefficients of the photosynthetically fixed carbon to plant pools (e.g. leaf, root and woody biomass), and $\xi(t)$ is an environmental scalar modifying the cycling rates and transfers among different ecosystem pools. Matrices **A** and **C** contain coefficients to calculate carbon transfers among the different pools and the amount of carbon release by respiration (Fig. 15.2). Each element of Eq. 15.9 represents an ecosystem process, which will be explored in more detail in the following sections.

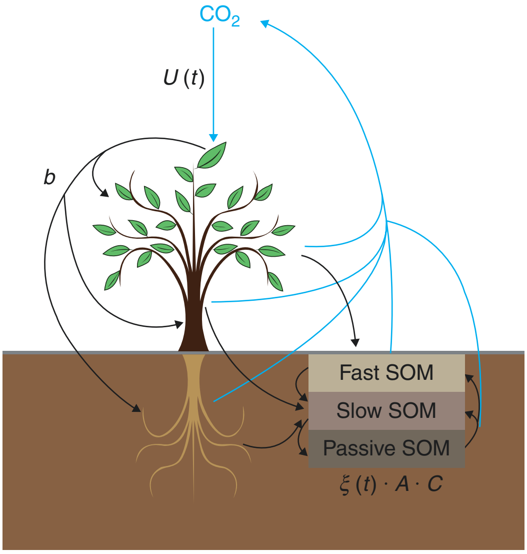


Fig. 15.2 Graphical representation of components of Eq. 15.9. CO_2 fixation by plants is included in the term $U(t)$, and the allocation of fixed carbon to plant pools is represented by the vector b. Cycling rates and transfers among different ecosystem pools are represented by the matrix product A·C, which can be modified by the environmental scalar $\xi(t)$. Fast, slow and passive soil organic matter (SOM) pools refer to pools with fast (e.g. within weeks) to very slow (e.g. within centuries) turnover rates

15.3.1 Carbon Uptake: *U*(*t*)

The first component of our general model is a function, $U(t)$, that determines the amount of carbon uptake in the ecosystem as a function of time. This function represents the total amount of fixed carbon by photosynthesis at the ecosystem level (Chap. 16). Most models describe photosynthesis using the biochemical model proposed by Farquhar et al. (1980) and Farquhar and Caemmerer (1982). This model contains equations that represent the rate of ribulose bisphosphate (RuBP)-saturated carboxylation, the ratio of photorespiration to carboxylation, and the rates of electron transport/photophosphorylation and dark respiration (Sect. 12.1 in Chap. 12). However, these processes occur at the cellular level in the leaf and need to be scaled up to the entire leaf, the canopy, the individual plant and the ecosystem (Bugmann 2001).

Many of the early ecosystem models represented photosynthesis at the leaf level and scaled up directly to the ecosystem level using information on the leaf area index. These types of models are sometimes referred to as **big leaf models**. Other models try to represent the vegetation canopy more explicitly accounting for the distribution of leaves on a vertical profile and their angle of sun exposure (Jones 1992). Still other models represent carbon uptake individually for each tree of a forest patch (i.e. **gap models**), applying an explicit scaling from leaves and individual trees to the ecosystem level (Bugmann 2001; Moorcroft et al. 2001; Shugart 2002).

15.3.2 Carbon Allocation: *b*

Once carbon is fixed by plants, it needs to be allocated to different plant parts with different functions and dynamics. This is described in our general model by the vector ***b***, which contains as elements coefficients that determine the proportion of the total inputs, $U(t)$, that are allocated to different vegetation pools.

Models differ widely in the type of vegetation pools they represent; they can be as simple as foliage, stem and roots, or finer pools such as sugars, starch, structural carbon and so forth. Allocation schemes in models could also be based on simple **fixed ratios**, on allometric **scaling rules** or on an **optimisation principle**, in which carbon is allocated in a dynamically driven manner by resource availability (Malhi et al. 2011; Franklin et al. 2012). In models based on an optimisation principle, allocation may depend on the availability of light, water and nutrients (Sect. 12.3 in Chap. 12). In general, an optimisation rule is applied to the partitioning of carbon to photosynthetic, woody and uptake pools (Franklin et al. 2012). For example, a balance between water loss and carbon uptake may dictate the proportion of carbon allocated to foliage and fine roots (Schulze et al. 1983) or available nitrogen in the soil may control foliage-to-root ratios (Reynolds and Chen 1996). In other models, the allocation strategy is not prescribed but rather emerges by the abiotic constraints on plant performance, for example, the allocation of carbon belowground as a response to low soil moisture content (Kleidon and Mooney 2000; Pavlick et al. 2013).

15.3.3 Cycling Rates in Ecosystem Pools: C

Organic compounds allocated to different plant parts reside there for a certain amount of time. In deciduous trees, carbon resides in the leaves for the duration of the growing season, while carbon in the stems resides there for decades. These differences in cycling rates are accounted for in the matrix **C** of the general model. The diagonal of this matrix contains the rates at which carbon cycles in each pool in units per time (1/[*time*]); therefore, the inverse of these rates represents the **turnover time** of carbon in each pool. In vegetation, cycling rates may depend on species composition or geographical location, while in soils, these rates may depend on the quality of the organic matter or its association with mineral surfaces (Ågren and Bosatta 1996; Sierra et al. 2011; Gleixner 2013).

15.3.4 Transfers and Transformations of Organic Material: A

In vegetation, carbon may be transferred among different pools or transformed into different organic compounds. For example, carbohydrates in the leaves may be transferred to stems and roots, or they can be transformed into more complex polymers, such as lignin and cellulose, that constitute structural growth. Similarly, carbon is also continuously transformed in the soils, from plant-derived compounds to microbe-derived organic acids (Ågren and Bosatta 1996; Gleixner 2013). These transfers and transformations imply that carbon gets transferred from one ecosystem pool to another, or in other words, it moves from one element to another of the vector $\boldsymbol{x}(t)$. The rates at which these transfers and transformations occur are represented as elements of the matrix **A** of the general model. This matrix contains only the value of −1 in the diagonal and the proportions at which carbon moves from one ecosystem pool to another in the off-diagonals.

15.3.5 Environmental Effects on Cycling Rates: $\xi(t)$

Cycling rates in ecosystems change on seasonal, annual and decadal time scales owing to changes in the environment, mostly caused by climatic fluctuations. Increasing temperature, for example, usually increases the rates of cycling in vegetation and soils (Ryan 1991; Davidson and Janssens 2006). Water deficits negatively affect plant and microbial growth, while excess water may create anoxic conditions in soils, negatively affecting plant and microbial physiology (Skopp et al. 1990).

Ecosystem models usually include functions that modify cycling rates (elements of the matrix **C**) based on changes in abiotic variables such as air temperature, soil moisture, vapour pressure deficit and so forth. In general, these functions are multiplicative and are expressed by the **scalar**

$$\xi(t) = \prod_i^n f_i\left(X_i(t)\right), \qquad (15.10)$$

where each $f_i(X_i(t))$ represents a function that takes as independent variable a time-dependent environmental variable $X_i(t)$. Each function produces a factor that indicates the proportion by which the environmental variable increases ($f_i(X_i(t)) > 1$) or decreases ($f_i(X_i(t)) < 1$) the cycling rates of the ecosystem pools.

15.4 Examples of Ecosystem Carbon Models

15.4.1 Simple Vegetation–Soil Model

The model in Fig. 15.1 can be represented using the general framework provided by Eq. 15.9. First, the dimension of the system needs to be defined, that is, how many entries are allowed in the vectors and matrices. In this particular case, the dimension of the system is 2, because there are only two carbon pools represented by two equations (Eqs. (15.3) and (15.4)). This means, then, that vectors will be of length 2 and our matrices will be of dimension 2 × 2.

Second, we define the vector $\boldsymbol{x}(t)$ as

$$\boldsymbol{x}(t) = \left(V(t), S(t)\right); \qquad (15.11)$$

therefore,

$$\frac{d\boldsymbol{x}(t)}{dt} = \begin{pmatrix} \frac{dV(t)}{dt} \\ \frac{dS(t)}{dt} \end{pmatrix}. \qquad (15.12)$$

Third, the first term of the right-hand side of Eq. 15.9, $U(t)\cdot\boldsymbol{b}$, is defined. In this case, photosynthetic inputs are assumed to stay constant over time, so $U(t) = P$, and the carbon allocation vector is defined as

$$\boldsymbol{b} = \begin{pmatrix} 1 \\ 0 \end{pmatrix} \qquad (15.13)$$

because the products of photosynthesis only enter directly into the vegetation pool. Now, the second term of the right-hand side of Eq. 15.9, $\xi(t) \cdot \mathbf{A} \cdot \mathbf{C} \cdot \boldsymbol{x}(t)$, is dependent on different pools and transfer rates. The proportion of transfer of carbon from vegetation to soil is given by the parameter α, so the matrix of transfer coefficients is given by

$$\mathbf{A} = \begin{pmatrix} -1 & 0 \\ \alpha & -1 \end{pmatrix}. \tag{15.14}$$

The coefficients determining the proportion of carbon leaving each pool determine the diagonal of the matrix

$$\mathbf{C} = \begin{pmatrix} c_1 & 0 \\ 0 & c_2 \end{pmatrix}, \tag{15.15}$$

so the multiplication between these two matrices results in

$$\mathbf{A} \cdot \mathbf{C} = \begin{pmatrix} -c_1 & 0 \\ \alpha c_1 & -c_2 \end{pmatrix}. \tag{15.16}$$

In this case, no climatic effects on the rates of carbon cycling are assumed; therefore, $\xi(t) = 1$. Putting this all together, the **two-pool ecosystem model** expressed in matrix form is given by

$$\frac{d\mathbf{x}(t)}{dt} = \begin{pmatrix} \frac{dV(t)}{dt} \\ \frac{dS(t)}{dt} \end{pmatrix} = P\begin{pmatrix} 1 \\ 0 \end{pmatrix} + \begin{pmatrix} -c_1 & 0 \\ \alpha c_1 & -c_2 \end{pmatrix}\begin{pmatrix} V(t) \\ S(t) \end{pmatrix}. \tag{15.17}$$

It is possible to recover the initial model in Eqs. (15.3) and (15.4) by performing the multiplication and addition of matrices and vectors.

15.4.2 Eight-Pool Model of Luo and Weng (2011)

Luo and Weng (2011) proposed an eight-pool model to simulate the observed C dynamics in a temperate forest in the state of North Carolina, USA (Fig. 15.3). The authors used data on carbon fluxes and stocks measured in this forest to parameterise the model. They found that the daily amount of photosynthetically fixed carbon (GPP) in this forest was $U = 3.37$ g C m^{-2} day^{-1}. The vector of carbon allocation in this model is given by **b**

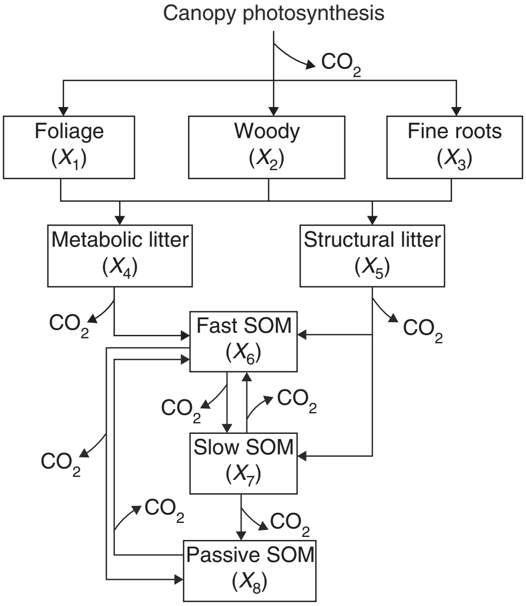


Fig. 15.3 Structure of Terrestrial Ecosystem Carbon Model (TECO). The structure represents flows through various pathways and partitioning to eight pools. The fraction to the plant pools is determined by partitioning the coefficient in vector ***b*** in Eq. 15.9. The fraction to litter and soil pools via each pathway is determined by the transfer coefficient matrix **A**. The values of vector ***b*** and matrix **A** are estimated from data collected in Duke Forest using a data assimilation approach (Weng and Luo 2011). The fraction of carbon from photosynthesis is large to plant pools and small to soil pools, particularly to the passive soil carbon pool

$$\boldsymbol{b} = \begin{pmatrix} 0.14 \\ 0.26 \\ 0.14 \\ 0 \\ 0 \\ 0 \\ 0 \\ 0 \end{pmatrix},$$

which shows that of all the photosynthetically fixed carbon, 14% is allocated to foliage, 26% to woody biomass and 14% to roots. Net primary production (NPP) in this case is the proportion of GPP that stays in the system, that is, NPP = $U(0.14 + 0.26 + 0.14) = 1.82\ \mathrm{g\ C\ m^{-2}\ day^{-1}}$.

Each pool in the model cycles at daily rates given by the matrix C

$$\mathbf{C}=\begin{pmatrix} 0.00258 & 0 & 0 & 0 & 0 & 0 & 0 & 0\\ 0 & 0.0000586 & 0 & 0 & 0 & 0 & 0 & 0\\ 0 & 0 & 0.00239 & 0 & 0 & 0 & 0 & 0\\ 0 & 0 & 0 & 0.0109 & 0 & 0 & 0 & 0\\ 0 & 0 & 0 & 0 & 0.00095 & 0 & 0 & 0\\ 0 & 0 & 0 & 0 & 0 & 0.0105 & 0 & 0\\ 0 & 0 & 0 & 0 & 0 & 0 & 0.0000995 & 0\\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.0000115 \end{pmatrix},$$

which shows the faster cycling rates in the metabolic litter ($1.09 \times 10^{-2}\ \mathrm{day^{-1}}$), the fast soil organic matter pools (e.g. labile organic matter such as fine roots, $1.05 \times 10^{-2}\ \mathrm{day^{-1}}$) and the slowest cycling rates in the passive SOM pool (e.g. recalcitrant organic matter such as woody debris of humic acids, $1.15 \times 10^{-5}\ \mathrm{day^{-1}}$) (Sect. 16.2 in Chap. 16).

The coefficients of the transfer and transformation matrix **A** are

$$\mathbf{A}=\begin{pmatrix} -1 & 0 & 0 & 0 & 0 & 0 & 0 & 0\\ 0 & -1 & 0 & 0 & 0 & 0 & 0 & 0\\ 0 & 0 & -1 & 0 & 0 & 0 & 0 & 0\\ 0.9 & 0 & 0.2 & -1 & 0 & 0 & 0 & 0\\ 0.1 & 1 & 0.8 & 0 & -1 & 0 & 0 & 0\\ 0 & 0 & 0 & 0.45 & 0.275 & -1 & 0.42 & 0.45\\ 0 & 0 & 0 & 0 & 0.275 & 0.296 & -1 & 0\\ 0 & 0 & 0 & 0 & 0 & 0.004 & 0.01 & -1 \end{pmatrix}$$

and show, for example, that 90% of the outputs from the foliage are transferred to the metabolic litter pool and 10% to the structural litter pool (fourth and fifth entries of the first column, respectively). Similarly, 45% of the outputs from the passive SOM pool are transferred to the fast SOM pool, while the slow SOM pool transfers 42% to the same fast SOM pool (sixth entries of the seventh and eight columns, respectively).

The behaviour of each pool over time can be obtained by solving the model numerically, that is, using some initial values of carbon storage in each pool and using the differential equation dx/dt to update the values of each pool at very small timesteps. Many methods can be used to compute numerical solutions, but a very accurate method is the **fourth-order Runge–Kutta method** (Soetaert and Herman 2009), which was used here to compute the time-dependent behaviour of the pools, assuming there is no carbon stored at the beginning of the simulation (Fig. 15.4). With this particular parameterisation, the model predicts accumulation of carbon up to a **steady-state** value for all pools, with larger storage in the woody biomass and the slow SOM pool and lower accumulation in the metabolic litter and the fast SOM pool.

As seen in the next section, all linear models, and therefore most ecosystem models, always reach a **steady-state carbon storage** where the inputs to each pool are equal to the outputs from them. Changes in the environment can either increase or decrease the steady-state carbon storage value depending on whether the environment increases or decreases the internal cycling rates.

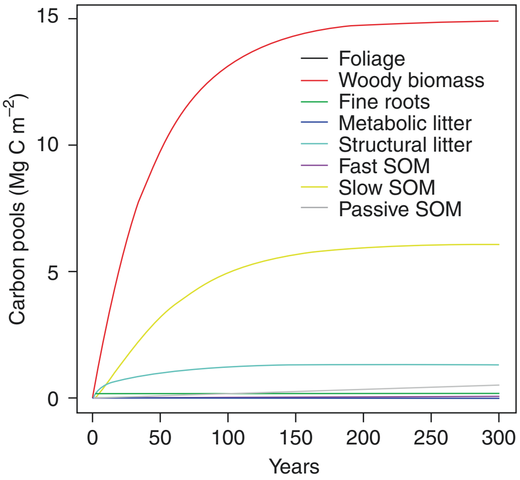
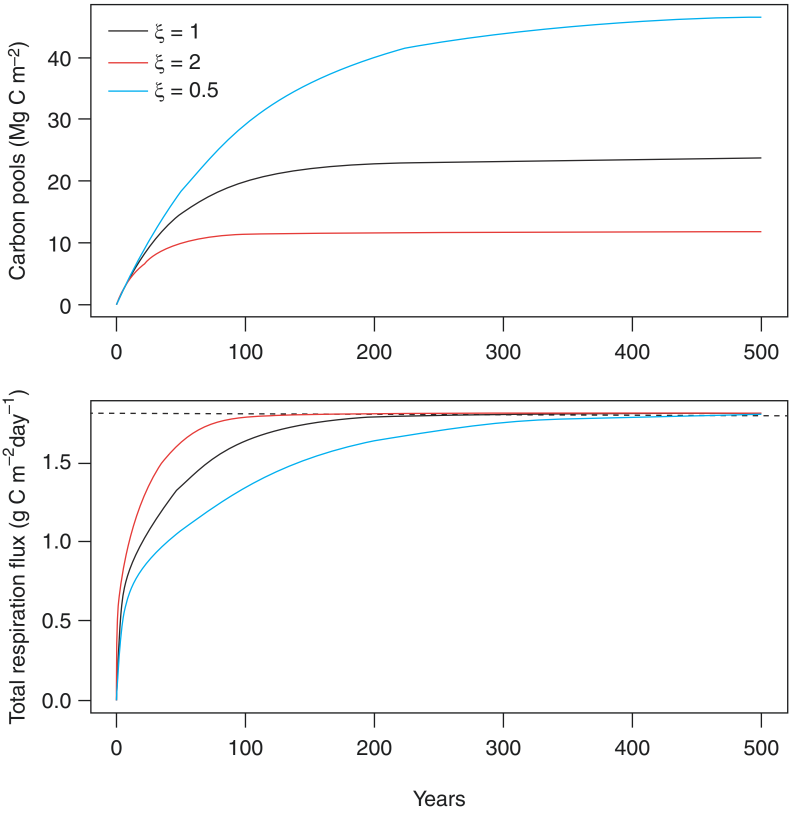


Fig. 15.4 Carbon accumulation in all ecosystem pools of the eight-pool model proposed by Luo and Weng (2011). The model is given by Eq. 15.9, with the parameterisation proposed by the authors (Sect. 15.2)

To explore the effects of the environment, two more simulations were run, in which the values of the elements in matrix **C** were either doubled or decreased by half. In other words, the effect of either doubling or reducing by half the rates of carbon flow out of the pools will be addressed. For example, changes in climate by 10 °C can double these rates, so this is a way to explore the effects of climate change on carbon storage and CO_2 exchanges with the atmosphere. This can be achieved by modifying the value of $\xi(t)$ in Eq. 15.9 (Fig. 15.5).

There are two important aspects to look at here: (1) decreasing the cycling rates increases the amount of carbon storage (e.g. as observed in boreal forests), while increasing the cycling rates decreases the amount of carbon storage (e.g. as observed in agricultural systems). In other words, carbon storage and cycling rates are inversely related; (2) as the cycling rates decrease, the amount of time required to reach equilibrium increases (Fig. 15.5). One can also gain important insights by studying the fluxes of respired

Fig. 15.5 Effects of environment on carbon pools and fluxes by doubling ($\xi = 2$) or halving cycling rates ($\xi = 0.5$) in the eight-pool ecosystem model proposed by Luo and Weng (2011). The upper panel shows the effect on carbon pools and the lower panel the effect on the total respiration flux



carbon: (1) All simulations converge to a constant respiration flux independent of the value of the cycling rates. Remember that at steady-state the outputs are equal to the inputs, and because in all cases the inputs are the same ($U \cdot \boldsymbol{b}$), the three simulations converge to a common value of 1.82 g C m^{-2} day^{-1}. (2) The time required to reach **equilibrium** depends on the value of the cycling rates. The lower the cycling rates, the longer it takes to reach equilibrium (Fig. 15.5).

15.5 Properties of Ecosystem Carbon Models

The properties observed in the 8-pool model can be generalised to most ecosystem models that conform to the structure of Eq. 15.9. Some of these simple mathematical concepts will be used below to explore these general properties of ecosystem models.

15.5.1 Role of Inputs and Cycling Rates on Ecosystem Carbon Storage

Assuming constant environmental conditions ($\xi(t) = 1$) and constant photosynthetic rates ($U(t) = U$), one can expect ecosystem models to reach a **steady-state**, in which the amount of inputs are equal to the outputs. From Eq. 15.9, the steady-state can be defined as

$$I = -\mathbf{D} \cdot \boldsymbol{x}, \tag{15.18}$$

where $\mathbf{D} = \mathbf{A} \cdot \mathbf{C}$, and $I = U \cdot \boldsymbol{b}$. The carbon stocks for each ecosystem pool at steady-state ($\boldsymbol{x}_{ss}$) can then be calculated by solving this equation as

$$\boldsymbol{x}_{ss} = -\mathbf{D}^{-1} \cdot I. \tag{15.19}$$

This simple equation shows that as the amount of photosynthetic inputs increases, the total amount of carbon that can be stored in steady-state increases as well, and as the cycling and transfer rates become faster, the capacity of carbon storage decreases. The effects of environmental change on carbon storage would depend then on how much the environment could modify photosynthetic rates $U(t)$ vs. cycling rates $\xi(t)$.

The **current generation of ecosystem models** focus on identifying how changes in atmospheric CO_2 concentration, nitrogen deposition, air temperatures and soil water status, among other factors, affect the rates of photosynthetic inputs, the allocation to different vegetation and soil pools, and the cycling rates in each pool. In other words, they evaluate how the environment modifies the elements of Eq. 15.9 and how they affect carbon storage capacity (Eq. 15.19). To investigate such dynamics of an ecosystem, it is important to start with reproducible steady-state conditions, which are reached after a (several centuries long) spin-up run, typically ending at pre-industrial conditions. In an actual modelling experiment, changes in the drivers are imposed, for example, anthropogenic disturbances or climate change, to learn how ecosystem processes are modified by changing environmental conditions. The comparison of different modelling experiments, i.e. runs, then allows the isolation of specific reactions to these drivers.

15.5.2 Residence and Response Times

A useful metric to compare ecosystem models is the concept of mean **transit time**, also known as mean **residence time**. It is defined as the average time a particle of carbon spends in a system since its time of entry (Eriksson 1971; Bolin and Rodhe 1973; Thompson and Randerson 1999; Manzoni et al. 2009). Residence times are computed only under an assumption of constant environmental conditions and steady-state (Eq. 15.19). For these linear time-invariant models, the output flux $O(t)$ can be calculated as

$$O(t) = \int_0^\infty \psi(T) I(t-T) dT, \tag{15.20}$$

where $\psi(T)$ is the residence time distribution. Under the assumption of an impulsive input, the **residence time distribution** is equal to the time evolution of the output flux, that is, $\psi(T) = O(t)$ (Thompson and Randerson 1999; Manzoni et al. 2009). Intuitively, this means that the transit or residence time distribution is equal to the time required to empty a system that is under steady-state and not subjected to external perturbations. The mean residence time therefore can be calculated as

$$\overline{\psi(t)} = \int_0^\infty t \cdot O(t)\, dt. \tag{15.21}$$

In practice, it is possible to calculate the residence time distribution by solving a model numerically with initial conditions at steady-state and an impulsive input. The model must be run for a period of time at least as long as the inverse of the smallest non-zero eigenvalue of matrix **D**.

The **eigenvalues** of matrix **D** in fact provide very interesting information about the rates of cycling and recovery of ecosystems after a perturbation. The **response time**, also called the **adjustment time**, of a system is defined as the time required for a system to attain steady-state conditions after a perturbation. Mathematically, it is defined as

$$\tau_{\text{cycle}} = \frac{1}{\min\left(\left|\lambda_i\right|\right)}, \tag{15.22}$$

where λ_i are the i eigenvalues of matrix **D**.

For example, the inverse of the eigenvalues of matrix **D** in the eight-pool model studied previously is given by

$$\frac{1}{|\lambda|} = \begin{pmatrix} 91.7 \\ 95.1 \\ 387.6 \\ 418.4 \\ 1052.6 \\ 11487.6 \\ 17064.8 \\ 87292.6 \end{pmatrix} \tag{15.23}$$

in units of days. Therefore, the response time of the eight-pool model is 87′292.6 days, or 239 years.

15.5.3 Disturbance Effects

Disturbances such as fires, windthrows or massive herbivory remove a significant part of the carbon stored in an ecosystem (Chap. 13). During these events, most but not all carbon is removed from the vegetation component (“slow in, rapid out”) (Körner 2003). A portion of the remaining carbon is left *in situ*, where it decomposes and may get transferred to the soil (Janisch and Harmon 2002). If the ecosystem does not suffer a major change in nutrient stocks or vegetation composition, it may return to the same equilibrium point if left to recover for a sufficient amount of time. In other words, if the elements of the vector I or the matrix **D** do not change, the ecosystem will reach the same steady-state $\boldsymbol{x}_{\text{ss}}$ after a disturbance event (Eq. 15.19).

Long-term carbon storage, however, can be affected dramatically even when I or **D** does not change but the frequency of disturbance events changes. Under frequent disturbances that do not allow enough time for the ecosystem to recover, long-term carbon storage would be reduced proportionally to the time between disturbances (Harmon et al. 1990; Harmon 2001; Luo and Weng 2011). As an example, let us consider the eight-pool model studied previously. An ecosystem can recover after a disturbance in about 239 years, so if disturbance events occur at 250-year intervals, the ecosystem has enough time to recover its total stock of carbon and reach the same steady-state value as the undisturbed system (Fig. 15.6). However, if disturbance events occur more frequently, the ecosystem cannot reach the steady-state value of the undisturbed condition and therefore would store, on average, less carbon in the long-term (Fig. 15.6).

Although in real ecosystems the recovery patterns may differ substantially from the patterns shown here, this mathematical analysis helps in formulating hypotheses, in predicting future responses of ecosystems to changing environments and thus in understanding the possible set of behaviours to be expected from an ecosystem, as represented by the model. Furthermore, the model can help in understanding possible changes in ecosystem carbon pools due to changes in disturbance

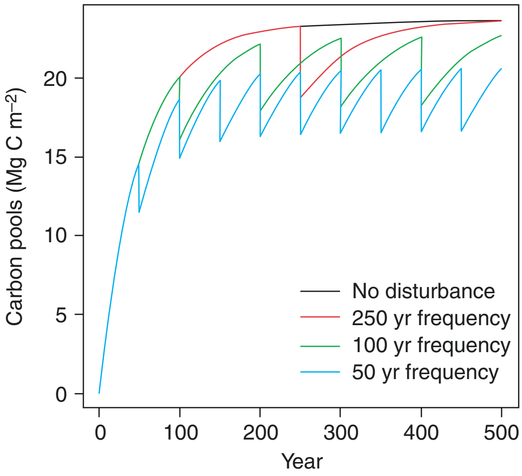


Fig. 15.6 Simple example of how frequent disturbance events affect long-term carbon storage in ecosystems. As the frequency of disturbances increases, the long-term average carbon stock decreases. In each simulation, the disturbance event removes 30% of the carbon stored in the foliage, woody biomass and metabolic litter pools

regimes and how disturbances shape the structure of natural landscapes.

In addition to carbon storage, disturbances related to natural processes (e.g. wind, fire, pests) as well as to human activities introduce a large degree of heterogeneity in forest landscapes. Each patch of forest that is subject to a disturbance event will recover by processes of natural regeneration and will accumulate biomass until the next disturbance event. The forest landscape can thus be thought of as a collection of patches of different sizes that are recovering from previous disturbances. Each patch may have different ages after the previous disturbance event, and the frequency of these different events may vary dramatically over space and time. This idea of a heterogeneous landscape was introduced by the concept of the “**shifting mosaic steady-state**” proposed by Bormann and Likens (1979). This concept helps one to understand the spatial and temporal heterogeneities of an ecosystem’s structure and function as shaped by disturbances.

For example, in tropical forests, a large heterogeneity in forest growth is usually observed in field surveys, and it is challenging to attribute long-term patterns of ecosystem function to particular predictors. Using an ecosystem model, Chambers et al. (2013) were able to attribute variability in tree growth and mortality to different sources of disturbance events for the Amazon region. Their analysis used an approach similar to the multiple simulations in Fig. 15.6, but repeated thousands of times over a 100-ha area. Chambers et al. (2013) could show how patterns of growth and mortality studied under the framework of the shifting mosaic steady-state gave better insights into ecosystem responses to climate change than previous analyses that did not consider disturbance-related heterogeneity.

Analysing the effects of disturbances on ecosystem processes with models also provides important insights for policy analysis. For instance, in the Pacific Northwest region of the USA, changes in forest management policies in the early 1990s led to significantly decreasing levels of timber harvest and increasing rotation lengths (times between successive harvests). Using an ecosystem carbon model, Krankina et al. (2012) were able to predict net increases in carbon pools for the entire region (4.3 million ha) due to the implementation of this new forest protection policy. This example shows how an ecosystem model helps to understand not only the dynamics of the system over time but also the effects of human actions and their policies on ecosystem properties.

Summary

- Mathematical models are used to conceptualise ecosystem processes and predict responses to changing environmental conditions. Depending on their scientific purpose, they include water, carbon, nutrient and energy fluxes and the competitive behaviour of individual organisms or organism groups.
- Ecosystem models are classified based on one main attribute and normally categorised in dichotomies. These can be, for example, empirical vs. mechanistic or static vs. dynamic but also qualitative vs. quantitative or global vs. regional.
- The five main classes of models are physiological, biogeochemical, gap, biogeophysical and dynamic global vegetation models.
- Ecosystem models are based on the principle of mass balance, that is, the balance of inputs

and outputs. Outputs can also be described as a fraction of a system's pools. The number of pools defines the dimension of the model.

- Models are commonly represented as vectors and matrices. Vectors describe pool sizes and partitioning rates, whereas matrices describe transfer rates and residence times between pools.
- Ecosystem models represent important tools that make it possible to attribute the variability of ecosystem responses to different sources of disturbance and change. Models thus allow for the formulation of hypotheses about future ecosystem behaviour and the consequences of changes in disturbance regimes, for example, due to a policy change.

References

Ågren GI, Andersson FO (2012) Terrestrial ecosystem ecology: principles and applications. Cambridge University Press, Cambridge

Ågren GI, Bosatta E (1996) Theoretical ecosystem ecology: understanding element cycles. Cambridge University Press, Cambridge

Ågren GI, McMurtrie RE, Parton WJ, Pastor J, Shugart HH (1991) State-of-the-art of models of production-decomposition linkages in conifer and grassland ecosystems. Ecol Appl 1:118–138

Bolin B, Rodhe H (1973) A note on the concepts of age distribution and transit time in natural reservoirs. Tellus 25:58–62

Bormann F, Likens G (1979) Pattern and process in a forested ecosystem: disturbance, development and the steady state based on the Hubbard Brook ecosystem study. Springer, New York

Botkin DB, Janak JJ, Wallis JR (1972) Some ecological consequences of a computer model of forest growth. J Ecol 60:849–872

Bugmann H (2001) A review of forest gap models. Clim Chang 51:259–305

Canham CD, Cole JJ, Lauenroth WK (eds) (2003) Models in ecosystem science. Princeton University Press, Princeton

Chambers JQ, Negron-Juarez RI, Marra DM, Di Vittorio A, Tews J, Roberts D, Ribeiro GHPM, Trumbore SE, Higuchi N (2013) The steady-state mosaic of disturbance and succession across an old-growth central Amazon forest landscape. Proc Natl Acad Sci 110:3949–3954

Davidson EA, Janssens IA (2006) Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. Nature 440:165–173

Eriksson E (1971) Compartment models and reservoir theory. Annu Rev Ecol Syst 2:67–84

Farquhar GD, Caemmerer S (1982) Modelling of photosynthetic response to environmental conditions. In: Lange OL, Nobel PS, Osmond CB, Ziegler H (eds) Physiological plant ecology II. Water relations and carbon assimilation. Encyclopedia of Plant Physiology, New series, Vol 12B. Springer, Berlin. pp 549–587

Farquhar GD, Caemmerer S, Berry JA (1980) A biochemical model of photosynthetic CO_2 assimilation in leaves of C_3 species. Planta 149:78–90

Franklin O, Johansson J, Dewar RC, Dieckmann U, McMurtrie RE, Brännström A, Dybzinski R (2012) Modeling carbon allocation in trees: a search for principles. Tree Physiol 32:648–666

Gleixner G (2013) Soil organic matter dynamics: a biological perspective derived from the use of compound-specific isotopes studies. Ecol Res 28:683–695

Harmon ME (2001) Carbon sequestration in forest: addressing the scale question. J For 99:24–29

Harmon ME, Ferrell WK, Franklin JF (1990) Effects on carbon storage of conversion of old-growth forests to young forests. Science 247:699–702

Huston AM, Smith T (1987) Plant succession: life history and competition. Am Nat 130:168–198

Janisch JE, Harmon ME (2002) Successional changes in live and dead wood carbon stores: implications for net ecosystem productivity. Tree Physiol 22:77–89

Jones HG (1992) Plants and microclimate: a quantitative approach to environmental plant physiology. Cambridge University Press, Cambridge

Kleidon A, Mooney HA (2000) A global distribution of biodiversity inferred from climatic constraints: Results from a process-based modelling study. Glob Change Biol 6:507–523

Körner C (2003) Slow in, rapid out—Carbon flux studies and Kyoto targets. Science 300:1242–1243

Krankina ON, Harmon ME, Schnekenburger F, Sierra CA (2012) Carbon balance on federal forest lands of western Oregon and Washington: the impact of the Northwest Forest Plan. For Ecol Manag 286:171–182

Luo Y, Weng E (2011) Dynamic disequilibrium of the terrestrial carbon cycle under global change. Trends Ecol Evol 26:96–104

Malhi Y, Doughty C, Galbraith D (2011) The allocation of ecosystem net primary productivity in tropical forests. Philos Trans R Soc B 366:3225–3245

Manzoni S, Katul GG, Porporato A (2009) Analysis of soil carbon transit times and age distributions using network theories. J Geophys Res 114:G04025

Moorcroft PR, Hurtt GC, Pacala SW (2001) A method for scaling vegetation dynamics: The ecosystem demography model (ED). Ecol Monogr 71:557–585

Pastor J (2008) Mathematical ecology of populations and ecosystems. Wiley-Blackwell, Chichester

Pavlick R, Drewry DT, Bohn K, Reu B, Kleidon A (2013) The Jena diversity-dynamic global vegetation model (JeDi-DGVM): a diverse approach to representing terrestrial biogeography and biogeochemistry based on plant functional trade-offs. Biogeosciences 10:4137–4177

Reynolds JF, Chen J (1996) Modelling whole-plant allocation in relation to carbon and nitrogen supply: coordination versus optimization: opinion. Plant Soil 185:65–74

Rodhe H (2000) Modeling biogeochemical cycles, Vol 72. Academic Press, Cambridge, USA

Ryan MG (1991) Effects of climate change on plant respiration. Ecol Appl 1:157–167

Schulze ED, Schilling K, Nagarajah S (1983) Carbohydrate partitioning in relation to whole plant production and water use of *Vigna unguiculata* (L.) Walp. Oecologia 58:169–177

Shugart HH (2002) Forest gap models. Volume 2: the earth system: biological and ecological dimensions of global environmental change. John Wiley & Sons, Ltd., Chichester

Sierra CA, Harmon ME (2008) Effects of processes at the population and community level on carbon dynamics of an ecosystem model. Available from Nature Proceedings, http://hdl.handle.net/10101/npre.2008.1918.1

Sierra CA, Harmon ME, Perakis SS (2011) Decomposition of heterogeneous organic matter and its long-term stabilization in soils. Ecol Monogr 81:619–634

Skopp S, Jawson MD, Doran JW (1990) Steady-state aerobic microbial activity as a function of soil water content. Soil Sci Soc Am J 54:1619–1625

Soetaert K, Herman PMJ (2009) A practical guide to ecological modelling: using R as a simulation platform. Springer, Dordrecht

Thompson MV, Randerson JT (1999) Impulse response functions of terrestrial carbon cycle models: method and application. Glob Change Biol 5:371–394

Weng E, Luo Y (2011) Relative information contributions of model vs. data to short- and long-term forecasts of forest carbon dynamics. Ecol Appl 21:1490–1505

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Biogeochemical Fluxes in Terrestrial Ecosystems

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Most element cycles in ecosystems are open, that is, gains and losses can occur, particularly of water, carbon and nitrogen. At the scale of landscapes, resources are often imported and exported from one ecosystem to another. The export of soluble organic carbon from boreal pine forest soils in Siberia in the form of humic and fulvic acids, which co-transport heavy metals, can be clearly seen in the “browning” of the creeks and rivers, transporting the dissolved organic carbon (DOC) from these freshwater systems to the ocean. The river shown here is the Dubces, a tributary of the Yenisei in Siberia. (Photo: E.-D. Schulze).

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Many definitions of biogeochemistry exist (e.g. Schlesinger 1990; Chapin et al. 2002), but here we consider **biogeochemistry** as the scientific study of the chemical, physical, geological and biological processes that govern the composition of the natural environment and the cycles of matter, chemical elements and energy in time and space. Thus, biogeochemistry includes the atmosphere, biosphere, pedosphere, hydrosphere, cryosphere and lithosphere. Often emphasis is placed on the study of water, carbon, nitrogen and phosphorus cycles. Biogeochemistry is a **systems science,** closely related to systems ecology (Chap. 13). The Ukrainian scientist **Vladimir Vernadsky** is often regarded as the founder of biogeochemistry as a science, since his 1926 book *The Biosphere* considered the physics of the Earth as a living whole.

Many different approaches are used to describe and quantify **biogeochemical cycles**, from observations to experiments and models (Chaps. 14 and 15). Research can be process-oriented, for example, studying decomposition or evapotranspiration, or oriented towards ecosystem budgets, for example, quantifying N inputs (atmospheric N deposition and N fertilisation) as well as N outputs (N leaching, gaseous N losses and harvests). Some of these cycles are of particular interest to multiple disciplines, such as ecology and atmospheric science, as certain processes within such biogeochemical cycles produce **greenhouse gases**. These gases, most importantly **CO_2, CH_4** and **N_2O**, are released to the atmosphere where their radiative forcing contributes to anthropogenic climate change (Chap. 21). Biogeochemical processes can be driven by abiotic factors, such as UV degradation of organic matter or weathering, but also by organisms, such as earthworms contributing to organic matter mineralisation or plants fixing CO_2 and symbiotic bacteria fixing N_2. Interactions between autotrophic and heterotrophic organisms within an ecosystem are key to biogeochemical cycles, for example, in the rhizosphere (Chap. 11). Similarly, coupled processes, for example, the release of C, N and other nutrients during plant litter degradation, combine various namely, plants, animals and microorganisms.

16.1 Water Fluxes in Terrestrial Ecosystems

16.1.1 Water Budget at Ecosystem Scale

Water flows through ecosystems, is stored only to a small degree in the soil profile, and leaves the ecosystem, either as water or water vapour. Thus, it is more appropriate to speak of a **water budget** than of a water cycle at the ecosystem scale. The ecosystem gains water via **precipitation** (rain, snow, fog, dew, rime and hail, adding up to total precipitation). Water reaches the ground below a plant canopy as throughfall or as stemflow (Fig. 16.1). **Throughfall** is defined as the sum of precipitation reaching the soil, that is, precipitation that either falls through canopy gaps or is intercepted by foliage, and what is not evaporated from these surfaces drips down leaves or needles (**leaf drip**). Throughfall is larger in open canopies and smaller in dense canopies because foliage, branches and stems intercept precipitation water (**interception**), of which a fraction evaporates and never reaches the ground. Interception by deciduous forests is typically much smaller than that by coniferous and evergreen forests (15–25% vs. 27–66%, respectively) (Fig. 16.1) owing to their clumped needle arrangements and long foliage presence throughout the year. **Stemflow** is higher for trees with smooth barks and a funnel-shaped crown architecture (such as beech, *Fagus* spp.) compared to trees with rough barks and irregularly shaped crowns (such as oak, *Quercus* spp.). Thus, throughfall is the difference between **bulk precipitation** (measured above the canopy or in the open), stemflow and interception (evaporation from plant surfaces), measured by rainfall collectors placed on the ground, stratified by canopy cover (accounting for gaps as well). The structure of the vegetation may modify the water input, for example, by "stripping" water from ground-reaching clouds (i.e. **fog**) via increased above-ground surface area that can intercept fog droplets. Examples are the laurel forests in Tenerife, which depend to a large extent on water harvested from clouds, or the tropical montane cloud forests in Puerto Rico. In *Sequoia semper-*

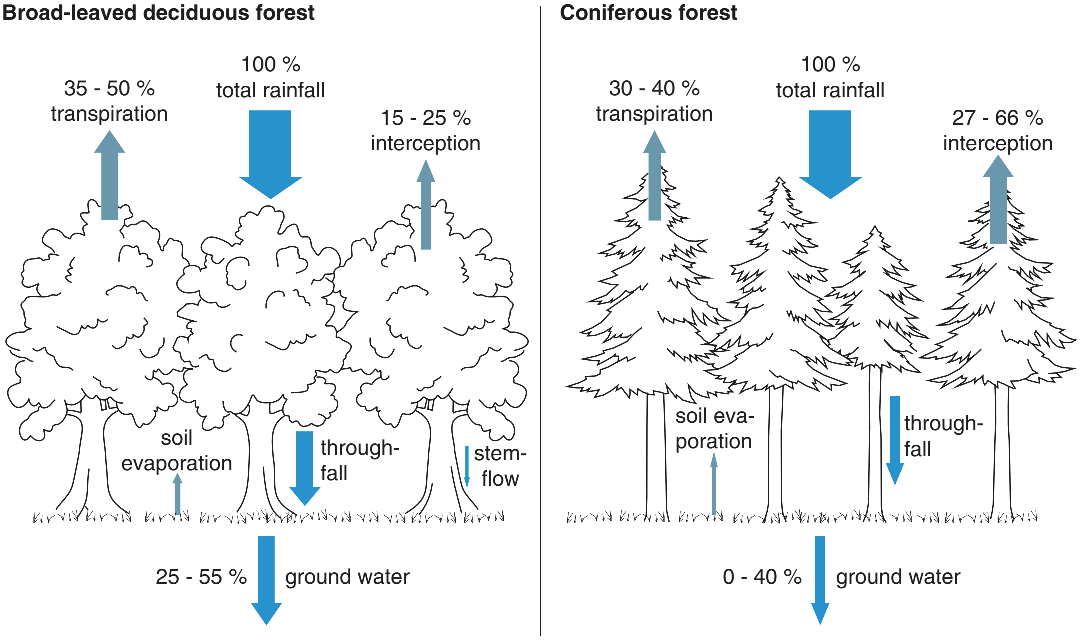


Fig. 16.1 Water fluxes in terrestrial ecosystems. Water enters the ecosystem as precipitation or as lateral water flow (not shown), is intercepted by the canopy, and reaches the ground via stemflow and throughfall. Water leaves the ecosystem via run-off (not shown), infiltrates into the soil, contributing to seepage and groundwater recharge, but also leaves as water vapour via transpiration and evaporation

virens (coastal redwood) forests in Northern California, 34% of the annual water input is due to fog drip, contributing 19% of transpired water during summer for large trees (Dawson 1998). Depending on how bulk precipitation is defined or where it is measured (above the canopy or in the open over low vegetation), interception can lead to water losses (relative to total precipitation measured above the canopy) or to water gains (relative to precipitation measured over low vegetation, which does not strip out fog). Moreover, ecosystems lose water by **run-off** and **infiltration** into the ground, contributing to seepage into the groundwater or river discharge, but also as water vapour lost to the atmosphere via **evaporation** from wet surfaces and via **transpiration** from plant foliage (Chaps. 9 and 10).

The **hydrological balance** can be described as follows:

$$P - E - F - \Delta S = 0, \tag{16.1}$$

where P denotes total precipitation, E evapotranspiration, F run-off and seepage, and ΔS change in soil water storage. Often, ΔS is considered zero and therefore omitted from this equation (Eq. 10.1, Chap. 10).

The water budget is positive if $P > E + F + \Delta S$, for example, in areas with high rainfall. It is negative if $P < E + F + \Delta S$, for example, when P is completely used by E or if E is fed by supplies other than P, such as **irrigation**. Spatially as well as temporally, the hydrological budget is highly variable, but on average, as much as 60% of total terrestrial precipitation is returned to the atmosphere by ecosystem evapotranspiration (Oki and Kanae 2006; Williams et al. 2012) (Chap. 10).

Understanding the partitioning of precipitation into evapotranspiration and run-off/seepage processes is one of the challenges in **ecohydrology**, since not only climate but also land cover (e.g. forest, grassland, cropland, urban area) and land use (e.g. crop rotation, intensive agriculture, extensive grazing), and thus terrestrial ecosystems, strongly affect this partitioning. Using the **concept of Budyko** (1974) (Fig. 16.2), one can separate the climatic radiative effect (driven by net radiation) from the land surface evaporative effect (driven by precipitation) and, thus, study the impacts of ecosystem characteristics. This makes it possible to compare effects for different vegetation and ecosystem types, but also to study impacts of inter- and intraseasonal variations. Plotting the ratio of mean annual **(actual) evapotranspiration** E and total precipitation P (E/P; also called the evaporative index, EI) versus the ratio of **potential evapotranspiration** E_p and total precipitation P (E_p/P; also called the dryness index, DI) results in the Budyko space. In theory, two profound upper limits can be hypothesised: the supply limit where evapotranspiration equals precipitation (horizontal line in Fig. 16.2) and the demand limit where actual evapotranspiration (controlled by meteorological conditions and ecophysiology) equals potential evapotranspira-

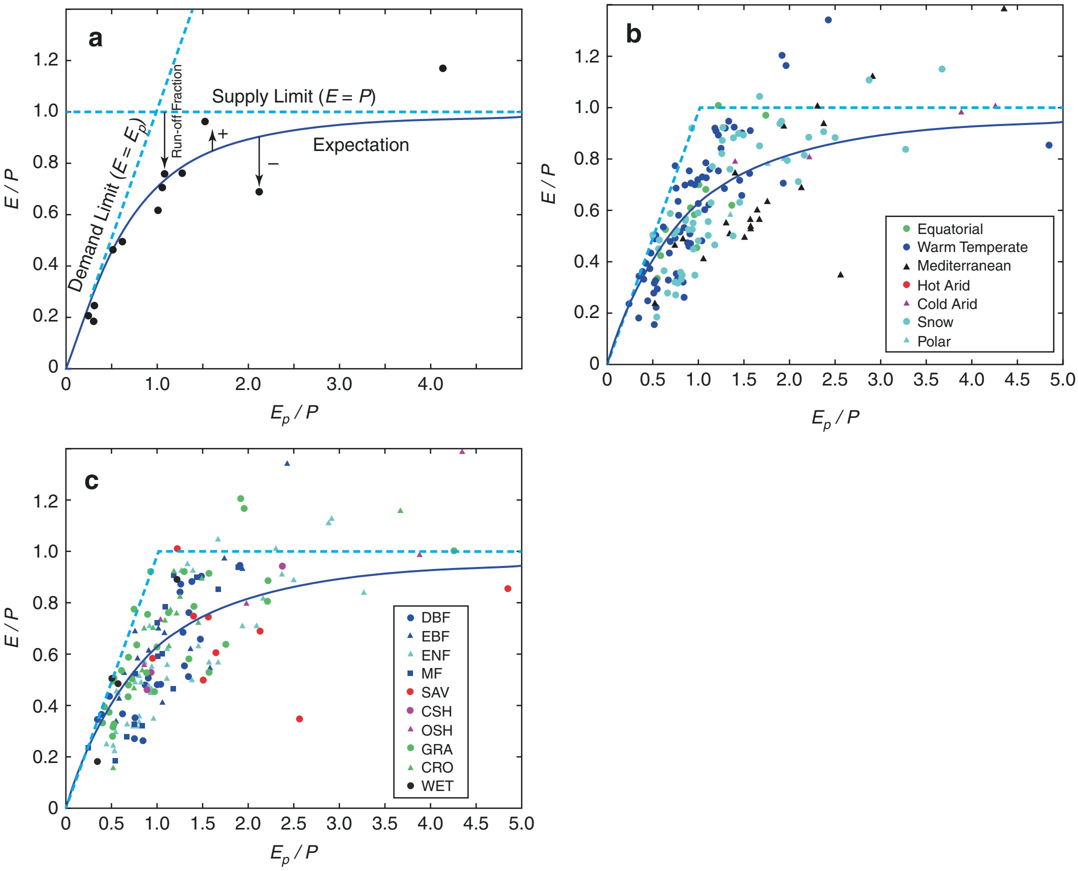


Fig. 16.2 Budyko concept. **a** Based on annual data for precipitation (P), potential evapotranspiration (E_p) and actual evapotranspiration (E), one can separate the radiative effect (driven by net radiation) from the evaporative effect (driven by precipitation) on ecosystem water vapour fluxes. The dashed lines represent the demand ($E = E_p$) and supply ($E = P$) limits. The black line represents expected ecosystem water vapour fluxes. The vertical arrows depict deviations from the expected value (plus or minus). The arrow from the supply limit line to the actual data point (i.e. the term $1 - E/P$) shows the percentage run-off and seepage relative to precipitation for this site. **b** Data from 167 ecosystem sites covering different climate types and **c** different ecosystem types across the globe are shown. The dashed lines in **b** and **c** represent the demand and supply limits. *DBF* deciduous broadleaf, *EBF* evergreen broadleaf, *ENF* evergreen needleleaf, *MF* mixed forest, *SAV* savanna including woody savanna, *CSH* closed shrubland, *OSH* open shrubland, *GRA* grassland, *CRO* cropland, *WET* wetland. (Modified from Williams et al. (2012))

tion E_p (controlled only by meteorological conditions). Here, E_p is defined as evapotranspiration by an ecosystem fully supplied with water to fulfil meteorological demands (calculated by Penman-Monteith; see following discussion). However, there exist many different definitions of $E_{p,}$ for example, evaporation from open water, and many ways to calculate E_p, for example, only taking temperature into account, adding wind speed or vapour pressure deficits. Here, exceeding $E_p/P = 1$ indicates an ecosystem water deficit at annual time scales, while the term $1 - E/P$ quantifies the annual run-off or seepage in any given ecosystem.

Based on 167 ecosystem flux sites (Sect. 14.1, Chap. 14) and 764 site-years, about 93% of all the sites were found to be at or below the demand and supply limits (Fig. 16.2b, c). The remaining 7% were outside the theoretical limits (e.g. more water used for evapotranspiration than supplied via precipitation), most likely owing to measurement biases (Chap. 14) and changes in soil water storage (which is assumed to be zero in the Budyko concept) (Williams et al. 2012). About 62% of the variation in E/P across sites, that is, the fraction of precipitation returned to the atmosphere by evapotranspiration, was driven by **net radiation** (energy-driven), and an additional 13% was explained by climate and vegetation types (physiology-driven). This showed that despite the **dominance of radiative controls** on E, further vegetation type-related controls on E must be included in models of water fluxes. Interestingly, grasslands had on average a higher E/P (65%) than forest ecosystems: E/P of 56% for **deciduous** broadleaf forests (DBF) and 63% for **evergreen** needleleaf forests (ENF) (Fig. 16.2c), quite similar to **croplands** (E/P of 69%). This is consistent with measured leaf transpiration rates (Larcher 2003) and various strategies observed for grasses vs. trees on how to deal with water stress (Chap. 10, Fig. 10.16). However, this contrasts with the better coupling of forests (leading to higher E), with trees having deeper root systems and, thus, access to deeper soil depths (with more water; but Chap. 10, Fig. 10.12) and maybe higher leaf area index (LAI) than **grasslands**.

16.1.2 Water Uptake of Trees

All plants need water to survive, for evapotranspiration as well as to maintain their turgor and to grow (Chap. 10). **Plant water uptake** is typically via the roots from the soil, although some plant species also rely on **fog**, for example, in deserts and montane cloud forests, not only epiphytes. Identifying and quantifying plant water uptake based on the distribution of roots is difficult for two reasons:

- The presence of **roots** at a certain depth does not necessarily mean that roots take up water at this depth (Chap. 10).
- Not all roots found in the soil are physiologically active.
- Assigning roots, particularly fine roots, to different species when studying a plant community is almost impossible. Genetic analyses have been used to determine the species, after roots have been dug out of the soil, but this approach is very laborious and expensive. More recently, near-infrared analyses of dried root material have been used to determine species identity, but this approach has a high uncertainty.

An alternative approach is to use stable isotopes of water, either **oxygen** or **hydrogen isotope ratios** ($\delta^{18}O$ or $\delta^{2}H$, respectively), to determine the soil **water source** or the **rooting depth** of water uptake. However, since precipitation changes its isotopic signature seasonally (Fig. 16.3), due to changes in temperature, atmospheric water vapour pressure and origin of air masses (Gat 1996), frequent sampling and hydrological modelling of the isotope ratios in soil water will best account for the biogeochemical variations of this important plant resource. Since no isotope fractionation takes place during root water uptake, isotope ratios in xylem water reflect the total soil water uptake of a plant. Non-transpiring tissues need to be sampled for these measurements, that is, root collars (Barnard et al. 2006), branches or twigs (Ehleringer et al. 2000), to avoid **evaporative enrichment**: During evaporation, lighter water molecules evaporate faster, so the remaining water pool becomes enriched in the heavier isotopes and no longer reflects the original water source. In a mixed forest, oxygen stable isotope ratios in soil water follow the precipitation inputs with some time lags, particularly in deeper soil layers, while the isotopic signatures in xylem water of temperate tree species show a pronounced seasonal course, but species also differ (Fig. 16.3).

Mixing of existing water pools in the soil profile with rain infiltrating into the soil depends on the soil structure, soil moisture content and precipitation regime. Based on these variables, the **mean residence time of water** at a particular soil depth can be modelled (Fig. 16.4). Such models account for **preferential flow** through macro

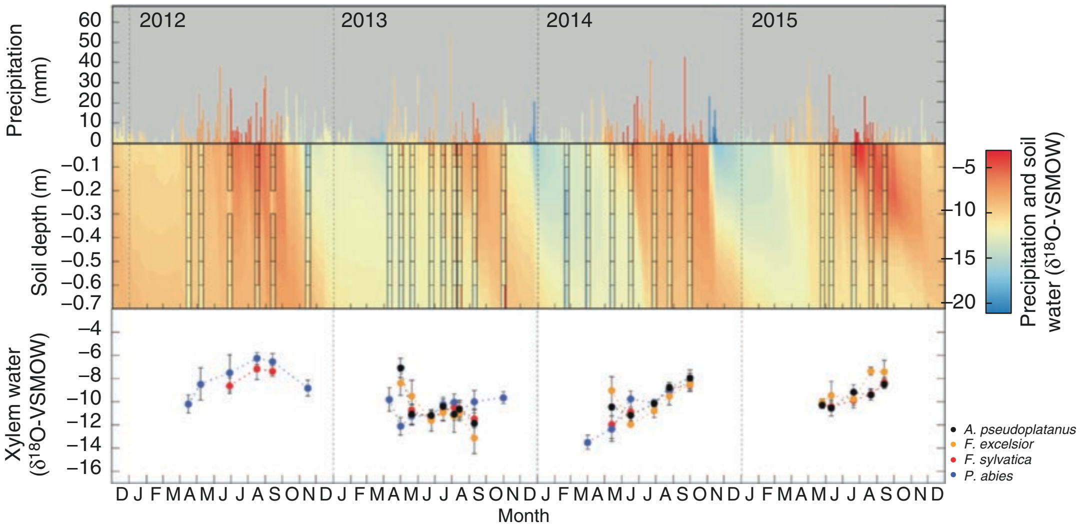


Fig. 16.3 Stable isotope ratios of oxygen in precipitation, soil water and xylem water. Oxygen isotope ratios were analysed with an isotope ratio mass spectrometer in precipitation samples, soil water of eight different depths, and in xylem water of four dominant tree species (*Fagus sylvatica, Picea abies, Fraxinus excelsior, Acer pseudoplatanus*) in a mixed forest (Lägeren, Switzerland) over 4 years. Coloured areas along the soil profiles were modelled using a soil hydraulic model. (Data from Brinkmann 2016)

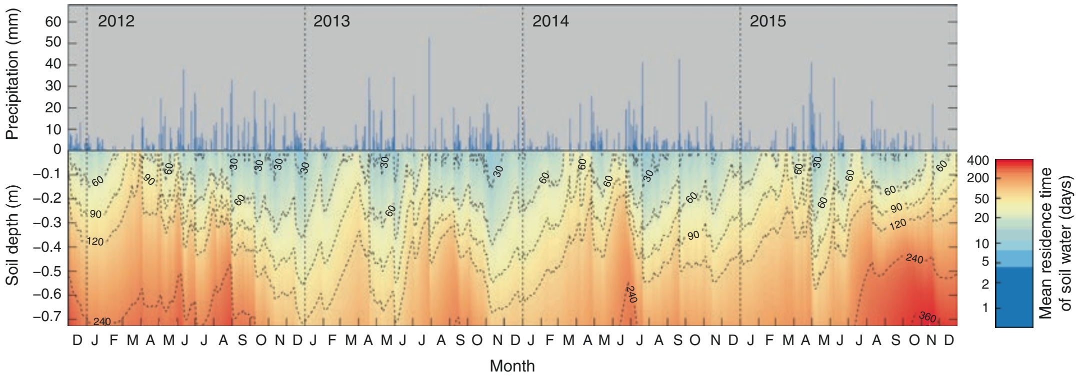


Fig. 16.4 Precipitation and mean residence time of soil water. Precipitation was collected in a mixed forest (Lägeren, Switzerland) over 4 years. Mean residence time of soil water at 0–0.8 m soil depth was modelled using a soil hydraulic model based on oxygen isotope ratio measurements. The colour scale indicates the mean residence time of soil water at a given depth. Dashed lines indicate the mean residence time of soil water at 30, 60, 120, 240 and 360 days. (Data from Brinkmann 2016)

pores (e.g. earthworm casts, root channels, cracks), which can lead to very high flow rates (within days). The "age" of water is higher at greater depths in the soil profile, and mean residence times can reach more than 1 year at a depth of 0.8 m. At more shallow depths, the impact of current precipitation is prevalent, and water pools mix over a period of about a month. Combining this information with the isotopic signatures of xylem water shows that *P. abies* takes up water from more shallow soil depths, while *F. sylvatica*, *A. pseudoplatanus* and *F. excelsior* take up water from deeper horizons. Since soil water is the ultimate pool to supply water for tree transpiration, **susceptibility** to short dry spells or **droughts** will also differ among these species (all other drivers for evapotranspiration being equal) (Sect. 16.1.3).

16.1.3 Evapotranspiration at Canopy and Ecosystem Scales

Evapotranspiration of ecosystems is both energy-driven and physiology-driven, as shown in the preceding section. Different processes are involved: transpiration via stomata and evaporation from surfaces. Ecosystem water vapour fluxes are thus composite fluxes since **evapotranspiration** can also originate from different surfaces: from soils and from vegetation (wet leaves, branches and stems). Sometimes a different partitioning method is used, canopy vs. sub-canopy layer, with the latter including soil and understorey vegetation. This means that attention needs to be paid to distinguishing different units (water vapour flux in mmol per m^2 leaf area or per m^2 ground area) and different spatial scales (leaf, soil, canopy, ecosystem; for leaf transpiration, Chap. 10).

The **energy budget equation** (also Eq. 9.4 in Chap. 9)

$$R_n = H + \lambda E + G \tag{16.2}$$

links the turbulent fluxes of latent (λE) and **sensible heat** ($H = \rho\, c_p\, G_H\, \Delta T$) (Chap. 9) to net radiation R_n, which, ultimately, is the energy input from the Sun that drives both turbulent fluxes and soil heat flux G. The flux of water from the ecosystem depends primarily on the energy that is available for vaporizing water, but H and λE are also substantially affected by turbulent conditions.

Since energy and water vapour fluxes are tightly coupled, evapotranspiration can be expressed as water vapour flux E in mm year^{-1} or mmol m^{-2} s^{-1} (or any other time unit), but also as **latent heat flux** λE in W m^{-2} (Fig. 16.5). This has the advantage that many energy-related and plant-related factors can be considered, such as

- Available solar energy for supplying the energy needed for the vaporisation of water.
- Precipitation input, water vapour pressure deficit of air, soil moisture, soil structure, supplying water and controlling water uptake.
- Roughness of surface (soil, canopy, ecosystem), which determines the coupling of the canopy to the atmosphere.
- Ecosystem structure, for example, fraction of bare soil, stand architecture, LAI, affecting energy budget of the ecosystem.
- Plant structural variables such as leaf area, and the leaf angle, affecting the absorption of incoming radiation.
- Leaf ecophysiology such as leaf conductance
- Spectral characteristics of surfaces, which determine the sensible heat flux.

The leaf-scale equation to describe **leaf transpiration** E_L (Chap. 10, Eq. 10.17) only accounted for two of these factors, namely stomatal conductance g_S and water vapour pressure deficit between leaf and air D_L. However, D_L is in turn dependent on E_L since higher transpiration rates humidify the air around the leaf. To account for this feedback (and others), the so-called **Penman-Monteith equation** (Eq. 16.3) describes evapotranspiration as energy flux, that is, as latent heat flux λE (in W m^{-2}) (Monteith 1965). The derivation of the equation is explained in Jones (2014). The latent heat flux of a terrestrial ecosystem depends on net radiation R_n (above canopy level) (Fig. 16.6), soil heat flux G, with $R_n - G$ also being called **available energy**, water vapour pressure deficit of air D, and the total conductances for water vapour G_w and for

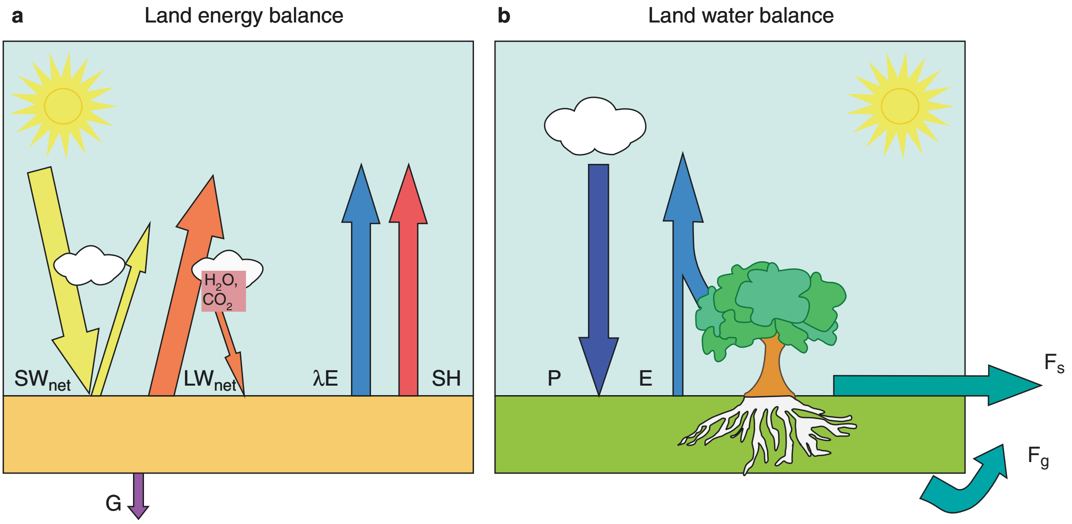


Fig. 16.5 Evapotranspiration as coupled energy and water flux. Energy **a** and water **b** fluxes are tightly coupled since the evaporation of water needs energy. SW_{net} = net shortwave radiation ($SW_{in} - SW_{out}$), LW_{net} = net longwave radiation ($LW_{in} - LW_{out}$), H_2O = atmospheric water vapour, CO_2 = atmospheric CO_2. For simplicity other greenhouse gases are not shown in the figure. SH = sensible heat flux, G = soil heat flux, P = precipitation, E = evapotranspiration, F_s = surface run-off, F_g = seepage. The sum of F_s and F_g represents the term F in Eq. (16.1). Changes of energy within the soil and changes in water content within the soil are omitted. (Modified from Seneviratne et al. (2010))

sensible heat G_H (uppercase G depicts ecosystem level compared to g at the leaf level):

$$\lambda E = \frac{s(R_n - G) + \rho c_p G_H D}{s + \gamma \left(\frac{G_H}{G_W} \right)}, \qquad (16.3)$$

where the coefficient s (in Pa K^{-1}) describes the change in saturation vapour pressure with temperature, D is the saturation vapour pressure (in Pa), ρ is the density of air (1.204 kg m^{-3} at sea level), c_p denotes the specific heat capacity of air (1012 J kg^{-1} K^{-1}), and γ (Pa K^{-1}) denotes the psychrometric constant (66.1 Pa K^{-1}) (Chap. 9). Both conductances G_W and G_H (in m s^{-1}) describe the entire pathway between the leaves and bulk air, including stomatal, cuticular and boundary layer components at the ecosystem level. The soil heat flux G is rather small, typically 2% of R_n in dense canopies, increasing to about 30% in very sparse canopies.

Under completely turbulent transport conditions for heat and water vapour in the boundary layer, G_H and G_W are similar and can be replaced by a **boundary layer conductance** (G_a, where a represents the atmosphere) and the **surface conductance** of the ecosystem (G_s). G_a describes the conductance between the free atmosphere and the surface(s) under study, that is, the soil surface and the canopy (leaf and stem surfaces), while G_s stands for the conductance out of the soil and into or out of the stomata of the foliage. Thus, for the sensible heat transfer H from a leaf or needle to the atmosphere, this transfer starts at the outer leaf surface and $G_H = G_a$ (which can also be expressed using resistance r instead of conductance: $G_H = 1/r_H = 1/r_a = G_a$). However, for the latent heat transfer λE from a leaf or needle and the soil surface to the atmosphere (water vapour leaving the foliage via evapotranspiration and the soil via evaporation), this transfer starts inside the leaf and from the soil, so $G_W = 1/r_w = 1/(r_a + r_s)$. Replacing G_H/G_w in Eq. (16.3) with $(1 + G_a/G_s)$, and recalling that $G_a = 1/r_a$ and $G_s = 1/r_s$, Eq. (16.3) can be expressed as

$$\lambda E = \frac{s(R_n - G) + \rho c_p G_a D}{s + \gamma \left(1 + \frac{G_a}{G_s} \right)}. \qquad (16.4)$$

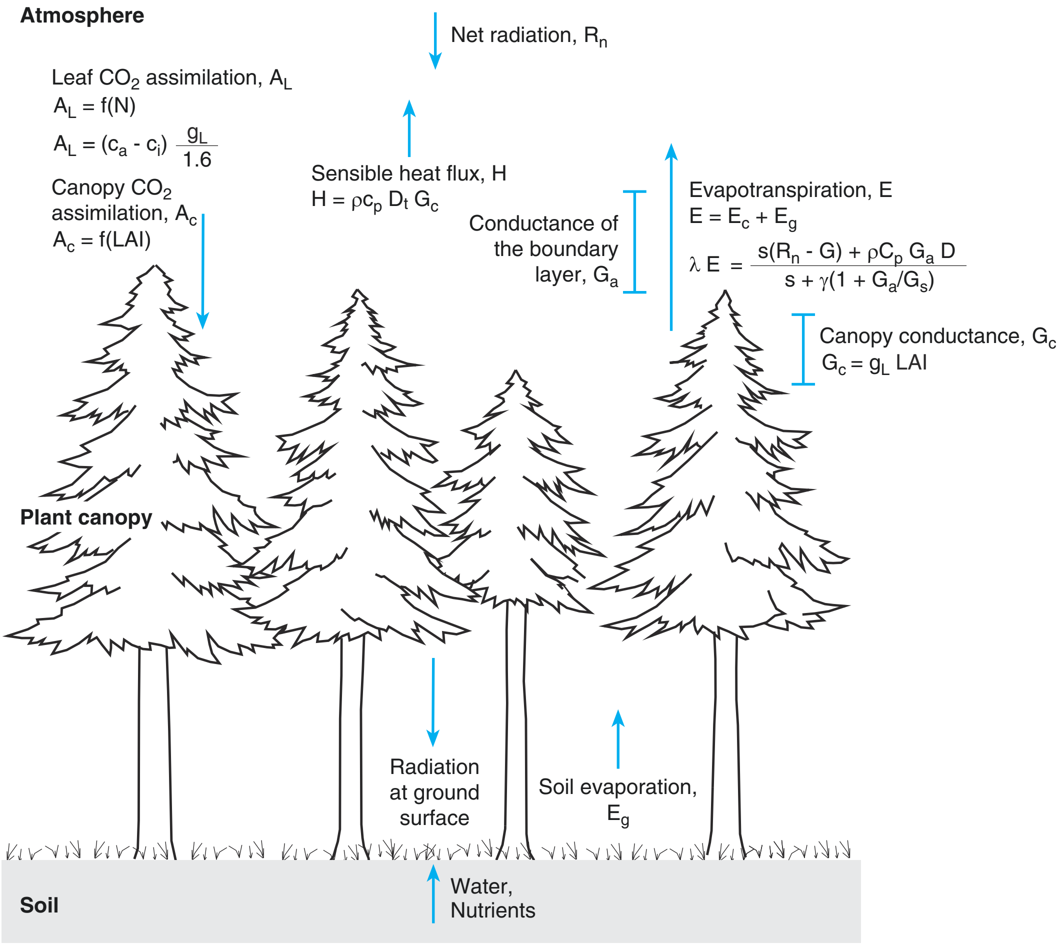


Fig. 16.6 Analytical representation of water vapour and CO_2 fluxes in a terrestrial ecosystem. Both water vapour and CO_2 fluxes are affected by abiotic and biotic drivers. See text for explanations and derivation of equations

Ecosystem-scale evapotranspiration (E) (Fig. 16.6) can be partitioned into canopy evapotranspiration (E_c) and **soil evaporation** (E_g) (following discussion) with

$$E = E_c + E_g. \tag{16.5}$$

If no measurements are available (Sect. 14.1 in Chap. 14), E_c can be scaled up from leaf transpiration (E_L) using a "**big-leaf model**", assuming all leaves in the canopy behave the same, as a single leaf:

$$E_c = E_L \ \text{LAI}. \tag{16.6}$$

However, to be closer to reality, currently also "two-leaf models" are used, which account for different behaviours of sunlit and shaded foliage within a canopy (Liu et al. 1997) (Chap. 15). Those interested in mathematics should read the work by Raupach and Finnigan (1988) with the remarkable title "Single-layer models of evaporation from plant canopies are incorrect but useful, whereas multi-layer models are correct but useless". Fortunately, since this publication, science and particularly model development have progressed, and optimisation theory and remote sensing approaches are used to describe canopies in more complex ways (e.g. Buckley et al. 2013; Peltoniemi et al. 2012).

Similarly, **surface conductance** G_s can be partitioned into

$$G_s = G_c + G_g, \tag{16.7}$$

with G_c = canopy conductance and G_g = soil conductance. The canopy conductance (G_c) is estimated by the conductance in the boundary layers around the leaves and the stomatal conductance.

Surface conductance G_s approaches **canopy conductance** G_c when the leaf area increases because soil evaporation becomes negligible in dense canopies (LAI > 3). It should also be noted that G_s is not equal to leaf conductance g_L because it includes not only the surfaces of vegetation in the ecosystem, but also the surface of the soil (Fig. 16.6) (Schulze et al. 1994).

Using the big leaf model, canopy conductance G_c can be approximated as

$$G_c = g_L \, \mathrm{LAI}. \tag{16.8}$$

Using a more stratified leaf model with i canopy strata, canopy conductance G_c can be approximated as

$$G_c = \Sigma\left(\overline{g_{L,i}} \, \mathrm{LA}_i\right), \tag{16.9}$$

with $\overline{g_{L,i}}$ = mean leaf conductance in stratum i and LA_i = leaf area in stratum i.

Because carbon dioxide and water vapour fluxes of a canopy are tightly coupled, we included **carbon dioxide assimilation** of the canopy A_c in Fig. 16.6 as well. A_c is determined by leaf net photosynthesis, which is controlled by the CO_2 gradient between the ambient air and the leaf intracellular air space ($= c_a - c_i$), the leaf conductance g_L, and foliar nitrogen nutrition, scaled up by canopy LAI (modulated by incoming radiation and leaf arrangement, for example, leaf angles, clumped needles and so forth).

Soil evaporation is dependent on the available energy at the soil surface (Fig. 16.6), the soil moisture available in the soil and D above the soil surface (for details, Seneviratne et al. 2010). The significance of soil evaporation becomes obvious when the maximum canopy conductance, the component of surface conductance related to the plant canopy, is plotted against the LAI (Fig. 16.7). As given by Eq. (16.6), both canopy and surface conductances are affected by different maximum stomatal and, hence, leaf conductances (g_{Lmax}). **Canopy conductance** increases with LAI and becomes saturated at about LAI 5 (for g_{Lmax} 4 mm s^{-1}) and at about LAI 9 (for g_{Lmax} 12 mm s^{-1}). In contrast, surface conductance behaves somewhat differently. With decreasing LAI, free evaporation from the wet soil surface becomes more important. At LAI 2 (at low g_{Lmax}), evaporation from the soil is as large as that from the canopy, as long as the soil surface is wet. For LAI < 1, surface conductance increases again because the water budget is determined by evaporation from the soil (Greenwood et al. 1992).

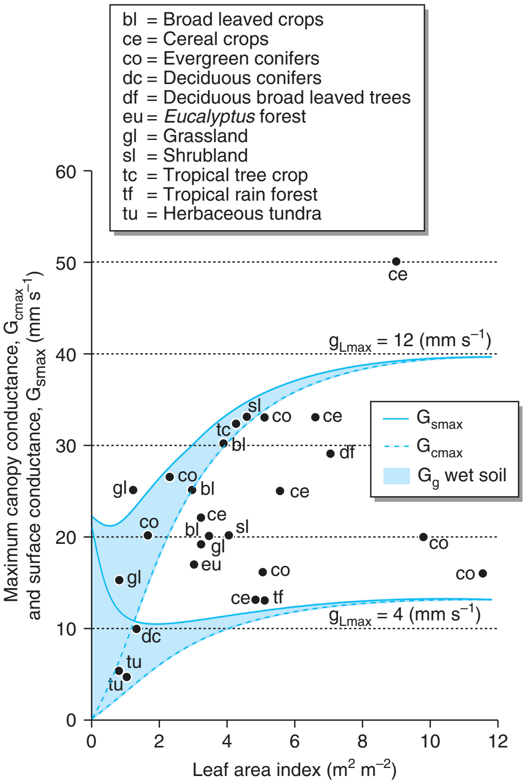


Fig. 16.7 Relationships between maximum canopy conductance (G_c from vegetation only) and surface conductance (G_s from soil and vegetation) and their relation to LAI. The continuous lines show the corresponding surface conductance, the hatched lines the canopy conductance. The shaded areas between the lines show the conductance of moist soil G_g. Two different sets of curves are given, based on maximum stomatal conductances of 4–12 mm s^{-1}, the range found on Earth. (After Schulze et al. 1994)

All **energy** components show a pronounced diel course on a cloudless day, driven by incident solar radiation (Fig. 16.8a). The grassland actively transpires during the day, so the latent heat flux consumes the largest share of the net radiation R_n. It takes about 2 h for the vegetation to increase transpiration with slowly increasing air temperatures and, thus, changes in water vapour deficit (Fig. 16.8b). The soil heat flux is the smallest term in the energy budget and shows the least diel variability, with a slightly shifted peak 1 h after the peaks for latent and sensible heat fluxes (Chap. 9). The soil temperatures lag behind air temperature: peak soil temperatures occur later for greater depths. During the day, air and soil surface temperatures can be very similar. Canopy surface temperatures are slightly lower than air temperatures during the night owing to longwave radiation losses but are much higher during the day. Although net radiation is dissipated in latent and sensible heat fluxes and ground heat flux, the **transpirational cooling** is not enough to cool the leaf surfaces below air temperatures (Sect. 9.4).

Depending on the overall environmental conditions, sensible and latent heat fluxes of different ecosystem types can account for a similar fraction of dissipated incoming energy (Table 16.1): this is

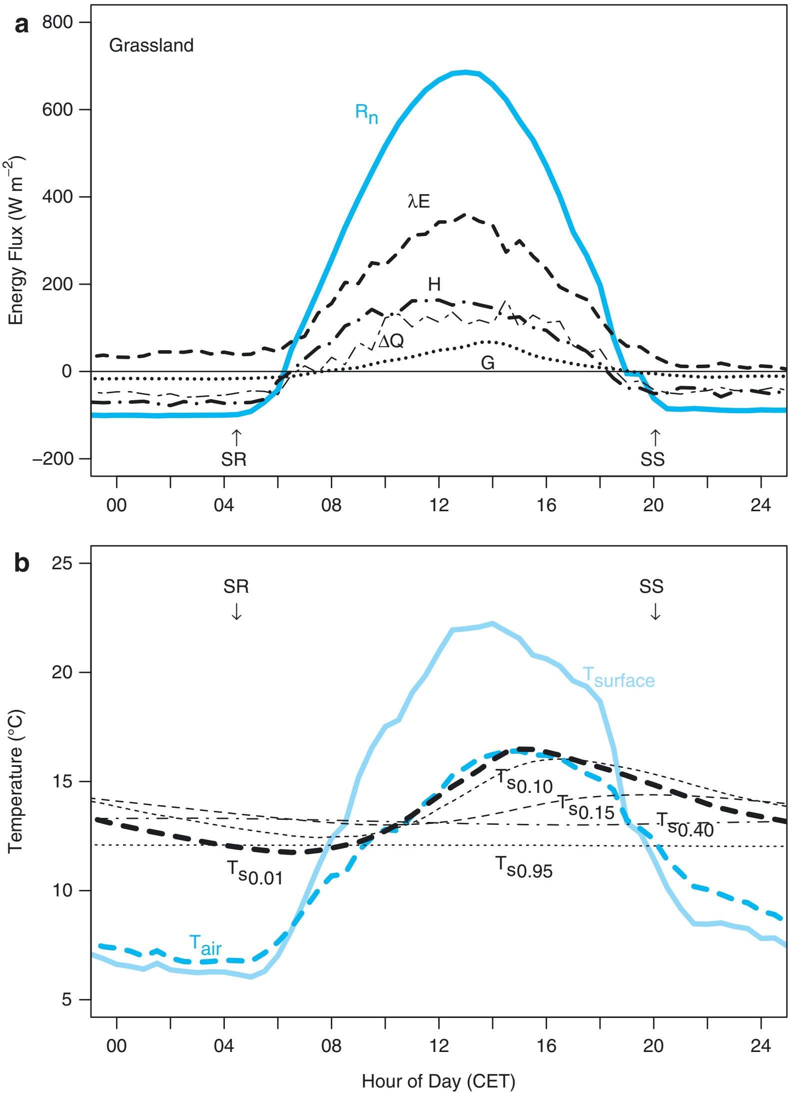


Fig. 16.8 Diel courses of the different components of the energy budget and corresponding temperatures over a medium intensively managed grassland in Switzerland (Früebüel, 1000 m asl, 30 May 2009). **a** The continuous line shows the net radiation R_n, the broken lines show λE, the latent heat flux, H the sensible heat flux, and G the soil heat flux. ΔQ represents the lack of energy balance closure, for example, the change in heat storage in the vegetation. **b** The continuous line shows the temperature at the top of the sward $T_{surface}$, the broken lines show the air temperature T_{air} and the soil temperatures T_s at five soil depths (soil depth given as subscript: 0.01, 0.10, 0.15, 0.40 and 0.95 m). *SR* sunrise, *SS* sunset. (Data from W. Eugster)

Table 16.1 Comparison of albedo, sensible and latent heat fluxes as well as Bowen ratios across ecosystem types

	Evergreen forests	Deciduous forest	Grasslands	Croplands
Albedo (%)	10 ± 2	13 ± 1	20 ± 2	17 ± 2
Sensible heat H (%)	44 ± 10	25 ± 7	44 ± 15	19 ± 4
Latent heat λE (%)	46 ± 10	62 ± 7	46 ± 15	64 ± 4
Bowen ratio ($H/\lambda E$)	0.5 to 1	0.25 to 0.5	highly variable	0.25 to 0.5

Means ±1 standard deviation are given based on multiple studies. Albedo is calculated based on incoming radiation. Data from Wilson et al. (2002), Cescatti et al. (2012)

often the case for grasslands and evergreen forests. However, deciduous forests and croplands often show a higher fraction of energy dissipated as latent heat, that is, evapotranspiration, compared to sensible heat. This results in a typical low **Bowen ratio (β)**, that is, the ratio of sensible to latent heat fluxes (Eq. 16.10), for croplands and deciduous forests, but higher ratios for evergreen forests. Grasslands, owing to their highly variable soil water supply, also have highly variable Bowen ratios:

$$\beta = \frac{H}{\lambda E} \tag{16.10}$$

It is interesting to note that the Bowen ratio increases when temperate ecosystems are converted to urban settlements, approaching values similar to deserts. In contrast, Bowen ratios decrease with irrigation, indicating higher water vapour and lower sensible heat fluxes due to evaporative cooling. Another useful ratio describes the fraction of available energy ($R_n - G$) used for latent heat λE, thus $\lambda E/(R_n - G)$, which is more intuitive and often more useful than the Bowen ratio.

16.1.4 Imposed and Equilibrium Evapotranspiration of Leaves and Canopies

Although one can use the Penman-Monteith equation (Eqs. 16.3 and 16.4) to calculate evapotranspiration, and this equation considers the feedback effects of E on D, one interesting question cannot easily be answered with this equation: What is the degree of **stomatal control** over leaf or canopy evapotranspiration? Here, Jarvis and McNaughton (1986) offered an interesting solution, partitioning the leaf or canopy evapotranspiration into two components, the equilibrium evaporation rate, E_{eq}, which depends only on radiation, the energy supply for evaporation, and the imposed evaporation rate, E_{imp}, which takes leaf or canopy conductance into account. Depending on the degree of **coupling** of the evaporating leaf or canopy surface to the atmosphere, either one of these two evaporation rates will prevail. Note that this approach does not consider soil evaporation (part of ecosystem evapotranspiration) but only plant-related evapotranspiration. One can thus look at the two extreme cases:

1. The leaf or canopy is well coupled to the atmosphere. This is the case for small leaves or isolated plants. Here, the boundary layer around the evaporating surfaces is very small, so the boundary layer conductance is very large, and the transfer of heat and mass (water vapour) is very efficient. This means that leaf or canopy temperatures approach air temperatures depending on the radiative input, and physiological controls dominate evapotranspiration. Thus, Eq. (16.4) is reduced to describe the **imposed evaporation** E_{imp}:

$$\text{At leaf level}: E_{imp} = \left(\frac{\rho c_p}{\lambda \gamma}\right) g_L D, \tag{16.11a}$$

$$\text{At canopy level}: E_{imp} = \left(\frac{\rho c_p}{\lambda \gamma}\right) G_c D, \tag{16.11b}$$

where g_L or G_c describes the corresponding physiological conductance of the leaf or the canopy. Owing to the full coupling, the conditions of the atmosphere are “forced or imposed” on the leaf or canopy, so that evapotranspiration is linearly related to conductance and water vapour deficit (which in turn is affected by conductance).

2. The leaf or canopy is not well coupled to the atmosphere. This is the case for large leaves, very short vegetation (short lawn), conditions with still air (no turbulence) or within a greenhouse. Here, the boundary layer around the evaporating surfaces is very large, so the boundary layer conductance is very small, and the transfer of heat and mass (water vapour) is very poor. This means that the energy supply R_n dominates evapotranspiration. Thus, Eq. (16.4) is reduced to describe **equilibrium evaporation** E_{eq}:

$$E_{eq} = \frac{sR_n}{\lambda(s+\gamma)}. \tag{16.12}$$

For both leaf and canopy evapotranspiration, water vapour loss is in equilibrium with the available net incoming radiation R_n, independent of leaf or canopy conductance. Such conditions exist for example on an even lawn. Leaf stomata may be wide open, but the canopy will lose little water because the transport of water vapour through the boundary layer does not take place. Thus, evapotranspiration saturates the boundary layer, and D will approach zero. Water vapour transport to the atmosphere is only enhanced if the temperature of the surface rises as a consequence of radiation. For large crop areas, actual evapotranspiration is about 26% larger than E_{eq} based on Eq. (16.12), so a factor 1.26 is introduced into the nominator (**Priestley–Taylor coefficient**) to increase the estimated evapotranspiration rate E_{eq}. The discrepancy arises because turbulent mixing in and above the field prevents the boundary layer from becoming fully saturated, so D is larger than zero.

Since E_{eq} is purely energy-driven, one can also interpret E_{eq} as **potential evaporation** (no physiological effect via transpiration). Physically, E_{eq} represents simply the water vapour flux from an open water surface that has the same surface temperature as a leaf or a canopy fully supplied with water, under conditions when the atmosphere is fully saturated with water vapour ($D = 0$). However, there are many different ways to calculate potential evaporation (for details, see climatology textbooks).

Under natural conditions, both extreme cases can happen, but usually a mixture of evapotranspiration occurs, driven by radiation inputs (E_{eq}) and imposed by the combination of atmospheric water vapour saturation deficit and leaf or canopy conductance (E_{imp}):

$$E = \Omega E_{eq} + (1-\Omega) E_{imp}, \tag{16.13}$$

where Ω is the **decoupling factor**, which quantifies the connection of the vegetation to the atmosphere. Ω can vary between 0 (perfect coupling) and 1 (complete isolation).

$$\text{At leaf level: } \Omega_L = \frac{s+1}{s+1+\dfrac{G_a}{g_L}}, \tag{16.14a}$$

$$\text{At canopy level: } \Omega_c = \frac{s+1}{s+1+\dfrac{G_a}{G_c}}. \tag{16.14b}$$

The sensitivity with which evapotranspiration reacts to changes in stomatal closure $(dE/E)/(dg_L/g_L)$ or $(dE/E)/(dG_c/G_c)$ is directly determined by Ω:

$$\text{At leaf level: } \frac{\dfrac{dE}{E}}{\dfrac{dg_L}{g_L}} = 1-\Omega_L, \tag{16.15a}$$

$$\text{At canopy level: } \frac{\dfrac{dE}{E}}{\dfrac{dG_c}{G_c}} = 1-\Omega_c. \tag{16.15b}$$

The aforementioned relations are very important in understanding water vapour loss from plant canopies. Under certain conditions, the characteristics of the vegetation are more important than stomatal regulation. A branch standing out from a wind-swept canopy of a forest experiences different evaporative conditions than other leaves protected in the canopy. The decoupling factor Ω decreases (coupling increases) with an increasing height of vegetation (Fig. 16.9) and increases with smaller leaves. However, this does not explain how and to what extent

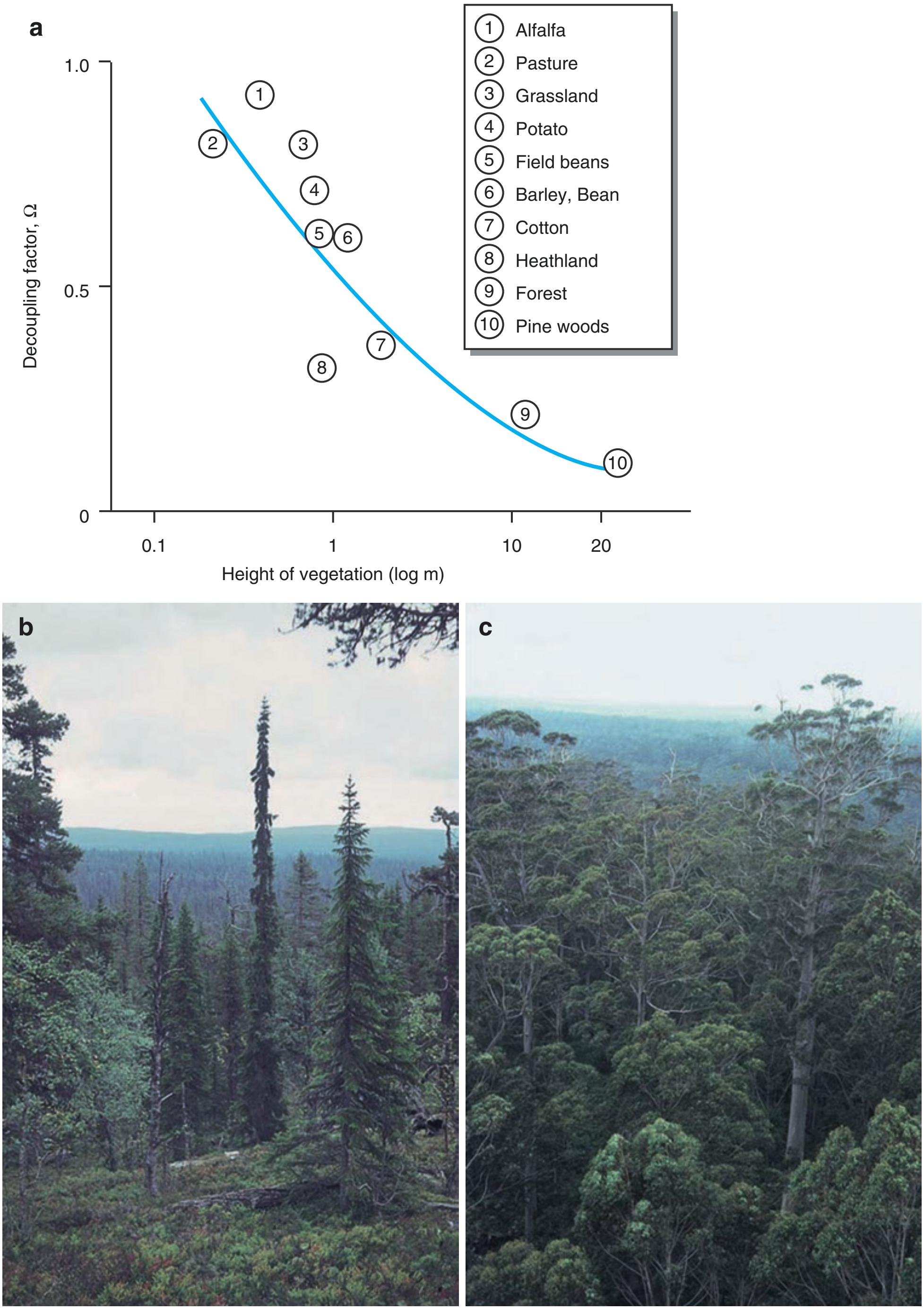


Fig. 16.9 Relationship between height of a canopy and its decoupling from the atmosphere. **a** Dependence of decoupling factor Ω on height of vegetation as a measure of roughness of surface (data from Kelliher et al. 1995). **b** In boreal forests, the ratio of latent to sensible heat flux is affected by the form of the tree canopy. *Picea obovata* x *excelsa* (narrow crown) is more densely covered with needles and therefore warms more than *Picea excelsa* (broad crown) or *Betula pubescens*. The thick ground vegetation with *Vaccinium myrtillus* does not have a very rough surface and thus warms more strongly. Gutulia, central Norway. **c** Canopy of a *Eucalyptus marginata* stand with an average height of 100 m in south-western Australia. *Eucalyptus marginata* reaches a height of 140 m. In contrast to boreal forests, the leaf surface is almost uniformly distributed in the canopy, although *Eucalyptus* forms leaf bundles at the ends of branches. Picture taken from the Gloucester tree near Pemperton. (Photos E-D Schulze)

evapotranspiration takes place, because at constant Ω, evapotranspiration is dependent on radiation, the water vapour saturation deficit and the corresponding conductance.

Decoupling can also be achieved by specific **morphological adaptations** at the leaf level, which reduce the boundary layer around the leaves. For example, leaf petioles with an elliptic, flattened cross section lead to leaf movements even at very low wind speeds. The fast-growing species *Populus tremula* has "shivering" leaves (Latin name *tremulus* = trembling) already in light breezes, decreasing the leaf boundary layer, thus increasing the boundary layer and leaf conductances and, in turn, leaf gas exchange (Sect. 9.3 in Chap. 9). Thus, E_{imp} dominates leaf and canopy E, being strongly driven by g_L and D (Eq. 16.11a). Growing on moist soils, this species can afford high transpirational losses due to high leaf conductances to enhance CO_2 uptake and, thus, growth.

Box 16.1: Techniques to Measure Transpiration and Evapotranspiration at Different Scales

Measurements at leaf scale:

- **Porometer**: Contains a sensor head onto which a leaf is pressed. The changes in air humidity and CO_2 concentration (facultative) over time are measured as the basis for flux calculations. **Advantage**: simple to use. **Disadvantage**: The leaf response is measured under artificial conditions.
- **Cuvettes**: These are controlled chambers in which a leaf is enclosed. Temperature and humidity can be controlled, so it is possible to determine plant responses to specific conditions. **Advantage**: Experiments can be conducted in the field. **Disadvantage**: The measured transpiration rate does not correspond to the transpiration rate under undisturbed conditions.

Measurements at single plant scale:

- **Xylem flux**: The water in the xylem is heated at a constant rate and the distribution of temperature in the stem is measured (Granier method). **Advantage**: It allows measurements of the natural rate of transpiration of plants. **Disadvantage**: The method is best suited for trees. Sapwood area needs to be known. Extrapolation to the whole vegetation surface is difficult.
- **Point dendrometers**: The girth of stems is measured continuously, with a small pin touching either the bark or the xylem. Measurements can be automated, frequency as high as 10 min. Stem radius changes are calculated. **Advantage**: Continuous, high-precision measurements. Cheap. **Disadvantage**: The method works best with trees. Secondary growth as well as shrinking and swelling due to water dynamics affect stem diameters; both processes need to be distinguished to estimate tree water deficit. (Zweifel et al. 2016)

Measurements at ecosystem scale:

- **Eddy covariance method**: The turbulent flux in the air above an ecosystem is derived from measurements of vertical wind speed and gas concentration in air parcels moving past the respective sensors. **Advantage**: Integrated measurement of fluxes for whole ecosystem (0.5–4 km^2), high temporal resolution (20 Hz, averaged over 30 min). **Disadvantage**: Needs stationary turbulent atmospheric conditions. Lots of post-processing needed. Assumes negligible advection. Expensive (Aubinet et al. 2012)

Measurements at landscape scale:

- **CBL budgeting** (CBL is the convective boundary layer of the atmosphere): The lower layer of the atmosphere is taken as a closed box (Lloyd et al. 2001). During the day, changes in gas concentration at different heights in this idealised box are measured from an airplane and fluxes within the box from the surface below can be estimated at landscape scale (50–100 km^2). **Advantage**: Quantification of flux budgets over heterogeneous landscapes. **Disadvantages**: Technically and meteorologically demanding. Limited to particular meteorological conditions (typically single nice weather days). Expensive

16.1.5 Responses of Terrestrial Ecosystems to Drought

Biogeochemical processes in ecosystems react to changes in environmental conditions just like physiological processes in leaves and individual plants. Using the appropriate measurement techniques for the scale under study, here the ecosystem scale (Box 16.1), one can quantify these changes and compare magnitudes of process rates and responses of different ecosystem types to the same driver. Moreover, one can study the interactions of different biogeochemical processes, like evapotranspiration (ET) and gross primary production (GPP). The ratio of GPP to ET (sometimes called **ecosystem water-use efficiency**) also provides insights into different survival strategies, that is, how the ecosystem reacts to environmental stress such as a severe drought. This is of particular interest since extreme events like droughts are expected to increase with anthropogenic climate change (Chap. 21).

Using the eddy covariance technique to measure ecosystem CO_2 and water vapour fluxes (Chap. 14), it was shown that during a year with a severe spring drought (2011), forests—in contrast to grasslands—increased GPP relative to ET compared to the (representative) year before (2010). All sites studied (subset of two shown in Fig. 16.10) showed an earlier start of the season, so GPP could be maintained also in 2011 (Wolf et al. 2013). However, owing to the water shortage in spring 2011, forests reduced their water loss (via stomatal regulation of transpiration), which led to increased GPP/ET ratios (steeper slope in Fig. 16.10). This is in stark contrast to the behaviour of grasslands: no change in water vapour losses was observed, the slopes of GPP over ET did not change, so grasslands showed the same GPP relative to ET in both years. Thus, **susceptibility to drought** strongly differs between grasslands and forests, probably owing to different evolutionary adaptation strategies (meristems of grasses are close to the ground, not at great height, ability of frequent regrowth after foliage loss).

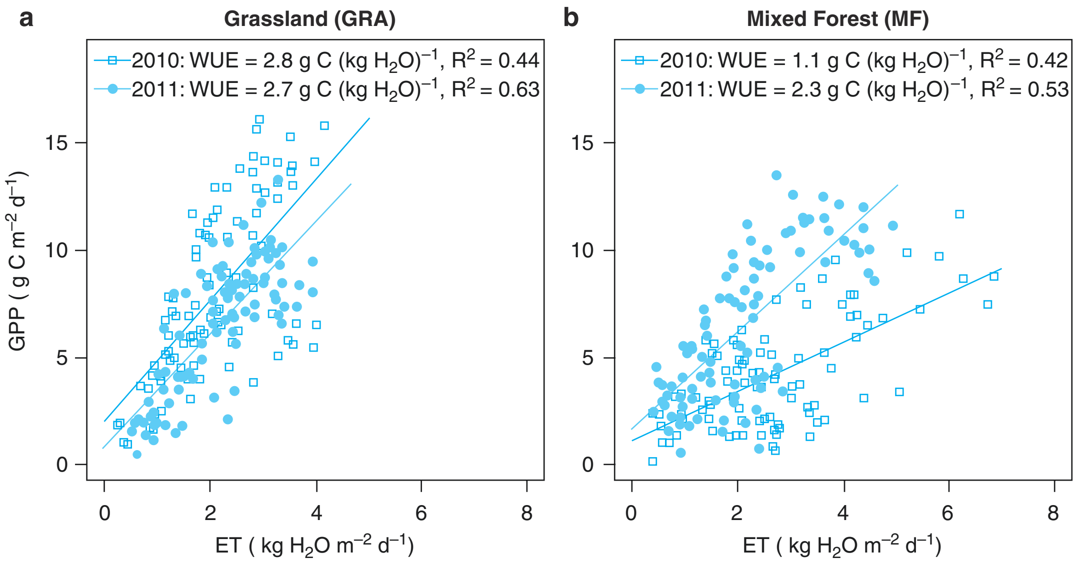


Fig. 16.10 Relationship between water vapour fluxes and gross primary production of grassland and mixed forest. The slope of the curves represents the ratio of GPP to ET of **a** a grassland (Oensingen, Switzerland) and **b** a mixed forest (Lägeren, Switzerland) over the course of 2 years. The year 2010 represents an average year for both sites, while 2011 was a year with a strong spring drought. (Wolf et al. 2013)

These different behaviours of grasslands and forests were supported by combining flux measurements and models at the next larger scale, the region. For the combined heatwave and drought in summer 2006 across Europe, grasslands showed much higher evapotranspiration rates at the beginning of the **heatwave** and drought than forests (Teuling et al. 2010). This resulted in a cooling of the atmosphere over grasslands but a heating over forests. Only longer into the extreme event, when grasslands started to wilt and die off, but forests still continued to transpire (although at a low rate), did this result in a cooling of the atmosphere over forests at later stages of the heatwave and drought. This shows how different ecosystems differ in their responses and feedbacks to changing environmental conditions, in this case to the atmosphere (Chap. 23).

16.2 Carbon Fluxes in Terrestrial Ecosystems

16.2.1 Carbon Pools and Fluxes in Terrestrial Ecosystems

Carbon enters terrestrial ecosystems as atmospheric carbon dioxide (CO_2) during **gross primary production** (Fig. 16.11). It is allocated as carbohydrates within plants and used to grow plant tissues and for storage (Chap. 12), but also to fuel **ecosystem respiration**, both from autotrophic plants and heterotrophic microbial organisms and soil fauna. Because of these two large ecosystem CO_2 fluxes (photosynthesis and respiration), there is a close coupling between the atmosphere and the biosphere, mediated by a turbulent exchange of air masses above and within the ecosystem. When plant tissues senesce and

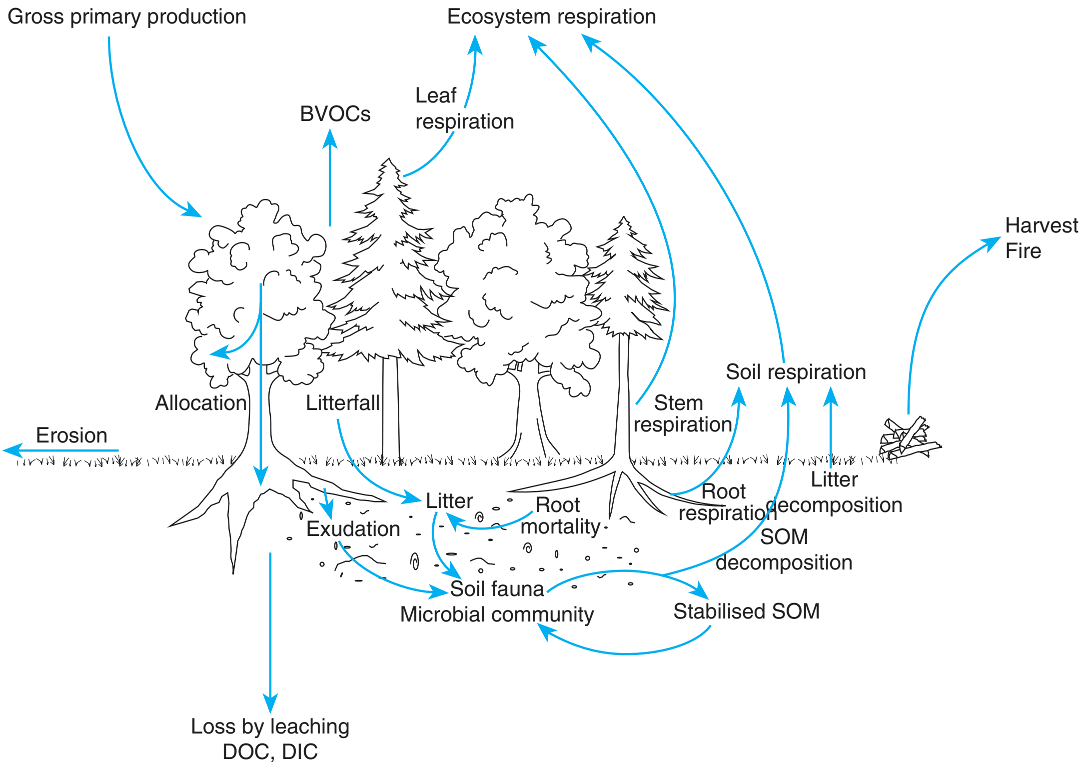


Fig. 16.11 Carbon pools and fluxes in terrestrial ecosystems. Carbon enters the ecosystem as carbon dioxide via photosynthesis and leaves the system as carbon dioxide via autotrophic (root, stem, foliage) and heterotrophic (microbial, soil fauna) respiration. Further carbon losses occur as leaching of dissolved organic and inorganic carbon (DOC and DIC, respectively) as well as via erosion. Additional losses result from harvests and fires

become litter, decomposition of this dead organic matter (necromass) sets in. **Decomposition** by soil fauna and microorganisms includes decay, that is, the biotic breakdown of organic matter, and mineralisation, that is, the release of inorganic nutrients, but also CH_4 and CO_2 (thus heterotrophic respiration). **Stabilisation** of organic matter, that is, the formation and protection of **soil organic matter** (SOM) (Sect. 20.4 in Chap. 20), contributes to carbon sequestration. Thus, the largest carbon pool in ecosystems is often in the soil (except in tropical forests). Additional losses occur during **leaching** of DOC and dissolved inorganic carbon (DIC) from the soil, but also during erosion. During fires and with harvests, large amounts of carbon are removed from ecosystems, although both fire and harvest residues also make large contributions to SOM. Depending on fire frequencies and the degree of ecosystem management, vegetation degeneration, **soil degradation** and erosion can occur. For the exchange of methane (CH_4) and other biogenic volatile organic compounds (BVOCs), Sect. 16.2.4.

One variable often used to address ecosystem carbon budgets is **net primary production** (**NPP**), in g C m^{-2} year^{-1}, defined as GPP minus respiration (Sect. 12.5 in Chap. 12 for leaf and plant levels and Chap. 23 for global change impacts). Thus, it includes, for example, production of fine roots, root exudation and emission of BVOVs for defence (Sect. 16.2.4). NPP constitutes about 50% of GPP (ranging from 30% to 80%) (Amthor 2000; DeLucia et al. 2007) and can be determined for above-ground and below-ground tissues (ANPP and BNPP, respectively). Moreover, **allometric relationships** (i.e. statistical relationships used to predict tree biomass) relate BNPP to total NPP. For example, for trees BNPP/NPP = 0.3, and for grasses BNPP/NPP = 0.5. These numbers are global means and thus do not account for species differences (Sect. 22.2 in Chap. 22). Moreover, most NPP estimates given in the literature are ANPP estimates only, neglecting below-ground production but also herbivory and other processes like exudation and BVOC emissions.

Thus, NPP should not be interpreted as **yield**, harvest or above-ground biomass production over time (e.g. ANPP per growing season, cropping time, year). Two examples illustrate this misconception: Farmers consider grain production as yield but are not necessarily interested in stem and root growth; foresters are mostly interested in cumulative stem growth and increase in wood volume at time of **harvest** but not in foliage growth or even stem mortality until harvest. Moreover, thinning and harvest residues are clearly part of NPP but not considered in assessments of net increment changes in forests. Both examples illustrate that the harvestable yield is only a small fraction of NPP.

Moreover, there exists no direct relationship between **standing biomass** (in g C m^{-2}) and NPP (in g C m^{-2} year^{-1}). Biomass produced by plants persists at the plant or in the ecosystem for very different time periods, leading to different values of standing biomass due to function (e.g. wood) and tissue longevity (Table 16.2). For annual species, the total biomass dies off at the end of the growing season (except seeds) and serves as substrate for heterotrophic organisms in the soil. For perennial herbaceous plants, almost all the total biomass produced also dies (except rhizomes, bulbs or corms, i.e. under-

Table 16.2 Standing biomass, above-ground net primary production (ANPP), and leaf litter production in different ecosystem types

Ecosystem type	Biomass (kg C m^{-2})	ANPP (kg C m^{-2} year^{-1})	Leaf litter (kg C m^{-2} year^{-1})
Tropical rainforest	20–32	3–10	0.5–1.4
Temperate deciduous forest	5–30	0.2–1.2	0.1–0.6
Temperate coniferous forest	15–75	0.4–1.3	0.1–0.6
Boreal coniferous forest	8–10	0.3–0.4	0.1–0.5
Savanna	1–2	0.4–0.6	0.1–0.4
Grassland	0.2–2.2	0.1–1.0	<0.1–1.0
Cropland	0.5	0.3–0.5	0.1–0.2
Desert	0.2–3	<0.1–0.5	<0.1–0.2
Tundra	0.1–2	<0.1–0.2	<0.1

Data from Schulze (1982), Blume et al. (2010) and Schlesinger and Bernhardt (2013) ground stem storage organs) and becomes litter within a year. Thus, for herbaceous species, this litter production corresponds to ANPP (Sect. 12.6 in Chap. 12). In contrast, in woody plants, about 50% of ANPP is invested in wood. Part of the sapwood is subsequently transformed into dead heartwood, which becomes woody debris and litter only with a long time delay. Moreover, only about 40 to 50% of deciduous tree ANPP and about 20% of evergreen tree ANPP reaches the soil each year as leaf, twig and root litter (Sect. 12.5 in Chap. 12). Thus, neither standing wood biomass nor litter fall reflects annual NPP or ANPP in forests.

A large proportion of total biomass is below-ground and thus "out of sight". Therefore, information about standing biomass, production and mortality, thus turnover, is more difficult to obtain than for above-ground biomass. On average, the proportion of **fine roots** as part of total biomass is about 28% (Table 16.3). Fine roots in forests reach a total length of 2–8 km m^{-2} and a projected area of 4–11 m^2 m^{-2}, corresponding in magnitude to the LAI. In grasslands, the length of fine roots (>100 km m^{-2}) is a factor of 10 greater than in forests. The NPP of fine roots probably corresponds to the turnover of leaves.

Thus, estimating NPP is difficult for different reasons. Plants might be difficult to reach or to measure, for example, tropical trees, epiphytes and lianas; some processes, particularly in the soil, might be difficult to determine, for example, root exudation or production and turnover of fine roots (<2 mm diameter). For example, different methods exist to estimate **fine root** biomass production and turnover, ranging from

- Sequential root biomass sampling.
- Ingrowth cores: mesh bags filled with root-free soil, placed into the rooting zone, and collected after some time to quantify the new roots grown into the cores.
- **Minirhizotrons**: cameras inserted into the soil to monitor root growth with transparent tubes.
- Stable isotope labelling: tracing the fate of ^{13}C–labelled photoassimilates into root growth.
- **Radiocarbon** dating based on **bomb-carbon:** ^{14}C created by above-ground nuclear tests done in the 1950s and 1960s (also called bomb-carbon), recovery of bomb-carbon in tissues, compounds or ecosystem compartments, relationship to decreasing atmospheric ^{14}C background values and thus to the age of the C analysed.

Each method has its own uncertainties, but generally sequential coring and minirhizotron estimates seem to overestimate turnover, while radiocarbon analyses seem to underestimate turnover (Gaul et al. 2009). Consequently, estimates of **mean life span** for the same fine roots might differ. In temperate forests, life spans of typically <1–2 years were found based on sequential coring and minirhizotron methods. However, fine root life spans were much larger, up to 8 years (top soil) and 18 years (deeper soil horizons),

Table 16.3 Biomass of fine roots (<2 mm diameter) and leaves in different ecosystem types on Earth (Data from Schulze 1982; Jackson et al. 1997)

Ecosystem type	Roots	Fine roots			Leaves or needles	
	Total (kg m^{-2})	Mass (kg m^{-2})	Length (km m^{-2})	Root surface index (m^2 m^{-2})	Mass (kg m^{-2})	Leaf area index (m^2 m^{-2})
Tropical rain forest	4.88	0.57	4.1	7.4	2.5	11
Temperate coniferous forest	4.40	0.82	6.1	11.0	1.3	9
Temperate deciduous forest	4.14	0.78	5.4	9.8	0.4	7
Boreal forest	2.92	0.60	2.6	4.6	1.8	11
Shrub vegetation	4.82	0.52	8.4	11.6	0.4	8
Savanna	1.40	0.99	60.4	42.5	0.9	3
Temperate grassland	1.56	1.51	112.0	79.1	0.6	3
Tundra	1.25	0.96	4.1	7.4	0.4	2
Desert	4.13	0.27	4.0	5.5	0.1	<1
Average	3.28	0.78				

based on radiocarbon analyses (Gaudinski et al. 2001). However, radiocarbon estimates can be biased, depending on which carbohydrate substrates with which age (i.e. time since bomb tests) are used for fine root production. Clear evidence was provided by Vargas et al. (2009) using radiocarbon analyses in five tropical forest stands before and after Hurricane Wilma hit. Fine roots grown into ingrowth cores installed after the hurricane were estimated to be 2–10 years old. Thus, trees had remobilised stored, that is, old, carbohydrates to supply new fine root production and did not use recently assimilated carbon. This made new roots look much older! Independently of the method used, most studies find thicker and deeper roots being older than fine roots in the top soil. Root turnover differs among different ecosystem types. For example, fine root turnover in grasslands is typically much greater than in forests, that is, the life span of fine roots in grasslands is much shorter. In comparison, leaves and needles in temperate forest ecosystems have a life span of 1–10 years (*Pinus aristata* even 30 years). Wood can remain at a plant >100 years (oldest living trees: 5000 years, *Pinus longaeva*, Bristlecone pine), while SOM is often >100–1000 years old.

One of the largest CO_2 fluxes in terrestrial ecosystems is **soil respiration** (also called **soil CO_2 efflux**), comprising between 50 and 70% of total ecosystem respiration (Raich and Schlesinger 1992). Soil respiration includes respiratory losses from plants and plant-root-related microorganisms in the rhizosphere (Box 11.1, Chap. 11), microbial respiration (MR) during decomposition of litter and SOM as well as respiration of soil fauna (Fig. 16.12). The strict separation into **auto-** and **heterotrophic soil respiration** is not useful since MR is intricately coupled to plant activity, particularly to canopy photosynthesis, not only in the **rhizosphere** via root production and exudation but also via litter production. Depending on the substrates used for respiration, turnover rates and, thus, residence times in the soil differ. While roots respire relatively young carbohydrates allocated below-ground (<1 year to several years), MR use substrates from root exudation (<1 year) or organic matter, ranging in age from leaf litter (<1 year to several years) to very old SOM (decades to millennia). Thus, the drivers of soil respiration are both biotic (carbon supply via photosynthesis and allocation belowground) and abiotic (environmental conditions), but they also interact with each other. For exam-

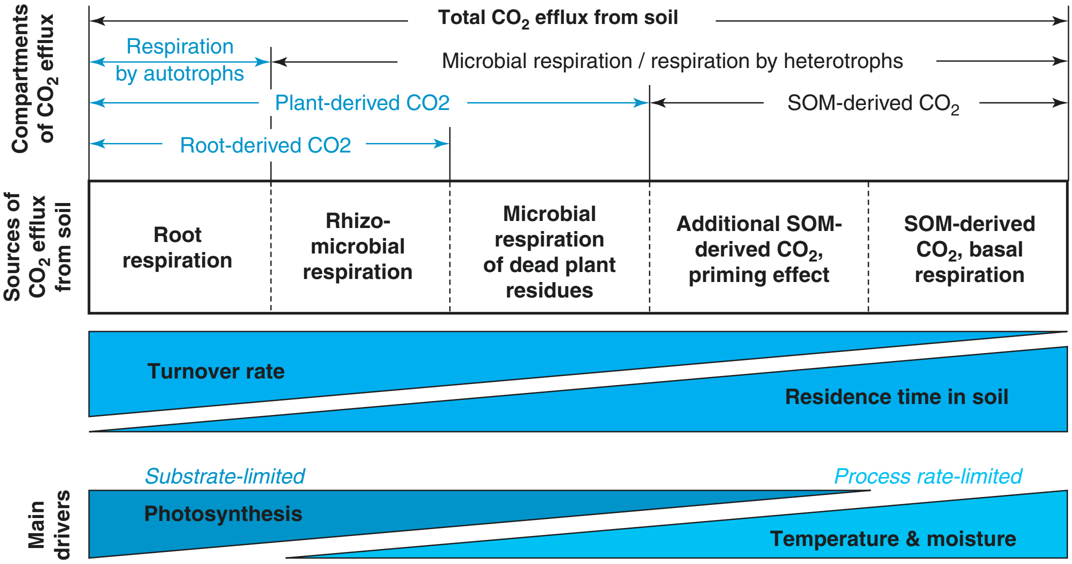


Fig. 16.12 Processes and organisms contributing to soil respiration in the form of soil CO_2 efflux to total ecosystem respiration. Turnover rates and, thus, residence times of the substrates differ among the different component fluxes, as do the main drivers. (Kuzyakov and Gavrichkova 2006)

ple, with increasing temperature, not only respiration increases, but also photosynthesis and in turn allocation below-ground may increase up to a certain limit. With increasing N supply, productivity increases, but also the root:shoot ratio and the litter quality change, affecting MR during mineralisation of plant litter.

Overall, the most important **driver of soil respiration** is canopy assimilation. This can be seen when above-ground biomass is cut, for example, in managed grasslands, while abiotic conditions like soil temperature and moisture remain unchanged. Soil respiration drops within a couple of days and only resumes when above-ground biomass, and thus LAI, is regrown. Högberg et al. (2001) used stem girdling in a northern pine forest to show for the first time the strong coupling of **canopy photosynthesis** to below-ground respiration (Sect. 14.2, Chap. 14). Girdling is the removal of the phloem in the bark of trees, which interrupts the supply with carbohydrates assimilated in the canopy to the root system. Depending on the starch pool in the roots, the drop in soil respiration occurred faster (low starch pool, end of season) when trees were girdled later in the year than when girdled in spring (still high starch pool, beginning of season). Similarly, drought slows down carbon allocation below-ground, affecting soil respiration negatively (Rühr et al. 2009). Thus, overall, soil respiration scales positively with GPP, NPP, LAI, litter production and carbohydrate supply below-ground. This affects both root-rhizosphere respiration (RR) and MR, which are tightly related to each other as well (Bond-Lamberty et al. 2004). Changes in **phenology**, co-occurring with changes in environmental conditions, thus affect soil respiration in mixed deciduous forests too (Ruehr and Buchmann 2010). During the growing season with full canopy cover, RR is greater than microbial soil respiration, contributing on average 50–60% to total soil respiration. However, during the dormant season, this contribution of RR drops to about 30%, with microbial soil respiration dominating the overall soil CO_2 flux.

Nevertheless, environmental conditions, particularly **soil temperature** and **soil moisture**, also regulate soil respiration (Sect. 13.3, Chap. 13). Since both abiotic factors also drive canopy photosynthesis and are more readily available than GPP, soil respiration is often modelled with climatic data, particularly at large spatial scales. Soil respiration increases exponentially with soil temperature, while low soil moisture contents decrease soil respiration below this general relationship. Phenology also affects these functional relationships (Fig. 16.13). During the growing season, both RR and MR show similar relationships with soil temperature. However, during the dormant sea-

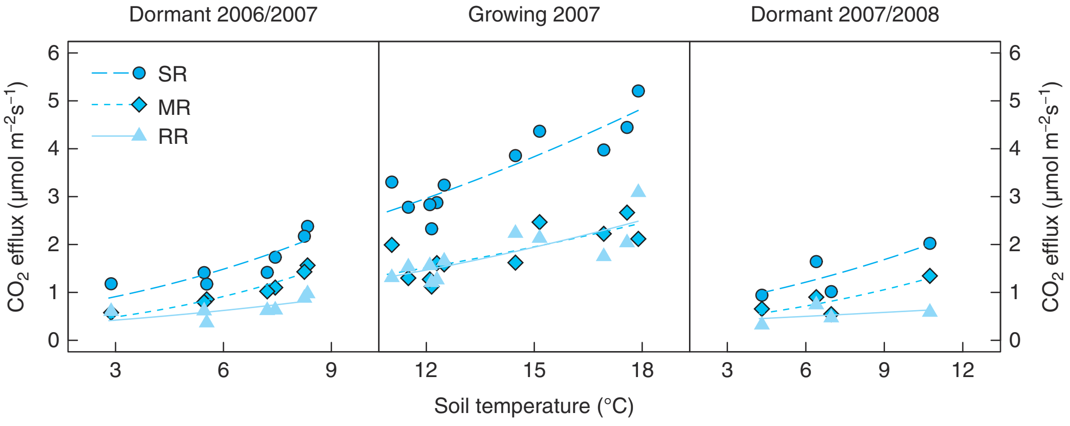


Fig. 16.13 Functional relationships of soil temperature with soil respiration (SR), microbial (MR) and root-rhizosphere respiration (RR). Fluxes were measured in a mixed deciduous forest during the dormant seasons (no tree foliage; 2006/2007 and 2007/2008) and the growing season (full canopy; 2007). SR was measured on grown forest soil. Using mesh bags, roots were excluded from the bags, and MR could be measured separately. RR was calculated by difference (RR = SR − MR). (Ruehr and Buchmann 2010)

Table 16.4 Soil respiration fluxes across different ecosystem types

Ecosystem type	Soil respiration ($g\ C\ m^{-2}\ year^{-1}$)
Tropical rainforest	666–1520
Temperate deciduous forest	304–1414
Temperate coniferous forest	250–1300
Boreal coniferous forest	120–550
Savanna	380–900
Grassland	132–1988
Cropland	224–1410
Desert	184–300
Tundra	29–95

Data from Raich and Schlesinger (1992), Bahn et al. (2008)

sons, when fluxes are lower, MR reacts more strongly to increasing soil temperatures (steeper slope) than root respiration. Most likely, RR during the dormant seasons is limited by carbon substrates compared to MR, which can use many organic matter substrates available in the soil. Owing to these interacting multiple drivers, a simple **Q_{10} value**, which describes the increase of an enzymatic process when temperature is increased by 10 K, cannot capture this complexity. Thus, it should not be used to describe soil respiration fluxes in response to changing environmental drivers, not even to temperature changes alone (for further details, Davidson et al. 2006). Instead, modelling needs to take into account both environmental and biotic variables (Chaps. 15 and 22).

Based on these interacting biotic and abiotic drivers, it is not surprising that total annual soil respiration fluxes vary strongly within and across ecosystem types (Table 16.4). Soil CO_2 fluxes can be as large in grasslands and croplands as in forests. Lower plant productivity due to climate limitations results in lower soil respiration rates, such as in desert, boreal forest and tundra ecosystems.

16.2.2 Decomposition and Stabilisation of Organic Matter in Terrestrial Ecosystems

If not harvested or eaten by animals, plant tissues naturally senesce and die, become (woody) debris or above- and below-ground litter, and are subsequently decomposed. Decomposition products can be stabilised, contributing to soil carbon pools. Thus, both decomposition and stabilisation of organic matter are tightly linked. Two main processes happening at the same time contribute to decomposition:

- **Decay**, which describes the biotic **breakdown** of dead plant organic matter (also called necromass) into smaller pieces (degradation) by soil fauna and microorganisms and the related mass loss (Sect. 20.4 in Chap. 20).
- **Mineralisation**, which describes the release of nutrients in inorganic forms from organic matter, including the release of CH_4 or CO_2 (Sect. 16.2.1).

Foliage decomposition is strongly linked to litter quality (in particularly to relative concentrations of water-soluble C compounds, cellulose, lignin and N) (Cotrufo et al. 2013) and to environmental conditions. The higher the quality, the faster the breakdown, under adequate soil moisture and temperature regimes for microbial activities (Sect. 20.4, Chap. 20). Simple **decay models** describe the patterns of exponential mass loss per year (Eq. 16.16). For parameterisation of organic matter decay and SOM formation in ecosystem and global models, Sects. 15.3 and 22.3 in Chaps. 15 and 22, respectively:

$$\frac{X}{X_o} = e^{-k}, \qquad (16.16)$$

with X/X_o describing the percentage mass remaining and k being the decomposition constant ($year^{-1}$).

Decomposition constants (also called k-values; under steady-state with $1/k$ = MRT, **mean residence time** or **turnover time**) for mass loss range from about 0.25 to 0.47 in Mediterranean and temperate regions vs. 2.3 in tropical areas. Thus, it takes on average 2.1–4 years vs. about 5 months to decompose foliage litter in Mediterranean and tropical climates, respectively. This first step of foliage decomposition occurs in several phases,

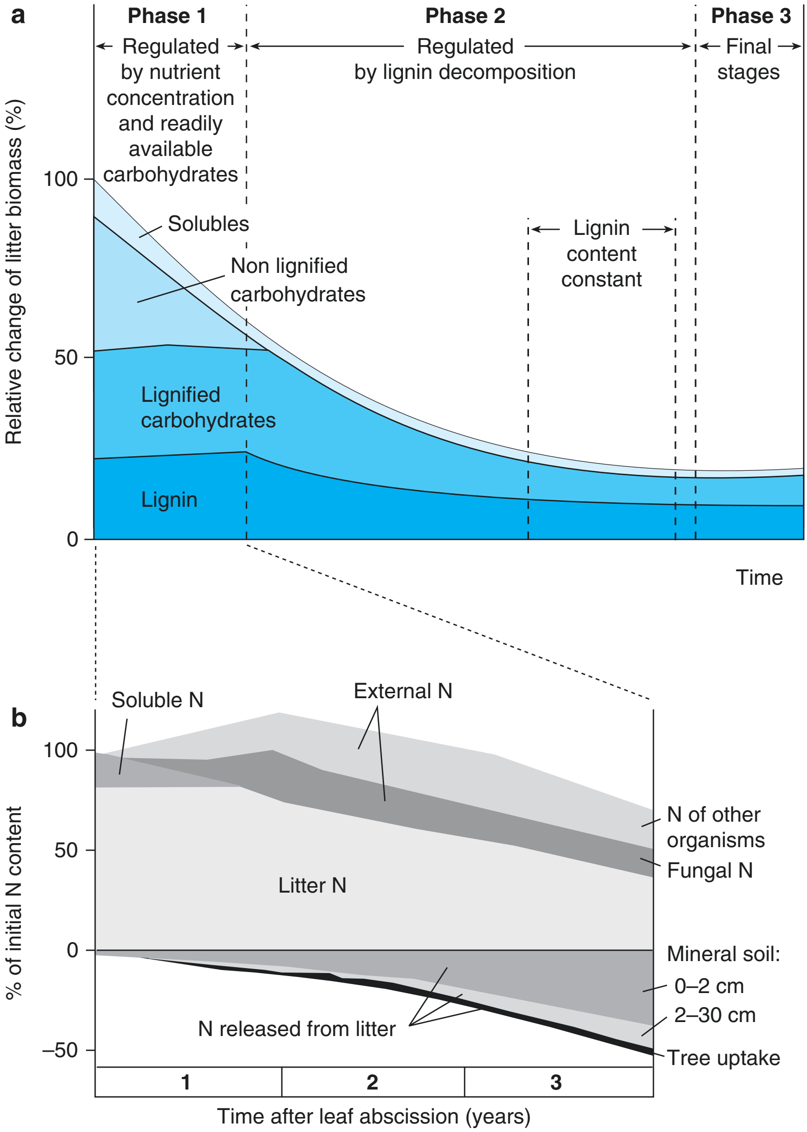


Fig. 16.14 Degradation of leaf litter from beech over time. **a** Initially, the easily available carbohydrates are consumed. Then lignin decomposition starts (after Berg and Matzner 1997). **b** Parallel with the decomposition of dry matter, decomposition of N-containing substances occurs. (Data from F. Cotrufo)

with the dynamics for C (Fig. 16.14a) being different to those for N (Fig. 16.14b). For a newly fallen leaf (leaf litter), its C content decreases because of the use of easily decomposable C compounds (sugar, hemicellulose, cellulose) by soil fauna and soil microorganisms. At the same time, the N content rises initially, as bacteria and fungi settle on the dead leaf (for beech, this takes about 1 year). Finally, N-containing substances are decomposed, and the N content of the leaf decreases as organisms retreat from the leaf (for beech, after about 3 years). After 3 years, the leaf has lost about 80% of its mass and 60% of its N content (Cotrufo et al. 2000). Further decomposition in later phases is much slower. Lignin is then decomposed by fungi, but for this process an additional C source is required (Gleixner et al. 2001).

Decomposition of wood takes much longer than leaf or fine root decomposition, often between 50 and >100 years. Reported *k*-values for coarse woody debris (>10 cm in diameter) range from 0.0025 (400 years) to 0.089 (11 years). However, these very long residence times are rather exceptions. In general, mean residence times are shorter in the tropics (8–21 years) than in temperate latitudes (21–29 years) or in high latitudes (25–28 years) (Bloom et al. 2016). Mass loss rates vary strongly with wood density and wood chemistry, but also with decomposer activities linked to environmental conditions. Due to higher lignin:N ratios, the wood of gymnosperms decomposes slower than that of angiosperms, when trees grew at the same site (Weedon et al. 2009). **Lignins** are high-molecular-mass, three-dimensionally structured compounds of phenylpropane units that enclose cellulose fibrils. Conifers form lignin from coniferyl alcohol and deciduous trees use both coniferyl and sinapyl alcohols. Grasses also use coumaryl alcohol. Degradation occurs by laccase-forming fungi (white rots), which break bonds in side chains and aromatic rings by forming oxygen radicals (Zech and Kögel-Knabner 1994). Mass loss of wood is also related to the fire history of the site (Fig. 16.15). In boreal coniferous forests, trunks killed by fire are degraded faster than in unburnt areas. Mass loss is finished after about 120 years, with part of the dead wood being burned because of periodic ground fires.

The **stabilisation** of organic matter, that is, the formation and protection of SOM, has received a lot of attention over the last decade. Stabilisation is related to chemical changes of decomposition products mediated by soil fauna (e.g. earthworms that change the chemistry of the organic residue) and microorganisms, but also to physical protection, for example, by the soil matrix, by association with minerals or occlusion in soil aggregates. Both factors can reduce the chance that organic matter will be decomposed and thus lead to the persistence of organic matter in the soil over long time periods (Schmidt et al. 2011; Cotrufo et al. 2013), contributing to long-term carbon (and nutrient) storage in soils. For example, newly formed microbial polysaccharides (bacterial slime) bind to clay and silt fractions in the soil and are thereby stabilised against further decomposition. Thus, the clay content determines the ability of soils to store C (Bird et al. 2001). In stark contrast to the initial steps of decomposition, during stabilisation, the molecular structure of the organic matter or the **recalcitrance** of organic matter as a substrate for decomposition is only marginally important. Even "easily decomposable" sugars can persist in the soil for decades when protected (or immobilised in constantly active microbial biomass), and even "recalcitrant" lignin and plant waxes can be decomposed at rates higher than the bulk soil when conditions are right. Similarly, the

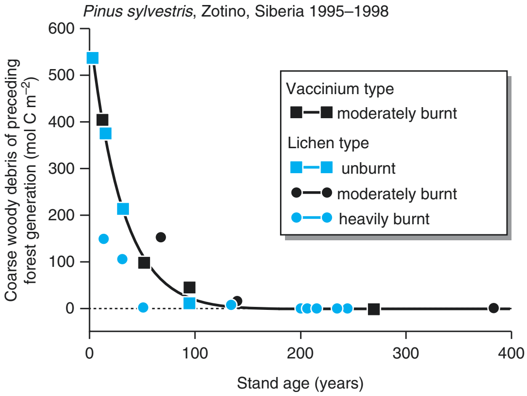


Fig. 16.15 Decomposition of dead wood after a fire in a Siberian pine forest. The mean residence time is only about 40 years, despite the cold climate. This is because of repeated fires at ground level. As these fires only burn the outside of the wood, single dead trunks can be traced back 400 years. (Wirth et al. 2002)

relevance of **humic substances** as very stable SOM fractions, formed *de novo* during decomposition, needs to be revisited. Inferred from the classical extraction methods in soil chemistry, the amount and relevance of humic substances have been largely overestimated. Their new formation is no longer considered quantitatively relevant for humus formation in soils. Nevertheless, most **soil carbon models** still use the structure and inferred decomposability of organic matter to drive their decomposition models (Chaps. 15 and 22). Instead, fire-derived organic matter has been identified as being highly relevant and can make up to 40% of total SOM in many forest and grassland soils (Box 16.2). Deep soil layers are still a black box, although globally they store more than 50% of total soil carbon pools.

Box 16.2: Black Carbon and Terra Preta Soils

A highly recalcitrant form of soil carbon, which is very difficult to degrade, is **charcoal** or **black carbon**. When organic matter is combusted under limited oxygen supply (charred), char, charcoal or soot (which can be distinguished by the molecular ratios of oxygen to carbon and hydrogen to carbon) is produced, forming condensed aromatic and carboxylic structures similar to graphite (Fig. 16.16a) (Gleixner et al. 2001; Glaser 2007). These structures are highly stable against microbial decomposition (but can be decomposed eventually).

In the central Amazon, “islands” with highly fertile soils, called **terra preta**, have been recorded, surrounded by very infertile soils, often ferralsols (Fig. 16.16b, c). These fertile soils contain about 3 times the amount of SOM, about 70 times more charcoal, higher nutrient content and a better nutrient retention capacity than their surrounding soils (Glaser 2007). These soils were formed in pre-Colombian times, about 7000 to 500 years BP, and have been used for agriculture ever since, so they are considered anthropogenic soils. The origin of the black carbon (also called **biochar**) is not entirely clear, but natural forest fires do not sufficiently explain the high black carbon content. Anthropogenic activities such as low-heat smouldering fires as used for cooking or spiritual uses have been proposed as source for the biochar. Higher microbial activities are found in terra preta soils as well as after charcoal additions to infertile ferralsols, probably due to the porous structure of charcoal, providing habitats for soil microorganisms. In addition, biochar is electrically conductive, so it can affect electron transfer processes by functioning as an electron shuttle, increasing, for example, N_2 fixation by free-living prokaryotes (Kappler et al. 2014). After the original combustion product has been oxidised on the edges by microorganisms in the soil (Glaser et al. 2002), black carbon also adds a cation exchange capacity to soils and, thus, a high nutrient retention capacity. Currently, the application of charcoal for sustainable agriculture is recommended.

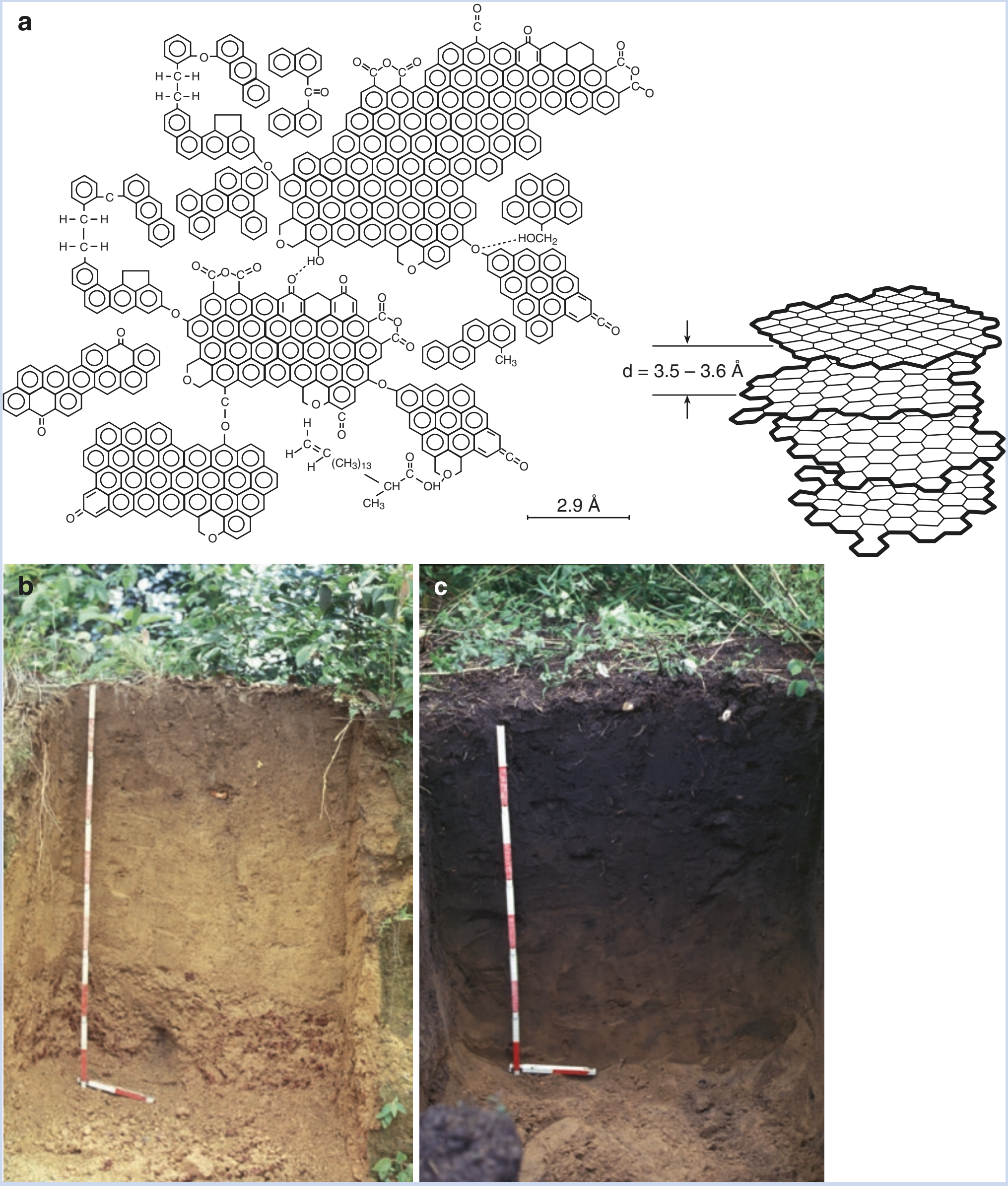


Fig. 16.16 Black carbon in terra preta soils in central Amazonia. **a** Putative structure of black carbon. In charcoal and soot, cyclic hydrocarbon molecules recrystallise into a condensed lattice of benzene rings (Gleixner et al. 2001). **b** Ferralsol, an abundant, but infertile, soil type in the tropics. **c** Terra preta, a black-earth-like anthropogenic soil in central Amazonia, also found in West and South Africa. (Photos B Glaser)

16.2.3 Net Ecosystem Production and Net Biome Production

Integrating over all assimilatory and respiratory processes taking place at the same time in a terrestrial ecosystem becomes necessary if one is interested in the response of ecosystems to management or climate or if one wants to compare flux magnitudes across ecosystem types. Measuring all processes separately and scaling them up to the ecosystem level is impossible and would introduce a huge uncertainty into the final flux estimate (Sect. 14.1, Chap. 14). Thus, one uses a micrometeorological approach (eddy covariance method, Box 16.1) to directly measure net carbon dioxide fluxes between the ecosystem and the atmosphere, that is, the **net ecosystem CO_2 exchange (NEE)** (in µmol CO_2 m^{-2} s^{-1}). NEE data are typically given using the meteorological sign convention (from an atmospheric perspective): negative values represent situations where the atmosphere loses CO_2 while the ecosystem takes up CO_2 and acts as carbon sink; positive values represent situations where the atmosphere gains CO_2 while the ecosystem loses CO_2 and acts as a carbon source. NEE is measured continuously over long time periods at high temporal resolution, typically at 10–20 Hz (10–20 times per second). The longest time series reaches back to 1992 (Harvard Forest, USA), and today data from >850 flux tower sites are available globally (Sect. 14.1, Chap. 14). Summing up NEE (generally aggregated to 30 min averages) to annual values results in **net ecosystem production NEP** (typically in g C m^{-2} $year^{-1}$), which is given as a positive number to represent a carbon sink (in contrast to NEE!). NEP is the small net difference between two large fluxes, GPP and all auto- and heterotrophic respiratory losses (Eq. 16.17), and can be approximated by NPP minus heterotrophic respiration. When no additional C inputs such as fertilisation and no additional C exports such as harvests, fire or erosion occur, NEP represents the ecosystem carbon budget, that is, the ecosystem **C sink** or **source**. However, when additional inputs and exports occur, these C fluxes need to be taken into account when calculating the ecosystem carbon budget. Then the C budget is called **net biome production (NBP)** (Eq. 16.18) (Schulze et al. 2000), even if a field or ecosystem type (and not a biome) is studied:

$$\mathrm{NEP} = \mathrm{GPP} - R_a - R_h = \mathrm{GPP} - R_e \approx \mathrm{NPP} - R_h, \qquad (16.17)$$

$$\mathrm{NBP} = \mathrm{NEP} - \mathrm{exports} + \mathrm{inputs}, \qquad (16.18)$$

where R_a is the respiration of autotrophic plants, R_h the respiration of heterotrophic organisms, and R_e the total **ecosystem respiration**, with $R_e = R_a + R_h$. Exports are additional C losses and can be harvests, C emitted as BVOCs, fire or erosion. Inputs are additional C sources such as organic fertilisers, that is, slurry and manure.

Most of the carbon enters the ecosystem as CO_2 via GPP (except organic fertilisation; see subsequent discussion). About 50% of GPP is used for NPP (Fig. 16.17). The **NPP/GPP ratio**, also called carbon use efficiency, varies with vegetation type and responds to changes in environmental conditions. Median values of NPP/GPP, considering ANPP and BNPP, range from about 0.3 for boreal forests, to 0.4 for temperate coniferous, 0.5 for tropical forests and 0.55 for temperate deciduous forests (DeLucia et al. 2007). Using remote sensing, the ANPP/GPP ratios can be estimated (Zhao et al. 2005), resulting in values between 0.35 and 0.54 for forests, 0.58 for cropland and 0.65 for grasslands, validated by inventories and flux measurements.

To know when an ecosystem is a carbon sink or a source, the net balance between gross photosynthesis and ecosystem respiration needs to be known. The **diurnal courses** of NEE clearly show when a particular process dominates. During the night, only respiration occurs. During the day, photosynthesis can be compensated by respiration (often the case in winter) or photosynthesis can overcompensate respiration (during most of the growing season). Thus, depending on the time of day and the day of the year, the ecosystem acts as either a CO_2 source (nighttime, winter) or a CO_2 sink (daytime, growing seasons). This general pattern occurs throughout the year, but environmental conditions, phenology

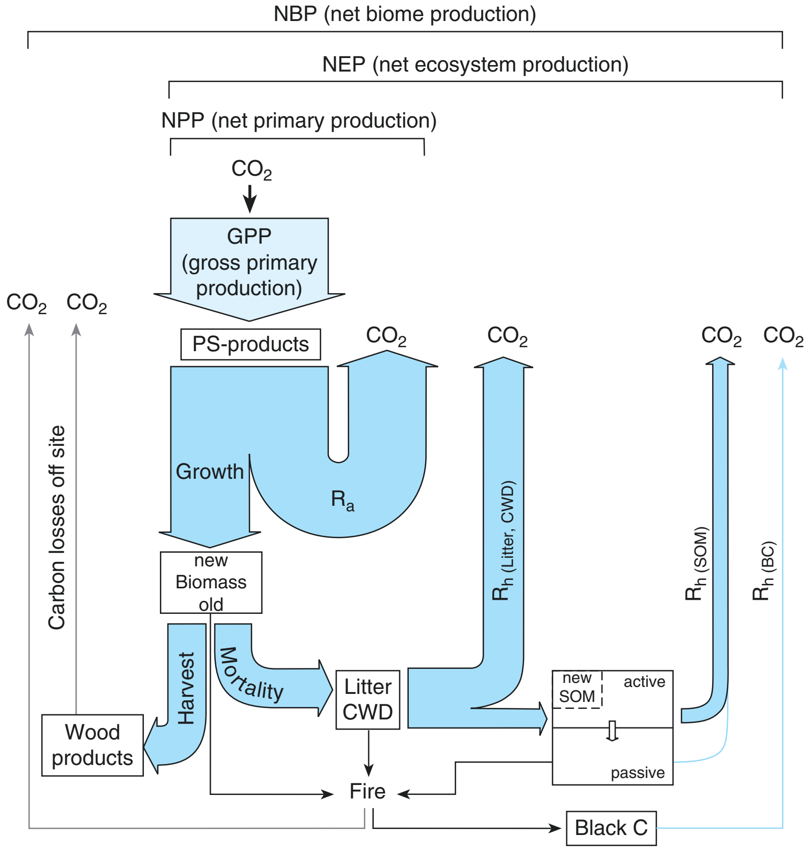


Fig. 16.17 Carbon budget of forest ecosystems. The initial process is gross primary production (GPP), which corresponds to gross photosynthesis. About 50% of the photoassimilates are used for net primary production (NPP); the rest is available for growth respiration and maintenance respiration. Accounting for heterotrophic respiration from litter, coarse woody debris (CWD) and from soils leads to net ecosystem production (NEP). If further processes are considered that remove or add C from or to the system, one talks about net biome production (NBP). CWD coarse woody debris, SOM soil organic matter, BC black carbon, R_h heterotrophic respiration, R_a respiration of autotrophic plants (After Schulze et al. 2000)

and management determine the relationship of CO_2 loss to uptake and, thus, the daily NEE flux.

The NEE of an intensively managed temperate **grassland** shows photosynthetic activities already in spring and highest uptake during summer (green and blue colours in Fig. 16.18a) (Zeeman et al. 2010). Therefore, sink activities start as early as February/March if the winter is mild (as in winter 2006/2007) but can also be delayed until April/May (as in winter 2005/2006). During the main growing season (May to September), high CO_2 uptake rates are measured during the day and only interrupted by management interventions, that is, frequent cuts of the meadow and subsequent manure applications. Then photosynthesis drops to very low rates and respiration dominates, both from the soil and the manure (orange and red colours in Fig. 16.18a). Presenting the cumulative NEE fluxes (Fig. 16.18b) reveals a typical zigzag pattern over the course of the growing season. When the grassland has grown well (NEE very negative, indicating high CO_2 uptake; data at the lowest point in a zigzag pattern), the farmer will cut the meadow to harvest the biomass and subsequently apply manure to fertilise the vegetation. Thus, after the harvest, photosynthesis is small and soil respiration dominates NEE for some days (NEE becomes less negative; data on the upward-pointing leg of a zigzag). When the regenerating vegetation carries out enough photosynthesis to overcompensate soil respiration, NEE will become more

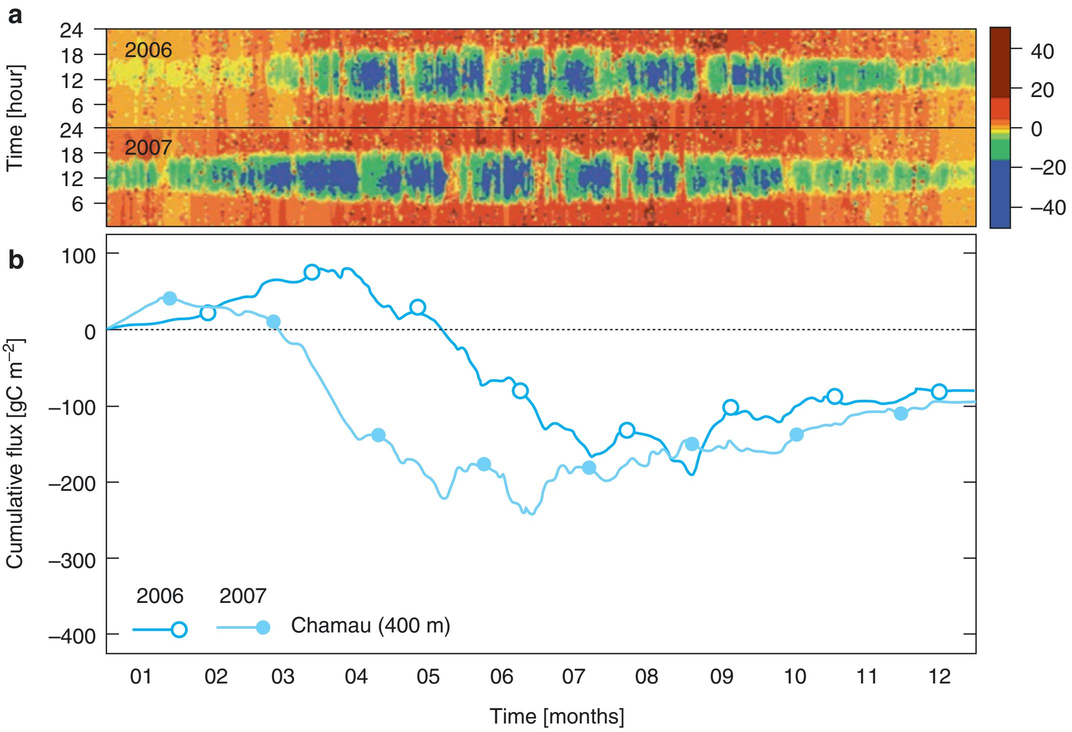


Fig. 16.18 Annual and diel courses of net ecosystem CO_2 exchange of an intensively managed grassland over 2 years. Net ecosystem CO_2 fluxes in µmol CO_2 m^{-2} s^{-1} were measured with the eddy-covariance method at Chamau, Switzerland, located 400 m asl. **a** Net ecosystem CO_2 fluxes are given in the micrometeorological sign convention over 24 h for the 2 years 2006–2007. **b** Seasonal courses of cumulative CO_2 fluxes differ between the 2 years. Frequent grass cuts (6–7 per year) and subsequent manure applications result in the typical zigzag pattern of CO_2 fluxes in grassland. (Data from M. J. Zeeman)

negative again (data on the downward-pointing leg of a zigzag). This zigzag pattern will repeat itself with each combined cut-and-manure event. At the end of the year, this grassland shows a carbon balance between assimilation and respiration of about 90 g C m^{-2} $year^{-1}$ (Fig. 16.18b). However, this balance is not yet the ecosystem carbon budget since the grassland was harvested multiple times (C exports) and received large amounts of organic fertiliser (C inputs). Accounting for the carbon in these additional exports (about 350 g C m^{-2} $year^{-1}$) and inputs (about 330 g C m^{-2} $year^{-1}$), the NBP and, thus, the ecosystem carbon sink was about 70 g C m^{-2} $year^{-1}$.

If an ecosystem does not experience additional exports and inputs during the year (e.g. by management or DOC fluxes), the final value of the cumulative NEE curve gives an estimate of the ecosystem carbon sink. This is often the case in **forests**, which are not managed on an annual basis. Evergreen forests can exhibit small sink activities also over winter, while sink activities in deciduous forests start with the leaf-out of the understorey vegetation (e.g. *Allium ursinum*, wild garlic, in temperate beech forests) and show peak NEE fluxes when the tree canopy is fully developed. Thus, **phenology** is an important driver of NEE and NEP. The longer the growing season, the higher the NEP: deciduous broadleaf forests increase their NEP by 5.6–5.8 g C m^{-2} per day of the growing season, evergreen needle-leaf forests by 3.4 g C m^{-2} day^{-1}, savannas by 3.7 g C m^{-2} day^{-1} and grasslands and croplands by 7.9 C m^{-2} day^{-1} (Churkina et al. 2005). Climate variables have large effects on NEE, but also on GPP and R_e. Both component fluxes depend primarily on light but increase with temperature and precipitation until limitations set in (heat or freezing stress, drought). This is true not only of the current year's weather but also of the previous year's weather, since carbon allocation and storage drive bud establishment and growth the following year. Furthermore, disturbances, either slow or sudden, affect ecosystem CO_2 fluxes. N deposition was shown to increase the NEP. Fire frequency and intensity affect both GPP and R_e. Drought and heatwaves affect GPP more negatively than R_e, shifting ecosystem NEE towards respiratory losses and even releasing CO_2 from SOM, sometimes worth several years of C sequestration (Ciais et al. 2005). Old forests still sequester carbon (Sect. 14.1, Chap. 14), although sometimes at lower rates than mature forests. For further examples, please see Baldocchi (2008, 2014).

Net ecosystem CO_2 fluxes, that is, the very small net difference between GPP and R_e, are measured using a micrometeorological approach (Table 16.5). However, these two very large component fluxes can be estimated using so-called **partitioning** techniques (e.g. Reichstein et al. 2005). Partitioning is typically based on the relationship of nighttime NEE (R_e only) to temperature, using relatively short time windows (often about 2 weeks). GPP is then calculated as the difference between NEE and R_e, assuming that leaf respiration during the day does not differ significantly from leaf respiration at night. Site-specific adjustments to this simple partitioning routine might be necessary, for example, when the site has been managed or a disturbance has occurred (fire, disease, extreme event). NEP is highest for forests (except boreal) and lowest for desert ecosystems (but data availability is very limited) (Table 16.5). Uncertainties are typically between 10 and 30% or between 30 and 50 g C m^{-2} $year^{-1}$. This uncertainty corresponds to about half the weight of normal printer paper (with about 80 g m^{-2}) covering 1 m^2 of ground (Baldocchi 2008). GPP and R_e estimates are much larger than NEP but follow the same patterns across ecosystem types. Fluxes of agricultural ecosystems, that is, grasslands and croplands, are comparable to those of temperate forests. While more than 850 site-years are available for NEE measurements and, thus, GPP and R_e estimates, not many NBP estimates exist, so uncertainties are very large. Those given in Table 16.5 rely on a combination of measurements and models. The **NBP/NPP ratio** can be used as a proxy for the carbon sequestration efficiency. It is reported to be 0.15 ± 0.05 for forests, 0.13 for grasslands and varies between −0.03 and 0.01 for croplands (Ciais et al. 2010; Luyssaert et al. 2010). These estimates support the more robust patterns based on NEP measurements, with forests being the largest carbon sinks, grasslands being small carbon sinks, and croplands being not carbon sinks at all but rather carbon sources.

The long-term development of the terrestrial carbon sink for any given ecosystem will depend on the fraction of how much carbon enters these sinks (e.g. expressed as NBP/NPP) and the longevity or MRT of the carbon sequestered in these sinks (Sect. 16.2.2). Both main sinks in ecosystems, wood and SOM, have MRTs that can be up to several decades

Table 16.5 NEP, GPP, R_e and NBP estimates across ecosystem types

Ecosystem type	NEP (g C m^{-2} $year^{-1}$)	GPP (g C m^{-2} $year^{-1}$)	R_e (g C m^{-2} $year^{-1}$)	NBP (g C m^{-2} $year^{-1}$)
Tropical rainforest	403 ± 102	3551 ± 160	3061 ± 162	NA
Temperate deciduous forest	311 ± 38	1375 ± 56	1048 ± 64	For Europe:
Temperate coniferous forest	398 ± 42	1762 ± 56	1336 ± 57	75 ± 20
Boreal coniferous forest	131 ± 79	973 ± 83	824 ± 112	NA
Savanna	360 ± 17	1380 ± 70	1020 ± 20	200
Grassland	247 ± 67	2296 ± 80	2104 ± 32	104 ± 73
Cropland	240 ± 113	1246 ± 248	1006 ± 222	−11 ± 33
Desert	28 ± 16	170 ± 39	143 ± 23	NA
Tundra	5 – 67[a]	15 – 130[a]	5 – 64[a]	NA

Means and standard deviations are given. Positive NEP values represent CO_2 uptake fluxes, but not C sinks (fertiliser inputs and harvest outputs are not considered yet). Negative NBP represents C sources, positive NBP represents C sinks. Data from Beringer et al. (2007), Ciais et al. (2010), Kutsch et al. (2010), Lafleur et al. (2012), Luyssaert et al. (2010), Soussana et al. (2007), Xie et al. (2015) and Zeeman et al. (2010)

NA: No data available

[a] Fluxes in g C m^{-2} $July^{-1}$

Table 16.6 Mean residence times of entire ecosystems

Ecosystem type	Mean MRT (years)	Range MRT (years)
Tropical rainforest	14.2	11.6–18.2
Temperate forest	23.5	18.9–30.8
Boreal forest	53.3	45.4–73.4
Savanna	16	12.2–22.1
Grassland	41.3	32.8–54.6
Cropland	22.1	17–30.1
Desert	36.3	27.6–49.9
Tundra	65.2	44.7–78.0

Means and ranges (2.5th and 97.5th percentiles) are given. MRT (turnover times) are calculated as the ratio of ecosystem carbon stocks in vegetation and soils to GPP, assuming steady-state. Data from Carvalhais et al. (2014)

(tropical, temperate climate) to centuries (boreal, arctic climate), but only very small amounts of C enter these long-term sinks. Integrating over all vegetation and soil carbon stocks, global **ecosystem MRT** has been calculated as 22.5 years, ranging from 18.1 to 29.4 years (Table 16.6) (Carvalhais et al. 2014). Thus, the longevity of global carbon sinks is rather short and thus sensitive to environmental change. The longest MRTs are found in tundra and boreal forests, while the shortest MRTs are found in tropical forests and savannas. Averaging all MRT > 75°N results in a MRT of 255 years, compared to 15 years in the equatorial tropics. Ecosystem MRTs vary with annual air temperature and annual precipitation, and climatic variables are predicted to change in the future (Chap. 23).

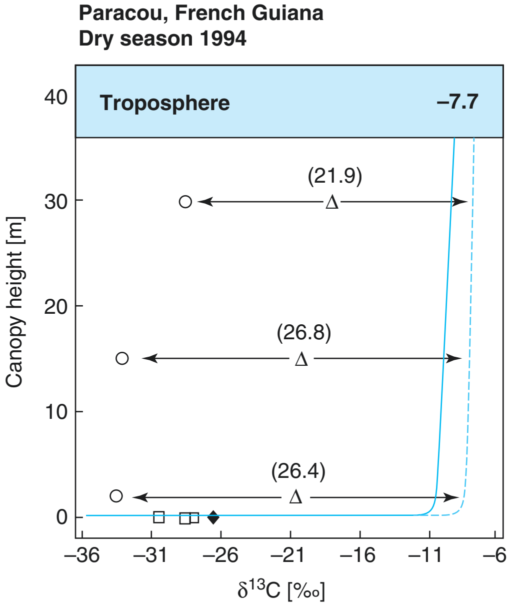


Fig. 16.19 Conceptual model of stable carbon isotope ratios δ^{13}C and leaf carbon isotope discrimination Δ (in per mil compared to an international standard) in a tropical forest in French Guiana. Foliage values (*circles*) are given for different heights within the canopy. Soil and litter (*squares*) and soil-respired CO$_2$ (*diamond*) signatures are given. Canopy CO$_2$ values (*lines*) are given for night- (solid) and daytime (dashed). (Buchmann et al. 1997)

Stable carbon isotopes as well as radiocarbon (Sect. 16.2.1) data provide further insights into the carbon turnover and the fate of carbon within an ecosystem. The source of carbon dioxide for plant photosynthesis is atmospheric CO$_2$, which currently has a δ^{13}C value of about −8.3‰ (declining due to fossil fuel burning; Sect. 23.3 in Chap. 23). Within the canopy, atmospheric CO$_2$ is mixed with respired CO$_2$, which has a δ^{13}C value close to the organic substrate being respired (between −30 and −18‰ for C$_3$ plants), resulting in canopy δ^{13}C profiles between the atmospheric background at the top of the canopy (Fig. 16.19) and a mix of both CO$_2$ sources close to the ground (reaching values of around −14 to −16‰). δ^{13}C gradients in canopy CO$_2$ vary with time of day, being small during the day when turbulent mixing occurs within the canopy and large at night under stable atmospheric conditions. This canopy CO$_2$ with its δ^{13}C is then the source for photosynthesis. Discrimination against ^{13}CO$_2$ happens during CO$_2$ diffusion into foliage as well as during CO$_2$ fixation (and respiration) (for detailed reviews see Ghashghaie and Badeck 2014 and Werner and Gessler 2011). Thus, depending on where the foliage is located within a canopy, not only the ecophysiology of foliage but also the source δ^{13}C determines the foliar δ^{13}C values in any ecosystem. As a result, foliage in the top canopy has higher δ^{13}C values than foliage closer to the ground (Fig. 16.19). In general, 30% of the gradients in foliar δ^{13}C are due to canopy CO$_2$, about 70% to ecophysiology (Buchmann et al. 2002). If foliage senesces and becomes litter and SOM, δ^{13}C values increase owing to fractionation during mineralisation and processes related to decomposition. Similarly, soil-respired CO$_2$ has a higher δ^{13}C than SOM. For further details, please refer to Brüggemann et al. (2011).

Moreover, the δ^{13}C in foliage integrates over the entire lifespan of a leaf, while δ^{13}C litter integrates over all species currently present in an ecosystem. In turn, δ^{13}C of SOM integrates over current and past vegetation. This is particularly interesting when vegetation had changed from **C_3 to C_4 vegetation** or vice versa, since carbon isotope discrimination differs strongly between these two photosynthesis types (Sect. 12.2, Chap. 12). Thus, δ^{13}C of SOM within a soil profile can give information about the dominant vegetation, forest or (C_4) grassland, over time, particularly when the age of SOM is known. The difference between the δ^{13}C of atmospheric CO_2 entering the ecosystem for GPP and the δ^{13}C of respired CO_2 of ecosystems, the so-called **isotopic disequilibrium**, is an important piece of information for global inverse atmospheric models that are used to estimate global sinks and sources.

16.2.4 Fluxes of CH_4 and Other Biogenic Volatile Organic Compounds

Although CO_2 dominates the discussion about the carbon dynamics of ecosystems, CO_2 is not the only carbon-containing gas being exchanged between ecosystems and the atmosphere: the exchange of methane (CH_4) and other **BVOCs** are highly relevant for many ecosystems as well.

Biogenic **methane** is produced by bacteria (*Archaea*; methanogenic bacteria) in anaerobic zones in soils and is a potent greenhouse gas (Fig. 16.20) (Chap. 23). The highest CH_4 production is thus found in wet or waterlogged soils, for example, in rice paddies and wetlands. However, between 60 and 90% of the CH_4 produced is oxidised to CO_2 by **methanotrophs**, that is, bacteria widespread in soils, representing a large sink for CH_4, which is relevant for global change (Le Mer and Roger 2001). CH_4 emissions from soils to the atmosphere can happen via diffusion or as bubbles from wetland soils (called **ebullition**), but also via vascular plants. Here, the **aerenchyma** of wetland plants (such as *Carex* species or *Eriophorum vaginatum*) acts like a chimney for CH_4, bypassing potential oxidation in the upper soil layers, thereby increasing **CH_4 emissions** from these ecosystems. The aerenchyma of aquatic or wetland plants (mainly

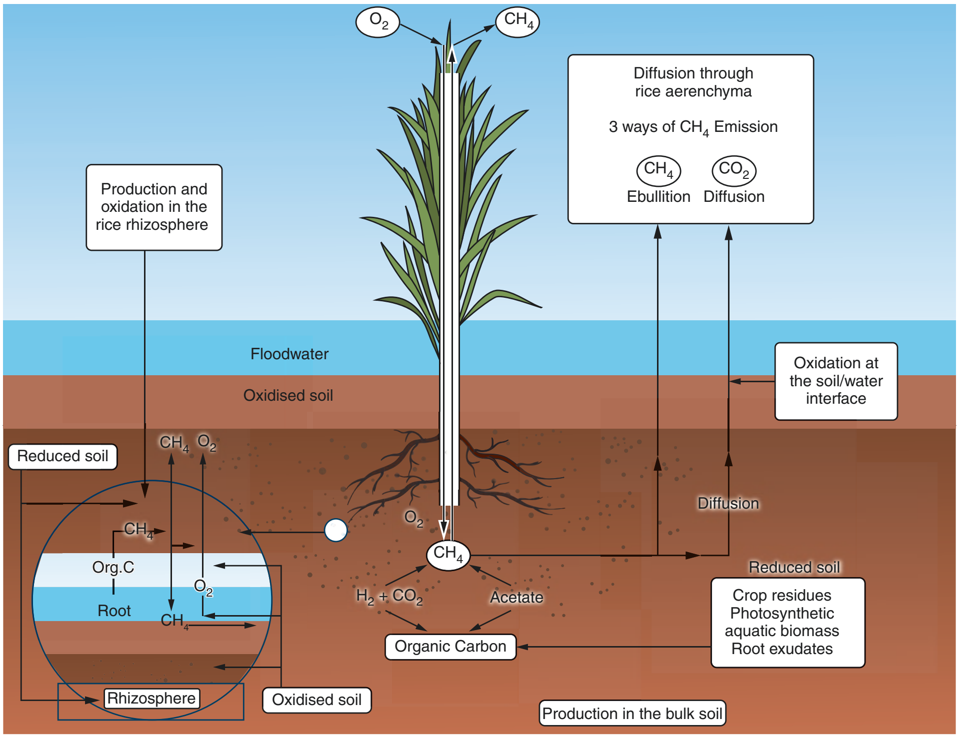


Fig. 16.20 CH_4 emissions from soils, mediated by vascular plants (Le Mer and Roger 2001)

in herbaceous plants but also in *Alnus*) is a modified parenchyma tissue with large cavities formed under anoxic conditions to mediate gas exchange (mainly of oxygen) between shoots and roots. Outgassing of CH_4 via aerenchyma tissues can be responsible for up to 90% of the CH_4 emissions during the growing season. The chimney effect increases with higher soil carbon contents, is higher under convective than under stable atmospheric conditions, and has been reported to scale with stomatal conductance (Joabsson et al. 1999; Le Mer and Roger 2001).

Plants emit a wide range of BVOCs such as **isoprene** (C_5H_8) and **methanol** (CH_3OH), the two most abundant BVOCs after CH_4 (Guenther et al. 2012), but up to 1700 substances have been reported (Loreto and Schnitzler 2010). Plants use BVOCs to communicate with each other, but also with other organisms, for example, as a wound signal (Sect. 19.3 in Chap. 19), and constitute up to 2–5% of the net carbon gain of heavily emitting broadleaf trees (e.g. *Eucalyptus*, *Quercus* and *Populus*). But BVOCs have also been found to relieve oxidative and thermal stresses. Two environmental factors typically increase foliar BVOC emissions, temperature and light, while water stress does not show an effect. While many of these flux measurements were made using small leaf enclosures (Guenther et al. 2012), such fluxes have also been measured at the ecosystem level using micrometeorological techniques (Sect. 14.1 in Chap. 14) (Wohlfahrt et al. 2015). Although these measurements supported environmental and biological controls, they also provided clear new evidence that, for example, ethanol fluxes are bi-directional: into and out of terrestrial ecosystems. In addition, land-use practices, such as clearing of understorey vegetation in forests or cutting of meadows with subsequent manure application, increased methanol emissions significantly over a couple of days (Fig. 16.21). Under a future climate, BVOC emissions are expected to increase owing to global warming, with large effects on atmospheric chemistry (Peñuelas and Staudt 2010).

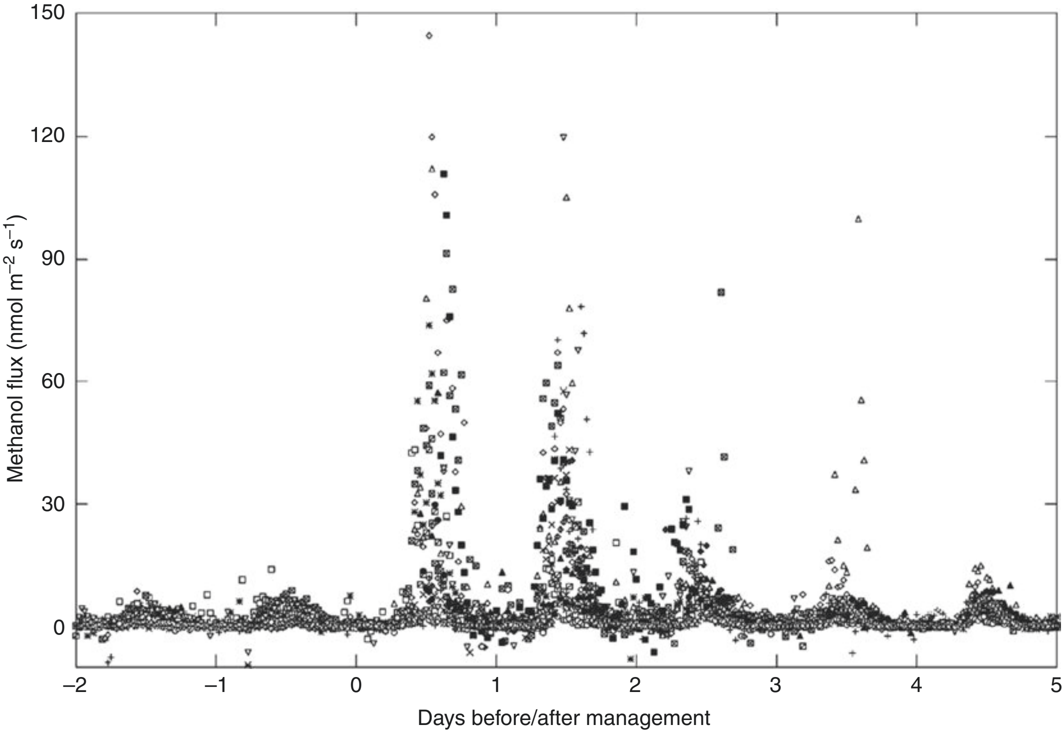


Fig. 16.21 Methanol emissions from three temperate grasslands in Austria and Switzerland measured using micrometeorological techniques. Large peaks can be seen 1–3 days after the corresponding management events. Different symbols depict different sites. (Wohlfahrt et al. 2015)

16.3 Nitrogen Fluxes in Terrestrial Ecosystems

The transformations of nitrogen in terrestrial ecosystems probably correspond most closely to what is generally called a biogeochemical cycle (Fig. 16.22). Elemental nitrogen N does not occur in nature, and most nitrogen is found in the atmosphere as gaseous N_2. This N_2 cannot be directly used by higher plants unless they are in symbiosis with microorganisms, for example, Fabaceae and **rhizobia**. In ecosystems, nitrogen occurs in inorganic oxidised and reduced forms (e.g. nitrate NO_3^- and ammonium NH_4^+) or together with C in organic compounds, particularly as amino groups (C–NH_2) or amide groups (C–N–C). Thus, the C and N cycles are tightly coupled. In what follows, “N” refers not to N_2 but to mole equivalents of nitrogen in different oxidised or reduced forms.

Overall, the nitrogen cycle in terrestrial ecosystems is characterised by interactions of organisms at different trophic levels (microorganisms, plants, animals, mainly soil fauna and herbivores), multiple origins of the same N species (e.g. NO and N_2O) and plant uptake of different N species (NH_4^+, NO_3^-, small amino acids). The entry point of nitrogen into ecosystems happens via **nitrogen fixation** (Fig. 16.23a). The change of gaseous N_2 from the atmosphere into organic compounds is achieved by N_2-fixing bacteria, which occur as free-living **cyanobacteria**, as bacteria in nodules of Fabaceae or as symbionts with other higher plants (e.g. alders, cycads plants) (Fig. 16.23b–d) and with fungi (e.g. lichens, biological crusts). Electrons are derived from the degradation of organic substances and used to reduce N_2 to NH_3. N_2 fixation is a process that needs a lot of energy, that is, 16 equivalents of ATP are hydrolysed during this reaction:

$$\begin{aligned} &N_2 + 8H^+ + 8e^- + 16ATP \\ &\rightarrow 2NH_3 + H_2 + 16ADP + 16P_i \end{aligned} \qquad (16.19)$$

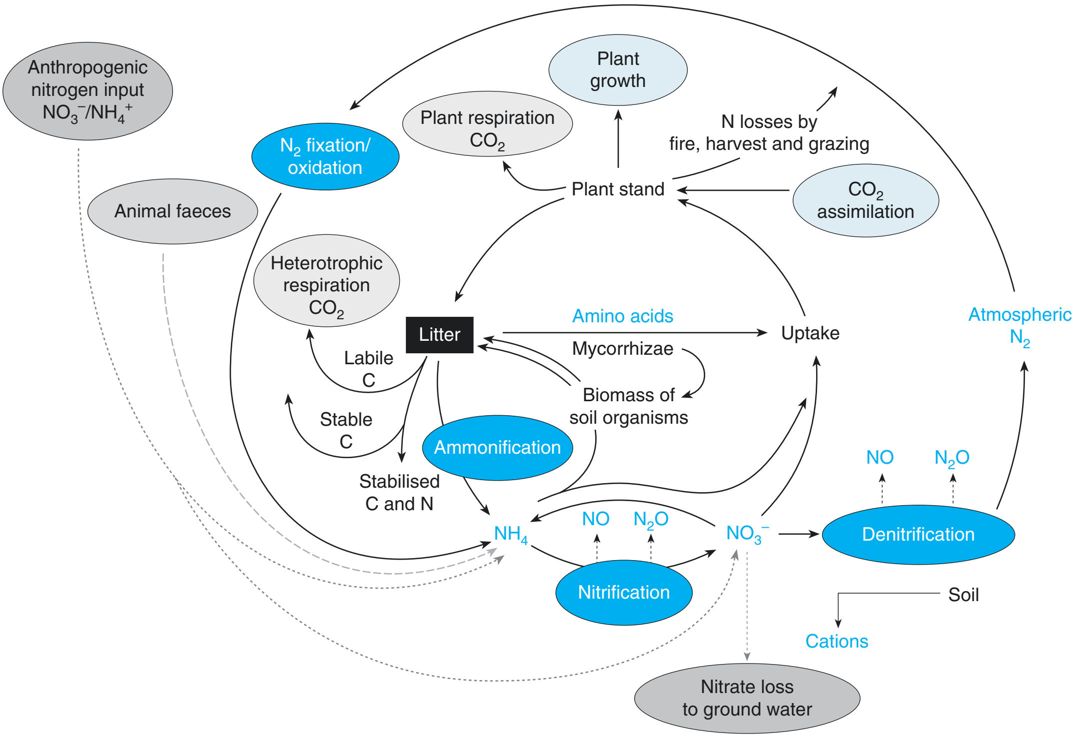


Fig. 16.22 Nitrogen cycle in terrestrial ecosystems with a focus on plant–microbe interactions (Modified from Schulze (2000)). Not all microbial processes are depicted

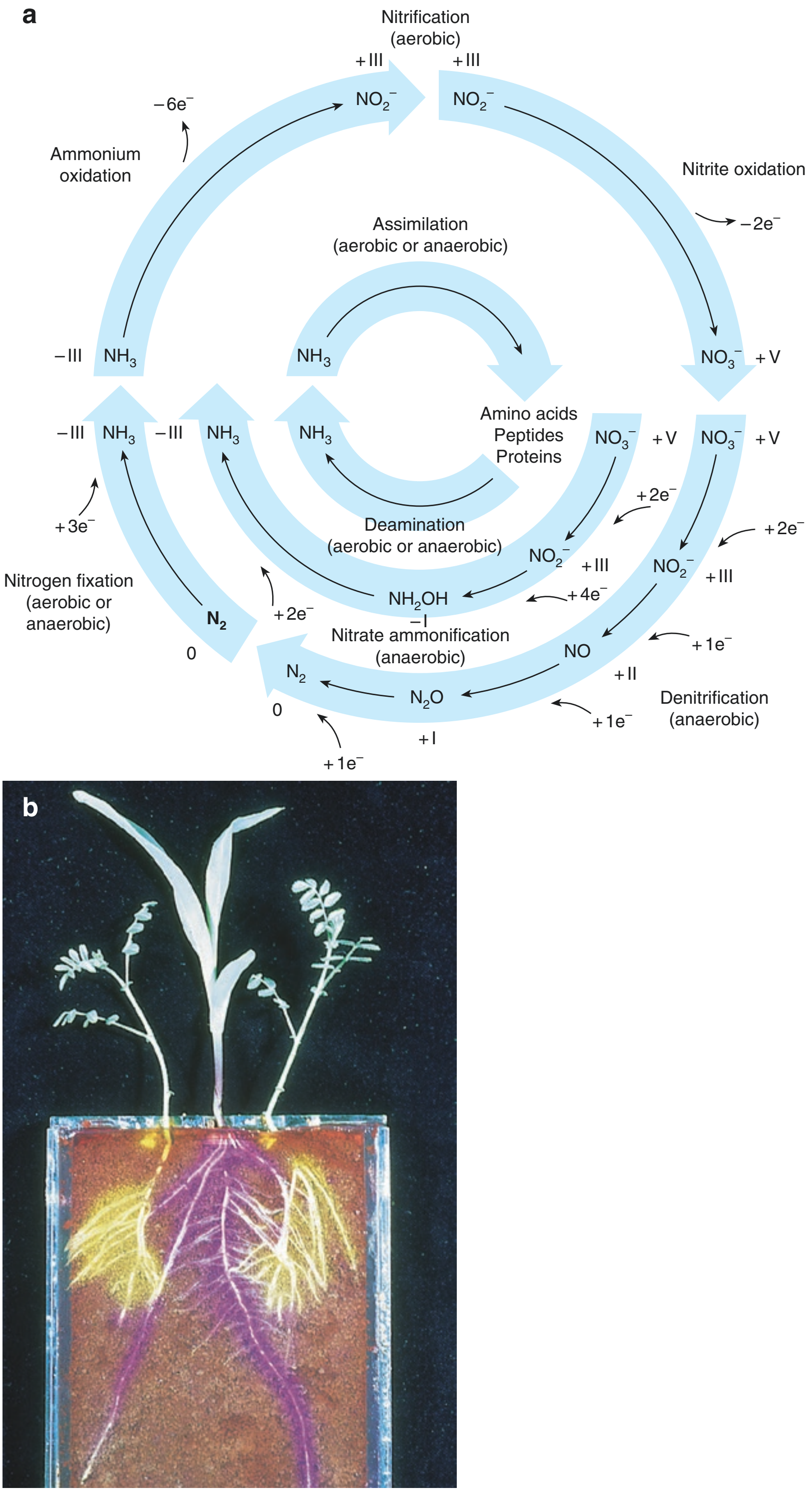


Fig. 16.23 Changes in oxidation states of N during N transformations and impacts of N_2 fixation. **a** Functional groups of microorganisms in biogeochemical nitrogen cycle. Blue arrows indicate reactions that occur within a single organism. Small black arrows are intermediate products. The figure also shows the oxidation state and the uptake or loss of electrons (after Meyer 1994). **b** Soil acidification as a result of N_2 fixation: During N_2 fixation, some plant roots release protons (derived from the dissociation of amino acids in the roots to keep ionic balance), which leads to acidification in many soil types. The low pH in the soil close to the pea root is in contrast to that close to the maize root, which raises the pH by absorbing nitrate. (Photo courtesy E. George). **c**, **d** *Macrozamia communis* as an example of the symbiosis between a plant and atmospheric N_2-fixing bacteria. The cycads form on their hypocotyls so-called coralloid (or coral-like) roots from the cortex that contain cyanobacteria recognisable by the blue-green colouring of roots. Several species of *Macrozamia* grow in the nutrient-deficient forests of Australia. (Photo: E.-D. Schulze)

Fig. 16.23 (continued)

N_2 fixation is low when N availability in the soil is high (e.g. in agriculture), because plants then use inorganic N forms instead of the energy-intensive N_2, or when P availability to the plant is low, because of the high need for ATP (Eq. 16.19). One can see already from this first reaction in the N cycle that the oxidation number of N changes depending on the N compound in question (Fig. 16.23a). In addition to N_2 fixation by bacteria, N_2 can also be oxidised by lightning or fire (for further details, Sect. 21.2 in Chap. 21).

In the reduction state of NH_3, nitrogen can be transformed in many metabolic processes without further changing its state. Only during the transformation of organic substances in the soil are electrons removed from nitrogen via binding to oxygen. A veritable "zoo" of very different soil bacteria is involved to handle the electrons. Distinction is made between the following dominant reactions. Transformation of NH_4^+ into oxidised nitrogen occurs via **ammonification** (to nitrite NO_2^-) (Eq. 16.20) and via **nitrification** (to nitrate NO_3^-) (Eq. 16.21):

$$4NH_4^+ + 6O_2 \rightarrow 4NO_2^- + 4H_2O + 8H^+, \tag{16.20}$$

$$2NO_2^- + O_2 \rightarrow 2NO_3^-. \tag{16.21}$$

Autotrophic soil bacteria of the genera *Nitrosomas* (ammonification) and *Nitrobacter* (nitrification) are responsible for these reaction and use the energy released as energy sources. The real reactions are (even more) complicated (than shown), as for example during the formation of nitrite the oxygen used as electron acceptor comes not from O_2 but from water. During the conversion of ammonium to nitrate, losses of intermediate products, particularly the gases NO_2, NO and N_2O, are also possible (Fig. 16.22). These losses affect the radiation balance of the Earth (Chap. 9).

In addition, microorganisms are able to use the oxidised NO_3^- as an electron acceptor, thereby gaining the oxygen required for oxidation of other substrates (**anaerobic nitrate ammonification**, also called **nitrate respiration**). NO_3^- thus returns to the reduction state of NO_2^- (Eq. 16.22) or directly into NH_4^+ (Eq. 16.23):

$$C_6H_{12}O_6 + 12NO_3^- \rightarrow 6CO_2 + 6H_2O + 12NO_2^-, \tag{16.22}$$

$$\begin{aligned} &C_6H_{12}O_6 + 3NO_3^- + 6H^+ \\ &\rightarrow 6CO_2 + 3NH_4^+ + 3H_2O. \end{aligned} \tag{16.23}$$

To close the N cycle of an ecosystem, nitrate needs to be transformed into molecular N_2 again. This takes place under anaerobic conditions during **denitrification**. Nitrate serves as electron acceptor. In addition, harvests, fire and leaching cause further N losses (Sect. 16.3). Denitrification is not just one reaction but multiple reactions that can take place in different organisms and that do not necessarily achieve the final product N_2. Depending on soil pH, redox conditions and other soil chemical conditions, products of intermediate steps, particularly NO_2, NO and N_2O, can be released, similar to the release during ammonification. The total balance of denitrification is

$$2NO_3^- + 10e^- + 12H^+ \rightarrow N_2 + 6H_2O. \tag{16.24}$$

Plants are able to take up different N species, NH_4^+ as well as NO_3^- and small amino acids (Chap. 11). For more details on the consequences of N uptake for biodiversity, Sect. 20.4 in Chap. 20. Uptake can be below-ground via roots, but also above-ground. Here, atmospheric N deposition comes into play. Anthropogenic sources of reactive nitrogen include NO_x, originating from burning and combustion processes, and NH_3, mainly from livestock, fertilisation, sewage systems or industrial production of ammonium. The **N deposition** in ecosystems from such sources often exceeds 5 kg N ha^{-1} year^{-1} (Sect. 21.2, Chap. 21). In some areas with intensive industry or agriculture, N deposition can reach 20 to >50 kg N ha^{-1} year^{-1} (Bobbink et al. 2010). N deposition has been shown to be one of the main drivers for changing species composition in many ecosystems, mainly due to the outcomes of resource competition. In addition, N inputs into ecosystems trigger soil acidification and can (Sect. 16.4). Using **stable nitrogen isotope labelling**, the fate of N deposition can be followed. It turns out that plant biomass distribution within an ecosystem is not a good indicator of short-term N retention (Buchmann et al. 1996). Understorey vegetation was a larger N sink (9–15%) than 15-year-old *Picea abies* trees (3–7%), although tree biomass was a factor 4 larger than understorey biomass. The main N sink was the soil (79–87%), particularly the top soil (46–63%). A recent meta-study revealed that soil carbon stocks were a good predictor of ^{15}N tracer retention in 48 ecosystems (Templer et al. 2012). Thus, soils represent a large sink for atmospheric N deposition, which can prevent N leaching as long as N deposition stays below approx. 46 kg N ha^{-1} year^{-1}.

Plant annual **N requirements** can be met by N mineralisation, N_2 fixation and N deposition or fertilisation. But also internal N fluxes, for example, remobilisation of amino acids prior to leaf shedding, can contribute to meeting these N requirements, although the extent varies widely. For example, N concentrations in litter vary between 5 and 10 mg g^{-1} dry matter in needles and leaves, up to 50 mg g^{-1} dry matter in crops and forage plants, and between 1 and 5 mg g^{-1} dry matter in wood. In a temperate beech forest, about 3 t dry matter ha^{-1} of litter reaches the soil each year, providing an annual input of plant-derived N of about 15–30 kg N ha^{-1} $year^{-1}$ for litter decomposition and mineralisation and, thus, in turn for plant uptake. On the other hand, the N requirements of a temperate spruce forest in Germany could not be met by soil N availability alone: about 12% of annual N requirements were met by atmospheric N deposition via **above-ground N uptake** in the canopy (Horn et al. 1989), compared to 10% in Eastern US conifer sites (Sievering et al. 2000). Nave and Curtis (2011) estimated that about half of the N deposition is intercepted and taken up in forest canopies.

The N supply via **N mineralisation** (i.e. ammonification and nitrification) is highly variable with respect to both the chemical species and the amount. At very low supply (N deficiency) and in acidic soils, fungi are the dominant microorganisms in the soil (Smith and Read 2008). They can make organic nitrogen available via proteases, which are particularly active at low pH, that is, fungi acidify the substrate by releasing protons and thus directly take up organic nitrogen from litter. Fungi generally have a higher N requirement than plants since in several species the cell walls are formed by N-rich glucosamine (chitin). Fungi also require carbohydrates that they obtain as mycorrhizae either directly from plants or as saprophytes living on organic substances from the decomposition of litter and debris. **Mycorrhizal fungi** supply amino acids derived from protein degradation to the plant, in exchange for carbohydrates. In boreal coniferous forests, this “short-circuited” nitrogen cycle, bypassing mineralisation by microbes, is so effective that no free nitrate or ammonium may be found in the soil solution (Wallenda et al. 2000). Despite the dominance of fungi in the degradation of organic substances and in the uptake of N in boreal forests, there are also ammonium-forming and nitrifying bacteria, as shown by the presence of spores that become active after long incubation times (Persson et al. 2000). Ammonium and nitrate only occur in soil solutions in boreal climates when the supply of calcium is high, so the soil pH increases (Nordin et al. 2001). Bacteria are more effective than fungi at mineralizing organic matter at higher pH values. Under these conditions, nitrate and ammonium can be detected in the soil solution as the main N products of decomposition (Sect. 16.2). In soil, oxidation and reduction of nitrogen compounds can take place concurrently in all horizons, since the inside of soil aggregates provide oxygen-free (anaerobic) zones.

An excess of ammonium or nitrate, also termed **nitrogen saturation**, occurs when external supply (by N deposition, fertilisation) or formation in the ecosystem (by mineralisation) exceeds consumption (e.g. by seasonal variation of growth). Nitrate leaching of 5 kg N ha^{-1} $year^{-1}$ is used as an indicator for N saturation thresholds. This has very significant consequences for the ecosystem (Sect. 16.4). Ammonium excess causes the release of cations, particularly K^+ and Al^{3+} from clay minerals (Chap. 11). In contrast, the highly mobile nitrate ion is not bound to the soil exchanger. Thus, nitrate excess can lead to **nitrate leaching** to lower soil horizons, but also to groundwater and, further, drainage systems. This loss of anions is coupled to an equimolar loss of cations. Deposition of N from air pollutants often accelerates N transformations and leads to increased nitrate loss, even without interaction with organisms in the ecosystem (Durka et al. 1994; de Vries et al. 2003). As a result of high N deposition rates and negative environmental effects, the **critical load concept** was developed in the 1980s. It calculates a threshold of N deposition for ecosystems below which one does not expect any negative effects. The set critical load for most temperate forests is between 10 and 20 kg N ha^{-1} $year^{-1}$. Over time, many studies have now identified the real critical loads. They range from 5 to 10 kg N ha^{-1} $year^{-1}$ for boreal forests, tundra, bogs and alpine ecosystems to 20–30 kg N ha^{-1} $year^{-1}$ for low- and medium-elevation hay meadows (Bobbink et al. 2010). The highest critical loads, 30–40 kg N ha^{-1} $year^{-1}$, have been reported for salt marshes. Still, more than 25% of all European forests suffer under N deposition rates higher than their corresponding critical loads. However, long-term fertilisation trials in Swedish forests contradict the notion that high N deposition directly translates to N leaching. Despite N fertilisation rates between 20 and 100 kg N ha^{-1} year^{-1} (as ammonium nitrate, adding up to about 2000 kg N ha^{-1} over 30 years), no N leaching occurred; instead N additions were used for increased forest growth (Binkley and Högberg 2016). Magnani et al. (2007) found a very strong positive relationship between net ecosystem production (Sect. 16.2) and wet N deposition (<15 kg N ha^{-1} year^{-1}) and questioned the risk of widespread N saturation under natural conditions. However, they were heavily criticised for their assumptions (de Vries et al. 2008).

16.4 Cation Fluxes in Terrestrial Ecosystems

Cation supply (in particular of K^+, Mg^{2+}, Ca^{2+}) occurs mainly from chemical **weathering** of primary minerals (Chap. 11) or via dust particles and sea spray entering the ecosystem from the atmosphere. Examples of **dust** inputs are the formation of loess in the post-glacial period (Blume et al. 2010), the supply of dust from the Sahara to the Amazon delta (Worobiec et al. 2007) and buffering of sulphur-containing emissions by industrial dusts in the 1960s, which delayed acidification of soils, as the ionic charge of deposited material was neutral. The deposition of sea salts from **sea spray** in coastal areas, that is, sea salt aerosols formed from the ocean, results in strong gradients of Ca^{2+}, Na^+ and Mg^{2+}, as well as Cl^- and SO_4^{2-} ions deposited on plant foliage to interior areas (Gustafsson and Franzen 2000).

Cations are taken up by roots and incorporated into plant tissues, where they remain for months to decades depending on foliage lifetimes and decomposition rates (Sect. 16.2.2). However, the return of cations into the soil occurs not only via decomposition but also through leaching from the canopy. **Canopy leaching** is a consequence of ammonium uptake from atmospheric pollution during which cations are leached buffering the input of protons. Thus, cation concentrations in throughfall are often larger than in bulk precipitation (Sect. 16.1). The accumulation of cations in the litter layer and in soil organic material and dense root systems in the top soil horizons enable direct resupply of cations from decomposing organic material to plants, particularly under nutrient-limited conditions (e.g. tropical and boreal systems). However, cations released from organic matter can also be leached from the soil together with **DOC**, for example, organic acids. As a consequence, cation concentrations (also aluminium and iron) in the soil solution of upper soil layers decrease and bleached horizons are formed, especially in nutrient-poor, sandy soils (eluvial E horizons). Alkaline saturation increases only in deeper soil layers (B and C horizons).

Table 16.7 Cation balance in a spruce forest (in mmol m^{-2} year^{-1})

	Calcium	Potassium	Magnesium
Soil			
Atmospheric input	25	19	10
Leaching from canopy	10	25	1
Weathering	79	52	36
Release from litter	189	54	29
Leaching into groundwater	−45	−21	−33
Available in soil	*258*	*129*	*43*
Plants			
Incorporation into wood	−59	−50	−13
Leaching from canopy	−10	−25	−1
Litter	−189	−54	−29
Total plant uptake	*−258*	*−129*	*−43*

The dynamics from uptake to release are very different for individual elements. In a spruce stand on granite, the calcium fluxes were about twice those of potassium and exceeded those of magnesium five-fold (Horn et al. 1989). As leaching into groundwater occurs for all elements at about the same magnitude, different amounts of Ca^{2+}, K^+ and Mg^{2+} must be supplied via the weathering of primary minerals in the soil profile (Table 16.7). Since weathering of granite is slow, this leads to decreased soil pH and to low forest productivity on acidic bedrock.

Ecosystems cannot avoid the loss of cations. Even in ecosystems without management and with a high root density, cations released during decomposition can be leached with organic acids into deeper layers or downslope. This process is known from the boreal zone as **podzolisation** (Blume et al. 2010; Weil and Brady 2009) and occurred in Scandinavia, for example, after the land rose (after glaciation) and was evident after only 400 years (Starr 1991). Leaching of cations from an ecosystem into groundwater and lateral transport into other ecosystems may have far-reaching consequences for nitrogen cycles of "supplier" and "receiver" systems. Two interactions are possible (Fig. 16.24). (A) Nitrate (or sulphate) is leached and carries cations away, leading to an increased total turnover; this is the "classic" assumption. (B) DOC is leached and cations accumulate in deeper soil horizons. As DOC is microbiologically mineralised during transport, there is secondary cation accumulation, leading to higher pH values deeper in the soil profile or downslope. Thus, nitrogen mineralisation also increases, allowing for high tree productivity (mechanism B in Fig. 16.24). The transport of DOC appears to dominate in the boreal climate (Högberg 2001) on acid substrates (granite), effecting relocation of cations, for example, on a slope (Guggenberger and Zech 1993). It is often assumed that other vegetation types, particularly in the tropics, are so well adapted to poor nutrient conditions that cation losses can be ignored. However, Chadwick et al. (1999) have shown that cation losses also occur in tropical climates, that is, for vegetation on lava flows of different ages (Fig. 16.25). As soon as weathering rates decline (after about 20,000 years), the ecosystems are supported by the atmospheric deposition of cations from Central Asia more than 6000 km away.

Natural processes causing cation loss may be accelerated by strong acids, particularly if they form acid anions that then enter the groundwater. Sulphate, but also chloride and nitrate, belongs

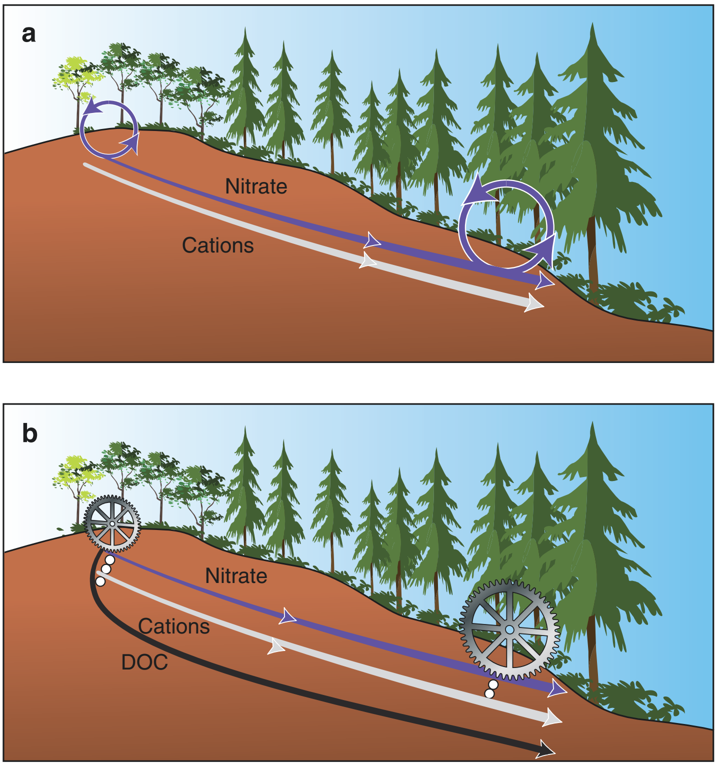


Fig. 16.24 Schematic representation of nitrate and cation fluxes downslope resulting from groundwater run-off in a boreal forest in Scandinavia. Two different mechanisms could explain the high productivity of trees downslope. **a** High nitrate leaching and associated cation loss that accumulate downslope and increase resource availability for growth downslope. **b** Low nitrate loss but large cation loss in association with DOC. (After Högberg 2001)

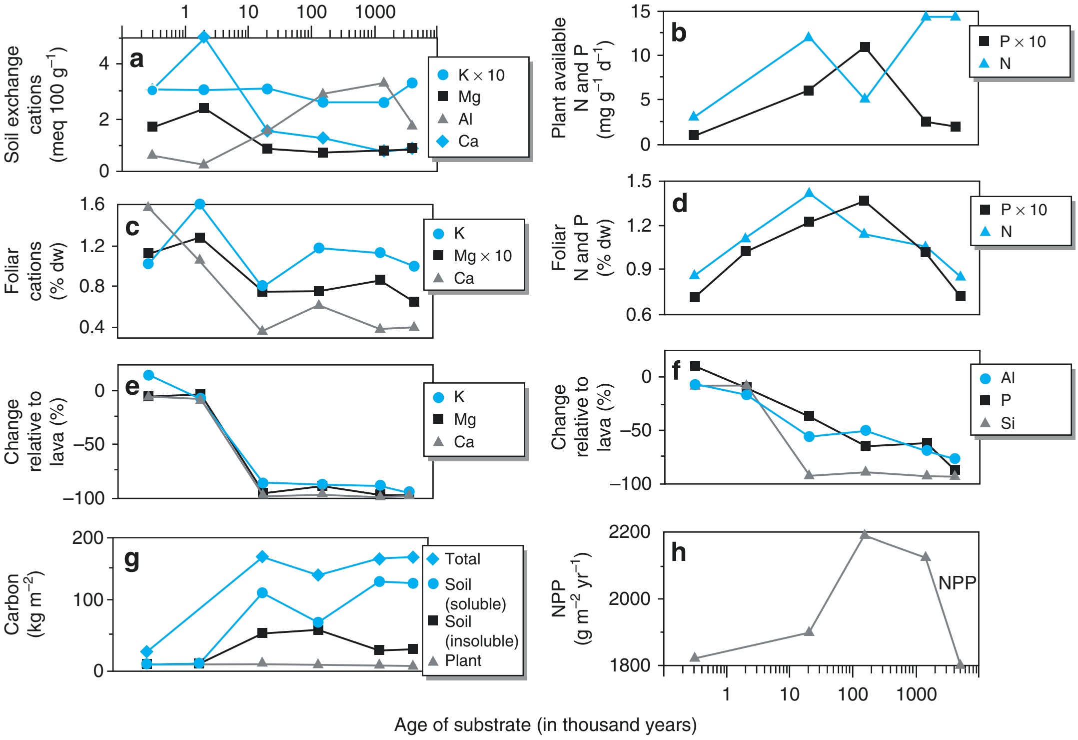


Fig. 16.25 **a**–**d** Changes in K, Mg, Al, Ca, P, and N concentrations in soils derived from weathered lava and in leaves along an age gradient on Hawaii. **e**, **f** The relative changes in soil nutrients compared to lava and **g** carbon pools as well as **h** NPP are also shown. (Vitousek et al. 1997; Chadwick et al. 1999)

to these acid anions, insofar as they are not used in lower soil layers and, thus, enter the groundwater. Such strong acids do not occur in excess under natural conditions. However, since industrialisation, ecosystems have been increasingly impacted by the atmospheric deposition of acids. In Europe, this has caused **soil acidification** over a period of about 30 years (Schulze 1989), with **base saturation** in all soil horizons decreasing from 10 to 50% at the start of the period to 5% on average a few decades later (Ulrich 1987). In Sweden, some soils even lost 70% of their exchangeable base cations in the mineral soil, but not in the organic layer (Högberg et al. 2006).

Forest vegetation should be adapted to soil acidification because under natural conditions, trees occupy sites across a very wide range of soil acidity (Ellenberg 1978). The phenomenon of **forest decline** in Central Europe prompted a controversy about whether:

- The observed loss of needles and discolouration were natural and would have occurred without the atmospheric input of acids.
- The damage was triggered by organisms (pests and pathogens).
- The damage was a direct response to atmospheric pollutants or a consequence of acidification of soils.

Schulze and Lange (1990) argued that the different paths leading to damage, decline and, eventually, death of trees did not need to be exclusive but become effective at different times over time (Fig. 16.26).

To evaluate this framework, it was necessary to examine the consequences of a wide range of possible factors and to identify the main cause(s):

- The primary impact of **pests** and **pathogens** could not be demonstrated, although several insects and pathogens (bark beetles, stem rot)

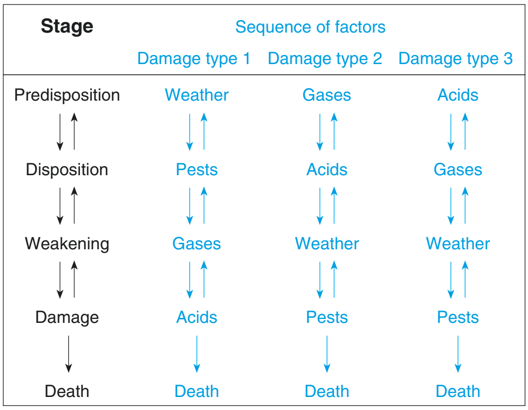


Fig. 16.26 Conceptual framework of a combination of factors leading to forest decline (Schulze and Lange 1990)

attack weakened trees and, ultimately, cause their death.

- During the twentieth century, high concentrations of pollutant gases, for example, SO_2 and NO_x, in emissions from industries caused damage, but the more recent damage symptoms were different. These new symptoms were related to tropospheric **ozone**, but the effect of ozone was shown to be rather complex and not straightforward (Chap. 5).
- Acidification of soils causes root damage, particularly due to the release of mono-nuclear **aluminium** (Al) species at low pH values (increased solubilisation of Al oxides and Al silicates at $pH < 5$; Sect. 11.5 in Chap. 11). However, individual tree species react differently to Al. Furthermore, Al also reacts with phosphate in the mycorrhiza and is immobilised (Kottke and Oberwinkler 1986). Thus, soil acidification alone could not explain the observed damage.
- One type of forest damage, characterised by yellowing of needles caused by **magnesium deficiency**, could be explained as a consequence of pollutants at the ecosystem scale (Schulze 1989). Soil acidification strongly reduces the availability of magnesium (and calcium) to plants. This is not only caused by the reduced base saturation of the soil exchanger occurring simultaneously with acidification, but also by competitive inhibition of Mg uptake by ammonium. In addition to ammonification, ammonium in the soil originates from atmospheric deposition, particularly from animal husbandry. Ammonium causes the release of Mg from exchangers in the soil and stimulates release of Al. Finally, Lange et al. (1989) proved in a very elegant experiment that the interaction of N with growth causes Mg deficiency in spruce. Buds were removed or not removed on opposite lateral twigs along the same branch. Damage was observed only on twigs where buds had not been removed and where growth had occurred (Chap. 11, Box 11.4). Obviously, the growth of trees is significantly regulated by N supply. Thus, canopy N uptake from airborne pollutants (in rain, fog and dew) becomes particularly important because this additional N supply is not balanced by cation uptake but leads to increased growth and the observed yellowing. The model of a nitrogen–cation interaction with limited cation supply due to soil acidification observed for forest decline could also be related to other observed cation deficiencies, particularly K deficiency on bogs, Mn and Fe deficiency on limestone, and the rarer Ca deficiency.

Air pollutants (gases in Fig. 16.26) were thus involved in each of these pathways of decline. The combination of soil acidification, N-triggered growth and ozone together with interactions of insect pests and microbial pathogens caused forest damage across Europe (Last and Watling 1991). Thus, ecological research provided clear evidence on the potential pathways of decline, upon which policy decisions could be taken. Based on scientific evidence, state regulations were put into place controlling emissions from large electric power plants. Thus, sulphur deposition into ecosystems decreased and, in turn, the rate of soil acidification. Additional measures in forest **management** were taken (liming, substantial clearing), and damaged areas were reforested. Heavy clearing reduced the density of trees in declining forests far below the recommended values of yield tables, for example, in the Fichtelgebirge

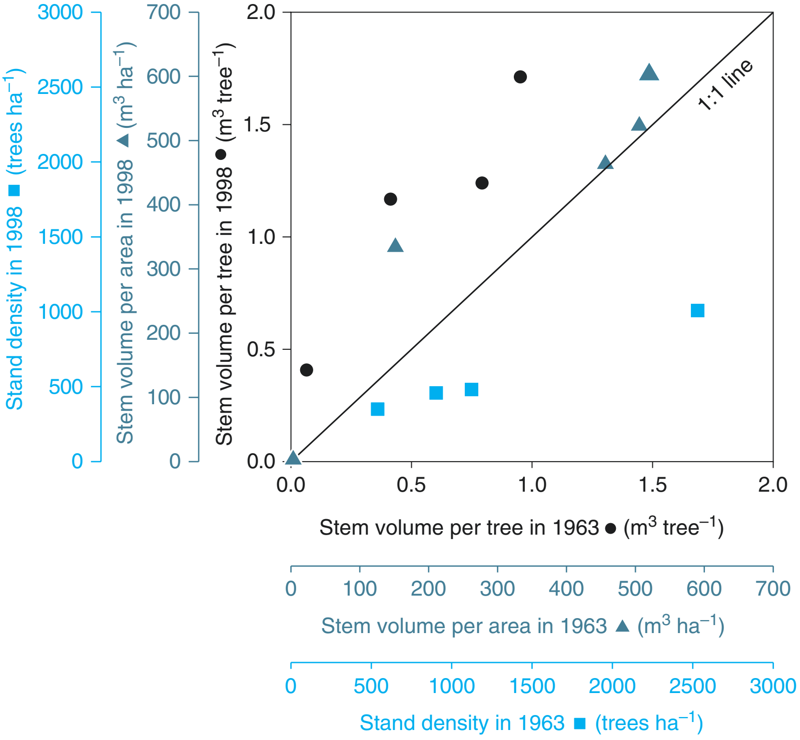


Fig. 16.27 Effects of management on forests. Logging in the 1980s left free-standing single trees. With smaller S, but still high N deposition rates, the remaining individual trees grew faster. Despite fewer trunks and a smaller leaf area, the volume of growth per stand remained the same. (Data from Mund et al. 2002)

(Germany) (Fig. 16.27). Thus, the cation supply per tree increased and, together with the (then) still high N deposition and the higher light availability, growth of individual trees improved. Despite the reduced density of stands, wood growth per area was eventually maintained. Today, damage to spruce and pine stands has been stabilised, but damage to deciduous trees continues to increase.

Summary

Water Fluxes

- Ecosystems have no water cycle but rather a hydrological balance between precipitation (rain, snow, fog, dew, rime and hail) and evapotranspiration, run-off and seepage. About 60% of total terrestrial precipitation is returned to the atmosphere via evapotranspiration.
- Ecosystem evapotranspiration, also called latent heat flux, is controlled by available energy and by plant ecophysiology. The Penman-Monteith equation describes this close link between energy and water fluxes.
- Ecosystem evapotranspiration consists of canopy transpiration and soil evaporation. Big-leaf or two-leaf models are often used to scale up leaf transpiration to the canopy scale. Evergreen forests have higher evapotranspiration rates than deciduous forests; grasslands lose more water than forests when well supplied with water.
- Canopy transpiration is controlled by two major drivers: leaf physiology (driving imposed evaporation) and available energy (driving equilibrium evaporation). Both evaporation processes occur at the same time and can be partitioned using the decoupling factor. Decoupling decreases with increasing height of vegetation and with smaller foliage of vegetation.
- Forest and grassland ecosystems respond differently to drought, with forests increasing their ratio of gross primary production to evapotranspiration, thus cooling the atmosphere less than grasslands early in the drought. This changes when the drought prevails and the grassland vegetation wilts, thereby decreasing evapotranspiration and the cooling feedback to the atmosphere.

Carbon Fluxes

- Important CO_2 fluxes in terrestrial ecosystems are GPP and autotrophic and heterotrophic respiration (R_e). About 50% of GPP is used for NPP. NPP is not the same as standing biomass or annual yield.
- Soil respiration accounts for 50 to 70% of R_e and is primarily driven by canopy assimilation. Environmental factors like temperature and moisture also have an effect. The decomposition of organic material comprises the decay of plant materials by soil fauna and microorganisms and mineralisation to inorganic forms, such as CO_2 and CH_4. Stabilisation of organic matter and decomposition products in the soil contribute to the long-term ecosystem carbon budget. Further C losses from ecosystems occur via leaching of dissolved carbon, harvests, fires and erosion, but also as BVOCs.
- The NEP, determined by the difference between GPP and R_e, is equivalent to the ecosystem carbon source or sink, when no further C inputs or exports occur. It can be measured with micrometeorological techniques. However, if the ecosystem is managed or disturbed, additional inputs and exports need to be considered, and the NBP represents the carbon sink or source strength.
- Stable carbon isotopes and radiocarbon analyses can be used to determine the fate of carbon in an ecosystem and MRTs. The MRTs determine how fast organic materials are mineralised and returned to the atmosphere as CO_2. MRTs are short for foliage and fine roots, longer for wood, and very long for SOM.

Nitrogen Fluxes

- The transformations of nitrogen in terrestrial ecosystems represent almost a closed cycle. Many organisms of different trophic levels are involved.
- Nitrogen enters an ecosystem via N_2 fixation, by symbiotic and by free-living N_2-fixing organisms, but also by lightning. Denitrification closes the ecosystem N cycle. Further inputs can be via fertilisation and N deposition, and further outputs occur via harvests, fire and leaching.
- The conversion of different N species, for example, of ammonium into nitrate (ammonification) or of nitrate into ammonium (nitrification), is controlled by microbial processes that are dependent on the redox potential. Soil chemical conditions determine whether organic nitrogen, ammonium or nitrate is the dominant form in the N cycle. Anaerobic conditions lead to the conversion of nitrate to ammonia or to denitrification, which releases NO_2, NO and N_2O. These intermediaries are or can be transformed into greenhouse gases that affect climate.
- Excess inputs of N into ecosystems can lead to N saturation, and leaching can occur, mainly as nitrate. The leaching of nitrate (and other strong acids) also results in equivalent cation losses, which are highly detrimental to ecosystem health.
- Stable isotope tracer studies help to understand the fate of N in ecosystems. Soils are the largest sink for N deposition.
- The concept of critical loads defines thresholds for N deposition into ecosystems below which no negative impacts are expected. They range from 5 to 40 kg N ha^{-1} $year^{-1}$.

Cation Fluxes

- Cation fluxes within ecosystems do not represent a closed cycle. Cations enter ecosystems naturally via weathering, dust or sea spray. Nowadays, atmospheric deposition plays an important role. Cycling within ecosystems includes uptake, release via decomposition and leaching from the canopy owing to atmospheric deposition and from the ecosystem because of podzolisation and soil acidification.
- Leaching from the soil occurs with DOC and strong acids that are produced anthropogenically. These acids displace cations from the exchange sites and lead to soil acidification when the losses are not compensated by weathering of primary minerals, import of dust, or by liming operations.
- Ecosystem flux rates of Ca^{2+} are larger than those of K^+, and both exceed those of Mg^{2+}.
- Lateral transport of cations, together with the transport of DOC, can explain the differentia-

tion of soil chemical characteristics and of vegetation even along short hydrological gradients.
- Forest damage and decline and tree death are rarely due to one factor only, but most often to multifactorial combinations of stressors, including soil acidification, N-triggered growth and ozone, together with interactions of insect pests and microbial pathogens.

References

Amthor JS (2000) The McCree-deWit-Penning de Vries-Thornley respiration paradigms: 30 years later. Ann Bot 86:1–20

Aubinet M, Vesala T, Papale D (2012) Eddy covariance—A practical guide to measurement and data analysis. Springer Publisher, New York

Bahn M, Rodeghiero M, Anderson-Dunn M, Dore S, Gimeno C, Drosler M, Williams M, Ammann C, Berninger F, Flechard C, Jones S, Balzarolo M, Kumar S, Newesely C, Priwitzer T, Raschi A, Siegwolf R, Susiluoto S, Tenhunen J, Wohlfahrt G, Cernusca A (2008) Soil respiration in European grasslands in relation to climate and assimilate supply. Ecosystems 11:1352–1367

Baldocchi D (2008) Breathing of the terrestrial biosphere: lessons learned from a global network of carbon dioxide flux measurement systems. Aust J Bot 56:1–26

Baldocchi D (2014) Measuring fluxes of trace gases and energy between ecosystems and the atmosphere—the state and future of the eddy covariance method. Glob Change Biol 20:3600–3609

Barnard RL, de Bello F, Gilgen AK, Buchmann N (2006) The $\delta^{18}O$ of root crown water best reflects source water $\delta^{18}O$ in different types of herbaceous species. Rapid Commun Mass Spectrom 20:3799–3802

Berg B, Matzner E (1997) Effect of N deposition on decomposition of plant litter and soil organic matter in forest systems. Environ Rev 5:1–25

Beringer J, Hutley LB, Tapper NJ, Cernusak LA (2007) Savanna fires and their impact on net ecosystem productivity in North Australia. Glob Change Biol 13:990–1004

Binkley D, Högberg P (2016) Tamm review: revisiting the influence of nitrogen deposition on Swedish forests. For Ecol Manag 368:222–239

Bird M, Santrùcková H, Lloyd J, Veenendaal E (2001) The global soil organic carbon pool. In: Schulze E-D, Heimann M, Harrison S, Holland E, Lloyd J, Prentice IC, Schimel D (eds) Global biogeochemical cycles in the climate system. Academic Press, San Diego

Bloom AA, Exbrayat JF, van der Velde IR, Feng L, Williams M (2016) The decadal state of the terrestrial carbon cycle: global retrievals of terrestrial carbon allocation, pools, and residence times. Proc Nat Acad Sci USA 113:1285–1290

Blume HP, Brümmer GW, Horn R, Kandeler E, Kögel-Knabner I, Stahr K, Thiele-Bruhn S, Welp G, Wilke BM (2010) Scheffer/Schachtschabel: Lehrbuch der Bodenkunde, 16th edn. Spektrum Akademischer Verlag, Heidelberg

Weil RR, Brady NC (2009) Elements of the nature and properties of soils, 3rd edn. Pearson, Upper Saddle River, USA

Brinkmann N (2016) Ecophysiological responses of four common Swiss tree species to global environmental change. PhD thesis, ETH Zurich, Switzerland

Brüggemann N, Gessler A, Kayler Z, Keel SG, Badeck F, Barthel M, Boeckx P, Buchmann N, Brugnoli E, Esperschütz J, Gavrichkova O, Ghashghaie J, Gomez-Casanovas N, Keitel C, Knohl A, Kuptz D, Palacio S, Salmon Y, Uchida Y, Bahn M (2011) Carbon allocation and carbon isotope fluxes in the plant–soil–atmosphere continuum: a review. Biogeosciences 8:3457–3489

Bobbink R, Hicks K, Galloway J, Spranger T, Alkemade R, Ashmore M, Bustamante M, Cinderby S, Davidson E, Dentener F, Emmett B, Erisman JW, Fenn M, Gilliam F, Nordin A, Pardo L, De Vries W (2010) Global assessment of nitrogen deposition effects on terrestrial plant diversity: a synthesis. Ecol Appl 20:30–59

Bond-Lamberty B, Wang C, Gower ST (2004) A global relationship between the heterotrophic and autotrophic components of soil respiration? Glob Change Biol 10:1756–1766

Buchmann N, Gebauer G, Schulze ED (1996) Partitioning of ^{15}N labeled ammonium and nitrate among soil, litter, below- and above-ground biomass of trees and understory in a 15-year-old *Picea abies* plantation. Biogeochemistry 33:1–23

Buchmann N, Guehl JM, Barigah TS, Ehleringer JR (1997) Interseasonal comparison of CO_2 concentrations, isotopic composition, and carbon dynamics in an Amazonian rainforest (French Guiana). Oecologia 110:120–131

Buchmann N, Brooks JR, Ehleringer JR (2002) Predicting carbon isotope ratios of atmospheric CO_2 within forest canopies. Funct Ecol 16:49–57

Buckley TN, Cescatti A, Farquhar GD (2013) What does optimization theory actually predict about crown profiles of photosynthetic capacity when models incorporate greater realism? Plant Cell Environ 36:1547–1563

Budyko MI (1974) Climate and life. Academic Press, New York

Carvalhais N, Forkel M, Khomik M, Bellarby J, Jung M, Migliavacca M, Mu M, Saatchi S, Santoro M, Thurner M, Weber U, Ahrens B, Beer C, Cescatti A, Randerson JT, Reichstein M (2014) Global covariation of carbon turnover times with climate in terrestrial ecosystems. Nature 514:213–220

Cescatti A, Marcolla B, Santhana Vannan SK, Yun Pan J, Román MO, Yang X, Ciais P, Cook RB, Law BE, Matteucci G, Migliavacca M, Moors E, Richardson AD, Seufert G, Schaaf CB (2012) Intercomparison of MODIS albedo retrievals and in situ measurements across the global FLUXNET network. Remote Sens Environ 121:323–334

Chadwick OA, Derry LA, Vitousek PM, Huebert BJ, Hedin LO (1999) Changing sources of nutrients during four million years of ecosystem development. Nature 397:491–497

Chapin FS III, Matson PA, Mooney HA (2002) Principles of terrestrial ecosystem ecology. Springer, New York

Churkina G, Schimel D, Braswell BH, Xiao XM (2005) Spatial analysis of growing season length control over net ecosystem exchange. Glob Change Biol 11:1777–1787

Ciais P, Reichstein M, Viovy N, Granier A, Ogée J, Allard V, Buchmann N, Aubinet M, Bernhofer C, Carrara A, Chevallier F, De Noblet N, Friend A, Friedlingstein P, Grünwald T, Heinesch B, Keronen P, Knohl A, Krinner G, Loustau D, Manca G, Matteucci G, Miglietta F, Ourcival JM, Pilegaard K, Rambal S, Seufert G, Soussana JF, Sanz MJ, Schulze ED, Vesala T, Valentini R (2005) Europe-wide reduction in primary productivity caused by the heat and drought in 2003. Nature 437:529–533

Ciais P, Wattenbach M, Vuichard N, Smith P, Piao SL, Don A, Luyssaert S, Janssens IA, Bondeau A, Dechow R, Leip A, Smith PC, van der Werf GR, Gervois S, van Oost K, Tomelleri E, Freibauer A, Schulze ED, Team CS (2010) The European carbon balance. Part 2: croplands. Glob Change Biol 16:1409–1428

Cotrufo MF, Miller M, Zeller B (2000) Litter decomposition. Ecol Stud 142:276–296

Cotrufo MF, Wallenstein MD, Boot CM, Denef K, Paul E (2013) The Microbial Efficiency-Matrix Stabilization (MEMS) framework integrates plant litter decomposition with soil organic matter stabilization: Do labile plant inputs form stable soil organic matter? Glob Change Biol 19:988–995

de Vries W, Reinds GJ, Vel E (2003) Intensive monitoring of forest ecosystems in Europe. 2: Atmospheric deposition and its impact on soil solution chemistry. For Ecol Manag 174:97–115

de Vries W, Solberg S, Dobbertin M, Sterba H, Laubhahn D, Reinds GJ, Nabuurs GJ, Gundersen P, Sutton MA (2008) Ecologically implausible carbon response? Nature 451:E1–E3

Davidson EA, Janssens IA, Luo Y (2006) On the variability of respiration in terrestrial ecosystems: moving beyond Q_{10}. Glob Change Biol 12:154–164

Dawson TE (1998) Fog in the California redwood forest: ecosystem inputs and use by plants. Oecologia 117:476–485

DeLucia EH, Drake JE, Thomas RB, Gonzalez-Meler M (2007) Forest carbon use efficiency: Is respiration a constant fraction of gross primary production? Glob Change Biol 13:1157–1167

Durka W, Schulze E-D, Gebauer G, Vorkelius S (1994) Effects of forest decline on uptake and leaching of deposited nitrate determined from ^{15}N and ^{18}O measurements. Nature 372:765–767

Ehleringer JR, Roden J, Dawson TE (2000) Assessing ecosystem-level water relations through stable isotope ratio analyses. Methods in ecosystem science, Part 2. Springer, New York, NY

Ellenberg H (1978) Vegetation Mitteleuropas mit den Alpen. Ulmer, Stuttgart

Gaudinski JB, Trumbore SE, Davidson EA, Cook AC, Markewitz D, Richter DD (2001) The age of fine-root carbon in three forests of the eastern United States measured by radiocarbon. Oecologia 129:420–429

Gaul D, Hertel D, Leuschner C (2009) Estimating fine root longevity in a temperate Norway spruce forest using three independent methods. Funct Plant Biol 36:11–19

Gat JR (1996) Oxygen and hydrogen isotopes in the hydrologic cycle. Annu Rev Earth Planet Sci 24:225–262

Ghashghaie J, Badeck FW (2014) Opposite carbon isotope discrimination during dark respiration in leaves versus roots – a review. New Phytol 201:751–769

Glaser B (2007) Prehistorically modified soils of central Amazonia: a model for sustainable agriculture in the twenty-first century. Philos Trans R Soc B 362:187–196

Glaser B, Lehmann J, Zech W (2002) Ameliorating physical and chemical properties of highly weathered soils in the tropics with charcoal—a review. Biol Fertil Soils 35:219–230

Gleixner G, Czimczik CJ, Kramer C, Lühker B, Schmidt MWI (2001) Plant compounds and their turnover and stabilization as soil organic matter. In: Schulze E-D, Heimann M, Harrison S, Holland E, Lloyd J, Prenice IC, Schimel D (eds) Global biogeochemical cycles in the climate system. Academic Press, San Diego. pp 201–215

Greenwood EAN, Turner NC, Schulze E-D, Watson GD, Venn NR (1992) Ground water management through increased water use by lupin crops. J Hydrol 134:1–11

Guenther AB, Jiang X, Heald CL, Sakulyanontvittaya T, Duhl T, Emmons LK, Wang X (2012) The model of emissions of gases and aerosols from nature version 2.1 (MEGAN2.1): an extended and updated framework for modeling biogenic emissions. Geosci Model Dev 5:1471–1492

Guggenberger G, Zech W (1993) Dissolved organic carbon control in acid forest soils of the Fichtelgebirge (Germany) as revealed by distribution pattern and structural analysis. Geoderma 59:109–129

Gustafsson MER, Franzen LG (2000) Inland transport of marine aerosols in southern Sweden. Atmos Environ 34:313–325

Högberg P (2001) Interactions between hillslope hydrochemistry, nitrogen dynamics and plants in Fennoscannian boreal forest. In: Schulze E-D, Heimann M, Harrison S, Holland E, Lloyd J, Prenice IC, Schimel D (eds) Global biogeochemical cycles in the climate system. Academic Press, San Diego. pp 227–233

Högberg P, Nordgren A, Buchmann N, Taylor AFS, Ekblad A, Högberg MN, Nyberg G, Ottosson-Löfvenius M, Read DJ (2001) Large-scale forest girdling shows that current photosynthesis drives soil respiration. Nature 411:89–792

Högberg P, Fan H, Quist M, Binkley D, Tamm CO (2006) Tree growth and soil acidification in response to 30 years of experimental N-loading on boreal forest. Glob Change Biol 12:489–499

Horn R, Schulze E-D, Hantschel R (1989) Nutrient balance and element cycling in healthy and declining Norway spruce stands. In: Schulze E-D, Lange OL, Oren R (eds) Forest decline and air pollution: a study of spruce (*Picea abies*) on acid soils. Ecological Studies, vol 77

Jackson RB, Mooney HA, Schulze E-D (1997) A global budget for fine root biomass, surface area and nutrient contents. Proc Nat Acad Sci USA 94:7362–7366

Jarvis PG, McNaughton KG (1986) Stomatal control of transpiration: scaling up from leaf to region. Adv Ecol Res 15:1–49

Joabsson A, Christensen TR, Wallen B (1999) Vascular plants controls on methane emissions from northern peatforming wetlands. TREE 14:385–388

Jones HG (2014) Plants and microclimate; a quantitative approach to environmental plant physiology. Cambridge University Press, Cambridge

Kappler A, Wuestner ML, Ruecker A, Harter J, Halama M, Behrens A (2014) Biochar as an electron shuttle between bacteria and Fe(III) minerals. Environ Sci Technol Lett 1:339–344

Kelliher FM, Leuning R, Raupach MR, Schulze ED (1995) Maximum conductance for evaporation of global vegetation types. Agric For Meteorol 73:1–16

Kottke I, Oberwinkler F (1986) Mycorrhiza of forest trees—structure and function. Trees 1:1–24

Kutsch WL, Aubinet M, Buchmann N, Smith P, Osborne B, Eugster W, Wattenbach M, Schrumpf M, Schulze ED, Tormellieri E, Ceschia E, Bernhofer C, Beziat P, Carrara A, Di Tommasi P, Grünwald T, Jones M, Magiulo V, Marloie O, Moureaux C, Olioso A, Sanz MJ, Saunders M, Søgaard H, Ziegler W (2010) The net biome production of full crop rotations in Europe. Agric Ecosyst Environ 139:336–345

Kuzyakov Y, Gavrichkova O (2006) Time lag between photosynthesis and carbon dioxide efflux from soil: a review of mechanisms and controls. Glob Change Biol 16:3386–3406

Lafleur PM, Humphreys ER, St. Louis VL, Myklebust MC, Papakyriakou T, Poissant L, Barker JD, Pilote M, Swystun KA (2012) Variation in peak growing season net ecosystem production across the Canadian Arctic. Environ Sci Technol 46:7971–7977

Lange OL, Weikert RM, Wedler M, Gebel J, Heber U (1989) Photosynthese und Nährstoffversorgung von Fichten aus einem Waldschadensgebiet auf basenarmem Untergrund. Allgemeine Forstzeitung 3:54–63

Larcher W (2003) Physiological plant ecology. Ecophysiology and stress physiology of functional groups, 4th edn. Springer, Berlin

Last FT, Watling R (1991) Acid deposition, its nature and impacts. Proc R Soc Edin Sec B 97:343

Le Mer J, Roger P (2001) Production, oxidation, emission and consumption of methane by soils: a review. Eur J Soil Biol 37:25–50

Liu J, Chen JM, Cihlar J, Park WM (1997) A process-based boreal ecosystem productivity simulator using remote sensing inputs. Remote Sens Environ 62:158–175

Lloyd J, Francey RJ, Mollicone D, Raupach MR, Sogachev A, Arneth A, Byers JB, Kelliher FM, Rebmann C, Valentini R, Wong SC, Bauer G, Schulze ED (2001) Vertical profiles, boundary layer budgets, and regional flux estimates for CO_2 and its ^{13}C ratio and for water vapor above a forest/bog mosaic in central Siberia. Glob Biogeochem Cycles 15:267–284

Loreto F, Schnitzler JP (2010) Abiotic stresses and induced BVOCs. Trends Plant Sci 15:154–166

Luyssaert S, Ciais P, Piao SL, Schulze ED, Jung M, Zaehle S, Schelhaas MJ, Reichstein M, Churkina G, Papale D, Abril G, Beer C, Grace J, Loustau D, Matteucci G, Magnani F, Nabuurs GJ, Verbeeck H, Sulkava M, Van der Werf GR, Janssens IA, Members of the Carboeurope—IP Synthesis Team (2010) The European carbon balance. Part 3: Forests. Glob Change Biol 16:1429–1450

Magnani F, Mencuccini M, Borghetti M, Berbigier P, Berninger F, Delzon S, Grelle G, Hari P, Jarvis PG, Kolari P, Kowalski AS, Lankreijer H, Law BE, Lindroth A, Loustau D, Manca G, Moncrieff JB, Rayment M, Tedeschi V, Valentini R, Grace J (2007) The human footprint in the carbon cycle of temperate and boreal forests. Nature 447:848–850

Meyer O (1994) Functional groups of microorganisms. Ecol Stud 99:67–96

Monteith JL (1965) Evaporation and environment. Symp Soc Exp Biol 19:205–234

Mund M, Kummetz E, Hein M, Bauer GA, Schulze E-D (2002) Growth and carbon stocks of a spruce forest chronosequence in central Europe. For Ecol Manag 171:275–296

Nave LE, Curtis PS (2011) Uptake and partitioning of simulated atmospheric N inputs in *Populus tremuloides—Pinus strobus* forest mesocosms. Botany 89:379–386

Nordin A, Högberg P, Näsholm T (2001) Soil nitrogen form and plant nitrogen uptake along a boreal forest productivity gradient. Oecologia 129:125–132

Oki T, Kanae S (2006) Global hydrological cycles and world water resources. Science 313:1068–1072

Peñuelas J, Staudt M (2010) BVOCs and global change. Trends Plant Sci 15:133–144

Peltoniemi MS, Duursma RA, Medlyn BE (2012) Co-optimal distribution of leaf nitrogen and hydraulic conductance in plant canopies. Tree Physiol 32:510–519

Persson T, Rudebeck A, Jussy JH, Clin-Belgrand M, Prieme A, Dambrine E, Karlsson PS, Sjöberg M (2000) Soil nitrogen turnover—mineralisation, nitrification and denitrification in European forest stands. Ecol Stud 142:297–331

Raich JW, Schlesinger WH (1992) The global carbon dioxide flux in soil respiration and its relationship to vegetation and climate. Tellus 44B:81–99

Raupach MR, Finnigan JJ (1988) Single-layer models of evaporation from plant canopies are incorrect but useful, whereas multi-layer models are correct but useless: Discuss. Aust J Plant Physiol 15:705–716

Reichstein M, Falge E, Baldocchi D, Papale D, Valentini R, Aubinet M, Berbigier P, Bernhofer C, Buchmann N, Falk M, Gilmanov T, Granier A, Grünwald T, Havránková K, Janous D, Knohl A, Laurela T, Lohila A, Loustau D, Matteucci G, Meyers T, Miglietta F, Ourcival JM, Perrin D, Pumpanen J, Rambal S, Rotenberg E, Sanz M, Tenhunen J, Seufert G, Vaccari F, Vesala T, Yakir D (2005) On the separation of net ecosystem exchange into assimilation and ecosystem respiration: review and improved algorithm. Glob Change Biol 11:1–16

Ruehr NK, Buchmann N (2010) Soil respiration fluxes in a temperate mixed forest: seasonality and temperature sensitivities differ among microbial and root-rhizosphere respiration. Tree Physiol 30:165–176

Rühr NK, Offermann CA, Gessler A, Winkler BJ, Ferrio JP, Buchmann N, Barnard RL (2009) Drought effects on allocation of recent carbon: From beech leaves to soil CO_2 efflux. New Phytologist 184:950–961

Schlesinger WH (1990) Evidence from chronosequence studies for a low carbon-storage potential of soils. Nature 348:232–239

Schlesinger WH, Bernhardt ES (2013) Biogeochemistry: an analysis of global change, 3rd edn. Academic Press, San Diego

Schmidt MWI, Torn MS, Abiven S, Dittmar T, Guggenberger G, Janssens IA, Kleber M, Kögel-Knabner I, Lehmann J, Manning DAC, Nannipieri P, Rasse DP, Weiner S, Trumbore SE (2011) Persistence of soil organic matter as an ecosystem property. Nature 478:49–56

Schulze E-D (1982) Plant life forms and their carbon, water and nutrient relations. In: Lange O, Nobel PS, Osmond CB, Ziegler H (eds) Physiological plant ecology II. Water relations and carbon assimilation. Encyclopedia in Plant Physiology. New series, vol 12B. Springer, Berlin. pp 616–676

Schulze E-D (1989) Air pollution and forest decline in a spruce (*Picea abies*) forest. Science 244:776–783

Schulze E-D (ed) (2000) Carbon and nutrient cycling in European forest ecosystems, Ecological studies, vol 142. Springer, Berlin

Schulze ED, Lange O (1990) Die Wirkungen von Luftverunreinigungen auf Waldökosysteme. Chemie in Unserer Zeit 24:117–130

Schulze ED, Kelliher FM, Körner C, Lloyd J, Leuning R (1994) Relationships among maximum stomatal conductance, ecosystem surface conductance, carbon assimilation rate, and plant nitrogen nutrition: a global ecology scaling exercise. Annu Rev Ecol Syst 25:629–660

Schulze E-D, Wirth C, Heimann M (2000) Managing forests after Kyoto. Science 289:2058–2059

Seneviratne SI, Corti T, Davin EL, Hirschi M, Jaeger EB, Lehner I, Orlowsky B, Teuling AJ (2010) Investigating soil moisture–climate interactions in a changing climate: a review. Earth Sci Rev 99:125–161

Sievering H, Fernandez I, Lee J, Hom J, Rustad L (2000) Forest canopy uptake of atmospheric nitrogen deposition at eastern US conifer sites: carbon storage implications? Glob Biogeochem Cycles 14:1153–1160

Smith DE, Read DJ (2008) Mycorrhizal symbiosis, 3rd edn. Academic Press, London

Soussana JF, Allard V, Pilegaard K, Ambus P, Amman C, Campbell C, Ceschia E, Clifton-Brown J, Czobel S, Domingues R, Flechard C, Fuhrer J, Hensen A, Horvath L, Jones M, Kasper G, Martin C, Nagy Z, Neftel A, Raschi A, Baronti S, Rees RM, Skiba U, Stefani P, Manca G, Sutton M, Tuba Z, Valentini R (2007) Full accounting of the greenhouse gas (CO_2, N_2O, CH_4) budget of nine European grassland sites. Agric Ecosyst Environ 121:121–134

Starr MR (1991) Soil formation and fertility along a 5000 year chronosequence. Geol Surv Finland Spec Pap 9:99–104

Templer PH, Mack MC, Chapin FS III, Christenson LM, Compton JE, Crook HD, Currie WS, Curtis CI, Dail DB, D'Antonio CM, Emmett BA, Epstein HE, Goodale CL, Gundersen P, Hobbie SE, Holland K, Hooper DU, Hungate BA, Lamontagne S, Nadelhoffer KJ, Osenberg CW, Perakis SS, Schleppi P, Schimel J, Schmidt IK, Sommerkorn M, Spoelstra J, Tietema A, Wessel WW, Zak DR (2012) Sinks for nitrogen inputs in terrestrial ecosystems: a meta-analysis of ^{15}N tracer field studies. Ecology 93:1816–1829

Teuling AJ, Seneviratne SI, Stöckli R, Reichstein M, Moors E, Ciais P, Luyssaert S, van den Hurk B, Ammann C, Bernhofer C, Dellwik E, Gianelle D, Gielen B, Grünwald T, Klumpp K, Montagnani L, Moureaux C, Sottocornola M, Wohlfahrt G (2010) Contrasting response of European forest and grassland energy exchange to heatwaves. Nat Geosci 3:722–727

Ulrich B (1987) Stability, elasticity, and resilience of terrestrial ecosystems with respect to matter balance. Ecol Stud 61:11–69

Vargas R, Trumbore SE, Allen MF (2009) Evidence of old carbon used to grow new fine roots in a tropical forest. New Phytol 182:710–718

Vitousek PM, Chadwick OA, Crews TE, Fownes JH, Hendricks DM, Herbert D (1997) Soil and ecosystem development across the Hawaiian Islands. GSAToday 7:1–8

Wallenda T, Stober C, Högbom L, Schinkel H, George E, Högberg P, Read DJ (2000) Nitrogen uptake processes in roots and mycorrhizae. Ecol Stud 142:122–143

Weedon JT, Cornwell WK, Cornelissen JHC, Zanne AE, Wirth C, Coomes DA (2009) Global meta-analysis of wood decomposition rates: a role for trait variation among tree species? Ecol Lett 12:45–56

Werner C, Gessler A (2011) Diel variations in the carbon isotope composition of respired CO_2 and associated carbon sources: a review of dynamics and mechanisms. Biogeosciences 8:2437–2459

Williams C, Reichstein M, Buchmann N, Baldocchi D, Beer C, Schwalm C, Wohlfahrt G, Hasler N, Bernhofer C, Foken T, Papale D, Schymanski S, Schaefer K (2012) Climate and vegetation controls on the surface water balance: Synthesis of evapotranspiration measured across a global network of flux towers. Water Resour Res 48:W06523

Wilson KB, Baldocchi DD, Aubinet M, Berbigier P, Bernhofer C, Dolman J, Falge E, Field C, Goldstein A, Granier A, Grelle A, Halldor T, Hollinger D, Katul G, Law BE, Lindroth A, Meyers T, Moncrieff J, Monson R, Oechel W, Tenhunen T, Valentini R, Verma S, Vesala T, Wofsy S (2002) Energy partitioning between latent and sensible heat flux during the warm season at FLUXNET sites. Water Resour Res 38:1294

Wirth C, Schulze E-D, Lühker B, Grigoriev S, Siry M, Hardes G, Ziegler W, Backor M, Bauer G, Vygodskaya NN (2002) Fire and site type effects on the long-term carbon and nitrogen balance in pristine Siberian Scots pine forest. Plant Soil 142:61–63

Wohlfahrt G, Amelynck C, Ammann C, Arneth A, Bamberger I, Goldstein AH, Gu L, Guenther A, Hansel A, Heinesch B, Holst T, Hörtnagl L, Karl T, Laffineur Q, Neftel A, McKinney K, Munger JM, Pallardy SG, Schade GW, Seco R, Schoon N (2015) An ecosystem-scale perspective of the net land methanol flux: synthesis of micrometeorological flux measurements. Atmos Chem Phys 15:7413–7427

Wolf S, Eugster W, Ammann C, Häni M, Zielis S, Hiller R, Stieger J, Imer D, Merbold L, Buchmann N (2013) Contrasting response of grassland *versus* forest carbon and water fluxes to spring drought in Switzerland. Environ Res Lett 8:035007

Worobiec A, Szaloki I, Osan J, Maenhaut W, Stefaniak EA, Van Grieken R (2007) Characterisation of Amazon Basin aerosols at the individual particle level by X-ray microanalytical techniques. Atmos Environ 41:9217–9230

Xie J, Zha T, Jia X, Qian D, Wu B, Zhang Y, Bourque CPA, Chen J, Sun G, Peltola H (2015) Irregular precipitation events in control of seasonal variations in CO_2 exchange in a cold desert-shrub ecosystem in northwest China. J Arid Environ 120:33–41

Zech W, Kögel-Knabner I (1994) Patterns and regulation of organic matter transformation in soils: Litter decomposition and humification. In: Schulze E-D (ed) Flux control in biological systems. Academic Press, San Diego

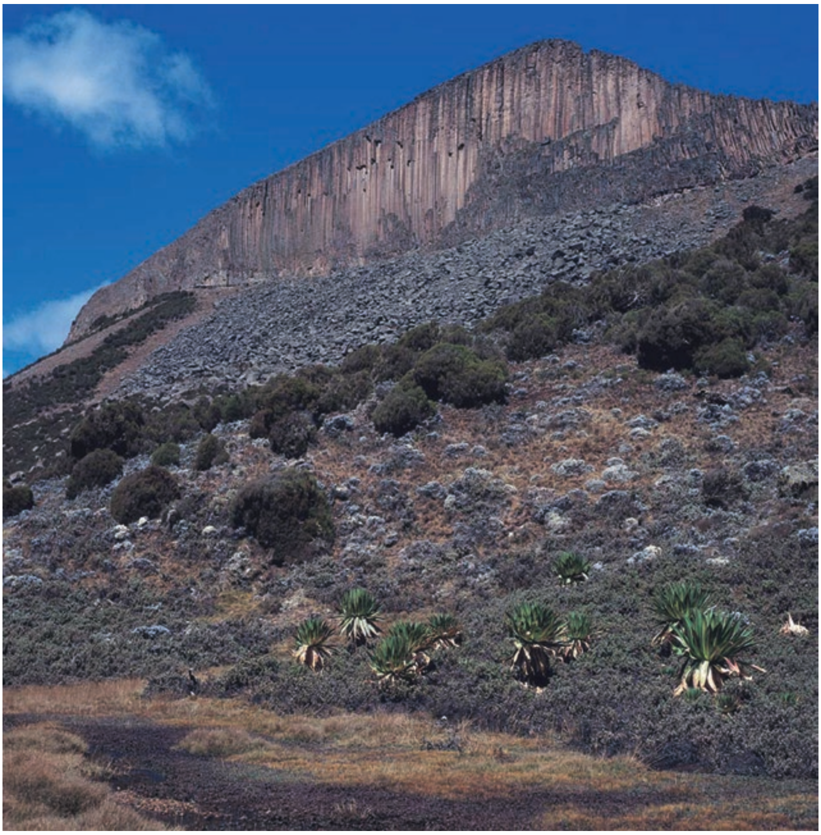
Zeeman MJ, Hiller R, Gilgen AK, Michna P, Plüss P, Buchmann N, Eugster W (2010) Management, not climate, controls net CO_2 fluxes and carbon budgets of three grasslands along an elevational gradient in Switzerland. Agric For Meteorol 150:519–530

Zhao M, Heinsch FA, Nemani RR, Running SW (2005) Improvements of the MODIS terrestrial gross and net primary production global data set. Remote Sens Environ 95:164–176

Zweifel R, Haeni M, Buchmann N, Eugster W (2016) Are trees able to grow in periods with shrunken stems? New Phytol 211:839–849

Part IV

Community Ecology and Biological Diversity



Small-scale vegetation mosaic in the Afro-Alpine region of the Bale Mountains (south-east Ethiopia) 3400 m above sea level with subalpine shrub communities (*Erica arborea*), dwarf shrub vegetation (different species of *Alchemilla* and *Helichrysum*) and individual giant lobelias (*Lobelia rhynchopetalum*) on the dry rocky slopes and also in the grassland communities and boggy depressions at the moist foot of the slopes. (Photo: K. Müller-Hohenstein)

In the chapters of Part IV, another level of ecological hierarchy is discussed, namely plant communities and their biological diversity. To fully understand the many aspects of the ecology of single plants, of plant communities and of ecosystems and their processes it is necessary to complement investigations under strictly controlled conditions in a laboratory by field studies. It is clear that no plant lives on its own in a natural environment; it can only exist in complex communities composed of plants, animals, fungi and microbes and their numerous interactions, that is in a "biocoenosis".

Along with the increasing complexity of processes to be considered at the community and ecosystem level comes a decreasing ability to make accurate predictions about plant community development in time and space. Thus, community ecology is mainly based on observations, comparisons and experiments, with an always changing spatio-temporal context. Many experiments in community ecology are carried out by nature itself, including all anthropogenic influences, which increases the complexity of the system considerably. The task is to recognise and to describe patterns of plant communities in time and space and to explain the underlying mechanisms and principles of plant community assembly. For this, quantitative data are needed but are sometimes difficult to obtain, and qualitative assessments gain importance.

In analysing ecosystems (Chap. 16), it already became obvious that two aspects are connected with the step from the laboratory into the field, namely the importance of space and time. Plant communities develop over the course of time and may display directed or cyclic dynamics. Their history of development must be known in order to understand their actual structure. Here, the influences of human activities are particularly important. The **historical development of plants** and of plant communities is discussed in Chap. 17. During their development over time, plants and plant communities conquer habitats and expand into new areas. However, the present-day global and regional differentiation of the plant cover can only be understood by taking into account the direct and indirect, intended or unintentional influences of humans.

The basis of the **spatial distribution** of plant communities is discussed in Chap. 18. During their development over time, plants and plant communities colonise new habitats and expand in space. Different vectors, such as wind, water and animals, are particularly responsible for the dispersal of propagules. The resulting final establishment and pattern of expansion depend furthermore on environmental conditions. A hierarchical order from species area types to plant kingdoms is the basis for plant geographical research. To illustrate, we focus on examples from Europe and Africa.

In Chap. 19, **biotic interactions** among plants and between plants, microorganisms and animals are considered. Plants and plant communities are strongly regulated by the environment, but they also influence their environment, resulting in feedbacks to the microclimatic conditions or soil conditions. Intra- and interspecific interactions, including competition or facilitation, structure plant communities and determine the coexistence of species. Finally, plants are embedded in a complex network of interactions with animals and microorganisms, some of which are essential for their reproductive success (pollination, dispersal), while others are primarily considered detrimental for plants (herbivory).

Chapter 20 introduces the concept of biodiversity and how plant diversity is controlled by environmental factors. It also describes the relationships between plant diversity and ecosystem functioning, i.e. raising the question about the role of plants and their diversity in regulating and maintaining ecosystem processes. Here, a trait-based approach to plant ecology is needed. This topic not only reveals the fundamental principles of community ecology but also has profound implications for ecosystem management and nature conservation.

17

Development of Plant Communities in Time

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The species-rich segetal flora in an annual crop of lentils and in a perennial crop of olive trees demonstrates the typical anthropogenic replacement of communities in an area of the European Mediterranean region that is still little influenced by herbicides. (Photo: K. Müller-Hohenstein)

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17.1 Introduction

The **historical development of plants** and of plant communities is discussed in Chapter 17. Plant communities develop over the course of time and may display directed or cyclic dynamics. Their history of development must be known to understand their actual structure. In the geological epochs up to the Holocene, plants and plant communities developed in close connection with numerous climatic changes. Only in the Anthropocene did the influences of human activities start to take on growing importance. Today the loss of plant species and the spread of neophytes are the main forces of change.

17.2 Development of Plants during Life History on Earth

Recent ecological interactions between plants and their environments are the basis of the present structure and spatial distribution of vegetation. However, the occurrence of species and communities may only be explained historically on the basis of knowledge of evolution and distribution. Three important geological events have contributed significantly to the formation of present-day patterns of distribution:

- Continuous **migration of the continents** in relation to the poles. According to measurements of palaeomagnetism, the magnetic North Pole in the Cambrian was in the Pacific, not far from the current location of the Japanese island group, whereas it was in north-eastern Asia in the Triassic (Fig. 17.1).
- The formation of continents arising from the permanent changes in the position of parts of the Earth's crust **(continental shift and plate tectonics)** (Fig. 17.2).

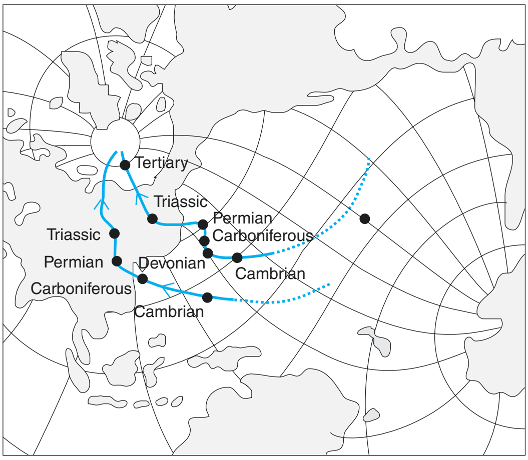


Fig. 17.1 Changes in position of magnetic North Pole during geological time, determined from palaeomagnetic measurements of North American (upper curve) and British rocks (lower curve). (after Kreeb 1983)

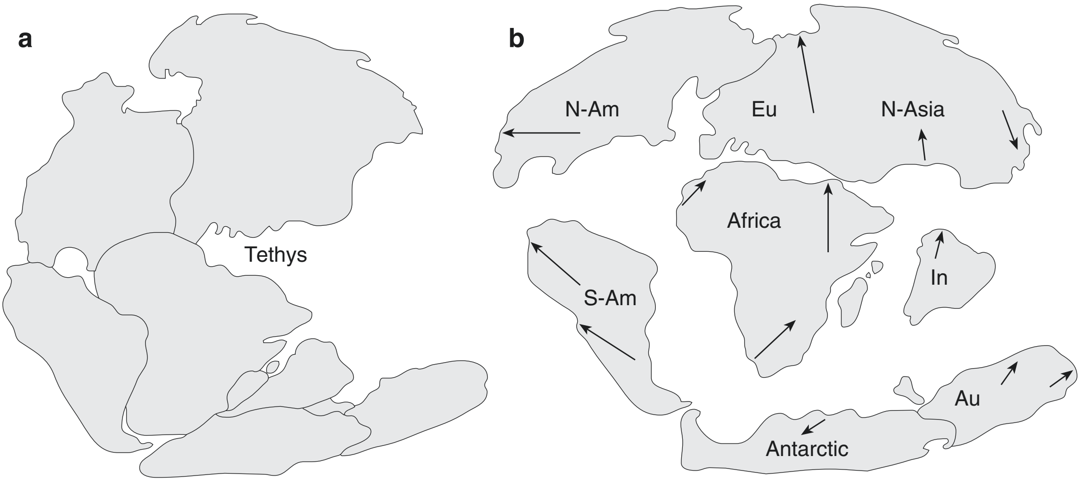


Fig. 17.2 Stages in development of present distribution of continents. **a** Joined landmass of Pangaea in Triassic. **b** Distribution of continents at end of Cretaceous. (after Bick 1993)

- **Solar effects** (different radiation conditions) arising from the composition of the atmosphere, coupled with changes in the Earth's eccentricity (orbit) around the Sun.

These events are linked to two influences directly affecting plants and their evolution. Firstly, climatic conditions have changed drastically and, secondly, the possibility for area expansion of plants and animals by the opening or closing of land bridges or by the rise of mountain barriers was either limited or enhanced. Furthermore, catastrophic **asteroid impacts** as well as changes in the CO_2 levels (Sun et al. 2012) that greatly reduced biodiversity at the end of the Permian and the Mesozoic should be mentioned.

More recently, the development of the patterns and distributions of vegetation has changed worldwide more rapidly and to a much greater extent by the continuously growing influence of human settlement and changes of land use. This shows clearly that palaeo-ecological links and historical development must be known to acquire a better understanding of present-day vegetation and its structure, composition and spatial distribution.

In the following section, periods of the history of life on Earth, including selected aspects of the phylogeny and coevolution of organisms (eophyticum, palaeophyticum, mesophyticum), will be outlined. The Neophyticum will be discussed in more detail, with special emphasis on late and postglacial development of vegetation, as well as direct and indirect influences of humans on plant cover. Problems of global change will be discussed more comprehensively in Chap. 21.

17.2.1 History of Vegetation to the End of the Tertiary

In the **Precambrian** Period two large separate landmasses existed, each near the poles: the **Laurasia** continent in the Northern Hemisphere, and the **Gondwana** continent in the Southern Hemisphere. These two continents over time merged and became the continent of **Pangaea**. Pangea remained one mass until the Palaeozoic Period, where changes in positions towards the poles and equator occurred. Traces of life and the first single-celled prokaryotes (bacteria, cyanobacteria) existed for about three billion years in an oxygen-poor atmosphere. Eukaryotes and multicellular forms could only develop when increases in oxygen occurred in the environment. This period, extending into the **Silurian**, is called the **eophytic** (proterophytic) or algal period.

An important plant developmental step occurred during the Silurian Period, where colonisation of land happened from the eophytic to the **palaeophytic** period. The first land plants possessed cells with large vacuoles, and some were able to develop stomata and other supporting tissues. These autotrophic plants lived together with fungi and bacteria (primary decomposers) communities and formed the first biocoenoses. From that period, plant diversity continuously increased through evolution.

Animal and plant communities evolved in unison (Table 17.1, Fig. 17.3). Psilophytes (archetypal ferns) are regarded as precursors of the Pteridophyta, to which Filicinae, Equisetinae and Lycopodiinae belong. Analysis of deposits of bituminous coal allow exact reconstruction of this vegetation, including indications of symbiotic interactions (mycorrhiza). At that time Bryophyta (mosses) split off and remained at this developmental stage. Other groups in the warm and humid climate of the **Carboniferous** formed luxuriant forests with tree-like Equisetinae, Lycopodiinae and Cordiates, which would later go extinct.

During the transition from the Carboniferous to the **Permian** Period, climatic conditions became much dryer. Many species became maladapted, which led to extinctions as many plant species were unable to adjust their water retention capabilities. Thus, the transition from the palaeophytic to the mesophytic is highlighted by a significant decrease in plant diversity. Colossal shifts in landmasses occurred at the beginning of the **Triassic**, when the Tethys Ocean separated from the eastern part of Pangaea. During the **Jurassic**, the North Atlantic developed, while the southern Atlantic formed during the Cretaceous

Period. In the early **Tertiary** Period, Antarctica and Australia broke off as well, and it took up until the **Pliocene** to arrive at the present position of the continents we see today.

Up to the **Cretaceous** Period, global flora was generally similar in diversity. The oceans at this point were still too small to be considered barriers to the exchange of flora. The history of vegetation up to the **mesophytic** is also called the period of the gymnosperms. Following the extinction of the larger club mosses and horsetails, gymnosperms, particularly conifers, were able to expand their distributions. In the northern regions the first representatives of the Pinaceae and the genus *Juniperus* are found. Cupressaceae occurred worldwide. The boundary between the Jurassic and Cretaceous Periods also divides the mesophytic from the neophytic and the gymnosperms from the angiosperms. The first angiosperms occurred at the end of the Jurassic Period.

In 25 million years of the Cretaceous Period, flowering plants developed rapidly and outcompeted many of the gymnosperms, which up until then had dominated. Almost at a snap of the finger all the main angiosperm groups developed, and all suitable habitats were colonised. Intercontinental flora exchange was still possible and helped facilitate the rapid rates of colonisation. A stronger floristic separation occurred during the Upper Cretaceous Period. The so-called **plant kingdoms** developed and created the three floristic realms in the Southern Hemisphere, Antarktis, Australis and Capensis, two tropical equatorial floristic realms, **Neotropics** and

Table 17.1 Putative evolution of life forms and ecosystems during Earth's history (after Kreeb 1983)

	Time in millions of years	Geological formation	Plant	Animal	Ecosystem type
Neophyticum (angiosperm period)	0	Present	Agricultural techniques	*Homo faber*	Anthropogenic ecosystem disruption
	0.005	Holocene	Cultivated plants	Domestication of animals	Anthropogenic changes in ecosystems
	0.5	Pleistocene		*Homo sapiens*	All land ecosystems, deserts, halophytic communities, cold areas
	30	Tertiary	Deciduous trees	Freshwater fish, humanisation	
	95	Cretaceous	Angiosperms		
Mesophyticum (gymnosperm period)	150	Jurassic	Pine trees, first flowering and seed plants	Early birds	Plant adaptation to different climate zones
	200	Triassic		Dinosaurs, early mammals	
Palaeophyticum (pteridophyte period)	230	Permian			Species diversity decreases slightly
	280	Carboniferous	First tree-like ferns:	Reptiles and dinosaurs	Swamp forests (dry land not colonised)
	340	Devonian	Lycopods Calamites Horsetails Ferns	Lung fish, amphibians, insects	First highly developed land ecosystems in moist places
	450	Silurian	First land plants: early ferns	First vertebrates	Simple ecosystems without consumers on land near coasts
Eophyticum (algae period)	500	Cambrian	Algae	All animal types except vertebrates	Higher developed aquatic ecosystems
	2000	Algoncium	Photosynthesis, respiration using oxygen		(Oxygen atmosphere) simple aquatic ecosystems
	3000	Archaean	First chemosynthetically active organisms		(Anaerobic aquatic ecosystems?) thermophilic organisms
	4000	Early ocean/ early atmosphere	Start of biological evolution: first cells		(Oxygen-free environment) (salt-free ocean?)

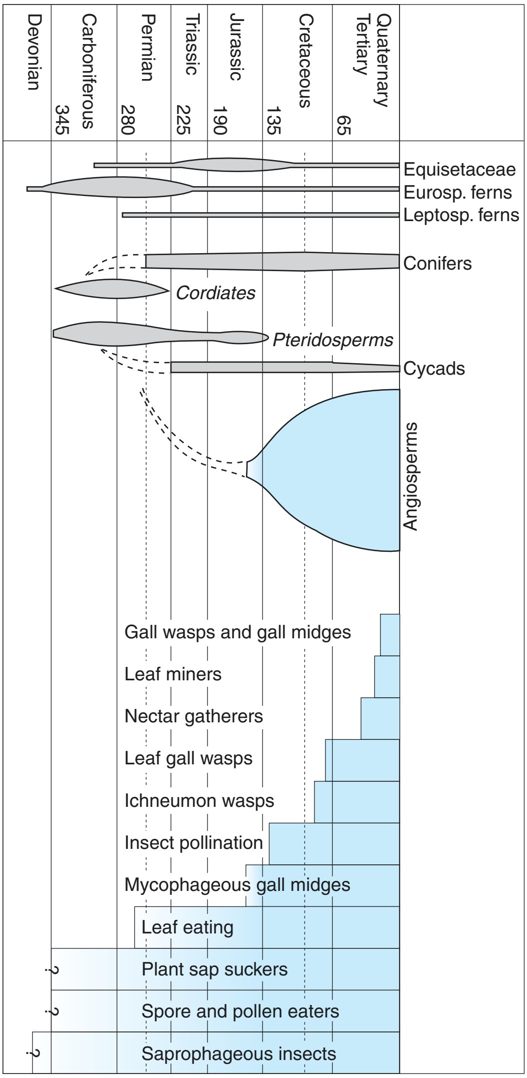


Fig. 17.3 Age and development of important groups of vascular plants and of phyto- and entomophageous insects. First occurrence of insect pollination and herbivory is also shown. (after Zwölfer 1978)

Palaeotropics, and the **Holarctic**, the sole Northern Hemisphere floristic realm.

Zwölfer (1978) gave the first overview of geological occurrences of vascular plants as well as phytophageous and entomophageous insects, which addressed the development of communities. It was reported that both pollen and dead plant material were eaten by arthropods as early as the Devonian Period, and in the Permian leaves were consumed. In the Triassic, insect pollination of flowers occurred, and there were entomophageous parasites and plant galls. From the Tertiary onwards, all present-day phytophages are represented: miners, gall flies and gall gnats (Fig. 17.3).

Mutual adaptations of floristic and faunistic partners (vertebrates as well as invertebrates) result when selective pressures are linked in development. Plants developed thorns, spines or chemical defence substances, whereas animals adapted through changes in their mouth parts or developing resistance against plant toxins. Some flowering plants were able to protect themselves against herbivory, for example, Gentianaceae (defence by indoalkaloids) or Solanaceae (defence by tropanalkaloids); however, again this led to the development in some animals of an ability to adapt to some of the most powerful plant toxins. In some cases animals made use of these substances for their own defence (Sect. 19.4, Chap. 19).

Most groups of flowering plants were present at the beginning of the Tertiary Period. The **neophytic** or angiosperm period is the current period. Among flowering plants, specialists are resilient in the most stressful environmental conditions (e.g. desert, highly saline soils, bare rocks). Along with the formation of mountain ranges, young mountain floras developed (**oreophytes**, sometimes closely related to flora in plains). Often individual altitudinal steps are characterised by **vicariad** species and genera. An example of altitudinal vicariation in the Alps is *Anthoxanthum odoratum* for grasslands at lower altitudes and *Anthoxanthum alpinum* at higher ones. Another example of ecological vicariation is the alpine *Rhododendron* species *R. ferrugineum*, which grows on siliceous rock, and *R. hirsutum*, which grows at the same altitude but on calcareous rock.

Holarctic flora has been found in Palaeozoic to Eocene lignite deposits in Spitsbergen, where not only the remains of plants growing in today's Central Europe under conditions of a temperate climate were found (e.g. *Acer*, *Betula*, *Fagus*, *Quercus*, *Pinus* and *Picea*) but also those that now grow only in humid, subtropical regions (e.g. *Taxodium*, *Magnolia*, *Liriodendron*). Plants found in Greenland represent the so-called **arcto-tertiary flora**, the basis of the Holarctic flora (e.g. *Aesculus*, *Castanea*, *Platanus*, *Vitis*). From the

Eocene “flora from the Geiseltal” near Merseburg, Germany, plant lists were compiled containing tropical plant families (e.g. families Annonaceae, Pandanaceae, Sterculiaceae). The question thus arises as to how tropical genera can grow in areas currently characterised by cold-temperate climatic conditions. Plate tectonics is the justifiable answer, where Europe had only taken up its current position in the Northern Hemisphere during the Tertiary Period.

In plant remains found from the **Pliocene** in Central Europe, tropical species are absent, but present-day genera (*Fagus*, *Quercus*) indicate a worldwide progressive cooling. In Europe, climate and vegetation zones shifted to the south. The development of new barriers began to become an issue, where the west–east extension of the Alps and the Mediterranean Sea made it difficult for certain species adapted to a warm climate to survive, where some species went extinct and others were able to survive in local refuges or simply migrated to more favourable regions. The relative uniformity of Pliocene flora in the Holarctic was lost. Large distribution ranges were separated into several spatially limited regions, the large **Tertiary disjunctions** (different separated parts of the former area of distribution, e.g. *Sequoia* and *Metasequoia*). For other species, for example, of the genera *Styrax*, *Platanus*, *Melia* and *Castanea*, a few moist warm sites became important refuges. The development of Mediterranean sclerophyllic vegetation is often connected to the general cooling of global climate in the Tertiary Period. Cooling in the Pliocene may be regarded as a precursor of the multiple quaternary climate changes, especially when compared with those occurring in the Pleistocene and Holocene.

17.2.2 Change of Climate and Vegetation in Pleistocene

The change from warm to cold periods is very important for the development of the vegetation in Central Europe. Temperatures continued to decrease in the Pleistocene for about two million years, which periodically would change to brief cold (“ice ages”) and warm periods. Average annual temperatures decreased here by at least 8 °C and as much as 12 °C below present-day temperatures. These climatic variations in the early Holocene are mainly explained by periodic changes of solar radiation caused by alterations in the orbit of the rotational axis of the Earth.

Direct and indirect consequences of **Quaternary climate variations** may be summarised as follows: On both hemispheres, starting from the polar regions, enormous inland ice masses up to 3000 m thick developed. Massive alpine glaciers also were present in the higher mountainous ranges. During the glacial maximum, few peaks rose beyond the alpine ice cover (nunataks). The glaciers extended far north into the foothills of mountainous regions, where a mere 300 km of ice-free area between alpine and polar ice caps in Europe remained. At the same time, sea level sank to about 200 m below the present level (eustatic changes) so that movement of plants in the cold period became easier between landmasses currently separated by shelf oceans (e.g. land connection between England and the European continent).

For Europe six cold periods are recognised with intermittent warm periods and short-term thermic oscillations. Glacial advances are typically named by the furthest northern-reaching point of the ice edge in Germany (alpine glacial periods):

Biber and Danube ice age in the early Pleistocene about one million years ago;
Günz and Mindel ice age in the middle Pleistocene, about 250,000 years ago;
Riss ice age about 230,000–120,000 years before the present (BP);
Würm glaciation (about 90,000–12,000 years BP) in the late Pleistocene.

The extinction of warmth-requiring tropical and subtropical species became more extensive, as did the alternating dominance of woody species during the warm periods and herbaceous species and grasses during cold ones. Trees in particular disappeared locally or survived unfavourable periods in **refuges** of eastern and southern latitudes. Because herbaceous plants, grasses and low-growing dwarf shrubs expand at much faster rates owing to their shorter regeneration times, this also resulted in far fewer losses of such species. Some thermophilic species were able to occupy refuges and survived, but their original continuous distribution was eventually separated into several **disjunct areas.** One of these **disjunct distributions** has cedars, with some species in the North African mountains (*Cedrus atlantica*), in the Near East (*Cedrus libani*) and in the Himalayas (*Cedrus deodora*).

During cold periods, very few species (mainly mosses, lichens and high alpine flowering plants) successfully inhabited mountainous regions surrounded by glaciers on the nunataks. The southern range expansion of some species has also been attributed to the changing climate during cold periods. There are several migratory paths, for example, the East African Rift Valley, the American mountain ranges and the bridge in South-East Asia-New Guinea-Australia, where these plants found places to grow and even today occur in bipolar distribution regions. Examples are the genera *Carex*, *Erica*, *Epilobium* and *Empetrum*.

A map of the vegetation in Europe during the peak of the Würm glaciation (Fig. 17.4) shows, compared to the present day, the shift of vegetation zones towards the south. Almost no trees could grow in the regions of Central Europe between the edges of the ice sheet. The vegetation of tundras and cold grasslands of that time were reconstructed using plant remains found in sedimentary lake cores, and it was found that the indicator species was the arctic alpine plant *Dryas octopetala.* During the warm periods, separated by cold periods, an **interglacial vegetation** developed, similar to the development steps of the postglacial vegetation.

17.2.3 Late and Postglacial Climate and Vegetation History

The vegetation history up to the Pleistocene has shown two main aspects:

- The enormous evolution of species and plant communities dependent on astronomic, tectonic and climatic events in biocoenoses.
- A distinct spatial separation of large parts of the Earth's crust occurred, with orogenesis reaching the actual situation.

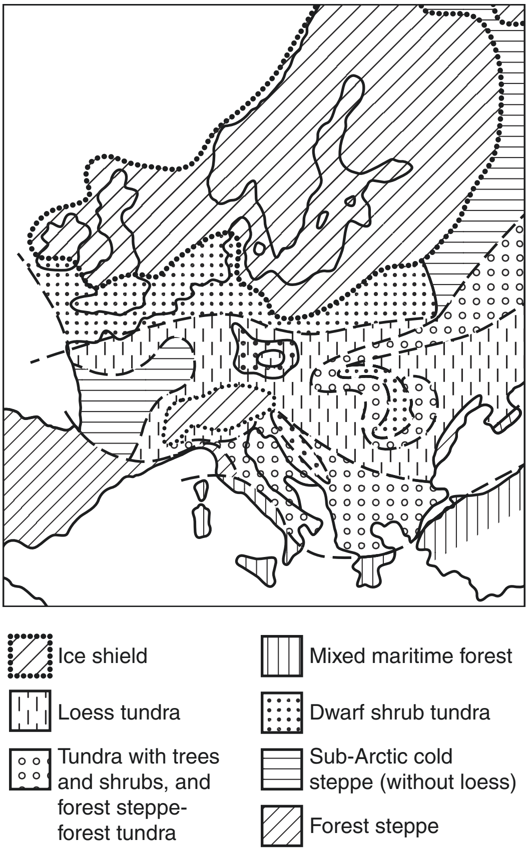


Fig. 17.4 Distribution of vegetation types in Europe during time of maximal glaciation in Würm glacial period. (after Kreeb 1983)

Now, in smaller areas, changes of the floristic characteristics due to small-scale differences in the site conditions are more important. Following the Holocene Period, the continents had almost reached their current position. The result was an irregular pattern with approximately 71% of the globe covered by water and the remaining 29% constituting continental land masses. The latter are unequally distributed with a large maximum in the Northern Hemisphere. Furthermore, large mountain ranges formed in Eurasia, extending mainly from west to east and north to south in the Americas. These main features have a determinant role in regional, continental and global climate, and, thus, impact the distribution and dynamics of vegetation.

Because of the outstanding example of the north–south extension of the Cordilleras, the different atmospheric conditions in the Americas, coupled with the regional pattern of glaciers and ice sheets, together form a developmental process different from what has occurred in Europe. Plant migration following the climatic changes was easier because difficult-to-cross west–east barriers like the European alpine mountain chains are missing. We concentrate here on the development in Eurasia and Africa.

The history of vegetation during the Holocene in Europe has been documented by **pollen analysis** and **radiocarbon dating** (Table 17.2). Almost all plant species found using these techniques have survived to the present day. Today, comprehensive data sets are available that are directly or indirectly linked to the vegetation development in postglacial and Holocene times. Not all historical analysis is done with pollen and radiocarbon dating; other techniques include macrofossils, tree-line changes (Fig. 17.5) and tree rings. Various waterborne traces have also been used, where the measurements of inorganic compounds within glaciers, ice sheets, eustatic terraces and lake levels can be taken. Furthermore, changes in orbital axes and solar radiation can also be used to draw inferences from the patterns and the likelihood of the presence of certain species in the past. Finally, for the last few centuries anthropogenic greenhouse gases and remarkable land cover changes have contributed directly or indirectly to more recent vegetation changes.

On the basis of the various sources of data, some models have been developed and have proposed findings that suggest detailed accounts of climate fluctuations leading to reactions of plant communities. Controversy still surrounds the causality of these findings, which continue to be discussed (Gallimore et al. 2005; Holzhauser et al. 2005). The difficulty in attributing the causes to one factor or a number of factors lies in the fact that there are many aspects that contribute in combination with a high order of complexity in terms of the processes and how they can change with climate. The differences are often due to the different data included in modelling that have been considered as decisive

Table 17.2 Vegetation and climatic elements of late- and postglacial times. Columns for time, pollination zone I–XII (from Overbeck 1975), vegetation period, climate history and human prehistory (after Walter and Straka 1970)

1000	XII	Forest plantations Beech	Post-interglacial period (sub-Atlanticum) (relatively cool and moist)	Postglacial	Historical period
0	XI				Iron Age
−1000	X	Beech-oak	Late interglacial period (Sub-Boreal) (warm and dry)		Bronze Age
−3000	IX	Mixed oak forest (oak, elm, lime, ash)	Middle interglacial period (Atlanticum) (warm and moist, climate optimum)		Late
−4000	VIII				Middle Neolithic
−5000					Early
−6000	VII	Hazel	Early interglacial (boreal) (warm and dry)		Mesolithic
−7000	VI	Hazel-pine			
−8000	V	Birch-pine	Pre-interglacial (increasing temperatures)		
	IV	Tree-poor tundra	Late subarctic period (return of cold)	Late Ice Age	Palaeolithic
−9000	III	Birch-pine	Middle subarctic period (Allerod) (temporarily warmer)		
−10000					
	II	Tree-poor tundra	Early subarctic period		
−11000	1	Treeless tundra	Late arctic period (cold)	Main glaciation	
−12000					

(e.g. atmosphere–ocean–land data, glacier or lake-level changes, solar activities or albedo changes).

So far, the results allow two general interpretations. The first involves researchers seeing a possibility or a necessity to put the results in a system of periods. This method has been traditionally done in pollen analysis, which was built from the diagrams of Firbas (1952 ff) and Overbeck (1975) and later improved by Holzhauser et al. (2005) and Joerin et al. (2006). The second interpretation involves incorporating variability in an attempt to discern general trends, for example, cooling or warming, under humid or arid conditions (Prentice and Jolly 2000; Wanner et al. 2008).

For a description of the late glacial time and the Holocene we have divided the following into three phases:

- Late- and postglacial times and early Holocene (18,000–9000 BP).
- Mid-Holocene (9000–6000 BP).
- Late-Holocene and preindustrial time (6000 BP–1700 AD).

In these three phases the development of the vegetation is closely connected with climatic changes. The influences of the late Holocene, where a remarkable human aspect begins to be identified on the vegetation, will be dealt with in the next subchapter.

In the **late glacial period**, also called the Dryas Period after the indicator species *Dryas octopetala*, a continental steppe dominated by scattered tree-free tundra islands was reconstructed after the results of pollen and macrofossil vegetation relics. All over the Northern Hemisphere, the cold, dry conditions led to dif-

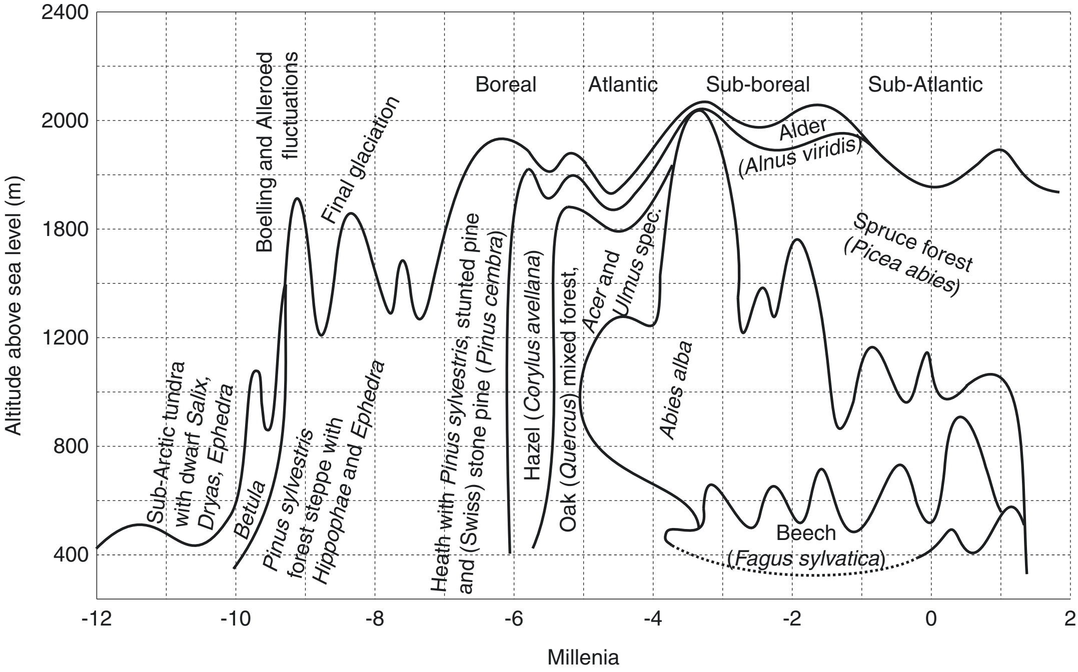


Fig. 17.5 Development of altitudinal zones of vegetation in northern Swiss Alps since maximum of Würm glaciation. (after Strasburger and Sitte 1998)

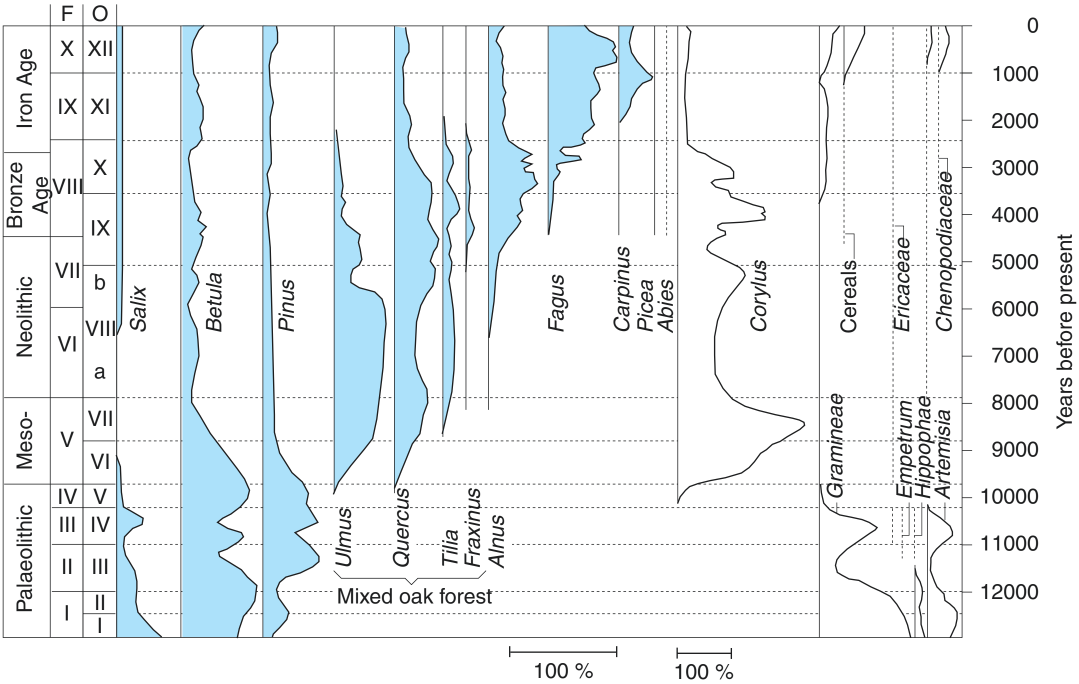


Fig. 17.6 Pollen diagram from Luttersee. The lake is situated near Göttingen, northern Germany, 160 m a.s.l.). Scale: sum of tree pollen 100%, without hazel (*Corylus*). (after Walter 1986)

ferent tundra and grassland types. Forest biomes were displaced southward, the boreal (i.e. taiga) biome became largely fragmented, while at the same time the moist tropical and temperate forests saw significant reductions. It is argued that during this period the arid Saharan mountains we know today may have been linked with the Mediterranean and tropical forest biomes and may have led to some of the discontinuous or fragmented range disjunctions, for example, *Acacia* spp. and *Euphorbia balsamifera* (Deil and Müller-Hohenstein 1984).

A noticeable warming of the climate occurred around 12,000 BP and was accompanied by the retreat of alpine and continental glaciers. As a result of this retreat of the glaciers, many species filled the newly created void of space. Warm-demanding species, in particular trees, were able to take advantage of this space in Central Europe. In Northern Europe, the forest biomes extended into the present-day tundras, while in the South, large parts of the Sahara were invaded by tropical grassland and dry shrubland.

This did not occur continuously. The migration of the tree species back to the earlier positions was reconstructed by comparing pollen profiles, so-called **iso-pollen maps**. This dynamic occurred in different ways and at different periods, according to the requirements of species for the site, the speed of migration and the location of the refuges during cold periods. Spruce (*Picea*) immigrated from an easterly direction, following the "northern path" from the southern Urals. Fir trees (*Abies*) and almost all deciduous trees (e.g. Fagus) originated from the Mediterranean areas and reached Central Europe via the Burgundian Gate or the Pannonian Basin. A pollen diagram from the Lutter Sea in northern Germany, representative of Central Europe, shows a detailed picture of the development of the temperate deciduous broadleaf forest biome from the late glacial period on (Figs. 17.6 and 17.7).

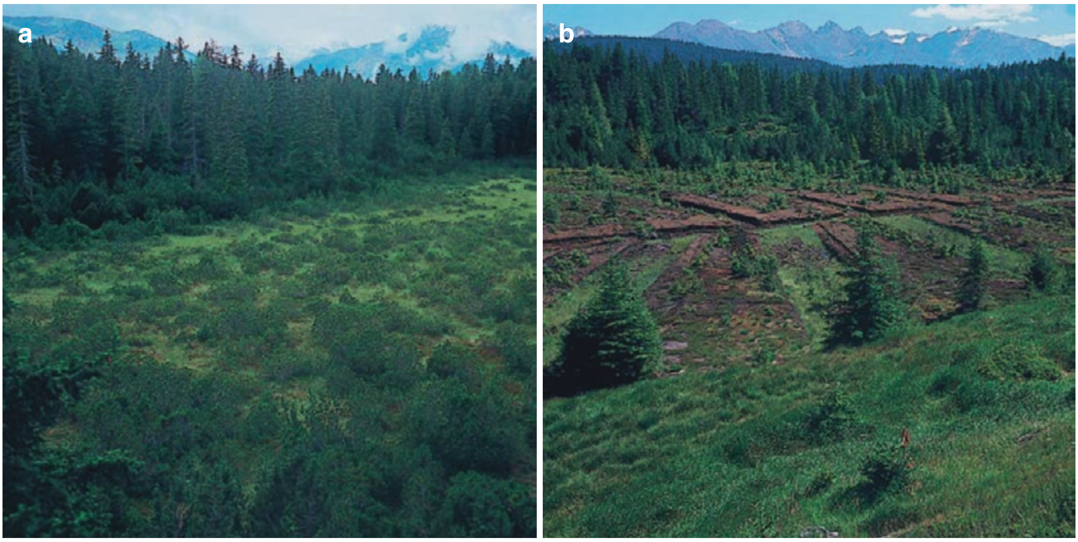


Fig. 17.7 Undisturbed and disturbed raised bogs. **a** Part of the almost natural "Pillermoor" (1600 m a.s.l.), which is a protected area in the lower Pitztal (Tyrol, Austria). **b** Part of same raised bog where peat was removed more than 30 years ago. Pollen analysis from this bog shows the postglacial development of vegetation of the montane region in Tyrol. (Photos: K. Müller-Hohenstein)

During the following 6000 years, the temperatures remained high with a number of distinct fluctuations. Consequently, the vegetation cover also changed; in the warmest periods (e.g. **Alleröd period, Atlantic period**), sparse spruce and birch forests and willow shrubs were able to exist. The steppes advanced from the east under the still extremely continental conditions. The temperate forest was able to extend; birch was methodically replaced by hazel and other deciduous trees. Human populations in the Mesolithic (about 8000 BP) were surrounded by species-rich forest communities. Remnants of tundra occupied the increasingly melting edges of the continental ice sheet, and steppes were pushed by invading forests towards the south and south-east.

This development is also confirmed by results of tree-line studies. The position of the alpine tree line in the last 12,000 years was approximately 1200 m lower in the last glacial period compared with present day conditions, outlined by the remarkable warming over this period (Fig. 17.5). The variation of the tree line, as well as a recently published temperature reconstruction, outlines similar temperature fluctuations following this temperature increase in the middle-late glacial period (Marcott et al. 2013). Throughout the early Holocene the temperatures stayed—with some regional variations—at this level. In the European Alps the tree line was about 400 m higher than today.

The warmest climatic conditions, and the corresponding development of vegetation, were experienced by the early Neolithic people in the **Atlantic period** about 6000–7000 BP. In Northern Europe, during this time of the "climatic optimum", mean annual temperatures were 2–3 K higher than present temperatures. Mixed oak forests with deciduous trees requiring warm climatic and nutrient-rich edaphic conditions were dominant. In the montane areas, fir dominated in the western Alps, spruce in the eastern Alps and pines in the eastern part of Central Europe on nutrient-poor sites. Thermophilic species still occurred at dry sites with grassland vegetation.

Glacial relicts from the cold periods are still maintained in present-day vegetation in isolated sites, for example, *Betula nana* in the foothills of the Alps in peat bogs. Similarly, species from the warmest periods were also able to persist on limestone outcrops. These **xerotherm relicts**, sub-Mediterranean species (*Quercus pubescens*) and those from the south Siberian and Pontic areas (*Stipa* spp.) were able to survive after the onset of cooling in the Sub-Boreal forest. To ensure their survival, both of these relict species required specific microclimatic or edaphic conditions. For xerotherm species, extremely shallow and southern facing, exposed sites, which inhibit the growth of trees, are needed. Beech only became dominant in the forests of Central Europe in the Atlantic period and took over the role of hornbeam (*Carpinus betulus*), which dominated in the interglacial period and was now predominant further to the east. Together with spruce and fir, beech forms forests up to the montane belt. Even though beech has dominated the forests of Central Europe for only a relatively short time period (30–50 tree generations), beech-dominated forests became established everywhere, up until increased human intervention became more intense (Hasel and Schwartz 2006).

Two main causes were responsible for further changes of the vegetation cover in the following millennia:

- a continuous decline in temperatures and.
- growing human influence (Sect. 17.2.4).

The climatic cooling (between 0.1 and 0.3 K over 1000 years) was the most important reason for large-scale plant migrations. Species that required higher temperatures migrated back into warmer regions and outcompeted the cold-period vegetation, except for a few relict species. Their expansion partly followed the edges of the ice sheet, and thus many closed areas became divided, and **disjunctions** were formed. Some of these disjunctions are concentrated on the Southern European mountains (e.g. species of the genera *Primula* and *Saxifraga*), while others form the arcto-alpine disjunctions with interspersed occurrence on the highest parts of the mountains of central Germany (e.g. *Nigritella nigra* agg.). Supplemental examples of disjunction distributions include the *Betula nana* and *Salix herbacea* and the circumpolar *Loiseleuria procumbens* and *Eriophorum scheuchzeri* in North America.

A reconstruction of the changes in global temperatures shows a constant decline in temperature, which ended only in the nineteenth century (Marcott et al. 2013). Especially thanks to a comprehensive palaeo Vegetation Mapping Project (BIOME 6000; Prentice and Jolly 2000), our knowledge about vegetation development from the mid-Holocene on has been considerably deepened. The reconstruction of the vegetation cover was made possible through the use of extensive pollen and macrofossil records. Vegetation was classified on the basis of plant functional types (PFTs), biomes, and megabiomes with worldwide contributions to this programme (Harrison and Prentice 2003). Because of high summer insolation and warmer temperatures, plant species with high heat demand experience very advantageous conditions. Therefore, the vegetation distribution compared to present-day conditions, and not including anthropogenic influences, has led to a significant northward shifting of boreal and temperate species in the Northern Hemisphere. Although variability exists and depends on the region, all distributions were more than 100 km further north compared to today. Warmer winter temperatures also favoured a change from cold-temperate mixed forests to temperate deciduous forests. The Mediterranean subtropics, however, were covered with temperate grassland and xerophytic shrubland.

Only in recent decades have new data been collected in connection with the history and climate of the arid African areas (Holzhauser et al. 2005; Knorr and Schnitzler 2006). According to these findings, the long-established views of a synchronous sequence of cold and warm periods in higher latitudes (e.g. Central Europe) and dry and humid ones in lower latitudes (e.g. Northern Africa) must be corrected.

During a long period (approximately between 18,000 and 6000 BP), most of the Sahara was "green", and warm-temperate mixed forests approached from the north as well as semi-evergreen broadleaf forests from the south (according to the original biome classification by Prentice and Jolly 2000). Mountains in the Sahara possessed a strongly **Mediterranean vegetation**. These conditions persisted up until the Atlantic period with semi-arid conditions and summer rains in the south and winter rains in the north, ultimately led to the Sahara being narrowed to a smaller region. Neumann (1988) assumes on the basis of charcoal analyses that Sahelian vegetation was approximately 600 km further north and dominated by such species as *Balanites aegyptiaca*, *Acacia albida* and *Cadaba farinosa*, which made up a sparse dry woodland, where grasslands advanced from 18.75° to 22.5°N. Other vegetation shifts were also identified, although smaller in size: the south-west shift of Mediterranean species is also assumed to have happened due to a positive precipitation–vegetation feedback, based on changes in albedo. It wasn't until about 6000 BP that everywhere in the Northern Hemisphere started cooling and experienced many more changes in vegetation. After weather conditions around 8000 BP began to cease, Neolithic man in the Sahara experienced increasing drought from 5000 years ago until now (Fig. 17.8). The tropical savanna reached its actual position again around 3300 BP. For the Sahara, even today, two relatively stable and interchanging vegetation phases are assumed, a "green" Sahara and a "red" Sahara

Fig. 17.8 Rock paintings and engravings indicate once more humid climatic conditions in central Saharan mountains. Pictures of hunters **a** and large grazing herds **b** near Sefar (Tassili), southern Algeria, are nearly 8000 years old. The "crying cows from Terarart" **c** near Djanet are about 5000 years old and indicate a gradual increase in aridity. (Photos: K. Müller-Hohenstein)

that is almost bare of vegetation (Claussen 2001). The actual human-influenced expansion of desert conditions in all sub-Saharan regions leads to increasing losses of both plants and animals, even if the situation for the flora is less dramatic (Le Houerou 1997).

There is sufficient evidence from glacier- and lake-level studies in the Swiss Alps with high-resolution data that natural driving forces still contribute to climate change (Holzhauser et al. 2005). Also, the results of tree-line studies from Russia underline a continuous cooling, at least more or less synchronous for the continents of the Northern Hemisphere (MacDonald et al. 2000a, b). Only in the last 300 years, despite the input of volcanic aerosols and a certain variability in solar insolation (both of which initiate cooling effects), has it been exceeded by the warming effect of the input of excessive greenhouse gases and land-use changes (shifting of forest to agricultural lands), which has ultimately led to a reverse forcing of the biophysical drivers for the continuous cooling seen in many regions. The main driving force for all these changes in the vegetation cover is no longer exclusively a change in climate; we must now consider anthropogenic effects in all biomes.

17.2.4 Changes in Vegetation Owing to Human Influence

Human activities have always affected vegetation because humans are directly or indirectly dependent on plants for raw materials, food and feed for agricultural livestock. The influence of humans historically was fairly small and restricted to simple consumption for themselves and their livestock. However, over time, with the rapid growth in population sizes, coupled with advances in technology and our use and the distribution of plants across the world, that influence has changed dramatically. The mosaic of anthropogenic plant communities became more diversified, corresponding to the type, duration, intensity and extent of human influence. Gathering beneficial wild plants for food and medicine, wood cutting, grazing and especially hunting and clearing, assisted by fire, led to specific "**substitute communities**". Soon, coppiced forests, managed meadows and other previously unknown plant communities arose. An important contribution to the diversification of human-made vegetation types brought the lessons learnt from hunting and gathering to all agricultural activities to improve plant cultivation and animal husbandry (Box 17.1).

Box 17.1: Typical Methods of Forest and Agricultural Management

A. Forestry

Coppice system ("Niederwald"): In the Middle Ages, such forests were used to obtain oak bark for tanning and firewood (Fig. 17.9d). The entire forest was used in 30-or-so-year cycles and regenerated from coppiced trees (regrowth from stump or roots). Thus, species that could regenerate were selected for (e.g. hazel, oak, hornbeam). Today, in many developing countries, afforestation efforts (e.g. with *Eucalyptus* species) are also used as coppiced forest.

Coppice with standard system ("Mittelwald"): This is a form of forest management applied in the Middle Ages (Fig. 17.9c) in combination with agriculture. The best individual trees (primarily oak) were harvested to supply timber for construction ("standards"), while the remaining trees were selected via coppicing. This technique is still used today to harvest valuable oak for veneers. Thus, an open canopy of uneven aged trees was consistently maintained to provide a sustainable supply of timber for use in construction.

High forest system ("Hochwald"): This consists of trees that grew from seeds (in contrast to regrowth from coppiced trees) (Fig. 17.9b). High forest systems are the dominant forest management strategy today. There are different varieties of this system: (1) **clear-felling (clear-cut)**, where all trees within a cutting block are cut at the same time; (2) **shelter-wood felling**, where a portion of the canopy trees are harvested, while the remaining portion provides canopy protection for the understorey and seed production and are typically distributed uniformly over the harvesting block. This management strategy leads to uneven aged stands, where successful regeneration in the European systems consists of beech, coming through the understorey, while pine and oak are harvested in the overstorey. As a result, canopy trees can be twice as old as the mean stand age. For example, oak becomes most valuable for timber beyond 300 years, where the space between individual trunks is filled with some younger tree generations in order to minimise the growth of shoots from dormant buds; (3) **selective cutting** and gap felling, whose tree harvests result in stands that are not of uniform age; only some of the trees are removed according to their size and usefulness. Regeneration in selectively thinned forests takes place where the individual trees have been removed. Because of variations of light and size in the regeneration area, a species-rich and multi-storey forest results.

ARD: *Afforestation, reforestation and deforestation* attained particular significance in the onset of the Kyoto Protocol (Chap. 21). **Deforestation** refers to harvesting an entire forest and converting the area into other uses (e.g. roads, agriculture), **reforestation** is re-establishing areas of forest that had previously been forested but changed to another land use (e.g. planting of forests in valley meadows), and **afforestation** means the establishment of forests on land that had not been forested earlier (e.g. forests on moorlands). **Revegetation** is the re-establishment of forests on areas that had been free of vegetation (e.g. slag heaps). **Degradation** is the result of harvesting of wood in excess of its natural growth, self-thinning and the density it would reach had the stand attained maximal growth. The current definition of a forest (10–30% cover, 2–4 m high) allows degradation of these limiting values before **conversion** (e.g. from primary to secondary forest or to plantations).

B. Agriculture

Managed grasslands: This term refers to meadows and swards that used in the production of hay or silage or for grazing. In Central Europe, these grasslands occur mainly on heavier (clay) soils, which are difficult to plough in spring, or in areas where the growing period is too short for cereals (mountain meadows). The species richness of this strategy depends on the intensity with which they are used (e.g. frequency of cutting, fertilisation).

Arable farming: Distinctions based on the following criteria are made (Swift and Anderson 1993):

Type of soil manipulation: ploughing, disc-harrowing. With the latter, a breakdown of organic matter in the soil is reduced and seed is sown in the furrows made by the disc harrow. This method decreases the compaction of soils and leads to deeper rooting, which may increase yields in semi-arid regions. There is no soil manipulation with zero tillage.

Type of crop: root crops (potatoes, beet) and **cereals**. Earlier agriculture employed intensive soil manipulation and thinning after sowing as a means of controlling weeds and crop density. Today, hoeing is less essential as weeds are controlled chemically and the number of crop plants is technically regulated by sowing density. In cereal cultivation, a distinction is made between **winter cereals**, sown in the autumn months, and **spring cereals**, sown in spring. Spring cereals have smaller yields, but they avoid the risk of frost damage in winter. Particular types of crops are those grown for **oil seed** (rape: sown in autumn; sunflower: sown in spring) and **maize**, which is sown in late spring after frost (typically in May) because it requires warm temperatures for growth. Cultivation of oil seeds and maize in Central Europe has increased considerably in recent decades. Also, crops for bioenergy have growing importance (e.g. straw from cereals).

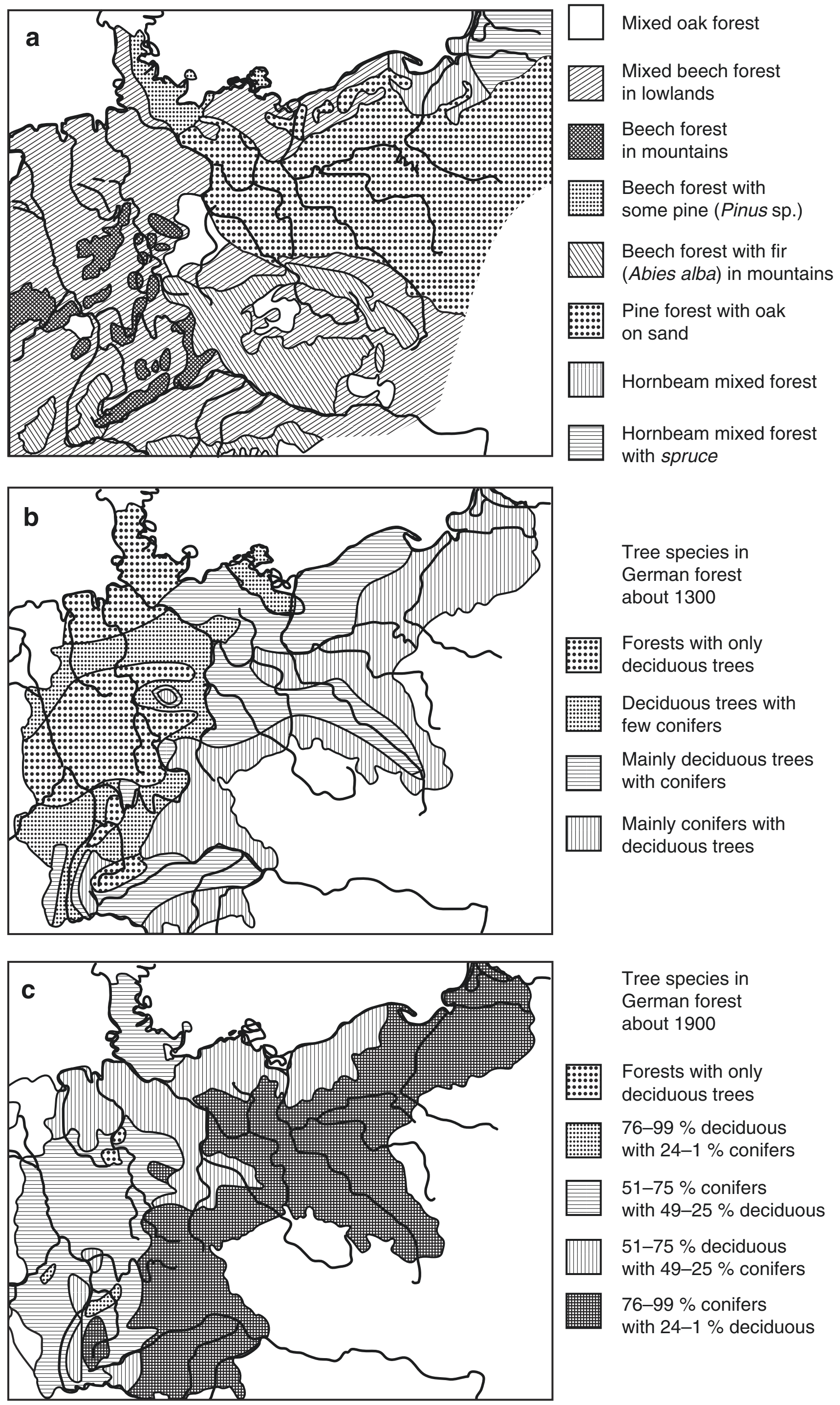


Fig. 17.9 Development of forests in Central Europe. From **a** after the warm period about 2000 BP (Firbas 1952) through **b** the Middle Ages until **c** the nineteenth century. (after Kreeb 1983)

Rain-fed agriculture occurs in dry areas (Fig. 17.10b): In the first year, fields are ploughed but not sown (fallow land). Precipitation is stored in the soil following rainfall, and the soil surface is harrowed in order to decrease evaporation, and the capillary action causes water to rise from deep in the soil to the surface. In the second year (or even later), the field is sown, so the crop can often benefit from 2 years of stored rainfall.

Shifting cultivation: This type of agriculture is dominant in tropical regions (Fig. 17.11a–c): smaller areas of forest are cleared and burnt in order to make nutrients available for cultivation, for example, of rice, manioc, banana, for a number of years. After

Fig. 17.10 Typical types of agricultural land use in countries around the Mediterranean. **a** Subsistence farming in a small area with mixed crops and many cultivated plant species (Central Atlas, Morocco). **b** Grain crops and fodder plants for national market on large-scale farms with high input of agrochemicals and machinery (Tuscan Hills, Italy). **c** Mixed agroforestry with grain crops for grower consumption and cork (*Quercus suber*) for national market (Extremadura, Spain). **d** Unregulated, excessive grazing with severely degraded forests and soil erosion (Central Atlas, Morocco). (Photos: K. Müller-Hohenstein)

some time, the nutrient availability is exhausted by the continuous harvesting and leads to the abandonment of the agricultural area and the clearing of a new area. Depending on the duration of this cycle, secondary forests can become established in abandoned areas. However, following very rapid or multiple rotations, degradation occurs because the fallow period is too short for the accumulation of nutrients in soils and vegetation. Grass species (e.g. *Imperata cylindrica*) invade; they are not preferred by animals because of their high Si content and must be controlled by fire. Consequently, there is a transition from species-rich forest to monotonous grassland.

Agroforestry (predominantly in the tropics) describes management systems in which forest regeneration and timber production (for fodder and fire wood respectively) are linked to field crop production in space and time. The overstorey is used for timber production, while field crops are grown in the understorey. Species of both strata are deliberately selected to optimise resource complementarity, which results in higher yields.

Multiple cropping (mainly in the humid tropics and oases of the Sahara): In this case (Fig. 17.12b), there is a permanent layer of fruit trees (mango, coconut) above useful shrubs (also herbs, banana), which in turn cover herbaceous crops (ginger, taro, manioc).

Fig. 17.11 Typical processes and sequences in exploitation of tropical rainforest. Examples from Central Sulawesi, Indonesia. **a** Uncontrolled clearing (slash and burn) of primary forest, done often by groups of people without knowledge of methods appropriate for the environment. **b** Agricultural use of the cleared forests for only a few years (without fertiliser application) until the fertility of the land is exhausted by the cultivated plants grown to fulfil people's needs. **c** The unproductive area is abandoned and quickly invaded by alang-alang grass (*Imperata cylindrica*) and bracken (*Pteridium aquilinum*). (Photos: K. Müller-Hohenstein)

Fig. 17.12 Types of sustainable agricultural land use in the humid as well as in seasonally moist tropical regions, across all continents. **a** "Continuous" rice cultivation in South-East Asia often combined with cultivation of different palm trees (Sulawesi, Indonesia). **b** In almost all tropical regions, small home gardens are multi-storied with different layers of cultivated plants, which "copies" the species-rich tropical forests, for example, trees such as oil palm (*Elaeis guineensis*), cashew nut (*Anacardium occidentale*) and banana (*Musa paradisiaca*) and annual vegetables below (Guinea-Bissau). **c** Sophisticated irrigation schemes on widespread terrace complexes have been in use for many centuries for cultivation of annual crops such as sorghum (*Sorghum bicolor*) and perennial shrubs such as coffee (*Coffea arabica*) and qat (*Catha edulis*) in the Yemen Arab Republic. (Photos: K. Müller-Hohenstein)

The present-day global distribution of vegetation can only be understood in light of human-induced influence and its associated effects on the plant community for the past few millennia. Nowadays, in Central Europe, no plant communities exist that have not been influenced by humans. In the absence of humans, it would be easy to have a vast closed cover forest across the entire European continent, for the exception of the area above the tree lines in the high mountains. At least in Europe and East Asia, the present vegetation is the result of interactions between the requirements of humans in different cultural situations and resources that offered natural landscapes. Most of these interventions are linked to the development of sedentary agricultural societies in Central America and—especially important for Europe—in East Asia.

17.2.4.1 Early Land-Use Influences

The area surrounding the Bay of Bengal, the northern Savanna landscapes of India, the Yangtze region of China and the highlands of Mexico are some of the **oldest centres of agriculture** (von Wissmann 1957). There is now proof that these agricultural centres had access to a number of different agricultural techniques since at least 14,000 years (Bar-Yosef 1998). Agriculturalists are thought to have come from the Levant about a thousand years later, where they arrived via Iran in Mesopotamia and essentially replaced the hunter-gatherers already located there (Hillman et al. 2001). The first technical advance was irrigation.

From this region of the Fertile Crescent agriculture and animal husbandry (cultivation) reached Central Europe via the Mediterranean region. The important steps in the shift away from a culture based on pure hunting-gathering to one that developed through the use of many techniques to improve crop growth had already taken place outside Europe. Neolithic agriculture in southern-central Europe has been found to have started about 7000 years ago, while the northern region began roughly 5500 years ago, generally limited to areas with the best climatic and edaphic conditions (dry, warm, but often nutrient-poor sites) as present in sparse mixed oak forests.

17.2.4.2 Land-Use Influences from Neolithic to Middle Ages

For a long time the **effect of prehistoric man** on the cover of vegetation was severely underestimated. Today, it is possible to prove the effect of these human activities for the periods in which, during postglacial times, the edges of the ice sheet retreated and woodland species immigrated. Agricultural activities (clearing and burning) contributed already during late-Neolithic times to the excessive release of greenhouse gases (GHGs) in the atmosphere and leading to human-induced climate warming. Furthermore, the intensified rice cultivation in Asia has consistently contributed to GHG emissions, where significant levels of methane are a primary by-product (Kerr 2013). Deforestation, soil erosion, nutrient depletion of soils, and land-use changes have led to often irreversible impacts worldwide, especially since the industrialisation of many larger countries over the past 300 years.

In the Neolithic Age, **"unregulated forest-field management"** was the most important type of land use in Central Europe. After clearing, agriculture was practised for a few years. Then the area was left fallow for a long period. Regulated rotation with sowing, grazing and use of wood in certain restricted periods in an area was only developed in the Bronze and Iron Ages (about 3700 BP), when sickles and iron ploughs replaced the wooden hook plough. The major crops grown during this period were primarily wheat, emmer and spelt. At the regional level, buckwheat was important, as were barley and rye later. The primary livestock of cattle and pigs were used to graze in forests, where the canopy trees provided wood for housing and firewood.

The first **coppiced forests** were developed in the Bronze Age. Wood was used for charcoal kilns and the smelting of iron ore. Hedges grew along species-rich edges of forests and nutrient-poor meadows, and dwarf shrub heathland expanded, leaving the regeneration of grazed forest areas endangered. Many deciduous trees were harvested for their branches (lopping) to provide livestock food for the winter. Thus, natural vegetation was not only considerably changed on arable fields and replaced by crop plants and their accompanying vegetation, but also in structure and species composition. In addition, large areas around settlements were influenced by grazing, trampling and tree felling and the use of other non-timber forest products, such as leaf litter.

For the last 2000 years, the youngest history of climate and vegetation development has been the focus of IGBP's "Past Global Change" (PAGES 2k) project (Kaufman et al. 2013). A continued cooling event has been confirmed with modest fluctuations (Little Ice Age between 1550 and 1850, with three warmer intervals) until the beginning of the industrial period (circa 1700 AD). During this period, on average, global temperature was still 0.3 K lower than that found over the last millennium. These findings should be taken with a grain of salt, as considerable variability and a combination of anthropogenic and natural drivers skew the effects at the local scale.

In Central Europe, until the beginning of modern times, human activity focused on clearing areas for agricultural purposes and settlements. Forests were degraded by grazing animals and by the increasing demand for wood, which was the sole energy source for cooking and heat prior to the use of coal. The ratio of forest to open land at the end of the first clearing period was approximately 70:30, despite Neolithic and Roman settlements. In the thirteenth century this ratio flipped to 30:70. Natural forests were restricted to areas unfavourable for agriculture. Not only was the vegetation cover changed drastically, but considerable soil erosion also occurred, outlined by the alluvial deposits in most European valleys (Dotterweich 2008). Towards the end of the Middle Ages, considerable breakdowns within the social system would lead to slight increases in forested areas. At the dawn of the sixteenth century, some of the first forest regulations were enacted as a means of protecting and limiting the use of forests. As early as the twelfth century, in some regions, the grazing of goats in forests was already forbidden.

The remaining forests were structurally and floristically changed. To maintain the energy requirements and to consciously save areas of forests for grazing, coppiced forests were managed. Oak and hornbeam were particularly suited to this kind of forest management because they regenerate easily through coppicing. The fruits of oak, beech and hazel were not only important feed for livestock but were also consumed by humans. These species were thus cultivated in open forests so shade-demanding woody species decreased. Oaks were grown not only for acorns (animal feed) but also for their bark, which was used for tanning. Large, emergent trees were retained as standards in the coppice system for timber, which was required for construction (Box 17.1A).

Forest management strategies like that of the "thinned coppice" allows several light-demanding herbaceous and woody plants to become established. However, losses of species can occur owing to heavy grazing from livestock, in addition to the use of leaf litter and humus-rich topsoil for barns. The excessive collection of humus and leaf litter contributed significantly to the loss of nutrients in the system and led to large differences in fertility between forests and arable land. Excessive use of forests on sandy soils caused the formation of **heathland** in Northern Europe. Chronicles describe the scarcity of wood, which led to the use of **peat from bogs**.

Today grazing and browsing in forests occur worldwide and are regarded as the anthropogenic factor that has had the most significant influence on vegetation (Ellenberg 2009) (Fig. 17.13). The increasing level of grazing had two consequences. First, depending on the original forest type and the number and type of grazing animals, many different plant communities, dominated by herbs and grasses, developed. Moist meadows, nutrient-deficient meadows, hay meadows and pastures with grasses able to regenerate rapidly expanded and excluded woody species. Occasional burning stimulated some herbaceous species, while others disappeared. More animals led to an increase of weeds in pastures, and plants sensitive to trampling disappeared. Poisonous species and those possessing protection (i.e. thorns) flourished and became dominant in the system. Animals contributed to the expansion of shrubs, dwarf shrubs and herbaceous species. To control the species composition within their fields, farmers would regulate the frequency of mowing, periods of grazing and the number of animals allowed to graze. A partic-

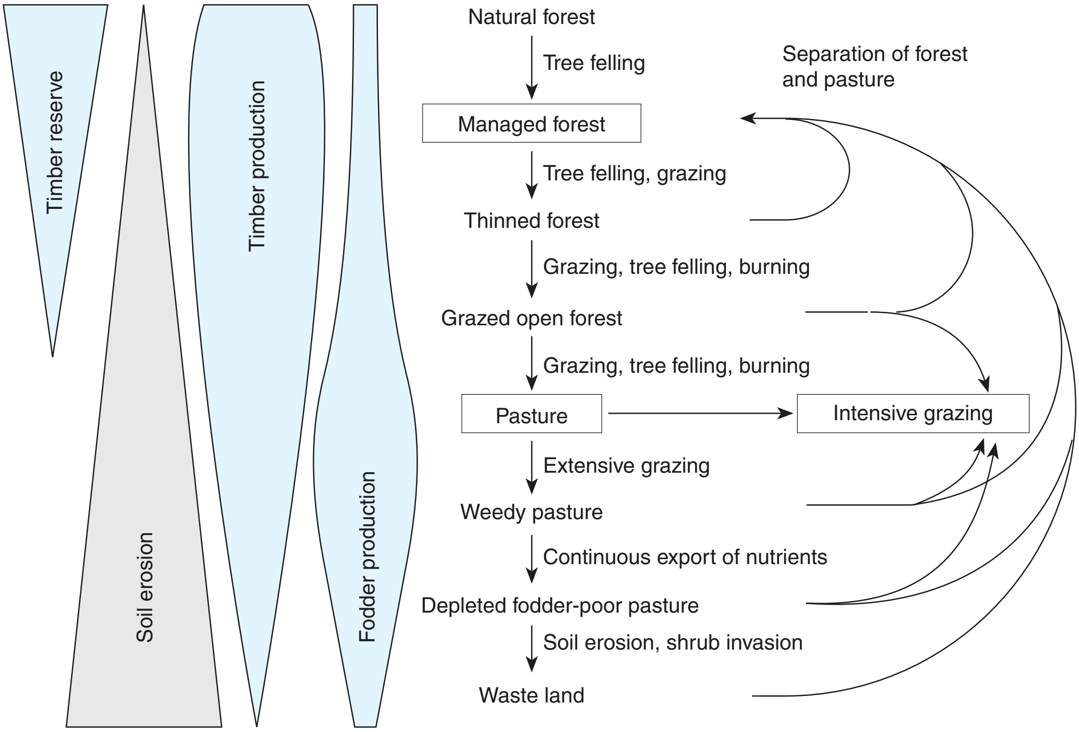


Fig. 17.13 Human influences on the vegetation of Central Europe. Including harvested timber and fodder yields, as well as estimates of timber reserves and soil erosion. (after Ellenberg 2009)

ular feature of this vegetation type is the large number of nitrophilic species in areas where many animals were kept ("Lägerflur", Sect. 20.3).

Previously unknown plant communities also developed with agriculture. During the Middle Ages, the permanent cultivation of rye without crop rotation, together with the growth of other cereals and buckwheat, led to so-called **three-field crop rotation**. The succession was winter cereals, summer cereals and usually a compulsory grazing fallow period that would regenerate the balance of nutrients through the input of manure as fertiliser. The first communities of weeds on arable land still contained many perennial species because of the fallow period and the relatively rare disruption from ploughing the soil. The highest species diversity in Central Europe occurred at the end of the Middle Ages as a result of human activities, which also led to a higher diversity of plant communities and habitat. In valley landscapes of Central Europe, a number of different important processes occurred that led to a number of different communities (Fig. 17.14). The valleys were important not only for the expansion of economic innovations but also for the dispersal of plants because of their small-scale differentiation of site conditions. The increase in the richness of the flora was only possible because of the disturbance of natural sites and resulted in the creation of new sites. The plant communities within the valleys were much different from those occurring within a forest or open fields because the depletion and accumulation of nutrients, irrigation and drainage were controlled by many different microclimatic processes.

The agricultural landscape of the Middle Ages was driven primarily by two developments. The first one was the introduction of crops from the Americas (e.g. potatoes, maize, quinoa). The second one concerns an extremely varied mosaic of plant communities, resulting in high compositional and structural diversity, which became very much endangered as a result of subsequent mechanisation in agriculture. The temporal development of species that have become naturalised (**archaeophytes and neophytes**), as well as those that have become extinct, have been

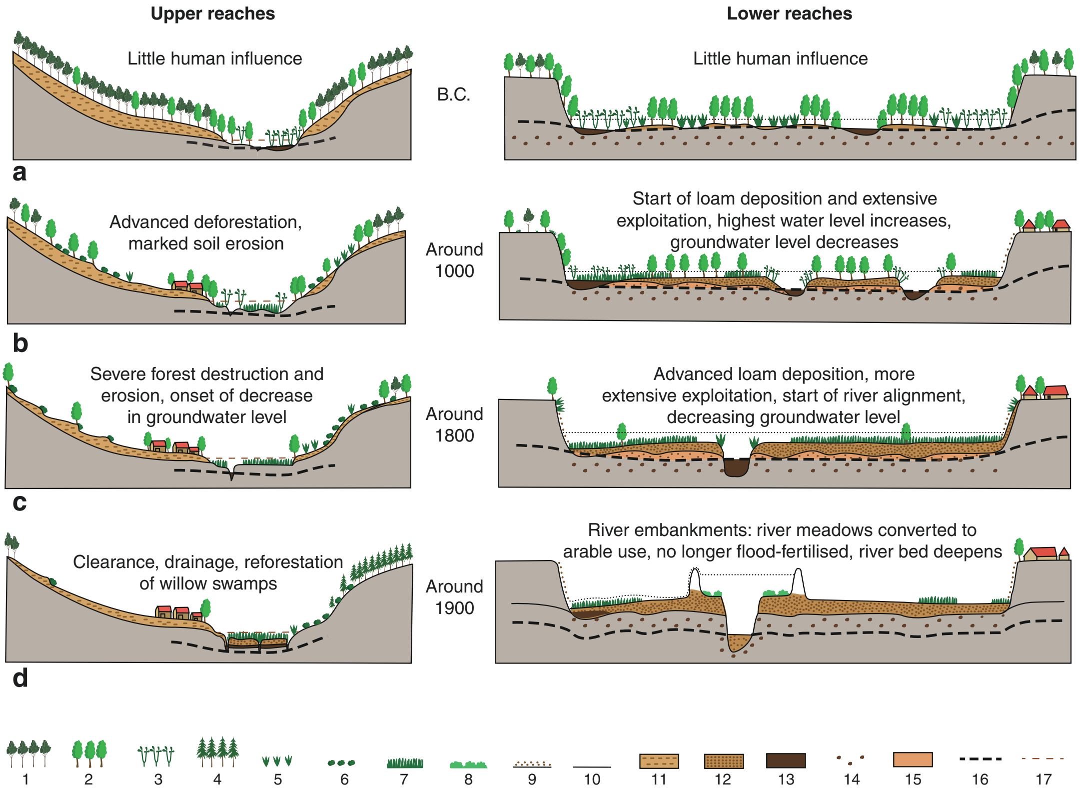


Fig. 17.14 Development of a central European river valley landscape. Increasing deforestation, drainage, erosion and deposition of loam in flood meadows in upper and lower reaches of river. *1* Beech forest; *2* oaks and other mixed deciduous forests; *3* alder swamp; *4* conifer reforestation; *5* willow scrub; *6* other scrub; *7* wet grassland; *8* moist grassland; *9* dry grassland; *10* arable fields; *11* loess soils; *12* meadow loam; *13* moorland; *14* gravel; *15* other soil types; *16* mean groundwater level; *17* highest water level. (after Ellenberg 2009)

summarised for Central Europe (Fig. 17.15). Despite the fact that species extinctions occurred mainly after the nineteenth century, the total number of plant species is still increasing owing to the continued emergence of more neophytes.

17.2.4.3 Agriculture and Forestry in Industrial Times

Since the onset of the Industrial Revolution and continued urban sprawl, significant changes have occurred in plant communities, where even the smallest of areas have now been affected (Sukopp and Wittig 1998). In the past, localised ploughing, watering and draining had an effect that was only apparent at a specific scale; however, as the influence of supplying and managing resources and their waste products increases, so does the effect on living systems. Pollutants and the effects of fertilisation have undoubtably influenced vegetation. For example, atmospheric deposition of nitrogen currently exceeds natural background levels by three orders of magnitude in some regions, leading to a steadily increasing eutrophication of terrestrial ecosystems (Galloway et al. 2004).

The beginning of the industrial period is linked with new anthropogenic influences on plant cover. At the onset of industrialisation, most of the remaining forests of Central Europe had already been degraded and the soils were much eroded or depleted of nutrients, which left the upper layers acidified. Although the conditions of the forest were maintained, the change in dominant energy source (coal) led to a significant makeover in terms of people thought about forest management. As the use of coal began to increase, many traditional forestry practices were no longer used; however, the demand for timber, paper and energy grew with the onset of the steam engine and railway.

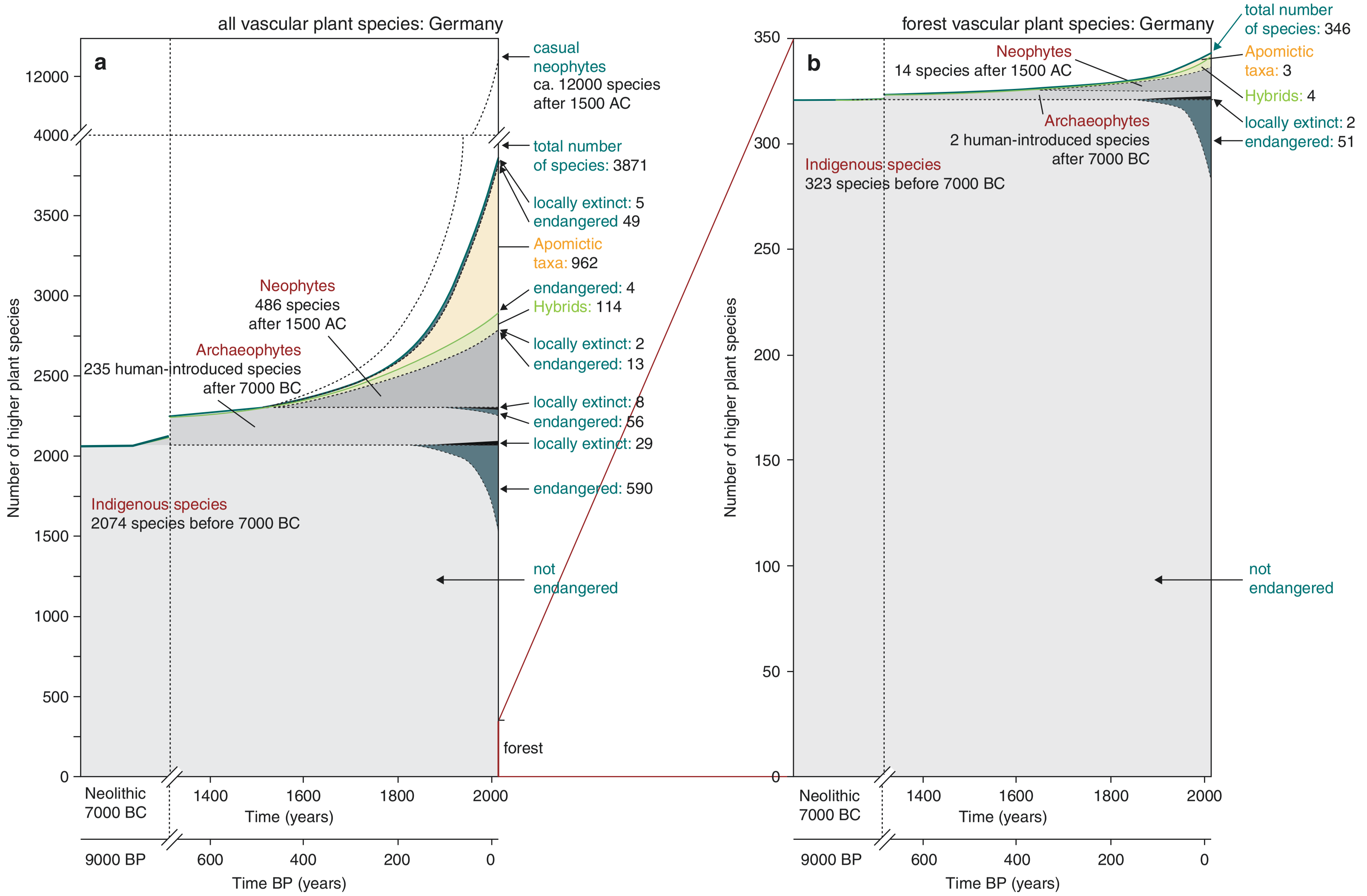


Fig. 17.15 Increase and decrease in plant species in Central Europe since Neolithic times. (after Scherer-Lorenzen et al. 2000; Schulze et al. 2016)

Attempts of reforestation occurred as early as the fourteenth century. However, it was only in the year 1713, when von Carlowitz put forth the "*principle of forest sustainability*", that large-scale afforestation projects were undertaken (Pretzsch 2005). It was at this time that the transition from deciduous forests to coniferous tree plantations commenced. Only some mixed forests were retained until the nineteenth century; however, they were considered to have become degraded. The so-called **new forest management** started with the intensive plantation of conifers on degraded lands and within abandoned fields, where this practice was used to meet the increasing requirements for construction-grade lumber. In Fig. 17.16, characteristic forms of forest management are shown. On the other hand, there are also individual steps of degradation

Fig. 17.16 Important human-made forest types in Central Europe and North Africa. **a** Almost naturally mixed forests (*Quercus faginea, Q. rotundifolia, Cedrus atlantica*) with trees of all age classes in central Atlas Mountains (Morocco). **b** Beech forest close to Bayreuth (Bavaria). Trees are clear felled or the largest trees are selectively removed. **c** Oak forest (*Quercus robur, Q. pubescens*) in Burgundy. The best stems for timber are only felled after 100 or more years, the rest for firewood every 30 years. **d** A *Eucalyptus* coppice in northern Morocco, cut 2 years before with new shoots forming that will be harvested after 12–15 years. (Photos: K. Müller-Hohenstein)

from a natural forest to wasteland (Fig. 17.13). Experiments with trees, such as the Douglas fir (*Pseudotsuga menziesii*), were successful, and spruce (*Picea*), pine (*Abies*) and larch (*Larix*) were planted beyond their natural ranges. Coppiced forests slowly transitioned to **high forests (mature)**. Various forms of forest management practices were used, for example, clear-cutting, shelterwood-compartment systems and shelterwood-selection systems (Box 17.1). The aim was to produce commercial timber as quickly as possible while maintaining a sustainable production yield (harvesting < regrowth).

Managing the forest using these strategies was successful for many reasons: forests were no longer used for livestock grazing, pruning or sod-cutting, and the use of leaf litter was significantly reduced, which in turn returned substantial amounts of nutrients back to the system. The most important change in these forests was the change from the once dominant deciduous trees to conifers, which triggered a change in vegetation dynamics. All coniferous species, particularly pine and spruce, are relatively undemanding in terms of regeneration and can be sown without major drawbacks. Furthermore, conifers tend to grow quite rapidly, resulting in much shorter rotational periods (80 years) than those of oak, which can be twice as long. The extent of this change from predominantly deciduous forests to coniferous forests is considerable, as depicted on maps of German forests over the last few centuries (Fig. 17.9).

Reforestation with only conifers can cause significant problems for forest communities. Soil erosion and acidification are higher in spruce plantations than in mixed deciduous forests. Bird diversity is also significantly reduced, where the number of species and their abundance is half as much in conifer stands as in deciduous forests (Goudie 1994). These findings were reinforced in the Chilean deciduous forest, where differences were more abrupt compared with exotic pine plantations (Finckh 1995). It is well known that coniferous plantations typically have much less food resources for birds and also lack the multi-tiered structures found in deciduous-dominated stands.

The separation of forest use and grazing was also important for the development of vegetation in open spaces. To protect forests and arable land from animals, fences were put around grazing areas. In early summer with a surplus of food, animals tend to favour the most palatable species. Areas of eutrophication due to the excrement deposits of livestock and grazing areas gave rise to a characteristic pattern. Particularly noticeable was the damage caused by trampling and erosion by too many animals. This can be counteracted to some extent through the use of mineral fertilisers, and changing the variety of crops can improve yields. Soils of low fertility were fertilised and sown with grass (***Vergrünlandung***). Meadows were mowed, often several times per year, to provide enough fodder for animals that were kept in stables during the winter months. Cereal fields were also used for grazing after harvests, which affected segetal flora. Nutrient-poor meadows were invaded by scrub, and sites for thermophilic and xerophilic species became rarer. These examples show how new agricultural techniques and trade patterns affected the composition of plant communities.

In agriculture, the **improved three-field crop rotation** was increasingly used. The fallow was abandoned and replaced by root crops, in particular potato. A significant agricultural advancement occurred in the middle of the nineteenth century, when N and P mineral fertilisers became available. As a result, the diversity of site conditions decreased, and flora diversity was reduced with fewer fallow fields occurring owing to the increased use of **fertilisers** and **herbicides**, where many perennial species of segetal flora disappeared. Marshes, bogs and river forests were drained and converted to meadows or pastures. Edges of fields, hedges, terraces and marginal biotopes, all with important interconnecting functions for non-crop plant and animal species, were drastically reduced. Schreiber (1995) demonstrated how various central European grassland communities, which had developed up to the middle of the nineteenth century, were converted into intensive grassland by new agricultural practices (Fig. 17.17). Currently, intensive land use has led to drastic losses of diversity in the

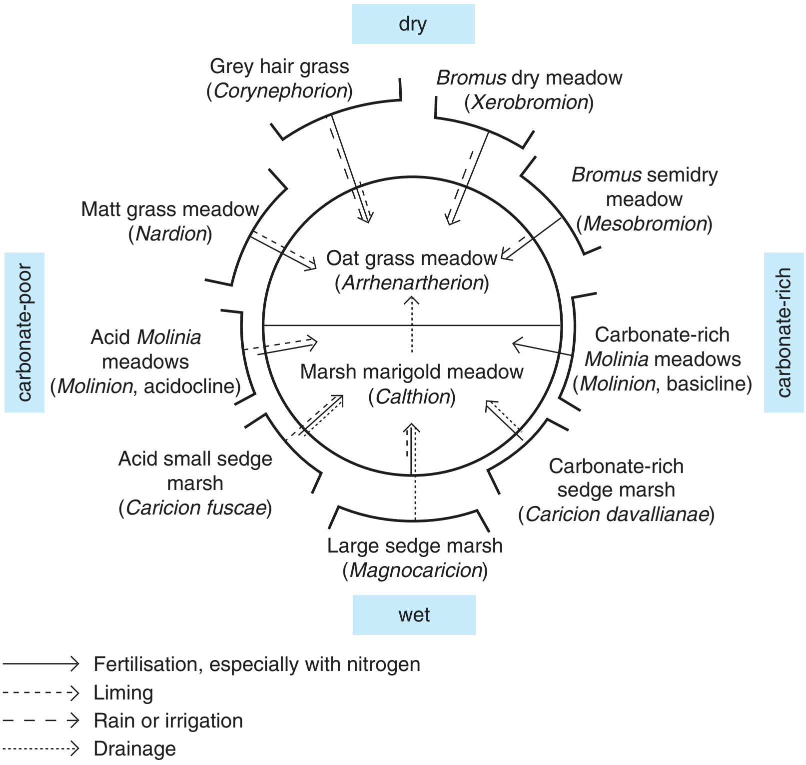


Fig. 17.17 Characteristic grassland communities in Central Europe according to water and carbonate availability. (modified from Schreiber (1995))

landscape and plant communities in all regions of Europe. The colourful mosaic of a rural landscape developed for extensive use since the Middle Ages has only been sustained in some remote areas.

Already 20 years ago, Vitousek et al. (1997) estimated that between one-third and a half of all terrestrial ecosystems had been transformed by human activities, more than half of the total surface of freshwater resources is used by humans, and one-quarter of the bird species on Earth have already gone extinct as a result of anthropogenic influences. More recently, Ellis et al. (2010) characterised the artificial changes in the terrestrial biosphere since the **Industrial Revolution** on the basis of gridded global data for human population density and land use. According to their evaluation of the past three centuries, the terrestrial biosphere passed from mainly "wild" to mainly "anthropogenic". With fewer small subsistence farms it is no longer necessary to combine arable crops with animal husbandry. The former "balance" of forest, grazing land and arable land once required in the rural landscape for reasons of greater self-sufficiency has now been lost. The impacts of human transformation of ecosystems over such a short time span during the last few decades has no parallel in the past with respect to intensity and consequences. Nowadays, even more drastic and irreversible shifts of global ecosystems are being discussed, potentially threatening Earth's ability to sustain humans and other species in the near future (Barnosky et al. 2012).

17.2.4.4 Recent Developments in Forests, Arable Fields and Settlements

Intensifying production in agriculture continues apace. Machines in agriculture are becoming increasingly heavier and cause increasing concerns regarding **soil compaction**. As a result, soil organisms suffer, particularly the macrofauna with Lumbricides. However, yields are still increasing, because modern plant-breeding programmes continuously provide new varieties (strains) with higher yield potential. Varieties must be continuously improved as they become resistant towards xenobiotica, which also require continuous changes. An unwanted "co-evolution" takes place, and the WBGU risk assessment (2000) points to the dangers posed by genetically modified crops that are resistant to herbicides and viruses if such transgenic crop plants become wild or cross with indigenous species.

Intensive agricultural practices also result in fewer species in the associated flora, which are often resistant to pesticides and herbicides. Therefore, measures for the protection of segetal flora are required. Various attempts have been made in this regarding, including mixed cropping, intercropping and managing strips at the edges of fields. However, the present-day agricultural landscape is characterised not only by mechanisation, specialisation and high production but also by homogenisation and contamination.

The use of land for settlement and industrial sites has grown enormously. Habitats and communities, which are without parallel in the natural landscape, are investigated in **urban ecology**. Changes are especially apparent for flora and fauna within an urban setting (Fig. 17.18). These areas are basically warm islands where warmth- and light-demanding species find refuge, but they need to be relatively insensitive to mechanical disturbance and pollutants.

Urban flora is fairly diverse and develops many rather constant plant communities owing to new non-natural sites being colonised mainly by ruderal species. **Lichen flora** is particularly well represented in towns. Especially epiphytic lichens are often taken as the standard for assessment of SO_2 pollution and evaluated regarding their **toxic tolerance**. New characteristic plant communities are also found in villages. Wittkamp et al. (1995) compared the vegetation of northern Bavarian and southern Thuringian villages on both sides of the former border between the western and eastern parts of Germany and found that variation in land use was closely linked to variation in vegetation. The comparison also showed that social structure and economic activity were important for this variability. Quite often, differences in vegetation caused by site conditions are of secondary importance compared with differences due to land use. The marked differences in the actual vegetation cover of landscapes north and south of the Strait of Gibraltar are strongly determined by different agro-political measures, culture-specific characteristics and economic activities. With almost identical natural initial conditions, a completely different inventory of communities developed with the intensive, market-orientated land use of Spain compared with the subsistence-orientated land use of Morocco (Deil 1995).

Recent human influences on vegetation in Central Europe is also well illustrated by the introduction of a new type of **forest decline**. Damage to trees and complete forest areas by smoke and other pollutants from industry has been reported since the beginning of the industrial age. It is also known that rejuvenation of forests in Central Europe has become more difficult, for several reasons, including damage by pests, attacks by fungi or other pathogens, climatic abnormalities and above all from acidification of the upper soil layer. It is now certain that the soils of many semi-natural woodlands and managed forests were depleted of nutrients because of litter removal, erosion and monoculture practices over the centuries.

The "new forest decline" affecting complete forest ecosystems has only been observed for the past 50 years. Significant damage has been attributed to the influx of acid from the atmosphere via long-distance transport in the form of **acid rain** and complex interactions with other drivers of environmental change (Sect. 16.4). However, analysis of the recent history of vegetation gives much evidence that the key to understanding present-day vegetation is a thorough recognition of past management methods and their effects. This is relevant not only for highly modified ecosystems such as agricultural fields, managed grasslands and heathlands but also for more natural vegetation types such as forests or bogs (Ellenberg 2009).

According to the results of the PAGES 2k project, the twentieth century was the warmest in the last 1400 years. The increase in temperature

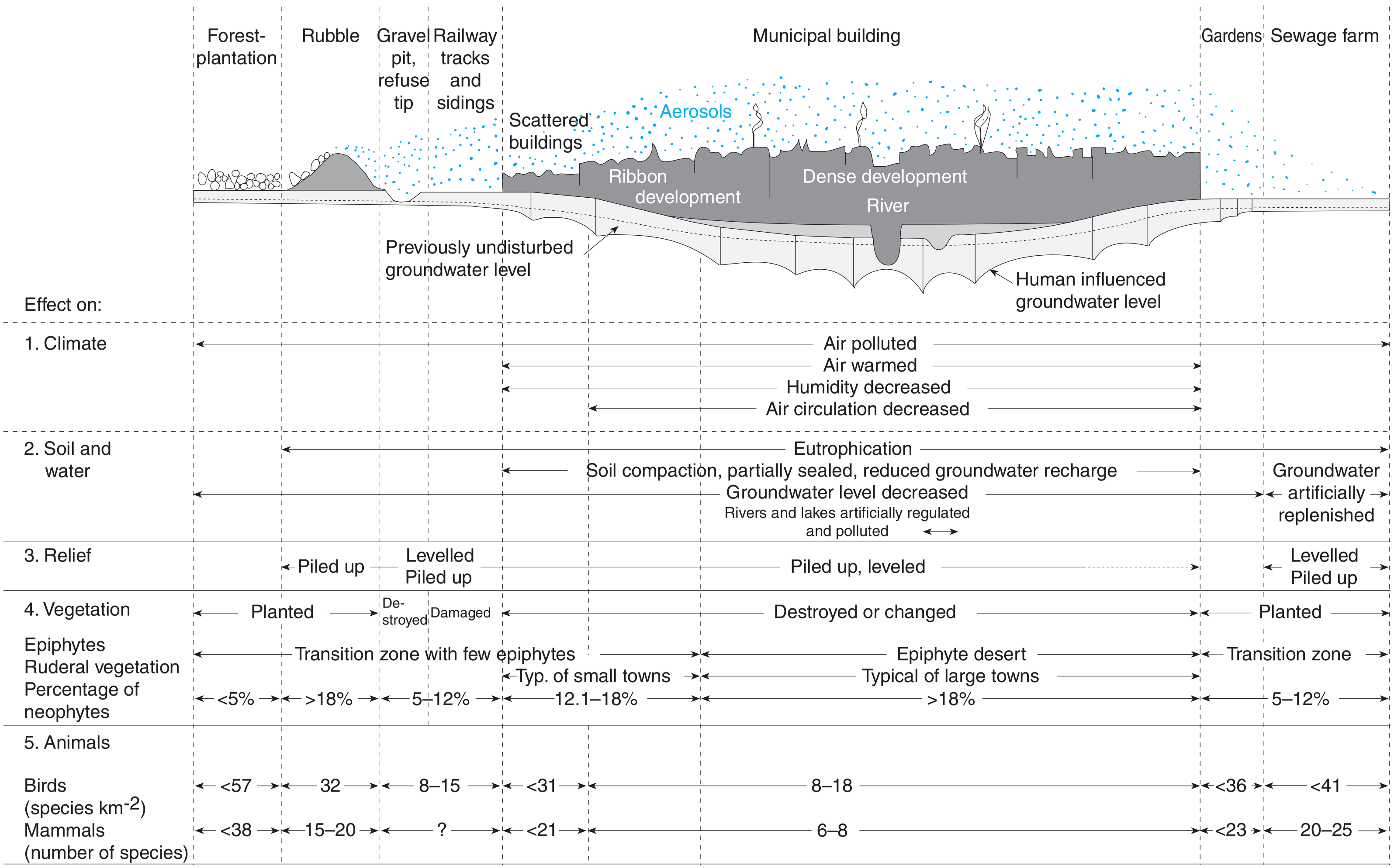


Fig. 17.18 Ecological characteristics of a large town, stressing interactions between human influences and abiotic and biotic conditions in this ecosystem. (after Sukopp and Wittig 1998)

between the nineteenth and twentieth centuries was the highest ever, and the long-term cooling trend was reversed as a result. Cooling in pre-industrial times was certainly mainly due to natural forces. Because these factors did not change, the actual warming, which has exceeded the known dimension until now, can only be explained by new anthropogenic influences, leading to actual global change (Chap. 21), and there will also be more changes in vegetation cover in the future.

17.2.5 Classification of Anthropogenic Influences and Their Consequences for Vegetation

The overall human impact on plant cover and the increase and decrease of plant species and communities have also led to further development of the classification system of plant communities in Europe. Jäger (1977) classified anthropogenic effects on vegetation into three main categories:

- **Original** (natural) **vegetation** (in sub-Atlantic period).
- **Actual** (recent) **vegetation** under present-day conditions of site and use.
- **Potential natural vegetation** (pnV), a term introduced by Tüxen (1956) describing the vegetation that would occur under present conditions at a site (without further changes in these site conditions).

Natural vegetation no longer exists in Central Europe. The pnV is important for some aspects of nature conservation and spatial planning. Recently, the pnV concept has been well criticised (Chiarucci et al. 2010; Loidi et al. 2012). In particular, non-predictable vegetation dynamics due to natural environmental changes, biological invasions and multiple human interventions have been ignored. We therefore concentrate on the actual vegetation and its environmental conditions here. Evaluating anthropogenic influences is essentially based on the balance between gain (introduction, immigration, naturalisation) and losses (displacement, extinction) of species. Compared with natural vegetation, gains as well as losses represent a change of the “natural” state. Therefore, a rather popular approach is to characterise and typify anthropogenic vegetation by defining the so-called **level of naturalness**. Several proposals have been made to scale naturalness.

One subdivision of **anthropochors** (non-indigenous species with expansion dependent on humans) was given by Sukopp (1972), using the following three criteria:

1. Based on the time of immigration: **archaeophytes** (old adventives) immigrating in prehistoric times are separated from **neophytes** (new adventives), which only immigrated in historical times after 1492 (Columbus’ arrival in the Americas);
2. According to the method of **immigration**, i.e. the type of human interaction in immigration: **ergasiophytes** (intentionally introduced species, for example, crop plants and their forms that grow wild, ornamental plants) as well as **xenophytes** (unintentionally introduced species, e.g. weeds accompanying imported seeds, plants from bird food);
3. According to the **degree of naturalisation**: how well they become established permanently at a new site (for example, **agriophytes**, i.e. new indigenous species that are competitive without human intervention; **ephemerophytes**, i.e. non-persistent, ephemeral species, which disappear quickly).

To be classified as a neophyte, a species must be introduced or imported, become established after reaching new sites, be naturalised permanently without direct help from humans, and finally expand. The hypothetical number of species that are successful in this sequence decreases with each new step. Plants must possess some of the characteristics listed in Table 17.3 in order to be successful.

What are the consequences of a gain and loss of species for the indigenous vegetation? The loss of distribution barriers leads to a mixing of the flora and fauna from various biomes. Already

Table 17.3 Characteristics of successful neophytes. Compiled from different sources by Sukopp and Wittig (1998)

1.	**Related to reproduction and biology of distribution** • Early capacity to reproduce (rapid flowering following vegetative phase = short juvenile period) • Single-parent reproduction • Self-compatibility; probable, although not obligatory self-pollination or apomictic • If cross-pollinated, then non-specific pollinator or wind pollinated • Seed production under a wide range of environmental conditions and continuous high reproductive capacity (production of many propagules) • Particularly large seed production under favourable conditions • Very resistant and long-lived seed (capacity to build up seed / diaspore bank) • Fruit and seed morphology suitable for extensive distribution by wind and animals including man • Unspecialised seedling and developmental processes; therefore, wide ecological potential • Discontinuous germination by induced dormancy • Rapid seedling growth
2.	**Related to vegetative growth and phenology** • Rapid growth as a consequence of fast exploitation of resources (large photosynthesis and respiration capacity) • Often able to exploit large N supply • Very flexible distribution of assimilates • If perennial, marked vegetative reproduction, able to regenerate from lower nodes and roots • Generally short and simple growth cycle • Frequently photoperiodic: day length neutral • Dormancy
3.	**Genetic characteristics** • Large genetic variability • Polyploidy; hybrids • Very flexible genetic system; thus alterations of recombination rates possible • Frequently phylogenetically young group
4.	**Population dynamics and ecological characteristics** • Generalists: broad climatic and edaphic range • Large acclimation potential; often phenotypically plastic = increases ecological potential • Rapid population increase due to high growth rates and early, as well as large, reproductive capacity • r Strategy • Very competitive through particular features such as rosette form, parasitic growth, allelopathy or fast and vigorous growth

Elton (1958) regarded this as a decisive, recent change in the biosphere. Two marked historical epochs must be distinguished: the time after the discovery of America until the sixteenth century, where increasing travel occurred between continents. Another important period also existed where, since the beginning of the nineteenth century, new anthropogenic sites opened up for the establishment of plants.

Lohmeier and Sukopp (1992) analysed the consequences of introduced foreign plants on the native vegetation present in the ecosystems of Europe. It was typically found that within industrial countries approximately 100 species per 100,000 km^2 were naturalised; however, variability exists in the system, whereas in Japan as many as 800 species were found where three floral regions meet. The proportion of **synanthropic species** is constantly increasing (Fig. 17.15); Sukopp (1972) assumed less than 1% of introduced plants, but this was modified by Lövei (1997) to 6%, coupled with 54% of total species in Germany originating from Europe and western Asia, 30% from moderate climates in North America, and 9% from Central and East Asia.

Because a cultivated landscape possesses a mosaic of different site conditions, the probability of species meeting and hybridising is greater. Thus, several families developed quickly and became species-rich, for example, the *Oenothera* species, following their introduction into Central Europe. Among the anthropochors, agriophytes are of special importance. These plants have been introduced for economic reasons in natural habitats (e.g. *Robinia pseudoacacia*, *Junglans regia*, *Prunus serotina*, *Castanea sativa*, *Helianthus tuberosus*), as ornamental plants (*Centranthus ruber*, *Heracleum mantegazzianum*, *Impatiens glandulifera*, *Tulipa sylvestris*, *Reynoutria japonica*), as species originating from botanical gardens (*Impatiens parviflora*, *Elodea canadensis*), and as species that were deliberately planted in natural areas (*Lupinus* spp.).

Agriophytes were not able to become established everywhere. They are particularly numerous on sites disturbed by humans, in towns and industrial areas. Only a few species became established in woodland regions. An example in forests is the wild cherry (*Prunus serotina*), which was originally introduced to accelerate the accumulation of humus, but it impedes natural regeneration. The spread of nitrogen-fixing species such as *Robinia pseudoacacia* leads to nitrogen accumulation in the soil and, consequently, to an increase of nitrophilic species. Along the coasts the cord grass (*Spartina anglica*), planted to take over land, has widely replaced glasswort (*Salicornia europaea*) and has thus become an unwanted invader. This applies also to the Canadian pond weed (*Elodea canadensis*), but in many waters it has decreased again owing to increasing eutrophication of waterways. Areas around river banks provide particularly favourable conditions for the **immigration and expansion** of agriophytes, as new open spaces always develop, due to the natural dynamics of water flow, and because there are few competitors to immigrants.

Are neophytes a danger to nature? The number of alien species in Central Europe exceeds the extinct species (Fig. 17.15). At present, about 5–25% of the flora in Central Europe may be anthropochor; in towns it reaches about 50%. There is much evidence for the decrease in indigenous species because of the advance of neophytes. Two species with a particularly high invasion potential, *Solidago canadensis* in Berlin and *Tribulus terrestris* in the east African savannas, were analysed using a key-lock model to explain their invasion of niches (Cornelius 1991). It was found that resource demand, tolerance to climate stress and strategies of adaptation to competition and regeneration (key traits) coincide with climatic conditions, disturbance and succession. Invasion is possible and endangers the existing mosaic of species and communities, where neophytes may become pests because they migrate at such a fast rate that their primary competitors and other negative influences, such as pathogens, stay behind.

Some important traits of neophytes are that they have a high potential of propagation and are highly efficient dispersal vectors. They are strong competitors who require no special climatic conditions while also showing the ability to efficiently exploit soil (for more traits, Table 17.3). Thus, they are often able to outcompete or suppress native species, especially in agricultural and forest communities, as they may produce high quantitative losses. At present, neophytes are not regarded as very dangerous for native species diversity in Europe; however, concern does arise on oceanic islands or other isolated habitats where more than 40% of the actual flora may be neophytes. The same is true of densely inhabited areas, as Lövei (1997) called this ongoing dynamic the “MacDonaldization” of the biosphere.

17.2.6 Anthropogenic Influences on Vegetation in Mediterranean, Saharan and Tropical Environments

Human influences have changed the natural vegetation in all climatic regions and biomes. Depending on the environment and the specific human influences, different consequences for the natural ecosystems may arise. Examples from three biomes are shown for the **Mediterranean region** (keywords “**deforestation** and **soil erosion**”), the **dry regions of Africa** (keyword **“desertification”)** and the **humid tropics of Africa** (keyword “**destruction of tropical forest**”).

17.2.6.1 Mediterranean Region

Plants in the Mediterranean region are particularly stressed because of the dry periods in summer. The influence of **fire** must also be considered, particularly when human intervention prevents it. Tree species found within the upper mountainous zones of the Mediterranean listed in the scheme of altitudinal zones in Fig. 17.19 typically have high drought resistance and are stimulated by fire (e.g. *Quercus suber*). Land-use changes began affecting large areas in the western Mediterranean region (bays of Alicante and Catalonia) in the early Neolithic Age, circa 7000 BP (Badal et al. 1994; Riera-Mora and Esteban-Amat 1994). The evergreen oak forest (*Quercus rotundifolia*) near the coast was mixed with deciduous oaks (*Quercus faginea*, *Q. pubescens*) and eventually thinned, and heliophilic shrubs became dominant.

Typical Mediterranean shrub communities (**macchie, garrigues**), developed. Inland areas

semihumid-humid zonation sequence		Altitudinal zone	semiarid-arid zonation sequence	
Reforestation with	Natural vegetation		Natural vegetation	Reforestation with
	Mountain grassland and dwarf shrub communities	subalpine/alpine (oro-mediterranean)	Mountain steppes, dwarf shrub communities and thorny cushion plants	
Pinus sylvestris	Mountain forests with *Fagus sylvatica* *Abies alba* *Pinus sylvestris* *Pinus uncinata*	montane (montane-mediterranean)	Mountain forests with *Cedrus atlantica* *Cedrus libani* *Abies pinsapo* *Abies cilicica, Pinus nigra*	*Pinus nigra* *Populus* spp.
Pinus radiata *Pinus pinaster* *Eucalyptus* spp. *Populus* spp.	Deciduous forests with *Quercus cerris* *Quercus pubescens* *Quercus faginea* *Carpinus orientalis*	submontane (sub-mediterranean, supra-mediterranean)	Evergreen and deciduous forests with *Quercus boissieri* *Quercus pubescens* *Quercus coccifera* *Quercus ilex, Pinus brutia*	*Pinus pinaster* *Eucalyptus* spp.
Pinus radiata *Pinus halepensis* *Eucalyptus* spp.	Evergreen forests with *Quercus ilex* *Quercus suber* *Pinus pinea* *Pinus pinaster*	basal/foothills (eu-mediterranean)	Evergreen forests with *Tetraclinis articulata* *Juniperus phoenicea* *Pinus halepensis*	*Pinus halepensis* *Eucalyptus* spp. *Tamaris* spp.

Fig. 17.19 Altitudinal belts of dominant tree species of natural vegetation and the most important exotic tree species used in reforestation in Mediterranean region. (Müller-Hohenstein 1991)

remained untouched for a long time, disregarding the first transhumance, for example, shepherds moving in the hot, dry summers from the plain into the mountains near the coast, and establishing a "vertical migratory pattern" of grazing management. The farms on the coastal plain, with favourable soils and availability of water, for example, the Spanish *huertas*, were the first areas with intensive agricultural crops. Evidence of crop plants introduced from the Mediterranean into North Africa demonstrates the development of an increasingly richer flora in agriculturally managed landscapes. In the Palaeolithic period, barley (*Hordeum vulgare*) was evident, whereas in the Neolithic period, wheat (*Triticum* spp.) emerged as well as fruit trees (*Phoenix dactylifera*, *Ziziphus* spp., *Lawsonia inermis*) and Fabaceae (*Lens culinaris*, *Pisum sativum*, *Vicia faba*).

The Phoenicians cultivated olives, vine, pomegranates and figs, while the Romans added garlic, onions, apples and pears. During the Arab period, species from Central and Eastern Asia arrived, for example, citrus, mulberry and carob trees, hemp and sugar cane. Species from the New World followed after the discovery of the Americas. Only at that time did some plant species often regarded as characteristic of the region reach the Mediterranean basin: agave, opuntia and maize, tobacco and tomato. In the nineteenth century many ornamental plants were added for economic reasons, and *Acacia* and *Eucalyptus* species were introduced. Today, about 200 exotic species are naturalised in North Africa, corresponding to 4% of the total regional flora (Le Floch et al. 1990). Some species were introduced unintentionally and, along with crop plants, became established. The number of those species originating from the New World is considerable, among them so-called aggressive invaders that became established particularly on ruderal sites (species of the genera *Amaranthus*, *Cuscuta* and *Conyza).* Currently, rapid expansion of *Heliotropium curassavicum*, *Solanum eleagnifolium* and *Xanthium spinosum* are occurring, as well as of some shrub species (*Ricinus communis* and *Nicotiana glauca*) into North Africa.

In the **segetal flora**, on the other hand, indigenous species found new niches. The approx. 50 species found within fields and fallow land include *Ammi majus*, *Ammi visnaga*, *Anagallis arvensis* and *Anagallis foemina*, *Ridolfia segetum*, *Sinapis arvensis* and *Carduncellus*, *Convolvulus*, *Cyperus* and *Diplotaxis* species. The number of sometimes thorny weeds on pastures is just as high (*Astragalus armatus*, *Calycotome villosa*, *Scolymus hispanicus* and *S. grandiflorum*) and also partly poisonous or at least non-edible (div. *Asphodelus spec.*, *Peganum harmala*, *Solanum nigrum*, *Stipagrostis pungens* and *Stipagrostis capensis*). The nutrient indicators (nitrophils) include *Aizoon* and *Mesembryanthemum* species, *Chenopodium murale*, *Hyoscyamus albus* and *Hyoscyamus niger* and *Withania somnifera.*

As for the Mediterranean regions, the same applies as for Central Europe: Naturalisation, expansion and disappearance of individual species are closely connected to the agricultural practices performed in those regions. Deil (1997) showed for the areas bordering the Strait of Gibraltar that vegetated landscapes can be read as a history book. Further, they can show how historic and actual forms of use demonstrate religious regulation as well as subsistence-orientated management of the indigenous population, or the market-orientated management of colonial times. Even today, it is possible to identify from the spectrum of different species an Islamic cemetery from the time before the reconquista. Similarly, it is possible to show the different uses of herbicides and the mechanical control of weeds in the fields of southern Spain or northern Morocco.

The recent history of forests in the Mediterranean regions is completely determined by human activities. During the Greek colonisation of Dalmatia around 3000 years BP, forests were intensively cleared. The Italian peninsula was largely deforested during Roman times, and the Iberian Peninsula mostly from the sixth century BC onwards. Severe consequences for vegetation and site quality have often been documented (Müller-Hohenstein 1973). Forest degradation starts with structural changes (age structure, density of stand and closure of canopy); livestock grazing in a forest leads to the invasion of ruderal species and the eventual decline of the forest, which causes a thinning of the stand. Forests on more favourable sites were cleared first, while arable fields extended on land with not very productive rain-fed agriculture. Clearing was also often supported by fires to take over grazing areas. Mediterranean dwarf shrub communities (**macchie** with various regionally different terms such as **garrigue**, **tomillares, phrygana, matorral**) and pastures differing in their floristic compositions are quite often determined by human activities.

Clearing was not just an intervention with irreversible consequences for vegetation; soil erosion down to the bed rock and sedimentation in valleys generally followed. The negative effects of soil degradation also has serious economic consequences, and a growing lack of wood has been an issue in the past 50 years. Reforestation efforts have increased in many southern European regions and North African countries, but so far such efforts have borne no discernible results. Exotic, fast-growing types of trees are chosen for reforestation, in particular some pine species *(Pinus radiata*), but a variety of *Eucalyptus* species are favoured for their fast growth rates (Fig. 17.19).

Where the reforestation has been successful, “forest” areas increased, but a uniformity also arose. The expected economic yields have not always materialised. The negative side effects on fauna and soil organic matter, attacks by pests and fires, for example, known from monocultures, increased. With the high diversity of Mediterranean woody species, the preferential use of exotic species would not have been necessary. The choice of fast-growing exotic species stemmed mainly from economic considerations, while ecological considerations were ignored. One could have limited those species to in areas where urgent protection from further erosion was required. In southern European countries, the pressure to harvest wood from forests is presently declining; the recovery of sclerophyllic and deciduous species can be observed. In North African countries, however, the pressure on the last near-natural remnants of forests is growing.

Also, in the European/North African-Mediterranean region, it is obvious that subsistence-oriented land management in small family farming systems coincides with a greater diversity of vegetation. Modern market-oriented management is always linked to a loss of diversity at all levels. Typical forms of Mediterranean land use are shown in Fig. 17.10.

17.2.6.2 Desertification on the Border of the Sahara

The term **desertification** has been used to describe environmental problems in arid areas, at least since the many years of drought in the Sahel in the late 1970s. Today it is obvious that this term describes not only **climatic stress** in long-lasting drought periods but also the complex interactions that include in particular human impacts on vegetation and landscapes. In the context of ecosystems in arid areas, and of the often-cited **man-made deserts**, it should be underlined that extended dry periods are a characteristic feature of arid areas. It is not only the small amount of available water after a precipitation event coupled with high temperatures but also the highly variable temporal, episodic and spatial distribution of this precipitation that cannot be anticipated.

In the Sahara region, it is not uncommon for prolonged periods of dryness to last for several years, as depicted historically through the interpretation of lake sediments (Nicholson 1978). The recent dry period in the 1970s in the Sahel had catastrophic consequences as it preceded a relatively moist period. During the moist period the human population grew considerably, but it found itself maladapted when the dry period arrived. Improved medical supplies and technical innovations (deep wells to tap fossil water) have improved grazing conditions and increased the number of animals being farmed in this area (Müller-Hohenstein 1993). However, it is not correct to regard ecosystems of arid areas as particularly labile systems. These ecosystems are adapted to extreme climatic variability. Autochthonous plants and animals are able to adapt in many ways, and thus are able to survive under such conditions. The human population in these areas has also adapted to maintain supplies and is prepared for variations in crop yield. A **"desertification scheme"** (Fig. 17.20) indicates the most important causes and consequences of land degradation in arid regions.

It is important to consider the discrepancy between population growth and—despite all the technological progress—the limited availability of renewable resources, in addition, as well as the substitution of traditional forms of management (nomadic life style) by modern forms of grazing and rain-fed agriculture. Up until the end of the twentieth century, the human population around the Sahara has grown five-fold (Goudie 1994). Today, owing to these increases in population, many examples of poor agricultural practices can be found in all areas near deserts, for example, agriculture in north-eastern Syria or eastern Jordan, which receives less than 200 mm of precipitation annually, or growing animal fodder through the use of fossil water from depths more than 1 km under the Algerian oases, all of which can further contribute to the degradation of vegetation in the area.

Human influence on the vegetation in arid areas is particularly linked to the disturbance of sites and original plant cover. As a result, many of the woody plants previously present in arid regions disappear as the requirements for energy are not met. The naturally sparse **contracted vegetation**, growing in areas with an above-average water supply, is damaged by overgrazing. While vegetation in drier areas with a high fodder quality typically becomes locally extinct, toxic or thorny plants can strongly expand. Local changes resulting from the increased loss of vegetation are seen in the **remobilisation of dunes** and increased number of **dust storms**. Also, water relations of areas are affected by modern irrigation installations, which result in the **salinisation of soils** and a rise in halophytes (Fig. 17.21).

The Sahara Desert area has probably grown by 15% in the last 100 years; indeed, it is believed that, just between the years 1958 and 1975, the Sahara extended 100 km to the north and to the south. However, such rates of desert growth are also questioned. Hellden (1991) found on the basis of satellite photos a close relationship between precipitation and vegetation, but no evidence for expansion of desert areas. It is still not exactly known whether the observed changes are permanent or whether regeneration is possible.

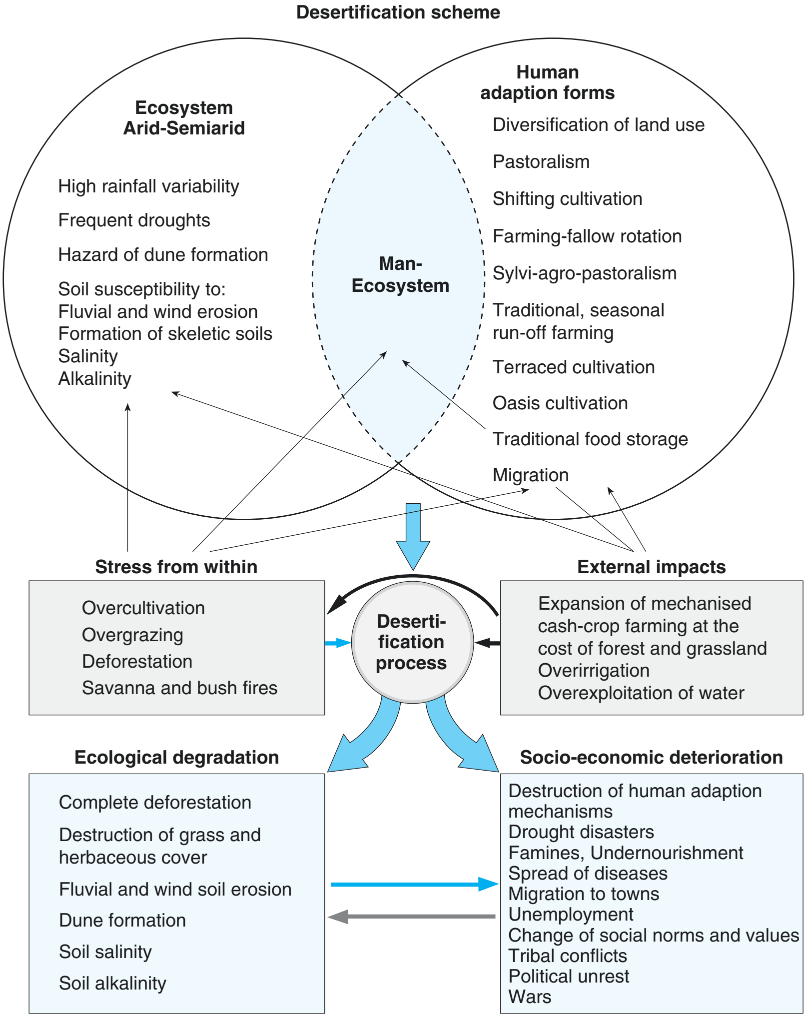


Fig. 17.20 Scheme of process of desertification. (after Ibrahim 1988)

The latter is understood as the sum of processes in an ecosystem by which lost elements may be regained and thus re-establish themselves to the point where they achieve a status equivalent to their original status. There are many positive and negative interactions between climatic events, the development of vegetation and abiotic site factors and human influences, all of which remain poorly understood. However, in all dry areas of the Old World, there have been examples of a rather rapid recovery of vegetation following a precipitation event. Obviously, the ability of species to regenerate in arid regions depends on the lower and upper variability of precipitation a plant can tolerate; however, this still remains largely unknown. Nevertheless, the existing alterations in the albedo, increasing dust load in the atmosphere and changes in soil moisture in arid regions also contribute to global climate changes and influence the regeneration of desert vegetation.

17.2.6.3 Destruction of Tropical Forests

The destruction of tropical forests has been a topic of public discussion even more than the problem of desertification. Not so much climatic but edaphic preconditions, particularly the availability of nutrients, are the limiting factors in this biome. It has long been known that soils weather intensively and **nutrients are leached** under conditions of high temperatures and continuous

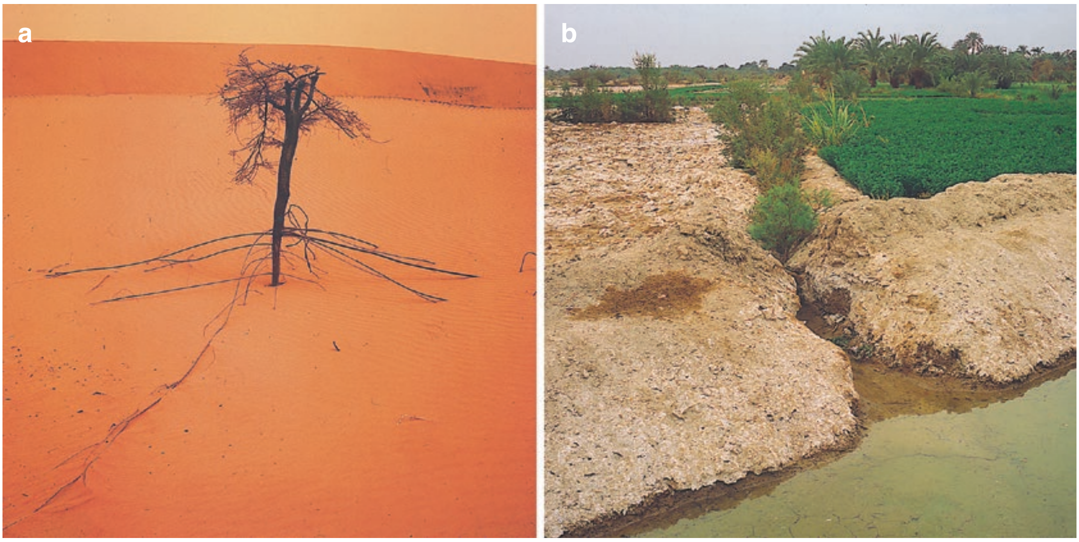


Fig. 17.21 Desertification in areas where people apply inappropriate forms of land use. **a** A single tree (*Commiphora africana*) in the southern Sahel of Mauretania is witness to former removal of dry forests, which disappeared because of excessive grazing and movement of sand dunes. **b** Incorrect irrigation with water of high salt content and inadequate drainage has caused salinisation in oases that had functioned for centuries with traditional cultivation (Dakhla Oasis, New Valley, Egypt). (Photos: K. Müller-Hohenstein)

moisture, two prominent features of tropical forest biomes. Although litter production is high, fast decomposition impedes the build-up of nutrient reserves, for example, in the form of humus. Even fertilisation is not sustainable in tropical soils with two-layered clay minerals, which have only weak ion-exchange capacities. The system can remain functional only if the **short-cut nutrient cycle** is maintained, with the help of mycorrhizae or fine roots present in the soil. The exportation of organic substances by harvesting has far-reaching consequences for the stability of soils and plant growth. Exceptions exist only where primary cations are released because of the mineralogical conditions, for example, in some regions of Java and Sulawesi, relatively young, nutrient-rich volcanic soils favour the establishment of permanent rice crops.

Clearing and changes in land use have taken place in tropical rain forests for thousands of years. However, the consequences of these early influences are considered to be much smaller than those occurring today. Intervention over large areas began with colonial times. Of the approximate 1.5 million described animal and plant species of the perhumid tropics—globally 10–11 million (Mora et al. 2011)—many thousands probably went extinct before they could be scientifically classified. In contrast to the forest management strategies used in temperate forests, these strategies have had negative effects in the tropics, as perhaps only one single tree trunk is used per hectare and many neighbouring trees are destroyed. Even the mangrove stands in tropical coastlands were intensively used for **wood extraction**, despite their protective functions against normal floods and tsunamis. Sites of these unique plant communities are used in East Asia, as well as Ecuador, for the breeding of shrimp.

Not only has the management of forests led to losses of species. The settlement that followed forest harvesting limited the development of secondary forests. Governments of several rain forest states saw the forests as a “valve” for the growing population pressure. Thus, many states subsidised their populations to help clear large patches of forest for agricultural purposes, more specifically ranching livestock. Grass seed was even sown from planes, but subsequent grazing was mostly given up after a few years as **substitute communities** with sclerophyllic grasses (e.g. *Imperata cylindrica*) developed, which were not suitable species for animal fodder. The practice of **shifting cultivation** with **slash and burn** was commonly used in all moist, tropical areas and was initially thought to be less damaging. Today this form of land clearing is regarded as less damaging, particularly if the periods of fallow last long enough, and the effect of fire is less harmful to the soil mycorrhizae, which is well known to help stabilise tropical forests and promote species biodiversity (Kottke et al. 2013). However, regeneration requires rather long fallow periods, which were often shortened because of the growing pressure from the human populations. Bruenig (1991) compared the consequences of "mild" intervention with "modern" intervention and assessed the consequences using two transects (Fig. 17.22). There are typical phases of the development of land use from the natural forest to unproductive fallow areas (Fig. 17.11).

Growing evidence supports significant losses of tropical moist forests, where in the period 2000–2012 it was found using Landsat satellite imagery a total of 2.3 million km^2 or 32% of the total biome was lost (Hansen et al. 2013). The tropical zone not only experienced the greatest total losses, it also suffered an estimated annual forest loss of 2101 km^2. Land-use changes are considered to have the highest impact on the decline of species richness and are still considered a major driver of change in ecosystem functions (Murphy and Romanuk 2014; Hooper et al. 2012).

If one starts with the assumption of a relatively low β-diversity (differences of diversity between different sites, Box 20.1), these habitat losses affect whole plant communities with highly endemic species, and particularly the specialists among plants and animals. Considerable losses in genetic material for breeding, species for medicinal purposes, food and various commodities have occurred (WBGU 2000). Cleared forest results in increases in soil erosion, which in turn leads to **changes in water relations**. These deleterious effects are expected to intensify with increases in atmospheric CO$_2$ concentrations associated with global **climate change**, which is expected to increase mean temperatures and the variability in precipitation (IPCC 2013) (Chap. 21).

In the wake of the destruction of tropical rain forests, various social movements have become involved in demanding increasing efforts to establish larger protected areas. It has been dif-

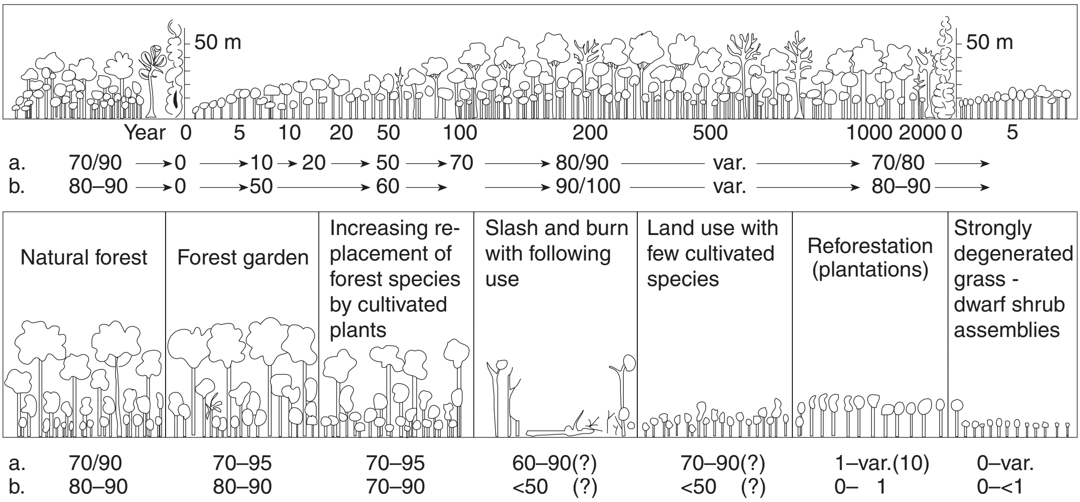


Fig. 17.22 Diversity of trees in undisturbed and disturbed tropical rainforests. Top: natural succession; bottom: following increasing intensity of land use. **a** Species richness as percentage of maximum attainable species number and **b** evenness as percentage of maximum attainable species number. (after Bruenig 1991)

ficult to convince the many millions of native people in these areas to change their way of life. It is often overlooked that concepts for sustainable management already exist in some areas. Earlier hunters-gatherers and the first settled farmers developed well-adapted forms of land use in most tropical regions. Low population densities allowed long fallow periods, which had a minimal effect on the land. The population was less mobile, stimulating a closed cover of several "storeys" from different crop plants. The original land use simulated (intuitively?) the structure and biodiversity of a natural rainforest with useful plants for daily life. Today, few examples exist of sustainable land use in permanent and seasonally moist rain forests of the tropics (Fig. 17.12).

Sustainable forest harvesting is extremely difficult to maintain owing to the imbalance of nutrient content in the soil post-harvest. New integrated approaches that take advantage of local crops that are adapted to current conditions (e.g. supply with nutrients), while limiting the effect of the site (e.g. creation of particular microclimatic conditions), must be developed to educate the local indigenous populations to improve management in the area. However, in doing this, the expectations of higher yields often linked to land use in the tropics must be revised. Sustainability must be thought of more than just as a rate of production or bottom line and more in terms of the maintenance of cultural and natural heritages in a particular environment or region. Some elements of sustainable use are generally valid. These are, for example, **agroforestry, mixed cropping, mulching and biological pest control**.

Many questions remain open about the scientific basis for nature protection in the tropics. It is assumed that a suitable number of plant individuals, able to reproduce, must be available to maintain a species. Assuming this number to be only 500, this could require, in the rain forest ecosystem, probably several hundred hectares for some species. This concerns the protection not only of species but of plant communities as a whole. Little is known about the protection of complete communities, about the minimum size of such areas and the bordering buffer zones required to ensure the persistence of a species. The borders of national parks and biosphere reserves are usually roughly estimated, even if not determined according to political and economic criteria. To define these borders is an important task for applied ecology, which is concerned with the protection of tropical ecosystems.

17.3 General Vegetation Dynamics

Vegetation units are permanently subject to spatial and temporal changes. This concerns changes in species composition as well as the constituent life forms and alterations in vegetation structure. Each recording of vegetation is only a momentary snapshot of a complex dynamic process. The temporal dynamics in the spatial arrangement of species are closely linked to the different demands of species, to their life cycle, mechanisms for reproduction, response to competitive pressures and to the resources available in that system.

Scientific approaches to **vegetation dynamics** aim to record and explain similarities of vegetation patterns and processes and then to derive characteristics or typical responses and models. The underlying causes of dynamic processes may be found in disturbances of very different kinds. The interpretation of vegetation dynamics is hampered by a confusing multitude of terms, which is caused by insufficient consideration of spatial and temporal scales. The description of vegetation dynamics on a few square centimetres of bare rock will necessarily be different to that within an area of several square kilometres in a forest. For boreal forests a different terminology should probably be used than for tropical rain forests, and taking temporal differences into consideration—hours, days, seasons, years, for example—is probably even more important (Fig. 17.23).

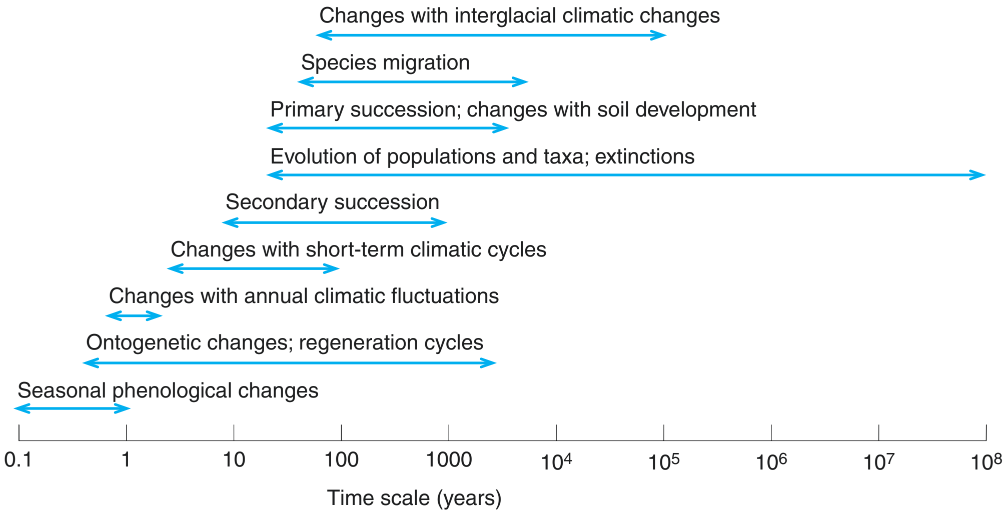


Fig. 17.23 Time scales for dynamic changes in vegetation. (after Miles 1987)

17.3.1 Short-Term and Seasonal Vegetation Dynamics

Plants need to adapt to changing daily and seasonal conditions in their habitat, particularly periodic changes of radiation, day length and temperatures, as well as the amount and distribution of precipitation. The **short-term dynamics** of plants and vegetation units are considered by the discipline of **phenology**, the science of seasonal sequences of life cycles of plants and plant communities. Visible changes in the life cycles of plants are recorded, stages of development defined and attempts made to explain these by changes over time, as well as biotic and abiotic factors in the habitat. Of interest are not just typical sequences but also differences in weather conditions from year to year, which may have a considerable effect on the timing of flowering, conditions for germination, the amount and allocation of biomass production and formation of fruit and seeds, as well as the start and duration of individual phenological stages.

Phenological characteristics have been known for a long time and are relatively easy to observe. In the **daily rhythm**, leaves and petals move (heliotropism) in order, for example, to protect against excessive radiation or to capture the highest possible amount of radiation. The production of odorous substances, the secretion of nectar or the supply of pollen by flowers may be coupled with the active phases of animal partners and change during the day. This is mainly regulated by the daily photoperiod.

Different aspects of flowering, harvesting or colouration of leaves are basic observations in phenology. These processes are regulated by **photoperiodic responses** and light quality. Further, important factors are temperature extremes and temperature integrals or even human intervention. Examples of such controls are the spatial mosaic of vegetation of snow combs, the use of light by spring geophytes in nemoral deciduous forests (Fig. 17.25) or the **flowering aspects** of meadows and pastures. Plants may require phases of particular low temperatures to germinate (**stratification**) or for flower induction (**vernalisation**). Annual, biennial and perennial species behave differently, making the derivation of general rules difficult.

There are also short-term periodic or episodic events that cannot be explained by the usual phenological characteristics but determine the dynamics of these communities decisively. These include regularly occurring floods in river basins, requiring particular adaptations to the extreme water supply and potential restrictions for root respiration (anaerobic conditions) and mechanical

Box 17.2: Methods in Phenology Research

Phenological studies focus on the appearance of plants during their temporal development throughout the year. The characteristics include floral development (reproduction) and leaves (vegetative growth). In spring, observations are usually made weekly and later at longer intervals. The numbers of flowers, shoots, leaves and fruits, as well as the degree of cover, are typically counted or measured.

Dierschke (1994) provides an example of such analysis for deciduous trees in nemoral forests and reproductive stages in phenology.

Vegetative phenological stages

0. Buds completely closed
1. Buds with green tips
2. Green leaf emergence
3. Leaves 25% unfolded
4. Leaves 50% unfolded
5. Leaves 75% unfolded
6. Leaves fully expanded
7. First leaves yellowing
8. Leaves 50% turned colour
9. Leaves 75% turned colour
10. Leaves 75% turned colour
11. Bare

Reproductive phenological stages

0. Without flower buds
1. Flower buds recognisable
2. Flower buds swollen
3. Shortly before flowering
4. Start of flowering
5. Up to 25% flowers mature
6. Up to 50% flowers mature
7. Full flowering
8. Flowering decreasing
9. Flowering ceased
10. Fruiting
11. Fruit abscission

Comparable categories have been developed for herbs, grasses and cryptogams. For general phenological examination, in which the whole plant community is considered, permanent areas are marked and regularly monitored. This may include all or only selected species in vegetative and reproductive stages of development (**phenophases**). In addition, environmental data are recorded, particularly those related to weather conditions (temperature, precipitation). For the visualisation of these data sets, species are sorted by the start of flowering or the length of the flowering period.

Development during the year is often subdivided into phenophases that are based on phenological plant types. They have the same developmental rhythm, which appears in comparable leaf characteristics, time of flowering and duration of the vegetative period. The applicability of these types is limited to particular regions because individual species may behave differently in different communities. Phenophases are initiated by the start of flowering, leaf unfolding, leaf colouration and leaf abscission of particular plant species.

In so-called phenophase diagrams, representatives of important phenological plant types are used to describe phenology over the course of the year (Fig. 17.24). These quantitative-synthetic phenological spectra provide a precise understanding of the floristic structural features of vegetation and elucidate connections between flowering, reproduction and dispersal, thereby providing the basis for the study of biocoenotic relationships. **Phenological maps** are widely used to show spatial differentiation, for example, of the start of spring (often based on flowering initiation of apple or lilac in Central Europe). The selected plant species used for this must fulfil two conditions: (1) they must occur in high numbers and be widely distributed and (2) they must show clearly distinguishable and easily assessable phenological characteristics. In mesoclimatic regions, trees are generally selected, while herbs are used to characterise the climatic conditions of the understorey. Phenological maps, which now are made with the help of aerial photographs and permanently installed automatic cameras (so-called phenocams), show differences within small areas such as towns and their suburbs. In agriculture, phenological characteristics are used to establish maps of growth climates and temperature ranges to assess the potential use or the probability of damage to particular types of crops.

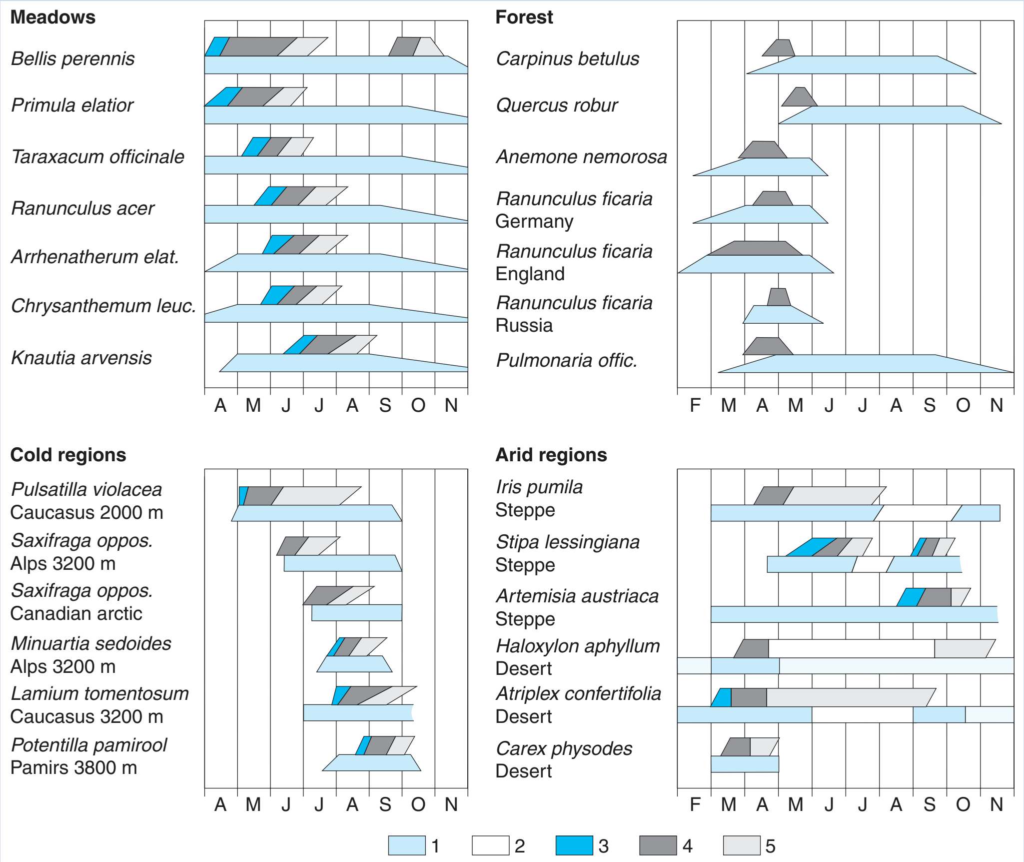


Fig. 17.24 Phenological phases in growing season. Examples of an oat grass-*Arrhenatherum*-grassland in Poland, for trees and herbs in a mixed oak forest in northern Germany (with comparison of *Ranunculus ficaria* to those in Russia and England) and for plant species from cold regions (high mountains, arctic regions) and from semi-arid and arid regions (steppe, deserts). *1* Time required for complete leaf cover; *2* death due to drought; *3* flower buds visible; *4* flowering period; *5* fruit ripening and seed dispersal. (after Larcher 2003)

disturbance (Fig. 17.26). Another example is the stress caused by avalanches in the Alpine belt.

Phases of activity and dormancy are characteristic of all regions with a seasonal climate. A distinction is made between phases of stronger activity of vegetative and reproductive growth. Occasionally, several **vegetative pulses of growth** occur, which can be detected as growth rings even in annual species (Schweingruber and Poschlod 2005). In late summer, some tree species rapidly form very distinct new shoots. Seasons may be determined by temperature or from the water supply. In the latter case, seasonal changes in water supply can prove to be the most important regulatory factor for the short-term dynamics of vegetation. In woody species, two types have evolved: Late flowering plants flower only after the development of leaves or after

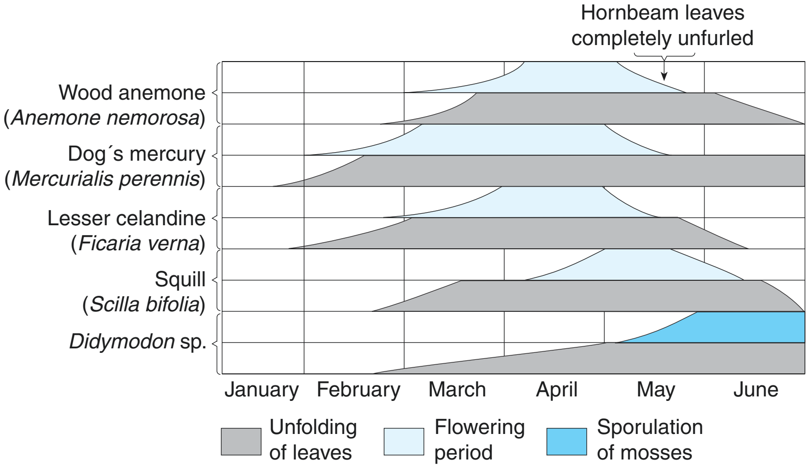


Fig. 17.25 Flowering period of geophytes during spring in a hornbeam (*Carpinus betulus*) forest. (after Schmidt 1969)

shedding of leaves at the end of the rainy season, while early flowering plants start to flower before the emergence of leaves, i.e. before the rainy season begins. Both types are adapted to the simultaneous occurrence of pollinators or seasonal periods with regular winds.

Because of the usually favourable conditions of temperature and moisture in the perhumid tropics, plants often grow continuously. Nevertheless, irregular bursts of growth may be observed, even with differences among different parts of individual plants. However, definite flowering periods or other phenological phases can hardly be established. Some individuals flower and carry ripe fruits at the same time. It is remarkable that several plant species only flower episodically, sometimes only after several decades.

The timing and duration of specific phenological phases within a year is very closely correlated with the sequence of weather conditions during the year. These short-term dynamics, occurring year by year, but not necessarily cyclical, are **fluctuations**. Changes are registered at the level of individual plants. The most important expression of fluctuation is a change in the dominance between co-occurring species. In contrast to successional dynamics, a return to the previous state is possible. In field studies, it is not easy to distinguish between fluctuation and succession because both overlap and influence each other. The phenological spectrum for species of woodland edges for two different annual sequences records the extent of such fluctuations (Fig. 17.24).

In extremely arid regions, where annuals dominate, definite flowering periods no longer occur because of the high variability of precipitation in time and space. But after several rain events a “flowering desert” quickly develops. Many annuals of arid areas may complete their life cycle within a few weeks (Fig. 17.27). The biblical seven fat and seven lean years point to fluctuations and their significance in rain-fed agriculture.

Furthermore, fluctuations may occur because of a massive attack by invertebrate herbivores. Not only climatologically but also genetically determined fluctuations are the so-called mast years of woody species with an annual production of a substantial amount of fruit compared to other years. Finally, fluctuations are often the result of human interventions, for example, rotations in grazing management or changing crops in agriculture. The phenological spectrum of species on woodland edges for two different annual sequences records the extent and yearly variability of such fluctuations (Fig. 17.28).

Evaluations of synecological and biocoenological links are only emerging, for example, of the temporal niches of flowering species in plant communities, of the synchronisation of insects and animals that distribute pollen, fruits and seeds. This would not only make pollen calendars available for those with allergies but would also help protect nature, i.e. by providing dates for mowing, for extensive maintenance or as a control for the success of different types of land use.

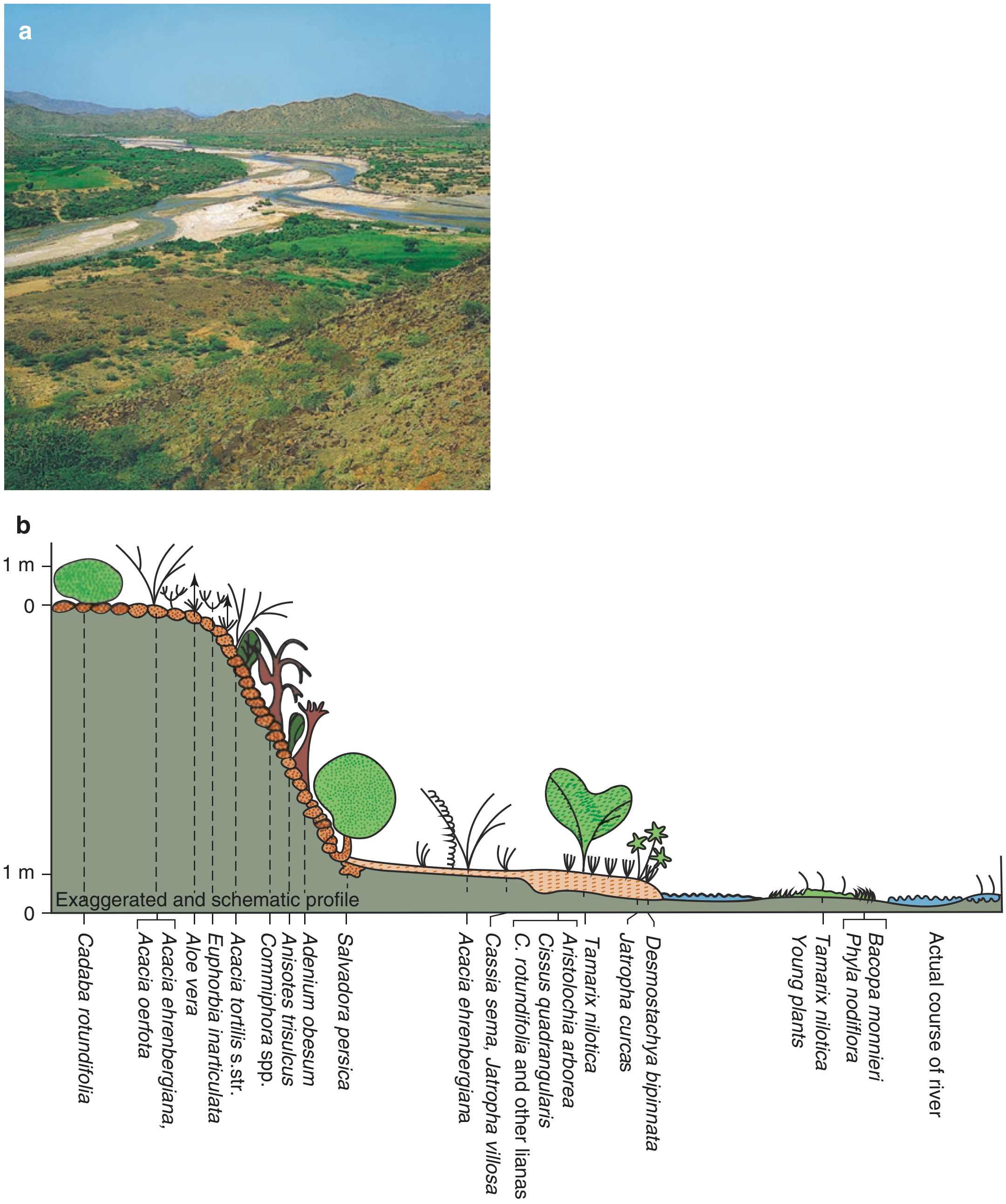


Fig. 17.26 Zonation of plant communities on borders of large wadis in North Yemen (Yemen Arab Republic), determined by different height of water flow. **a** Wadi Mawr in Tihama Mountains with highly variable water discharge during year (Photo: K. Müller-Hohenstein). **b** Schematic transect from bed of wadi to lower terraces and to top of wadi bank. Only therophytes such as *Bacopa monnieri* and *Phyla nodiflora* are able to colonise the frequently moving gravel banks. In the more strongly consolidated parts of the banks, grasses with particular root systems (rhizomes), such as *Desmostachya bipinnata*, and very elastic woody species, such as *Tamarix nilotica*, are able to survive episodic flooding. The resulting changes in vegetation are relatively rapid and aperiodic. (Deil and Müller-Hohenstein 1985)

Fig. 17.27 "Flowering desert" (Arabic, *acheb*) after one of the rare rainfall events in extreme deserts. Such an unpredictable change in vegetation is called a fluctuation; the plant community is composed of only therophytes. This example is from the Arabian Desert (United Arab Emirates) and contains *Silene villosa*, *Senecio glaucus* and *Plantago amplexicaulis.* (Photo: K. Müller-Hohenstein)

17.3.2 Long-Term Vegetation Dynamics

Medium- and long-term changes in plant cover over several decades and up to millennia are analysed in research on **successions**. Only some decades ago, the principles and models of these successions were derived from empirical data. However, from the beginning there was controversy in the scientific discussions between those with a holistic approach who consider the complete ecosystem and those with a reductionist approach who focus on individual functions and processes in succession. Both approaches had the same aim in trying to recognise the causes of vegetation dynamics by explaining the resulting effects and predicting them. There remains a belief that there are basic rules of dynamic sequences, but many processes are now seen as stochastic. This is demonstrated by the influence of extreme climatic events such as prolonged drought (Kreyling et al. 2011). The necessity of considering spatial and temporal scales in greater detail is generally accepted.

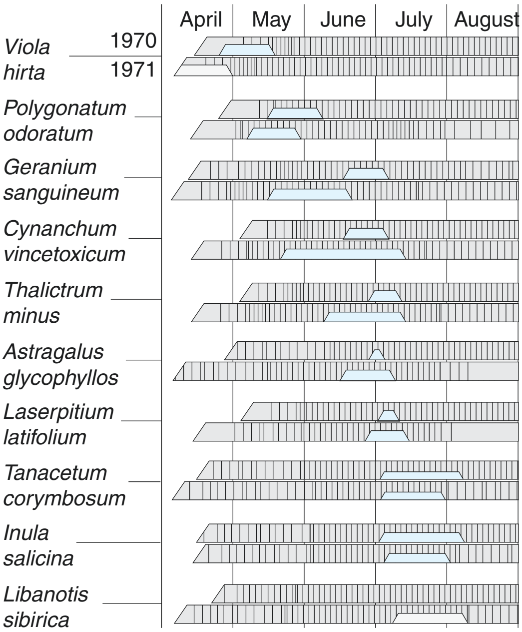


Fig. 17.28 Phenological spectra for species on woodland edges. The small trapezoidal areas show the flowering period. (after Dierschke 1994)

17.3.2.1 Beginnings of Succession Research

Systematic research on vegetation dynamics is connected with the names of the ecologists Clements and Gleason. Clements (1916) is regarded as the founder of the discipline of successional research, starting from the idea that only undemanding species grow first on bare substrates. Once established, species change and influence the conditions and community of their site, which then facilitates invasion by others. Clear temporal periods are recognisable until the development of a uniform, final community, the so-called **climax community**, representing a relative equilibrium. Small fluctuations in community assemblages are possible, but a reversal of the clearly directed processes leading to this climax community is not.

Later Clements assumed three **succession sequences**. One of these sequences has its origin in a freshwater basin. During the processes of receding water and emerging land in temperate latitudes, deciduous forests develop as a climax via a boggy and pre-forest stage (**hydroseries**). Another sequence starts from a saline substrate (**haloseries**) and a third on bare rock (**xeroseries**),

Box 17.3: Methods for Studying Succession

Research on succession has followed two complementary paths. In one, the development of the vegetation over time is studied at a particular site, including experimental treatments. In the other approach, the focus is on the current spatial composition of vegetation, which is used to reconstruct changes over time (false time series, or **space-for-time substitution**). An example of this is the littoral zone of a lake, which in its spatial development may be seen as an ecological series, while its temporal processes at the same site may be interpreted as succession.

Indicator plants, the age structure and diversity of stands or an analysis of seed banks can often help to establish the temporal sequence of particular developmental stages. In addition, external indicators are often used, such as differences in soil profiles or historical records from archives or land-use registries and account books of farms, which often have data about fertilisation or the use of herbicides at particular times.

Nevertheless, there are inherent problems in drawing conclusions from space for time substitutions. Therefore, more direct methods of understanding successions are increasingly being used. Spatially limited units of vegetation are established and plant individuals are monitored in regular sequences (**biomonitoring**). This long-term observation on **permanent plots** provides detailed analysis about population dynamics as the vegetation changes. Evaluation of aerial photographs and repeated satellite data are increasingly being used, although the scale is often not sufficient for the observation of individuals. Quickbird, with a resolution down to 0.6 m (but only panchromatic), has some of the best satellite imaging capabilities. It can be used to make comparisons of the average performance of stands; the structural aspects of plant cover are most obvious, while inventories of species are often not comparable. Experimental studies of succession are carried out on comparable areas using a range of treatments (e.g. different fertiliser applications, mowing regimes, single or multiple soil tillage, fencing and exclusion of grazing or other sorts of herbivory), and the effects on the vegetation during the following period are measured. Biomonitoring is also used in applied analyses of succession for the regulation and modification of measures in nature conservation in order to depict future trends in the development of the vegetation.

but all end in the same forest climax. Changes in the site always originate from plants themselves. Also, in larger areas with the same climatic conditions, the same final community will always emerge (**monoclimax**). This concept was well received, but there were critics who could not empirically confirm this theory. The reason for the discrepancy was that Clements concentrated on the dynamics of undisturbed vegetation (**primary succession**) and interferences of any kind, and developments arising from them (**secondary succession**), were disregarded.

Clements' theory, which regarded plant communities as "organisms", was rejected by Gleason (1926), who stressed that there was also an individualistic type of vegetation dynamics without clear steps and without formation of the different vegetation units. He started from the assumption that changes in species at a site depended on the species composition and the influx of diaspores to that site.

Today, the concepts of Clements and Gleason are no longer accepted in their pure form. In particular, the idea of a final monoclimax has been rejected in the scientific community, which now favours continuously dynamic or cyclical views. However, following this rejection, two important movements emerged and helped set the tone for successional research today:

- A relatively general interpretation of the broad spectrum of dynamic events in ecosystems
- A recognition of the enormous complexity of conditions and attempts to clarify individual aspects

Definitions of succession or **vegetation dynamics** are today broader and more general. These dynamics comprise changes in structure and species in vegetation units in space and time. Short-term, daily and seasonal changes are included. All forms may be described by the term **patch dynamics** (Pickett and White 1985). Another general definition underlines the notion that successions are medium- to long-term dynamic processes in a **directed, temporal sequence** of plant communities in an ecosystem. It is often stressed that these sequences are irreversible—within limits—and predictable and may be triggered by endogenous or exogenous processes. During succession, self-organisation in the ecosystem (on the precondition that there is no disturbance) increases and a balance between primary production and mineralisation develops.

Odum (1980) lists a total of 24 different ecosystem characteristics that are able to change during a succession sequence. He regarded development as a well-ordered process resulting from changes caused by vegetation and ultimately leading to a stable ecosystem, where maximum functional interconnections are achieved. The hypothetical final state is understood as a complex community of organisms with complex links and interactions, in which once equilibrium is achieved, it can change again, for example, after a new disturbance.

However, successions are often also understood as stochastic processes, basically because the seed input in a biocoenosis at a site is random; the same applies to the germination and establishment rates or the availability of necessary safe sites and the occurrence of disturbance—their type, intensity and degree—which are generally not predictable.

17.3.2.2 Succession Types

Succession may be considered over large or small areas, with fast or slow changes. It may be directed or cyclical and may be affected by endogenous or exogenous processes, which may differ by type, intensity, duration or extent. It is important to consider the geographical location within different climatic zones and whether development occurs on newly formed soils or on those previously colonised. Finally, participating plant species will differ in their ability to disperse and compete and in their life history strategies and resource demands/strategies. Dynamic processes are triggered if net production and mineralisation in an ecosystem are not balanced. In such cases it is possible, for example, to accumulate organic matter (formation of bogs, **autotrophic succession**) or for organic matter to be consumed (use of humus by agricultural systems, **heterotrophic succession**).

Considering all these aspects, many succession types on different spatial and temporal scales have been described. Spatial and temporal relations and how these aspects are related and differ are shown in Table 17.4. In Fig. 17.29, the successional types are schematically arranged. These are the most important examples of progressive and regressive, directed as well as cyclical vegetation dynamics.

Table 17.4 Relationships between spatial and temporal dimensions in changes in vegetation

	Individual	Patch	Population	Community	Landscape	Region
Fluctuation	×	××	××			
Gap dynamics	×	××	××			
Patch dynamics	×	×	×			
Cyclical succession		×	××	×		
Regeneration succession		××	××	××		
Secondary succession		×	××	××	××	
Primary succession			××	××	××	
Secular succession				×	×	×

The terms in the table headers refer to spatial dimensions. A patch is a small homogeneous area (ecotope), a gap a small open space in the forest (after van der Maarel 1988)

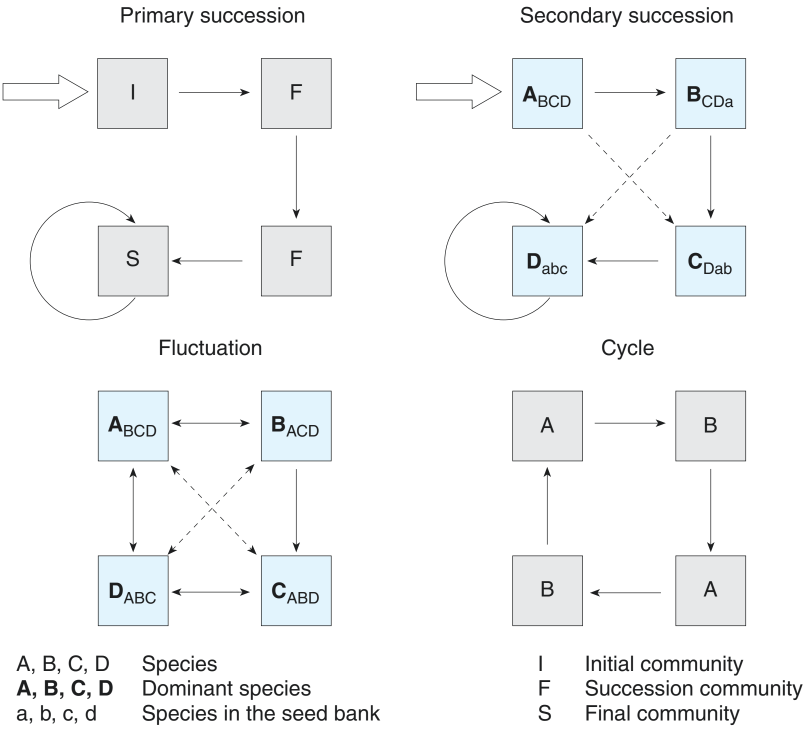


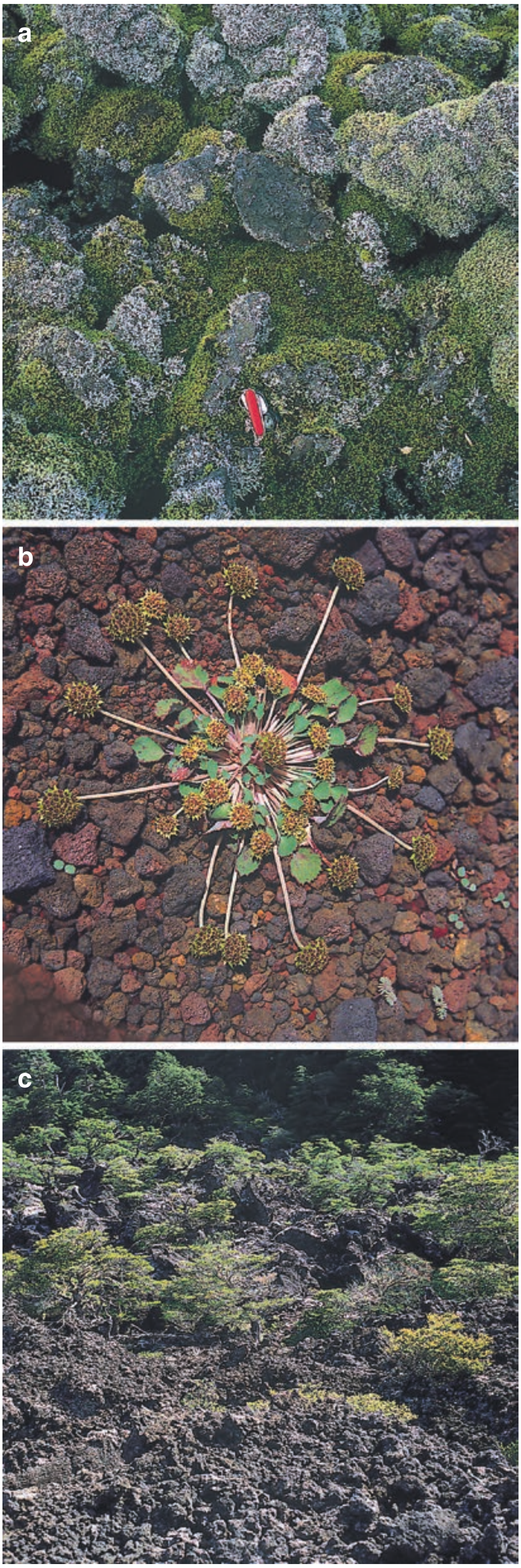
Fig. 17.29 Types of directed and cyclical vegetation dynamics. (after Jochimsen 1993)

Primary Successions

Primary successions are important for understanding processes of vegetation dynamics, but in reality they are rarely observed because they typically occur over long time periods where an uninhabited abiotic substrate needs to be present. Knowledge of individual stages of the sequence of primary successions derives mainly from newly formed sites, for example, following a volcanic eruption (Fig. 17.30) or in newly developed coastal regions or at the receding edge of a melting glacier (Fig. 17.31). Also anthropogenic sites, such as rubble heaps, quarries, road cuts and so forth, may be regarded as starting points of primary succession. Despite the differences in sites, similar trends and basic patterns may be discerned in such situations.

Very few plants are able to cope with the hostile conditions of a site during the initial phases. On rocks, cryptogamic communities develop first, perhaps lithophilic lichens, then fruticose lichens, mosses and ferns. In unfavourable exposed positions, for example on steep rock walls or on mobile debris, development rarely goes beyond this phase (permanent pioneer communities). Usually, the pioneer communities, which themselves depend on the input of propagules from the surrounding areas, change the site over the course of time, which allows for the formation of a soil substrate. Many Leguminosae are herbaceous pioneers that facilitate the accumulation of nitrogen in this new substrate. Upon the establishment of later pioneer plants, these will help change the local microclimate. If flowering plants have not become established during the first phase of succession, they will now follow. These are predominantly heliophilic, epigaeically germinating annuals or, where climatic conditions do not allow such establishment, undemanding (i.e. able to grow on a nutrient-deficient substrate) herbaceous hemicryptophytes and chamaephytes.

As succession progresses, the pioneer species are excluded more and more with each step by more demanding species. When this change takes place solely because of the changes in the vegetation itself, it is called **autogenic succession**. If other causes are more important— for example, natural climate change or a lower groundwater table caused by human extraction of water—this



is called **allogenic succession**. If successions proceed under steady external conditions, there are further stages, after the pioneer stage where competing species occur, that are superior to the pioneer species in vegetative and reproductive growth. These species grow taller, despite lower rates of growth, because of their longer life span (occurrence and increase of shrubs and trees), and they are more shade tolerant but often have less effective mechanisms for distribution, despite their more effective occupation of space in the long-term. Trees are superior to shrubs, forming **polycormones**, which enable them to dominate for a certain time. In the final phase of such development, trees dominate. This type of primary succession is understood to be progressive because the diversity increases at the level of the species as well as with regard to structure.

Common dynamic trends, despite the apparent individuality of responses, are summarised in Fig. 17.32. At the beginning of primary succession, chaotic interactions dominate, which cannot be predicted, because input and the establishment of propagules are, to a high degree, stochastic; widely distributed annuals dominate. Between the development of vegetation and changes in the site, feedback mechanisms trigger (Table 17.5). This means that plants themselves contribute, to a considerable degree, to creating environmental conditions that favour conspecific species. The dominance of exogenous factors is only slowly substituted by endogenous factors and is accompanied by a change in species and life forms. In the labile pioneer stages, intra- and interspecific competition is not very important, but in the later stages competition plays a decisive role in the

Fig. 17.30 Different stages of primary succession. **a** On fresh volcanic lava dense moss and lichen communities have developed after 8 years. **b** Only specialists among the vascular plants (e.g. *Pozoa volcanica*) become established quickly on almost unweathered rocks without soil. **c** Only after several decades do the first trees (*Nothofagus obliqua, N. dombeyi*) form open woodland vegetation. Photos were taken on sites on Llaima Volcano in southern Chile. (Photos: K. Müller-Hohenstein)

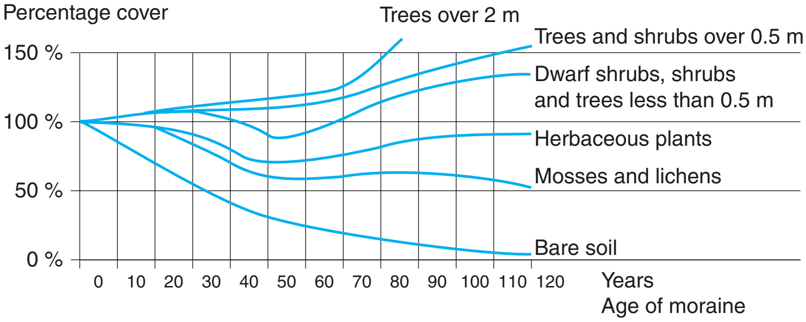


Fig. 17.31 Succession on moraines of Aletsch Glacier (Switzerland) (after Klötzli 1993)

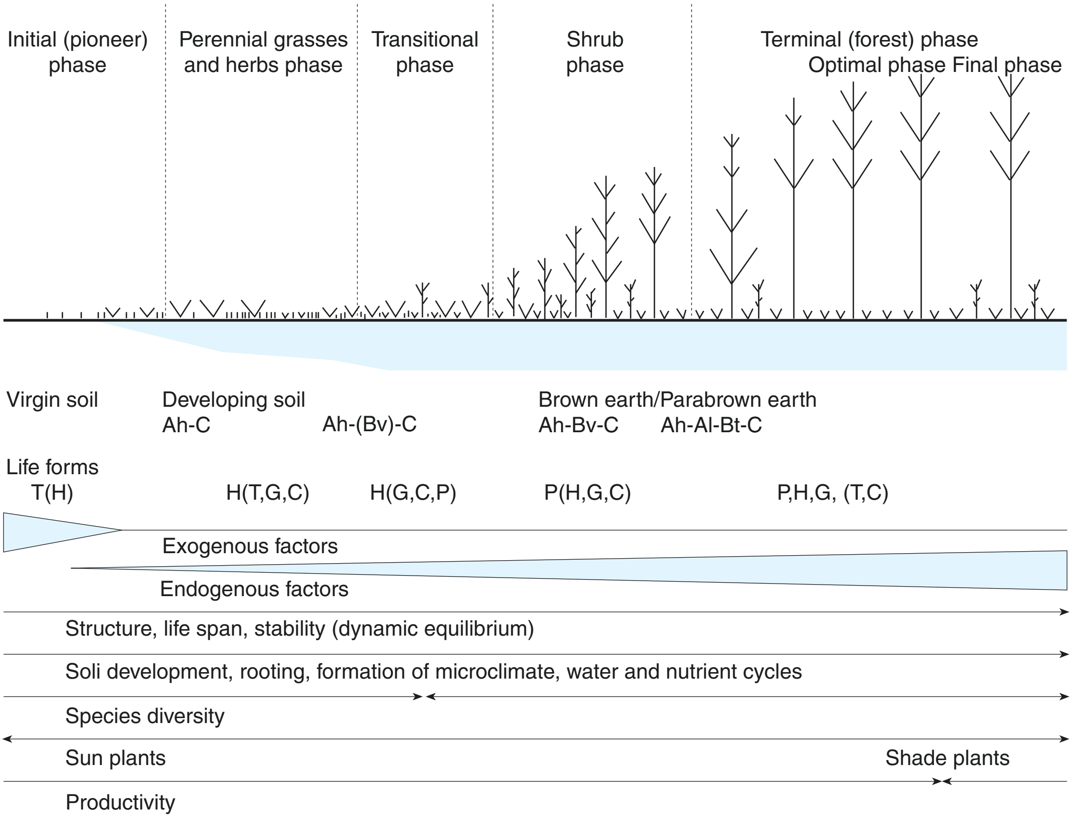


Fig. 17.32 Main characteristics of progress of primary succession. Exemplified for silicate rock and under sub-Atlantic climatic conditions. *T*: Therophytes; *H*: Hemicryptophytes; *G*: Geophytes; *C*: Chamaephytes; *P*: Phanerophytes. (after Dierschke 1994)

development of communities that become increasingly resistant to external disturbances.

Disturbances and Secondary Successions

Primary successions occur faster under warm, humid climatic conditions than under cold or dry conditions. However, it is most important that development of these successions are not affected by disturbances, which can only be rarely excluded. Thus, primary successions are particularly important for a better understanding of the processes of secondary successions, which dominate the actual vegetation dynamics in our environment.

Table 17.5 Environmental changes during succession (after Klötzli 1993)

1. Species structure	
Species composition	First rapid, then stepwise change
Number of autotrophic species (autotrophic diversity)	Increasing, often early in secondary succession
Number of heterotrophic species (heterotrophic diversity)	Increasing, until late in secondary succession
Species diversity	Initially increasing, then stable or again decreasing
Niche specialists	Initially broad then narrow
Size of organism	Initially small then large
Life cycle	Initially brief and simple, then long and complex
Selection pressure	Initially r-selection then K-selective
Type of production	Initially quantitative then qualitative
2. Nutrient cycles	
Cycles	Initially open then closed
Nutrient exchange	Initially rapid then slow
Role of organic debris (detritus)	Initially unimportant then very important
3. Organic structure	
Total biomass	Initially small then large
Stratification	Initially one layer then multiple
Inorganic nutrients	Initially in soil then in biomass
Recalcitrant organic material (e.g. humus)	Initially little then much
Biochemical diversity (e.g. pigments)	Initially low then high (increasing accumulation of toxins!)
Chlorophyll amount	Initially small then large (in secondary succession little difference!)
4. Energy flow	
Relation to food chain	Initially simple (food chain) then complex (food web)
Gross primary production	During early phase of primary succession increasing (only limited or no increase in secondary succession)
Net primary production	Continuously decreasing
Total respiration	Continuously increasing
Primary production per unit respiration	Initially primary production greater than equal to respiration (steady-state condition)
Primary production per unit biomass	Initially large then small
Biomass per unit of energy	Initially small then large; therefore, minimal use of energy per unit of biomass
5. Homeostasis (ecological steady-state, result of irreversible processes)	
Internal symbiosis	Initially not developed then developed
Nutrient storage	Initially small then large
Stability (resistance to disturbance)	Initially small then large
Entropy (increasing entropy)	Initially large (small) then small (constant)
Information	Initially small then large

Disturbances are the main causes of spatial heterogeneity and also affect environmental conditions and plant competition. They may disturb but at the same time also maintain biodiversity. For instance, grazing by large herbivores is an important disturbance because it can control vegetative dynamics, structure and diversity. All successional concepts, from patch dynamics to mosaic cycles, are based on disturbance regimes. Disturbances can have a profound influence on the species composition, changes and vegetative matter fluxes at a site, which can regulate habitat fragmentation. These factors concern plant communities as well as entire ecosystems, and the loss, gain and turnover of organic matter and disturbances may be the result of natural events or human interventions (Fig. 17.33).

There are several definitions and a multitude of different types of disturbances (Box 17.4).

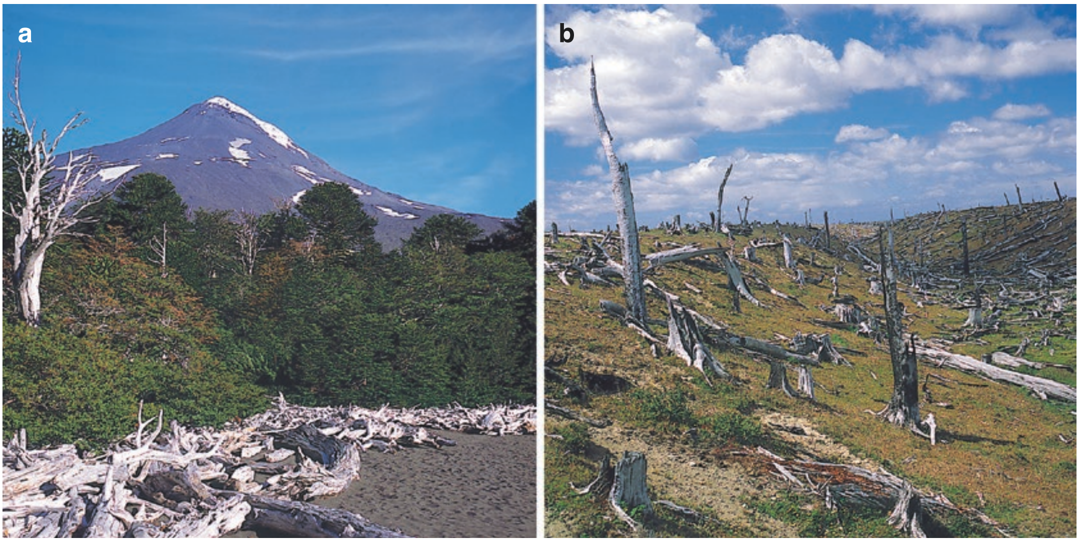


Fig. 17.33 Secondary successions develop after disturbances, which may be natural, for example, **a** when dead wood accumulates after volcanic activity and subsequent fire in a forest community on the Lanin Volcano in southern Chile. However, **b** the disturbances can also be human-made, for example, forests cleared by fire for range lands, not for timber, in southern Chile near Aisen. (Photos: K. Müller-Hohenstein)

Box 17.4: Disturbances: Definitions and Properties

A disturbance is a relatively discrete event in time that concerns an ecosystem, community or population structure (of vegetation) and changes the resources, substrate availability or physical environment (Pickett and White 1985). Because this is an absolute definition, all changes must be measured and accounted for. In contrast, by some relative definitions, disturbances are regarded as events leading to deviations from the normal dynamics in an ecosystem or plant community, based on the assumption that a "normal" state is known. Furthermore, severe disturbances can range from having very far-reaching consequences, up to a complete floristically and structurally different plant community, to very small ones, for example, affecting the ability of a single plant to resprout.

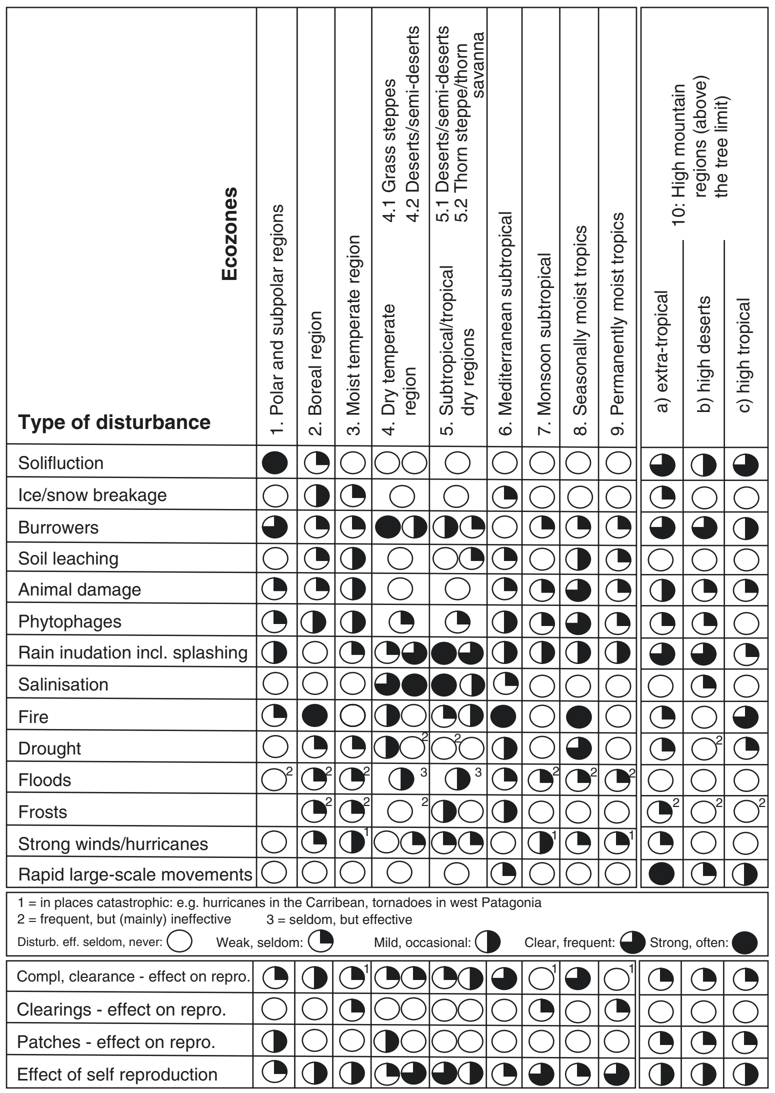
Richter (1997) distinguishes between endogenous and exogenous disturbances. The former occur regularly; they are a feature of a system, so organisms in the community adapt. This is the case for seasonal changes and for changes such as frequent, regular flooding of meadows. Most disturbances that then lead to secondary successions are exogenous and are typically natural in origin (e.g. catastrophic storms or landslides and avalanches); however, they can also be caused by human activity.

To overcome the high complexity of disturbance regimes, Buhk et al. (2007) established a classification scheme that takes into account the disturbance type (e.g. felling, flooding), disturbance space, form and distribution (spatial dimensions) and disturbance frequency, seasonality and duration (time dimensions).

The intermediate disturbance hypothesis (IDH) puts forth an often discussed theoretical background to evaluate the effects of a given disturbance (Sect. 13.5 and Sect. 20.3). This hypothesis describes the relations between the type and force of the disturbance and the species diversity in the area concerned (Huston 1979). It states that at intermediate levels of disturbance, species diversity is at its highest.

No species will be lost by being overly disturbed, and the competitive exclusion of a species is not very likely. Field tests of the IDH showed mixed support for and against this hypothesis (Mackey and Currie 2001).

In our managed landscapes, anthropogenic disturbance dominates because it begins with processes that immediately affect individual plants or that alter the environment and affect the whole community. It is therefore useful to differentiate between natural and anthropogenic disturbances, such as unusual weather conditions, flooding and landslides versus logging, mowing and trampling. However, some disturbances may be a combination of both, for example, fire (Fig. 17.33). There are spatial and temporal patterns in disturbances that help to understand the patterns of succession. Richter (1997) attempted to characterise disturbances in different climate zones (Fig. 17.34).



Ecozones Type of disturbance	1. Polar and subpolar regions	2. Boreal region	3. Moist temperate region	4. Dry temperate region	5. Subtropical/tropical dry regions	6. Mediterranean subtropical	7. Monsoon subtropical	8. Seasonally moist tropics	9. Permanently moist tropics	10: High mountain regions (above) the tree limit)		
				4.1 Grass steppes 4.2 Deserts/semi-deserts	5.1 Deserts/semi-deserts 5.2 Thorn steppe/thorn savanna					a) extra-tropical	b) high deserts	c) high tropical
Solifluction	●	◔	○	○○	○	○	○	○	○	◕	◑	◕
Ice/snow breakage	○	◑	◔	○	○	◔	○	○	○	◔	○	○
Burrowers	◕	◔	◔	●◑	◑◔	○	◔	◔	◔	◕	◕	◑
Soil leaching	○	◔	◑	○	○◔	◔	○	◑	◔	○	○	○
Animal damage	◔	◔	◑	○	○	◔	◔	◕	◔	◑	◔	◔
Phytophages	◔	◑	◑	◔	◔	◑	◔	◕	◔	◔	◔	○
Rain inudation incl. splashing	◑	○	◔	◔◕	●◕	◑	◑	◑	◑	◕	◕	◔
Salinisation	○	○	○	◕●	●◑	◔	○	○	○	○	◔	○
Fire	◔	●	○	◑○	◔◑	●	○	●	○	◔	○	◕
Drought	○	◔	◔	◑○[2]	○[2]○	◑	○	◕	○	◔	○[2]	◔
Floods	○[2]	◔[2]	◔[2]	◑[3]	◑[3]	◔	◔[2]	◔[2]	◔[2]	○	○	○
Frosts		◔[2]	◔[2]	○[2]	◑○	◑	○	○	○	◔[2]	○[2]	○[2]
Strong winds/hurricanes	○	◔	◑[1]	○◔	◔◔	○	◑[1]	◔	◔[1]	◔	○	○
Rapid large-scale movements	○	○	○	○	○	◔	○	○	○	●	◔	◑

1 = in places catastrophic: e.g. hurricanes in the Carribean, tornadoes in west Patagonia
2 = frequent, but (mainly) ineffective 3 = seldom, but effective
Disturb. eff. seldom, never: ○ Weak, seldom: ◔ Mild, occasional: ◑ Clear, frequent: ◕ Strong, often: ●

Compl, clearance - effect on repro.	◔	◑	◔[1]	◔◔	◔◑	◕	○[1]	◕	○[1]	◔	◔	◔
Clearings - effect on repro.	○	○	◔	○○	○○	○	◔	○	◔	○	○	○
Patches - effect on repro.	◑	○	○	◑○	○○	○	○	○	○	◔	◔	◔
Effect of self reproduction	◔	◑	◑	◔◕	◕◑	◔	◕	◔	◕	◑	◑	◑

Fig. 17.34 Type and occurrence of disturbances in different ecozones. (after Böhmer and Richter 1996)

Secondary succession sequences may be classified according to the responses to disturbance (regarding the material balance of an ecosystem):

- Disturbances may interrupt the dynamics and the vegetation but leave the ecosystem at a certain stage (permanent communities).
- Changes occur without clear direction within vegetation, for example, because of long-term fluctuations in the water level.

Influences mentioned can lead to faster or slower, as well as irreversible, alterations. A response that reverses the process or sets it back to a previous step or direction of change is known as **regressive succession**. These include successions that occur as a consequence of overexploitation or selective use of forests and pastures.

Most often secondary succession leads to reestablishment of the state that preeceded the disturbance. Here, too, the changes in direction lead to a more complex form of organisation in the plant community. However, secondary successions have different initial stages. Their dynamic changes start from an already settled substrate and may build on an existing seed bank. This means that secondary successions progress faster than primary successions; right from the start there is competition for space and resources, and only species that can compete are able to invade.

In Central Europe, numerous studies investigate secondary succession on fallow land and meadows. Schmidt (1993) describes succession over 25 years on (previously sterilised) fallow fields and found that after only 2 years of occupation by annuals, the persistence of herbaceous plants allowed them to become established by the eighth year, after which dwarf shrubs and shrubs occurred up to the twentieth year. Finally, successions continued with pioneer forests, or a pre-forest stage. These phases were initially limited by nutrients. Even if individual phases develop relatively regularly, it is difficult to analyse this development and to define the decisive factors determining the succession because of the many factors influencing and feeding back into the process (Fig. 17.35).

Secondary succession in fallow pastures is delayed because of the dense grass layer.

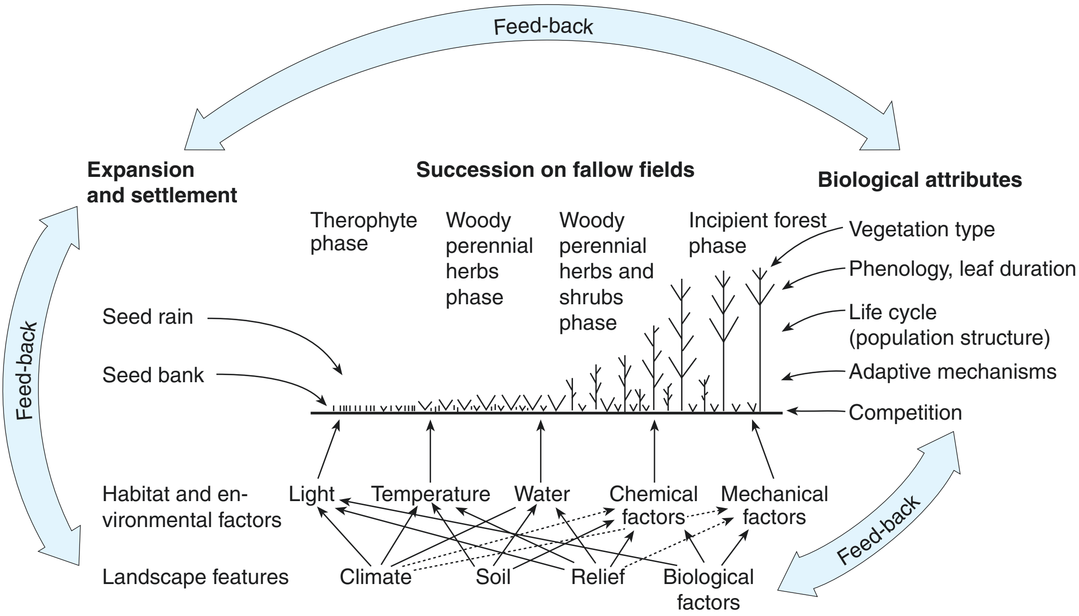


Fig. 17.35 Successions on fallowed agricultural fields: influencing factors and interrelations. (after Schmidt 1993)

Schreiber (1995) shows from observations over 20 years that the establishment of woody plants can occur in several ways. Occasionally, well-known basic processes in the succession of different functional types of plants from annuals to woody species occur. However, pastures, initially relatively homogeneous, often show the formation of dominance patterns with few species that cover the area well after just a few years. With good nutrient supply, herbs dominate because biomass is not removed (auto-eutrophication), but with poor nutrient supply grasses dominate. The temporal sequence of individual stages differs considerably. In some areas, 10–15 m high pre-forest vegetation occurs, while on other potential forest sites neither trees nor shrubs grow. The difference in the establishment of woody plants does not fit any succession model so far described; a prediction about changes in life forms and species is not yet possible, even if occasionally such phases in vegetation dynamics may be clearly seen.

A special case of secondary succession is **polycormophyte succession**. Vegetative lateral shoots of plants form colonies that are able to expand in closely covered herbaceous plant communities even faster than via seeds. This type of succession usually starts with a pioneer woody species possessing a superior defence against herbivores, for example, *Prunus spinosa*. Such plants are able to expand over large areas for decades. Finally, taller, unprotected shrubs and trees become established in centres of such areas, so that forest islands and, ultimately, closed forest areas may result. This development can be interpreted as an autogenous succession, regulated by the vegetation itself. The study of this form of succession allows strategies of competition in woody species to be recognised (Fig. 17.36).

The concept of succession as a directed, more or less deterministic, although predictable, process must therefore be corrected according to empirical results obtained in recent decades. These changes over time are very complex, with many variables influencing development, for example, site, biological reproduction, space and time. Particularly important are the type, intensity and duration of disturbance. All these factors make it difficult to regulate and predict successions.

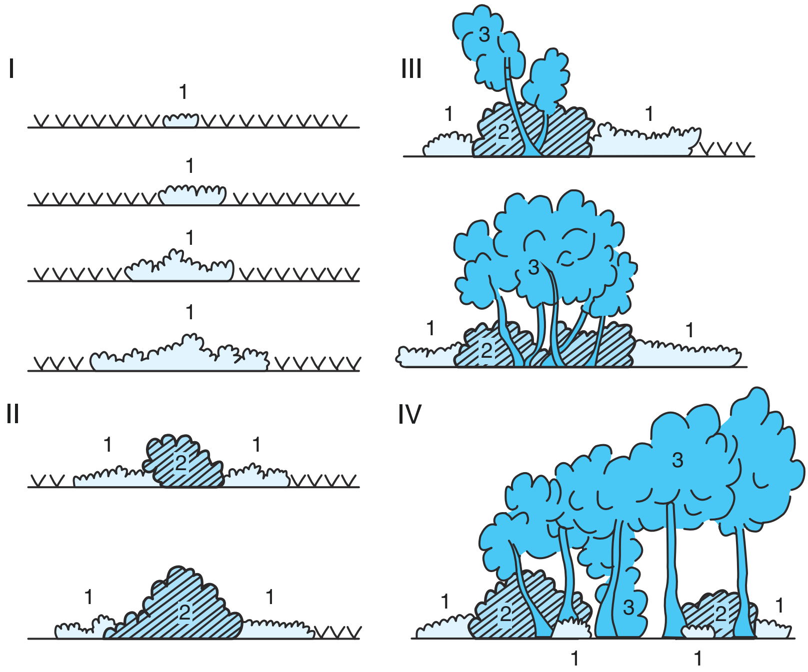


Fig. 17.36 Polycormophyte succession of woody species in grassland. *1* With establishment of low-growing woody species; *2* followed by tall-growing woody species; *3* with woody, tall trees. (after Dierschke 1994)

Cyclical Vegetation Dynamics

Secondary successions not only develop on fallow or abandoned land but also in plant communities affected by all kinds of disturbances. Here processes directed towards a re-establishment of the original status may occur and fit into a **cyclical regeneration scheme**. Examples originate from managed forests where humans are the driving force, ensuring that the cycle is maintained. Pignatti and Pignatti (1984) analysed such regeneration cycles for Mediterranean forests (Fig. 17.37) and showed two variants—one for regeneration after clearing and one, more regressive, succession after several fires. After clearing, various weeds become established that are later on outcompeted by oaks. Reoccurring fires will lead to a permanent stage where regeneration takes place—if at all—only after a long period.

The final phase of secondary succession can be understood as a kind of self-preservation cycle. In a cyclical succession, plants of different ages enter and replace each other in the same vegetation community. Structural changes with the same or different species at one site are important. Further concepts about **cyclical vegetation dynamics** originated from Watt (1947), who introduced the **"gap"** into the discussion, that is, sites where these processes take place. Remmert (1991) coined the term **mosaic-cycle concept** to describe such cyclical dynamics. An important observation was that the climax stage (mature stage) does not extend over enormous areas in natural forests, but that various phases of development are spread out like a mosaic. All stages co-occur adjacent to each other in small patches. For Central European forest areas three phases are distinguished:

- A rejuvenating and juvenile phase, with young plants of the same or different tree species, with the previous phases occurring again. Often light-demanding trees invade first, followed by shade-tolerant trees.
- An optimal phase corresponding to a forest of uniform age with few species, a closed stand with little undergrowth.
- Ageing and decaying phases when the tree layer is disrupted over large areas and species requiring light are able to invade.

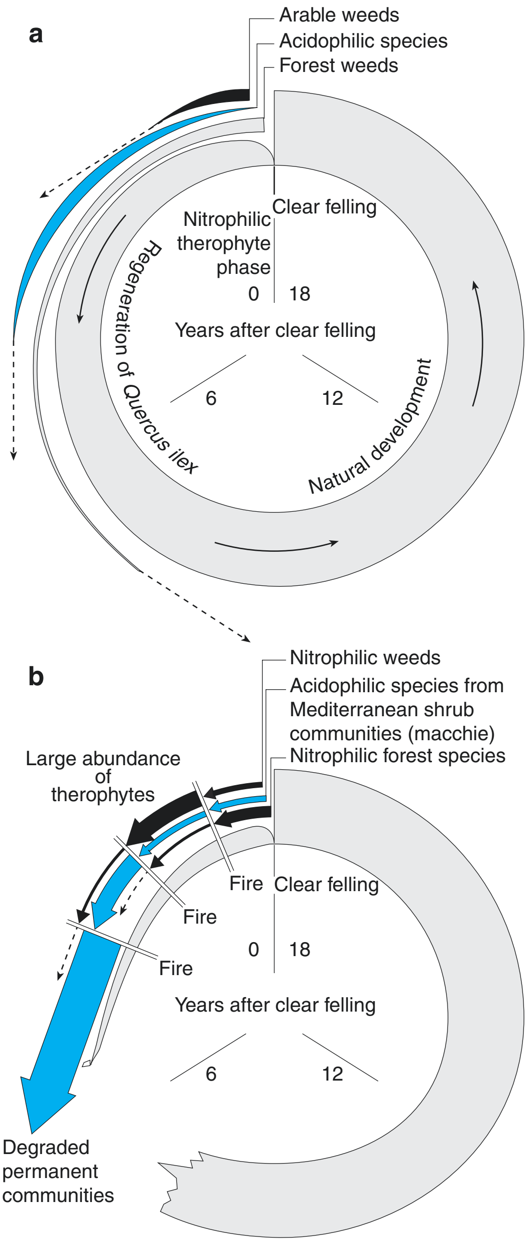


Fig. 17.37 Succession in Mediterranean oak forest. **a** Cycles following clear felling. **b** Regression after multiple fires. (after Dierschke 1994)

These phases may be regarded as a continuous process of **self-thinning**.

Figure 17.38 shows schematically the cyclical vegetation dynamics for a tropical rain forest. The size of the pieces of the mosaic differs, depending on the diversity of species. In nemoral

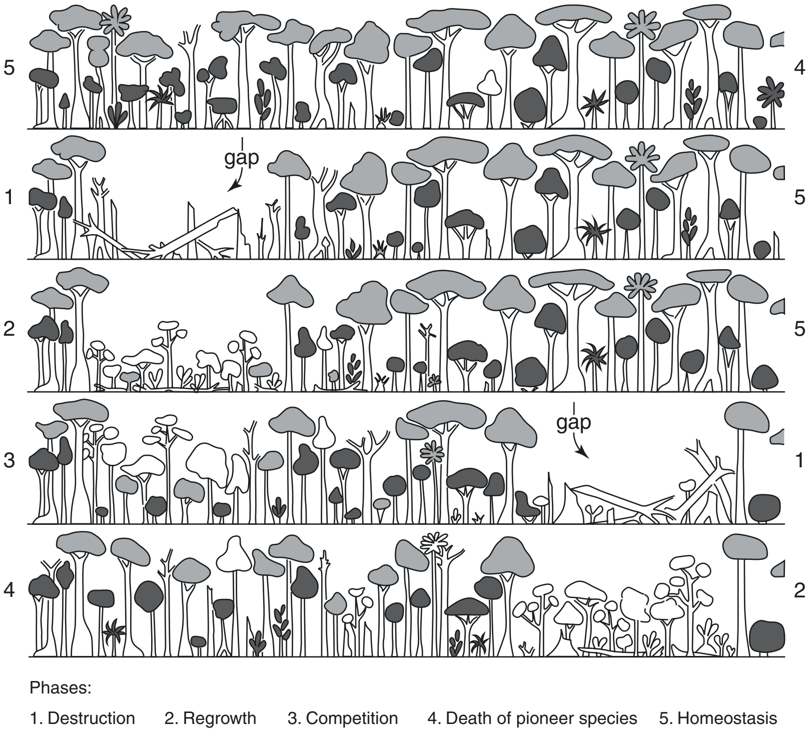


Fig. 17.38 Mosaic cycle in tropical rainforest. Open tree crown pioneer species; thick tree crown canopy species; medium tree crown shade-tolerant species. (after Richter 1997)

deciduous forests an average size of 1–2 ha is assumed; in boreal forests the pieces of the mosaic cover several square kilometres because of the influence of fires. In contrast, in tropical rain forests they are hardly ever larger than 100 m^2 (**treefall gaps**). The duration of cycles also differs. For the well-analysed forests of the boreal zone several centuries are assumed; in the North American sequoia forests cycles last several thousand years. Processes of vegetation dynamics similar to **mosaic cycles** also exist in North Atlantic heath and bog complexes.

Disturbance is again seen as the driving force for cyclic vegetation dynamics. The life span of "key organisms" is important, and competition following their death is centred on obtaining light and nutrients. The same is true for mechanical influences (wind breakage, fire). Constant conditions are not to be expected in a **pristine forest**, which is also a mosaic of asynchronous phases of cyclical vegetation dynamics. During the individual phases, the structural characteristics of forests and their species diversity change.

Today, additional types of cyclical vegetation dynamics are distinguished based on questions of scale and preferential occurrence in different biomes. The formation of mosaics over large areas in Hawaii is known as a consequence of the "death of cohorts" (Müller-Dombois 1995). Demographically unfavourable situations caused and maintained by fire and storm damage are the driving force. In this context, the mass die-off of bamboo-like grasses in all tropical regions should also be included. However, it is still not clear whether only endogenous (age) or also exogenous (climate) influences are responsible; it is likely that a combination of both is responsible.

In **cohort dynamics**, as in the mosaic cycle, the species composition may change. However, in so-called **carousel dynamics**, the pattern formation in grasslands occurring over small areas is not included according to van der Maarel and Sykes (1993). The basic idea of this change over time is that species are able to recycle in a very short time period on the smallest of scales. A **regeneration gap** is a sufficient free space for seeds to germinate and become established. These spaces become available through the death of individual plants and are conquered in a sort of "guerrilla strategy" or even according to the

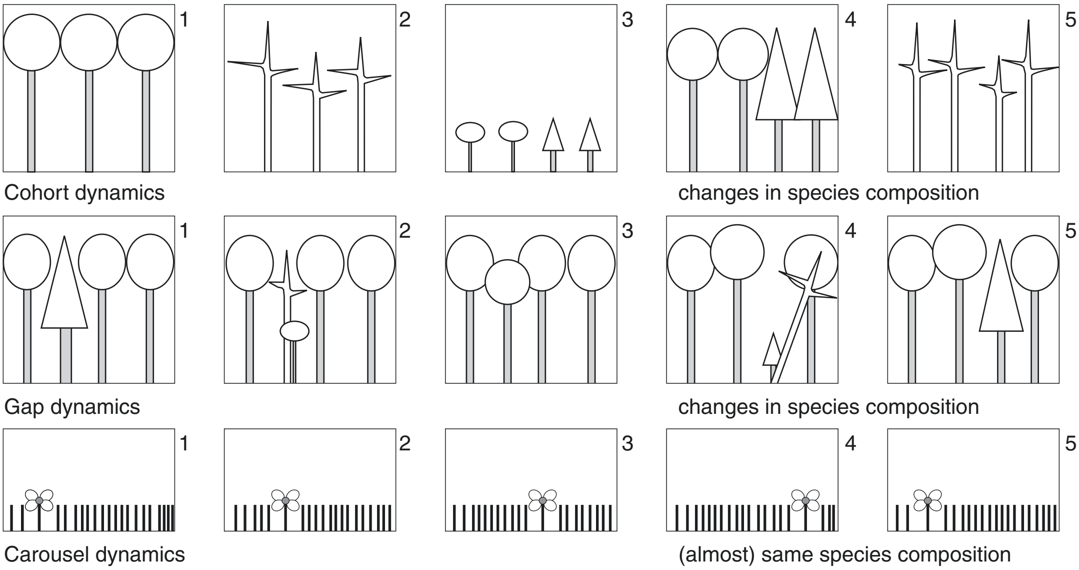


Fig. 17.39 Developmental phases of different types of plants during changes in vegetation. (after Richter 1997)

lottery principle of species in the community in which all have occupied the same regeneration niche, or a first-come, first-served approach. Because these species are short lived, the carousel model describes vegetation dynamics in the smallest space and of the shortest duration. Populations of a species are always available, but they are very mobile, and the species composition remains constant. Figure 17.39 compares different spatial and temporal scales of cohort, gap and carousel dynamics schematically.

17.3.2.3 Aspects of Applied Succession Research

The dynamic nature of plant communities has often been identified via bio-indicators. It is assumed that the response of a plant community to disturbances is specific, and perhaps quantifiable. The vitality of species of the plant community and shifts in the species spectrum are measured. Knowledge about the formation of plant communities and their regulation is gained by empirical findings of many succession studies. For instance, pioneer plants with uniform seeds are selected for the greening of open spaces or to stabilise open slopes after road building (Fig. 17.40).

Today, we know about asynchronous vegetation cycles and therefore understand the limits to the practical application of current knowledge of vegetation dynamics. Management recommendations for the maintenance of certain ecosystems also need to be revisited, as do the minimum spatial dimensions of protected areas. Current knowledge of vegetation dynamics helps in the selection of “replacement areas”, where disturbed or lost communities may develop again.

Biomonitoring was developed in order to understand syndynamic processes, to identify damaging influences so that they could be quickly counteracted or minimised. Examples are the indication of air pollution and the eutrophication of water. Vegetation changes resulting from interventions at certain sites can also be recorded by continuous biomonitoring. Multiple scales on the hemeroby (level of naturalness) of spaces for vegetation have been devised. Red List species, loss of species, proportion of annuals and neophytes are important values for structuring vegetation units according to the degree of human intervention. Ultimately, knowledge about vegetation dynamics is applied in attempts to improve areas to be used for agriculture or forestry and to control such attempts. Thus, for example, the application of Ca-containing fertilisers in order to combat the acidification of soils in forests and the effects of herbicide application in vineyards, leading to the loss of endangered species, were assessed in this way.

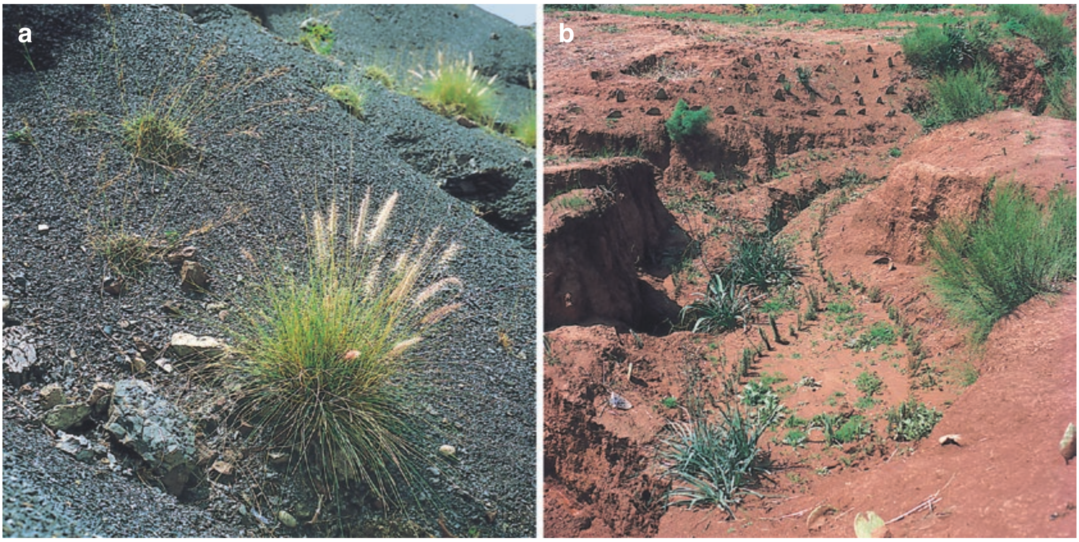


Fig. 17.40 Pioneer plant species are able to start the succession in areas requiring protection, such as those subject to erosion. *Pennisetum setaceum* **a** is a tussock grass with extensive roots that is suitable for the stabilisation of steep slopes (mountains in Yemen Arab Republic). **b** As part of a project to protect against severe degradation of vegetation and soils in the Central Atlas Mountains (Morocco), a mixture of suitable plant species, such as dwarf and brushwood scrubs, dwarf palms and *Opuntia cactus* was used to achieve the initial stages in regeneration of area. (Photos: K. Müller-Hohenstein)

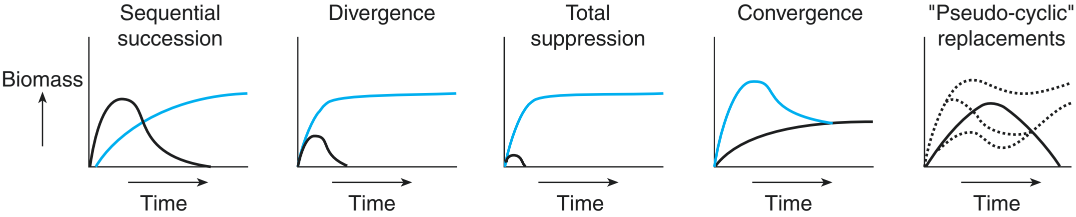


Fig. 17.41 Possible behaviour of two species over the course of succession. (after McCook 1994)

17.3.3 Vegetation Dynamics and Strategy Models

Variability within a single plant can be considerable, growth can be fast or slow, tolerance to shade can be high or low, and dispersal from the parent plant can be far or near, to name a few parameters. Such characteristics, acquired during the course of evolution, enable plants to successfully compete with other individuals and to become established and are often summarised by the term “strategy”. It is defined as the sum of genetically fixed physiological and morphological adaptations required to cope with different environmental conditions, conquer a habitat and persist with optimal use of resources. Individual plants, populations and species are also classified using strategic aspects as plant functional types (Sect. 20.2).

McCook (1994) showed how two plant species with different characteristics may behave in competitive ways (Fig. 17.41). The following basic variants are possible. One species gets suppressed at different temporal rates, both species achieve a similar abundance, or both species become dominant at different times. All strategic models are based on such assumed forms of performance and differ only in the way they are interpreted. External influences are not always considered (e.g. climate change, herbivory). Because overlapping anthropogenic interference is also excluded, the knowledge gained is relatively limited. Other models originate from functional characteristics of the whole ecosystem and ask which of these have changed over time and how. These models usually generalise too much, where some are exclusively descriptive, while others try to make predictions or attempt to explain current dynamic processes. Ultimately, no single model provides a comprehensive explanation for the empirical findings from the field, at least none has to date.

17.3.3.1 Initial Floristic Composition

The model of initial floristic composition (IFC), based on Egler (1954), is still used to describe the sequence of successions because it represents sequences that are physiognomically recognisable. According to this model, the complete set of species is present from the beginning, and a sequence of starts results in only a few of these species becoming dominant. Figure 17.42 shows the course of growth for six species from germination via establishment of seedlings, through to the vegetative stage, and finally to the reproductive growth phase. Species 1–4 are relatively short-lived therophytes to short-lived woody species, and species 5 and 6 are long-lived, shade-tolerant species. When the latter species are fully developed, the short-lived ones are no longer able to persist. IFC is still accepted as a descriptive model of primary as well as of secondary successions. There are no generally valid succession sequences because of external disturbances and stress situations caused by them. Egler introduced this concept of gradual change as the centre point and prefers the term "development of vegetation" to that of succession. The limitation of such a model is the exclusion of the propagule influx.

17.3.3.2 r and K Strategies

The concept of r and K selection is based on models of population growth in animals, which was developed by MacArthur and Wilson (1967). This concept is used by botanists and zoologists to stress particularly contrasting characteristics of species. "**r**" is the intrinsic rate of population growth or rate of reproduction, while "**K**" represents the carrying capacity or maximum population size. Essentially, the r and K concepts stress the allocation patterns of limiting resources that are inversely related.

***r*-strategists** form a large number of very small seeds representing a high proportion of their phytomass; they also tend to have an efficient mechanism for dispersal and grow fast without high biomass accumulation. This leads to a much quicker time to reach reproductive maturity, and such plants also tolerate long periods of seed dormancy, but the seeds can be activated very quickly. Species that are r-strategists are **short-lived opportunists** that are able to become established faster in their environment than shade-tolerant species, but they are inferior competitors to *K*-strategists.

***K*-strategists** are **long-lived** and slow-growing and accumulate large amounts of biomass over time. For this reason, and because they are shade tolerant, they are able to outcompete r-strategists.

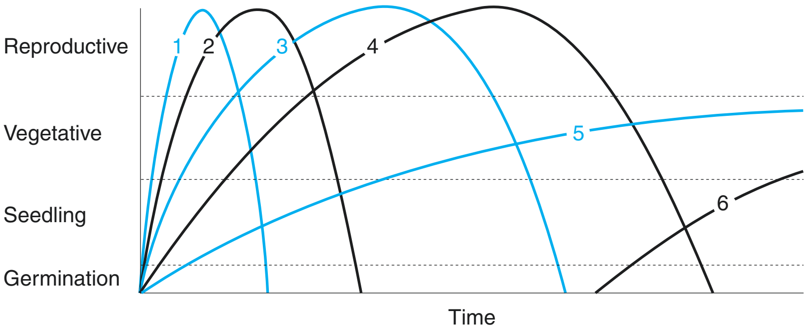


Fig. 17.42 Scheme of initial floristic composition model of succession. The curves show the behaviour of six different species. (after Finegan 1984)

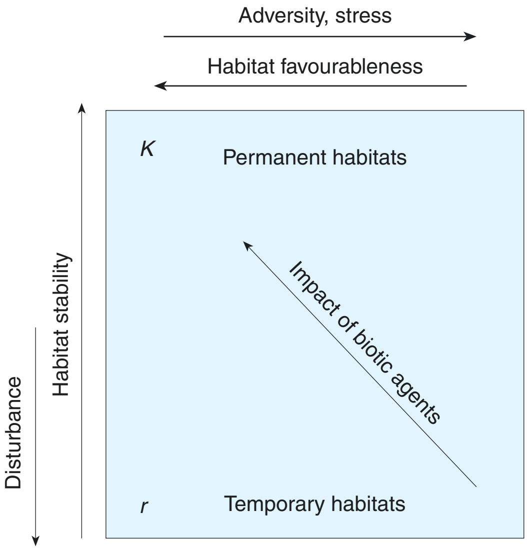


Fig. 17.43 Model of *K*- and *r*-selection considering effects of stress. (after Brown 1985 and Brown and Southwood 1987)

They invest less into reproduction and will typically produce a small number of seeds that are larger than those of *r*-strategists. However, they need to form metabolites for defence to protect long-lived leaves and other organs from herbivory. In terms of successional stages, it is easy to determine that early stages are dominated by *r*-strategists, while later stages are dominated by *K*-strategists. On fallow land, for example, annual and biennial species are replaced over time by shrubs, which are then taken over by trees.

The aforementioned characteristics are accepted as important trade-offs, but a continuum is seen between the extreme positions of *r*- and *K*-strategists. This continuum also indicates not only that disturbed habitats are colonised by *r*-strategists in the short-term (Fig. 17.43) but also that those habitats permanently dominated by *K*-strategists do not necessarily allow stress-free growth. With the requirement for **stress tolerance**, a further strategy type is indicated.

17.3.3.3 Strategy Types of Grime (C-S-R Model)

Grime (1974) and Grime et al. (1988) worked out one of the most well-known models of vegetation dynamics: the **triangle model of primary ecological strategies**. Stress tolerance, adaptation to unfavourable conditions and reaction to disturbance missing in the r/K strategy model were regarded as particularly important. Three strategy types were introduced (Sect. 19.3):

Competitor strategist (C): long-lived, competitive species on favourable sites without limitation of resources and almost stress free. They use resources particularly well, often possess storage organs and show considerable plasticity in root and shoot formation, continuously produce leaves that live for only a short time, and have low seed production. These are perennial herbs, shrubs and trees, which form in mid to late successional stages.

Stress-Tolerant Strategist (S): species adapted to unfavourable sites with limited or poor availability of resources (e.g. inadequate light, drought, nutrient deficiency, frequent frosts). They are long-lived, but with low productivity and reproductive rates and are often restricted to sites with little or no competition. Extremely stress-tolerant species are lichens on cold and dry sites.

Ruderal Strategist (R): short-lived, usually herbaceous species with fast growth rates and high seed production, usually self-pollinated with rapid seed ripening and dispersal, disturbance-tolerant opportunists and pioneers, but weak competitors. Therefore, they grow on sites with frequent, natural disturbances.

However, it is difficult to classify many plant species into only one of these three strategies. Intermediates are frequently observed, where plants with characteristics of several strategic types in different combinations are possible. On favourable sites where competitor strategists should dominate, C-R transition forms are found if the favourable conditions are temporarily disturbed, for example, by mowing meadows. Stress-tolerant competitor strategists (C-S) are long-lived species; for example, many tree species of nemoral forests have adapted to non-optimum sites. Stress-tolerant ruderal strategists (S-R) grow on unfavourable sites that are often disturbed. Included is also an intermediate type (C-S-R) combining several strategies and may also occur in temporal sequence within the same species.

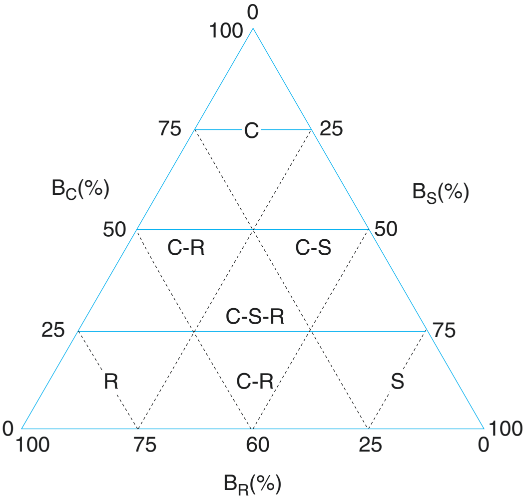


Fig. 17.44 C-S-R diagram of different types of strategy according to Grime. C competitor species; S stress-tolerant species; R ruderal and intermediate types with relative importance of competition (B_C), stress (B_S) and disturbance (B_R). (after Grime et al. 1988)

Grime et al. (1988) attributed life forms to some of his strategy types and included them in areas of his so-called **strategic triangle** (Fig. 17.44). These strategy types are linked to succession sequences, assuming different productivities. On productive sites, development proceeded from ruderals via competitively strong types to those plants with competitive-stress strategies. This applies in Central Europe to beech forests on limestone, where on unproductive sites the final stage is determined by stress-tolerant species. The more productive the site, the higher the proportion of competitively strong species in the mid-successional period. The intensity of competition increases with increasing productivity at the site. However, Tilman (1990) argues against this conclusion.

17.3.3.4 Resource Ratio Model of Tilman

All plant species are limited in their distribution by resources, which are often difficult to acquire but are required for survival. A species is deemed successful in competition for such a **limiting resource** if it is able to reduce the level of nutrients to the lowest level (called **R***), resulting in competitive exclusion (Sect. 19.3). Tilman (1982) developed this model to describe the growth of algae, while for terrestrial systems the assumption is made that the most important limiting resource is within the soil (typically nitrogen) or is light. Any limitation in either of these resources will lead to increased stress within the plant. Often, these resources are inversely related, that is, a low nitrogen supply is typically associated with favourable light conditions, and low light levels (in the understorey) are commonly found at sites with favourable conditions for plant nutrition. Gradients between those two extremes lead to succession stages where plants replace each other according to their demands and their specific competitiveness. Each species grows fastest and reproduces best with the resources to which it is best adapted and where it can outcompete other species. Sufficient root biomass is very important for obtaining sufficient nutrients in the soil, but also sufficient above-ground biomass is essential for light capture by producing leaves. In primary succession, species able to cope with a poor nitrogen supply typically exclude species that require a great deal of nitrogen. As time passes, however, soil nutrition gradually improves thanks to mineralisation and nitrogen input into the system. Now, species able to cope with less light are more competitive. This hypothesis is the basis of the resource ratio model or the nutrient-light relation model.

Simpler than the ideas of this model are those of the nutrient-colonisation and light-colonisation models, or the “competition-colonisation trade-off”. The former again applies to nutrient-limited habitats. Colonists producing many seeds, which they are able to disperse quickly, are initially successful. However, they are weak in the competition for nutrients, and thus species that allocate their resources in such a way as to establish their rooting system to gain more nutrients are favoured. The corresponding situation applies to nutrient-rich habitats for light as the limiting factor. These interactions for five grass species demonstrating their ability for competition and colonisation are shown in Fig. 17.45.

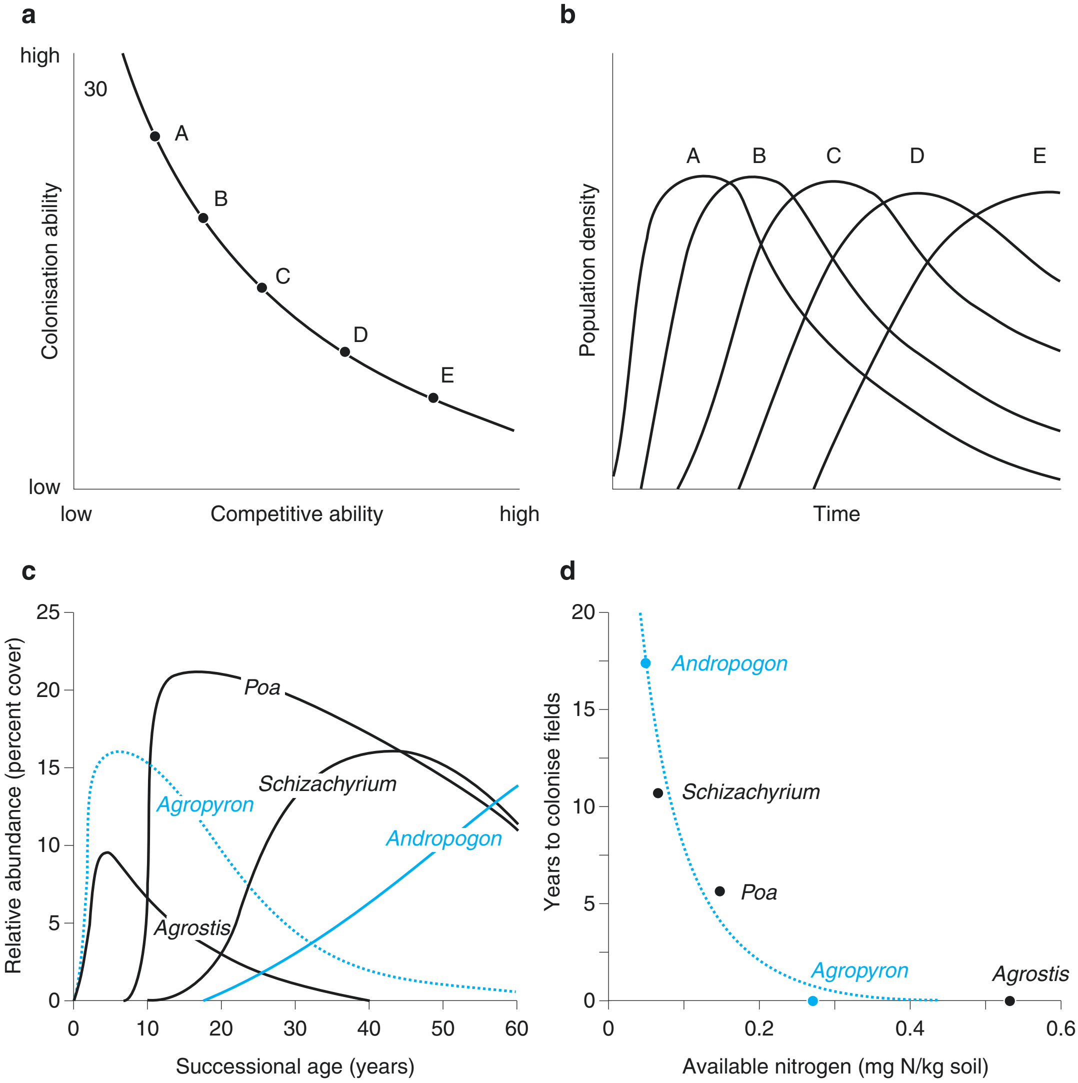


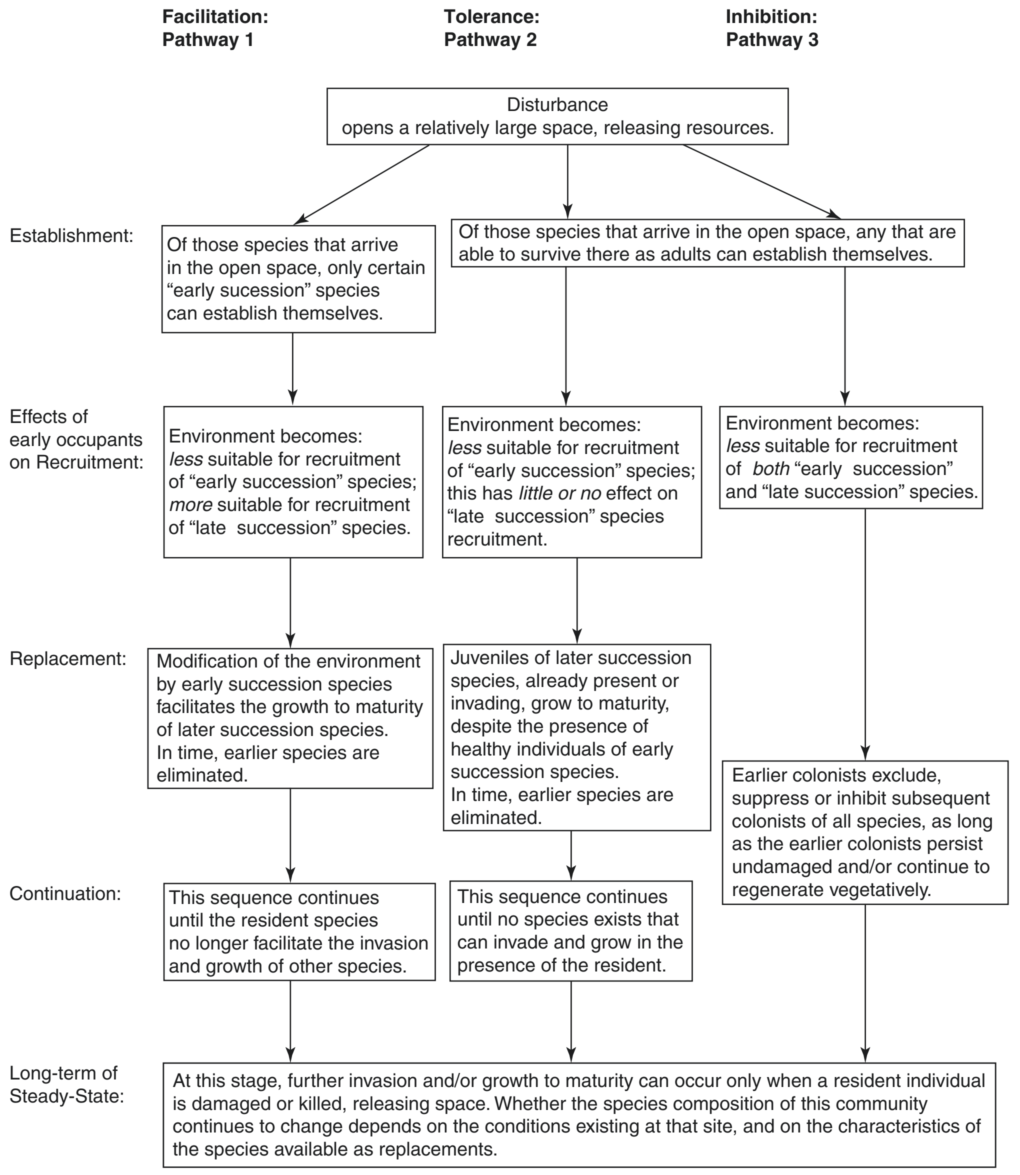
Fig. 17.45 Relationship between competition and colonisation capability. **a** Curve represents a hypothetical interspecific trade-off between competitive ability. Each point on this curve could represent a distinct plant species. The five points shown are for species A, B, C, D, and E. **b** Species A–E will have qualitative successional dynamics because of their colonisation–competition trade-offs. **c** Successional dynamics of dominant grass species of Cedar Creek Natural History Area (after Tilman 1988). **d** Observed interdependence of competitive ability and colonisation rates for five dominant grasses of Cedar Creek Natural History Area. R* for nitrogen is the observed level to which monocultures of each species reduced the concentration of dissolved ammonium and nitrate on fertile, low-nitrogen soils (Tilman and Wedin 1991a). Lower R* values correspond to a greater competitive ability (Tilman and Wedin 1991b). The colonisation rate is inversely related to the years each species required to colonise newly abandoned fields at Cedar Creek Natural History Area. (after Tilman 1994)

From these models, the consequences for biodiversity within areas may be derived. The more heterogeneous a space to be colonised is—particularly regarding its environmental conditions (e.g. nutrients, light, water) and natural and anthropogenic disturbances—the more species are able to coexist. It follows that with increasing heterogeneity not only does biodiversity increase but, in the habitat, resources should ideally be available at intermediate levels (Sect. 20.3).

17.3.3.5 Facilitation-Tolerance-Inhibition Models of Connell and Slatyer

Competition for resources may change by type and amount over time, especially when disturbance regimes are considered. Connell and Slatyer (1977) pointed out that the driving force behind vegetation dynamics and stress is the issue of scale, where certain dynamics only occur at certain scales. As such, three models, or **succession pathways**, are considered (Box 17.5):

Box 17.5: Three "Succession Pathways" of Connell and Slatyer (1977) (after McCook 1994)



Disturbance opens a relatively large space, releasing resources.

Of those species that arrive in the open space, only certain "early sucession" species can establish themselves.

Of those species that arrive in the open space, any that are able to survive there as adults can establish themselves.

Environment becomes: *less* suitable for recruitment of "early succession" species; *more* suitable for recruitment of "late succession" species.

Environment becomes: *less* suitable for recruitment of "early succession" species; this has *little or no* effect on "late succession" species recruitment.

Environment becomes: *less* suitable for recruitment of *both* "early succession" and "late succession" species.

Modification of the environment by early succession species facilitates the growth to maturity of later succession species. In time, earlier species are eliminated.

Juveniles of later succession species, already present or invading, grow to maturity, despite the presence of healthy individuals of early succession species. In time, earlier species are eliminated.

Earlier colonists exclude, suppress or inhibit subsequent colonists of all species, as long as the earlier colonists persist undamaged and/or continue to regenerate vegetatively.

This sequence continues until the resident species no longer facilitate the invasion and growth of other species.

This sequence continues until no species exists that can invade and grow in the presence of the resident.

At this stage, further invasion and/or growth to maturity can occur only when a resident individual is damaged or killed, releasing space. Whether the species composition of this community continues to change depends on the conditions existing at that site, and on the characteristics of the species available as replacements.

Facilitation model: Facilitation is understood as the "promotion" or "enabling" of other species, starting from the assumption that the first colonists change site conditions over the course of time autogenically in such a way (e.g. change in substrate, formation of humus) that colonisation by more demanding species is stimulated. This is usually linked to the displacement of the first colonists as they become unable to cope with the competitive advantage of the incoming species.

Tolerance model: Late successional species are neither stimulated nor inhibited. However, they are only able to establish themselves if previously established individuals die or are removed, leaving an area to invade. The species now present compete with one another and behave similarly to the resource ratio model of Tilman, where species with lower R* gain dominance.

Inhibition model: Earlier colonists suppress or inhibit subsequent invaders, which will only be able to become established in the event of a disturbance or by the creation of open space for short time spans due to an individual's death and not because of their competitive advantage.

All three models have been tested in field experiments. The facilitation model may be observed in primary successions, where pioneer species prepare the substrate, as well as following disturbance, because the succession is thrown back into an earlier phase. Both of the other model versions were tested in later, species-rich successional stages. The final steady-state stage is regarded as relatively stable, but cyclical dynamics are not excluded.

Also, the question of stability is taken into consideration. Consequently, succession is regarded as a balancing reaction of a "stable" system that has been heavily disturbed. The spatial and temporal extent of the disturbance as well as their type and intensity are decisive for the following new initial stage of succession.

17.3.4 Vegetation Dynamics and Influence of Animals

At any time during succession, two important influences by animals must be taken into account (Sect. 19.4). The spectrum of species may be changed by herbivory, or at least the conditions for competition are changed. This is rarely fully taken into account because **herbivores** often eat seeds (granivores) and seedlings, and the extent of such disturbance is difficult to measure. Often it is a matter of speculation as to how vegetation would have developed without herbivory. However, **animals** are also **vectors for propagules** and, thus, for the distribution of species, and they participate decisively in the formation of spatial patterns and the composition of vegetation units. In addition, animals change site conditions by their excrement and by their mechanical activities and soil disturbance.

There is much evidence that animals, too, exhibit distinct dynamics. In the initial stages of succession, arthropod herbivores dominate, with 93% of all insect species; however, these proportions drop drastically within older successional stages (51%) and even more so in forest communities (44%). During the initial stages, sap-sucking phytophages make up half of that population, later only a quarter. Macroinvertebrates and predators associated with them increase with the age of the succession.

Brown and Southwood (1987) tried to derive from these observations basic adaptation strategies for plants and animals during succession (Fig. 17.46). They concluded that faunistic partners in the early stages of succession are usually opportunists (*r*-strategists) investing their resources in their reproduction. Many insects are able to fly, promising fast colonisation. The phytophages are mostly generalists, and food webs are rather simple. In the mid-successional stage, secondary consumers are also represented among the animals, particularly insectivores. Food webs and the structural organisation of the habitat become more complex. Few of the occurring

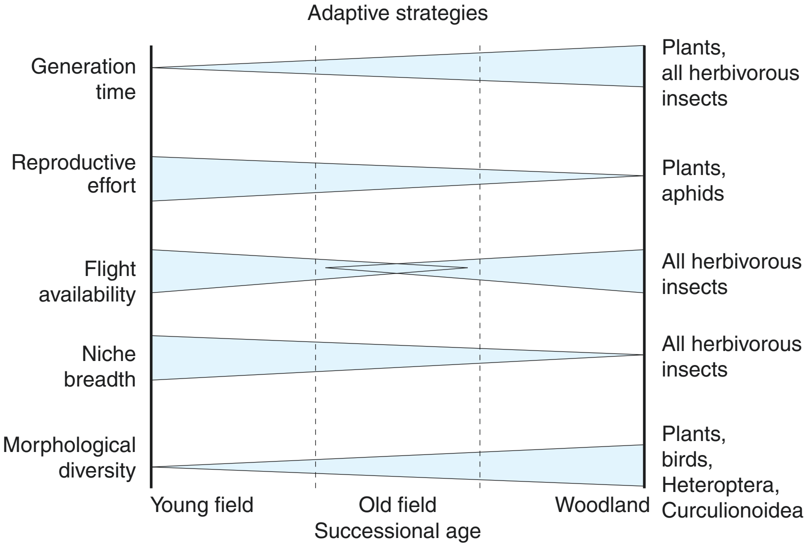


Fig. 17.46 Adaptive strategies of plants and animals during secondary succession. (after Brown and Southwood 1987)

insects have wings, and the invertebrates are uniformly distributed. The high structural diversity of vegetation in the late successional phase begets a large number of niches for specialists. Morphological and trophic diversity in invertebrates (particularly insects) and vertebrates (particularly birds) is high, and *K*-strategists dominate even for animals.

17.3.5 Further Aspects for Understanding Vegetation Dynamics

In addition to the concepts of vegetation dynamics mentioned so far, other ideas that incorporate the enormous complexity of ecosystems could be discussed, for example, those concerning **convergence** and **divergence** in the development of successions (Leps and Rejmanek 1991), the **continuum concept** by Austin (1985) or the discussion of **chaos theory** and **non-linear systems** (Stone and Ezrati 1996). These models, as well as those with partially overlapping concepts covered previously, show that it is not possible to describe all aspects of vegetation dynamics with "one simple formula". Complex processes and patterns of vegetation dynamics may only be generalised or modelled to a certain extent. Descriptive models of the sequence of individual species are accepted, but they explain little. Also, little emphasis is placed on the fact that a species performs differently in juvenile stages than in older stages. As summarised by Bazzaz (1990: 258), "Despite much progress in modelling succession, the tension between simplicity of models for prediction and complexity to include all relevant parameters remains unsolved."

A path towards a better understanding of processes and mechanisms of vegetation dynamics should integrate previous and new information from experimental approaches. Note should be made of different spatial and temporal scales, as well as of the organisational hierarchies of plants—individual, species, population, community. Recently, dynamic simulation models have been used to describe vegetation dynamics. In southern Ecuador, Dislich et al. (2009) used the FORMIND model to simulate the dynamics of tropical mountain forests and regarded this model as being well adapted to investigate disturbances to forest structure and species composition. The empirical results of long-term studies should be used for verification. For example, the results obtained by Schreiber (1995) on very detailed succession studies over more than 20 years (on fallow land) do not fit into any succession model. This means that succession can hardly be exactly predicted, and planning based on such predictions is risky.

17.4 Ecological Stability of Plant Communities and Disturbances

The topics of succession and cyclical vegetation dynamics touch on questions of the "**stability**" of plant communities and whole ecosystems, as well as the concept of **ecological equilibrium**, sometimes naively termed the "balance of nature". Much controversy continues to surround this complex topic, particularly in relation to the definitions of stability and of the characteristics required for stability (Grimm et al. 1992). Temporal and spatial scales are often not considered sufficiently: stability is related to momentary conditions, years or centuries, of plant communities considering a span of only a few square centimetres up to many square kilometres. In all cases, stability/instability is linked to species interactions and demographic stochasticity (internal sources) or disturbance, environmental change and stress (external sources). The relations between stability and diversity or complexity are discussed in Sect 20.4.

Generally, definitions of ecological stability are linked to a system capable of maintaining its structures and functions over the long-term and that is properly used by humans. Population sizes of species may fluctuate little around a mean value, and turnover of species is possible to a limited extent (but not that of life forms or functional groups). Functional relations, such as within food webs, and the many different niches and feedback mechanisms in a system strongly determine stability. Theoretically, **stability** may thus be explained via the sum of all functional connections within a system. It is a dynamic concept that also includes the stability of processes. Stable systems react to disturbance and return to the initial stage by self-regulation. Ecological stability includes cyclical changes, but not successions. In contrast, a labile system is not able to withstand changing external influences.

There is a clear differentiation between complexity and stability. For the complexity in a system, the number of species**, connectance, interaction strength** and the **evenness** of species distribution are most important. Several **components of stability** may be distinguished as additional variables of interest that could be applied to species abundances, species composition or ecosystem properties and processes within plant communities (Pimm 1984):

- **Qualitative stability**: property of a system that returns to its original state after a perturbation.
- **Resistance**: a measure of the ability of a system to maintain its original state in the face of an external disturbance or perturbation.
- **Resilience**: a measure of the speed at which a system returns to its original state after a perturbation.
- **Robustness**: a measure of the amount of perturbation that a system can tolerate before switching to another state.
- **Variability**: a phenomenological measure of the magnitude of temporal changes in a system property.
- **Persistence**: a measure of the ability of a system to maintain itself through time.

Disturbance and strain are generally seen as influences that indicate a "situation deviating from the norm" and that lead to stress situations. The extent to which a system can cope with strain depends on the type, intensity, duration and spatial extent of the disturbance (Fig. 17.47).

Gigon (1982) also suggested that ecological stability should not only be related to some vaguely defined "balance". Other stabilising mechanisms, such as inertia, buffer effects, the replacement principle and risk distribution, also affect ecosystems. Important characteristics are the basic dynamic behaviour of ecosystems and the occurrence (or absence) of disturbances. He also states that imbalances and instabilities in nature are just as decisive for evolution as balance and stability. Gigon thus distinguishes between the following aspects:

- **Ecological stability**, which includes the resistance of a system or its ability to return to its original state after a disturbance (resilience).
- **Ecological instability**, where changes after a disturbance cannot be reversed.
- **Ecological lability**, which is a transient phase with a strong disposition to change as a result of disturbance.

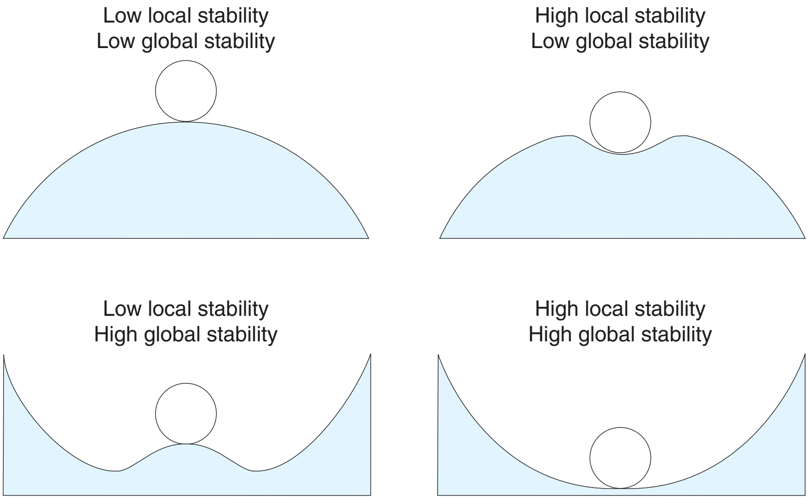


Fig. 17.47 Relations between different spatial scales (local, global) and stability. (after Begon et al. 1999)

Forms of ecological stability may be described as constancy if no actual changes take place (except changes of individual plants) or as resistance if disturbances are buffered (Fig. 17.48). In these cases, the affected systems remain almost unchanged. Other forms where a major dynamic is apparent but the original state is still reached may be called cyclical with regular fluctuations and regeneration cycles or resilient if regeneration takes place after irregularly occurring disturbances.

Forms of instability (Fig. 17.49) lead to changes in the ecological characteristics of a system. These may be triggered endogenously (e.g. in autogenic successions) or exogenously (owing to disturbances). Instability may also result in endogenous or exogenous fluctuations (e.g. insect calamities or fluctuations of agricultural yield because of pathogen attack). These forms of stability and instability may occur in the same system. An individual tree performs differently when it is part of a complete forest; a locally destructive fire may be necessary for the maintenance of the system over a large area. Only a few cases fail to fit into this concept because of insufficient observations or insufficient knowledge of the interfering factors.

Disturbances or perturbations are not necessarily negative for the stability of ecosystems or communities. They can even be essential for the maintenance of a dynamic ecological equilibrium. A boreal larch forest would develop into quite a different system without the regular influence of fires. The same interfering factors may thus have different consequences for a system. Disturbances may be seen as inherent properties of a system or as stochastic external events, the latter caused naturally or anthropogenically. Several years without precipitation in desert regions is an internal disturbance to the system, as is the regulation of population density based on predator–prey relationships, or the dynamics of avalanches in montane ecosystems. It is often difficult to distinguish between disturbances caused by endogenous biological processes and those caused by exogenous environmental influences. Variances in spatial and temporal scales must be taken into account. The scale extends from disturbances by continental drift, on a scale of millions of square kilometres taking millennia to occur, to damage by spring tides, late frosts or extreme herbivory affecting a few hectares over a much shorter time frame.

Finally, it must be stressed that there is no “balance of nature” in the sense of completely stable ecosystems: ecosystems are always dynamic and undergoing change. In addition, no value judgement is implied by the concept of

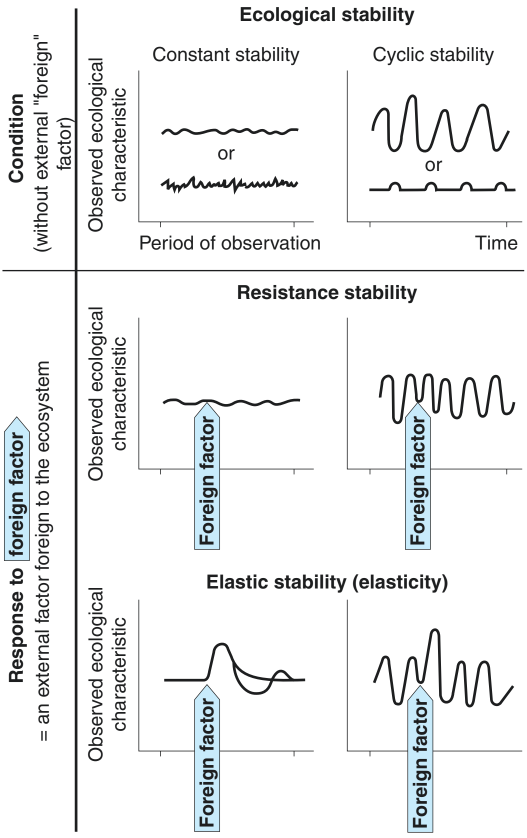


Fig. 17.48 Basic types of ecological stability. These types differ according to the dynamics of chosen characteristics and to the presence or absence of external factors. (after Gigon 1982)

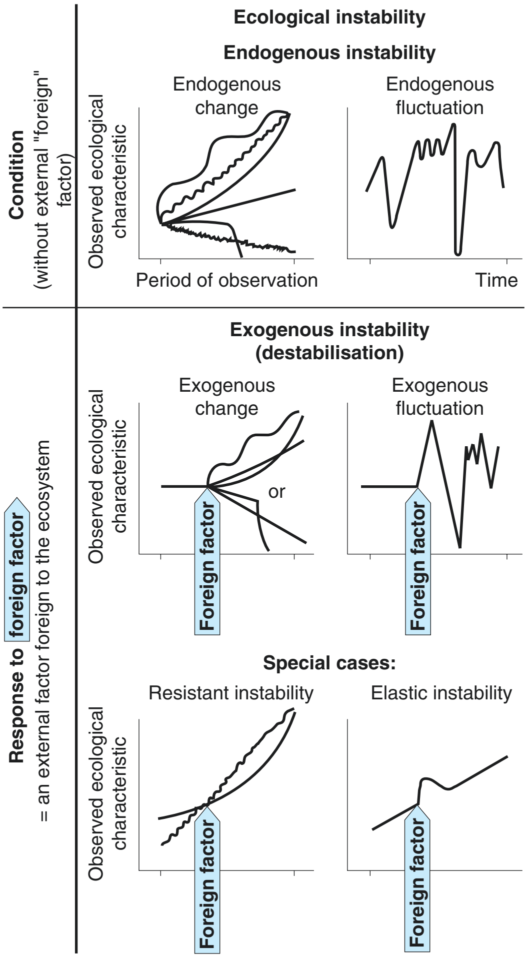


Fig. 17.49 Basic types of ecological instability. These types differ according to the dynamic of chosen characteristics and to the presence or absence of external foreign factors. (after Gigon 1982)

ecological stability. A stable system might be judged differently by a farmer than by an environmentalist, by a skier differently than by a hunter. A **practice-oriented synecology** must include an **evaluation of stability**, which is based on accepted standards and models.

Summary

- Beginning around the algae period/Eophyticum (about 4000 million years ago), the development of plants began with single-cell prokaryotes, which developed into algae. At the beginning of the Palaeozoic Period (about 450 million years ago), the first ferns and gymnosperms evolved. This development was largely influenced by geologic-tectonic and climatic events. It wasn't until the Cretaceous Period (about 95 million years ago) when angiosperms completed the current flora arrangement, which remained quite uniform on the existing continents for a while. A diversification of the flora into plant kingdoms only developed in the Tertiary Period (30 million years ago).
- A worldwide climatic cooling and periodic alternations between cold and warm periods

in the Pleistocene (0.5 million years ago) were responsible for further vegetation change and discrete spatial separation of plant communities. Large disjunctions of species over hundreds of kilometres in latitude and in altitude are geographical vicariants resulting from these climatic fluctuations.
- However, the present-day global and regional differentiation of the plant cover can only be understood by taking into account the direct and indirect, intended or unintentional influences of humans. Completely undisturbed plant communities no longer exist. Plant species are going and will continue to go extinct, and neophytes are spreading and dominating. In this chapter, examples from Central Europe, the Mediterranean, Saharan and tropical environments were presented in detail.
- General models of short- and long-term vegetation dynamics have been elaborated. In short-term dynamics, the daily and seasonal processes are best known (phenology). Long-term dynamics include successions. Of general importance for successional dynamics are developments on bare soil and without any disturbance (primary succession). However, most successions are secondary following more or less regular natural or human-caused disturbances. There are several models for these dynamics (mosaic cycles, cohort dynamics and others). Different strategy models (r and K, CSR, resource-ratio and facilitation-tolerance-inhibition model) can also be related to successional dynamics. In this context the different facets of ecological stability are discussed, which include qualitative stability, resistance, resilience, robustness, variability and persistence.

References

Austin MP (1985) Continuum concept, ordination methods and niche theory. Annu Rev Ecol Syst 16:39–61

Badal E, Bernabeu J, Vernet JL (1994) Vegetation changes and human action from the Neolithic to the Bronze Age (7000–4000 bp) in Alicante, Spain, based on charcoal analysis. Veg Hist Archaeobotany 3:155–166

Barnosky AD, Hadly EA, Bascompte J, Berlow EL, Brown JH, Fortelius M, Getz WM, Harte J, Hastings A, Marquet PA, Martinez ND, Mooers A, Roopnarine P, Vermeij G, Williams JW, Gillespie R, Kitzes J, Marshall C, Matzke N, Mindell DP, Revilla E, Smith AB (2012) Approaching a state shift in Earth's biosphere. Nature 486:52–58

Bar-Yosef O (1998) The Natufian culture in the Levant, threshold to the origins of agriculture. Evol Anthropol 6:159–177

Bazzaz FA (1990) Plant-plant interactions in successional environment. In: Grace JB, Tilman D (eds) Perspectives on plant competition. Academic Press, San Diego

Begon M, Harper JL, Townsend C (1999) Ecology, 3rd edn. Blackwell, Oxford

Bick H (1993) Ökologie. Fischer, Stuttgart

Böhmer HJ, Richter M (1996) Regeneration—Versuch einer Typisierung und zonalen Ordnung. Geogr Rundsch 48(11):626–632

Brown VK (1985) Insect herbivores and plant succession. Oikos 44(1):17–22

Brown VK, Southwood TRE (1987) Secondary succession: patterns and strategies. In: Gray AJ, Crawley MJ, Edwards PJ (eds) Colonisation, succession and stability. Blackwell, Oxford

Bruenig EF (1991) Functions of the tropical rainforest in the local and global context. Gießener Beitr Entwicklungsforsch Reihe 1(19):1–13

Buhk C, Retzer V, Beierkuhnlein C, Jentsch A (2007) Predicting plant species richness and vegetation patterns in cultural landscapes using disturbance parameters. Agric Ecosyst Environ 122:446–457

Chiarucci A, Araujo MB, Decocq G, Beierkuhnlein C, Fernández-Palacios JM (2010) The concept of potential natural vegetation: an epitaph? J Veg Sci 21:1–7

Claussen M (2001) Biogeographical feedbacks and the dynamics of climate. In: Schulze ED (ed) Global biogeochemical cycles in the climate system. Academic Press, San Diego, pp 61–71

Clements FE (1916) Plant succession: an analysis of the development of vegetation. Carnegie Inst., Washington.

Connell JH, Slatyer RO (1977) Mechanisms of succession in natural communities and their role in community stability and organisation. Am Nat 111:1119–1144

Cornelius R (1991) Populationsbiologische Grundlagen des speziellen Artenschutzes. Verh Ges Ökol 20:905–916

Deil U (1995) Vegetation und rezenter Landschaftswandel im Campo de Gibraltar (Südwestspanien) und im Tangerois (Nordwestmarokko). Geoökodynamik 16:109–136

Deil U (1997) Zur geobotanischen Kennzeichnung von Kulturlandschaften—Vergleichende Untersuchungen in Südspanien und Nordmarokko. Erdwissenschaftliche Forschung 36, Wiesbaden Stuttgart

Deil U, Müller-Hohenstein K (1984) Fragmenta Phytosociologica Arabiae-Felicis I: Eine Euphorbia balsamifera-Gesellschaft aus dem jemenitischen Hochland und ihre Beziehungen zu makaronesischen Pflanzengesellschaften. Flora 175:307–326

Deil U, Müller-Hohenstein K (1985) Beiträge zur Vegetation des Jemen. I. Pflanzengesellschaften und Ökotopgefüge der Gebirgstihamah am Beispiel des Beckens von At Tur (J.A.R.) Phytocoenologia 13:1–102

Dierschke H (1994) Pflanzensoziologie. Grundlagen und Methoden. Ulmer, Stuttgart

Dislich C, Günther S, Homeier J, Schröder B, Huth A (2009) Simulating forest dynamics of a tropical mountain forest in South Ecuador. Erdkunde 63:347–364

Dotterweich M (2008) The history of soil erosion and fluvial deposits in small catchments of Central Europe: deciphering the long-term interaction between humans and the environment—a review. Geomorphology 101:192–208

Egler FE (1954) Vegetation science concepts I. Initial floristic composition, a factor in old-field vegetation development. Vegetatio 4:412–417

Ellenberg H (2009) Vegetation ecology of Central Europe, 4th edn. Cambridge University Press, Cambridge

Ellis CD, Goldewyik KK, Siebert S, Lightman D, Ramakutty N (2010) Anthropogenic transformation of the biomes, 1700 to 2000. Glob Ecol Biogeogr 19:589–606

Elton CS (1958) The ecology of invasion by animals and plants. Methuen, London

Finckh M (1995) Die Wälder des Villarrica-Nationalparks (Südchile)—Lebensgemeinschaften als Grundlage für ein Schutzkonzept. Diss Bot 259:1–181

Finegan B (1984) Forest succession. Nature 312:109–114

Firbas F (1949–1952) Waldgeschichte Mitteleuropas. 3 Bd. Fischer, Jena

Gallimore R, Jakob R, Ktzbach J (2005) Coupled atmosphere-ocean-vegetation simulations for modern and mid-holocene climates: role of extratropical vegetation cover feedbacks. Clim Dyn 25:755–776

Galloway JN, Dentener FJ, Capone DG, Boyer EW, Howarth RW, Seitzinger SP, Asner GP, Cleveland CC, Green PA, Holland EA, Karl DM, Michaels AF, Porter JH, Townsend AR, Vörösmarty CJ (2004) Nitrogen cycles: past, present, and future. Biogeochemistry 70:153

Gigon A (1982) Typologie und Erfassung der ökologischen Stabilität und Instabilität mit Beispielen aus Gebirgsökosystemen. Verh Ges Ökol 12:13–30

Gleason HA (1926) The individualistic concept of the plant association. Bull Torrey Bot Club 53:7–26

Goudie A (1994) Mensch und Umwelt. Spektrum, Heidelberg

Grime JP (1974) Vegetation classification by reference to strategies. Nature 250:26–31

Grime JP, Hodgson JP, Hunt R (1988) Comparative plant ecology. Unwin, London

Grimm V, Schmidt E, Wissel C (1992) On the application of stability concepts in ecology. Ecol Model 63:143–161

Hansen MC, Potapov PV, Moore R, Hancher M, Turubanova SA, Tyukavina A, Thau D, Stehman SV, Goetz SJ, Loveland TR, Kommareddy A, Egorov A, Chini L, Justice CO, Townshend JRG (2013) High-resolution global maps of 21st-century forest cover change. Science 342:850–853

Harrison SP, Prentice IC (2003) Climate and CO_2 controls on global vegetation distribution at the last glacial maximum analysis based on palaeovegetation data, biome modeling and palaeclimatic simulations. Glob Change Biol 9:983–1004

Hasel K, Schwartz E (2006) Forstgeschichte. Ein Grundriß für Studium und Praxis, 3rd edn. Kessel, Remagen

Hellden U (1991) Desertification—time for an assessment? Ambio 20:372–383

Hillmann GC, Hedges R, Moore A, Colledge S, Pettitt P (2001) New evidence for Lateglacial cereal cultivation at Abu Hureyra on the Euphrates. The Holocene 11:383–393

Holzhauser H, Magny M, Zumbühl JZ (2005) Glacier and lake-level variations in west-central Europe over the last 3500 years. The Holocene 15:789–801

Hooper DU, Adair EC, Bradley JC, Byrnes JEK, Hungate BA, Matulich KL, Gonzales A, Duffy JE, Gamfeldt L, O'Connor MI (2012) A global synthesis reveals biodiversity loss as a major driver of ecosystem change. Nature 486:105–108

Huston MA (1979) A general hypothesis of species diversity. Am Nat 113:81–101

Ibrahim FN (1988) Ecological imbalance in the Republic of the Sudan—with reference to desertification in Darfur, Bayreuther Geowissenschaftliche Arbeiten, vol 6. Druckhaus Bayreuth Verlagsgessellschaft, Bayreuth

IPCC—Intergovernmental Panel on Climate Change (2013) Climate change 2013: the physical science basis. Contribution of Working Group I to the 5th Assessment Report. Cambridge University Press, Cambridge

Jäger EJ (1977) Veränderungen des Artenbestandes von Floren unter dem Einfluß des Menschen. Biol Rdsch 15(5):287–300

Jochimsen ME (1993) Sukzession. In: Kuttler W (ed) Handbuch zur Ökologie. Analytica, Berlin, pp 418–424

Joerin UE, Stocker TF, Schlüchter C (2006) Multicentury glacier fluctations in the Swiss Alps during the Holocene. Holocene 16:697–704

Kaufman D, McKay N, Kiefer T, von Gunten L (2013) A regional view of global climate change. IGBP's Global Change magazine, Issue 81

Kerr RA (2013) Humans fueled global warming millennia ago. Science 342:918

Klötzli F (1993) Ökosysteme, 3. Aufl. Fischer, Stuttgart

Knorr W, Schnitzler KG (2006) Enhanced albedo feedback in North Africa from possible combined vegetation and soil-formation processes. Clim Dyn 26:55–63

Kottke I, Setaro S, Haug I, Herrera P, Cruz D, Fries A, Gawlik J, Homeier J, Werner FA, Gerique A, Suárez JP (2013) Mycorrhiza networks promote biodiversity and stabilise the tropical mountain rain forest ecosystem: perspectives for understanding complex communities. In: Bendix J, Beck E, Bräunig A, Makeschin F, Mosandl R, Scheu S, Wicke W (eds) Ecosystem services, biodiversity and environmental change in a tropical mountain ecosystem of South Ecuador, Ecological studies, vol 221. Springer, Berlin, pp 187–203

Kreeb KH (1983) Vegetationskunde. Ulmer, Stuttgart

Kreyling J, Jentsch A, Beierkuhnlein C (2011) Stochastic trajectories of succession initiated by extreme climatic events. Ecol Lett 14:758–764

Larcher W (2003) Physiological plant ecology—ecophysiology and stress physiology of functional groups, 3rd edn. Springer, Berlin

Le Floch E, Le Houerou HN, Mathez J (1990) History and patterns of plant invasion in northern Africa. In: Di Castri F, Hansen AJ, Debussche M (eds) Biological invasion and the Mediterranean basin. Kluwer, Dordrecht, pp 105–133

Le Houerou HN (1997) Climate, flora and fauna changes in the Sahara over the past 500 million years. J Arid Environ 37:619–647

Leps J, Rejmanek M (1991) Convergence or divergence: what should we expect from vegetation succession? Oikos 62(2):261–264

Lohmeier W, Sukopp H (1992) Agriophyten in der Vegetation Mitteleuropas. Schriften Vegetationskde 25

Loidi J, Fernández-González F (2012) Potential natural vegetation: reburying or reboring? J Veg Sci 23:596–604

Lövei GL (1997) Global change through invasion. Nature 388:627–628

MacArthur RH, Wilson EO (1967) Biogeographie von Inseln. Wissenschaftliche Taschenbücher, Goldmann, München

MacDonald GM, Velichko AA, Kremenetski CV, Andreev A (2000a) History and climate change across northern Eurasia. Quat Res 53:302–311

MacDonald GM, Velichko AA, Kremenetski BOK, Goleva AA, Andreev AA, Cwynar LC, Riding T, Forman SL, TWD E, Aravena R, Hammarlund D, Szeicz JM, Gattaulin VN (2000b) Holocene treeline history and climate change across northern Eurasia. Quat Res 53:302–311

Mackey RL, Currie D (2001) Diversity-disturbance relationship: is it generally strong and peaked? Ecology 82:3479–3492

Marcott SA, Shakin JR, Clark PU, Mix AC (2013) A reconstruction of regional and global temperature for the past 11,300 years. Science 339:1198

McCook LJ (1994) Understanding ecological community succession. Vegetatio 110:115–147

Miles J (1987) Vegetation succession: past and present perceptions. In: Gray AJ, Crawley MJ (eds) Colonisation, succession and stability. Blackwell Scientific, Oxford, pp 1–29

Mora C, Tittensor DP, Adl S, Simpson AGP, Worm B (2011) How many species are there on earth and in the ocean? PLoS Biol 9(8):e1001127.

Müller-Dombois D (1995) Biological diversity and disturbance regimes in island ecosystems. In: Vitousek PM, Loope LL, Andersen H (eds) Islands. Springer, Berlin, pp 163–175

Müller-Hohenstein K (1973) Die anthropogene Beeinflussung der Wälder im westlichen Mittelmeerraum unter besonderer Berücksichtigung der Aufforstungen. Erdkunde 27:55–68

Müller-Hohenstein K (1991) Der Mittelmeerraum. Ein vegetationsgeographischer Überblick. Geogr Rundsch 43(7–8):409–411

Müller-Hohenstein K (1993) Auf dem Weg zu einem neuen Verständnis von Desertifikation—Überlegungen aus der Sicht einer praxisorientierten Geobotanik. Phytocoenologia 23:499–518

Murphy GEC, Romanuk TN (2014) A meta-analysis of declines in local species richness from human disturbances. Ecol Evol 4:91–103

Neumann K (1988) Die Bedeutung der Holzkohlenuntersuchungen für die Vegetationsgeschichte der Sahara—das Beispiel Fachi/Niger. Würzb Geogr Arb 69:71–85

Nicholson SE (1978) Climatic variations in the Sahel and other African regions during the past five centuries. J Arid Environ 1:3–24

Odum EP (1980) Grundlagen der Ökologie. Bd 1. Thieme, Stuttgart

Overbeck F (1975) Botanisch-geologische Moorkunde unter besonderer Berücksichtigung der Moore Nordwestdeutschlands als Quellen zur Vegetations-, Klima- und Siedlungsgeschichte. Wacholtz, Neumünster

Pickett STA, White PS (1985) The ecology of natural disturbance and patch dynamics. Academic Press, New York

Pignatti E, Pignatti S (1984) Sekundäre Vegetation und floristische Vielfalt im Mittelmeerraum. Phytocoenologia 12:351–358

Pimm SL (1984) The complexity and stability of ecosystems. Nature 307:321–326

Prentice IC, Jolly D (2000) Mid-Holocene and glacial-maximum vegetation geography of northern continents and Africa. J Biogeogr 27:507–519

Pretzsch H (2005) Diversity and productivity in forests: evidence from long-term experimental plots. In: Scherer-Lorenzen M, Körner C, Schulze E-D (eds) Forest diversity and function. Temperate and boreal systems, vol 176. Springer, Berlin, pp 41–64

Remmert H (ed) (1991) The mosaic-cycle concept of ecosystems. Springer, Berlin

Richter M (1997) Allgemeine Pflanzengeographie. Teubner, Stuttgart

Riera-Mora S, Esteban-Amat A (1994) Vegetation history and human activity during the last 6000 years on the central Catalan coast (northeastern Iberian peninsula). Veg Hist Archaeobotany 3:7–23

Scherer-Lorenzen M, Elend A, Nöllert S, Schulze E-D (2000) Plant invasions in Germany—general aspects and impact of nitrogen deposition. In: Mooney HA, Hobbs RJ (eds) Invasive species in a changing world. Island Press, Washington, DC, pp 351–368

Schmidt G (1969) Vegetationsgeographie auf ökologisch-soziologischer Grundlage: Einführung und Probleme. Teubner, Leipzig

Schmidt W (1993) Sukzession und Sukzessionslenkung auf Brachäckern—neue Ergebnisse aus einem Dauerflächenversuch. Scripta Geobot 20:65–104

Schreiber KF (1995) Renaturierung von Grünland—Erfahrungen aus langjährigen Untersuchungen und Managementmaßnahmen. Ber Tüxen-Ges 7:111–113

Schulze ED, Aas G, Grimm GW, Gossner MM, Walentowski H, Ammer C, Kühn I, Bouriaud O, von Gadow K (2016) A review on plant diversity and forest management of European beech forest. Eur J For Res 135:51–67

Schweingruber F, Poschlod P (2005) Growth rings in herbs and shrubs: life span, age determination and stem anatomy. Forest Snow Landsc Res 79:195–415

Stone L, Ezrati I (1996) Chaos, cycles and spatio-temporal dynamics in plant ecology. J Ecol 84:279–291

Strasburger E, Sitte P (1998) Lehrbuch der Botanik für Hochschulen. Fischer, Stuttgart

Sukopp H (1972) Wandel von Flora und Vegetation in Mitteleuropa unter dem Einfluß des Menschen. Ber Landwirtsch 50(1):112–139

Sukopp H, Wittig R (eds) (1998) Stadtökologie, 2nd edn. Gustav Fischer, Stuttgart

Sun D, Joachimski MM, Wignall PB, Yan C, Chen Y, Jiang H, Wang L, Lai X (2012) Lethally hot temperatures during the early triassic greenhouse. Science 338:366–370

Swift MJ, Anderson JM (1993) Biodiversity and ecosystem function in agricultural systems, Ecological studies, vol 99. Springer, Berlin, pp 15–41

Tilman D (1982) Resource competition and community structure. Princeton University Press, Princeton, NJ

Tilman D (1988) Plant strategies and the dynamic and structure of plant communities. Princeton University Press, Princeton

Tilman D (1990) Constraints and tradeoffs: towards a predictive theory of competition and succession. Oikos 58:3–15

Tilman D (1994) Community diversity and succession: the roles of competition, dispersal, and habitat modification. In: Schulze ED, Mooney HA (eds) Biodiversity and ecosystem function. Springer, Berlin, pp 327–344

Tilman D, Wedin D (1991a) Plant traits and resource reduction for five grasses growing on anitrogen gradient. Ecology 72:685–700

Tilman D, Wedin D (1991b) Dynamics of nitrogen competition between successional grasses. Ecology 72:1038–1049

Tüxen R (1956) Die heutige potentielle natürliche Vegetation als Gegenstand der Vegetationskartierung. Angew Pflanzensoziol 13:5–42

Vitousek M, Mooney HA, Lubchenko J, Melillo JM (1997) Domination of earth's ecosystems. Science 277:494–499

Walter H (1986) Allgemeine Geobotanik. Eugen Ulmer, Stuttgart

Walter H, Straka H (1970) Grundlagen der Pflanzenverbreitung. Bd 3,2. Arealkunde (Floristisch-historische Geobotanik), 2. Aufl. Ulmer, Stuttgart

Wanner H, Beer J, Bütikofer J, Crowley TJ, Cubasch U, Flückiger J, Goosse H, Grosjean M, Joos F, Kaplan JO, Küttel M, Müller SA, Prentice IC, Solomina O, Stocker TF, Tarasov P, Wagner M, Widmann M (2008) Mid- to late Holocene climate change: an overview. Quat Sci Rev 27:1791–1828

Watt AS (1947) Pattern and process in the plant community. J Ecol 35:1–22

WBGU (Wissenschaftlicher Beirat der Bundesregierung Globale Umweltveränderungen) (2000) Welt im Wandel: Erhaltung und nachhaltige Nutzung der Biosphäre. Springer, Berlin

Weiss H, Bradley RS (2001) What drives societal collapse? Science 291:609–610

van der Maarel E (1988) Vegetation dynamics: patterns in time and space. Vegetatio 77:7–19

van der Maarel E, Sykes MT (1993) Small scale species turnover in a limestone grassland: the carousel model and some comments on the niche concept. J Veg Sci 4:179–188

von Wissmann H (1957) Ursprungsherde und Ausbreitungswege von Pflanzen- und Tierzucht und ihre Abhängigkeit von der Klimageschichte. Erdkunde 11:175–193

Wittkamp J, Deil U, Beierkuhnlein C (1995) Sozialstruktur und Dorfvegetation—im Vergleich von Dörfern beiderseits der ehemaligen innerdeutschen Grenze. Erde 126:107–126

Zwölfer H (1978) Mechanismen und Ergebnisse der Co-Evolution von phytophagen und entomophagen Insekten und höheren Pflanzen. Sonderb Naturwiss Ver Hamburg 2:7–50

18

Spatial Distribution of Plants and Plant Communities

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Vegetation mosaic of evergreen gallery riverine forest and dry woodlands of deciduous species in higher elevations in seasonally wet, tropical Ethiopia (Photo: K. Müller-Hohenstein)

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18.1 Introduction

The previous chapter showed how plants and plant communities develop over time and focused on short- and long-term temporal dynamics. These temporal dynamics lead to varying distributional patterns of species and communities. It is the task of **spatial ecology** to recognise such distribution patterns, to describe them, and to mechanistically explain their formation. Recognition and understanding of both the temporal and spatial dynamics of plant communities are indispensable for a thorough comprehension of biotic interactions within ecosystems, which is the topic of discussion in this chapter. The current chapter deals with the ecological basis of plant distribution, followed by a discussion of the relationships between species and area, with a particular emphasis on island biogeography.

18.2 Plant Dispersal

The **life cycle** of sessile plants includes a mobile phase, **propagule dispersal**. Plants will typically use one of the following two strategies: production of (1) **generative propagules**, where the plant produces spores, seeds, fruits, syncarps or even complete plants carrying seeds, and of (2) **vegetative propagules**, which include bulbs, shoots, runners, adventitious buds, parts of rhizomes and clonal growth (Fig. 18.1). Depending on the strategy of the plant in question, the distance travelled

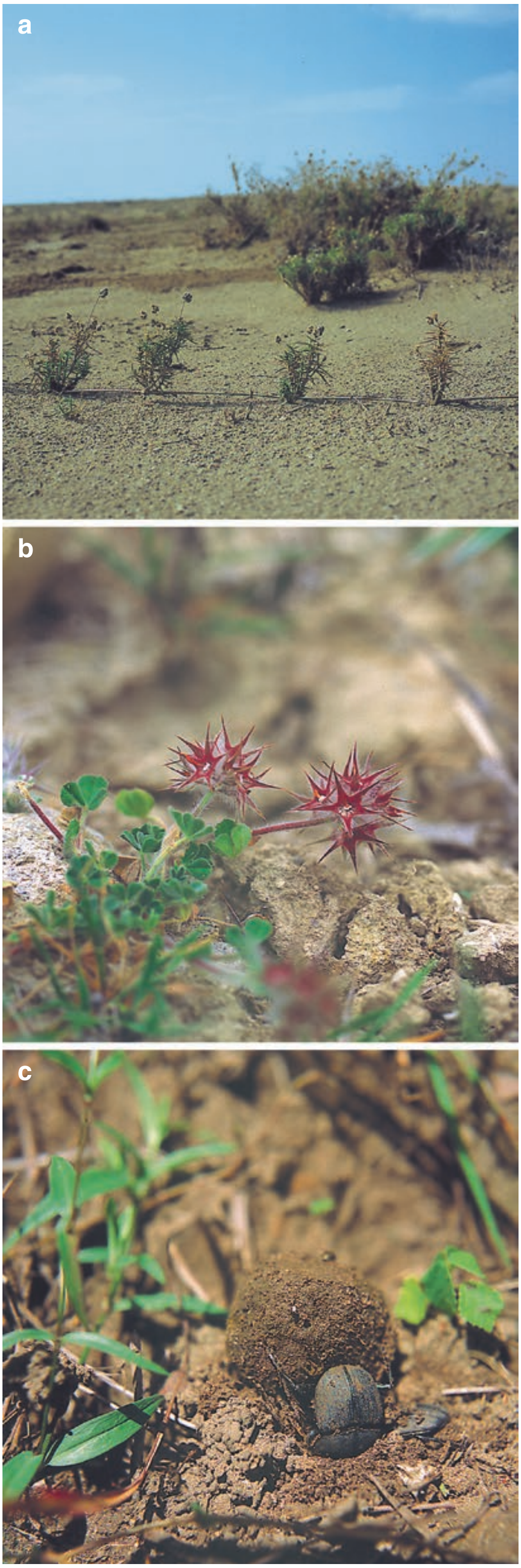


Fig. 18.1 Plants have many different methods of effective dispersal. **a** *Aeloropus littoralis* is a salt-tolerant coastal grass which spreads by vegetative runners (blastochory) as in south-western Arabia. **b** Self-dispersal (autochory) in *Trifolium stellatum* takes a special form (herpochory) with awns on the fruit having hygroscopic characteristics which enables the seed to move over short distances. **c** A special form of secondary animal dispersal (zoochory) is provided by coprochory. Dung beetles (many types of scarabs) collect the droppings of animals (e.g. cattle) and form it into balls. The dung contains seeds that are then buried just below the soil surface, where they may have a chance to germinate (Photos: K. Müller-Hohenstein)

by the propagule will vary significantly and can be influenced through the help of abiotic or biotic factors. The aim of this process is to find a site that will facilitate the establishment and long-term survival of the plant, a so-called **safe site.** Finding a suitable site on which to become established is an extremely important stage in any plant's life cycle, particularly in a highly competitive site. In any case, dispersal is crucial to the future presence of the plant's population and to the plant's capacity to persist in the vegetative community.

Successful plant dispersal is typically improved when propagules possess certain morphological traits that improve their likelihood of finding an ideal site on which to become established. These traits can take advantage of external vectors to facilitate transport, which could include wind, water or even animals.

18.2.1 Traits and Vectors

Propagules are the **functional units** of plants and have adapted over time to be transported by wind, water, animals or through their own means of dispersal. Such traits include, for example, morphological structures on seeds, such as barbs and hooks, which cling to fur or feathers and can be transported long distances by the animal it gets attached to. Lightweight seeds or those possessing samaras (wings) can have significantly increased dispersal distances from the parent plants through wind. Nutritious, fleshy fruits attract animals by their smell, taste and colour. Most of the characteristics of seeds connected with transport are special parts of the pericarp. Some seeds still have adequate resources (coupled with resistant seed coats) for germination even if they have been eaten by animals, and they eventually find an ideal substrate medium (e.g. seeds from *Argania spinosa*, which are eaten by goats). Some **dispersal strategies**, modification and derivation are outlined in Table 18.1. Relationships between propagules and dispersal agents, especially by vertebrates, were compiled by Howe and Westley (1986) (Table 18.2).

Dispersal vectors may change over time depending on environmental conditions. Species that can use multiple dispersal vectors are considered "**polychor**". Many plants do not use only one vector but possess different morphological adaptations to exploit several vectors. The ability to use several strategies improves a plant's chances of finding an ideal site for establishment. In special cases, however, a "secondary" dispersal strategy could prove more important. For example, an African elephant eats its favourite fruit, containing seeds, which are passed later in the day, 20 km from where they were eaten (**primary dispersal**). The surviving seeds are then further dispersed by dung beetles, which transport the seeds over short distances before burying them (**secondary dispersal**) (Fig. 18.1c) (Engel 2000). The importance of "secondary" dispersal is often underestimated. The example of dung beetles shows that the most favourable microsites are often only found in the secondary transport phase. Secondary transport may also lead to a wider range of dispersal.

However, the great variety of plant traits and different means of propagule transport requires a structured overview of the vectors and mechanisms associated with dispersal. Two large groups and many small subgroups are distinguished:

1. Propagation by the plant itself (**autochory**)
2. Propagation by other vectors (**allochory**)

18.2.1.1 Autochory

Over time, plants have evolved various mechanisms to ensure successful dispersal. In its simplest form, **autochory**, propagules are dispersed via gravity. Typically, the highest proportion of seeds is found closest to the parent tree, which is also known as the seed shadow. On rare occasions (i.e. steep slope or following a disturbance), dispersal can occur over longer distances. Such plants have no special traits for dispersal.

Table 18.1 Major dispersal strategies of fruits and seeds (after Howe and Smallwood 1982)

Dispersal agent	General adaptation	Modification	Derivation	Comment
Animal	Chemical attractant	Aril, pericarp, pulp	Seed coat or floral part	Vertebrate dispersal
	Fleshy nutrient	Elaiosome	Seed integument	Ant dispersal
	Clinging structures	Hooks, viscous material	Usually floral parts	Sticks to fur or feathers
	Mimesis	Coloured seed coat	Seed coat	Eaten by birds
Wind	Size reduction	Dustlike seeds	Seeds	Up to millions/plant
	High surface/volume ratio	Wings, plumes, balloons	Seed coat or fruit	Balloons uncommon
	Tumbleweeds	Shoot breaks loose	Entire shoot	Seeds scattered
Water	Resistance to sinking	Hairs or slime	Seed coat	Submerged transport
	Uses surface tension	Small size, unwettable	Seed coat	Float until wetted
	Low specific gravity	Air spaces, cork, oil	Seed or fruits	Floats long distances
Self dispersal	Explosive fruits	Varied	Fruits	Secondary transport common
	Creeping diasporas	Hydroscopic bristles	Fruits	Occurs with varying humidity

Table 18.2 Relationship between propagules and dispersal by vertebrates (after Howe and Westley 1986, with additions)

Animal/animal group	Propagule colour	Propagule smell	Propagule form	Use to animals
Mammals in herds	Brown	Little smell	Thick husked nuts, do not burst open	Seeds
Birds in flocks	Green, brown	Without	Seeds without wings and small nuts	Seeds
Frugivor mammals in trees	Yellow, green, white, orange, brown	Aromatic	Seeds often with arils, whole fruits, burst open	Arils, pulp rich in proteins and sugars
Bats	Green, white, light yellow	Aromatic, musty	Diverse, often pendent fruit	Lipid- and starch-rich fruits
Ground living and frugivorous mammals	Green, brown	Without	Hard, over 50 mm long fruits, do not burst open	Lipid-rich fruits
Frugivorous birds (obligate)	Black, blue, red, green	Without	Big seeds with arils, whole seeds often burst open	Lipid- and protein-rich fruit flesh
Frugivorous birds (facultative)	Black, blue, red, white	Without	Small seeds with arils, berries and stone fruits	Mostly carbohydrate-rich fruit
Furry or feathery	Insignificant	Without	Sticky and barbed hooks	None

Propagules can also reach suitable growing sites by growth processes, for example, via scions (vegetative shoots) or flower stalks (pedicels, e.g. *Cymbalaria muralis*). Propagules are even able to move by themselves over short distances, for example, by twisting awns due to changes in humidity (Fig. 18.1b). In addition, some plants have even evolved mechanisms to project propagules by a single impulse or shot, which helps ensure further distances travelled from the parent plant. The propagule ejections can be triggered by a series of different vectors: animals, wind or even a simple raindrop (e.g. *Impatiens noli-tangere*). In some species, these triggers are not required, where certain changes in abiotic factors must occur for projection of the propagule to occur. For example, differences in turgor pressure in a plant (e.g. *Ecballium elaterium*) or changes in moisture exchange through the seed coat (e.g. *Bauhinia purpurea*) can trigger this phenomenon. Seed dispersal through this mechanism can easily cover several metres in some cases.

18.2.1.2 Allochory

Wind is an important abiotic dispersal vector for allochoric seed transport **(anemochory).** Even when seeds reach the ground or soil substrate, they can continue to be blown along the surface. Plant propagules have been able to adapt morphologically to ground dispersal, especially in dry arid regions of the world where there are rarely impediments or barriers to such transport. More importantly, however, is transport by air currents. Small, light propagules are particularly benefactors of this mode of dispersal as they can easily be dispersed multiple times under the right gusts of wind, for example, seeds of orchids or spores of cryptograms. Some other interesting wind-dispersed adaptations include **balloon fliers** (e.g. *Astragalus spinosus*) that possess special morphological adaptations, as do seeds or fruits with **parachutes** (e.g. *Taraxacum officinale*). A number of tree species (e.g. *Acer* and *Fraxinus* spp.) have adapted special **wings** (or **samaras**) to help keep propagules in the air and increase dispersal distances. Wind also triggers seed transport in plants that scatter seeds (e.g. *Papaver* spp.).

Hydrochory involves the transportation of propagules either in or with the help of water as a dispersal vector. Some propagules are able to float because of special tissues or large intercellular spaces that have a low specific weight and that typically possess a hydrophobic seed coat, which makes it difficult for the seed to absorb water (e.g. *Nymphea* species). Coconuts and certain seeds and seedlings of some mangrove species are excellent examples of this adaptation, where they are able to stay in salt water for extended periods of time with little or no effect on seed viability. A seed that falls into a moving body of water (i.e. river, lake or ocean) can almost ensure successful **long-distance dispersal**; however, a body of water is not always required. In drier, more arid areas, seeds can travel substantial distances from their parent plant with the help of a few raindrops (e.g. *Anastatica hierochuntica* in dry regions). There are disadvantages to this mode of dispersal, however, as floating for prolonged periods of time can cause premature germination with a lack of an anchoring substrate. Plants usually prepare their offspring for this encounter by certain dormancy cues, where a seed must meet specific environmental conditions (typically moisture and temperature) prior to breaking dormancy and allowing germination to ensue.

The most important and ecologically most complex form of **allochoric dispersal** that exists is **zoochory**. Zoochory involves the use of animals as dispersal vectors for plants. Plants have developed different mechanisms and traits to entice or attract animals to disperse their seed, where, interestingly, animal foraging and behaviour can determine patterns of seed dispersal. Close interrelations between some plant and animal species point towards a long co-evolutionary development. This applies particularly to **endozoochory**, where propagules are transported internally by the animal. To do so successfully, seeds should have a relatively hard shell that ensures they are resistant to conditions within the animal's digestive system (i.e. high acidity). After excretion, seeds are usually provided with good starting conditions for germination in the nutrient-rich excrement. Although propagules can be taken up randomly, very close links between birds, bats and herbivores with plant species through the use of fruit can entice attraction and increase the likelihood of seed dispersal. These are especially evident in the humid tropical regions of the world (Table 18.2). Zoochory does have some disadvantages as a dispersal medium;

foraging animals can hoard or cache seeds (i.e. squirrels) in a safe site, which could reduce the likelihood of future germination (e.g. seeds of *Pinus cembra* collected by *Nucifraga caryocatactes*), but some of them still have a chance to survive because not all hiding places are found again and some seeds are also lost during transport.

Birds (**ornithochory**), bats, ants (**myrmecochory**) and many larger animals are especially attracted to the fruit of plants. Plants invest in nutrient-rich fruits and have evolved to attract dispersal vectors by the use of bright vibrant colours and strong odours. Ants may carry seeds possessing lipid-rich **elaiosomes** (e.g. *Corydalis cava*), but the seeds remain untouched. Birds are especially attracted by the colouring of fruits and are even able to distinguish ripe seeds from unripe ones. Sometimes propagules are eaten or damaged. These are often starch-rich and can provide nourishment for an animal. In some instances a monkey, for example, will ingest the fruit pulp and then spit out the seed.

Epizoochory is a form of passive dispersal by animals, where the seed possesses mechanisms to cling to the hair or fur of the animal. Typical mechanisms include glue-like excretions, glandular hair, barbs with awns and other outgrowths formed from the pericarp that can attach to the animal. By doing so, the seed greatly improves its dispersal distance; however, unlike in earlier cases, the animal is not rewarded for its transportation through nutrient supplementation. In endozoochory, close interaction exists between plant and animal, where dispersal is regulated, sometimes even targeted. As a result, epizoochory is mainly random.

Two additional dispersal mechanisms exist that do not really fit well with the previously mentioned groups. The first is **atelochory** (also called **achory**), where dispersal does not occur, and in fact it is prevented. The consequence of this evolutionary development is that reproduction takes place at the site where the mother plant grows, which is favourable to the species. This lack of dispersal allows the offspring to take advantage of similar conditions its parents have. *Arachis hypogaea* or *Trifolium subterraneum* provide examples of such a strategy, where, following pollination, the pedicel and ovary penetrate into the soil and become established.

The final mode of dispersal for propagules involves humans (**anthropochory**), which with the onset of the **Anthropocene** has played an increasingly important role in the recent history of plant dispersal. In this particular form, any dispersal distances can be achieved, and essentially, no geographical or ecological barriers exist. Anthropochory dispersal occurs when humans are looking to move certain species of plants to specific areas for either food or ornamental purposes. If dispersal occurs unintentionally along with other propagules (e.g. weeds disperse along with crops of cereal), their distribution and the pattern of the species concerned typically almost always occur randomly. Both forms are closely linked to the problems with neophytes (Sect. 17.3).

18.2.2 Effectiveness of Dispersal Mechanisms

Dispersal can be limited by physical barriers, such as large differences in altitude of mountainous regions, oceans and large arid regions. The absence of certain environmental conditions or requirements (i.e. temperature, water, light, soil nutrients, symbiotic patterns) may significantly limit successful establishment following dispersal. Keep in mind that these barriers or requirements can be manipulated in plants favoured by the human vector, where people can improve growing conditions by removing competition, improving soil conditions through fertilisation or aeration.

A clear understanding of how far propagules can disperse is especially important in the field of **ecosystem restoration**, which could provide key information about species' ability to persist in fragmented habitats. As this fragmentation is quite common in human-altered landscapes, better knowledge about successful seed dispersal is indispensable. This is especially true for ballistic and other autochoric species, including ant- and bat-dispersed vectors, where **dispersal distances** travel is rarely beyond a few metres. In contrast, many vertebrates, wind and water are able to disperse propagules for distances exceeding 10 km. In some of the best-case dispersal distance scenarios, orchid seeds and spores from ferns have been known to travel distances of several hundred kilometres.

When flora becomes established on young islands or within post-disturbance landscapes, it will occur primarily by anemochoric species, unless a human vector facilitates its introduction. Once established, primary dispersal mechanisms tend to shift from primarily wind to water or birds, as illustrated in a fallow field (Fig. 18.2). During the first few years, wind-dispersed species become established predominantly via long-distance transport; however, as time passes, allochoric species become more dominant after the first two decades and, finally, typically within a century, replace wind-dispersed species (Sect. 17.2). Other quantitative aspects of seed dispersal to consider include (1) the number of seeds produced and dispersed, (2) the number of visits of dispersers (e.g. birds), and (3) the continuity of favourable weather conditions (e.g. duration of air flow). The efficiency of seed dispersal also has qualitative aspects. The quality of a seed may determine whether or not a bird will decide to disperse it, how the bird manipulates it and, finally, how it is transported, all of which will affect the probability of seed germination.

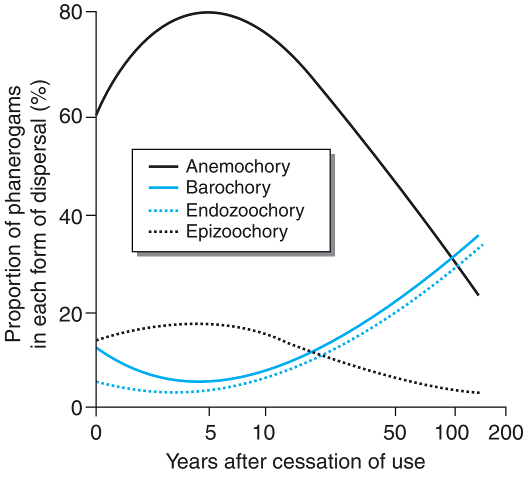


Fig. 18.2 Dispersal mechanisms can change during succession. Relative frequency of four dispersal mechanisms in phanerogamic flora of fallow fields close to Montpellier (France) at different times after their abandonment (after Lepart and Escarre 1983)

The dispersal of propagules is usually deemed successful if they reach a site that is favourable for their germination and establishment and ensures growth till flowering and seed production (**safe site**). Following germination and establishment it is extremely important to the long-term survival of the species that it exploit its new site, which is at some distance from the parent plant, contributing to the expansion of the species range or area. An expanding range or shift provides a few benefits, especially if it occurs at fast enough rates. A fast shift can allow a plant species to escape certain pathogens and enhance the population's chances of survival. To a large degree this depends on the available mechanisms for dispersal and their effectiveness regarding a targeted (suitable site for growth) and far-reaching (gain space) transport of propagules. However, such substrate "targets" are typically not achieved through a single form of dispersal. To ensure successful colonisation, a series of different dispersal vectors and their associated interactions can be used to improve seed dispersal (**heterospory**). Multiple dispersal mechanisms can supplement each other to ensure successful dispersal. Under unfavourable external conditions (i.e. a short vegetation period in high mountains or long dry periods), reproductive dispersal is combined with vegetative propagation. For example, the alpine species *Polygonum viviparum* produces both seeds and bulbils on the same stalk, with the bulbil fraction increasing with altitude.

These particular advantages associated with specific regions typically occur when the species adapts to the local conditions over time (local adaptation). For instance, wind-dispersed propagules in arid regions are often transported over long distances because only minimal obstacles occur over land. Another example of plant-dispersal local adaption is the production of flashy or tasty fruit-bearing plants, which increase the likelihood of attracting animal dispersal vectors. Essentially, different strategies have evolved in which successful arrival at safe sites and spatial expansion provide a niche balance. Studies on seed dispersal in forests have shown that many trees in the humid tropics with rainy and dry seasons have created morphologically adapted seeds that facilitate transportation by animals. In temperate forests this also applies to shrubs, but here seeds from trees are predominantly transported by wind. This change in the form of dispersal is explained by regular winds occurring in temperate latitudes. Also in dry areas, where almost no obstacles impede air currents, wind dispersal dominates. All this is to say that there is no concrete evidence for certain dispersal vectors being exclusively used or associated with specific biomes (Tables 18.1 and 18.2).

Several hypotheses and models have been developed to help explain the link between certain plant species and their vectors. The **low investment model** is associated with plants' investing little per propagule produced, resulting in a large number of small seeds. This model favours dispersal vectors associated with long-distance dispersal (wind-dispersed, attached to animals). Because little is invested in each seed, the recruitment rate is quiet low; however, this can be offset by volume. This strategy is typically used by early successional species. The second model, the **high investment model**, is essentially the opposite, where plants produce very few, large seeds. The large seed size provides ample amounts of energy and nutrients to ensure good rates of germination, assuming it attracts the appropriate dispersing agent (bird or bat) and falls upon a favourable substrate. The seeds in this strategy are only distributed over short distances, but they usually find relatively safe conditions for germination. In animal-dispersed species, both strategies are used: seeds externally attached to animals (with low investment) and those transported in the gut (with high investment). The **directed dispersal hypothesis** first proposed by Howe and Smallwood (1982), regarding targeted, relatively safe dispersal, also aligns with the high investment model. This contrasts with the **colonisation hypothesis**, where opportunists exploit opportunities for rapid dispersal over large areas. The premise for the **escape hypothesis** is that the chances for establishment and germination depend on the low density of conspecifics, so the mother plant cannot be nearby (e.g. Janzen-Connell effect) (Sect. 19.3).

Table 18.3 Factors affecting efficiency of dispersal (after Schupp 1993)

I.	**Quantity of seed dispersal**
A.	*Number of visitors*
	1. Density of dispersal agent
	2. Type of nutrition
	3. Reliability of the visit
B.	*Number of seeds dispersed per visit*
	1. Number of seeds touched per visit
	2. Probability of dispersal of a seed touched
II.	**Quality of seed dispersal**
A.	*Quality of treatment*
	1. Seeds are transported intact or broken
	2. Change in germination rate
B.	*Quality of seed deposition*
	1. Transport type
	(a) Targeted choice of habitat
	(b) Targeted transport
	2. Deposition type
	(a) Proportion of deposited seeds
	(b) Mixing of different seeds

Only a few experimental results have confirmed these particular hypotheses. It is certain, however, that many plants do not use only one vector but possess morphological and other adaptations to exploit several vectors. Such **polychory** improves successful dispersal considerably. The most important components for efficient seed dispersal are summarised in a hierarchical classification (Table 18.3).

18.2.3 Propagule Bank and Seedling Establishment

Seed dispersal is deemed successful only if the transported propagules germinate at a potential site or are incorporated into the soil (in which case it will become established at a later time). The stock of all dispersal units in the soil is called the **propagule or seed bank**, also a **seed pool.**

Seeds may remain viable for several years, in some cases up to a few centuries, until more favourable conditions for development occur. Seeds from *Medicago lupulina* have been found to be viable in the soil after 26 years, significantly lower than the seed of *Spergula arvensis*, which has been shown to maintain viability up to 1700 years (Urbanska 1992). Many propagules reduce metabolic activity before germination. Germination-inhibiting chemical substances may prevent further development. Sometimes temperatures must fall below a certain minimum value (**vernalisation**) before the seedling can develop. Such periods are called **dormancy** and may be determined genetically or by external conditions. Many seeds are protected by a thick pericarp, which can be impermeable to water. Dormancy acts as an environmental checklist for the seed, where until all environmental condition (typically light and temperature) cues are checked off, the seed will remain in the soil until conditions are met. The amount of time a seed will remain viable in a seed bank will vary from species to species.

Baskin and Baskin (2001) identified the differences between dormancy types; the first, **endogenous dormancy**, is where the properties associated with the seed embryo inhibit germination (e.g. physiological inhibiting mechanisms or an undeveloped embryo), whereas **exogenous dormancy** is described as where the properties of the endosperm or any other tissues of the seed or fruit inhibit germination (e.g. physical, chemical or mechanical constraints on germination and embryo growth).

The period of dormancy is different for different types of propagules. In tropical rainforests, seeds of shade-tolerant trees will tend to germinate immediately if they are found within a suitable growing site. Seeds of shade-tolerant trees often remain dormant until favourable conditions emerge, which will then allow for germination to occur, for example, after a fallen tree opens a gap in the canopy. In dry regions with very variable wet periods, species differ considerably in dormancy, even within individuals of the same species. In general, there is a clear favourability for seeds to be non-dormant in wet tropical rain forests (60% of species are non-dormant), mirroring an environmental gradient of decreasing precipitation and increasing seasonality or uncertainty of rainfall events. Generally, it may be assumed that the dormancy of propagules serves to tune germination to growth conditions that will provide a suitability bridge for a cold winter or a dry season.

A seed bank is usually located in the uppermost 10 cm of soil. Seed banks are made up of two types: **temporary** and **long-term. Temporary propagule banks** consist of the accumulation of seeds that will germinate in the short-term (next year). **Long-term propagule banks** are particularly important for the regeneration of plant communities. Propagules in temporary banks have only limited ability to germinate—as for tropical shade trees—and the regeneration of forests after a severe disturbance is unlikely. This also applies to rainforests in southern Chile outside the tropics. A few years after clearing of the almost natural stands and reforestations of the area with *Pinus radiata*, the local seed banks contained hardly any propagules of indigenous species (Scherer and Deil 1997**.** This underlines the importance of seed banks for the protection of species and biotopes.

The phase of **seedling establishment** is particularly sensitive in the life cycle of plants. Pathogens, herbivores and competitors, but also climatic abnormalities, may lead to large losses. Some seedlings require the protection of neighbouring species (e.g. *Arabis hirsuta*, *Primula viridis*), but for others germination is reduced by neighbouring species (*Plantago lanceolata*, *Sanguisorba minor*). A third group of species was able to germinate under all experimental conditions (e.g. *Medicago lupulina*). Large, time-dependent fluctuations have also been observed. There are close relations between rates of germination and interannual fluctuations of climatic conditions, particularly of temperatures. Most species germinate more successfully at higher temperatures, while others germinate better at lower temperatures (Espigares and Peco 1993). In some species of *Acer*, seed germination can commence only if it experiences a certain number of cool, moist days (known as stratification) near the freezing point to break dormancy and allow for germination to ensue (Solarik et al. 2016).

While the molecular and biochemical bases for dormancy and germination are well known for certain model species under controlled environmental conditions, we still lack a clear understanding of some of the fundamental processes under natural conditions that inhibit or promote seed germination and establishment. The successful establishment of a plant population is only secured by a permanent input of propagules, even if edaphic and climatic conditions at the growing site are suitable, pollinators (when necessary) are present, and the species is able to successfully compete with co-occurring individuals and protect itself against pathogens.

18.2.4 Distribution Patterns

As a result of different dispersal mechanisms, plant species develop distinct **spatial patterns of distribution**. These patterns are not permanently fixed in space because they depend largely on abiotic and biotic factors, which continuously fluctuate over time (daily, weekly, monthly, seasonally and yearly). Among these factors especially those related to climate, soil and mechanical impacts (flooding, thunderstorms) and—in cultural landscapes—agrochemical and agrotechnical influences are important. Accurately identifying the propagule distribution pattern will depend on the spatial scale, where variability from the local-scale small patches to large-scale landscapes must be considered. A several-square-kilometre area with small forest islands, grasslands and bogs will show different patterns when compared with dispersal at finer scales (cm^2, m^2) in the same area, which typically will yield much different results. Today, a species' distribution is typically assessed by the use of a grid system in analysis. Although results will depend on the size of the grid chosen for analysis, the **spatial scale** (e.g. "**patch**", "**local**" or "landscape") becomes essential when considering dispersal patterns.

Distribution patterns will typically fall under three main types: **clumped, regular** and **random** distributions. The **clumped distribution** is the most common type in natural vegetation, mainly because of a close relationship between abiotic and biotic resources associated with plant establishment and growth. As these resources often present a mosaic structure, species and plant communities often become clumped. The introductory photo of Part IV shows an example of clumped distribution in a tropical high-mountain belt with abiotic site factors changing on a large scale. On a smaller scale, spatially aggregated clumped distribution can be the result of a restricted seed shadow, where seed is either dispersed or animals fail to travel far before excreting or dropping the seed. Fangliang et al. (1997) found in the highly diverse tropical rainforests of Malaysia a 4:1 relation of clumped to random distributed tree species, which suggests a strong influence of animal-dispersed seeds in these systems.

A regular distribution occurs when the propagule is dispersed evenly over an area, where a comparable amount of seeds are found at long and short distances from the parent tree. This distribution pattern is rarely found in nature. The regular distribution can occur when the environmental conditions across the dispersal distance change in a regular way: the zonation of different plant community changes with a significant change in the landscape. Vegetation along a riverside is an example. The mechanical force of the water during the rainy season and the different water storage capacities of the sediments on the low fluvial terraces with different grain sizes can result in the formation of a regular sequence of different species and communities (Fig. 17.25). Regular patterns are also sometimes observed in tropical dry woodlands ("**leopard skin**") if the distance between plant individuals is the result of competition for water, the limiting resource. The introductory photo of Chap. 18 shows an example of regular vegetation patterns at the landscape scale, with an evergreen gallery riverine forest and a seasonally moist dry woodland. Most examples of regular patterns found in nature are actually artificial, for example, in fruit tree plantations or even crop cultivation (introductory photo in Chap. 17).

Although rare, regular spatial patterns are typically determined by animals and wind vectors, they are most important for **random distributions**. One precondition is that the plant species concerned must be generalists, that is, they have a wide resource-based spatial niche (area where species-specific requirements are met), and the spatial distribution of the environmental resources is rather homogeneous. Abiotic and biotic factors are thus spaced in an unpredictable way, as are the individuals of plant species.

18.3 Vegetation Geography

One consequence of short-range dispersal is that the site where propagules fall to the ground is already occupied by conspecific plants, often offspring of the same mother plant. Hence, growing seedlings will typically face **intraspecific competition** because a favourable abiotic environment is likely. In contrast, for propagules transported by long-distance dispersal, there is typically a higher chance of facing unfavourable abiotic and biotic factors. Although the likelihood of establishment at less favourable sites is lower, a successful establishment can still lead to spatial expansion. The result is an increased **species range** or **area**, which is a geographically defined region where individuals of a species can be found.

The science of **spatial distribution** of plants (**chorology**) aims (1) to recognise the various types and characteristic patterns of distribution, which provide the ability to map and to describe species organisation, and (2) to explain the development of patterns of distribution. A comparative assessment of geographical areas leads to the characterisation of **floristic elements** and **areal types** or **geo-elements**.

18.3.1 Characterisation and Interpretation of Areas

There are various ways to map areas. Frequently, when considering species distributions, only borders are drawn without providing any additional information concerning the distribution and abundance of species within the area. This can be avoided by creating **dot maps**, which can provide species locations. The most popular way to represent species distributions is through the use of **species range maps**. However, these maps often show only a portion of the entire range and rarely contain any information about species abundance. Such maps also show the climatic differentiation of areas often better than those based on meteorological data. Regardless of their shortcomings, these maps are indispensable for applied tasks, for example, nature protection.

The **species range** or **area** is essentially the spatial distribution in which a biological taxon is found, that is, where the environment is typically favourable for that species. The range limits are typically controlled by a number of historical and ecological factors, for example, climate, interspecific (other species) and intraspecific (same species) competition, site quality, food resources, water and landscape. Isolating the contribution of each of these factors individually is extremely difficult, especially since they can be co-dependent on each other. One attempt at determining range limits has been done through the use of isotherms (average temperatures); however, plants rarely react to average conditions. For example, the eastern species range of beech (*Fagus sylvatica*) is constrained by the lack of precipitation; however, another constraint is the severe cold winter (> −30 °C), which is known to cause extensive damage to bud development. At the species' southern range limit, the opposite occurs, where a combination of a lack of summer precipitation and high temperatures causes significant drought events. Finally, beech's northern limit has been determined by a combination of prolonged winters and late-season frost events. However, it has been speculated that beech reached its northern limit in the north-west of the British Isles after the last glaciation. These observations have relied on the current distribution patterns of adult trees while ignoring environmental constraints on seed germination and seedling establishment, key processes in determining any long-term presence of a species. This will be of special importance in studies about climate-change-driven dynamics as species attempt to maintain their climatic niches by expanding their ranges in altitude and latitude. As decisive for alpine plant communities and their upper distribution boundary is summer frost resistance (Taschler and Neuner 2004).

Identifying the constraining factors influencing range limit is particularly important for olive trees in the Mediterranean region (Fig. 18.3). In the mountainous portion of these regions, prolonged frost, coupled with a shorter growing season, minimises biomass accumulation in the stem. In southern Europe, early summer is often too moist, inhibiting pollination and making fruit setting difficult. In North Africa, towards the south, increasing drought is limiting. At these limits, **Walter's law of the relative constancy of habitats** can be applied to understand the occurrence of plants. In the southern species range of *Quercus pubescens*, for example, its occurrence indicates moist outposts of Mediterranean habitats, while at the northern range, in the upper Rhine Valley, it is found only on the warmest and driest, south-facing slopes. If the climate within the area of a plant species is changing in a particular direction, this species moves into a habitat that compensates for this climate change, so that the environmental conditions remain rather constant, assuming that the demands of a specific plant species remain constant (Walter 1986).

It should be mentioned that species range limits are dynamic, under constant flux, and can change quite readily owing to climatic factors influencing the biological system. The postglacial retreat of ice caused by climate warming led to significant species range shifts, which made it possible to make inferences on the rates of possible migration. For some important Central European tree species a range expansion of approximately 100 m/year was calculated, a considerable rate when one considers that trees are sessile organisms that typically require decades to reach reproductive maturity. Furthermore, quiet often many tree species will produce ample seed crops only once every several years (**masting**).

Considering the changes associated with climate change, species invasion, natural disturbances and new land-use practices, inventorying species ranges will continue. Complicating matters, the presence of **synanthropic species** or species that benefit from the presence of humans makes mapping species' ranges and range limits extremely difficult. Ecologists have

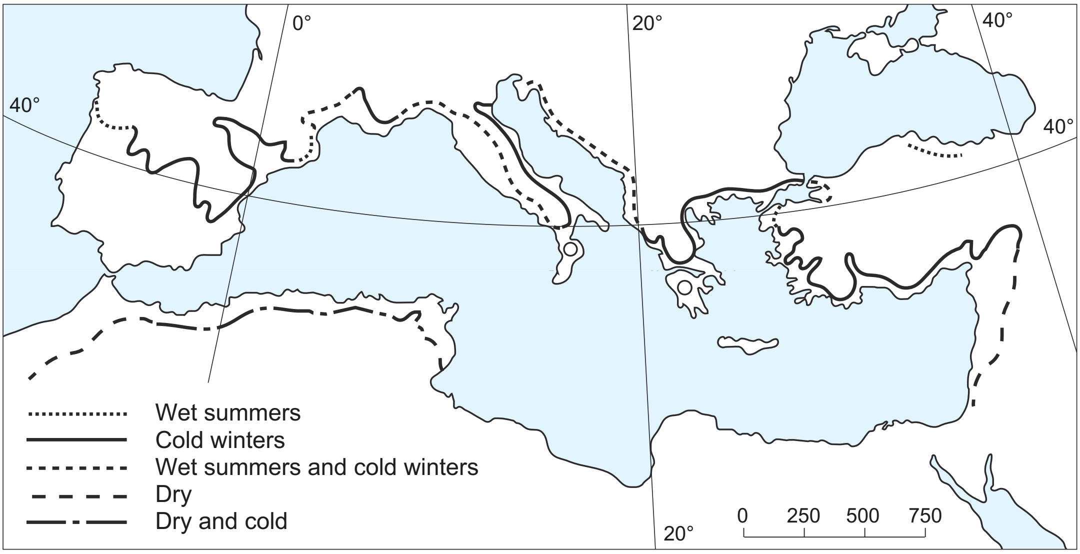


Fig. 18.3 Limit of the distribution of olive trees (*Olea europaea*) in the Mediterranean area and the most important climatic factors determining it (after Müller-Hohenstein 1981)

thus introduced the concept of a potential or fundamental range and a realised range. A **potential range** is an area where the range of environmental conditions is suitable for existence without the influence of competition or predation from interspecific species, whereas a **realised range** is the part of the potential range that is actually occupied by the species. A realised range is typically limited by various site conditions. Figure 18.4 shows schematically how differently the spatio-temporal formation of areas may occur. Areas may grow or shrink; they can also divide (**disjunction**), and new taxa may evolve by **allopatric differentiation** (metapopulations of the same species live in clearly separated geographical areas).

Species ranges are also characterised by their (1) size, (2) form and (3) geographical location. The differentiation between **cosmopolitan** and **endemic species** is based on the size of distribution areas. **Cosmopolitan species** typically occur over large areas, commonly extending over continents and different climatic zones. These species have extremely effective dispersal mechanisms, are highly competitive and can be categorised as phylogenetically old. Some common examples of cosmopolitan species include bracken (*Pteridium aquilinum*) and annual meadow grass (*Poa annua*). Cosmopolitans are differentiated from species that are generalists in terms of their site requirements (e.g. *Pinus sylvestris*).

Endemic species are species unique to one specific location or distribution, for example, in isolated mountain regions or islands. Two types of endemic species exist: **palaeo-endemic and neo-endemic.** A **palaeo-endemic** (sometimes referred to as **relict-endemic**) **species** is a species that historically was known to be widely distributed but, owing to either a disturbance (natural or anthropogenic) or competition, is now restricted to a much smaller native area. Typically, these species are phylogenetically old species. The giant redwoods (*Sequoia gigantea*) of California and the Eastern Asian *Ginkgo biloba* are both classic examples of these types of species. In contrast, **neo-endemics**, the phylogenetically younger counterpart, are species that have not had the opportunity temporally to benefit from

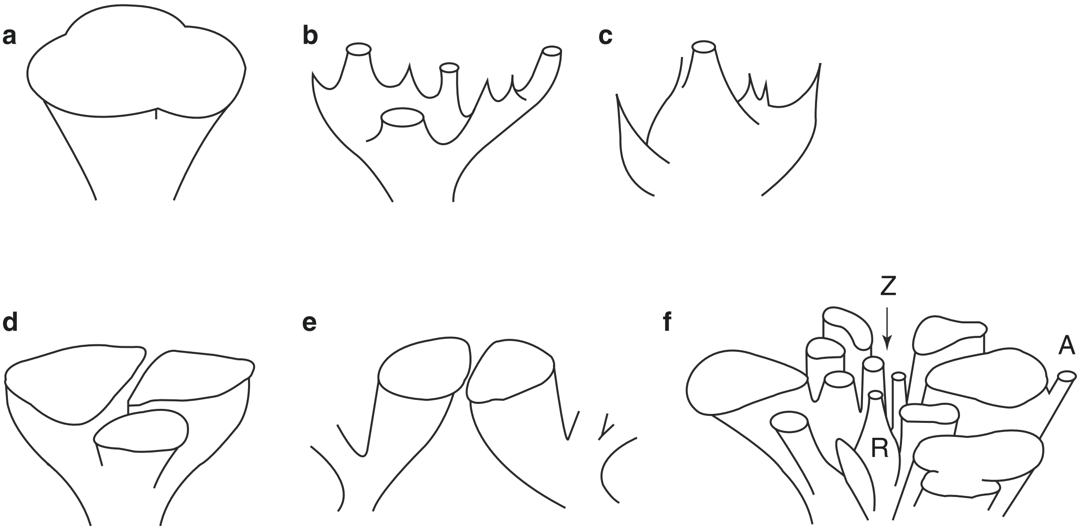


Fig. 18.4 Possible means by which plants exploit space over a period of time. Time axis vertical, space axis horizontal, cut surfaces show the current situation. **a** Area expansion; **b** death of populations and shrinkage to disjunct areas; **c** as in **b** with development of relict palaeoendemic areas; **d** allopatric differentiation of three vicarious related groups; **e** pseudovicarious species, living in ecologically or geographically similar conditions; **f** distribution of closely related species with a centre of diversity (Z), relict endemics (R) and neoendemic species (A). There are no fixed relationships between the age of the species, diversity of the group or size of the area (from Strasburger and Sitte 1998)

inhabiting a larger range. Another reason for their lack of distribution could be attributed to physical barriers in the landscape, which has limited such movement. Island biogeographers have collected data from island groups that have shown that the distance of an island to the mainland, coupled with the duration of isolation, reflects the proportion of endemics in flora composition (Table 18.4).

Species areas are also differentiated by their form, particularly whether they are closed areas, that is, the species is established in a single, clearly delimited space, or whether the area consists of several partial areas and is thus **disjunct.** In closed areas, gaps between individual growing sites are so small that they may be bridged easily and quickly by the transport of propagules or pollen. In **disjunct areas**, this is no longer possible. It may be assumed that polyphyletic origin of the same species does not occur and therefore other explanations for the genesis of disjunct areas must be found. One explanation might be an extremely rare distribution event, for example, by migrating birds or through some anthropogenic influence. In many cases, however, it is known that present disjunct areas were once closed and were separated by tectonic events (e.g. continental drift), the formation of mountains or climatic changes (e.g. change in cold and warm periods). A good example of the latter are **arcto-alpine species**, which were widely distributed in Europe during the Pleistocene, growing in the lowland tundra habitats between the Scandinavian and alpine glaciers. Today, under a warmer period, they are restricted to high alpine and arctic habitats, as well as to isolated patches in lower mountain ranges in Central Europe (e.g. *Dryas octopetala*).

Table 18.4 Proportion of endemics in the flora of different islands and island groups (after Frey and Lösch 1998)

Island/island group	Endemics in %	Distance to the nearest mainland (in km)
Fernando Po	12.0	100
Canary Islands	53.5	170
Sao Tomé	19.4	250
Cape Verde Islands	15.0	500
Juan Fernandez	66.7	750
Madeira	10.5	970
Galapagos	40.9	1120
Azoren	36.0	1460
St. Helena	88.9	1920
Hawaii	94.4	4400
Marquesas	52.3	6000

With the separation of once closed areas, so-called **vicarious areas** may develop. In these partial areas, the populations of once uniform species developed further in different ways. This would be called **geographical vicariance** with examples of the genera *Kleinia* and *Aeonium* (Fig. 18.5). The

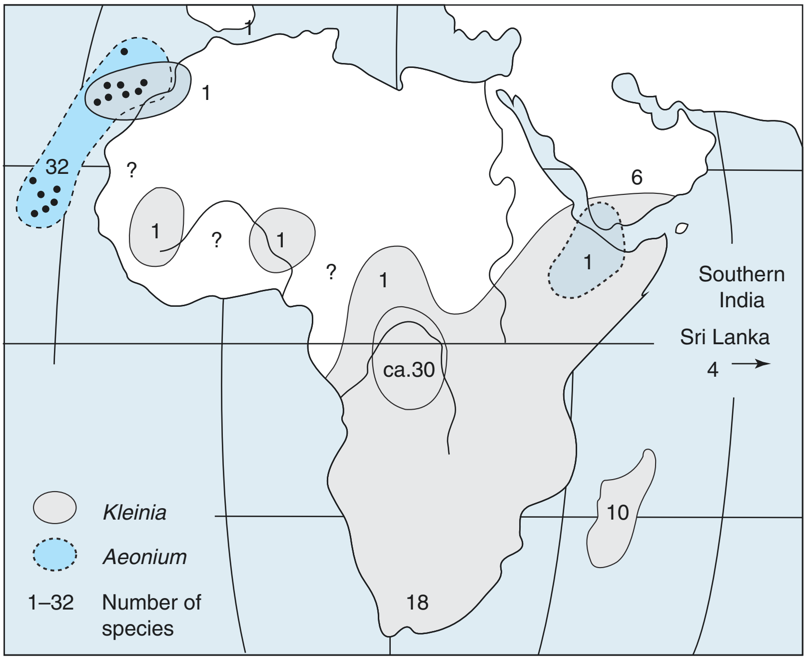


Fig. 18.5 Vicariance of the two genera *Kleinia* and *Aeonium* (Deil and Müller-Hohenstein 1984, after Richter 1997)

centres of diversity of these species in southern and eastern tropical Africa as well as in Macaronesia (including the Cape Verde islands) are separated by the North African dry regions. If subspecies or other species of a genus are established in the same space at different sites, this is called **ecological vicariance**; examples are the two alpine rhododendrons *Rhododendron hirsutum* and *R. ferrugineum*, respectively, on soils of limestone and silicate rocks.

In general terms, differences in geological site conditions are related to differences in flora. The question of what factors cause these changes in a flora can only be answered at the level of the ecosystem. For example, on siliceous and limestone bedrock, the following ecological conditions of the site are altered:

- Limestone sites are usually drier than siliceous sites, because the water from precipitation seeps rapidly into deep soil layers.
- Limestone sites are warmer than siliceous sites because of the lower soil water content.
- Siliceous: deficient in Mo and alkaline cations but with an excess of Al.
- On limestone sites litter decomposition leads to mulch (mull) as the dominating form of humus, while siliceous sites are characterised by raw humus or moder.
- N mineralisation on limestone sites leads to nitrate as the dominating N form, whereas on siliceous sites it is ammonium.

The multitude of factors affecting a site shows that there is not a single factor that explains differences in vegetation. Most plants growing on siliceous substrates do not grow on limestone because of the soil chemistry (Fig. 18.6). Conversely, competition in the root layer stops the immigration of limestone species into siliceous sites, although they could

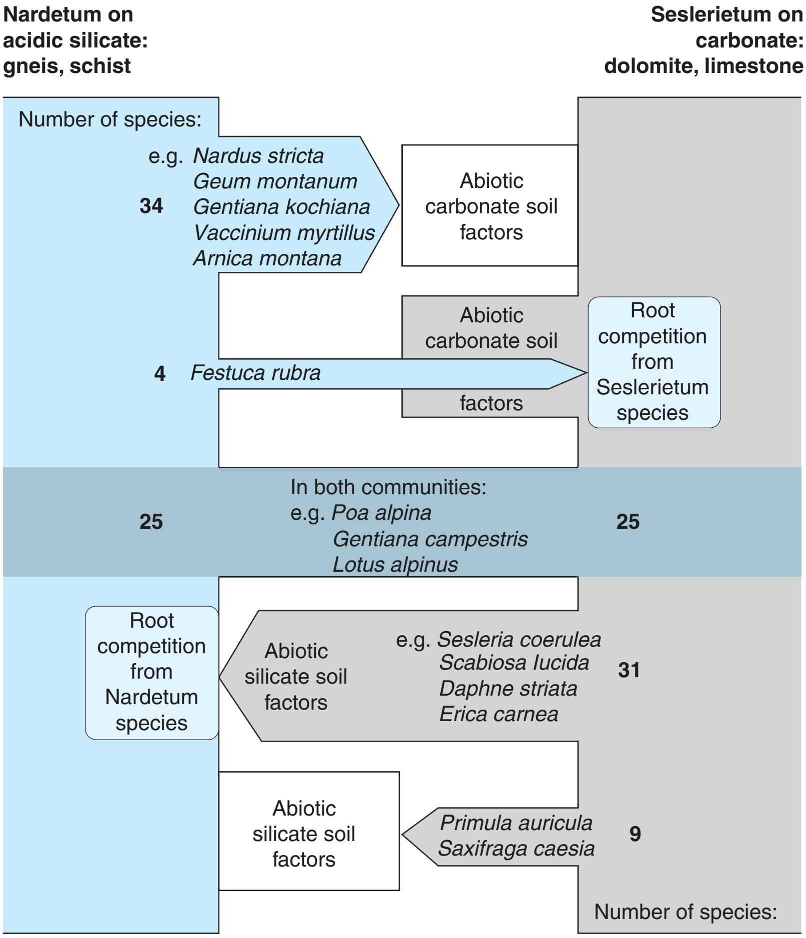


Fig. 18.6 Relationship between calcareous and siliceous vegetation of two alpine plant ecosystems. Matgrass communities (*Nardus stricta*) occur on siliceous sites, and bluegrass meadows (*Sesleria coerulea*) occupy calcareous sites. The number of species unable to invade the other's root space, either because of root competition or other abiotic factors, is shown (after Gigon 1987)

grow there without competition. While 34 species of the siliceous **matgrass meadows** (Nardetum) are not able to colonise calcareous **bluegrass meadows** (Seslerietum) because of abiotic factors such as Fe deficiency, a large supply of phosphate or Al toxicity, it is mainly competition by roots of the matgrass species that stops invasion by bluegrass species. These abiotic factors, on the other hand, only affect nine species (Gigon 1987).

If phylogenetically related species are distributed closely together, it may be concluded that they have developed within the same region and that the area is a **centre of diversity** (**genetic centre**, central zone of related groups), or at least a **maintenance centre** of this genus. Plant breeders aim to find such centres for economically important plants because they hope to find important gene reserves.

18.3.2 Area Types-Floristic Elements-Plant Kingdoms

Areas of similar basic structures, size and geographical positions are categorised into **area types**. Various species do not occupy absolutely identical areas, but all species of the same area type are considered to be **geo-elements** if spatial aspects are considered more and **floristic elements** if floristic aspects are considered. Nevertheless, these terms may be regarded as synonyms.

The spatial distribution of area types is linked to climatic characteristics: (1) zonal temperature dependence with latitude, (2) dependence on the duration of the growing season with altitude above sea level, (3) dependence on the influence of oceanic or continental climates that affect temperature ranges. Groups of geo-elements for Europe are shown on the map in Fig. 18.7. The following

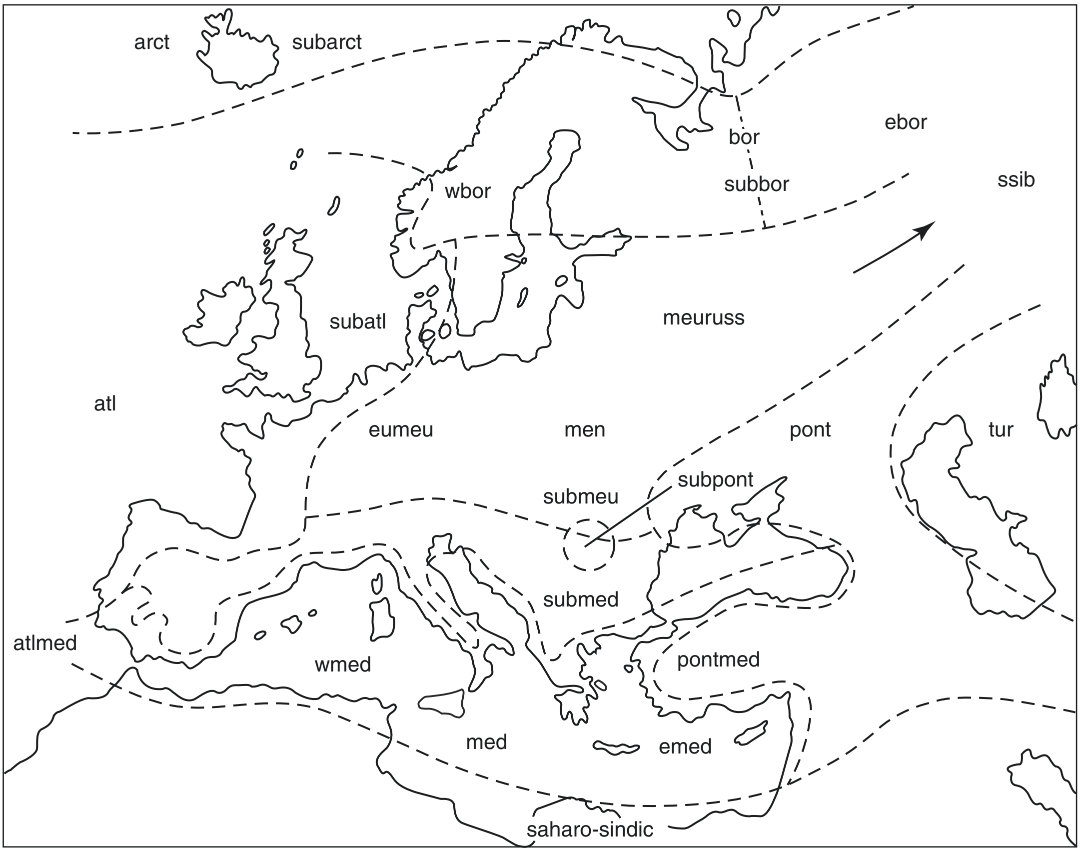


Fig. 18.7 Classification of geoelements (similar area types) of Central Europe. *atl* atlantic, *arct* arctic, *bor* boreal, *eu* European, *m* central, *med* mediterranean, *pont* pontic, *russ* russian, *saharo* saharian, *sindic* indian, *tur* turanic, *e* east, *s* south, *w* west (after Kreeb 1983)

abbreviations are generally used for the zonal sequence from north to south, which can be further subdivided based on clearly defined floristic contrasts between the observed areas (e.g. sub-Mediterranean).

For altitudinal belts the following terms are used:

- plan (planar belt of lowlands).
- coll (colline belt).
- mont (montane belt).
- subalp (subalpine belt to the timberline).
- alp (alpine belt).
- niv (nival belt).

For the west–east changes in Europe the following terms are used:

- atl (atlantic).
- cen (central European).
- ssib (southern Siberian).

Examples of geo-elements influencing Central Europe are listed in Table 18.5.

Table 18.5 Examples of types of central European geoelements and neighbouring geoelements

Central European (eu-mi):	*Fagus sylvatica, Quercus petraea, Hedera helix*
Sub-arctic (subarct):	*Betula nana, Salix herbacea, Rubus chamaemorus*
Boreal (bor);	*Picea abies, Larix decidua, Ledum palustre*
Atlantic (atl):	*Erica tetralix, E. cinerea Sarothamnus scoparius, Ilex aquifolium*
Central Russian (mi-ru):	*Carpinus betulus, Quercus robur, Alnus glutinosa, Melampyrum nemorosum*
Sub Mediterranean (submed):	*Acer monspessulanum, Quercus pubescens, Sorbus torminalis, Bromus erectus*
Mediterranean (med):	*Quercus rotundifolia, Arbutus unedo, A. andrachne*
Pontic: (pont):	*Adonis vernalis, Anemone sylvestris, Stipa pennata, S. capillata*
South-Siberian (ssib):	*Daphne mezereum, Betula verrucosa, Astragalus danicus*
Arctic-alpine (arct-alp):	*Loiseleuria procumbens, Poa alpina, Arctostaphylos alpinus*

Vegetation may thus be regarded as the combination of species of a certain area or geo-element. The causes of boundaries between areas and types remain poorly understood; however, their evaluation and interpretation can be based on ecological characteristics of the species. For example, Müller-Hohenstein (1988) characterised vegetation units on the Arabian peninsula using an **area typological approach** (Fig. 18.8). The figures show the different interpretations of the boundaries, which could then be used by climatologists and plant geographers. It is easy to see from this figure that there is a lot of variability between boundaries, suggesting that the north-eastern Arabian coastal regions should not be classified as tropical, according to neither the climate nor the vegetation.

Area types and the corresponding geo-elements are the basis of a hierarchical division of the Earth according to floral relationships. At the highest level of this hierarchy are the six **plant kingdoms**. This division is made on the best possible homogeneity within and the greatest contrast between neighbouring units. The differentiation is mainly based on the geographical positions in which these species have developed for different periods in isolation. To define the plant kingdoms, mainly higher taxonomic units (families) are used, which are based on not only their exclusive distribution but also the spatial centres of their distributions. Plant kingdoms can be further subdivided into **floral regions** and **floral provinces** (Fig. 18.9). The early separation of the southern continents with the corresponding formation of three plant kingdoms, **Antarctic, Capensis** and **Australis,** is particularly important. The sole plant kingdom in the northern hemisphere, which covers the middle and higher latitudes, is the **Holarctic**. In the lower latitudes of the tropics, the **Palaeotropics** and **Neotropics are differentiated**.

The **Holarctic** is the largest plant kingdom with distribution centres of many plant families (Apiaceae, Betulaceae, Brassicaceae, Caryophyllaceae, Fagaceae, Primulaceae, Ranunculaceae, Rosaceae, Salicaceae). Current differences, for example, between holarctic regions in North America and Eurasia, are caused

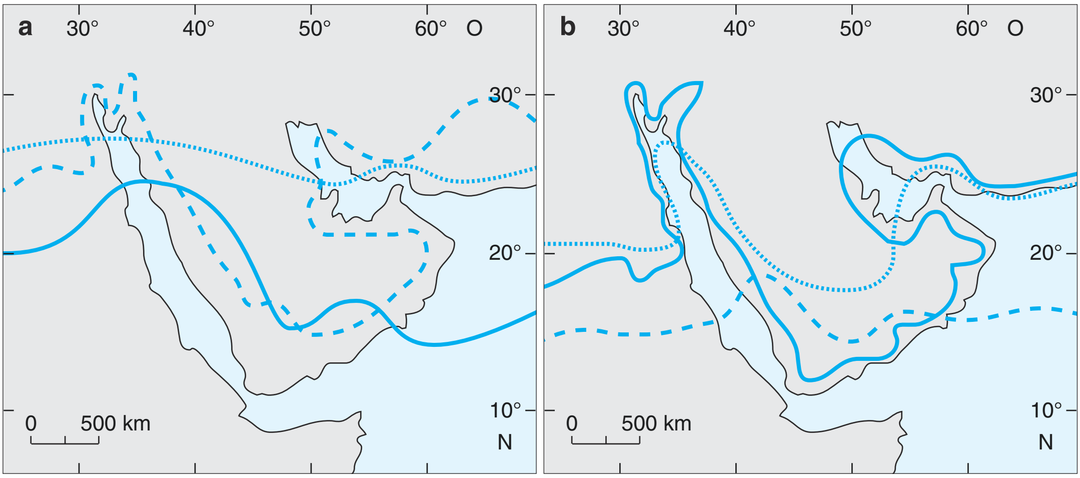


Fig. 18.8 The position of plant kingdoms or climatic zones on the Arabian Peninsula. **a** Position of the boundaries between the Holarctic and the Palaeotropic plant kingdoms according to plant geographers Diels (1908, dotted line), Al Hubaishi and Müller-Hohenstein (1984, continuous line) and Kürschner (1986, broken line). **b** Boundaries between the subtropics and tropics on the Arabian Peninsula according to climatologists Troll and Paffen (1964, dotted line), von Wissmann (1964, continuous line), Blüthgen (1964, broken line) (after Müller-Hohenstein 1988)

by recent geological events (ice ages). However, in more recent geological time periods, no insurmountable barriers have arisen.

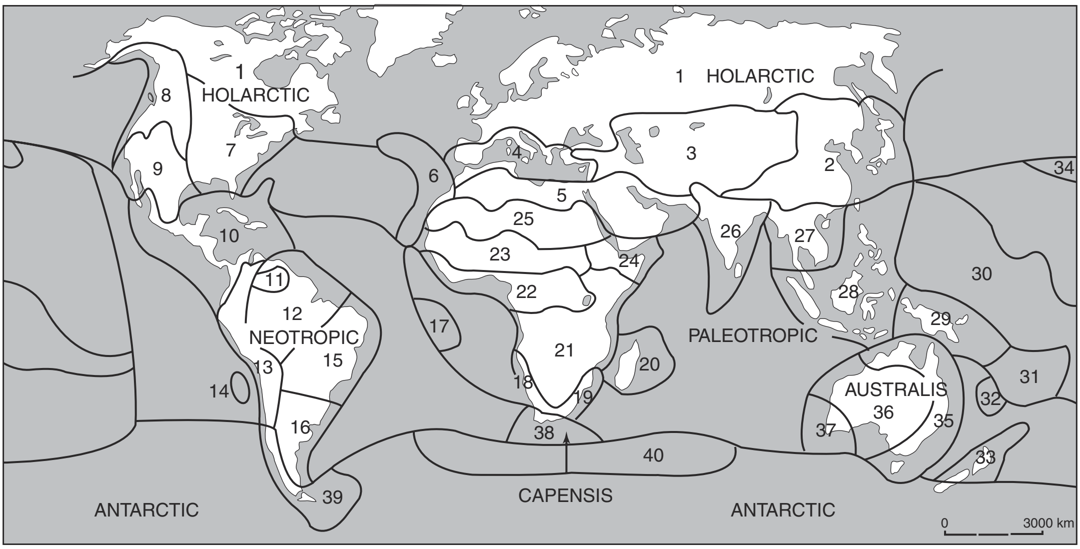
This does not apply to the southern, tropical regions. The separation of the African continent from South America led to the subdivision of two tropical plant kingdoms; this subdivision is justified, despite existing parallels (pantropical species and families, e.g. Annonaceae). Particularly characteristic families in the **Palaeotropics**, including the African continent and the South-East Asian archipelagos, are Combretaceae, Dipterocarpaceae, Euphorbiaceae, Moraceae (with over 1000 species of the genus *Ficus*), Nepenthaceae, Pandanaceae and Zingiberaceae. For the **Neotropics**, including most parts of Central and South America, species of Araceae, Bromeliaceae, Cactaceae and Solanaceae are particularly characteristic. Tropaeolaceae are entirely limited to this plant kingdom.

The **Capensis** in the south of the African continent is the smallest plant kingdom, but it is a particularly autonomous realm, where some families have developed into many species. This applies particularly to Ericaceae and Mesembryanthemaceae. In these two families relations to the Holarctic and Antarctic become obvious. The Bruniaceae is an endemic family of the cape, and representatives of the Proteaceae and Restionaceae are dominant.

The Southern Hemisphere plant kingdom of **Australis** comprises only the Australian continent and Tasmania; at the level of genera and species it is rich in endemic species. *Eucalyptus* species (Myrtaceae) are particularly important and are now distributed worldwide. The neighbouring New Zealand belongs in part to the Palaeotropics, but in the south partly to the Southern Hemisphere, the **Antarctic**, which has its largest area almost completely inhabited by plants. However, in the southern tip of South America, southern beeches (genus *Nothofagus*) developed.

18.4 Species–Area Relationships

The spatial distribution of co-occurring plants depends on the dispersal mechanisms of species, rates of reproduction, competitiveness, growth and other factors. In nature, clumped distributions are particularly frequent, rather "island-like", where patches are covered more densely, so that there are differences in **abundance**. Ecologists seeking the origin of such patterns need to know how many



Plant kingdom: Holarctic *(can be divided into Paleoarctic and Nearctic)*

Floral regions:

1 Circumboreal
2 East Asian
3 Irano-Turanic
4 Mediterranean
5 North Saharan-Arabian
6 Macaronesian
7 North American-Atlantic
8 Rocky Mountains region
9 Madric

Plant kingdom: Neotropic

Floral regions:

10 Caribbean
11 Guyanese
12 Amazonian
13 Andean region
14 Juan-Fernandez islands
15 Brazilian
16 Argentinian-East Patagonian

Plant kingdom: Paleotropic *(can be divided into African, Indomalaysian and Polynesian regions)*

Floral regions:

17 Acenscion Island and St. Helena
18 Karoo-Namibian
19 Zulu region
20 Madagascan
21 Angolo-Zambesian
22 Guinean-Congolesian
23 Sudano-Sahelian
24 Eritreo-Jemenitic
25 South Saharan
26 Indian
27 Indochinese
28 Malaysian
29 Papua-New Guinean
30 Polynesian
31 Fijian
32 New Caledonian
33 New Zealand
34 Hawaiian

Plant kingdom: Australis

Floral regions:

35 Northeast Australian
36 Central Australian
37 West Australian

Plant kingdom: Capensis

Floral regions:

38 Capensic

Plant kingdom: Antarctic

Floral regions:

39 South Chilenian-Magellanic
40 Subantarctic

Fig. 18.9 Plant kingdoms and floral regions (after Richter 1997)

species (and individuals) are able to live in a certain area, known as the so-called **species–area relationship (SAR).**

Species–area relationships are an important background for understanding **biodiversity**. No single factor determines these relationships, and our present knowledge about how many factors there are and how they interact (e.g. **random placement, minimum area effects** and **evolutionary independence**) remains limited. Incomplete surveys in heterogeneous habitats contribute to the present difficulties in formulating a clear definition of these relationships, where several types currently exist. Further, attempts at clarifying species–area relations have sometimes been based on a rather small empirical basis for mathematical modelling. While **mathematical models** provide some insight into these interactions, they usually are based on initially simple equations, reflecting reality to only some degree, sometimes leading to incorrect conclusions. In contrast, holistic attempts have also been limited in their success, which have often led to superficial descriptive conclusions.

In this complex context it is most important to consider the **spatial scales**, which may differ with respect to the importance of the interactions that occur. The variability of scale is vast, from tiny soil crusts in an extreme desert to large species-rich tropical forests. Since long-term global vegetation surveys are well established—especially in the context of the relationship between climate and vegetation—large-scale maps and graphs are widely used and generally well accepted (Köppen 1900; Holdridge 1966). In these examples, vegetation is based on a classification of **vegetation formations**, such as evergreen rainforest, dry savanna and desert shrubland, which are characterised by floristic as well as **structural/physiognomic features**. More recently, computer simulations have led to a better understanding of the dynamics of global vegetation models, where most recently they have been used to predict species range shifts under climate change. For simplicity's sake, often both climate and vegetation models are combined. This requires a reduction of the parameters—such as plant cover, water balance, biomass, soil carbon and many more—chosen for a single vegetation model. Such a reduction with respect to vegetation has even been proposed using only two plant functional types (Brovkin et al. 1997). At least two problems arise: there are too many parameters and the choice of parameters may always be comprehensible but still be arbitrary. Modellers are thus faced with the challenge of answering many questions: Should plant species, plant growth forms or plant functional types be taken into account? Further, what scale, grid size and time steps should be used for data collection in the field? The attempt to simplify often complicates one's task because major uncertainties still surround the question of what variables to include. A model based on all ecologically important factors collected from the field for landscape and global spatial scales can prove troublesome when the focus is providing actual vegetation cover. Developing models that can accurately predict reliable changes for the future vegetation dynamics is extremely difficult and represents a major challenge facing the scientific community today.

However, recent developments in global ecosystem modelling have led to much more detailed representations of the world's vegetation types, for example, the Lund–Potsdam–Jena (LPJ) **Dynamic Global Vegetation Model** (Sitch et al. 2003). Such models are based mainly on land surface biophysics and on plant functional types with different physiological, morphological and phenological attributes with field data evaluation on different time steps (Sect. 22.1).

18.4.1 Equilibrium Theory of Island Biogeography

Relations between the distribution and establishment of organisms and the size of areas have been analysed in particular for **islands**. Islands are clearly bound with a limited number of different habitats, often under relatively uniform climatic conditions. They occur in various sizes and are situated at different distances from the mainland. Therefore, they have been chosen as examples to clarify basic relations between number of species and size of area.

Two main questions must be answered:

1. How do plants establish themselves on islands?
2. What limits the number of species on islands?

The first question is easily answered. Dispersal to islands situated far from the mainland, and thus from the closest source of propagules, can only be achieved by a form of **long-distance dispersal**. Transport by sea birds may be a method of dispersal (particularly **epizoochoric**), but also abiotic vectors, such as air and sea currents, or exceptional events, for example, tropical cyclones, must be considered.

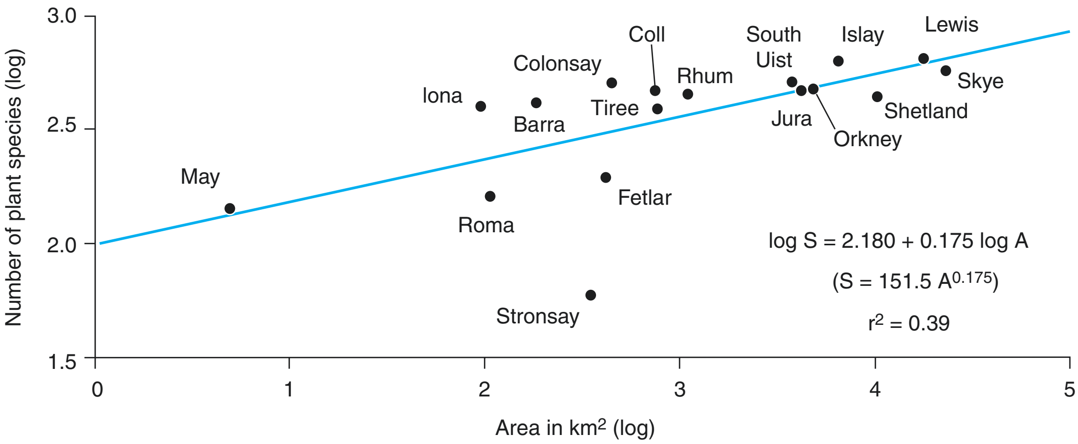


Fig. 18.10 Species-area relationships for plant species from selected Scottish islands (after Johnson and Simberloff 1974)

On islands in closer proximity to the mainland, birds remain important; however, at greater distances dispersal by wind and water is more prevalent. Propagules can be transported to islands from several directions. Almost half of all species on Hawaii originate from the Indo-Pacific region, more than a quarter from the Holarctic and 17% from cold temperate Southern Hemisphere areas (Fenner 1985). A simple equation was developed to explain how plants can become established on islands. Arrhenius (1921) showed that the relationship between the size of an island and the number of species it maintains can be described by

$$S = c \cdot A^z \qquad (18.1)$$

or

$$\log S = \log c + z \log A, \qquad (18.2)$$

where S is the number of species of a taxon on the island, A denotes the area, z is a constant that changes little worldwide (i.e. the slope of the linear regression, when log S is plotted against log A, has values between 0.17 and 0.4), and c is a constant of proportionality and is dependent on the dimensions in which A was measured, in terms of the biogeographical area and taxonomic group.

The relationship between species and area is shown in Eqs. 18.1 and 18.2, where the number of species of a given group is halved if the area is reduced by a factor of 10. This attempt to provide a mathematically comprehensible theoretical expression relating the number of species to the size of islands is one of the important bases of the **equilibrium theory of island biogeography** by MacArthur and Wilson (1967). This has been confirmed, for instance, for plant species of the Scottish islands (Fig. 18.10). These relationships are explained by two hypotheses: (1) the **habitat diversity hypothesis** (Gorman 1979), which suggests that on larger islands there is a greater number of diverse habitats, and (2) the **area-alone hypothesis** (Kohn and Walsh 1994), which assumes a direct relationship between island size and number of species.

MacArthur and Wilson (1967) built on previous knowledge about the establishment and number of species on islands. They started from the following premises:

- Fewer species occur on islands than in the same area on the mainland.
- The number of species on islands increases exponentially with the size of the island.
- The pool of species on the mainland supplies propagules.
- The distance from the mainland is a very important determinant of the number of species on an island.

In addition, the researchers assumed that the number of species on islands depends on the diversity of habitat, and that if other islands exist between the island and the mainland, those will play an important role as a **stepping stone**. It was also concluded that islands possess a limited capacity for harbouring new species, which results in a sensitive equilibrium between the rate of **colonisation** and **extinction**. It should be noted that some islands may be **"oceanic" islands** (e.g. formed by volcanic eruptions) and as a result have never had direct contact with the mainland, or "continental" islands, where species contact has existed as a proportion of established species originating from some period of contact.

In summary, these observations and considerations lead to the formulation of a general theory attempting to explain the distributions of organisms found in island ecosystems. Ultimately, the most important parameters for such an explanation are the size of the island and its distance to the mainland. As such, three general conclusions were drawn:

- Larger islands have more species, also known as the "target effect" (higher colonisation rates on larger islands because they represent a larger "target").
- Increased distance from the mainland (supplier of propagules) results in decreased numbers of species.
- At a constant number of species there is a continuous turnover of species due to colonisation and extinction.

The course of **colonisation and extinction** is shown schematically in Fig. 18.11a, where the intersection of both curves shows the equilibrium state, where similar rates of colonisation and extinction lead to a constant **number of species**, that is, the loss of species is compensated by the arrival of new species. While the number of species at equilibrium is constant, the identity of species and species composition may change, that is, there is a **turnover** of species. The **rate of colonisation** (establishment on the island) is dependent on the distance from the mainland. The greater the distance, the more difficult it is

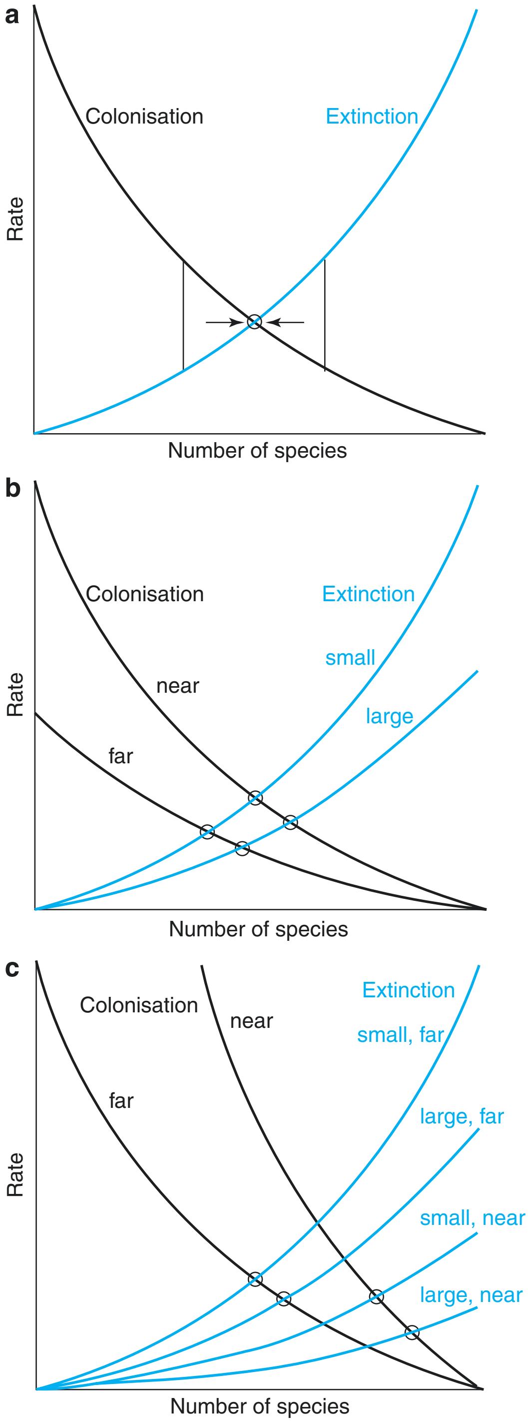


Fig. 18.11 Basic concepts in the theory of island biogeography. **a** Processes of colonisation and extinction. **b** Equilibrium (after MacArthur and Wilson 1967). **c** "Rescue effect" according to the equilibrium theory (after Brown and Gibson 1983)

for a species to become established there. The quality, type and quantity of the "source" of propagules that might arrive on the island must also be noted. The **rate of extinction**, however, is determined by the size of the island and will be much higher on small islands than on large ones because small islands can only support smaller population sizes, which have a higher risk of extinction. These conclusions have led to additional modification (Fig. 18.11b), where the following points may be deduced:

- Small islands have smaller numbers of species and higher turnover rates than large islands.
- Islands near the mainland have more species and a higher turnover rate than those further away.
- An island near the mainland returns to equilibrium after disturbance more quickly than one further away.

The equilibrium theory (or **steady-state theory**) was not generally well accepted at first. Some of the predictions of the model were verified empirically by Simberloff and Wilson (1969), who observed four islands off the coast of Florida following complete defaunation (sterilisation) and found re-establishment with the expected number of species and turnover rates in relation to size and position of the islands. Bush and Whittaker (1991) reconstructed rates of colonisation and extinction for spermatophytes on the volcano Rakata (Krakatau islands) on the basis of expedition reports and confirmed this theory as well (Fig. 18.12). On the other hand, different observations suggested that the extinction rate was dependent not only on the size of the island but also on the position of the island relative to the pool of propagules. The turnover of species on islands near the pool of propagules is rather low because of the continuous supply of propagules, which is of greater significance than the size of the island, which is known as the **rescue effect**, that is, a decreased rate of extinction due to recolonisation and immigration (Fig. 18.11c).

Criticism of the MacArthur and Wilson (1967) model is also directed at the type of predictive mathematical models used. Barkman (1990) believed that to describe complex functional relations in ecosystems, only descriptive models with limited validity should be considered. The characteristics of individual plant species and their interactions among each other have not been taken into account at all in these models. It is also assumed that the increased number of species is exclusive due to colonisation; genetic evolution is not considered, nor are the aspects of species saturation.

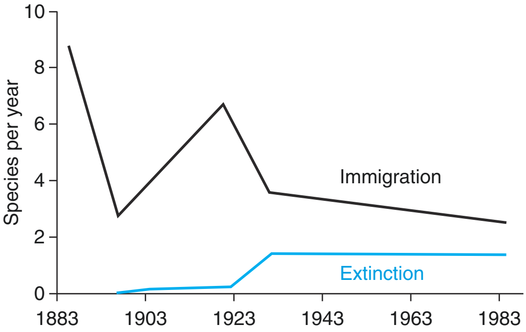


Fig. 18.12 Immigration and extinction of vascular plants on volcano Rakata, Krakatau islands, between 1883 and 1989 (after Bush and Whittaker 1991)

Lomolino and Weiser (2001) suggested that species richness may vary independently of island area, especially on small islands, and they termed this the **small island effect.** Responsible for a higher and more predictable speciation rate on larger islands is the internal geographical isolation of very different habitats such as large river basins and high mountain ranges, which are necessary for in situ speciation. Within-island speciation rates can exceed immigration as a source of species richness, at least on islands larger than 3000 km^2.

It has also been argued that phylogenetic diversification takes place on the same time scale as immigration and extinction. In this case, species richness on islands seems to be almost independent of all discussed factors. Finally, in a number of recent publications it has been highlighted more frequently that habitat heterogeneity, spatial scale and time scales (geological) are not sufficiently taken into consideration. Whittaker et al. (2008) proposed a **general dynamic model** (GDM) that provides explanations of biodiversity patterns by describing the relations between speciation, immigration and extinction, taking into account the life cycle of islands because climatic changes and geological tectonic events question the equilibrium model as well. In a proposed GDM, the most important variables considered remain—speciation, immigration and extinction—but are now combined with the evolutionary history of single islands and complete island archipelagos. The age of islands is also now taken into account; in particular, the geological history and the major tectonic events help to extend the thus far discussed conceptions of the equilibrium theory of island biogeography.

The theory of island biogeography also demonstrates that **ecological equilibrium** does not imply that ecosystems are constant and unchanging. The theory is based on a stochastic dynamic equilibrium, with a constant change in the rates of colonisation and extinction, which results in interannual variability for the actual number of species on islands and does not include speciation. Today it is becoming even more difficult to test empirically the simple assumptions of the theory of island biogeography simply due to the increasing anthropogenic influences. Although this theory has been criticised, it will be increasingly difficult to dispute, as empirical studies become increasingly harder to conduct, where the theory's application can go beyond oceanic islands.

18.4.2 "Oceanic" and "Mainland" Islands

The results of island biogeography were formulated for islands and island groups surrounded by seawater and thus lack application for terrestrial island-like habitats. Nevertheless, attempts have been made to transfer this knowledge to the mainland and island-like habitats. These habitats are islands in lakes, mountain peaks in mountainous areas, "Inselberge" in the tropics and very small, well-isolated systems such as individual deciduous trees in a coniferous forest, caves or flower heads. Nowadays, all **anthropogenic forests** or **biotope fragments** in our managed landscapes could be interpreted to some extent as islands.

However, there are a number of commonalities to justify the application of island biogeography models to mainland islands. They have defined areas, relatively sharp borders with neighbouring habitats, are smaller than the surrounding area, and are often situated in a hostile surrounding area, at least for the taxa occurring within them. However, differences should not be overlooked, such as **isolations** (genetic separation) and **separations** (spatial separation). Usually, the distance to neighbouring islands (e.g. other forest fragments) is not very large, and the surrounding area may be hostile, but it allows at least some short-term bridging. Most of all, species turnover is faster because immigration rates are higher (e.g. from species avoiding intensive agriculture and fleeing into residual forests), as are emigration rates (e.g. because of the relative proximity of comparable neighbouring islands or sudden external disturbances).

The disappearance of a species in a habitat does not necessarily result in the extinction of the species at all. If the tree line in mountains gets lower because of a climate cooling, species will probably find refuge in the valley. Ultimately, the risk of extinction is low. With subsequent warming certain species will become established again in higher altitudes. The same principle can be applied to the diversity of species in regions that became mainland species during prolonged cold periods and then, owing to certain climatic constraints within the species, became islands again in warm periods. In this case the equilibrium theory was contrasted with the **relict theory**, which states that the present-day occurrence of species and communities is the result of changes in the past.

For intensively used landscapes with many small habitats a **mosaic concept** was developed (Duelli 1993). The number of species is explained as individual "stones" in a mosaic; within the habitat the number of species increases with the number of habitat types (even those created by humans). In a mosaic landscape there are several transitional stages (**ecotones**) that may be colonised by specialists. Among animals **habitat diversity** favours those that are dependent on a seasonal change of habitats. This concept underlines the importance of transitions and edges between neighbouring habitats.

For small forest islands, species-rich **edge zones** can be observed where light-demanding species occur, but not typical forest species. In near-natural ecosystems, edge zones often act as **buffer zones** that reduce the immigration of external species to the inside of the island, which provides the habitat for obligate forest species. In intensively used agricultural landscapes such buffer zones are often lacking and the environmental gradients to the island edges are steeper. The relationship between area and number of species may thus differ according to the proportion of the edge and the core zone. In small forest patches species composition is determined by the species of the edge zone. With increasing area, species density decreases and species typical of continuous forest zones appear. The highest diversity is achieved within this transition zone between the edge and the core. In special cases this apparently simple relation is complicated by the differences in the quality and range of influences within this zone. A distinction must also be made between natural (wind, radiation) and anthropogenic (emissions, fertilisers, mechanical disturbances) environmental factors.

The function of **habitat fragment corridors** or **stepping stones** between larger mainland islands should also be noted. These may stimulate **connectivity** between habitats by assisting movement across the landscape, that is, by allowing transient residence of taxa without providing a permanent habitat. At the same time they may act as **refuges**. It is assumed that species are able to be more successful in expanding their range when stepping stones are present. This has been empirically shown for the assisted movement of animal species in fragmented landscapes, for example, for birds (Fischer and Lindenmayer 2002), but evidence on plants remains unclear.

Plants must move within landscapes as vegetative parts (ramets), pollen or seeds, assisted by wind, water or animals (Sect. 18.2.1). Therefore, the characteristics of the spatial pattern within the mainland might be equally or even more important than that of the stepping stones or corridors. However, because plants are sessile organisms, they are much more limited in their ability to decide whether a habitat is "suitable" or "hostile", where mobile species can respond more readily to gradients of resource availability. Thus, more recently, the simple corridor–matrix model of metapopulations and landscape ecology has been replaced by an integrative functional mosaic model, where the landscape is composed of patches of different movement and flow characteristics, which provides a much more natural interpretation of the relationships (Murphy and Lovett-Doust 2004).

There are examples showing that mainland islands serve as solid proof of the validity of species–area relationships according to the theory of island biogeography if the influences of humans on the island are not too significant (Fig. 18.13a). These were confirmed, for example, for island

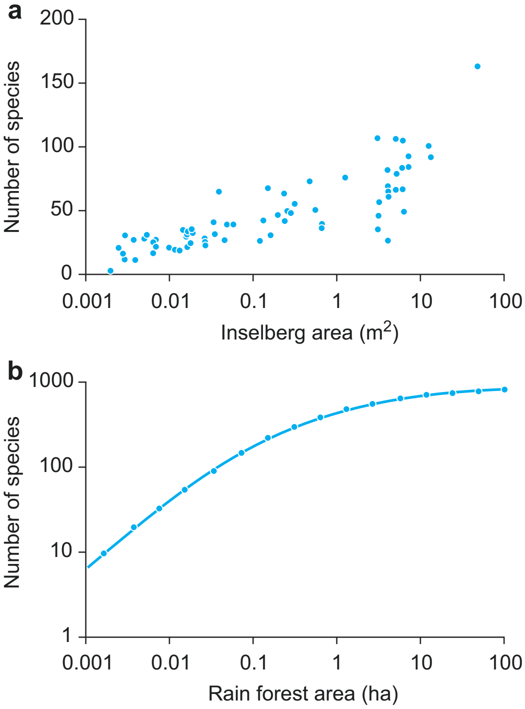


Fig. 18.13 Relationship between the number of species and habitat area. **a** On "Inselbergs" on the Ivory Coast (after Porembski and Barthlott 1993); **b** In a tropical rainforest in Malaysia (after May and Stumpf 2000)

mountains on the Ivory Coast, where the number of species increases steadily with increasing area (Porembski et al. 1995). However, in the tropical rainforests of Malaysia, increasing areas led to a significant saturation of species (in the reported case with an area of around 50 ha) (Fig. 18.13b). This contradiction has far-reaching consequences, particularly since nowadays **extinction rates** of plant and animal species are on the rise. For example, owing to the increasing losses of tropical rainforests, species extinction rates are calculated on the basis of species–area curves. The course of the curves in the figures shown here therefore allows a (too) broad spread of extinction rates. The saturation rate in tropical rainforests for an area of about 50 ha also indicates that plant sociological research examining minimum areas is possible theoretically but not practically.

Because most of us today live in managed landscapes that typically have a high degree of fragmentation, it becomes more relevant to apply the theory of island biogeography to current problems, most prominently for questions surrounding **protected areas**. The relation of core to edge zones in small habitats becomes extremely important. With a spatial decrease in such habitats the diversity of conditions at a site decreases linearly, but the quality decreases exponentially (Mader 1983). Species that are locally adapted to specific site conditions may go locally extinct if abrupt changes in these environments occur. In contrast, more widely distributed species, which have broader habitat requirements, may suffer limited consequences in these edge environments, unless habitat is lost due to a large or frequent disturbance. Therefore, application of the theory of island biogeography is, at the moment, only limited. Akatov (2012) discusses in more detail the shortcomings of this theory, its possible uses and recommendations for practical planning of nature conservation projects.

In spite of these known shortcomings, conservation planning is still mainly based on island theory, although established relations between the size of an area and distance (for mainland islands, the distance to the next suitable habitat) have stimulated further discussions on the **minimum size of areas that should be sustained**. Of course, the size of a protected area should not be calculated according to the assumptions of island biogeography exclusively. Habitats of the same or similar quality should be maintained not too far away as (perhaps only intermittently required) refuge areas, in connection with the previously mentioned **stepping stones.** These stepping stones are an important component of the concept of **biotope connectivity** for protected areas. In our agriculturally managed landscapes, such stepping stones could be small forest islands (refuge) as well as hedges, edges of fields, long-term fallow land, abandoned stone quarries or railway lines. Concepts of nature protection must incorporate, along with the protected areas, buffer zones and smaller areas of habitat fragments around the protected area, and these areas should be maximised.

Preserving a given number of species should not be the sole aim of protection measures. Large areas of **mosaics of optimal and suboptimal habitats** should be the primary goal of such an area. As such, there is no one-size-fits-all approach when considering the size and spatial patterns for a protected area and stepping stones (particularly the distances between **stepping stones** and the protected area). Each of these aspects depends on the communities one is interested in protecting and can vary substantially. Very few empirical studies have been conducted to determine the minimum distances and areas that should be used for individual groups and organisms. Currently, urgent attempts to create protected areas are based on local conditions, the plausibility of plans and the availability of land. Increasingly, the more dynamic **metapopulation concept** and especially the **functional mosaic model** (Murphy and Lovett-Doust 2004) are becoming more important to help determine these issues of protected areas. The latter not only considers the dichotomy between unsuitable and suitable habitat patches but underlines the nature of the composite landscape mosaic as a key determinant of the fate of plant populations.

18.4.3 More Models of Island Biogeography Related to the Number of Species and Area

The theory of island biogeography was taken as a paradigm. Since the 1970s and 1980s various alternative interpretations have been advanced and discussed. Those who emphasise stochastic processes explain the establishment of plant species on islands differently to those who favour determinism. All theoretical considerations are based more or less on the same factors, which are regarded as decisive for the establishment of plants; however, they are interpreted differently. As the state of knowledge currently stands, the following factors have been identified as important in this theory: the pool of propagules on the mainland, mechanisms for dispersal, distance to the island and its size, habitat characteristics, phases of succession and the conditions of competition on the island.

Connor and Simberloff (1979) assumed in their simulation model that the establishment of plants occurs stochastically without competition. They tested this model with actual data and concluded that competition does not play a role. In their interpretation, it was the parameters of dispersal that determined the success of a coloniser. Gilpin and Diamond (1982), regarding **competition** as the decisive factor, criticised this interpretation. They mentioned that closely neighbouring islands possess different species compositions, although an exchange of species would be possible. However, this exchange does not take place because the appropriate species niches are already occupied, where invading species will not displace species already established. In this more empirical model the explanation of diversity on islands is not possible without considering competition, so the species first present will be a contributing factor to succession and the plant community.

These and other models use only those parameters that are considered important. Often, the dimension of the temporal scale has not been considered. Time has been shown to be an important component for the establishment of different species, as pointed out by the models developed by Grime (1979) and Tilman (1988, Sect. 17.3). For the early establishment phase, a stochastic interpretation is more relevant, whereas for the later phases, a deterministic one is possible.

Models developed by Whittaker and Jones (1994), which criticise purely stochastic models, show how much the immigration of species depends on the dispersing vector and on the stage of succession, as exemplified by their data from the island of Krakatau during the course of colonisation over 100 years (Fig. 18.14). They found that during the initial phase, colonising species reaching the island became established on undeveloped substrates. During the second phase, anemochoric species became more important.

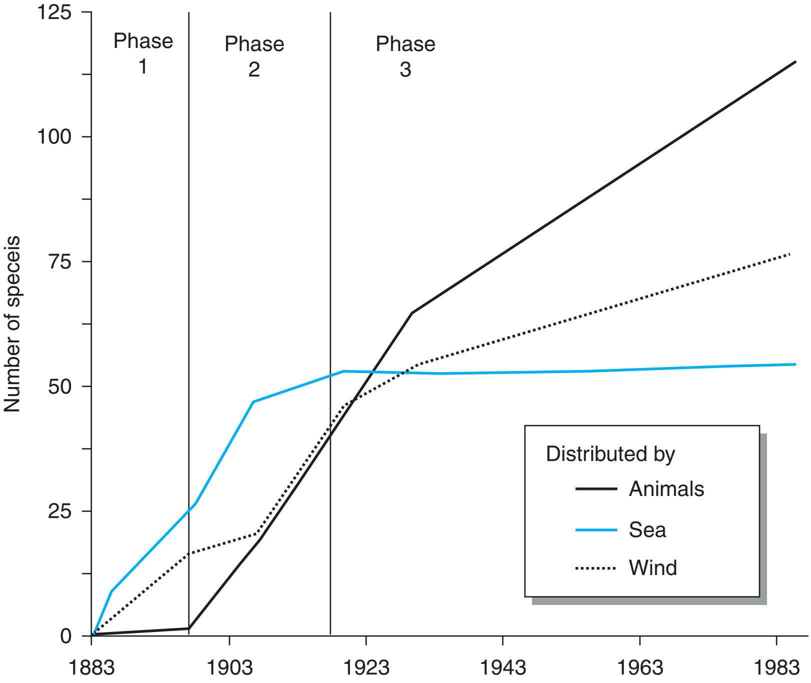


Fig. 18.14 Pioneer spermatophytes on volcano Rakata, Krakatau islands, from 1883 to 1989. The calculation is based on the assumption of minimum turnover. On the *y*-axis the data for number of species observed during different expeditions are shown. Species introduced by man are not considered (after Whittaker and Jones 1994)

However, it was only during the third phase, after substrates and the first succession stages of vegetation had developed, that zoochory played an increasingly important role. These results also suggest **an initial stochastic but later deterministic establishment of species**. It is overlooked in many interpretations that the turnover of species is not an inherent feature of a system but is largely regulated by changes in the environment. In this analysis and calculations, a minimum turnover rate is considered, but actual speciation rates are not available.

18.5 Problems of Pattern and Scale

Community ecology is often based on the concept of a continuum in time and space. **Spatial scale** has been neglected for a long time, and spatial homogeneity was often taken for granted, with spatial heterogeneity being seen as a necessary evil. However, there are different spatial levels of distribution of single plants and plant communities according to species composition and structural characteristics (e.g. forest trees or communities in small island patches or in extensive areas of several thousand hectares on large plains). Furthermore, today most landscapes are structured and determined by human activities, which influence the patterns of land and forest use depending on their size. If we deal with problems of pattern and processes of vegetation, plant coexistence and competition, then scaling issues are regarded as indispensable and fundamental to all ecological investigations because many single processes occur on different spatial scales, for example, photosynthesis (**cellular scale**), growth (**individual scale**) and species distribution (**landscape scale**) (Levin 1992).

Although fixing the scale along a hierarchy can be subjective, understanding the difference between fine (small) and coarse (large) processes becomes important. Furthermore, it is important to know the difference between the ecological and geographical understanding of scale. For landscape ecologists, cartographers and geographers, a small scale is a large area seen on a map with few details (e.g. landscape mosaic, array of patches, 1:100,000). In contrast, for a biological ecologist, small scale means a small part of a map showing many details (e.g. a habitat patch, 1:1000). Even patches can apply to different scales; special patterns demand special scales. For example, in applied ecology, for decision makers in agricultural planning or nature conservation, three **spatial scales** are most frequently used: **within habitat**, **habitat mosaic** (landscape) and **macro-scale** (**regional, landscape mosaic**).

The basis for choosing a certain scale is the degree of heterogeneity of a given environment and the specific research question being asked. There is no single "correct" natural scale. Patterns will also change across scales, where differences within a square-metre patch are likely to differ from those at the landscape scale. Further, describing an ecosystem will typically require multiple scales, ranging from the flower head of a thistle to the presence of a tree species across the Mediterranean landscape. In a fine-scale approach, species "a" and "b" may occur in different plots. In such a fine-scale approach, the diverse zonation of plant communities of a complex riverside vegetation becomes visible (Fig. 17.25). These details would be lost in a broad-scale approach using a landscape transect of a large river valley owing to necessary generalisation (Fig. 17.12).

In this context it is important to define the finest details (units), which should be visible in the chosen scale (grain), and the area chosen for investigation (extent). All three depend largely on the size of the organism or the community. In a fragmented landscape, the distance between fragments of the same quality is taken into account for the choice of an adapted scale. Grain and extent change with every change of scale. For large-scale investigations remote sensing has quite often been used; it is even useful for plant communities but would not be used at the individual scale.

Even if all these aspects are considered, we must realise that the choice of a certain scale for a certain spatial analysis is based on the individual perception of the research problem. The chosen scale seems “right” or “appropriate”, but ultimately it is still arbitrary. To obtain better answers to the comprehensive questions surrounding how **environmental heterogeneity** changes with scale, Wiens (1989) proposed a multiscale approach, where better insight into the interrelations between scale-dependent patterns and their causes occurs within different ecosystems. New macro-scale approaches have also been suggested, prompted by problems of global change and also based on methodological reflections coming from **landscape ecology**. These concern especially the study of the arrangement of larger ecological systems in space. Certain spatial patterns can only be interpreted on a larger scale, and only on such a scale can a better understanding of these patterns and ecological processes in this new field of **macroecology** be obtained (Gaston and Blackburn 2000). We illustrate these aspects with some examples in what follows.

Two centuries ago, Alexander von Humboldt (1807) recognised that species richness declined significantly as one follows the latitudinal gradient from the tropics to the extratropical regions. Based on the distribution of mammals, Rapoport (1975) found also a greater species diversity in the tropics, and Stevens (1992) underlined these findings and added an **altitudinal gradient** to this so-called **Rapaport’s rule**, to which also many exceptions have been noted. Latitude can be regarded as a surrogate for different environmental gradients, for example, changes in temperature, insolation, seasonality—on large scales, such as hemispheres, continents and countries (Sect. 20.3). Moles et al. (2009) studied global patterns in plant height, a decisive character of a species’ ability to compete for light, and found a close relationship between latitude and height due to a major difference in plant strategy between low- and high-latitude systems. Nobis et al. (2012) used a **large-scale global approach** to analyse the variation of morphological traits (especially needle characteristics). They detected a strong latitudinal correlation with phylogenetic signals due to a phylogenetic structural environmental variation among the 103 *Pinus* species they studied.

In Switzerland, the relationships between species richness, neophytes and their environment were analysed using a 1-km^2-grid-system approach. The results suggest that climate and land use are the primary forces behind environmental change. **Neophytes** were found to increase in abundance with global warming, with the highest rates occurring within urban regions. Again in Switzerland, along an elevation gradient (263–3175 m a.s.l.) within 400 km^2 plots the interspecific variation of 708 plant species of adult age showed clearly that temperature was the most important environmental factor in increases in age with higher elevations. Further, it was found that under warmer conditions at lower elevations the lifespan of many species was shorter. This indicates that global warming could contribute to faster species turnover, favouring short-lived species (Nobis and Schweingruber 2013).

The **altitudinal gradient** is a very powerful basis for testing ecological and evolutionary responses of plants and plant communities to natural environmental influences (Körner 2003). Changing temperature, together with radiation and other climatic trends, leads not only to a zonation of communities with different floristic composition but also different structurally defined communities. The phenotypic variations of pine needles (including their xeromorphic characteristics) have been assessed along a transect (ranging from lowland desert to a mountainous cloud forest) within five Canary islands as a means of describing large-scale altitudinal differentiation, and it was found that environmental changes mainly described the differences, taking into account phylogenetic influences (Lopez et al. 2008).

There are still methodological problems in the complex field of scale-based plant and plant community monitoring and in applying the results for issues such as agricultural and forest management and conservation planning. However, large-scale projects such as the Swiss Biodiversity Biomonitoring Programme are being designed to produce information about the dynamics of biodiversity at different, but especially large, scales.

Summary

- Closely related to the development of plants and plant communities in time is their spatial distribution. The temporal dynamic leads to distribution patterns of species and plant communities. It is also the task of plant ecology to recognise, describe and explain such distribution patterns. Knowledge about the temporal and spatial dynamics of plant communities is indispensable for understanding biotic interactions within ecosystems
- The distribution of plants starts with a mobile phase in the life cycle of all plants, with the dispersal of propagules (seeds, fruits, parts of adult plants and even whole plants). Rarely do plants just drop ripened seeds; typically, most benefit from the use of a variety of dispersal vectors such as wind, water and animals in order to distribute their propagules while trying to find suitable places for germination and final establishment
- There is no guarantee that, following dispersal, a suitable substrate (safe site) will be found or adequate time for germination will be given. Many propagules may remain dormant for some time in a seed bank, waiting for favourable environmental conditions (light, temperature and water availability)
- Some species, with very effective dispersal vectors and low demands of habitat conditions, are today widespread, despite continental and climatic barriers (cosmopolites). Others are bound to only small territories owing to their species-specific requirements for habitat quality, slow dispersal or young existence (endemics). Species with similar characteristics often coexist in areas with similar environmental conditions (habitat filtering). This is the basis for the area types (floristic elements, geo-elements). The interpretation of the spatial distribution of area types led to a hierarchical order, ranging from these basic areas over floral provinces and regions up to the plant kingdoms (Holarctic, Neo- and Palaetropic, Capensis, Australis and Antarctic)
- Area types have also been an important starting point for ongoing discussions of species area relations and for the classical island biogeography equilibrium theory. On the basis of this theory, many new models were developed to acquire a better understanding of how plants become established on islands and of area limits. In some of these models islands are not only understood as small continental parts surrounded by the sea but also as a forest “island” in an otherwise tree-free area. There are two kinds of general models: (1) stochastic models, which possess some inherent randomness, and (2) deterministic models, in which the output is fully determined by the parameter values and the initial conditions (i.e. competition, habitat diversity or some degree of disturbance). However, currently our knowledge about how many factors and their interactions with each other influence species–area relations remains limited

References

Akatov VV (2012) 60 years of the equilibrium theory of insular biogeography: problems of testing, results of the field studies, applied importance. Zh Obshch 73:163–182

Al Hubaishi A, Müller-Hohenstein K (1984) An introduction to the vegetation of Yemen. Ecological basis, floristic composition, human influence. GTZ, Eschborn

Arrhenius O (1921) Species and area. J Ecol 9:95–99

Barkman JJ (1990) Controversies and perspectives in plant ecology and vegetation science. Phytocoenologia 18:565–590

Baskin CC, Baskin JM (2001) Seeds: ecology, biogeography, and evolution of dormancy and germination. Acad Press, San Diego

Blüthgen J (1964) Allgemeine Klimageographie. Lehrbuch der Allgemeinen Geographie Band 2. De Gruyter, Berlin

Brovkin V, Ganopolski A, Svirezher Y (1997) A continuous climate-vegetation classification for use in climate-biosphere studies. Ecol Model 101:251–261

Brown JH, Gibson AC (1983) Biogeography. Mosby, St. Louis

Bush MB, Whittaker RJ (1991) Krakatau: colonisation patterns and hierarchies. J Biogeogr 18:341–356

Connor EF, Simberloff D (1979) The assembly of species communities: change or competition? Ecology 60:1132–1140

Deil U, Müller-Hohenstein K (1984) Fragmenta Phytosociologica Arabiae-Felicis I—Eine Euphorbia-balsamifera-Gesellschaft aus dem jemenitischen Hochland und ihre Beziehungen zu makaronesichen Pflanzengesellschaften. Flora 175:407–426

Diels L (1908) Pflanzengeographie. GJ Göschen, Leipzig

Duelli P (1993) Ökologischer Ausgleich in der Kulturlandschaft: Eine Herausforderung für Politik, Naturschutz und ökologische Forschung. Verh Ges Ökol 22:3–8

Engel TR (2000) Seed dispersal and forest regeneration in a tropical lowland biocoenosis (Shimba Hills, Kenya). PhD Thesis, University of Bayreuth, Germany

Espigares T, Peco B (1993) Mediterranean pasture dynamics: the role of germination. J Veg Sci 4:189–194

Fangliang H, Legendre P, LaFrankie JV (1997) Distribution patterns of tree species in a Malaysian tropical rain forest. J Veg Sci 8:105–114

Fenner M (1985) Seed ecology. Chapman and Hall, London

Fischer J, Lindenmayer D (2002) The conservation value of paddock trees for birds in a variegated landscape in southern New Wales. 2. Paddock trees as stepping stones. Biodivers Conserv 11:833–849

Frey W, Lösch R (1998) Lehrbuch der Geobotanik. Pflanze und Vegetation in Raum und Zeit. Fischer, Stuttgart

Gaston KJ, Blackburn TM (2000) Pattern and processes in macroecology. Blackwell, Oxford

Gigon A (1987) A hierarchic approach in causal ecosystem analysis. The calcifuge-calcicole problem in alpine grasslands. Ecological studies, vol 61. Springer, Berlin Heidelberg New York

Gilpin ME, Diamond JM (1982) Factors contributing to non-randomness in species co-occurrences on islands. Oecologia 52:75–84

Gorman (1979) Island Ecology. Chapman & Hall, London

Grime JP (1979) Plant strategies and vegetation processes. Wiley, Chichester

Holdridge LR (1966) The life zone system. Adansonia VI 2:199–203

Howe HF, Smallwood J (1982) Ecology of seed dispersal. Ann Rev Ecol Syst 13:201–228

Howe HF, Westley LC (1986) Ecology of pollination and seed dispersal. In: Crawley MG (ed) Plant ecology. Blackwell, Oxford, pp 262–283

Humboldt von A (1807) Essai sur la Géographie des Plantes, Paris

Johnson MP, Simberloff DS (1974) Environmental determinants of island species in the British Isles. J Biogeogr 1:149–154

Köppen W (1900) Versuch einer Klassifikation der Klimate vorzugsweise nach ihren Beziehungen zur Pflanzenwelt. Geogr Zeitschr 6(593–611):657–679

Körner C (2003) Alpine plant life. Functional plant ecology of high mountain ecosystems. Springer, Berlin, Heidelberg, New York

Kohn DD, Walsh DM (1994) Plant species richness - the effect of island size and habitat diversity. J Ecol 82:367–377

Kürschner H (1986) Omanisch-makranische Disjunktion. Ein Beitrag zur pflanzengeographischen Stellung und zu den florengenetischen Beziehungen Omans. Bot Jahrb Syst 106:541–562

Lepart J, Escarre J (1983) La succession végétale, mécanismes et modèles: analyse bibliographique. Bull Ecol 14:133–178

Levin SA (1992) The problem of pattern and scale in ecology. Ecol 73:1943–1967

Lomolino MV, Weiser MD (2001) Towards a more general species-area relationship: diversity on all islands, great and small. J Biogeogr 28:431–445

Lopez R, Climent J, Gil L (2008) From desert to cloud forest: the non-trivial phenotypic variation of Canary Island pine needles. Trees 22:843–849

MacArthur RH, Wilson EO (1967) The theory of Island biogeography. Princeton University Press, Princeton

Mader HJ (1983) Warum haben kleine Inselbiotope hohe Artenzahlen? Natur Landschaft 58:367–370

May RM, Stumpf PH (2000) Species area relations in tropical forests. Science 290:2084–2086

Moles AT, Warton DI, Warman L, Swenson NG, Laffan SW, Zanne AE, Pitman A, Hemmings FA, Leishman MR (2009) Global patterns in plant height. J Ecol 97:923–932

Müller-Hohenstein K (1981) Die Landschaftsgürtel der Erde. 2. Auf. Teuber, Stuttgart

Müller-Hohenstein K (1988) Zur Arealkunde der arabischen Halbinsel. Erde 119:65–74

Murphy HT, Lovett-Doust J (2004) Context and connectivity in plant metapopulations and landscape mosaics: does the matrix matter? Oikos 105:3–14

Nobis MP, Schweingruber FH (2013) Adult age of vascular plant species along an elevational land-use and climate gradient. Ecography 36:1076–1085

Nobis MP, Traiser C, Roth-Nebelsick A (2012) Latitudinal variation in morphological traits of the genus Pinus and its relation to environmental and phylogentic signals. Plant Ecol and Div 5:1–11

Porembski S, Barthlott W (1993) Ökogeographische Differenzierung und Diversität der Vegetation von Inselbergen in der Elfenbeinküste. In: Barthlott W, Naumann CM, Schmidt-Loske K, Schuchmann K (eds) Animal-plant interactions in tropical environments. Results of the Annual Meeting of the German Society for Tropical Ecology, Bonn, pp 149–158

Porembski S, Brown G, Barthlott W (1995) An inverted latitudinal gradient of plant diversity in shallow depressions on Ivorian inselbergs. Vegetatio 117:151–163

Rapoport EH (1975) Areografia: Estrategias Geograficas de las Especies. Fondo de Cultura Economica, Mexico

Richter M (1997) Allgemeine Pflanzengeographie. Teubner, Stuttgart

Scherer M, Deil U (1997) Floristische Diversität und Vegetationsstruktur in traditionellen und modernen Kulturlandschaften—untersucht an Beispielen aus

Chile und dem westlichen Mittelmeerraum. Z für Ökologie und Naturschutz 6:19–31

Schupp EW (1993) Quantity, quality and the effectiveness of seed dispersal by animals. Vegetatio 107:15–29

Simberloff DS, Wilson EO (1969) Experimental zoogeography of islands: the colonisation of empty islands. Ecology 50:278–298

Sitch S, Smith B, Prentice IC, Arneth A, Bondeau A, Cramer W, Kaplan JO, Levis S, Lucht W, Sykes MT, Thonicke K, Venevsky S (2003) Evaluation of ecosystem dynamics, plant geography and terrestrial carbon cycling in the LPJ dynamic global vegetation Model. Glob Change Biol 9:161–185

Solarik KA, Gravel D, Ameztegui A, Bergeron Y, Messier C (2016) Assessing tree germination resilience to global warming: a manipulative experiment using sugar maple (Acer saccharum). Seed Sci Res 26:153–164

Stevens GC (1992) The elevational gradient in altitudinal range: an extension of Rapoports latitudinal rule to altitude. Am Nat 140:893–911

Strasburger E, Sitte P (1998) Lehrbuch der Botanik für Hochschulen. Fischer, Stuttgart

Taschler D, Neuner G (2004) Summer frost resistance and freezing patterns measured in situ in leaves of major alpine plant growth forms in relation to their upper distribution boundary. Plant Cell Environ 27: 737–746

Tilman D (1988) Plant strategies and the dynamic and structure of plant communities. Princeton University Press, Princeton

Troll C, Paffen KH (1964) Karte der Jahreszeitenklimate der Erde. Erdkunde 18:5–29

Urbanska KM (1992) Populationsbiologie der Pflanzen. Grundlagen, Probleme, Perspektiven. UTB 1631, C. Fischer, Stuttgart

von Wissmann H (1964) Zur Geschichte und Landeskunde von Alt-Südarabien. Kommission bei Rudolf M. Rohrer, Graz

Walter H (1986) Allgemeine Geobotanik. Ulmer, Stuttgart

Whittaker RJ, Jones SH (1994) Structure in rebuilding insular ecosystems: an empirically derived model. Oikos 69:524–529

Whittaker RJ, Triantis KA, Ladle RJ (2008) A general dynamic theory of oceanic island biogeography. J Biogeogr 35:977–994

Wiens JA (1989) Spatial scaling in ecology. Funct Ecol 3:385–397

19

Interactions Between Plants, Plant Communities and the Abiotic and Biotic Environment

With Contributions from C. F. Dormann and H. M. Schaefer

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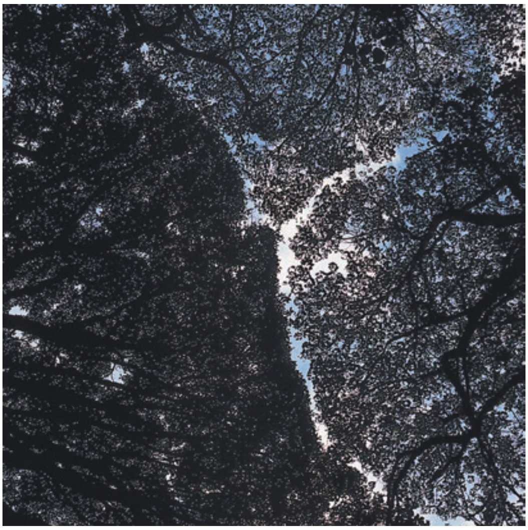

Competition or coexistence? View of the almost completely closed canopy of a mountain rainforest on Kilimanjaro (Machame, 2400 m above sea level) (Photo: K. Müller-Hohenstein)

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19.1 Introduction

In the previous chapters we discussed aspects of the development of plants and plant communities over the course of time (Chap. 17) and their distribution in space (Chap. 18). In this chapter, the **interrelations and interactions between plants and their environment** are described. Plants and plant communities not only depend on environmental conditions but also affect their environment, changing climatic conditions and soils, and thus contribute to temporal dynamics and spatial changes.

The formation of plant communities involves interactions between different plant species (interspecific) as well as between the individuals of the same species (intraspecific).The niches for plant species in a community are determined by **competition and coexistence.** And finally, plants are only one part of the entire community of organisms. In particular, animals play an important role as pollinators, seed dispersers and herbivores.

It must be underlined that many interactions are extremely complex and far from being completely understood, especially if one considers not just the interactions between single individuals or plant species but also within the community of all organisms (**biocoenosis**). Furthermore, it should not be forgotten that over the course of these interactions plants may change the abiotic site conditions.

19.2 Influences of Vegetation on Site Conditions

The extent to which vegetation influences the growing conditions on a site becomes clear when the vegetation is disturbed or completely removed. According to Lovelock (1992), drastic changes would occur on Earth if there was no life, particularly the composition of the atmosphere, which would become oxygen free, and the current surface temperatures of about 300 K would be affected.

Plant cover influences the entire biological community and the abiotic environment. Already **microclimatic conditions** change over small distances. Increased **soil erosion** at an intermediate scale is witness to the change in run-off of water and to the protective effect of vegetation cover (Fig. 19.1).

Fig. 19.1 Vegetation affecting the environment. Lower hill slope, with advanced degradation of vegetation, in central Atlas Mountains (Morocco). The roots of the few remaining bushes (*Quercus rotundifolia*, *Pistacia lentiscus*) protect the soil from erosion. The plants seem to be growing on a pedestal. (Photo: K. Müller-Hohenstein)

Plants and plant communities not only fulfill their requirements for light, water and nutrients at the site where they grow, they also affect it. This may improve the conditions at the site to the plant's advantage, for example, by increasing the humus content of the soil, which provides a better water supply owing to the increased water storage capacity, or they make conditions worse because they create conditions for species that outcompete them (see the facilitation model according to Connel and Slatyer 1977) (Chap. 17). Undemanding pioneers (e.g. lichens on bare rock) must make way for more demanding species, for example, mosses and flowering plants on substrates prepared by **biogenic weathering**.

Wilson and Agnew (1992) distinguished various feedback switches, almost like electrical control systems, that are triggered by vegetation in relation to changes on a site. Thus, a plant community not only changes its environment but in addition also affects neighbouring plant communities (e.g. by shading, wind protection). In each of these cases such effects must be regarded as dynamic processes. They concern mostly climatic and edaphic relations, but also aspects of relief formation at several spatial and temporal scales. In what follows, these connections will be explained using examples at the level of the plant community.

19.2.1 Influences of Vegetation on Climatic Conditions

Climatic factors (especially temperature and precipitation) are directly related to vegetation cover and structure, with the effects varying on different spatial scales. In the case of a closed forest, these influences lead also to microclimatic changes (between the soil surface and the canopy) in terms of climatic differentiations in the stem region, the crown and the entire forested area. Within the space occupied by vegetation, horizontal and vertical patterns and gradients of climatic parameters must be measured in order to be able to recognise the interactions between vegetation and climate. Figure 19.2 shows the variability of temperatures within a forest-edge ecosystem, which largely depends on exposure to sun. Surface temperatures measured at places only a few metres apart at the edge of a forest in the Netherlands at noon on a clear day in March correspond, in their extremes, to those in boreal forests (north side) and temperate deserts (south side). However, these differences apply only under direct solar radiation and disappear completely under cloudy skies. It is obvious that characterisation of the climate in a stand requires the temporal course of a climatic variable and its spatial differentiation.

For the climate of a stand, the **albedo** is just as important as the layers of vegetation, the type of branching of trees and shrubs, and the density and position of leaves. These structural characteristics of plant communities determine the amount of light that reaches the assimilating organs of individual plants. A dense tree canopy may severely decrease the light available for light-demanding species while also providing shade for shade-demanding plants. Oasis cultures occur in arid regions all over the world; their multiple layers of annual and permanent crops—cereals and vegetables, fruit-bearing shrubs and small trees, closed palm canopies—would not be possible without the shade provided by the date palms in the strong radiation conditions and with the dry air in arid regions.

In low, one-layered stands, for example, in lichen communities and on moss carpets during

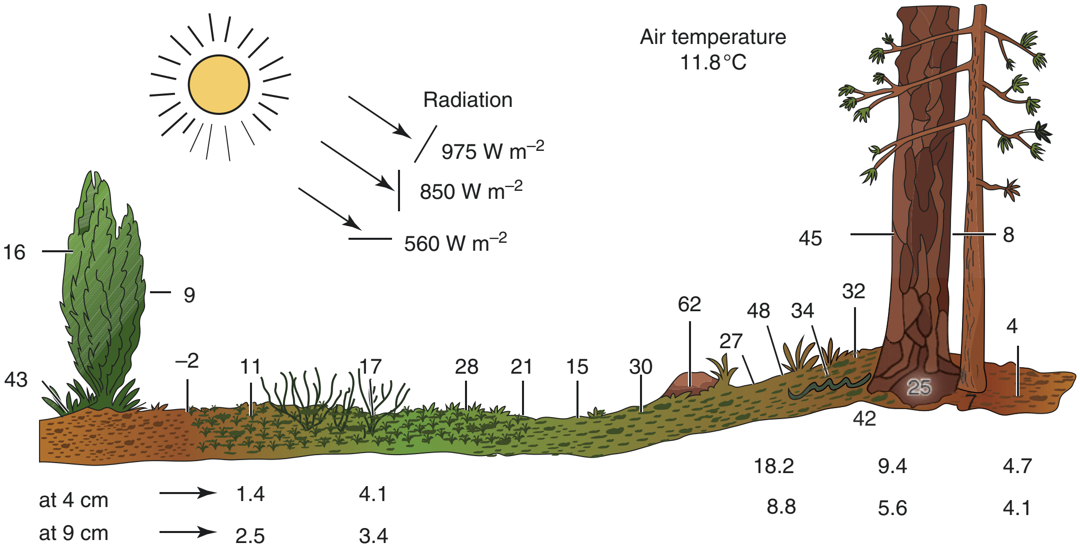

Fig. 19.2 Vegetation affecting temperature regimes. Surface temperatures along a transect from a forest edge to a juniper heath in the Netherlands. Soil temperatures were measured at 4 and 9 cm depth, air temperature at 1 m above the ground, the input radiation to surfaces at different inclinations was 560, 850 and 975 W m^{-2}. (After Stoudtjesdijk and Barkman 1992)

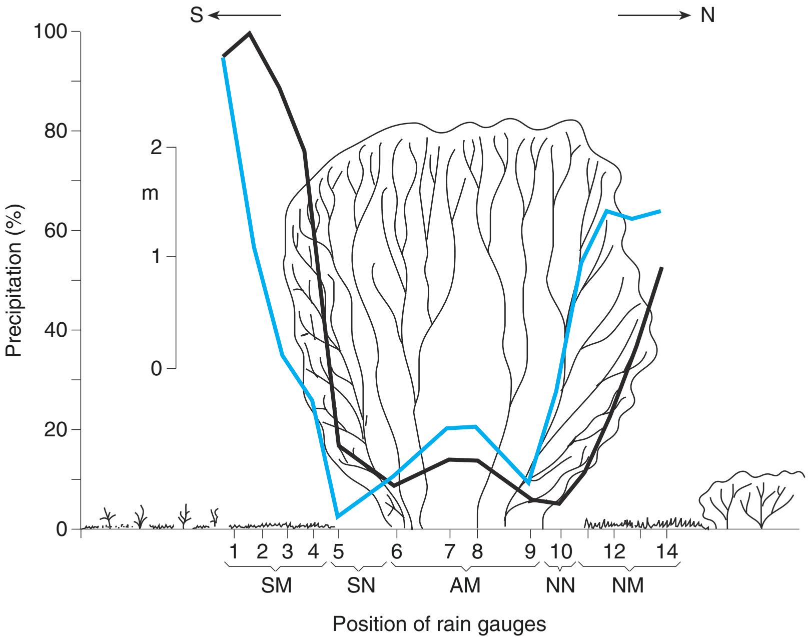

Fig. 19.3 Vegetation effects on small-scale distribution of rainfall. Distribution of rainfall along transect through juniper bush, measured with 14 rain gauges with a northerly wind (black line) and southerly wind (blue line). Maximum rainfall is equal to 100%. SM South, mossy; SN south, needle litter; AM without moss; NN north, needle litter; NM north mossy. (After Stoudtjesdijk and Barkman 1992)

the day, higher temperatures are reached than in neighbouring open areas. However, because of the high surface radiation during the night, temperatures may fall much more than in multilayered stands. In the latter, temperature layers can be observed. The first maximum, higher than the temperature in open spaces, is reached in the canopy at higher daytime temperature fluctuations; a second occurs at the ground surface, especially in more open areas. In the space between the canopy and soil surface, temperatures are more balanced. Temperatures on the ground may even be further affected by the consistency of litter. According to Stoutjesdijk and Barkman (1992) on a clear winter night −4 °C was measured under Douglas fir, under pine −9 °C, but under larch and oaks −14 °C. Thus, in species-rich forests, considerable differences occur over small distances. For the development of spring geophytes, the favourable light and temperature conditions in deciduous forests are decisive. Conditions under oak are usually more favourable than under beech and hornbeam.

Vegetation also influences precipitation over small distances. This was measured at different wind speeds (Stoudtjesdijk and Barkman 1992) for isolated juniper bushes with dense needles on the southern side in a shrub and grass community (Fig. 19.3). **Interception** is very important in multilayered stands (Sect. 16.1). The path of a raindrop is determined primarily by the structural characteristics of the plant cover. Some plant species are able, because of the form of their leaves or needles, to comb out precipitation (*Pinus patula*, *P. canariense*). Run-off paths on branches and stems and the distribution of water at the base of the stem are also important. In total, the measured interception by conifers is about twice that of deciduous trees, but it also depends on the abundance and intensity of precipitation. Gaps in a stand, development of the leaves in different seasons and layering of the stand are important determinants of the amount of water that actually reaches the ground. Also the relative humidity inside a stand is higher and more balanced than in open spaces.

Various forms of **wind shear** show the influence of wind on vegetation. It may be concluded that plant stands also weaken wind, since hedges provide **protective wind barriers** (Fig. 19.4). This depends on the height, width and permeability of the vegetation, and the reduction in wind speed and the development of turbulence, in turn, cause large differences in microclimatic conditions within small scales. Also the energy transport and transport of materials—such as atmospheric inputs, soil particles and litter—and how they are affected by vegetation must be considered.

Dune systems along coastlines worldwide characterise littoral zones. The sequence of different

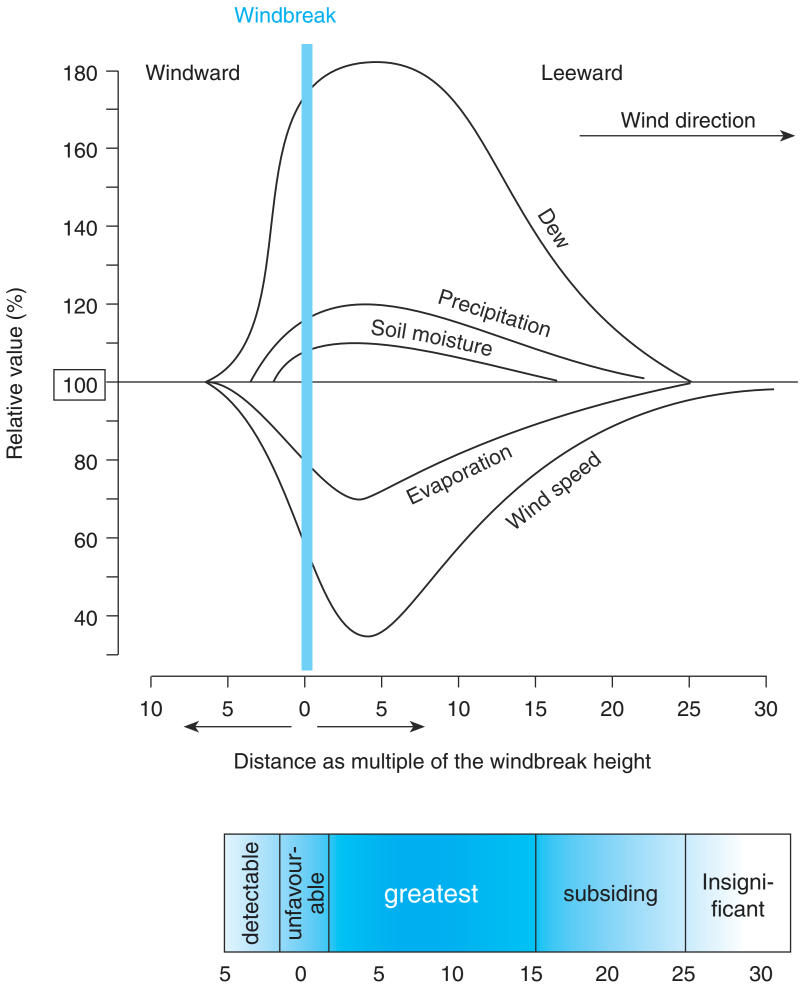

Fig. 19.4 Influence of a shelter belt on the microclimate. (After Reichelt and Wilmanns 1973)

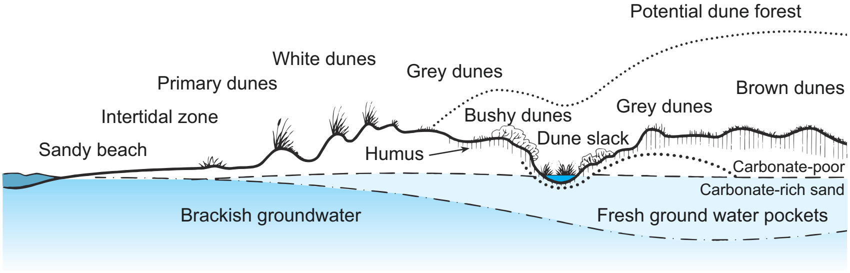

Fig. 19.5 Sequence of habitats in coastal regions with dune formation. (After Ellenberg and Leuschner 2010)

sites along the coast into the hinterland is shown in Fig. 19.5. Some plant species are able to stabilise mobile sand, which is transported by **wind**, and influence transitions from the coast to the hinterland. These plants are able to withstand the mechanical effects of wind and the salt carried by it. Following from the sea towards the land, communities include sea rocket (*Cakile maritima*), lyme grass (*Elymus arenarius*) and marram grass (*Ammophila arenaria*). The latter is the most important primary dune species and is not only able to stabilise dunes but also to tolerate being covered by sand because it forms layers of rhizomes and survives the cover of **primary dunes** (**white dunes**), which are often metres high. If marram grass is not covered by sand, **secondary** and **tertiary dunes** (**grey** and **brown dunes**) develop from the gradual accumulation of humus from the decaying plant material. Tertiary dunes are recognised by an increasingly closed cover of dune grasses and shrub communities. Without plant species adapted in such a way, this formation of relief and zonation would not be possible. At the moment, dune complexes disturbed by tourists are successfully protected by planting with the salt-tolerant sand dune couch grass (*Agropyron junceum*) and marram grass (*Ammophila arenaria*), which are tolerant to sand cover.

Plants also play a role in triggering the formation of inland dunes. Long (1954) traced the origin of the **Nebket** (Arabic term for a special dune system) in North Africa to single, particularly resistant, dwarf shrubs. Sand blown in by the wind is deposited on the leeward and windward sides of these shrubs. With time, the accumulation of sand serves as a water reservoir and improves the nutrient supply of the "initial shrub", which is able to grow better and thus offers possibilities for other plants to establish and finally for animals to settle. Thus, particularly at the edges of deserts, island-like dune systems develop with communities surprisingly rich in species in an otherwise hostile environment.

This shows that vegetation, with its floristic composition and, above all, with its structural characteristics, greatly influences the variability of environmental conditions. Many vegetation patterns can be understood only if the influences of vegetation that cause the differences in the local climate are known.

19.2.2 Influences of Vegetation on Weathering and Topography

Even though climatic and tectonic factors are most important for geomorphological processes, the influences of organisms on the formation of relief and, thus, for changing site conditions must not be overlooked. Viles (1988) distinguishes between active and passive relations between organisms and the site factors that depend on relief. The former are biogenic weathering, formation of **biogenic sediments** (e.g. lime deposits), **bioturbation** (e.g. burrowing animals) and **bioerosion** (e.g. from grazing animals). Passive relations, arising from the mere presence of the vegetation, can be seen in dune formation and in the accumulation of organic matter (e.g. in bogs or as a consequence of damming rivers).

Weathering or **soil formation** was generally interpreted as an exogenous, climatic and physicochemically regulated process. Today, organisms are regarded as playing an important role in weathering in all climatic zones. For example, **cyanobacteria** participate in the formation of **desert varnish**, a covering of iron and manganese compounds, thereby securing their own habitat with a protective crust. The metabolic processes of lichens, cyanobacteria and fungi result in the release of acids and chelating compounds that, under humid conditions, dissolve some components in rocks either completely (as with limestone) or selectively and remove the mineral components. **Endolithic lichens,** living within rocks (e.g. from the genera *Caloplaca* and *Buellia*), and the many different species living on the surface of rocks (**epilithic**) contribute to biophysical and biochemical weathering in all climatic conditions (Belnap and Lange 2001). Under moist conditions, crusted rocky surfaces are conserved by lichen cover, but in arid regions lichens can be very destructive. Danin (1986) recognised in the weathering forms observed in the Negev a dynamic equilibrium between surface destruction and crust formation. The formation of particular types of crusts and patterns of dissolution caused by different moisture conditions also allow conclusions to be drawn about more humid palaeoclimatic conditions.

Bioturbation and its various forms (e.g. by earthworms in temperate habitats, ground-dwelling small mammals in tropical high mountains) and consequences for habitats are only mentioned here, as is **bioerosion**, with its often catastrophic consequences in overgrazed mountain regions (Fig. 17.17d, Chap. 17). An example of the passive role of vegetation in forming reliefs is living submerged macrophytic vegetation. The **dynamics of river beds** and **river valleys** are particularly regulated by vegetation. Plants occupying river banks or that are submerged influence water flow and, thus, affect erosion and the deposition of materials transported in rivers. In non-canalised rivers in Europe, islands covered with canary grass (*Phalaris canariensis*) develop in the river bed. The German tamarisk (*Myricaria germanica*) not only withstands the mechanical strain of floods but also contributes considerably to the stabilisation of river banks in the valleys of the alpine lowlands.

Other climatic zones see similar, typical influences of vegetation on the topography along rivers and their banks. For example, in the lowland tropics, vegetation near river banks acts as zones trapping sediment and floating materials, thereby slowing the flow of the river and providing protection from erosion by damming the river. In near-natural river valleys, small mosaics of different plant communities frequently occur. These communities provide information on the water supply and the **mechanical strain** caused by water, as well as about the modifying influences of plants. Such mosaics can only be understood if the interactions between vegetation and site are considered (Fig. 17.25, Chap. 17).

19.2.3 Influences of Vegetation on Soils

Influences of vegetation on the fertility and water relations of soils belong to the most important biotic–abiotic interactions in ecosystems. Earlier discussion of primary successions emphasised the contribution of pioneer plants in providing the first **organic litter** in the formation of soils and, thus, in preparing conditions at a site for more demanding plants. The quality and amount of organic litter are very important for **pedogenic processes** and the characteristics of soils. This litter determines the C/N ratio of soils (especially the A-horizons) as well as possibly starts or increases soil acidification.

Plants also influence the input of nitrogen and other nutrients (as well as pollutants) either directly through N-fixation (Leguminosae) or indirectly through their effects on atmospheric nutrient deposition. Rode et al. (1996) showed how diverse these inputs can be depending on the species of trees and shrubs at a given site. Input is high in birch-pine forests, mainly owing to the roughness of these stands and the presence of needles on pines in winter. Interception is three to ten times higher than for oak and beech forests. That individual tree species are able to determine the chemical characteristics of soils was proved by Reich et al. (2005) using 30-year old plantations of 14 different tree species. Especially those species that have high calcium concentrations in their litter increase soil pH, exchangeable calcium, per cent base saturation and forest floor turnover rate. In addition, such species also favour earthworm diversity and abundance.

One result of current experimental studies on biodiversity shows that increasing plant species diversity increases availability of N in the soil (Dybzinski et al. 2008). An important reason for this higher N (and C) accumulation is most probably the complementarity of species belonging to different plant functional groups such as legumes and C4 grasses (Fornara and Tilman 2008) by increasing the supply of nutrients via both greater inputs and greater retention (Sect. 20.4). Not only the content of certain nutrients but particularly their availability are closely linked to the organic material in soil. However, the accumulation of **allelochemicals** and organic substances that are difficult to degrade may render a site unsuitable for particular plant species.

Vegetation affects not only the chemistry of soils but also their physical characteristics. Depending on the rooting systems of plant species and on the type of litter, soil structures are formed that allow aeration of the soil and contribute to the transformation of an abiotic substrate into a habitat for a very wide range of organisms in the soil (**edaphon**).

The structural characteristics of soils and their content of organic substances brought about by vegetation are closely linked to the water relations of the soil. A dense plant cover not only protects against erosion but may also increase water retention, contributing to more balanced run-off, and may limit flooding over large areas.

19.3 Interactions Among Plants (Contribution by C. F. Dormann)

The growth of an individual plant is strongly affected, both negatively and positively, by its neighbours. Overall, negative effects—competition—are the more prevalent form of plant–plant interactions, but in specific situations positive effects (facilitation) are also detectable. Table 19.1 shows the potential types of interactions between organisms. We shall address positive and neutral plant–plant interactions first before looking more closely at competition.

19.3.1 Positive and Neutral Plant–Plant Interactions

19.3.1.1 Symbiosis and Other Non-negative Relations of Plants and Fungi

Symbiosis refers to close positive interactions between two partners from different taxa (Fig. 19.6, top row). Traditionally, and in most of Europe, symbiosis refers to a mutualistic interaction. In other parts of the world and particularly in zoology, symbiosis refers to any kind of interaction, or at least any kind of cohabitation, including parasitism. Here we use the term in the traditional, strict sense. The most famous symbiosis with plants outside the marine world involves fungi. We include this interaction here to construct a gradient from obligatory symbiosis to facultative (and temporary) facilitation.

Above-ground, fungi of the phylum Ascomycetes form a symbiosis with green algae of the division Chlorophyta in the form of **lichens**. In this symbiosis, the algal partner provides the capacity to fix CO_2, the end product of which they share with the fungi, while the fungal partner provides access to nutrients and serves as the holdfast in the substrate. It can be argued that fungi have domesticated algae for their own benefit. The advantage of this symbiosis is that, while both species have free-living forms in other habitats, only in combination can they colonise the barren rocks and tree barks on which they grow. Lichens form, in some sense, a new organism. Sexual reproduction of each partner is sometimes still possible, but propagation of lichens occurs largely through the dispersal of lichen fragments comprising both partners.

Below-ground, various fungi interact with plant roots as **mycorrhizae**. Depending on the specialisation of this interaction, it varies from obligatory partnership (e.g. in epiphytic tropical orchids, where fungal spores may even travel on dust-fine seeds) over high host specificity (in ericoid mycorrhizae) to more opportunistic matches (in vascular–arbuscular mycorrhizae (VAM) and ecto-mycorrhizae). In the latter cases the evolutionary parasitic history of this association is still evident, as plant roots "forage" for mycorrhizae, and the subsequent colonisation of roots through fungi shares a close resemblance with fungal infections, and in the case of VAM the plant seeks to enclose the invading mycelium to prevent its spread in the roots (Sect. 19.3).

A **commensal relationship**, where one plant benefits from the other without affecting it, is exhibited by **epiphytes** (in particular many orchids, bromeliads, ferns and mosses) growing on the

Table 19.1 Potential interactions between two organisms

Type of interaction	Organism 1	Organism 2	Type of interaction
Symbiosis (mutalism and protocooperation)	+	+	Interaction beneficial to both organisms
Commensalism (parabiosis, epecology, e.g. epiphytes, epizoics, metabiosts)	+	o	Interaction beneficial to one organism, without disadvantaging the other
Parasitism (antibiosis, allelopathy and antagonism)	+	–	Interaction benefits one organism to the detriment of the other
Neutralism	o	o	Interaction without a beneficial or detrimental effect
Amensalism	–	o	Interaction leads to a detrimental influence on one organism without aiding the other
Competition	–	–	Interaction leads to mutual disadvantage

o *Neutral influence*, + *Positive, advantageous influence*, – *Negative, disadvantageous influence*

Fig. 19.6 Examples of plant–plant and plant–fungi interactions. Close symbiosis (lichens: top left), mycorrhization of *Picea glauca* roots (top right), bromeliad epiphyte on tree (bottom left) and facilitation of *Poa alpina* by alpine cushion plant *Silene acaulis* (bottom right). (Photos: top left: N. Nagel, top right: Silk666, bottom left: M. Scherer-Lorenzen, bottom right: C.F. Dormann)

branches of trees. In most cases, the host tree has no benefit but also no disadvantage from the presence of the other plants. Since the host trees serve merely as substrate-near-the-light, species associations between epiphytes and their hosts are highly generalistic and indistinguishable from random associations.

Lianas rely on their hosts for structural support. Typically starting growth on a branch where their seeds were deposited by fruit-eating birds or mammals, they send aerial roots to the ground to then climb the host to reach the light without investing in support structures ("hemi-epiphytes"). In some cases (strangler figs of the genus *Ficus*, Moraceae, e.g. *F. benghalensis*, *F. virens*), lianas encircle the host so tightly that they "strangle" it, preventing effective phloem transport, progressing from commensalism to parasitism (and parasitoidy, Chap. 12).

Similar to commensalism, **facilitation** of individuals of one species by those of another is a relatively common phenomenon (Brooker et al.

2008). In the case of **nurse plants**, seedlings of one species profit from the physical environment created by another plant (e.g. hydrolic redistribution in arid systems, thorny thickets reducing grazing, reduction of wind chill in artic/alpine systems) (Chap. 10). In only a few cases have these systems been investigated well enough to explore whether the facilitated plant eventually returns this benefit. It rather seems that facilitation may well be a transient state, moving from commensalism to competition as the plant matures and becomes independent of the sheltered environment. This phenomenon can be observed particularly well along stress gradients, where competitive interactions become less and mutualistic interactions more important as environmental harshness increases ("**stress gradient hypothesis**": Bertness and Callaway 1994).

19.3.1.2 Parasitism and Hemiparasitism

Parasitism occurs in all biomes under very different climatic conditions (Fig. 19.7).

Many plant species developed the ability to live off other plants. In pure parasitism, as exhibited in *Cuscuta* (dodder: Fig. 19.8), *Orobanche* (broom-rape) or the spectacular *Rafflesia*, the parasite forms host-penetrating organs, so-called haustoria, which tap the phloem to extract sugars, nutrients, amino acids, water and all other substances required for growth.

Semiparasites, such as *Striga* (witchweed, a common generalist parasite of tropical crops) or *Rhinanthus* (rattleweed now also in the Orobanchaceae, formerly Scrophulariaceae), also draw water or nutrients from the host but are typically green and photosynthesise fully. While *Rhinanthus* can survive without a host, *Viscum album* (mistletoe) is an obligate hemiparasite and cannot.

The evolution of parasitism in plants from epiphytes over **hemiparasites** to obligate parasites (or over lianas towards strangler figs) is associated with a moderate increase in specialisation. Hemiparasites still have a wide host spectrum (*Rhinanthus minor*, yellow rattle, for example, parasitises over 50 species in 18 families), but even **obligate parasites**, such as *Orobanche* and *Cuscuta*, can have tens of host species. In the extreme, orchids, the most species-rich plant

Fig. 19.7 Parasitic plants have developed in all biomes. **a** In cool, temperate southern Chile *Misodendron punctatum* on southern beech (*Nothofagus antarctica*), **b** in semiarid northern Chile a completely leafless Loranthacea (*Tristerix aphyllus*) lives on many cacti (e.g. *Trichocereus* spp.) **c** In the extremely arid Arabian Desert *Cistanche violacea* lives on various host plants, for example, even on halophytes like *Suaeda fruticosa*. (Photos: K. Müller-Hohenstein)

Fig. 19.8 Parasitic plants. Dodder, *Cuscuta europaea* **a**, and witchweed, *Striga hermonthica* **b**. Dodder penetrates leaves and branches to access the sap flow of the host. It can spectacularly overgrow its host in a hair-like web (here on dwarf elder, *Sambucus ebulus*), although its economic impact is often limited. Pretty-looking witchweed is one of the worst tropical plant pests, threatening in particular small self-sustaining farmers, draining the resources from the crops on which roots it parasitises (here maize *Zea mays*). (Photos under creative commons license from Wikipedia (dodder), and Jan Grenz (witchweed))

family, are largely parasitic, even photosynthetic active species. Generalist parasitism is akin to generalist herbivory and can hence have suppressive effects on competitively dominant species and hence positive effects on plant community diversity (Sect 19.2).

19.3.1.3 Allelopathy

Chemical suppression of the growth of neighbours is called **allelopathy** (Greek: harm to others), because the allelopathic species was incorrectly assumed to be unaffected by its own chemical warfare (Molisch 1937). It may lead to reduced growth of competitors and occurs in a wide range of plant species and life forms, but it is not yet clear how significant allelopathy is under natural conditions and for the structure of plant communities. The list of allelopathic species is constantly growing because all plants produce substances of moderate to high toxicity to others, albeit to varying extents. Allelopathy received renewed attention in the context of invasion of introduced species, as some European species (e.g. *Centaurea maculosa*: spotted knapweed; *Alliaria petiolata*: garlic mustard) decimated their surrounding vegetation following introduction into the USA.

The chemical substances are released either directly, for example, as **root exudates** (e.g. in the macrophyte *Stratiotes aloides*: water soldier), or indirectly, for example, during decomposition of litter (*Juglans regia*, walnut, or *Eucalyptus* spec.). They affect the germination or growth of the plants in the surroundings, but they also often affect the soil community in general. Attempts to turn allelochemicals into herbicides have proven ineffective, suggesting low root uptake under natural conditions, but a chemical analogue (mesotrione) to the original leptospermone (formed by species of the Myrtaceae) is available commercially (Syngenta's Callisto and Tenacity herbicides).

Individuals of the same species, and offspring of the allelopathic individual in particular, are not immune to their own species' toxin. Indeed, walnut understorey will be devoid of all plant life, excluding also walnut seedlings. Allelopathy is being particularly investigated in crop species such as rice (*Oryza sativa*) and barley (*Hordeum vulgare*). The benefit to the allelopathic species is obvious: it reduces competition for water, nutrients and, eventually, light. The costs are relatively high, however, as these substances are broken down by soil biota and need to be replenished continuously. Since allelopathy goes hand in hand with competition for nutrients or even herbivory (Halsey 2004), it is often difficult to tease the causal effects apart experimentally (usually by using activated coal to absorb aromatic substances). The "obvious" pattern in the field may thus be multicausal and not merely the effect of chemical interactions.

19.3.2 Competition and Coexistence

Without impediments, even the slowest growing, poorest reproducing plant species would be able to cover the inhabitable surface of the planet within only a few dozen generations. This Malthusian law of exponential growth led Darwin (1859) to understand competition as one of the main selective forces behind natural selection. Of all the seeds that fall onto a given area, only a few can become established, and only a species that is able to win this struggle for space is part of the next generation (i.e. has fitness >0). Thus, conceptually, the link between competition and evolution is a very close one. As a consequence, competition has existed as a research topic in plant ecology for at least a century, with a wide variety of approaches, models and, regrettably, misunderstandings. Competition not only affects individual populations but also community structure and ecosystem-level processes (Chap. 13).

19.3.2.1 Concepts and Definitions of Competition

Competition, in the widest possible definition of the term, represents a situation where the winner (read: competitively superior, dominant species or individual) is picked from a set of candidates (**contest competition**). Superiority is not sufficient for survival, however: many individuals may compete without any of them "winning" enough to make a living (**scramble competition**). In plant competition, the establishing individual may be picked independently of the species (see the lottery model below) or its success may be correlated with some trait such as shade tolerance or seed mass. Competition, ubiquitous as we assume it to be in plant communities, is difficult to detect "in action", requiring tracer experiments and manipulation of resources. And even failure to detect competition may well be due to generations of intense competition having removed unsuccessful species from the species pool ("the ghost of competition past": Connell 1980).

Often competition changes qualitatively during the lifetime of a plant. It starts with competition for a germination site (called the "regeneration niche" by Grubb 1977), and it may then turn into competition for water or nitrogen, to possibly end in a competition for light (as in forest trees). Competition for light, nutrients and water is called resource competition; it has attracted the bulk of scientific interest. Allelopathy, discussed earlier, is sometimes referred to as "interference competition" to highlight the active initiative of a plant in preventing other plants exploiting the resources in its immediate vicinity. While the production of allelochemicals is common, our understanding is that **scramble or diffuse competition** is the more common mode of interaction. Scrambling refers to the disorderly uptake of resources by all plant individuals (of possibly several species). Since any resource unit used by one plant is no longer available to another plant (which is why it is sometimes referred to as "pre-emptive competition"), and since plants acquiring more resources can grow more and hence continue foraging for resources, scrambling often leads to a run-away process, resulting in the dominance of a small number of individual plants. This process becomes particularly prominent for light, where competition is strongly asymmetric: taller trees shade smaller ones (pre-empting the struggle for light), but not the other way around. The taller trees can thus grow even more and will hence shade out the smaller trees in forests even more. In the case of *Fagus sylvatica* (European beech, Fagaceae, but also for *Nothofagus* spp., southern beeches), this can lead to a complete suppression of all other tree species in its understorey (although differential sensitivity to deer browsing may contribute to this outcome; Sect. 19.2). Competition for nutrients, for example, nitrogen and water, is much less asymmetric, allowing in particular small individuals to snatch up some resources.

19.3.2.2 Competition for Resources

The most obvious resource plants compete for are nutrients (N, P, cations), water and light. The reason these resources are the target of competition is that they become limiting under some circumstances (see Liebig's law of minimum, Chap. 11). Only when plants deplete the local resource pool does competition come into play. If nitrogen is still available in the soil but shading limits plant growth (say in forest understorey), then competition for nitrogen is ecologically irrelevant.

Across all biomes, **nitrogen** is the de facto most commonly limiting resource (Vitousek and Howarth 1991). This can be explained by its virtual absence in bedrock, its erratic non-biotic production through volcanic eruptions and lightning, and its high abundance in plants and animals. Before the invention of chemical nitrogen fertilisers in the early twentieth century (winning Haber and Bosch the 1918 Nobel Prize in Chemistry), all nitrogen in plants and animals had been fixed by bacteria (free-living marine and terrestrial cyanobacteria, endo-symbiontic protobacteria (*Rhizobia* in legumes) or actinobacteria (e.g. *Frankia* in alder; see also Sect. 7.4 in Chap. 7 and Sect. 16.3 in Chap. 16 for more details on nitrogen fixation). Today, industrial N fixation is about twice that of all natural N fixation (both biogenic and lightning). It is unsurprising that this huge increase in nitrogen availability had substantial effects on plant communities (Sect. 19.4).

The obvious agricultural implication of nitrogen limitation and the "green revolution" of fertilisation have blinded plant ecologists to the probably far more ubiquitous and observable limiting resource for plants: **light**. Trees are the result of the struggle for adapting to taller competitors, leading to a run-away process of investing a huge proportion of assimilates into structural support (stem, roots and branches), which delays reproduction and increases susceptibility to damage and pests. But forests are not the only light-competition systems; even grassland systems, less than 1 m tall, can be light-limited, as has been shown experimentally (Sect. 20.3 in Chap. 20). Surprisingly, even for aquatic systems, where algal blooms reduce light penetration further down the water column, only recently has a theory of light competition been properly developed (Huisman and Weissing 1995). The key feature of light competition, and its biggest difference to competition for nutrients or water, is the asymmetry mentioned earlier. The consequence is a strong evolutionary pressure towards tallness in light-limiting systems or an adaptation to low-light conditions (exhibited by many light-sensitive forest understorey plants such as *Paris quadrifolia*: herb-paris, or the seedling stages of dominant tree species such as European beech or sycamore maple, or indeed many tropical tree species).

The other common limiting resources (such as **phosphorus** or **water**) are covered in Chaps. 10 and 11. They are also common subjects of competition but provide no known qualitative difference to nitrogen in terms of the way competition is carried out. Nitrogen (because of the tremendously increased availability) and light (because of its asymmetry) cover most situations of competition.

Much less investigated is the role of "negative resources", that is, substances or settings that impair plant growth and that plants may thus compete for to avoid. While soil water, which transports soluble nutrients and allows their transpirational transport up into plant leaves (Chap. 10), is imperative for growth, too much or too little soil water is detrimental to many plant species. Avoiding water-logged soils (on which only a minority of plants are actually able to grow, while many more can briefly tolerate it) or soil desiccation (which stimulates root abscission and impairs photosynthesis by inducing stomata closure) actually means that plants are now competing for positions along gradients where environmental conditions are favourable ("mesic") in all aspects. On dry, wet, polluted, nutrient-poor, cold, dark sites, any adaptation to adversity will immediately also give competitive advantage with respect to all other resources since only a few species will be able to survive. For example, light competition on lead-/arsenic-rich soils is virtually absent, since few species have adapted to such conditions, none of them a shrub or tree able to outshade others. **Competition** for herbivore- or pathogen-free space will be discussed in what follows (Sect. 19.4).

19.3.2.3 Plant Traits and Competition

Can traits (sensu Chap. 20) be identified that indicate probable establishment or superior growth in plant communities? As a first pass, different limiting resources require different traits: light competition will favour taller plants, while low nitrogen levels in the soil should favour longer roots (Table 19.2). In a study of shoreline plants, Gaudet and Keddy (1988) found that plant biomass was the single best predictor of competition

Table 19.2 Examples of plant characteristics related to competitive strength

Primary attribute: mechanism
Rate of water depletion
Rate of nutrient depletion (e.g. N, P, K)
Rate of light depletion
Ability to attract pollinators
Ability to attract dispersal agents
Interference with dispersal agents of neighbours
Interference with pollination of neighbours
Allelopathic activity
Tolerance to water depletion
Tolerance to nutrient depletion
Tolerance to light depletion
Resistance to allelopathic chemicals
Resource use efficiency
Secondary attribute: trait
Root density
Lateral root extension
Uptake efficiency into root hairs
Density of root hairs
Plant height
Leaf area
Lateral extension of shoots
Leaf orientation
Number/density of flowers
Floral attractiveness/rewards
Number of seeds/fruits
Attractivity of seeds/fruits for dispersers
Litter deposition
Litter chemical properties
Pollen allelopathy
Relative growth rate
Tertiary attribute: strategy
Arrival time of dispersal agents
Germination time
Seed size
Photosynthetic capacity
Luxury consumption
Mycorrhizal association
Allelopathy
Pathogen resistance
Temperature niche
Ability to attract pathogens to neighbours
Tolerance of disturbance
Longevity (e.g. clonality)
Resource-ratio niche

Primary attributes represent mechanisms of competition effects, secondary attributes represent measurable plant traits, while tertiary attributes are more general elements of plant strategies. There is no one-to-one relationship; rather (groups of) tertiary attributes affect multiple secondary attributes, and those multiple primary attributes (after Aarssen 1989)

outcome. They reason that nutrient uptake as well as light competition will benefit from more biomass. But is nutrient competition also pre-emptive, that is, will those plant win that can take up nutrients fastest? In this shoreline system that may very well be the case. However, in arid environments, plant tolerance to drought and their ability to extract nutrients at low nutrient levels may be more important than the ability to thrive under high-N conditions. Tilman (e.g. 1997) demonstrated that indeed those plant species that tolerate the lowest resource levels ("R*") may in some systems determine the outcome of competition (see subsequent discussion for more details and consequences for coexistence).

Competitive strength will thus in many cases not be readily reflected in obvious characteristics such as plant height or root nodules. It is also a matter of exerting competitive effects on neighbouring plant individuals (competitive effect). It is appealing to attempt a concept of plant types according to their competitive behaviour, but before we do so, it should be made clear that this is a phenomenological framework, and the actual processes need to be confirmed in every system anew. The best known scheme of plant strategies is Grime's (1977) **C-S-R concept** (Sect. 17.3 in Chap. 17) of competitive dominance (C), ability to tolerate stress (S) and ability to use resource pulses (R). This is directly reflected in plant traits, with dominant plants being larger and richer in storage organs, stress adapted displaying specific morphological adaptations to that stress (e.g. aerenchymas in water-logged soils, stomata-poor leaves with rolled margins in dry conditions, cushion growth form in exposed alpine environments) (Fig. 19.9), while resource-craving ruderals display extreme phenotypic plasticity in size and growth rate with low allocation to storage and roots. In any given site, environmental conditions may thus lead to a clear competitive hierarchy, with the best-adapted trait combination occupying the most growth-favouring conditions, displacing other trait combinations to inferior sites (Box 19.3). To explore whether such concepts reflect actual competitive processes, experiments are inevitable.

Fig. 19.9 A relatively robust cushion plant (*Plantago rigida*) in a Paramo community in Equador protects a much more sensitive species (*Castilleja pumila*) with red flowers. The former species may be termed a "nurse plant", the latter a "cushion guest". (Photo: K. Müller-Hohenstein)

19.3.2.4 Experimental Approaches to Clarify Phenomena of Competition

It is one thing to expect **competition** to be an important process in plant ecology, but quite another to actually demonstrate its effects experimentally. Three different lines of experiments have developed over the years: (1) **laboratory experiments** on species pairs, (2) **neighbour-removal experiments** in the field and (3) **phytometer studies**. Additionally, observational, non-manipulative studies attempt to attribute patterns in occurrence, abundance or growth to competition, but since they are purely correlative, this line of evidence is much weaker. To differentiate competition from the indirect effects of trophic interactions (Sect. 19.2), experiments also manipulate grazing pressure, fungal infections and mycorrhization. These experiments may be additionally necessary to understand plant–plant interactions comprehensively, but they do not quantify competition itself.

Laboratory studies allow standardised conditions, controlled densities of plants and detailed assessments of root growth, nutrient leaching and so forth. Additionally, only lab experiments allow the implementation of sophisticated competition designs (Box 19.1). Lab experiments have consistently revealed strong below- and above-ground competition in a wide range of species. This line of research has been largely discontinued, as the evidence is clear. Moreover, lab experiments primarily confirmed that competition *can* occur, not that they actually matter in the field.

Accordingly, neighbour removal studies have been the main approach to investigating effects of competition in the field. In this approach, a target plant individual is cleared of all neighbours, while in the control it remains untouched. Better growth in isolation is then taken as evidence of suppression of growth when the plant is grown with neighbours. And indeed, reviews and meta-analyses of neighbour-removal experiments unequivocally confirm the importance of competition for plant growth in virtually any system (Gurevitch et al. 1992). The main shortcoming of this approach is that above-ground neighbour removal leads to dead below-ground biomass, which releases nutrients as it decomposes, confounding neighbour competition with fertilisation. Tying shoots aside reduces **light competition**, but split-root experiments are only possible in the lab. It seems that neighbour-removal experiments are falling out of favour, too, and mesocosm experiments, linking lab and field setups, are rarely used to address plant competition.

The third experimental approach to plant competition focuses on measuring the intensity of competition in the entire plant community. The focus is on the *intensity* of competition, not the exact effect of one species on another. Accordingly, the idea of using a so-called competition-o-meter was born, building on using organisms as sensors for soil moisture or nutrient status ("**phytometer**"). Effectively, identical individuals of a "suitable" plant species are transplanted into existing plant communities and neighbour-free controls. The difference in growth quantifies competition. The results of this approach are equivocal with respect to competition intensity. This is largely due to the

Box 19.1: Designs for Competition Experiments

The actual set-up of an experiment depends on the specific hypothesis it sets out to test. We introduce the additive, the substitutive and the response surface design and the questions they try to address. In all designs, we distinguish between the target species and the competitor that exerts an influence on the target.

In additive designs, the competitor is added to whatever density the target grows to (Fig. 19.10a). It answers questions such as: Does the competitor have an effect on the target species? How does the effect depend on competitor density? In substitutive designs (Fig. 19.10b), density is kept constant, but the proportions of the two species change. This is a useful design to evaluate the strength of inter- relative to intraspecific competition. Combining different densities of both species leads to the response surface design (Fig. 19.10c), clearly the most complex and labour-intensive set-up. Only this design allows the parameterisation of a competition model with varying densities. In principle, this design can also be used for descriptive studies along gradients of densities of two (or more) species (e.g. Rees et al. 1996).

Designs of this type are typically not analysed using the Lotka–Volterra equations of Sect. 19.2 but by a function fitted to additive and surface design experiments derived by Firbank and Watkinson (1985):

$$w_A = \frac{\bar{w}_A}{(1+a_A\left(N_A+\alpha N_B\right)^b}, \qquad (19.1)$$

where w is the biomass of species A and N is the number of individuals; $\bar{w}_A$ is the average biomass of A without competition; and α, a_A and b are fitted parameters.

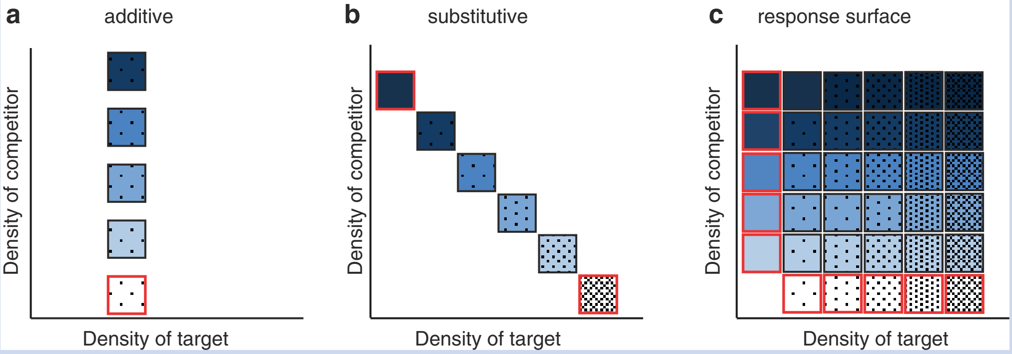

Fig. 19.10 Different designs for competition experiments. *Blue shades* represent density of competitor, dot density that of the target species. Monocultures are indicated by a *red box*

choice of the phytometer, which affects the results as well as the confounding effects of grazing and mycorrhization. This line of experimentation has thus not been able to deliver as reliable results as the two previously mentioned approaches.

All three approaches have been used to address the question of competition intensity along productivity gradients. One might expect competition to be more severe at high productivity, when growth is fast and plant individuals tall (Grime 2001). At low productivity, Grime argued, the environment is so challenging that competition plays only a minor role. In contrast, Oksanen (1990) argued that under stress any additional adversity imposed by competition will have more severe consequences. Eventually, this debate was resolved: biomass was much less reduced by competition under stressful conditions, but since plants also grow less there, the *relative* effect of competition was as pronounced under nutrient limitation as under fertile conditions.

19.3.2.5 Models of Intra- and Interspecific Competition

Any simple concept can be couched in mathematical terms, which offers completely new approaches to investigating the effects of competition for populations and communities. However, such models can "only" explore the consequences of their assumptions and, hence, must be shown to apply to any given situation. Still, the conceptual clarity such models can provide far outweighs their limitations.

The key idea in competition models is to express the competitive effects of species A on B in multiples of the effect of A on A, that is, the balance of inter- versus intraspecific competition. All else being equal, if B is twice the biomass of A, each individual of B should have twice as much effect on A as an individual of A. To be able to put this into a simple formula, we first recall that the density-dependent growth of a population of species A can be represented by a logistic equation:

$$\frac{dN_\text{A}}{dt} = r_\text{A}\frac{N_\text{A}}{K_\text{A}}\left(K_\text{A} - N_\text{A}\right), \tag{19.2}$$

which can be rewritten as

$$\frac{1}{N_\text{A}}\frac{dN_\text{A}}{dt} = r_\text{A}\left(1 - \alpha_\text{AA}N_\text{A}\right). \tag{19.3}$$

Now we add species B's effects on A:

$$\frac{1}{N_\text{A}}\frac{dN_\text{A}}{dt} = r_\text{A}\left(1 - \alpha_\text{AA}N_\text{A} - \alpha_\text{AB}N_\text{B}\right). \tag{19.4}$$

Thus, the coefficient α_AA represents **intraspecific competition** (read: A affected by A), while α_AB (read: A as affected by B, or B on A) represents **interspecific competition** of B on A. By analogy, we have another equation describing the population dynamics of B, which is identical apart from the indices. This set of equations is known as Lotka–Volterra competition (Case 2000). Typically, competition is not symmetric, that is, $\alpha_\text{AB} \neq \alpha_\text{BA}$. The competition coefficients represent the overlap of niches between the two species: more overlap means more competition.

The coexistence of the two species is possible if either species can invade a monoculture of the other species. For example, species B can invade a monoculture of species A if the effect of A on itself is larger than that on B: $\alpha_\text{AA} > \alpha_\text{BA}$ and $\alpha_\text{BB} > \alpha_\text{AB}$ (Chesson 2000). In simple words: coexistence requires intraspecific competition to be stronger than interspecific competition. (Coexistence is achieved if the *relative* competition coefficients are less than one: $\frac{\alpha_\text{AB}}{\alpha_\text{BB}} < 1$ and $\frac{\alpha_\text{BA}}{\alpha_\text{AA}} < 1$. Note that a quantity often reported, $\frac{\alpha_\text{AB}}{\alpha_\text{AA}} < 1$, is uninformative about coexistence. We need to know how strongly the resident is affecting the invader, not how strongly it is affected by the invader!)

The Lotka–Volterra system was initially without reference to a mechanism, but it can be derived from diffuse competition for a single resource (MacArthur 1969; Tilman 1982).

It is worth recalling that intraspecific competition is **density-dependent**, leading to **self-thinning**, for example, in forest stands (Yoda et al. 1963). It is therefore not unreasonable to consider that also competition is density-dependent *on competitor B* and, hence, that competition coefficient α_AB varies (non-linearly) with the number of individuals of B: $\alpha_\text{AB} = f(N_\text{B})$. This makes no difference for the preceding situation, as long as we investigate only the moment of invasion (i.e. resident at equilibrium, invader at zero). For two-species systems, we can still manipulate densities across both species and determine the competition coefficients (in what is called a response surface design; Box 19.1). For multiple species, this becomes practically impossible.

One mechanistic interpretation was offered by Tilman (1982), the so-called **R*** rule. It states that the winning species in a competition is the one that tolerates lower resource concentrations for persistence (survival and reproduction). This lowest level is symbolised by R*, and the species with the lowest R* value wins (Box 19.2, Chap. 17)

Box 19.2: Graphical Model of Plant Coexistence Under Multiple Resources

Tilman (1982) proposed a graphical model to understand the competition of two species for two resources. A crucial feature of this model is that resources get depleted, so competition is decided in favour of the species that can survive on the lowest amount of resources. This level of minimum resource requirement is called R^*, and it differs between species and resources.

Figure 19.11 illustrates competition between species A (red) and B (blue) for resources 1 and 2. The lines ("zero-growth isoclines") indicate the minimum requirements for the two resources. In Fig. 19.11a, species B has lower resource requirements than A for both resources (indicated by the dashed lines). In this situation, B will always deplete resources to a value below A's requirements, so A will go extinct.

The situation changes if A and B have a resource for which their R^* is lower than that of the other species (in Fig. 19.11b, c, $R^*_{1A} < R^*_{1B}$ and $R^*_{2B} < R^*_{2A}$). This alone, however, does not guarantee coexistence. Imagine a level of resources indicated by the green point. The two species will now consume the two resources, indicated by the arrows (consumption vectors). In Fig. 19.11b, species A hits its minimum requirement of resource 2, but species B continues to exploit resource 2 below A's R^*_2—and species A goes extinct.

In Fig. 19.11c, the consumption vectors are swapped: now species A consumes resource 2 *slower* than species B. As resource 2 is depleted to A's minimum level, B can further deplete it. At some point (in the blue corner), resource 1 will become limiting for B. Here, its consumption of resource 2 will stop, too. As resource 2 recovers, species B cannot profit from it because it is still limited by resource 1. Hence, resource levels will move to the point where the zero-growth isoclines for the two species intersect and where both species can coexist (indicated by *).

Along a gradient of *resource ratios*, species with different R* values replace each other. To see that, we must extend the previous figure to more species (Fig. 19.12).

As the ratio of resources changes (Fig. 19.12 right: R1:R2), different pairs of species coexist at different positions of the resource-ratio gradient. In systems with spatially variable resource ratios, the coexistence of several species becomes possible.

Experimental confirmation of this concept comes from work on competition between five grass species, each lowering the concentration of soil N below the minimum requirement of their inferior competitors (Tilman and Wedin 1993). However, because such experiments are extremely laborious, the role of this theory in realised vegetation remains unclear.

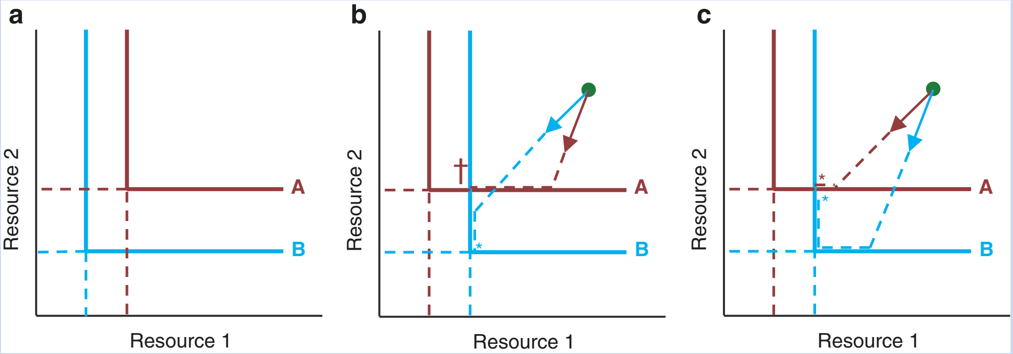

Fig. 19.11 Competition between two species for two resources. **a** B has lower resource requirements than A for both resources and hence wins. **b** Resource consumption (*arrows*) reduces resource 2 more than resource 1, again leading to dominance of B. **c** Resource requirements and consumption match, coexistence is possible. (Tilman 1982)

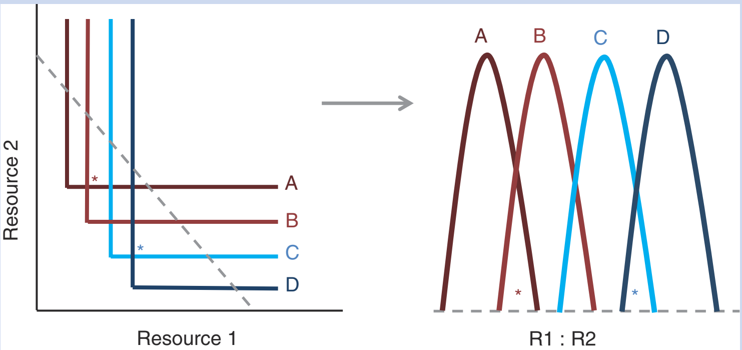

Fig. 19.12 Competition between four species for two resources. (Tilman 1982)

Chesson (2000) made the important theoretical distinction between two different kinds of mechanisms contributing to coexistence: **stabilising processes** (e.g. the Janzen–Connell effect discussed subsequently) are typically linked to density dependence and allow a species to increase at low densities, thereby preventing its local extinction. **Equalising processes** (such as disturbance or environmental harshness) contribute to averaging out fitness differences between species; they slow down the extinction of one species by another but cannot ultimately prevent it. The density-dependent competition effect would be a stabilising force (as low densities lead to no competition and, hence, prevent extinction), while species with similar or even identical R^* values would only be equalised, but not stabilised. If, through a stochastic disturbance, one of them decreased, there is no process that would allow it to rebound to higher abundance, a mechanism required for stabilisation. Apart from the aforementioned balance of intra-/interspecific competition, there are two more involved fluctuation-dependent processes, which require a variable resource: the relative non-linearity of competition and the storage effect. Note that, in general, the Lotka–Volterra system also works in variable environments, but these two new processes *require* such variability.

The relative non-linearity of competition describes two species whose growth rates respond differently (e.g. one linearly, the other non-linearly) to the limiting resource. As this resource fluctuates, sometimes one will grow better and be competitively superior, sometimes the other. While it is unclear how relevant this effect is in real communities, the theoretical potential for allowing coexistence among many species under multiple fluctuation resources is great (Huisman and Weissing 1999).

The second, and possibly more commonly known, fluctuation-dependent stabilising mechanism is the **storage effect**. It actually requires that three assumptions be met: (1) species must respond differentially to the environment; (2) competition must be driven by the environment, such that growth and competition co-vary; and (3) poor growth conditions must be tolerated, for example, population growth must be buffered (e.g. by seed banks). The “spatial” storage effect occurs when competing plant species grow in monospecific patches, so that each species has conditions in which it thrives and those in which it is subdued. The “temporal” storage effect is exemplified by spring geophytes in deciduous forests (such as wild garlic *Allium ursinum*, lesser celandine *Ranunculus ficaria*, wood anemone *Anemone nemorosa*) (Sect. 9.2, Chap. 9). Spring geophytes emerge in late winter or early spring and use the period before trees regrow their foliage. They then translocate their nutrients into below-ground storage organs, awaiting the next season.

Apart from these coexistence mechanisms, there is also an important spatially explicit coexistence mechanism: the **competition–colonisation trade-off**. The premise of the competition–colonisation trade-off is that plant species are either good colonisers *or* good competitors in the establishment phase (Slatkin 1974). An obvious trait to look at would be seed size: small seeds are dispersed more readily and over larger distances, while large-seeded species will have an easier time germinating and living off the seed's resources for longer. In this way small-seeded species will find empty patches in a wider part of the landscape, while large-seeded species will only disperse close to the mother plant but dominate over the smaller-seeded species there. Coexistence is achieved at the landscape scale, and over multiple generations, rather than in any given patch at any time (if at all: the competition–colonisation trade-off is an equalising mechanism, not a stabilising one). While this mechanism resembles the **r-K strategies**, it is a bit more specific and, hence, more readily testable. Experimentally, the benefit of large seeds is difficult to verify, and recently the ability of large seeds to tolerate droughts and shade has been proposed as a more plausible mechanism (Muller-Landau 2010).

In recent years, **neutral mechanisms** of coexistence have become more prominent (Hubbell 2001) (Fig. 19.13). Neutral refers to the assumption that species (e.g. within a functional group or guild) are equivalent in all aspects relevant for competition, such as dispersal, competitive strength and so forth. In such a situation, a species filling a vacant patch in the community is drawn randomly from the species pool, as in a lottery. Over many generations, this will lead to "ecological drift" in community composition, sometimes one, sometimes another species being most abundant, and rare species going extinct. Unless new species are added from outside, eventually only one species will remain, but which one cannot be predicted. Such lottery competition is an old theoretical hypothesis of **coexistence**, which does not chime well with our current understanding of stabilising and equalising mechanisms and remains difficult to test because of its long-term prediction and high stochasticity.

Finally, we shall be looking at competition and coexistence involving other trophic levels, such as the Janzen–Connell effect, in Sect. 19.3.3.1.

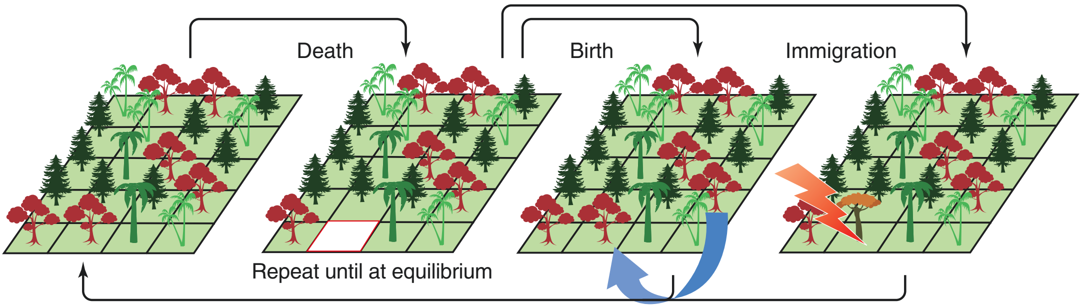

Fig. 19.13 Neutral community dynamics. All species are assumed to be equivalent to each other; death, birth and immigration processes are purely stochastic. Such neutral dynamics lack stabilising processes and hence do not lead to coexistence. Thus, any given local community will display species turnover ("ecological drift"), with amount and distance of dispersal and the size of the entire community determining local species richness (Rosindell et al. 2011). Reproduced with permission from Elsevier

19.3.3 Competition and Its Consequences for Plant Community Structure and Diversity

So far, this chapter has largely focused on pairwise interactions, where one species is (temporarily) superior to another. In a community setting, many species are simultaneously competing with each other, typically more so the nearer they are to each other. The consequences of plant competition for plant communities as a whole are much less straightforward. The key problem is the existence of competitive loops, where species A, B and C compete for several resources. For any resource alone, we may find a competitive hierarchy (e.g. for nitrogen: A > B > C), but that hierarchy may be different for another resource (e.g. for light: B > C > A). In such circumstances, the dominance of C over A for light might actually benefit B in its nitrogen competition. This situation has been called "my enemy's enemy is my friend", and it leads to a rather unpredictable outcome of competition for multiple resources. In fact, since experimental effort increases dramatically with the number of species considered, competition is often invoked in community experiments, rather than being directly proven. What can be observed is a decrease in the biomass of a target species, called a phytometer, for example, as diversity increases or soils become more fertile. This is attributed to greater resource depletion due to competition. Thus, **competition** is typically *inferred* as a driving force, either conceptually or mathematically.

Certain concepts link competition to abundance patterns in vegetation. For example, Keddy (1989) suggested the idea of competitive hierarchies, where a superior species is able to exclude all others, the second-most dominant all those below it and so forth. This would lead to a zonation pattern, with the most dominant species occupying the best growth conditions, although all species would grow best there. Experimental evidence dates back to the legendary ***Hohenheimer Grundwasserversuch*** of Ellenberg and Walter in 1952 (Box 19.3). It shows that the individual niche optimum (the **"autecological optimum"**) will differ from a plant's position in the vegetation, surrounded by other species (the "**synecological optimum**", although optimum is arguably the wrong word here). However, not all experimental evidence, of which there is little, agrees.

As competition changes species composition, transitions from one kind of plant community to another occur, altering the environment in the process (succession). In some systems these alterations are cyclical, for example, because the new community is more flammable and fire will burn the vegetation down to the ground, restarting a succession. At the landscape level, several different stages of this cycle are present, so species coexist, not in a patch, but at a higher spatial scale. The resulting dynamic mosaic of successional stages has been observed in heathlands and rain forests (the "**mosaic-cycle concept**" of Remmert 1991). As this concept is phenomenological (i.e. describes the outcome rather than the mechanisms), it is more of historic interest and adds little to our understanding of competitive interactions in plant communities.

19.3.3.1 Competition in Concert with Trophic Interactions

In any given plant community, competition is not the only biotic interaction at work. In fact, a rich literature investigates the effect of other interactions on the importance of competition. Livestock **grazing**, as well as the more selective **browsing** of wood plants by ungulates, is the most commonly investigated form of biotic process interfering with plant competition. The field evidence is unequivocal: grazing suppresses the dominant species, increases light availability, creates open sites for germination, removes nutrients from the system and, overall, leads to or maintains higher species richness. The main reason for the overall positive effect of grazing is that dominant species lose more biomass, in absolute terms, than rare ones. Thus, grazing, as well as other frequency-dependent damage such as hemiparasitism, often acts as an equalising mechanism. Browsing effects in contrast are highly specific to the herbivore and its level of foraging preferences. An indiscriminate browser suppresses the dominant species, similar to grazing, but strongly discriminating browsers (or grazers) can have effects similar to those of plant pathogens.

Less obvious, but probably even more common, is the effect of **pathogens**, in particular fungal infections and **herbivory** by caterpillars, weevils and suchlike, on plant communities. In contrast to grazers, these pathogens are typically highly specialised and may locally exterminate their host. Still, pathogens can contribute to the dynamic long-term coexistence of plant species by suppressing the most abundant species. A key feature is that pathogen transmission is density dependent, so that as a species becomes rarer in the community, it is less often attacked by pathogens. Hence, pathogens lead to the stabilising condition required for coexistence among competing species (Janzen–Connell hypothesis, initially proposed particularly for tropical tree seedlings) (Fig. 19.14). The mechanism resembles the effect of competition, that is, one species dominating another, but the actual agent is not the dominating plant, but the pathogen that suppresses the subdominant. The term *apparent competition* describes this situation aptly: it looks like competition but is really the outcome of selective suppression by a higher trophic level. From a theoretical point of view, herbivory can be seen as competition for attack-free space and has been shown to be mathematically equivalent (Chesson and Kuang 2008).

Similar to the ambivalent effect of facilitation (which may shift from a beneficial to a competitive relationship), "pathogens" (fungi, endophytic algae) may also occasionally have positive effects on host plants. Fungal **endophytes** spend their lives in the tissue of commercially important grasses, increasing or decreasing their transpiration, reducing their palatability to grazers and sometimes increasing their growth rate. This relationship progresses, depending on the plant species, from antagonistic to commensalistic to symbiotic. Accordingly, the way pathogens affect plant community composition and diversity is not easy to anticipate.

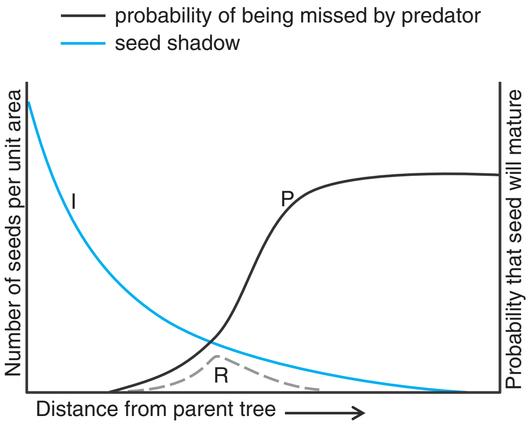

Fig. 19.14 The Janzen–Connell hypothesis. Shown is the recruitment curve R as the result of two distance-dependent processes: the number of seeds decreases with distance to the parent tree (I), while the chance of escaping predation by a specialist seed predator (P) increases. Modified from Janzen (1970), but independently derived also by Connell (1971)

19.3.3.2 Consistent Determinants of Plant Community Structure and Diversity

Predicting the effects of competition on community structure is, in principle, difficult: all species interact in slightly different ways, and these interactions vary through time. Additionally, the outcome of this confusion of interactions should change with resource availability, depend on the sequence of establishments (founder effect) and be susceptible to disturbances and management. In reality, however, plant communities are far more predictable than the variety of possible interactions would suggest. There are several reasons:

1. Often one environmental factor overrides all the biotic interaction details. This is obvious in stressful environments, such as deserts, polar regions or salt marshes. It is, however, also true in dark forest understoreys, waterlogged soils or highly grazed pastures. Only species able to cope with such constraints will be able to survive, and we find only few alter-

native survival strategies for each situation (e.g. succulence or seed banks in the case of deserts; thorns, toxins or growth meristems close to the ground in the case of grazing). In a simple sentence: competition may be intense, but it is unimportant relative to other factors.

2. Evolution cannot combine growth strategies and plant traits freely. New species come with the baggage of a phylogenetic past, and they are modifications of existing species, not optimally assembled from whatever Nature has to offer. Hence, many plant families have never managed to become established in regions beyond their evolutionary origin, have never been able to grow rapidly or develop a tolerance to drought. Crassulaceae, for example, have developed a rare photosynthetic trick (C4-CAM, Sect. 12.1 in Chap. 12), but they are void of secondary growth (Sect. 12.5, Chap. 12) and hence do not grow into trees. As a consequence of the phylogenetic conservatism in trait evolution, we find specific families or even genera dominating specific systems (e.g. Dipterocarpaceae in the Asian tropics, Poaceae in temperate grasslands, Cactaceae/Euphorbiaceae in deserts).
3. Plasticity within species leads to local acclimation (phenotypic plasticity) and allows a dominant species to be dominant over a large range of environmental conditions (including local adaptations due to genotypic plasticity, e.g. ecotypes). Temperate European forests are dominated, in their natural state, by European beech *Fagus sylvatica* over a wide range of soil and climatic conditions (Fig. 19.4). Similarly, couch grass *Elymus repens* is a pioneer grass species worldwide, in nutrient-rich arid systems as much as fertile salt marshes, on sand as much as on loamy soils. Both species display phenotypic plasticity, as well as high genetic diversity across their distributional range and adaptive polyploidy.
4. During successional developments (be it primary succession of glacial deposits, landslides or volcanic rock, or secondary succession following logging or abandonment of arable land), environmental constraints alternate. We can imagine a glacial foreland to be primarily nutrient limited, favouring species with symbiotic nitrogen fixers. Such early pioneers are soon replaced by larger forbs, then shrubs. In due course, as an organic soil layer builds up, nutrient limitations are replaced by competition for light, which is won by trees. Succession is thus a relative predictable sequence of traits and species (Sect. 17.2, Chap. 17).
5. Most species are rare. The reasons are manifold, but point 2 above (limited genetic variability within any given clade) is certainly one of the main culprits. Over centuries and millennia, dominance patterns of plants remain surprisingly stable, as witnessed in pollen records. Despite thousands of plant species in the continental species pool, only the same few handful dominate the pollen record. Abundance is thus not a mere fluke or outcome of ecologic drift, as Hubbell's neutral theory suggests (Hubbell 2001). Whatever trait combination makes these few species superior, the common species are apparently able to hold on to their dominance and are rarely replaced by (native or non-native) invading species. When this does happen, it can be spectacular (such as the red chinona *Cinchona pubescens* on the Galapagos Islands or Japanese knotweed *Fallopia japonica* in parts of Europe). Still, species-induced system changes are rare, and most often human land and pest management are behind observed dramatic changes in species abundances (Sect. 17.2, Chap. 17: human impacts and climate change).

19.3.4 Relevance of Plant–Plant Interactions for Practical Applications

The last section argued that despite the large idiosyncrasy of **plant–plant interactions**, some degree of generalisation is possible. In applied plant ecology, two relevant approaches follow from the overall effects of plant competition: **indicator values** and **ecograms**. To understand them, we need to briefly touch on niche concepts.

19.3.4.1 Fundamental and Realised Niches

Since Hutchinson's (1957) famous "remarks" publication that introduced the ecological niche, ecologists have understood a niche as a set of environmental and biotic conditions under which a species is able to have a non-negative population growth rate (*vulgo*: is able to survive). A **fundamental niche** is typically wider and only limited by ecophysiological constraints (e.g. too cold or too dry). Biotic interactions (with pathogens, herbivores, competitors) reduce this niche space towards a **realised niche**, while mutualists (pollinators, nurse plants) can also increase the realised niche beyond the fundamental niche. Plants from a wide range of climates can be successfully grown in temperate botanic gardens as long as their physiological needs are satisfied. This clearly demonstrates that the realised distribution of, say, the arctic-alpine mountain avens *Dryas octopetala* (Rosaceae) does not reflect its fundamental niche, which would encompass at least the whole temperate zone, too.

The way competition alters the fundamental towards the realised niche was demonstrated nicely by the seminal Hohenheimer groundwater experiment (Box 19.3). It has since been repeated and confirmed for various plant communities. One important conclusion is that for many species the realised niche is much narrower than their fundamental niche, and hence it actually indicates the conditions under which a plant is growing. Only in a narrow band of environmental values, say pH between 6.5 and 7, can a specific plant be found. Thus, if we find some plant in the wild, we can be relatively certain of the pH at these sites: the plant serves as an **indicator** for abiotic conditions.

19.3.4.2 Indicator Values, Indicator Species and Ecograms

A plant's niche has several abiotic dimensions: soil water content, temperature, pH, nutrient availability, light conditions and so forth. Not all of them will limit plant growth in the same way, that is, to some the plant responds more strongly than to others. As a consequence, plant occurrence may be indicative of the actual environmental value for one or two niche dimensions, but much less for a third or fourth (for more details Chap. 10).

In the 1970s, the same Heinz Ellenberg who had conducted the groundwater experiment (Box 19.3) summarised his immense field experience from vegetation recordings in Central Europe by assigning to most vascular plant species **indicator values** between 1 and 9 for light (L), temperature (T), continentality (K), soil moisture (F), soil pH (R), nitrogen availability (N) and, occasionally, salinity (S) (most recent version: Ellenberg et al. 1992). These values indicate the preference for an environmental condition in the presence of competitors, rather than an ecophysiological tolerance. To follow up on the example of *Dryas octopetala*, it would be characterised by the following indicator value sequence: L9 T2 K7 F4 R8 N4 S- ("-" indicates that no value has been assigned for salinity). Extreme values indicate extreme positions in the corresponding dimension, that is, here for very high light, continentality and pH values and very low temperature. *Dryas* can be grown also in moderate temperatures and high nitrogen conditions, for example, in European botanical gardens, but only after exclusion of competitors.

Given that the biotic environment changes over the range of a plant species, it is not surprising to find that these indicator values require some regional fine-tuning. The same species may be a limestone specialist in Austria but occur on high-pH schist in Norway (in the case of *Dryas octopetala*). Still, Ellenberg's indicator value scheme has proven so robust, useful and pragmatic that it has been adopted in other countries (e.g. Austria, Italy, Greece, Switzerland, UK) and extended to other species groups (e.g. mosses).

Because many plant species have some value to indicate light, soil or nutrient conditions, we can move from understanding a plant's environmental niche to its converse, using plants to indicate environmental conditions (Dufrêne and Legendre 1997). Plant species whose occurrence can consistently and reliably be related to, say, soil salinity are called **indicator species**. Only a small subset of all plant species

Box 19.3: Hohenheimer Groundwater Experiment (*"Grundwasserversuch"*)

In this experiment, Ellenberg (1953) wanted to investigate whether the **realised niche** of four grass species in mixture differed from their **fundamental niche** in monoculture along an environmental niche dimension (distance to groundwater). In an idealised Fig. 19.15a, this is what we may expect. The actual results are less spectacular but confirm the general idea (Fig. 19.15b).

In a re-analysis with more complete data retrieved in Ellenberg's old notebooks, both different fundamental niches *and* niche displacement under competition could be detected, confirming the initial interpretation (Hector et al. 2012).

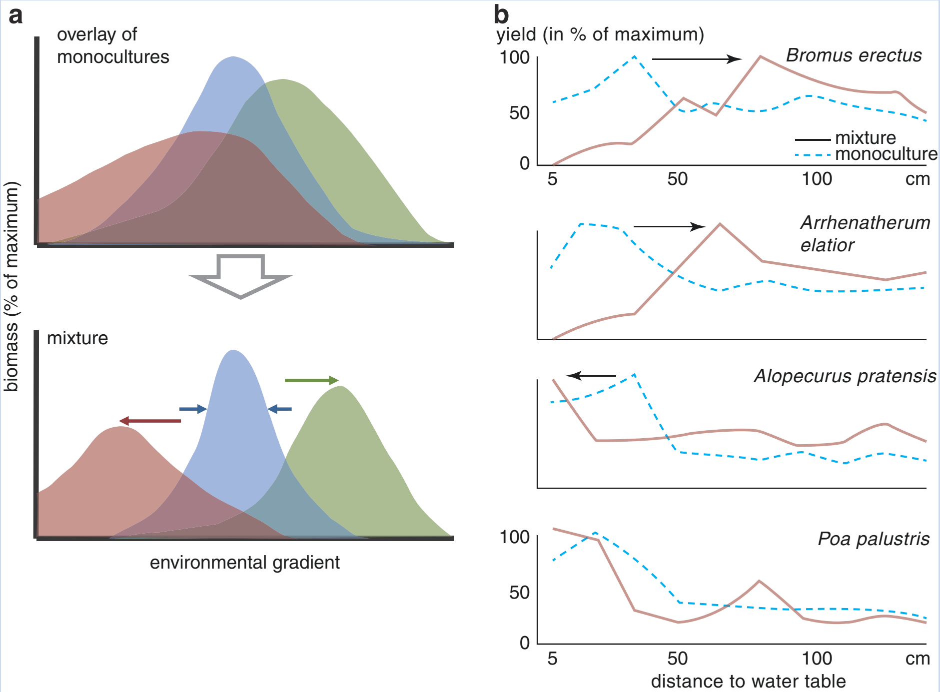

Fig. 19.15 Shift from fundamental to realised niches under interspecific competition. **a** Three hypothetical species having overlapping niches in fundamental niches (as measured in monocultures), which are affected by co-occurring species in mixture (bottom). Arrows indicate in which direction niches have shifted. Overlap (darker shaded parts) is substantially reduced. **b** Results of the actual experiment. Growth is represented as percentage of maximum growth of that species. Tall oat grass (*Arrhenatherum elatius*) takes the central position, with the three other species being pushed to the extremes (as indicated by the arrows). (Modified from Hector et al. (2012))

has a wide ecological niche in all dimensions except one, making it a reliable estimate for this one, narrow dimension. More commonly, evolutionary selective pressures have led to environmental formations, where climate and nutrient conditions co-vary (e.g. in nutrient-poor, unstable and dry sand dunes). Species adapted to these conditions indicate a formation rather than only a specific site feature. Such consistent vegetation formations are the topic of vegetation classification (Chap. 20), and here typical plant species characterise and delineate plant associations, which by themselves have indication value.

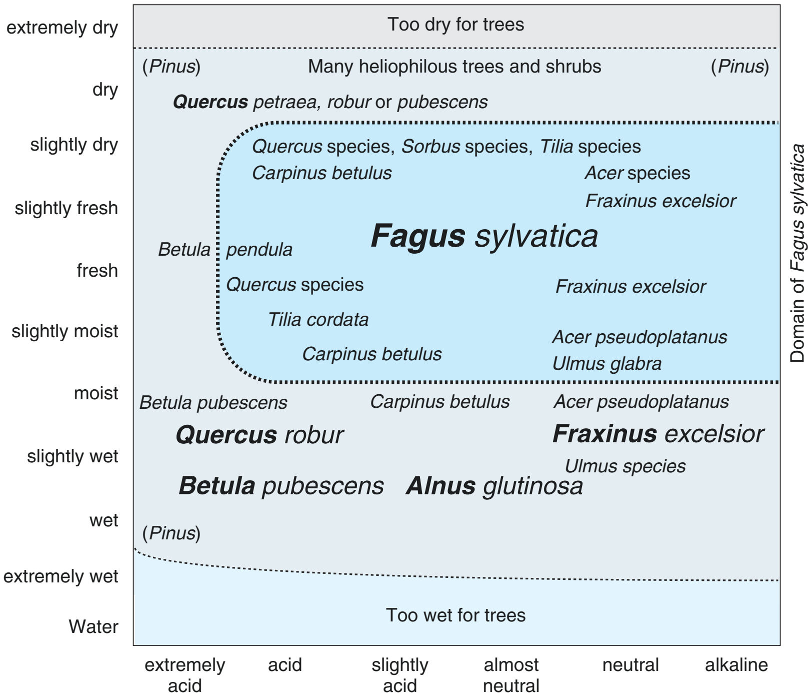

Fig. 19.16 Ecogram of submontane Central European trees showing realised niche positions along pH and soil moisture dimensions. Heavily dashed area delimits dominance region of beech *Fagus sylvatica*. Font size represents dominance status. (After Ellenberg and Leuschner 2010)

It must be pointed out that using plant occurrence (or performance) as a "bioassay" to measure environmental conditions is only a first approximation. Plants integrate environmental conditions over months and years, and dispersal limitation may lead to their absence and, hence, distort the derived value. Still, indicator values often correlate nicely with actual measurements of the environment (Ertsen et al. 1998), particularly across plots within the same vegetation type.

In a next step, we can depict the realised niches across two dimensions, for example, pH *and* soil moisture. This leads to so-called **ecograms** (Fig. 19.16), which represent niches in an idealised way, since often the actual composition is heavily modified through human management.

Ecograms can also provide a first assessment of environmental change effects, for example, of which plant species and communities we would expect when restoring drained wetlands or under greater drought stress due to climatic changes. They are necessarily incomplete, as the niche is multidimensional, but the ecogram depicts only two axes. Their added value lies in communicating our understanding to interested laypersons and to practitioners such as foresters and conservationists.

19.4 Interactions Between Plants and Animals (Contribution by H. M. Schaefer)

Plants and animals interact in a myriad of ways (Figs. 19.17 and 19.18), resulting in complex interaction webs at the community or ecosystem level. For example, animals need particular species of plants for their food supply, and many flowering plants depend on animals for pollination, and especially woody plants in tropical forests depend on animals to disperse their seeds.

The far-reaching effects of animals on plant communities become obvious in terms like "**termite savanna**" and "**beaver meadow**" or if we regard the transport of large amounts of nutrients from the sea to the mainland, for example, the Guano deposits in the North Chilean coastal regions. Animals not only sometimes depend on

Fig. 19.17 Examples of manifold plant–animal interactions. Carnivory: The Mediterranean Portugese sundown (*Drosophyllum lusitanicum*) captures insects to complement nutrient uptake **a**. Commensalism: Thorn bugs use the stems of a Solanaceae in the montane forests of Ecuador as a mating place **b**. Termites can play an important role in nutrient cycling and thereby affect plant species composition as in the example of termite savannas in Africa **c**. (Photos: K. Müller-Hohenstein)

specific plant species but also on the structure of single plants or plant communities. For example, canopy height and layering of plant communities are key variables affecting the availability of resting and nesting sites—and thus habitat quality—for bird species, such as the Capercaillie (*Tetrao urogallus*), for example (Fig. 19.19). Numerous invertebrates find shelter under the leaves or bark of trees.

Thus, many characteristics of plants and plant communities have a considerable influence on animals, via:

- Food supply (e.g. leaf mass, fruits, wood, nectar, pollen).
- Carnivory
- Availability of physical structures (e.g. horizontal branches, closed canopy, dead wood).

Conversely, animals influence plants and plant communities in different ways, which can be partly understood as a response to the use of resources provided by plants, such as

- Herbivory (e.g. eating whole plants or only leaves, fruits).
- Pollination.
- Dispersal of seeds (and other propagules).
- Change of soil properties (e.g. bioturbation, degradation of organic matter by invertebrates).

Some of these interactions have long been the focus of ecologists and evolutionary biologists alike because they represent the backbone of structuring terrestrial biodiversity. However, plant and animal communities differ in some ways. Animal communities are usually richer in species. Animals use different resources in time and space, which obliges them to move between sites. Table 19.3 shows the temporal turnover in the population of ground-dwelling beetles (Coleoptera) in a semidesert species poor plant community. Therefore, for animal ecologists it is practically impossible to take a complete inventory of all animal species at one time, and recording of this diversity is a very time-consuming task requiring the cooperation of several taxonomic specialists.

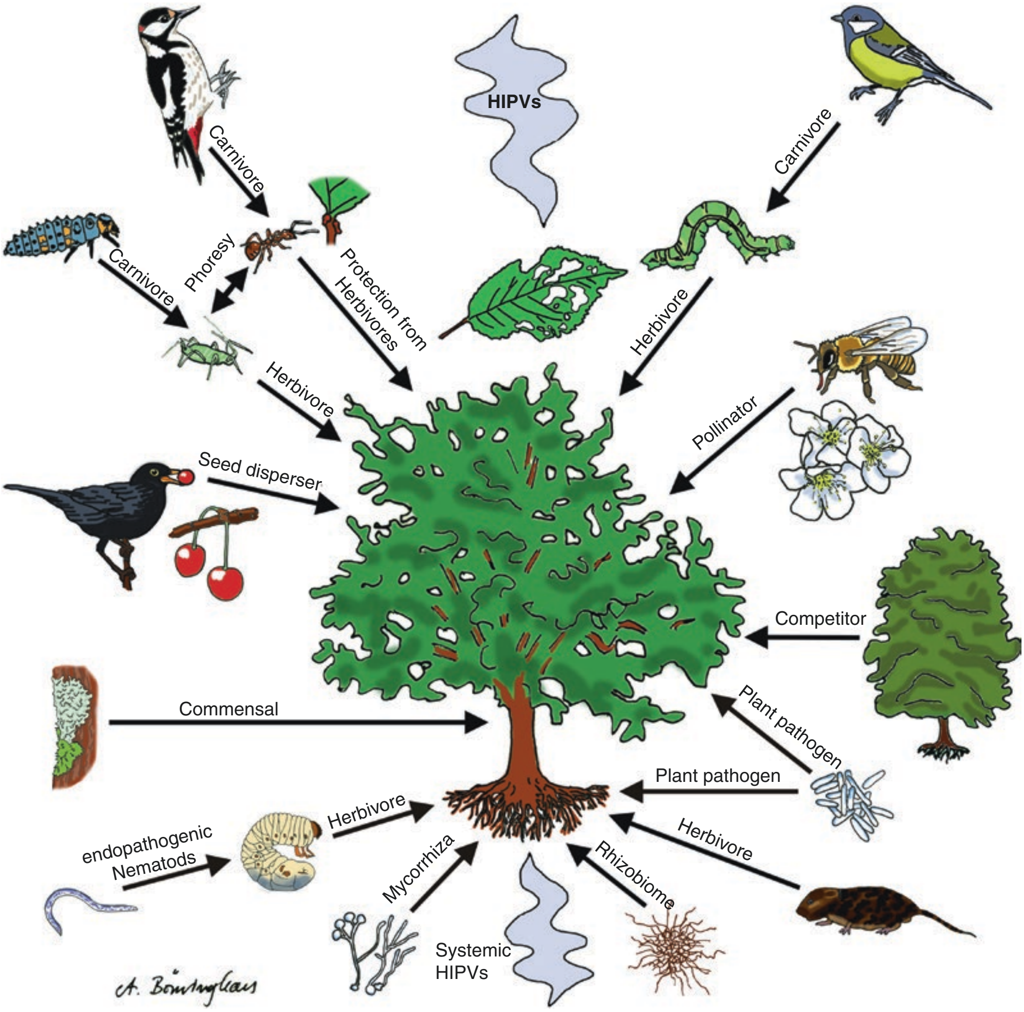

Fig. 19.18 Biological interactions between plants and other organisms (HIPVs: herbivore-induced plant volatiles)

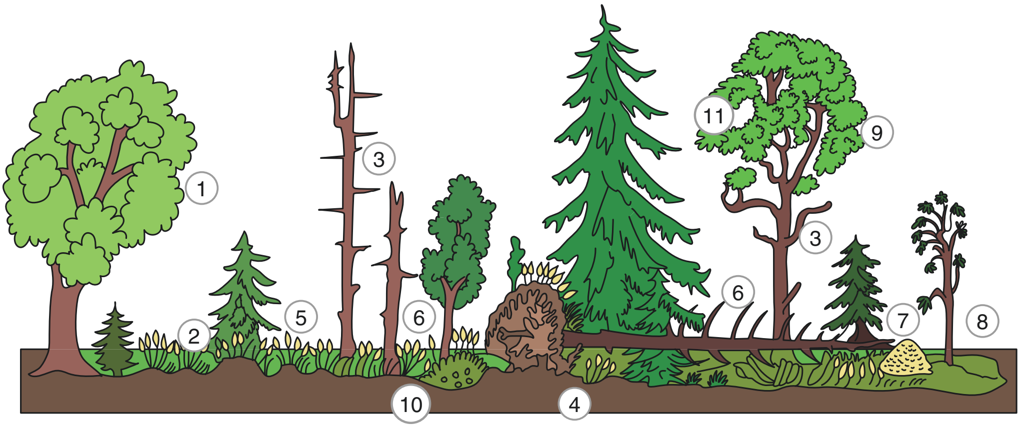

Fig. 19.19 Schematic of capercaillie (*Tetrao urogallus*) habitat requierements. A variety of different plant species, vegetation structures and environmental conditions are needed to fulfil habitat requirements for this bird species. 1: forage for beech buds in spring 2: protected nesting site 3: mating tree 4: grit uptake at root plates of fallen trees 5: forage for blueberries in summer 6: forage for xylobiontic insects on deadwood 7: forage for ants 8: mating site on the ground 9: forage for pine needles in winter 10: dusting sites 11: protected roosting site. (After von Hessberg 1998)

Table 19.3 Temporal dynamics of beetle species in a *Stipa tenacissima* community on high plateau of eastern Morocco (Müller-Hohenstein 1978). Beetles were caught in the same area at approximately monthly intervals between October 1973 and June 1974 (• = Only one, 1 = Several, 2 = Many)

Date caught	26	14	17	25	20	25	24	15
	Oct.	Nov.	Jan	Feb.	Mar.	Apr.	May	Jun.
Pachychila lesnei	1	1						
Scaurus tristis	•	2						
Pachyscleodes semiasperula	•	•						
Trox barbarus	1		1					
Geotrupes puncticollis	•		1					
Paracelia simplex	1	1		•			•	
Ontophagus taurus	•	•			1	•		
Gonocephalum prolixum	2	2	2	1	2	2	1	
Cymindis setifensis	2	1	1	1	1	1		1
Micipsa instriata	1	1	2	1		•	•	1
Timarcha latipes	1	**1**	1	2	•	1	•	1
Pimelia boyeri	1	1	•	•	1	1	1	1
Hoplarion tumidum		2	1		•			
Gonocephalum rusticum		1		1		•		
Adelostema sulcatum		•		•			1	
Hoplarion latissimus			1	1		2		
Rhytirrhinus compressipennis			•			•	•	
Chrysomela hyperici			1			•	1	
Adesmia metallica ssp. faremonti			1		1	1	•	•
Entemocelis rumicis				1	•			
Chrysomela sanguinolenta				1	1		•	
Scarabaeus puncticollis					1	•		
Scarabaeus laticollis					1	•	2	
Onitis ion					**2**		•	
Scarabaeus variolosus					1	1		•
Pimelia gibba						•	1	
Graphopterus exclamationis						•	1	
Chrysomela bicolor						•	1	
Scaurus dubius						2		1
Julodis manipularis						•	1	•
Mylabris brevicollis							1	1
Mylabris baulnyi							1	2
Acinopus sabulosus							•	•
Aethiessa floralis							•	1
Zophosis ghilianii							1	1

19.4.1 Classification of Plant–Animal Interactions

The interactions between plants and animals can best be understood by looking at their evolutionary effects on both groups. A classification of these interactions must consider two different directions: the influence of plants on animals and, conversely, that of animals on plants. The interactions can be beneficial for both groups, beneficial for one group only and either neutral (**commensalism**) or detrimental to the other group, or neutral to both sides. Mutually beneficial interactions are termed **mutualism**; they occur predominantly in **pollination** and **seed dispersal** where animals typically obtain a nutritional reward for dispersing the genes of plants. However, mutualisms occur also in **mycorrhizal** symbiosis where plants provide carbohydrates to the mycorrhizal fungi, which supply minerals in exchange. Well known are also mutualistic interactions between ants and several *Acacia* species, for example, *Acacia drepanolobium*. The ants use nectar from glands produced by the tree and defend the tree from herbivores (Fig. 19.20).

Fig. 19.20 *Acacia drepanolobium* is an important partner for mutualistic interactions with different ant species in semi-arid tropical woodlands. (Photo: K. Müller-Hohenstein)

Mutualisms can be viewed as **biological markets** (Werner et al. 2014; Stournaras et al. 2015). In general, reciprocal rewards stabilise mutualisms, which occur if both partners can exert control over the interaction, for example, by directing resources to reward partners. **Herbivory** and **carnivory** are examples of interactions that are beneficial to only one group, the consumer, and detrimental to the other. Such interactions are termed **antagonisms**. Herbivory occurs if animals consume plants or parts of them, whereas carnivory occurs if plants consume animals. Neutral interactions are those that do not affect the fitness of interacting partners. An example of a **neutralism** is if a bird uses a plant as a lookout or to broadcast its song but does not interact with the plant in other ways, for example, by consuming herbivorous insects on it. This would be an example of commensalism. Considering the fitness effects of plant–animal interactions allows us thus to trace the evolutionary history that has shaped these interactions and the traits of both the plants and animals involved.

19.4.2 Evolutionary History of Biological Interactions

During most of the twentieth century, researchers assumed a coevolutionary framework for plant–animal interactions. **Coevolution** occurs if species or groups of species undergo mutual **adaptations**. Mutual adaptations occur if a change in the traits of one group leads to a change in traits of the other group, which is followed again by a change in the traits of the first group. Coevolution can occur in mutualisms as well as antagonisms and is assumed to have produced much of the Earth's biodiversity. While adaptations undoubtedly occur—for example, figs dispersed by primarily visually guided birds are typically small, conspicuously coloured and have little scent, while figs dispersed by primarily olfactory guided nocturnal bats are relatively large, predominantly green or yellow and have a strong smell (Lomáscolo et al. 2010)—they are often difficult to pinpoint. Even in the example of figs, it is unclear whether coevolution has taken place since the sensory systems of birds and bats may not have evolved in response to the sensory stimuli of figs or, more generally, fruits. A very good system to study coevolution is the resistance among crop plants and their herbivores, which can evolve adaptations to overcome resistance within a decade (Rausher 2001).

While early classical work on coevolution focused mostly on interactions among a single species of plant and a single species of animal, there is now a consensus that the majority of plants interact simultaneously with many animal species and that these interactions are not independent of each other. Multispecies interactions are embedded in, and thus significantly influenced by, the community context (Strauss and Irwin 2004). This realisation has transformed the concept of coevolution into **diffuse coevolution** among multiple species where interactions with one species can alter the likelihood and strength of interactions with other species. Diffuse coevolution implies that the selective pressures of different species are not independent of each other. This interdependence is found, for example, in the selection for resistance against herbivores in the ivy-leaf morning glory (*Ipomoea hederacea*). Significant negative genetic correlations exist between resistance to deer and to generalist insect herbivory (Stinchcombe and Rausher 2001). In addition, the resistance loci under selection differ according to the composition of the local herbivore community. Finally, selection for deer resistance depends on the presence of insects. In the absence of insects, the deer resistance of ivy-leaf morning glory is effectively neutral. Thus, the sign and strength of selection can be influenced by the composition of the local community of animals and plants. This is important to note because animal communities can fluctuate widely in species composition and relative abundance of species over time and space. An important implication of this concept is, thus, that the fitness effects of plant–animal interactions are spatially and temporally variable, leading to a mosaic of coevolution (Thompson 2005).

Diffuse coevolution is most apparent if different species interact with the same traits. For example, ants that steal nectar but do not pollinate the flowers of the alpine sky pilot (*Polemonium viscosum*) select for smaller, narrower corollas, whereas bumblebees, the regular pollinator of that species, select for larger, wider corollas (Galen and Cuba 2001). Galen also showed that corolla shape is influenced by the abiotic environment, which again underscores that the net effects of animals on plants will be spatially and temporally variable. How intricately the interactions among different species can be linked is less apparent if distinct animal species interact with distinct plant traits. The interactions of the wild tobacco *Nicotiana attenuata* with its pollinators and herbivores provide a good example. Typically, wild tobacco flowers at night and is pollinated by hawkmoths, which are also important herbivores for that species. When hawkmoth larvae vigorously attack the leaves, their oral secretions trigger hormonal responses by the plant, which lead to flowers opening during day time (Fig. 19.21). These flowers are then pollinated by hummingbirds, suggesting that wild tobacco changes pollinators to reduce its herbivory load (Kessler et al. 2010). This study highlights that even seemingly independent interactions, such as those between plants and their pollinators and plants and their herbivores, can be linked by systemic responses by the plant. Consequently, the traditional focus of studying pairwise interactions among plants and animals has shifted towards a more encompassing approach of simultaneously considering multiple interactions.

Expanding the concept of coevolution to **diffuse coevolution** enables a more encompassing view of plant ecology that has many implications. A first important implication of the concept of diffuse coevolution is that the most apparent animals interacting with plants are not always the most important agents of selection on plants. Microbes and bacteria are ubiquitous selective agents whose effects on plants are often overlooked but widespread. For example, while **pollinators** and **seed dispersers** are the animals most evidently interacting with flowers and fruits, respectively, their interactions with plants cannot explain why resources that are made to be eaten, such as nectar and fruits, can be toxic to the extent that they are rarely consumed. For example, deterrent nectar has been found in at least 21 plant families (Adler 2000). Typically, combinations of chemical repellents and attractants will help reproductive organs to avoid predators while attracting animals' dispersing genes. The second implication is thus that the effects of all organisms interacting with a given plant trait must be considered in order to understand the mechanisms that structure interactions. The third implication is the lack of reciprocity that is necessarily found in strict coevolution among one plant population and one animal population. The fourth implication is that the results of studies can rarely be generalised across space and time, simply because fluctuations in the biotic and abiotic environment can alter how plants interact with a given species.

An alternative framework to coevolution is **ecological fitting**. Ecological fitting describes

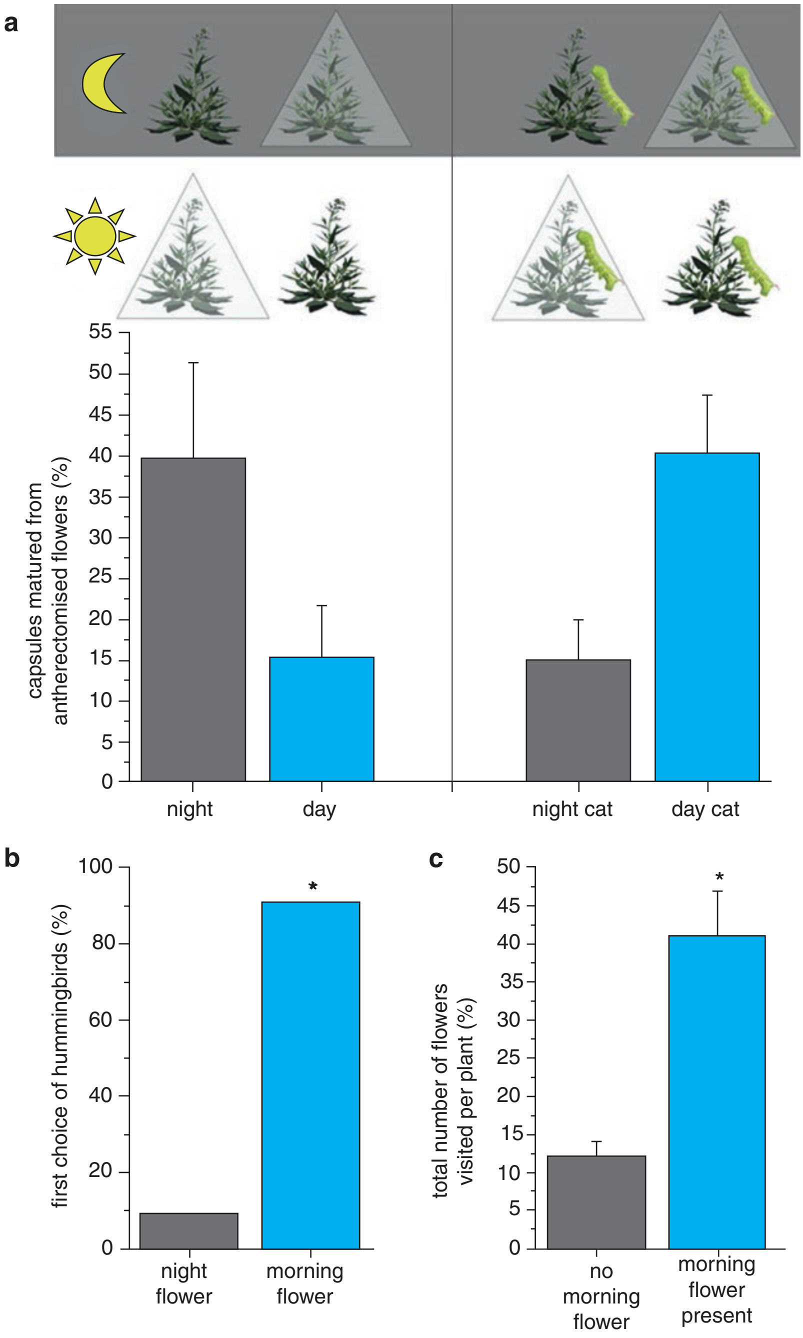

Fig. 19.21 Herbivory influencing pollination system. Herbivory by the larvae of the main pollinator *Manduca sexta* changed the pollination system in the tobacco plant *Nicotiana attenuata*. When no herbivores were present, *Manduca sexta* was the most important pollinator because plants dropped more seeds that were accessible only at night (to *Manduca sexta*) compared to those that were accessible to pollinators (hummingbirds) only during the day **a**, left. This pattern was reversed when herbivorous larvae were present on the plants **a**, right. The shift to hummingbird pollination is explicable by the way plants change to opening flowers in the morning when infested by herbivorous larvae, and hummingbirds prefer to visit flowers that open in the morning **b** and plants that have flowers in the morning **c**. (Kessler et al. 2010)

interactions among partners without mutual adaptations and is an appropriate null hypothesis for the concept of diffuse coevolution. Ecological fitting occurs if species interact with those species in a community that match best their own traits without a shared evolutionary history (Janzen 1985). Importantly, however, the concept of ecological fitting can be difficult to disentangle from diffuse coevolution because historical information on coexistence and mutual adaptations is rarely available (except for **invasive species**). The key difference is that coevolution expects interactions to be structured by mutual adaptations and thus genetic changes in plants and animals, whereas no genetic change in response to interactions occurs under the concept of ecological fitting.

Although ecological fitting is an inevitable and probably frequent process in nature that results from the interaction between highly flexible organisms and highly variable biotic and abiotic environments, it is not easily recognisable. Ecological fitting is thus perhaps most easily recognised in communities with frequent **species turnover**. Often the species assemblage within communities is not stable, whether owing to climatic changes such as glaciation cycles or to current human-induced changes to the environment such as grazing regimes of livestock. A context in which ecological fitting has attracted a lot of attention recently is that of invasive species, which obviously integrate into communities without sharing a coevolutionary history with the native species. For example, *Impatiens glandulifera* is an Asian invader in Central Europe reducing the pollination success of native species by attracting pollinators with its rich nectar resources (Chittka and Schürkens 2001). More generally, it is hypothesised that **phenotypic plasticity** is an important prerequisite for ecological fitting and for establishing new interactions with other species (Agosta and Klemens 2008).

Independent of whether or not the interactions among plants and animals instill evolutionary change, it is important to note that plants typically interact not only with a multitude of herbivores, pollinators and seed dispersers but also with bacteria and fungi. Even though bacteria and fungi typically outnumber herbivores and pollinators, the consequences of their interactions with plants are often not fully understood. The pungent taste of chilli (*Capsicum* spp.) is a good example. In *Capsicum chacoense* in south-eastern Bolivia there is a strong variability in pungency within and among populations. Interestingly, this variability is directly linked to variations in the damage caused by the fungal pathogen *Fusarium semitectum* that attacks the seeds. This fungus is the primary cause of seed mortality in *C. chacoense*, but the likelihood of infection is contingent upon secondary plant constituents. Fungal infection was twice as high in seeds from non-pungent fruits compared to pungent fruits (Fig. 19.22) (Tewksbury et al. 2008). Hemipterans foraging on the fruits facilitate the

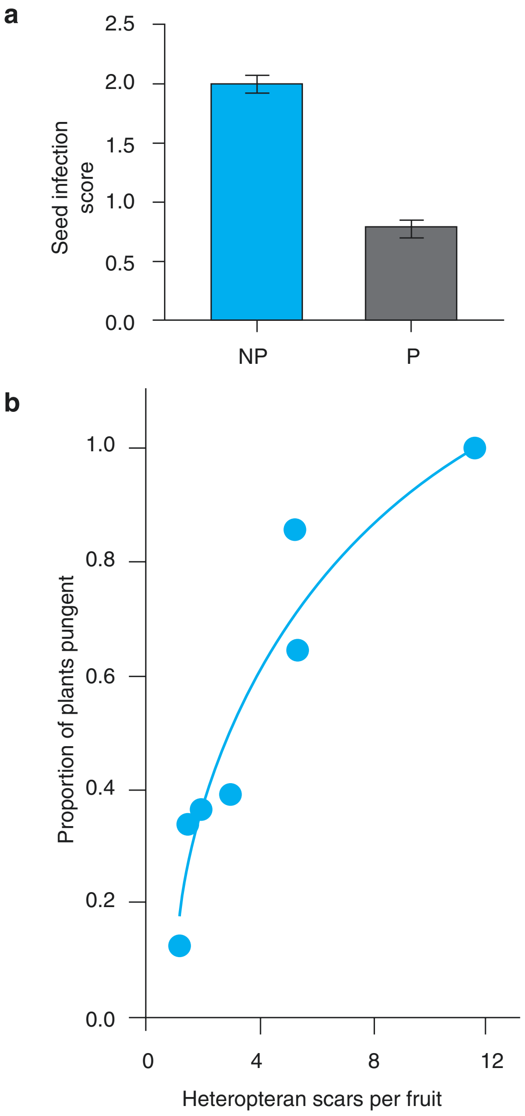

Fig. 19.22 Plant–herbivore–fungi interactions. *Capsicum chacoense* is naturally polymorphic for the production of pungent capsaicin. **a** Non-pungent seeds (NP) are twice as likely to be colonised by fungi (*Fusarium semitectum*) as pungent seeds (P). **b** The proportion of plants producing capsaicin within populations is a function of the predation pressures by Hemiptera, which puncture fruit skin and thereby facilitate the infection by the fungi (Tewksbury et al. 2008)

entry of the fungi into the fruit and its spread between fruits. Most notably, the foraging pressure of Hemipterans was a strong predictor of the proportion of pungent plants at a given site. Taken together, these results suggest that pungency in chillies is an adaptive response to the likelihood of fungal attack. More importantly, it is an example of the use of biochemistry to mediate the interactions with animals and pathogens.

Biochemistry is among the main mechanism by which plants structure interactions with their environment as their immobility precludes their seeking out favourable environmental conditions. Plants' biochemicals can be either very specific, targeting only one group or even species (see volatile signalling in what follows), or relatively general, affecting multiple groups of species. An important reason to expect general effects is that many biochemical pathways in plants produce a variety of end products that in turn can affect a variety of animals. Again, pungency in chilli illustrates broad as well as specific effects. Pungency does not only defend the chilli plant against fungi attack but also against seed predation by mammals which is reduced in pungent seeds (Tewksbury et al. 2008). In contrast, birds, the legitimate seed dispersers of chilli plants, are unaffected by the presence of capsaicin, the substance that gives chilli its pungent taste. Thus, capsaicin has general deterrent effects on both mammals and fungi but does not affect birds.

The fact that plants mediate their interactions through biochemistry can lead to the deceiving impression that plants are relatively inactive compared to animals. Yet this is not the case, as we will see in the following sections. Plants are active players that can quickly increase their defences in response to attacks by herbivores; they attract the enemies of their herbivores and use "signals" to increase their visibility and memorability for the animals they depend on.

Plants possess a very diverse array of **secondary compounds** with far more than 200,000 substances known so far and many more being discovered each year. The term secondary compounds encompasses all metabolic products without a known function in the primary metabolism of plants. In other words, all substances that are not known to be involved in the vital functions of growth, development, maintenance and reproduction of plants are included under this umbrella term. While the functions of the majority of secondary compounds are not known, a large number of them contribute to mediate plant–animal interactions. In general, three classes of substances are involved: pigments that impart colour to flowers and fruits, volatiles that attract pollinators but also recruit the enemies of herbivores, and deterrent substances that alter the quality of food.

19.4.3 Herbivory

Herbivores consume large proportions of the biomass of plants in most ecosystems. It is thus not surprising that herbivores can alter the composition of plant communities. Herbivory also forms the major process through which energy enters the food chain and is of major economic importance as it causes huge economic losses in plant crops cultivated for human consumption, for example, when swarms of locusts plague farmers or by post-harvest losses.

However, herbivory represents a very complex field of interactions between plants and animals. Plants are not just eaten. Herbivores influence plants in many ways, affecting their fitness and growth, as well as the composition, diversity, structure and dynamics of plant communities. Some results of grazing and browsing in plant communities are shown in Fig. 19.23.

Globally, the most important herbivores are the "wild" large vertebrates, such as African and Eurasian ungulates grazing in semiarid tropical regions. Domestic grazers, such as cows and sheep, prevail on artificial pastures in temperate climates. There are also many herbivorous invertebrate species which consume leaves, and also other plant resources; they suck sap, eat pollen or seeds, buds or young shoots. Insects in all stages of development are the most important group of herbivorous invertebrates. They are more specialised than vertebrates (i.e. are mono- or oligophagous), while vertebrates are mostly polyphagous. A special case of herbivory with enormous economic impact is granivory.

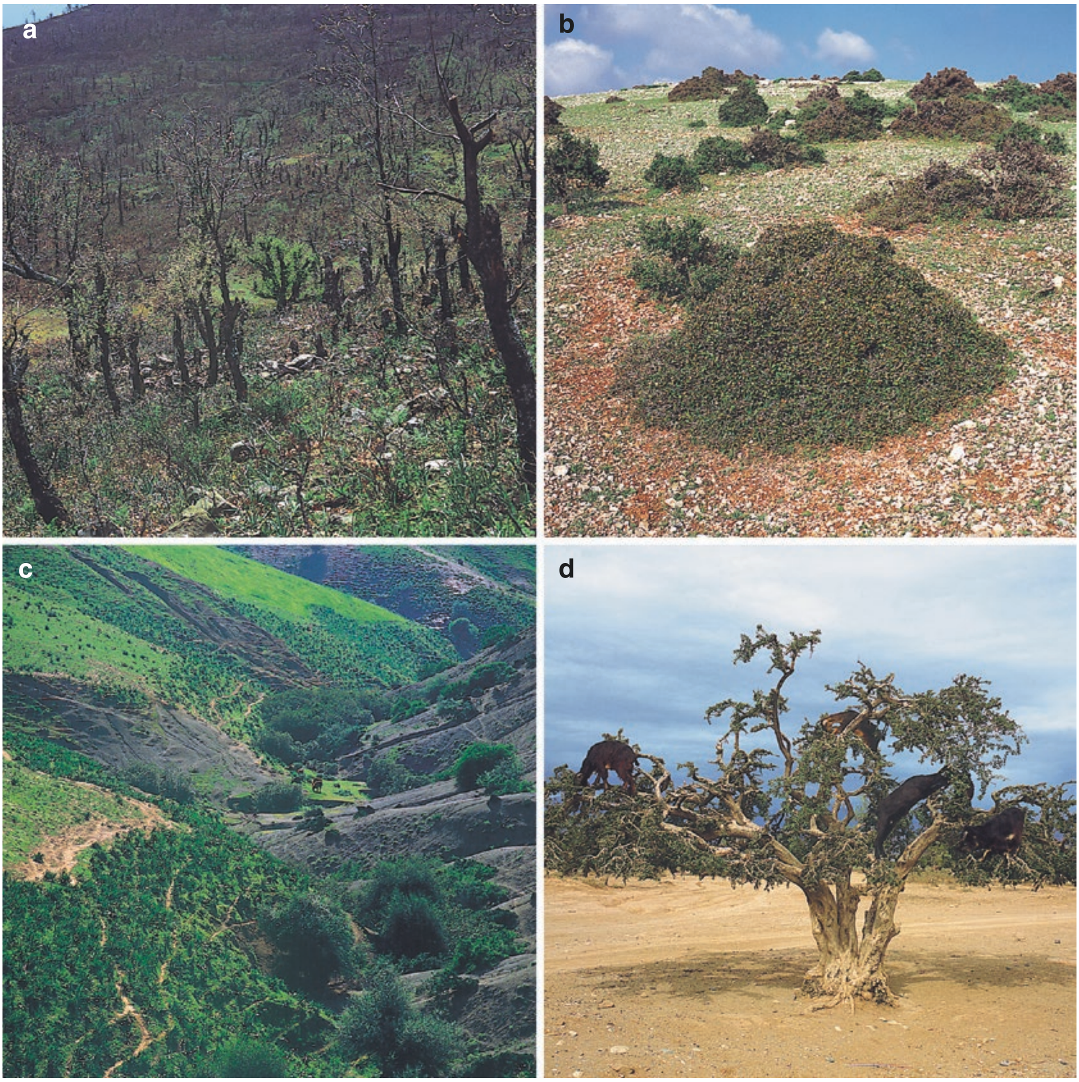

Fig. 19.23 Fodder production, grazing and browsing may have very different consequences for plant communities. **a** In the Rif Mountains in northern Morocco, branches of summer green oaks (*Quercus faginea*) are cut when animal fodder is in short supply. The trees appear stunted. **b** Extreme browsing pressure on *Quercus coccifera* in Jordan leads to sharper and stronger thorns on the small oak bushes. **c** Strong grazing pressure can also lead to increased frequency of toxic species, for example, *Asphodelus* div. spec. shown here in pastures of the Plateau Central in Morocco. **d** If herbs and grasses have already been lost due to excessive grazing, the remaining trees, for example, *Argania spinose*, are browsed by goats in the Sousse plain in southern Morocco. (Photos: K. Müller-Hohenstein)

Granivores feed mainly or even exclusively on seeds. Only recently has more attention been paid to root feeders (Stein et al. 2010). There is evidence that **below-ground herbivory** may sometimes be more important in its quantity and effects on plant communities than **above-ground herbivory**.

Extreme grazing generally leads to the loss of palatable species in plant communities, while especially poisonous and thorny species may expand their population sizes. However, herbivores can also promote plant species richness in many plant communities with medium grazing pressure by reducing the dominance of otherwise highly competitive plant species. The manifold consequences of herbivory depend also on the seasonal development of the different plant tissues. Especially in arid regions, early grazing of not yet fully developed plants has a significant influence on plant survival and fitness.

Two major hypotheses have been formulated concerning plant–herbivore relations: the **plant stress hypothesis** proposes that physiologically stressed plants become more susceptible to herbivores (Louda and Collinge 1992), while the **plant vigour hypothesi**s postulates that herbivores prefer plants growing vigorously (Price 1991).

Plants use two strategies to cope with herbivores, **tolerance** and **resistance**. Resistance is the reduction of the amount of damage caused by herbivores, whereas tolerance describes the reduction of the impact of herbivores on plant reproduction, for example, through rapid regrowth or increased photosynthetic activity. Resistance can be caused by biochemical and mechanical traits; the latter include thorns, latex, trichomes and other structures that impede browsing.

A fundamental principle is that both tolerance and resistance are costly to plants but that these costs are balanced through an increase in growth, reproduction and survival (Fig. 19.24). The costs of both strategies can also explain why there is a large interspecific difference among plants in their levels of resistance and tolerance. Costs are opportunity costs, for example, of resources devoted to defences or regrowth that could otherwise be used for reproduction. Biochemical defences also include the potential costs of deterring those animals plants want to attract, such as seed dispersers and pollinators, if the biochemicals are broadly deterrent and not restricted to the tissue vulnerable only to herbivores.

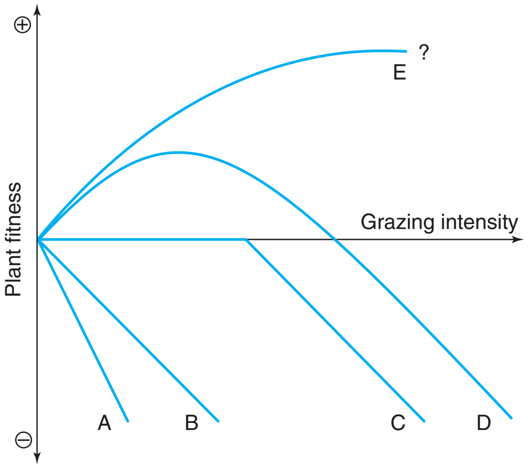

Fig. 19.24 Effects of herbivory on plant growth and fitness. Cases **A** and **B** assume that there is a linear relation between the intensity with which a plant is eaten and fitness (e.g. seed yield per plant). In case **C** herbivore pressure without visible effects is initially tolerated; only later do significant losses occur. In cases **D** and **E** grazing stimulates at first, stimulation may lead to increased fitness **E**, after the initial transient increase there may also be a decrease **D**. (After McNaughton 1983)

Plant defences can be classified according to their specificity. Most plants possess an array of general, broadly deterrent defences against herbivores such as tannins, for example. These defences are typically not very strong and can be overcome by herbivores. Thus, in addition to those broadly active defences, many plants produce more potent, specific defences that act against specialist herbivores. It is here where an **arms race** can occur between plants and their herbivores. Arms races are characterised by three steps. First, plants develop secondary compounds by which they defend themselves against herbivores. Plants producing biologically active compounds gain fitness benefits by reducing the numbers of herbivores. Second, as those defences reduce the fitness of herbivores, there is often strong selection on herbivores to overcome plant defences. This step is facilitated by two factors, the significantly shorter generation times of herbivores and pathogens (compared to most plants) and the higher population density of most antagonists. Third, plants develop new secondary compounds to fend off the antagonists that developed resistance to the previously evolved substances. A given plant still retains the original secondary compound because not all of its enemies will have evolved to overcome it. Thus, within-plant diversity of secondary compounds is driven, at least in part, by the ecological diversity of the enemies a plant may face and escalating arms races with some of these enemies. It is easy to see that arms races are a form of coevolution. Interestingly, such arms races of mutual counteradaptations are not found if plants employ a strategy of tolerance to cope with herbivores because tolerance does not reduce the fitness of herbivores, so it does not lead to counteradaptations by them.

Another way of classifying plant defences is according to their presence in plant tissue. Constitutive defences are continuously present, whereas induced defences are produced by a plant only if it is attacked by herbivores or if another plant in its direct vicinity is attacked. Induced defences are thus one way for plants to reduce the costs of defending themselves since they incur them only when the defences are actually needed. This is particularly so because attacks by herbivores are unpredictable in space and time. Notably, a plant relying solely on induced defences to fend off herbivores may be at a selective disadvantage relative to plants relying also on constitutive defences because there is a time lag before induced defences can be mobilised. This time lag can be reduced if plants prepare for the mobilisation of defences, a process known as **priming**, which refers to the synthesis of precursors of induced defences so that the time lag is reduced. For example, plants can use basic building blocks in the phenolpropanoid pathway such as chalcone to synthesise defensive compounds such as tannins. Indeed, priming can be induced by volatiles released from other plants that are associated with herbivore attack (Heil and Karban 2010). Another area in which priming is important is when a plant's reaction to one stressor enables a faster or stronger response to a second stressor. This often occurs if the biochemicals used in response to the two different stressors are derived from the same biosynthetic pathway because the same precursors can be used for both types of biochemicals. A good example of such a pathway is, again, the phenylpropane pathway in plants from which diverse substances originate from anthocyanins as plant pigments to various defensive compounds such as tannins and flavones (Schaefer and Rolshausen 2006).

Induced defences thus require that a plant senses that an attack by herbivores is likely to occur. This occurs obviously if the plant itself is attacked. Induced defence may result from the systemic transport of defensive metabolites from the area under attack to other parts of the same plant. As such it could be an unavoidable but slow process. Yet, the alert of an attack can also be transmitted through new substances produced after the attack has occurred. This chemical signal can be transmitted through the vascular system of the plant, or the signal can involve the release of volatile chemicals into the air from affected leaves of the plant and their detection by other parts or be transported through the networks of roots. How plants perceive airborne signals remains unknown. What is known, though, is that plants can adsorb and rerelease volatiles from neighbouring plants (Himanen et al. 2010).

Airborne signalling can be more rapid than vascular signalling, particularly in neighbouring leaves from different branches. It is easy to understand how an airborne signalling system can evolve since herbivory entails the destruction of cells with an unavoidable emission of substances into the air. Volatiles may thus be the unavoidable consequence of tissue destruction by herbivores, or they may constitute alerting signals specifically evolved to transmit information. Several factors, such as wind, temperature and nutrient availability, are known to influence the emission of volatiles. Distinguishing whether volatiles are necessary consequences of tissue destruction or evolved signals will allow us to understand whether plants evolved a communication system of alerting signals or whether they obtain information from cues, which are unavoidable by-products of herbivory.

Given that volatiles can indicate an attack of herbivores, plants may also be able to "sense" the attack on a neighbouring plant. One classical study (Karban et al. 2000) demonstrated that wild tobacco (*Nicotiana attenuata*) growing in a field in 0-15 cm distance to experimentally-clipped sagebush (*Artemisia tridentata*) became more resistant to herbivores than control plants near to unclipped sagebush (Fig. 19.25). The volatile signal inducing resistance in wild tobacco was an epimer of methyl jasmonate. Undamaged sagebrush individuals near clipped conspecifics also experienced reduced herbivore damage relative to controls. Although, in general, odours can travel large distances, distances recorded in

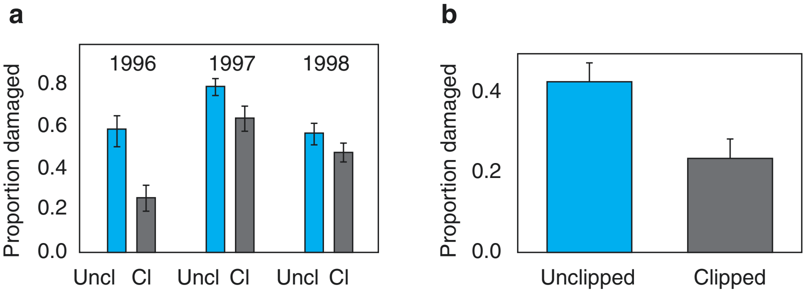

Fig. 19.25 Communication between plants through volatiles induces resistance to herbivores. **a** Maximum proportion of leaves damaged by grasshoppers during three seasons on tobacco plants near clipped (Cl) or unclipped (Uncl) sagebrush (means ± 1 SE). **b** Maximum proportion of leaves damaged by cutworms during 1996 season on tobacco plants near clipped or unclipped sagebrush (means ± 1 SE). (Karban et al. 2000)

experiments were typically only in the range of 10–15 cm. Thus, communication among plants through induced volatiles seems to be restricted to short distances. Such short distances are typical in grasslands but unlikely to occur commonly among trees in forests because the effects of competition among neighbouring plants are likely to outweigh the benefits of interchanging alerting signals. Hence, the topic of alerting signals between different plant individuals has not been fully resolved.

Apart from indicating the likelihood of an imminent attack by herbivores, induced volatiles can also have other functions: they can deter herbivores directly or attract their enemies, both predators and parasites. That plants can attract predators and parasites of herbivores underscores again the point that plants are active players in their interactions with other organisms. While there had been a debate on the effectiveness of volatiles under natural conditions, a few studies have shown a twofold reduction in the rate of oviposition by other herbivores and a fivefold increase in the rate of predation on eggs in response to induced volatiles. These numbers correspond to 90% reduction in herbivore load through the use of induced volatiles (Kessler and Baldwin 2001), suggesting that communication to the enemies of their enemies can be strongly beneficial for plants.

There is evidence that plants actively modify their olfactory communication in response to herbivory attack. Herbivore-damaged tobacco plants release volatile blends during the day that attract **parasitoids** of their herbivores, whereas those released at night repel herbivores that forage during the night. This evidence suggests that plants have indeed evolved an active SOS communication to fend off herbivores. Given that many predators and parasites of herbivores are insects such as wasps that search for their prey using volatiles, it is easy to envision how plants' SOS communication system evolved as those predators are already pre-adapted to react to odours.

Another intriguing aspect is that some plant species have evolved **mutualisms** with other animals, often ants, as a protection against herbivory. These plants provide ants with food and with housing (domatia) in the form of hollow swellings. The ants, in return, protect their host plant from herbivores and sometimes also from competitors. In addition, plants can take up nutrients from the decomposing detritus transported into the plants by the ants, as well as from the CO_2 respired by the ants (Treseder et al. 1995).

Interestingly, as in most mutualisms, the effects of plants and ants on their partners can vary. While some interactions evolved to the state of obligate mutualisms where ants are truly symbionts living only on those plants, other ant species destroy the flowers of their hosts to induce them to invest in growth rather than reproduction as these ants benefit more from plant growth. Again, plant chemistry can play an important role in structuring these ant–plant mutualisms. In exceptional cases, ants can only digest the type of carbohydrates produced by their host plant, effectively limiting their options to thrive on other plant species.

Another potential form of protection against herbivores is **mimicry.** Mimicry describes the adaptive resemblance between a model species and a mimic. Mimicry occurs if the mimic gains adaptive benefits by duping animals into confusing it with the model (Fig. 19.26). This confusion between mimic and model is the central element in mimicry and distinguishes it from related phenomena such as the exploitation of innate sensory biases of perceivers, which arise through their sensory system. Pollinators, for example, can have innate biases for visiting large floral displays (Naug and Arathi 2007).

Mimicry may occur interspecifically if individuals from a poorly defended species resemble individuals from a better defended species and, thus, gain protection from herbivores. This is a long-standing hypothesis that may pertain to mistletoes and vines that might benefit from being mistaken as host plants. One of the main challenges has been to show an adaptive benefit of such a resemblance. A recent study on the Neotropical vine *Boquila trifoliolata* is consistent with the mimicry hypothesis by showing (1) that leaves of this species resemble the foliage of the tree *B. trifoliolata* it is climbing and (2) that leaf herbivory is greater on vines climbing leafless trunks compared to those climbing trees with foliage (Gianoli and Carrasco-Urra 2014).

Fig. 19.26 Mimicry as a protection against herbivory. Seeds of *Margaritaria nobilis* are brightly coloured, like fruits, but offer no reward to seed dispersers in terms of fruit pulp. (Photo: M. Kuhlman, www.frutosatrativosdocerrado.bio.br)

Over the last 15 years a hotly debated question has been whether plants use leaf colour as a visual signal to communicate their defensive strength to potential herbivores. The idea was originally proposed to explain the exuberant yellow and red leaf colours during fall in the Northern Hemisphere (Archetti 2000; Hamilton and Brown 2001). The basic reasoning behind this hypothesis is that plants could benefit from such a signal of strength by reducing the attack rate of herbivores, while herbivores could benefit from such a signal by finding the least defended plants more quickly. While studies were quick to show a correlation between non-green leaf colours and herbivore attack rates (e.g. Hagen et al. 2003), it proved more difficult to establish that herbivores respond to leaf colour (and not to an associated trait) and that this association represents actually a signal that evolved for the effect of communicating to herbivores. Arguably, the best experimental evidence stems from the Southern Hemisphere. Leaves of the shrub *Pseudowintera colorata* vary in colour from green to red. Leaves with wider red margins contained higher concentrations of the secondary compound polygodial and experienced less herbivory. Crucially, experiments demonstrated that larvae of the generalist herbivore *Ctenopseustis obliquana* responded to the colouration of leaves when they avoided red leaves (Cooney et al. 2012). This study suggests that plants can use aposematic warning colours to communicate to herbivores and that herbivores attend to variation in leaf colouration.

19.4.4 Carnivory

Carnivory is very interesting because it has evolved perhaps as often as ten times. There are over 600 species of carnivorous plants, spread across 6 subclasses of angiosperms and distributed worldwide. Given the multiple, independent evolution of carnivory, it is not surprising that plants have evolved morphologically very distinct mechanisms to capture animals. The most common forms are pitchers filled with a fluid that digests small animals falling into the pitcher from a slippery rim formed by epicuticular waxes. Animals can also be caught with sticky fluids on the outside of the plant, through suction or through movement in response to physical pressure from the victim, as in the Venus flytrap (*Dionaea muscipula*). Carnivory occurs if plants have (1) evolved specific adaptations to attract and capture animals and (2) are capable of absorbing nutrients either directly from the dead animal or via an obligate and host-specific digestive mutualism. Such a mutualism occurs, for example, in some pitcher plants where a specialised microfauna living in the fluid thrives on the animal prey but also facilitates digestion for the plant. Again, mutualisms with ants occur as well, where ants clean the rim of pitchers and thereby increase the efficiency of prey capture, which is typically quite low in carnivorous plants. Ants, in turn, benefit from receiving food and nesting space by the pitcher plant. Other plant–animal interactions also occur in carnivorous plants; for example, small mites are able to live as commensals below the glandular, adhesive hairs on the surface of trap leaves of *Pinguicula*, feeding on the trapped insects (Antor and García 1995).

Despite having evolved multiple times, carnivory remains a very uncommon trait in plants (occurring in less than 0.2% of angiosperm taxa). While it is often difficult to reconstruct the evolution of traits without a good fossil record, there is the idea that sticky traps originally evolved as a defence against herbivores and that those defences later evolved into specialised traps for capturing insects. The scarcity of carnivory by plants suggests that carnivory is not an efficient way for a plant to gather energy compared to photosynthesis. Carnivorous plants are typically found on nutrient-poor soils such as heathlands, suggesting that carnivory is an adaptation for finding alternative sources of nitrogen (and other nutrients) rather than a means of gathering energy. The conjecture that nutrients rather than energy are limited is supported by the facultative expression of traps for carnivory that many species exhibit. This observation is easily made with respect to carnivorous species that are kept in one's home. When watered with tap water, they tend to grow quicker but reduce investment in traps, while they grow slowly but invest in many traps when watered with distilled water.

Many carnivorous plants use sugar rewards to lure animals to their trap. This fact suggests that carnivorous plants capture animals primarily to increase their intake of nitrogen and less for the intake of energy. As stated earlier, the efficiency of traps is relatively low, and it is not uncommon for only 1% of prey attracted to a plant to actually be caught. **Carnivorous plants** do not appear to specialise in particular types of prey. To increase capture efficiency, carnivorous plants may use volatiles and colour to lure prey, which are typically insects but can occasionally also be small rodents. There is substantial variation in the colouration of traps, mainly from green to red but also in the UV range. Because many insects are not particularly sensitive to the colour red, it is doubtful whether red colouration functions primarily to attract prey, even though such effects have been reported. The role of colour has not yet been fully elucidated. **Volatiles** released from traps include components that are commonly found in flowers and fruits and may serve an attractive function. Based on such similarities in bouquets, it has been suggested that traps mimic flowers. This is a fascinating suggestion, but similarities can occur for a variety of reasons and are thus not necessarily caused by mimicry. So far, no compelling evidence has emerged to show that prey confuse flowers with traps. Indeed, it has been suggested that carnivorous plants have evolved mechanisms, such as temporal and spatial separation between flowers and traps, to reduce possible conflicts that would involve potential pollinators being preyed upon. For example, many species have elongated flower stalks that separate flowers from their traps, for example, in the genus *Drosera* (Fig. 19.27). Hence, it has not been conclusively shown that mimicry exists in carnivorous plants.

19.4.5 Pollination

Wind and animals are the most important vectors for pollen. **Pollination** by wind can occur over greater distances, but the success declines remarkably with distance. The distance of pollen transported by animals is usually much more restricted, but

Fig. 19.27 *Drosera rotundifolia*, one of the frequent carnivorous species in undisturbed moorlands. (Photo: K. Müller-Hohenstein)

pollen carried by animals often has higher chances of ending up on the stigma of a conspecific. This is because animals do not move randomly within an area but rather direct their movements to locate food resources thereby increasing the probability that pollen will be deposited on flowers.

The key element in pollination is thus that pollen needs to be moved from one flower to the next conspecific one for successful pollination. To enable that movement, pollen must stick to animals, for example, the hairs of insects or feathers of hummingbirds, and be brushed off on the stigma of the next flower. Flowers typically offer rewards to entice animals to visit them. The most common types of rewards are nectar and pollen; less common rewards include resins, fragrances that insects collect in specific grooves and heat. For example, male orchid bees (Euglossini) collect fragrances from flowers and other resources and store them in specialised tibia pockets to use them later in courtship (Eltz et al. 2008). In some cases, insects visit flowers not for their nutritional rewards but because they have a high likelihood of finding mating partners on flowers.

Not all animals visiting flowers to collect rewards are **legitimate pollinators**; some leave flowers without having transferred pollen or taken it up. To complicate the issue further, species such as bumblebees or hummingbirds that may be legitimate pollinators in one plant species may be nectar thieves in another. To study pollination systems, it is thus essential to verify the effect of animals on pollination.

Flowers that exceed the mean ambient temperature can offer considerable metabolic rewards in terms of heat to **ectothermic insects**. **Self-heating flowers** evolved independently in 6 families, with an estimated number of 900 species alone being pollinated by scarab beetles of the genus *Cyclocephala*. Seymour et al. (2003) showed that beetles resting inside 3–4 °C warmer flowers had two- to five-fold lower metabolic rates than those outside the flowers. **Thermogenesis** is associated with elevated respiratory rates, which is why CO_2 emission can be a reliable indicator of heat production. Because insects spend a considerable amount of time in warm flowers, there is a high probability of successful pollen transfer. Plants can also increase the probability of pollen transfer by trapping insects until pollen has been transferred.

Because floral rewards can be unpredictable and are often not immediately visible to approaching floral visitors, many pollinators learn quickly to associate floral phenotypes with the expected average rewards. Learning of variable phenotype–reward associations can lead to an important behaviour for plant fitness, **floral constancy**. Floral constancy describes the behaviour of preferentially visiting one or a few rewarding floral phenotypes in subsequent visits. Flower constancy is an important behaviour that leads to a high probability of the arrival of conspecific pollen. Hence, flowers should be under selection to be memorisable for animals, a selection that is not necessarily found in fruits since successful seed dispersal does not require animals to visit conspecific plants.

Because plants have a high interest in not losing pollen on flowers of different species, interactions with pollinators are on average more specialised than are those with seed dispersers. The higher specialisation is explicable because floral phenotypes represent important filters that structure the interactions between flowers and floral visitors. Perhaps the most important filter is floral morphology, which can severely restrict the ability of animals to reach the nutritional rewards of the flower. In addition, floral morphology obviously influences not only the likelihood that pollen will be transmitted by a floral visitor but also the sequence of events. Presenting pollen and stigmata that receive pollen so that pollinators touch them before they can exploit nutritional rewards (referred to as approach **herkogamy**) can be adaptive because pollinators provide their pollination service before plants deliver payment in nectar. This situation contrasts with that of seed dispersal, where plants have no control over the movements of animal vectors once they leave the fruiting plant. Here, plants necessarily pay in advance—in terms of the energy provided by fleshy fruits—prior to the seed dispersal event. Third, flowers of a given species are under greater selective pressure to be recognisable and visited repeatedly than the fruits of the same species. Consequently, phenotypes that are important in species recognition such as colours and scent are more diverse in flowers than they are in fruits. For example, the diversity of floral colours is twice that of fruit colours, and flowers sport colour patterns more often than fruits, which creates further diversity in visual floral displays (Stournaras et al. 2013).

Even though pollination systems are more specialised than **seed dispersal systems**, there is strong variation in the degree of specialisation. On one end of the generalisation–specialisation continuum, only a single species pollinates flowers, whereas other plants are pollinated by more than 50 different species. Figs are often quoted as a remarkable example of a particularly specialised **pollination system**. Bertin (1989) described the cycle for *Ficus sycomorus* (Fig. 19.28). The

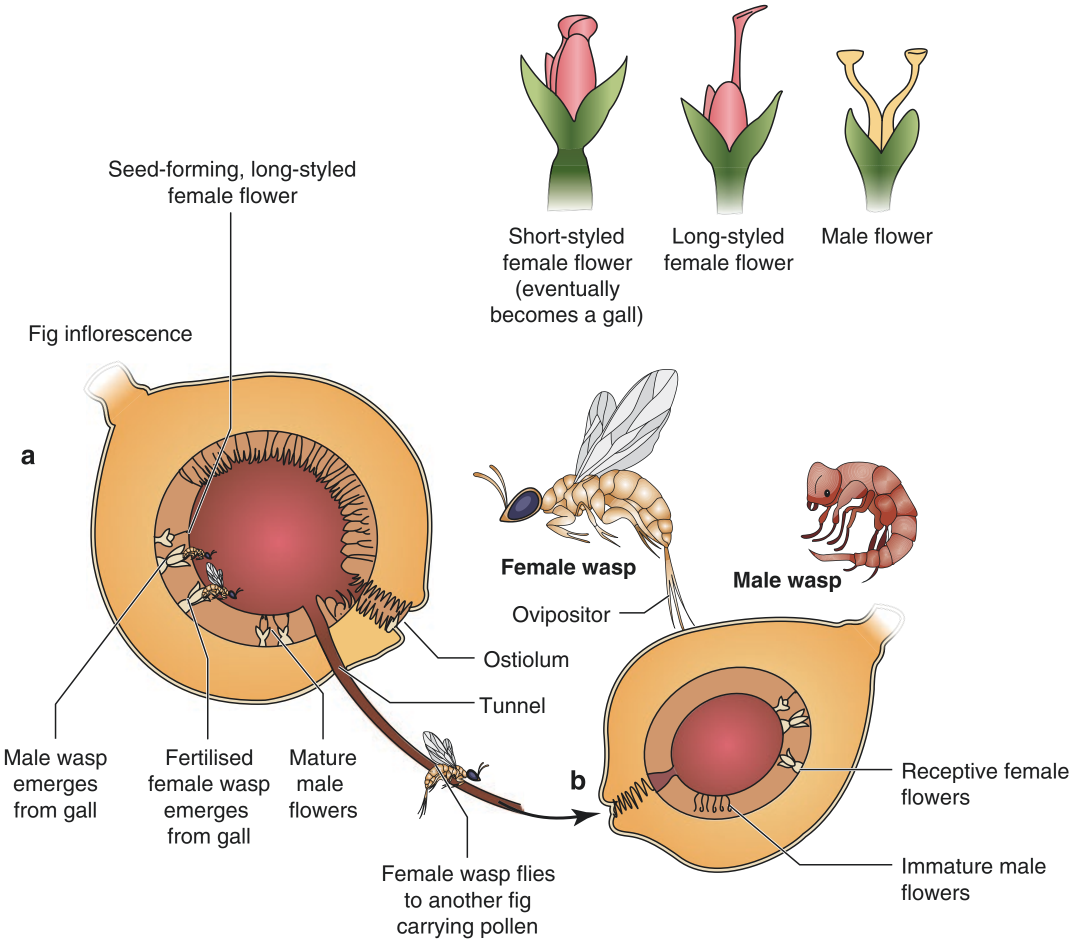

Fig. 19.28 *Ficus sycomorus* and its wasp pollinators. (Bertin 1989)

syconium, the large, almost closed inflorescence of this fig species, has a small distal opening, the ostiulum. Females of one group of wasps from the family Agaonides are attracted by the smell of the flowers and carry pollen through this opening into the inner space (in one direction only). They distribute pollen to the numerous individual female flowers in the inner space. In some of them, particularly those with shorter pistils, they lay eggs before they die. At the same time, individual figs develop and the larvae of the fig wasp feed on the gall-like growing fig tissue. First male wasps hatch and find galls with females and fertilise them. The males die or dig tunnels and reach the outside. The females pass through these tunnels to the outside, taking up pollen near the tunnel. This is a very specialised pollination system with coevolutionary, morphological and physiological adaptations of wasps and figs.

There appears to be a latitudinal gradient, with the pollination system of tropical species being on average more specialised than that of temperate species. Floral morphology is key to understanding the degree of specialisation. Open, radial symmetric flowers (**actinomorphic**) are less efficient at directing pollinator movement within flowers to the stigmata and thus often exhibit a "generalised pollination system". In contrast, closed **zygomorphic** flowers with bilateral symmetry restrict the directionality of approach and movement within the flowers, leading to more efficient pollen transfer. Radial symmetry is the ancestral form, with zygomorphic flowers having evolved independently several times. The length of flower tubes is a further morphological trait that can strongly influence which animals are able to enjoy the floral rewards. The longer the tubes, the more restricted and, hence, specialised the pollination system will be.

The most important function of **floral morphology** is to ensure effective pollination. As discussed earlier, this can partly be achieved by screening out nectar thieves or unreliable pollinators. Unreliable pollinatores are those visiting a species only irregularly and thereby increasing the risk of losing pollen. However, plants can also increase pollination effectiveness by guiding pollinators to the reproductive organs. It is here where flower morphology is particularly important. For example, Muchhala (2007) showed that bats and hummingbirds selected for different corolla widths. In an experiment, he showed that wide corollas guided bat snouts better, whereas narrow corollas guided hummingbirds' bills better. A poor fit between floral morphology and pollinator morphology resulted in variable entry angles and decreased pollen transfer. Interestingly, generalisation in plant traits was never favoured in this experiment because intermediate corollas always had lower **pollen transfer** rates.

Nectar guides are another morphological feature to help pollinators orient on flowers. Nectar guides can be morphological, for example, elevated rims on the surface of the petals, or visual, such as coloured marks or UV stripes radiating from the floral rewards (Fig. 19.29). There is also possibly an olfactory correspondent of nectar guides because flower parts of the tall buttercup (*Ranunculus acris*) differed in odour profiles (Bergström et al. 1995). Most remarkably, pollen odour differed strongly

Fig. 19.29 Plants guide pollinators to their reproductive organs. Nectar guides are morphological or visual traits such as rims that radiate from the centre of a flower and help pollinators to orient on it and find the nutritional rewards. (Photo: by HM Schaefer)

from all other plant parts, and emission from the petals differed among apical and basal petal regions, paralleling **optical nectar guides**.

Earlier, we stated that animals typically visit flowers to collect **nutritional rewards**. Yet flower visitors need to be tolerant to variable nutritional returns. Even in highly rewarding species that offer abundant nectar or pollen resources, the flower may have been depleted by recent visits of competing pollinators. Pollinators thus need to be tolerant to variable nutritional returns linked to a given floral trait. This tolerance is important in evolutionary terms. It facilitates, for example, the repeated evolution of rewardless flowers precisely because tolerance leads to weaker selection against rewardlessness. Although flower species from 32 families are permanently rewardless (Renner 2005), detailed data are available only for orchids, which are the prime example of deceptive flowers, with roughly a third of all species not offering any rewards to pollinators. To achieve pollination, the most commonly employed strategies of rewardless orchids are food and sexual deception. Food-deceptive species may mimic rewarding species or rely on perceptual exploitation of innate biases in the sensory system of pollinators. For example, a widespread innate bias of pollinators is that they preferentially visit large floral displays. Large floral displays are more easily detected from a distance, but the preference for large displays persists even in lab conditions where distances are typically small. Sexually deceptive orchids are probably the prime example of **mimicry in plants**. They mimic the scent of female pollinators and entice males to attempt to copulate with the flower, which also provides some visual resemblance to female pollinators. According to Jersáková et al. (2006), food deception is six times as common as the more specialised sexual deception in orchids. An important consequence of rewardlessness is an increased outcrossing rate as pollinators leave unrewarding plants more quickly than rewarding plants. As such, they may visit fewer flowers of the same individual, which means the pollen of the flowers they did visit will be disproportionally deposited on the flowers of different individuals.

Although pollinators need to be tolerant to variable nutritional returns, there can also be selection for more reliable signals. For example, flowers of at least 77 families change colour once they are pollinated (Weiss 1995). These **unrewarding flowers** still contribute to attracting pollinators from a distance to as yet unpollinated flowers of the same plant. At the same time, they also increase the foraging efficiency of pollinators by directing them to rewarding flowers. The repeated evolution of the trait of colour change is thus thought to originate from a coevolutionary process between plants and their pollinators that increases the efficiency of pollen transfer.

Flowers and pollination are important in **premating isolation** and speciation in plants. In particular, pollinators can drive speciation in plants if they restrict their visit to specific phenotypes. This is termed **ethological isolation**, and it can constitute an important premating isolating barrier. The proximate basis for ethological isolation is the distinct sensory world of pollinators. Ethological isolation is typically studied in hybrid zones, for example, that of *Ipomopsis aggregata* and *I. tenuituba*. In this hybrid zone, ethological isolation mediated by difference in flower colour was more important than mechanical isolation owing to distinct floral morphologies. *I. aggregata* is characterised by red flowers with wide corolla tubes and a high nectar production, whereas *I. tenuituba* has white to pink flowers with long and narrow corolla tubes and low nectar production. Painting flowers of both species red increased the percentage of conspecific seeds (Campbell and Aldridge 2006), demonstrating the importance of **plant–animal communication** in directing gene flow.

Although the concept of diversifying selection exerted by pollinators upon floral traits is intuitively plausible, and although this process has likely played an important role in the diversification of angiosperms, it remains to some extent controversial. While interspecific comparisons consistently suggest that animal-pollinated clades are more species-rich than clades with other pollination systems, it has been difficult to exclude the possibility that this pattern is caused by animal-mediated pollination rather than other selective agents not controlled for in analyses.

Odours are likely to be the primary communication channel of higher plants because fragrances were nearly universally employed among the early angiosperms. However, **olfactory communication** by plants is not as well known as **visual communication**, partly reflecting our own bias as visual animals, partly reflecting the more complex nature of olfactory signals. For example, more than 1700 substances are known from floral scent (Knudsen et al. 2006). However, many of these substances are not known to function in attracting pollinators. For example, only 9 of more than 60 volatiles in sacred datura (*Datura wrightii*) elicit a behavioural response in its pollinator, the moth *Manduca sexta* (Riffel et al. 2009). The complexity of odour blends means that it is often not a single substance that attracts animals but a mix of various compounds. In a few pollination systems, odours constitute the reward, such as in Euglossini bees that collect perfumes from flowers (Eltz et al. 2008).

It should be emphasised that pollinators use both floral odour and colour to identify and discriminate among flowers. Visual and olfactory stimuli can have additive effects on pollinators. The additive salience of visual and olfactory stimuli was a good predictor of bumblebees' initial behaviour and learning performance of floral stimuli (Katzenberger et al. 2013). Importantly, this study showed that floral displays consisting of olfactory and visual stimuli with low individual salience were more effective than the summed predicted compound salience, pointing to a multiplicative effect of the combination of olfactory and visual signals. In other words, the simultaneous integration of olfactory and visual stimuli disproportionately increased perceivers' discrimination abilities of less efficient stimuli. This effect was not identical for vision and scent in bumblebees: Multimodal floral signals increased learning relative to only olfactory cues, but not relative to only visual cues. Hence, this and other studies document that pollinators select not a single trait but a combination of different traits, which has been termed a pollination syndrome.

19.4.6 Seed Dispersal By Animals

The general characteristics of seed dispersal were already treated in Sect. 18.1 of Chap. 18. Here we limit the discussion to issues directly relevant to interactions with animals. Most animals are mobile for at least one stage of their development; in contrast, plants are fundamentally sessile, with their only chance of dispersal being as seeds. Dispersal of seeds away from the parent may have a number of selective advantages. Firstly, it may reduce the exposure of the seed to predators or pathogens that are attracted to, or supported by, the parent. Further, it reduces the potential for competition between parent and offspring and among offspring. These concepts have been encapsulated in the **Janzen–Connell hypothesis** (Fig. 19.14) for the high species diversity in many plant communities (introduced independently by Daniel Janzen (1970) and Joseph Connell (1971).

This hypothesis suggests that diversity is maintained by two mechanisms:

1. **Mortality of seeds** and seedlings increases as their density increases, and
2. **Survival of seeds** or seedlings increases with increasing distance from the parent.

The likelihood of being dispersed an increasing distance from the parent decreases very strongly, however, beyond the immediate vicinity of the parent plant. This phenomenon is encapsulated in the key concept of the dispersal kernel. The dispersal kernel describes either the probability of a seed being dispersed or of dispersal and successful establishment as a function of distance from the parent plant (Cousens et al. 2008). Given the decreasing probability of a seed being dispersed greater and greater distances from the parent plant, the dispersal kernel of dispersal distances will generally show a monotonic decline to zero with increasing distance, whereas the likelihood of seed establishment may initially increase with distance before declining to zero again.

Dispersal distances by frugivores are highly variable; long-range dispersal over several kilometres does occur. Some large frugivores have long gut-retention times. Birds and primates can be very fast moving, covering distances of hundreds of metres in a few minutes. Thus, dispersal distances of up to tens of kilometres are certainly possible by this dispersal mode, and distances of tens or hundreds of metres are commonplace (Hardesty et al. 2006; Seidler and Plotkin 2006; Jordano et al. 2007). Dispersal distances will be very different for different frugivores. For example, while mammals were primarily responsible for long-distance dispersal of seeds of the cherry tree *Prunus mahaleb* (Jordano et al. 2007), birds and bats achieved longer **dispersal distances** than other mammals in a Neotropical forest (Seidler and Plotkin 2006). Although a good dispersal agent transports seeds away from the parent, there may not be selection for ever-further dispersal. Wenny (2000) followed the success of bird-dispersed seeds of the tree *Beilschmiedia pendula* in Costa Rica. Those transported less than 10 m from the parent suffered high mortality through predation and fungal diseases. However, those transported more than 30 m had lower survival than those transported 10–20 m. This effect likely arises because the environment close to the parent is more likely than more distant environments to be suitable to this species.

A very important characteristic of animal dispersal is that animals move non-randomly through a landscape, so they may deposit seeds non-randomly in ways that benefit subsequent germination. Wenny and Levey (1998) followed individuals of five bird species dispersing seeds of *Ocotea endresiana* in Costa Rica, monitoring the success of seeds through to the seedling stage a year after fruits were consumed. For four of the disperser species, dispersal distances were low (less than 20 m) and so were seed survival rates. However, over half the seeds transported by three-wattled bellbirds (*Procnias tricarunculata*) travelled over 40 m and often ended up under gaps in the canopy, where seedling success was high. The reason for this particular distribution is linked to male bellbirds commonly displaying to females from exposed perches where they are well-lit and can be seen from a distance. This behaviour of **non-random seed dispersal** can have important consequences, even at the landscape level. A landmark study based on data from 90,000 forest plots across Spain demonstrated that the distribution of animal-dispersed species is more resilient to fragmentation than that of wind-dispersed species (Montoya et al. 2008). Notably, dispersal mode was a better predictor of resistance to habitat fragmentation than any other variable, including seed size, and the results could not simply be explained by phylogeny. This effect is likely to be due to non-random movements of animal seed dispersers.

Defecation or regurgitation by frugivores is not always beneficial for seed preservation and subsequent germination. Quite often it results in seed clumping (Poulsen et al. 2001; Potthoff et al. 2006), particularly at sleeping sites (Russo and Augspurger 2004). Thus seed dispersal by animals may increase competition between seeds. However, this may lead to increased seed predation, for example, by ants and rodents, but sometimes these seed predators will also disperse seeds on the ground, for example, by caching them. Caching can lead to secondary seed dispersal when caches are not retrieved. For example, Central American agoutis (*Dasyprocta punctata*) scatter-hoard seeds across their home ranges of approx. 3 ha as food reserves for the low-fruit season. While agoutis initially cached seeds only over short distances, they subsequently recached the seeds up to 36 times, leading to total dispersal distances of >100 m (Jansen et al. 2012). This study shows that seed dispersal is a complex process that can consist of several different steps. It also shows that categorising animals as either mutualists or antagonists can oversimplify the interactions between plants and animals since even typically antagonistic animals such as seed predators (applying also to jays and squirrels) can confer fitness benefits to plants.

The insight that plants interact simultaneously with a variety of animals, bacteria and microbes is particularly important for explaining the contents of fleshy fruits. Nutrients, in particular lipids and carbohydrates, generally favour fruit consumption, whereas defensive **secondary compounds**, such as tannins and phenols, reduce fruit consumption (Schaefer et al. 2003b). Fruits can be very rich in either **lipids** or **carbohydrates** such as avocado and blackberries, respectively. There is a strong negative correlation between both types of nutrients, which can be explained by their biochemical properties; carbohydrates are water soluble, whereas lipids are hydrophobic. However, they contain more than double the energy of carbohydrates or proteins per weight unit.

Given that the meaning of fleshy fruits is that they are consumed and dispersed, the existence of deterrent secondary compounds may appear puzzling. However, there are myriads of organisms that consume fruit pulp but do not disperse seeds, such as microbes and fungi. The evolutionary triad between plants, their **seed dispersers** and **fruit predators** can explain the relative investment in nutrients and secondary compounds. Plants defend themselves against these unwanted fruit consumers with deterrent secondary compounds, some of which also affect the consumption rate of legitimate seed dispersers. Several studies (Cipollini and Levey 1997; Schaefer et al. 2003b; Cazetta et al. 2008) have found a negative relationship between the nutritional contents of fruits and their contents of secondary compounds, suggesting that plants employ alternative strategies to achieve seed dispersal. Nutrient-rich fruits are quickly consumed by seed dispersers, reducing the likelihood of predation by microbes and fungi. In contrast, less nutritious fruits are more strongly defended and can persist for months on plants, such as the guelder rose (*Viburnum opulus*).

19.4.7 Mycorrhizal Symbiosis

The symbiosis between **fungal mycorrhizae** and plants provides a good example of how plants trade resources with their mutualists from fungi to animals. As explained in Sect. 7.4 in Chap. 7, plants trade carbohydrates for fungal growth and survival in exchange for mineral nutrients and protection. This exchange of resources can be viewed as a biological market in which both plants and fungi try to optimise resource utilisation (Werner et al. 2014). Core assumptions about biological markets are that both plants and the consumers trade resources and services so as to maximise their respective benefits and that there is partner choice among the distinct classes of plants and consumers. Crucially, the quality of different potential partners varies, and there can be competition over which will be the preferred trading partner for other players. Finally, supply and demand govern the exchange value of resources for services, and all players can advertise the resources they offer. Market theory offers a good perspective from which to understand the dynamic interactions between plants, fungi and animals.

This **mycorrhizal mutualism** evolved long before plants engaged in mutualisms with insects and vertebrates and contributed to plants' colonisation of the land. Conforming to fundamental assumptions in biological markets, experimental studies demonstrated that plants could detect variation in nutritional returns provided by fungi, discriminate the best fungal partners and reward them (Kiers et al. 2011). Likewise, fungal partners increase nutrient transfer only to those roots that provide more carbohydrates in return. More specifically, the supply of carbohydrates by plants triggers nutrient uptake and transport by fungi in this symbiosis. Only when plants deliver carbohydrates across the **mycorrhizal interface** do fungi increase nutrient transport, but not when they can obtain carbohydrates directly (Fellbaum et al. 2012). That each partner attempts to optimise nutritional returns by choosing the best partner leads to bidirectional control, which in turn stabilises the mutualism through reciprocal rewards. This distinguishes biological markets from obligate symbiosis, where at least one partner has lost the outside option, which can lead to domestication as in endosymbionts.

The fundamental principle of partner choice does not only apply to mycorrhizae but also occurs in the **biological markets** of **pollination** and **seed dispersal** (Stournaras et al. 2015). Most animals are sensitive to variation in the nutritional rewards offered by plants. Seed-dispersing birds, for example, can discriminate 1–2% differences in the carbohydrate contents of fruits and perceive variation in the composition of amino acids (Schaefer et al. 2003a). Importantly, animals can use a simple self-serving strategy to direct their interactions to more rewarding partners and thereby reduce the fitness of less rewarding ones. A good example are hawkmoths, which reduce probing time on less rewarding flowers to increase their foraging efficiency and thereby reduce the pollination and seed set of relatively unrewarding flowers (Brandenburg et al. 2012). Self-serving behaviour is an effective strategy only if the fitness effects of multiple, repeated interactions between two partners have a pronounced influence on the fitness of each, but a single interaction does not strongly determine their fitness (Schaefer et al. 2014). This is the case for seed dispersal and for pollination.

The dynamics between plants and mycorrhizae differ, however, from those of pollination and seed dispersal because plants have greater control over partner choice among mycorrhizal fungi than among animals that disperse their genes. In other words, only animals, not plants, can apply self-serving behaviour to choose optimal partners in pollination and seed dispersal. As stated earlier, plants influence partner choice through their biochemistry. Plants may be able to adjust biochemicals to achieve optimal partner choice in tight coevolutionary interactions with animals over evolutionary time spans. However, coevolutionary interactions incur high risks of being interrupted in communities with high species turnover, such as those occurring during glacial and anthropogenic changes. This leads to a higher probability of deviations from optimal partner choice in pollination and seed dispersal than in mycorrhizal symbiosis.

19.4.8 Influences of Abiotic Environment on Plant–Animal Interactions

The interactions between plants and their abiotic environment can influence plant–animal interactions to a similar extent as the interactions between plants and one type of animal can affect their interactions with another type of animal. A well-known case is, for example, UV radiation. Field experiments show that plants as different as southern beeches (*Nothofagus spec.*) and jimsonweed (*Datura spec.)* ward off insect herbivory more effectively if they had received higher **UV-B radiation** during plant growth (Ballaré et al. 1996; Rousseaux et al. 2004). The underlying mechanism is called priming and relies on the fact that either the same or biochemically similar components are used in defence against biotic and abiotic stressors. Plants can thus react more quickly or more vigorously against a second stressor (e.g. herbivores) if UV radiation had already stimulated the production of defensive compounds or precursors thereof. Priming is an important phenomenon in plants because they cannot spatially evade their stressors and predators. This can also explain why in species that are polymorphic in floral colour it is usually the anthocyanin-pigmented morph that is not only more tolerant to **abiotic conditions** such as drought, extreme temperatures and high irradiance but also avoided by herbivores (Strauss and Whittall 2006).

Many complex phenotypes in plants may be best explained by the interplay between abiotic and biotic factors acting upon plant traits. This probably applies to the conspicuous changes in leaf colouration during senescence but also in emerging leaves because this colour change is strongly influenced by illumination and temperature but can also affect herbivores. It likewise applies to the red colouration of peduncles and pedicels in the infructescences of many plant species from different families (Fig. 19.30). Again, the colouration of peduncles is typically a light-induced response—suggesting that non-green pigmentation serves primarily a photoprotective function—but it can also serve a communicative function to attract seed dispersers by increasing conspicuousness through contrasts to the green foliage and through indicating the quality of nutritional fruit rewards, which is typically higher in strongly illuminated plants owing to higher photosynthetic rates (Schaefer and Braun 2009). The environmental effects on plant–animal interactions provide a mechanistic explanation for why **coevolutionary dynamics** between populations of plants and animals are temporally and spatially variable (Thompson 2005).

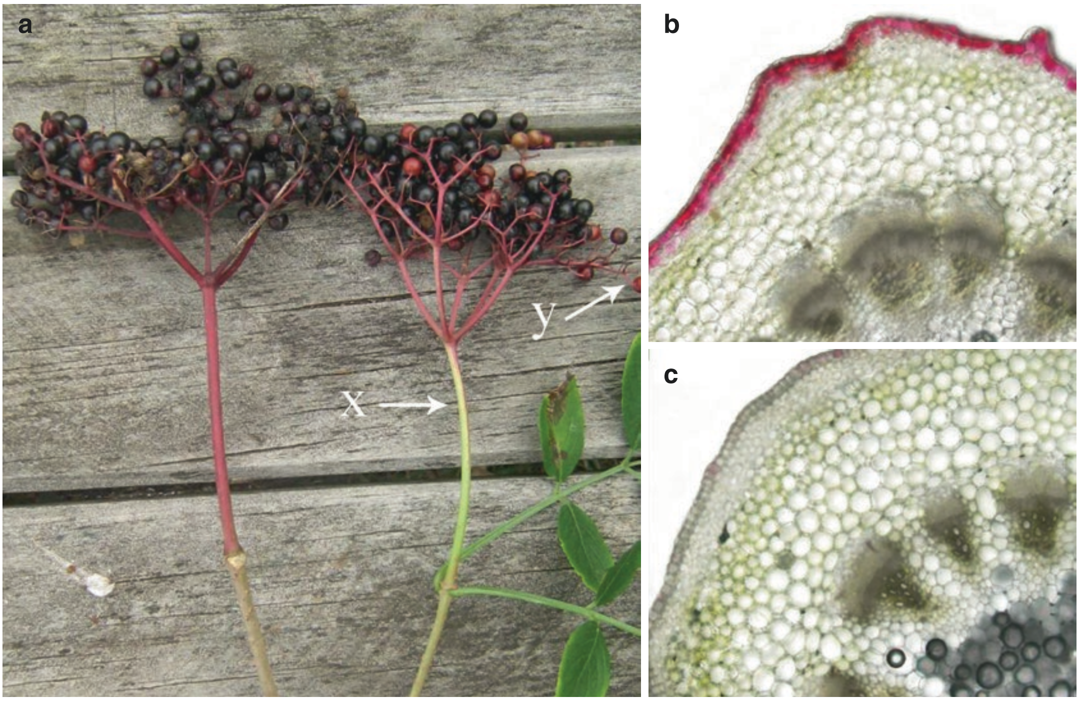

Fig. 19.30 Phenotypic plasticity influencing seed dispersal. The red peduncles of black elder (*Sambucus nigra*) are a stress response that may also be related to senescence, and they attract seed dispersers to the infructescence. The peduncles (*X*) vary predictably in their colour from red to green **a** according to the intensity of ambient light. Pedicles (*Y*) are mostly red. Anthocyanin pigmentation in the peduncle is restricted to the outermost layers of hypodermal collenchyma **b** and absent in green peduncles **c**. (Cooney et al. 2015) (Photos: HM Schaefer and L Cooney)

In sum, plants use **biochemicals** to mediate their interactions with the biotic and abiotic environment. They interact simultaneously with a variety of organisms and abiotic factors. These interactions are interdependent, which leads to variable outcomes depending on the composition of the community and the abiotic environment. The interdependence of plant–animal interactions makes the study of plant ecology a particularly fascinating and intellectually challenging topic. An important implication is that, similar to other fields of ecology, care needs to be taken when generalising from single studies. Nevertheless, many dynamics in the market between plants and their interacting organisms have been elucidated. One of the lessons from those studies and the many factors acting upon plants is that studies should thrive to assess the relative importance of different selective forces in order to understand the evolution of the ecological processes in plants.

Summary

- Plants interact with the abiotic environment, with other plants, and with animals and microorganisms. Plants and plant communities also influence and change the local, regional and global environment.
- Plant communities affect the local microclimate by changing albedo, temperature distribution, wind speed and water fluxes.
- Soils are influenced by plants, especially through bioweathering and litter production and subsequent decomposition. Plants can also protect soils from erosion. In semiarid areas, dunes and coastal regions may be stabilised by plants.
- Plants affect each other both negatively and positively. They compete and coexist. Symbiosis is the result of a positive, mutualistic interaction. Lichens are a good example of an above-ground symbiosis, mycorrhizae of a below-ground one. A commensal relationship,

where only one partner benefits, can often be found in epiphytes on trees. Parasitism, where one partner suffers, is widespread.

- Different forms of competition, especially for important resources, and plant traits that favour successful competition are discussed, including experimental approaches and models for intra- and interspecific competition.
- The effects of competition (and coexistence) on the diversity and structure of plant communities are shown using various examples.
- Indicator plants, indicator values and ecograms are examples of the practical application of results from studies on plant–plant interactions.
- Pollination, seed dispersal and herbivory are the most important plant–animal interactions that developed often in coevolution and processes of ecological fitting, for example, in pollination and seed dispersal systems.
- Plants use two strategies to cope with herbivores, tolerance and resistance. Most plants possess an array of general, broadly deterrent defences against generalist herbivores, but can also produce more potent, specific defences against specialist herbivores. Through chemical signalling, plants can sense herbivore attack within the plant and of neighbouring plants, which can induce the production of defence compounds.

References

Aarssen LW (1989) Competitive ability and species coexistence: a “plant’s-eye” view. Oikos 3:386–401

Adler LS (2000) The ecological significance of toxic nectar. Oikos 91:409–420

Agosta SJ, Klemens JA (2008) Ecological fitting by phenotypically flexible genotypes: implications for species associations, community assembly and evolution. Ecol Lett 11:1123–1134

Antor RJ, García MB (1995) A new mite-plant association: mites living amidst the adhesive traps of carnivorous plants. Oecologia 101:51–54

Archetti M (2000) The origin of autumn colours by coevolution. J Theor Biol 205:625–630

Ballaré CL, Scope AL, Stapleton AE, Yanovsky MJ (1996) Solar ultraviolet-B radiation affects seedling emergence, DNA integrity, plant morphology, growth rate, and attractiveness to herbivore insects in *Datura ferox*. Plant Physiol 112:161–170

Belnap J, Lange OL (eds) (2001) Biological soil crusts. Structure, function and management, Ecological studies, vol 150. Springer, Berlin

Bergström G, Dobson HEM, Groth I (1995) Spatial fragrance patterns within the flowers of *Ranunculus acris* (Ranunculaceae). Plant Syst Evol 195:221–242

Bertin RI (1989) Pollination biology. In: Abrahamson WG (ed) Plant-animal interactions. McGraw-Hill, New York, pp 23–83

Bertness MD, Callaway RM (1994) Positive interactions in communities. Trends Ecol Evol 9(5):191–193

Brandenburg A, Kuhlemeier C, Bshary R (2012) Hawkmoth pollinators decrease seed set of a low-nectar *Petunia axillaris* line through reduced probing time. Curr Biol 22:1635–1639

Brooker RW, Maestre FT, Callaway RM, Lortie CL, Cavieres LA, Kunstler G, Liancourt P, Tielbörger K, Travis JMJ, Anthelme F, Armas C, Coll L, Corcket E, Delzon S, Forey E, Kikvidze Z, Olofsson J, Pugnaire F, Quiroz CL, Saccone P, Schiffers K, Seifan M, Touzard B, Michalet R (2008) Facilitation in plant communities: the past, the present, and the future. J Ecol 96:18–34

Campbell DR, Aldridge G (2006) Floral biology and hybrid zones. In: Harder LD, Barrett SCH (eds) Ecology and evolution of flowers. Oxford University Press, Oxford, pp 326–345

Case TJ (2000) An illustrated guide to theoretical ecology. Oxford University Press, Oxford

Cazetta E, Schaefer HM, Galetti M (2008) Does attraction to frugivores or defense against pathogens shape fruit pulp composition? Oecologia 155:277–286

Chesson P (2000) Mechanisms of maintenance of species diversity. Annu Rev Ecol Syst 31:343–366

Chesson P, Kuang JJ (2008) The interaction between predation and competition. Nature 456:235–238

Chittka L, Schürkens S (2001) Successful invason of a floral market. Nature 411:653

Cipollini ML, Levey DJ (1997) Why are some fruits toxic? Glycoalkaloids in Solanum and fruit choice by vertebrates. Ecology 78:782–798

Connell JH (1971) On the role of natural enemies in preventing exclusion in some marine animals and in rain forest trees. In: den Boer PJ, Gradwell GR (eds) Dynamics of populations. Centre for Agricultual Publishing and Documentation, Wageningen, pp 298–310

Connell JH (1980) Diversity and the coevolution of competitors, or the ghost of competition past. Oikos 35:131–138

Connell JH, Slatyer RO (1977) Mechanisms of succession in natural communities and their role in community stability and organisation. Am Nat 111:1119–1144

Cooney LJ, Schaefer HM, Logan BA, Cox B, Gould KS (2015) Functional significance of anthocyanins in peduncles of *Sambucus nigra*. Environ Exp Bot 119:18–26

Cooney LJ, van Klink JW, Hughes NM, Perry NB, Schaefer HM, Menzies IJ, Gould KS (2012) Red leaf margins indicate increased polygodial content and function as visual signals to reduce herbivory in *Pseudowinteria colorata*. New Phytol 194:488–497

Cousens R, Wiegand T, Taghizadeh M (2008) Small-scale spatial structure within patterns of seed dispersal. Oecologia 158:437–448

Danin A (1986) Patterns of biogenic weathering as indicators of palaeoclimates in Israel. Proc R Soc Edinb Sect B (Biol) 89b:243–253

Darwin CR (1859) The origin of species by means of natural selection or the preservation of favoured races in the struggle for life. J. Murray, London

Dufrêne M, Legendre P (1997) Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecol Monogr 67:345–366

Dybzinski R, Fargione JF, Zak DR, Fornara D, Tilman D (2008) Soil fertility increases with plant species diversity in a long-term biodiversity experiment. Oecologia 158:85–93

Ellenberg H (1953) Physiologisches und ökologisches Verhalten derselben Pflanzenarten. Bericht der Dtsch Bot Gesellschaft 65:351–361

Ellenberg H, Leuschner C (2010) Vegetation Mitteleuropas mit den Alpen: In ökologischer, dynamischer und historischer Sicht, 6th edn. UTB, Stuttgart

Ellenberg H, Weber HE, Düll R, Wirth V, Werner W, Paulißen D (1992) Zeigerwerte von Pflanzen in Mitteleuropa, 2. Aufl. Ser Geobot 18:1–258

Eltz T, Zimmermann Y, Pfeiffer C, Pech JR, Twele R, Francke W, Quezada-Euan JJ, Lunau K (2008) An olfactory shift is associated with male perfume differentiation and species divergence in orchid bees. Curr Biol 18:1844–1848

Ertsen A, Alkemade J, Wassen M (1998) Calibrating Ellenberg indicator values for moisture, acidity, nutrient availability and salinity in the Netherlands. Plant Ecol 135:113–124

Fellbaum CR, Gachomo EW, Beesetty Y, Choudhari S, Strahan GD, Pfeffer PE, Kiers ET, Bücking H (2012) Carbon availability triggers fungal nitrogen uptake and transport in arbuscular mycorrhizal symbiosis. Proceedings National Academy of Sciences 109:2666–2671

Firbank LG, Watkinson AR (1985) On the analysis of competition within two-species mixtures of plants. J Appl Ecol 22:503–517

Fornara DA, Tilman D (2008) Plant functional composition in fluencies rates of soil carbon and nitrogen accumulation. J Ecol 96:314–322

Galen C, Cuba J (2001) Down the tube: pollinators, predators, and the evolution of flower shape in the alpine skypilot, *Polemonium viscosum*. Evolution 55:1963–1971

Gaudet CL, Keddy PA (1988) A comparative approach to predicting competitive ability from plant traits. Nature 334:242–243

Gianoli E, Carrasco-Urra F (2014) Leaf mimicry in a climbing plant protects against herbivory. Curr Biol 24:R357–R359

Grime JP (1977) Evidence for the existence of three primary strategies in plants and its relevance for ecological and evolutionary theory. Am Nat 111:1169–1194

Grime JP (2001) Plant strategies and vegetation processes, 2nd edn. John Wiley, Chichester

Grubb PJ (1977) The maintenance of species richness in plant communities: the importance of the regeneration niche. Biol Rev 52:107–145

Gurevitch J, Morrow LL, Wallace A, Walsh JS (1992) A meta-analysis of competition in field experiments. Am Nat 140:539–572

Hagen SB, Folstad I, Jakobsen SW (2003) Autumn colouration and herbivore resistance in mountain birch (*Betula pubescens*). Ecol Lett 6:807–811

Halsey RW (2004) In search of allelopathy: an ecohistorical view of the investigation of chemical inhibition in California coastal sage scrub and chamise chaparral. J Torrey Bot Soc 131:343–367

Hamilton WD, Brown SP (2001) Autumn tree colours as a handicap signal. Proc R Soc Lond B 268:1489–1493

Hardesty BD, Hubbell SP, Bermingham E (2006) Genetic evidence of frequent long-distance recruitment in a vertebrate-dispersed tree. Ecol Lett 9:516–525

Hector A, von Felten S, Hautier Y, Weilenmann M, Bruelheide H (2012) Effects of dominance and diversity on productivity along Ellenberg's experimental water table gradients. PLoS One 7:e43358

Heil M, Karban R (2010) Explaining evolution of plant communication by airborne signals. Trends Ecol Evol 25:137–144

Himanen SJ, Blande JD, Klemola T, Pulkkinen J, Heijari J, Holopainen JK (2010) Birch (Betula spp.) leaves adsorb and re-release volatiles specific to neighbouring plants—a mechanism for associational herbivore resistance? New Phytol 186:722–732

Hubbell SP (2001) The unified neutral theory of biodiversity and biogeography. Princeton University Press, Princeton

Huisman J, Weissing FJ (1995) Competition for nutrients and light in a mixed water column: a theoretical analysis. Am Nat 146:536–564

Huisman J, Weissing FJ (1999) Biodiversity of plankton by species oscillations and chaos. Nature 402: 407–410

Hutchinson GE (1957) Concluding remarks. Cold Spring Harb Symp Quant Biol 22:415–427

Jansen PA, Hirsch BT, Emsens W-J, Zamora-Gutierrez V, Wikelski M, Kays R (2012) Thieving rodents as substitute dispersers of megafaunal seeds. Proc Natl Acad Sci U S A 109:12610–12615

Janzen DH (1970) Herbivores and number of tree species in tropical forests. Am Nat 104:501–528

Janzen DH (1985) On ecological fitting. Oikos 45: 308–310

Jersáková J, Johnson SD, Kindlmann P (2006) Mechanisms and evolution of deceptive pollination in orchids. Biol Rev 81:219–235

Jordano P, García C, Godoy JA, García-Castaño JL (2007) Differential contribution of frugivores to complex seed dispersal patterns. Proceedings National Academy of Sciences 104:3278–3282

Karban R, Baldwin IT, Baxter KJ, Laue G, Felton GW (2000) Communication between plants: induced resistance in wild tobacco plants following clipping of neighboring sagebrush. Oecologia 125:66–71

Katzenberger TD, Lunau K, Junker RR (2013) Salience of multimodal flower cues manipulates initial responses and facilitates learning performance of bumblebees. Behav Ecol Sociobiol 67:1587–1599

Keddy PA (1989) Competition. Chapman & Hall, London

Kessler A, Baldwin IT (2001) Defensive function of herbivore-induced plant volatile emissions in nature. Science 291:2141–2144

Kessler D, Diezel C, Baldwin IT (2010) Changing pollinators as a means of escaping herbivores. Curr Biol 20:237–242

Kiers ET, Duhamel M, Beesetty Y, Mensah JA, Franken O, Verbruggen E, Fellbaum CR, Kowalchuk GA, Hart MM, Bago A, Palmer TM, West SA, Vandenkoornhuyse P, Jansa J, Bücking H (2011) Reciprocal rewards stabilise cooperation in the mycorrhizal symbiosis. Science 333(6044):880–882.

Knudsen JT, Eriksson R, Gershenzon J, Stähl B (2006) Diversity and distribution of floral scent. Bot Rev 72:1–120

Lomáscolo SB, Levey DJ, Kimball RT, Bolker BM, Alborn HT (2010) Dispersers shape fruit diversity in *Ficus* (Moraceae). Proc Natl Acad Sci U S A 107:14668–14672

Long G (1954) Contribution a l'étude de la végétation de la Tunisie centrale. Ann Serv Bot et Agric Tunisie 27:1–38

Louda SM, Collinge SK (1992) Plant resistence to insect herbivores: a field test of environmental stress hypothesis. Ecology 73:153–169

Lovelock J (1992) Gaia—Die Erde ist ein Lebewesen. Scherz, Munich

MacArthur RH (1969) Species packing, and what interspecific competition minimizes. Proc Natl Acad Sci U S A 64:1369–1371

McNaughton SJ (1983) Compensatory plant growth as a response to herbivory. Oikos 40:329–336

Molisch H (1937) Der Einfluss einer Pflanze auf die andere. Allelopathie. Gustav Fischer, Jena

Montoya D, Zavala MA, Rodriguez MA, Purves DW (2008) Animal versus wind dispersal and the robustness of tree species to deforestation. Science 320:1502–1504

Muchhala N (2007) Adaptive trade-off in floral morphology mediates specialisation for flowers pollinated by bats and hummingbirds. Am Nat 169:494–504

Müller-Hohenstein K (1978) Die ostmarokkanischen Hochplateaus. Erlanger geographische Arbeiten 7, Erlangen

Muller-Landau HC (2010) The tolerance-fecundity tradeoff and the maintenance of diversity in seed size. Proc Natl Acad Sci U S A 107:4242–4247

Naug D, Arathi HS (2007) Receiver bias for exaggerated signals in honeybees and its implications for the evolution of floral displays. Biol Lett 3:635–637

Oksanen L (1990) Predation, herbivory, and plant strategies along gradients of primary productivity. In: Grace JB, Tilman D (eds) Perspectives on plant competition. Academic Press, London, pp 445–474

Potthoff M, Johst K, Gutt J, Wissel C (2006) Clumped dispersal and species coexistence. Ecol Model 198:247–254

Poulsen JR, Clark CJ, Smith TB (2001) Seed dispersal by a diurnal primate community in the Dja Reserve, Cameroon. J Trop Ecol 17:787–808

Price PW (1991) The plant vigor hypothesis and herbivore attack. Oikos 62:244–251

Rausher MD (2001) Co-evolution and plant resistance to natural enemies. Nature 411:857–864

Rees M, Grubb PJ, Kelly D (1996) Quantifying the impact of competition and spatial heterogeneity on the structure and dynamics of a four-species guild of winter annuals. Am Nat 147:1–32

Reich PB, Oleksyn J, Modrzynski J, Mrozinski P, Hobbie SE, Eissenstat DM, Chorover J, Chadwick OA, Hale CM, Tjoelker MG (2005) Linking litter calcium, earthworms and soil properties: a common garden test with 14 tree species. Ecol Lett 8:811-818

Reichelt G, Wilmanns O (1973) Vegetationsgeographie. Das geographische Seminar. Westermann, Braunschweig

Remmert H (1991) The mosaic-cycle concept of ecosystems. Springer, Heidelberg

Renner SS (2005) Rewardless flowers in the angiosperms and the role of insect cognition in their evolution. In: Waser NM, Ollerton J (eds) Specialisation and generalisation in pollination systems. University of Chicago Press, Chicago, pp 123–144

Riffel JA, Lei H, Christensen TA, Hildebrand JG (2009) Characterisation and coding of behaviorally significant odor mixtures. Curr Biol 19:335–340

Rode MW, Dageförde A, Görlitz G (1996) Einfluss der Baumart auf den Nährstoffeintrag und seine Bedeutung für die natürliche Waldentwicklung auf nährstoffarmen Böden Norddeutschlands. Verh Ges Ökol 26:139–145

Rosindell J, Hubbell SP, Etienne RS (2011) The unified neutral theory of biodiversity and biogeography at age ten. Trends Ecol Evol 26:340–348

Rousseaux MC, Julkunen-Tiitto R, Searles PS, Scope AL, Aphalo PJ, Ballaré CL (2004) Solar UV-B radiation affects leaf quality and insect herbivory in the southern beech tree *Nothofagus antartica*. Oecologia 138:505–512

Russo SE, Augspurger CK (2004) Aggregated seed dispersal by spider monkeys limits recruitment to clumped patterns in *Virola calophylla*. Ecol Lett 7:1058–1067

Schaefer HM, Braun J (2009) Reliable cues and signals of fruit quality are contingent on the habitat in black elder (*Sambucus nigra*). Ecology 90:1564–1573

Schaefer HM, Rolshausen G (2006) Plants on red alert—do insects pay attention? BioEssays 28:65–71

Schaefer HM, Schmidt V, Bairlein F (2003a) Discrimination abilities for nutrients: which difference matters for choosy birds and why? Anim Behav 65:531–541

Schaefer HM, Schmidt V, Winkler H (2003b) Testing the defence trade-off hypothesis: how contents of nutrients and secondary compounds affect fruit removal. Oikos 102:318–328

Schaefer HM, Valido A, Jordano P (2014) Birds see the true colours of fruits to live off the fat of the land. Proc Biol Sci 281:20132516

Seidler TG, Plotkin JB (2006) Seed dispersal and spatial pattern in tropical trees. PLoS Biol 4:2132–2137

Seymour RS, Gibernan M, Ito K (2003) Thermogenesis and respiration of inflorescences of the dead horse arum *Helicodiceros muscivorus,* a pseudotermoregulatory aroid associated with fly pollination. Funct Ecol 17:886–894

Slatkin M (1974) Competition and regional coexistence. Ecology 55:128–134

Stein C, Unsicher SB, Kahmen A, Wagner M, Audorff V, Auge H, Prati D, Weiser WW (2010) Impact of invertebrate herbivory in grasslands depends on plant species diversity. Ecol 91:1639–1650

Stinchcombe JR, Rausher MD (2001) Diffuse selection on resistance to deer herbivory in the ivyleaf morning glory, *Ipomoea hederacea*. Am Nat 158: 376–388

Stoudtjesdijk PH, Barkman JJ (1992) Microclimate, vegetation and fauna. Opulus Press, Knivsta

Stournaras KE, Lo E, Böhning-Gaese K, Cazetta E, Dehling DM, Schleuning M, Stoddard MC, Donoghue MJ, Prum RO, Schaefer HM (2013) How colorful are fruits? Limited color diversity in fleshy fruits on local and global scales. New Phytol 198:617–629

Stournaras KE, Prum RO, Schaefer HM (2015) Fruit advertisement strategies in two Neotropical plant-seed disperser markets. Evol Ecol 29:489–509

Strauss SY, Irwin RE (2004) Ecological and evolutionary consequences of multispecies plant-animal interactions. Annu Rev Ecol Syst 35:433–466

Strauss SY, Whittall JB (2006) Non-pollinator agents of selection on floral traits. In: Harder LD, Barrett SCH (eds) Ecology and evolution of flowers. Oxford University Press, Oxford, pp 120–138

Tewksbury JJ, Reagan KM, Machnicki NJ, Carlo TA, Haak DC, Calderón Peñaloza AL, Levey DJ (2008) Evolutionary ecology of pungency in wild chilies. Proc Natl Acad Sci U S A 105:11808–11811

Thompson JN (2005) The geographic mosaic of coevolution. University of Chicago Press, Chicago

Tilman D (1982) Resource competition and community structure. Princeton University Press, Princeton, NJ

Tilman D (1997) Mechanisms of plant competition. In: Crawley MJ (ed) Plant ecology, 2nd edn. Blackwell, Oxford, pp 239–261

Tilman D, Wedin DA (1993) Competition among grasses along a nitrogen gradient: initial conditions and mechanisms of competition. Ecol Monogr 63:199–229

Treseder KK, Davidson DW, Ehleringer JB (1995) Absorption of ant-provided carbon dioxide and nitrogen by a tropical epiphyte. Nature 375:137–139

Viles HA (1988) Biogeomorphology. Blackwell, Oxford

Vitousek PM, Howarth RW (1991) Nitrogen limitation on land and in the sea: How can it occur? Biogeochemistry 13:87–115

von Hessberg A (1998) Vegetationsstrukturen in den Habitaten des Auerhuhns (Tetrao urogallus) im Fichtelgebirge. Dipl. Thesis Lehrstuhl Biogeographie, Universität Bayreuth

Weiss MR (1995) Floral color change: a widespread functional convergence. Am J Bot 82:167–185

Wenny DG (2000) Seed dispersal, seed predation, and seedling recruitment of a neotropical montane tree. Ecol Monogr 70:331–351

Wenny DG, Levey DJ (1998) Directed seed dispersal by bellbirds in a tropical cloud forest. Proc Natl Acad Sci U S A 95:6204–6207

Werner GDA, Strassmann JE, Ivens ABF, Engelmoer DJP, Verbruggen E, Queller DC, DC NR, Johnson NC, Hammerstein P, Kiers ET (2014) Evolution of microbial markets. Proc Natl Acad Sci U S A 111:1237–1244

Wilson JB, Agnew DQ (1992) Positive-feedback switches in plant communities. In: Begon M, Fitter AH (eds) Advances in ecological research 23. Academic Press, London, pp 263–336

Yoda K, Kira T, Ogawa H, Hozumi K (1963) Self-thinning in overcrowded pure stands under cultivated and natural conditions. J Biol 14:107–129

Biodiversity

20

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Mixed deciduous forest in Central Europe, Hainich National Park. (Photo: courtesy of S. Getzin)

E.-D. Schulze et al., *Plant Ecology*, https://doi.org/10.1007/978-3-662-56233-8_20

"I fly window seat, incurably. It doesn't matter that I've been on countless flights over the past four decades and stared downward over numberless vistas of forest and wetland, prairie and river. When the flight attendants ask for people to lower the window shade so that you can see the movie better, that's my shade still up, my face pressed against the glass.

I revel in the details of geography and sweep of biology that can be seen from the air. I trace trails into box canyons and along mountain ridges; search tundra for oriented lakes; look at sediment roiling downcast from a turbulent river mouth; scan bayous for cypress islands; enjoy the dendritic meanderings of channels through a tide flat; discover oxbow lakes along the fringes of a river basin.

Anyone who shares this affliction with me knows, however, that what one sees most of the time along too many common routes is the human footprint: dams and dikes, farmland, shopping malls and roads, hills bulldozed, forests flattened, massive works of civil (and uncivil) engineering."

John Peterson Myers (Myers 1997, page xvii)

20.1 Introduction

Biological diversity—or **biodiversity**—is one of the most striking elements of planet Earth and has always fascinated people. By provisioning food, shelter and all materials needed for survival, biodiversity has been the very foundation of human life for thousands of years. Perhaps not surprisingly, early human cultures obviously adored the many creatures living with them, and they left remarkable legacies of their view of life in the oldest human cave paintings, dating back to the Upper Palaeolithic, approx. 17,000 years BC. The many naturalists and artists travelling around the world in the seventeenth and eighteenth centuries also beautifully documented the astonishing diversity of life as they entered new territories. Even today, biodiversity is an inexhaustible source of inspiration and creativity in arts, and many people make excursions to watch birds and plants or to simply enjoy being outside in nature. The affinity towards and admiration of the rich diversity of life forms and ecosystems around us are obviously fundamental features of human life, which has been recognised as the biophilia hypothesis by Erich Fromm (1964) and Edward O. Wilson (1984).

Biodiversity has also been an important subject of study in ecology: trying to understand the development of biodiversity over time, the causes of its spatial distribution, and more recently, its functional implications, are some of the topics that scientists continue to work on. It has been found that biodiversity developed through evolutionary processes by adaptation to abiotic conditions and resources and in interaction with established competitors, herbivores or pathogens. But why do some plants form communities with few species and others with many species? What regulates the assembly of species, and how does this influence ecosystem processes? What kind of human management results in losses or gains in biodiversity? The answers to these and other questions remain largely unknown (Fig. 20.1).

Beyond science, biodiversity attracted the interest of the general public following the Earth Summit in Rio de Janeiro in 1992, as a result of which the conservation of biodiversity, the sustainable use of its components and the fair and equitable sharing of the benefits arising from the utilisation of genetic resources became regulated (United Nations Convention on Biological Diversity, CBD). People from all walks of life, including politicians, became aware of the global loss of species, a loss caused by a situation in which human influences grew to become significantly greater than natural rates of extinction. Scientists recognised that knowledge of biodiversity was rather modest and feared that numerous organisms would become extinct without ever having been scientifically recorded. Since that time, research on the functional consequences of biodiversity has gained strong momentum. Mere numbers of species were not regarded sufficient to understand communities in their habitats; it was recognised that other aspects of biodiversity, such as the functional characteristics of species, also play an important role in how ecosystems work. Plants and animals were to be regarded not only as resources but as decisive factors controlling processes in ecosystems.

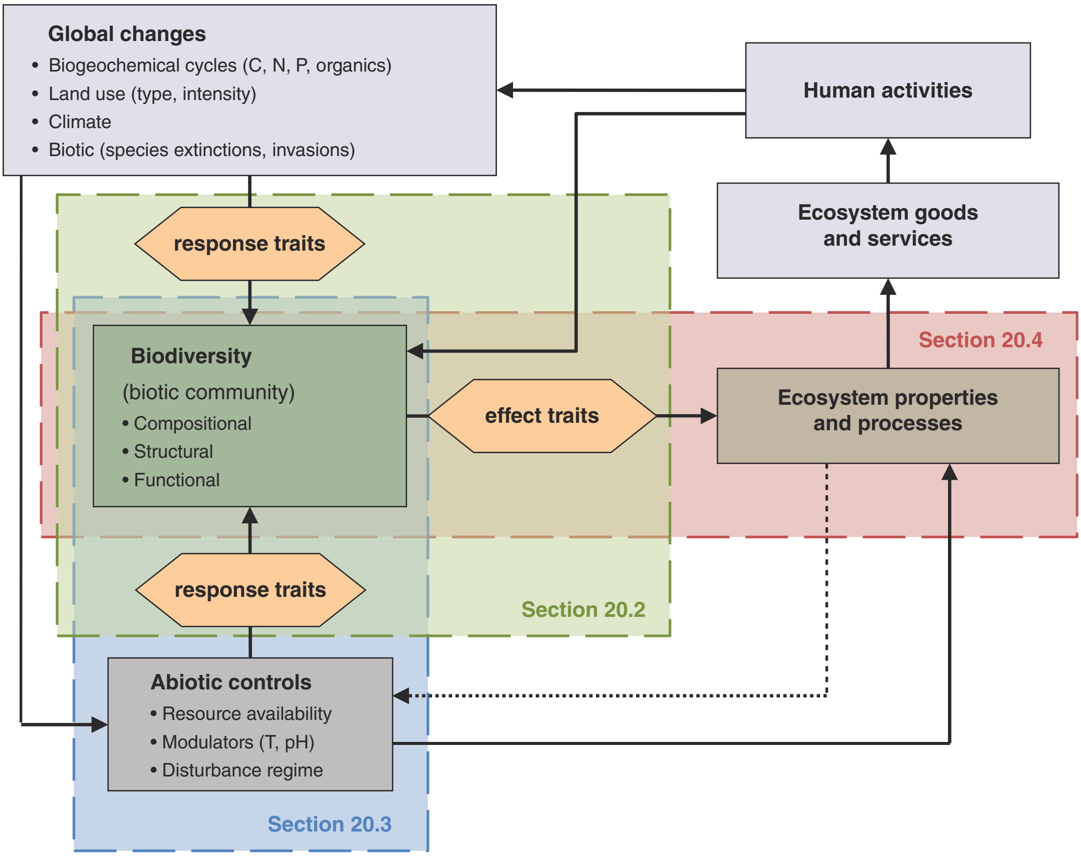


Fig. 20.1 Conceptual framework of this chapter. The biotic community can be characterised by different biodiversity components (Sect. 20.2). Biodiversity is controlled by the environment (Sect. 20.3) but also affects ecosystem functioning (Sect. 20.4). Interactions within biotic communities are described in Chap. 19, while influences and feedbacks between ecosystem services, human activities, global changes and ecosystems are dealt with in Chap. 23. Solid lines represent direct influences and the dotted line shows a feedback loop. Modified from Hooper et al. (2005), reproduced with permission from John Wiley & Sons

Currently, ecosystems are being increasingly disturbed by different drivers of global change, including altered biogeochemical cycles and eutrophication, changing land use and its intensity, changing climate and biotic changes (Chap. 23). In consequence, habitats and species are being lost and gained, while new conditions are created by human interference; for instance, human management is responsible for the previously unknown diversity in traditional agricultural landscapes of central Europe. Therefore, it is very urgent to clarify important questions on the development, loss and function of biodiversity.

This chapter presents the various facets and definitions of biodiversity, focusing on compositional, structural and functional aspects, where also the concept of plant traits will be introduced (Sect. 20.2). In a subsequent part, observed patterns of biodiversity in response to environmental factors will be presented (Sect. 20.3). Finally, Sect. 20.4 discusses the effects that biodiversity changes have on the properties and functions of ecosystems. The effects of management and human activities are dealt with in Chaps. 17 and 23.

20.2 Various Facets of Biodiversity

Mostly, the term **biodiversity** is used as a synonym for species richness, both in the media, but also still often in science. While early biodiversity

Table 20.1 Hierarchical organisation of biodiversity

Genetic diversity	Organismic diversity	Ecological diversity
	Kingdoms	Biomes
	Phyla	Bioregions
	Families	Landscapes
	Genera	Ecosystems
	Species	Habitats
	Subspecies	Niches
Populations	Populations	Populations
Individuals	Individuals	
Chromosomes		
Genes		
Nucleotides		

Three basic groups of biodiversity, forming a nested hierarchy of their elements (Heywood and Watson 1995)

research focused mainly on the number of species in an area, biodiversity is now seen as a broad concept, and it has been defined in numerous ways (Heywood and Watson 1995). In essence, it encompasses the **variability of biological entities across all levels of biological hierarchies**, that is, from the level of genes to ecosystems. Edward O. Wilson has simply coined it the "variety of life" (Wilson 1992).

Perhaps the most far-reaching definition is that from the UN Convention on Biological Diversity (CBD), signed at the UN Conference on Environment and Development in Rio de Janeiro 1992: "'Biological diversity' means the variability among living organisms from all sources including, *inter alia*, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems". This definition clearly distinguishes three basic levels of biodiversity: **genetic diversity**, **organismic diversity** and **ecological diversity**. These three broad groups are strongly linked to each other and share elements in common (Table 20.1). Ecological diversity is sometimes further separated into community/ecosystem and landscape/regional diversity (Table 20.2). The CBD also recognises the important role of biodiversity for sustaining the life-support functions of our planet and underlies its importance for human health and quality of life.

Clearly, these broad descriptions of the term are not very helpful for more specific questions such as whether an ecosystem is functioning in different ways if biodiversity is lost. Thus, **biodiversity must be defined more specifically for any given study**, for example, by referring to a specific element listed in Table 20.1; these elements are hierarchically nested within each group.

In addition, biodiversity can be categorised into a second set of three different aspects: **compositional**, **structural** and **functional diversity**. In contrast to the aforementioned categorisation into genetic, organismal and ecological diversity that is based on the fundamental hierarchies of biological organisation, the distinction into compositional, structural and functional diversity focuses on the elements of which biodiversity is composed and the resulting physical structures and functional consequences. The biological hierarchies, ranging from the genetic to the landscape level, can also be nested within these three aspects (Fig. 20.2). A variety of indicators and tools are applicable to assess, monitor and quantify biodiversity along those three axes (Table 20.2). More recently, the **diversity of interactions** among organisms (e.g. competition, facilitation, pollination, herbivory) has been highlighted as a component of biodiversity that strongly influences ecological processes. For the purpose of this chapter, we will use the categorisation suggested in Fig. 20.2 because it is more closely related to the underlying mechanisms of the role of biodiversity in ecosystems. The diversity of interactions is hereby included within the functional aspects of biodiversity.

20.2.1 Compositional Diversity

The number and identity of different biological entities can be used to describe the compositional diversity of ecosystems, for example, by listing how many and which plant species are growing there. Most often, compositional diversity is based on the number and variety of taxonomic units, such as species, genera or families, but it can also be based on alleles, populations, communities, ecosystems or landscape types (Fig. 20.2, Table 20.1). In biodiversity assessments and inventories the dimensionless number of species per unit of area (**species richness**) is often used (Fig. 20.3). More information is gained

Table 20.2 Indicators and measures of biodiversity

Indicators			
	Composition	Structure	Function
Regional-landscape	Identity, distribution, richness, and proportions of patch (habitat) types and multipatch landscape types; collective patterns of species distributions (richness, endemism)	Heterogeneity; connectivity; spatial linkage; patchiness; porosity; contrast; grain size; fragmentation; configuration; juxtaposition; patch size frequency distribution; perimeter-area ratio; pattern of habitat layer distribution	Disturbance processes (areal extent, frequency or return interval, rotation period, predictability, intensity, severity, seasonality); biogeochemical fluxes, nutrient cycling rates; energy flow rates; patch persistence and turnover rates; rates of erosion and geomorphic and hydrologic processes; human land-use trends
Community-ecosystem	Identity, relative abundance, frequency, richness, evenness and diversity of species and guilds; proportions of endemic, exotic, threatened and endangered species; dominance-diversity curves; life-form proportions; similarity coefficients; C4:C3 plant species ratios	Substrate and soil variables; slope and aspect; vegetation biomass and physiognomy; foliage density and layering; horizontal patchiness; canopy packing, openness and gap proportions; abundance, density and distribution of key physical features (e.g. cliffs, outcrops, sinks) and structural elements (snags, down logs); water and resource (e.g. mast) availability; snow cover	Biomass and resource productivity; herbivory, parasitism, and predation rates; colonisation and local extinction rates; patch dynamics (fine-scale disturbance processes); biogeochemical fluxes, nutrient cycling rates; human intrusion rates and intensities
Population-species	Absolute or relative abundance; frequency; importance or cover value; biomass; density	Dispersion (microdistribution); range (macrodistribution); population structure (sex ratio, age ratio); habitat variables (see community-ecosystem structure, above); within-individual morphological variability	Demographic processes (fertility, recruitment rate, survivorship, mortality); metapopulation dynamics; population genetics (see below); population fluctuations; functional traits; physiology; life history; phenology; growth rate (of individuals); acclimation; adaptation
Genetic	Allelic diversity; presence of particular rare alleles, deleterious recessives or karyotypic variants	Census and effective population size; heterozygosity; chromosomal or phenotypic polymorphism; generation overlap; heritability	Inbreeding depression; outbreeding rate; rate of genetic drift; gene flow; mutation rate; selection intensity

Examples of inventorying, monitoring and assessing terrestrial biodiversity at different levels of organisation, including compositional, structural and functional components (Noss 1990)

by adding abundance or dominance values (Box 20.1) and the distribution in space (e.g. spatial patterns such as clumped, regular or random distribution) (Sect. 18.2).

While the number of distinct species per area or of an entire ecosystem (= species richness or species density) is by far the most frequently used metric, it should be kept in mind that biodiversity not only comprises the number of species. In fact, **there is no single measure of biodiversity**, and it is impossible to define *the* biodiversity of an ecosystem (Gaston and Spicer 1998). However, species richness has turned into a kind of "currency" in biodiversity research, because it is relatively easy to measure and because species differ in their genetic composition and functional traits, in their growth forms and stature, in their habitat requirements and biocoenotic interactions. Therefore, species diversity can also be seen as a "surrogate" for certain facets of genetic, organismal, struc-

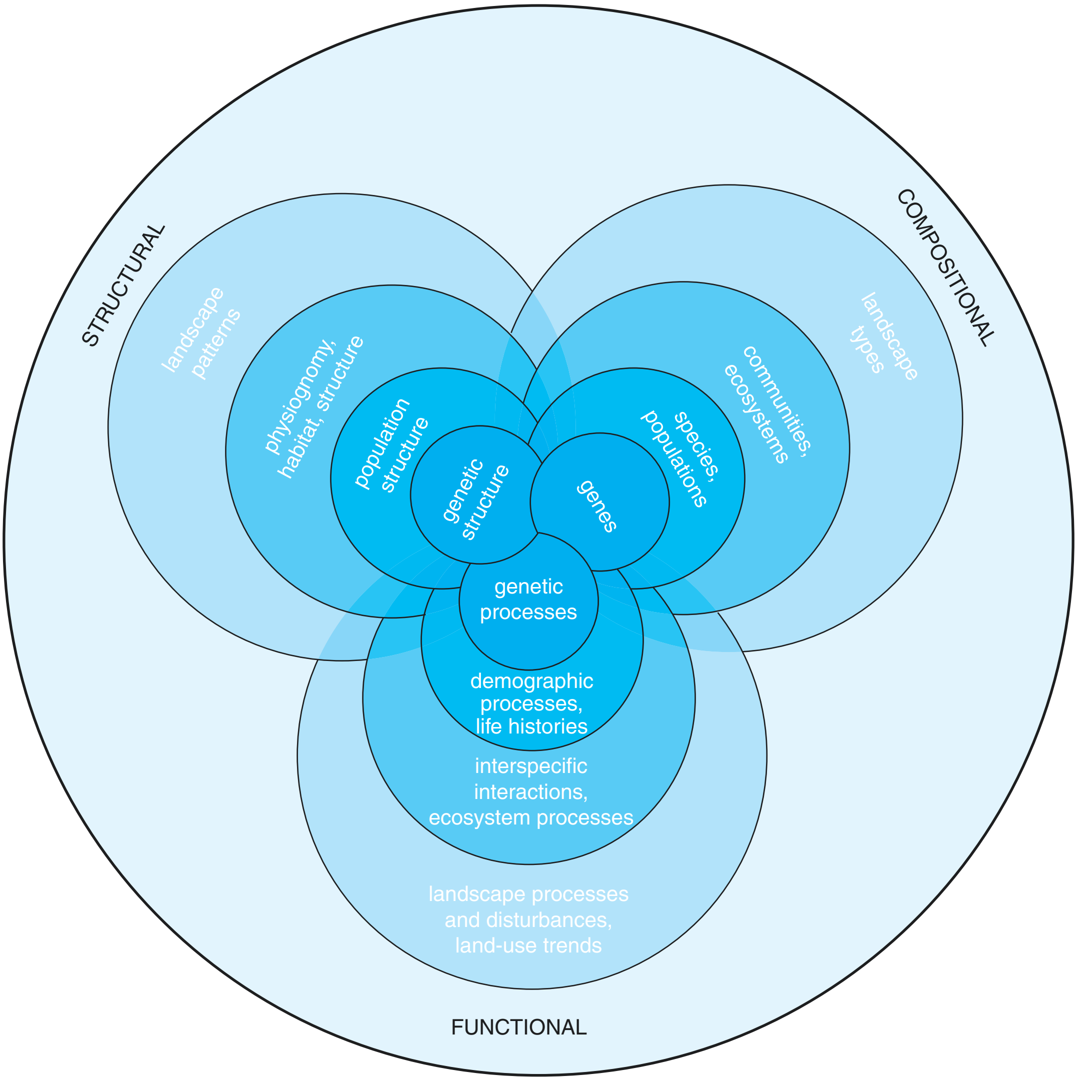


Fig. 20.2 Three spheres of biodiversity. Biodiversity can be categorised into compositional, structural and functional spheres that are interconnected. Each sphere encompasses multiple levels of organisation (Noss 1990). Reproduced with permission from John Wiley & Sons

tural, functional and ecological diversity. Species diversity and genetic diversity, for example, are sometimes well correlated, presumably because the processes determining genetic diversity should also determine species diversity. However, this covariation is mainly found in small-scale, isolated ecosystems such as oceanic islands or forest patches. In contrast, genetic diversity might be more related to demographic history in more widespread, well-connected populations where these two facets of biodiversity are less correlated (Taberlet et al. 2012).

The strong focus on species diversity calls for a proper designation of the species concept, which is not as easy as one might expect (Box 20.2). In what follows, we will also focus on the species level to illustrate some global patterns of compositional diversity.

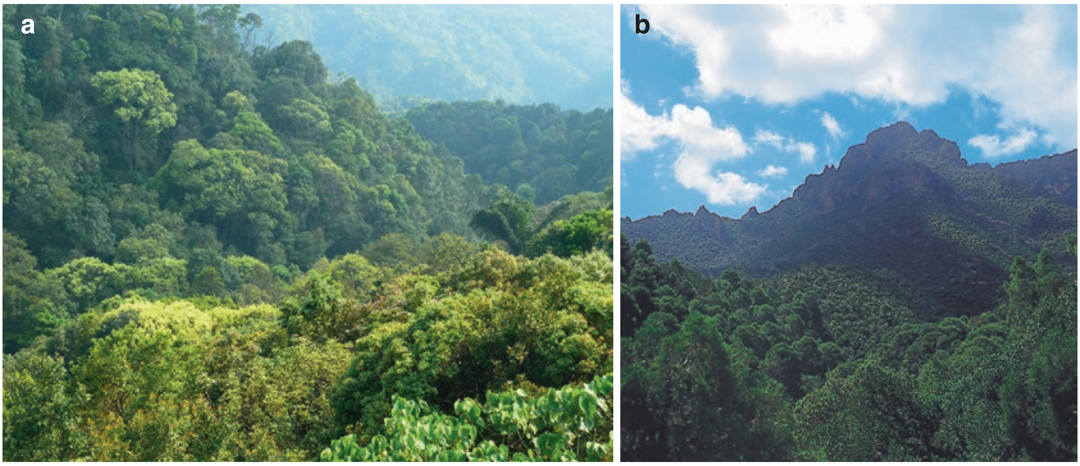


Fig. 20.3 Differences in plant species richness. Plant communities differ largely in species richness depending on environmental conditions, evolutionary history or human interference. **a** Species-rich natural, moist tropical forest with more than 8000 mm precipitation per year in the Bach Ma National Park in the central highlands of Vietnam, at 1000—1400 m a.s.l. **b** Coniferous forest in the Mediterranean region dominated by only one tree species (*Pinus halepensis*). In both cases, there has been little human interference in the forests. (Photos: E. Beck, K. Müller-Hohenstein)

Box 20.1: Quantification of Biodiversity

How diverse is an ecosystem, and does this diversity change over time? Do distinct landscapes differ in their biodiversity? Which aspect of biodiversity responds first to changes in environmental conditions or management? To answer such typical questions in ecology, biodiversity must be quantified. However, the concept of biodiversity with its numerous facets is difficult to handle without proper definition and measures.

In essence, any measure of biodiversity should encompass the **richness** of different entities, and the degree of difference or **dissimilarity** between those entities, for example, species in a sample or in a community. One way to represent the differences between such entities is to account for the relative abundance or **evenness** of those entities. Other ways to differentiate between entities include aspects of genetics, morphology, biochemistry, biogeography or the functional role within ecosystems. Therefore, it has to be noted that "there is no single all-embracing measure of biodiversity—nor will there ever be one!" (Gaston and Spicer 2004).

The measure of **species richness** is simply the total number of species within a sample or community. The number of individuals of each species is irrelevant for this measure. If the number of species is related to an area (e.g. per square metre), the term **species density** is also used.

To distinguish diversity at different spatial scales, the concept introduced by Whittaker (1960) is often used, which distinguishes the following categories:

Point diversity: number of species in a small or micro-habitat sample, taken within a community regarded as homogeneous;

α-diversity: within-habitat diversity, that is, the number of species within a community and per area;

β-diversity: between-habitat diversity differentiation, that is, a dimensionless comparative number of species in different units of vegetation or habitats;

γ-diversity: landscape diversity, that is, the number of species in larger units, such as an island or landscapes that include more than one community.

Later, he added two levels at higher spatial scales, which, however, are rarely used:

δ-diversity: geographic diversity differentiation, that is, dimensionless comparative number of species applied to changes over large scales (e.g. along climatic gradients or between geographic areas); it is the functional equivalent of beta diversity at the higher organisational level of the landscape;

ε-diversity: regional diversity, that is, the total number of species in a broad geographic area, including different landscapes or groups of areas of gamma diversity.

α-, γ- and ε-diversity are thus measured in particular areas, the first in those that are occupied by a community, the latter in larger spatial units, such as ecosystems, landscapes or regions. β- and δ-diversity, in contrast, must be calculated and describe changes in the number of species between habitats or landscapes or along ecological gradients. β-diversity may also be used for comparisons of number of species in the same habitat over time and is then a measure of **species turnover**.

Beside species richness, one of the most frequently used indices of diversity is that of **Shannon and Weaver** (1949):

$$H' = -\sum_{i=1}^{S} \left(p_i \times \ln p_i \right) \tag{20.1}$$

where $p_i = \frac{n_i}{N}$

H' Shannon's diversity index,
S number of species present in sample,
p_i relative frequency per area (abundance) of ith species, measured from 0–1,
n_i number of individuals of species i,
N total number of individuals.

In this index, the **richness** and proportional **abundance** of species are included because both aspects determine the heterogeneity—and therefore the diversity—of a community. H' rises with an increasing number of species or increasing uniformity of distribution of relative abundance (e.g. cover or biomass) of individual species. In habitats with single species, the value is zero. If all species have the same relative abundance, H' is at its maximum. Shannon's index is independent of the functional characteristics of the individual species: all are treated equally.

The same index can also be used to calculate the genetic diversity within a population, with p_i being the relative frequency of the ith allele.

The Shannon indices of different communities do not tell us whether a high value is due to a higher number of species or to a more even distribution of individuals. To compare communities with different species richness, the **evenness** can be calculated, that is, the uniformity of species distribution in a habitat. Evenness indices reflect the ratio of dominant to rare species within a single value, and several such indices exist, all of which have specific features (Smith and Wilson 1996). The index by Pielou (1966) is based on Shannon's index:

$$J' = \frac{H'}{H'_{\max}} \tag{20.2}$$

where $H'_{\max}$ is the maximum value of H' and equal to $H'_{\max} = \ln S$.

To describe the **dominance** distribution of species within a community, indices can be used that give more weight to the more abundant species, while the addition of rare species results in only minor changes. Such an index is **Simpson's index** (Simpson 1949), which describes the probability that two individuals randomly selected from a sample will belong to the same species:

$$D = \sum_{i=1}^{S} p_i^2 \tag{20.3}$$

To obtain an increasing value with increasing diversity, this index is most often presented as Simpson's index of diversity $1 - D$ (ranging from 0 to 1) or as Simpson's reciprocal index $1/D$.

To describe the similarity or dissimilarity in species composition between different floristic regions, plant communities or sample quadrats, several indices have been developed, for example:

The **Jaccard similarity coefficient**, which uses information on species absence or presence in two samples (Jaccard 1912):

$$S_J = \frac{a}{a+b+c} \tag{20.4}$$

- a number of species common to both samples,
- b number of species unique to the first sample,
- c number of species unique to the second sample.

It is often multiplied by 100% and can also be presented as an index of dissimilarity by

$$D_J = 1 - S_J \tag{20.5}$$

Very similar is the **Sørensen–Dice similarity coefficient**, which gives more weight to species common in both samples (Dice 1945; Sørensen 1948):

$$S_S = \frac{2a}{2a+b+c} \tag{20.6}$$

As with the Jaccard index, it can also be expressed as a percentage, or as dissimilarity, the latter representing the **Bray–Curtis dissimilarity** (Bray and Curtis 1957):

$$D_{\mathrm{BC}} = 1 - S_S \tag{20.7}$$

This index is bound between 1 and 0, with 1 representing a situation where the two samples do not share any species, and 0 meaning the two samples have identical species compositions.

Other indices to compare species compositions have been developed, for example, by including information on abundances, by generalising to more than two samples or by using other distance measures such as Euclidean distances. More details can be found in textbooks dealing with analyses of ecological data (e.g. Legendre and Legendre 2012).

Box 20.2: The Species Concept

A species is the central taxonomic rank of biological systematics, and species are one of the fundamental units in biology, similar to genes, cells and organisms. Species names are binomial, meaning they include the genus (e.g. *Abies*) and the species rank (e.g. *alba*), when naming silver fir, for instance. In botany, species can be further subdivided into subspecies, varieties and forms (so-called infraspecific taxa). The way to name species is defined in the "International Code of Nomenclature for algae, fungi, and plants (Melbourne Code)", adopted by the Eighteenth International Botanical Congress Melbourne, Australia, July 2011.

Despite this clear taxonomic classification, it is not always easy to determine what a species actually is. A central question related to species concepts is thus the determination of clear boundaries between species, which must be based on well-defined criteria: What degree of morphological differences is enough to separate morphospecies? How large must the genetic difference be to separate two species? Evolutionary processes (speciation) are dynamic and ongoing, and so boundaries between species are constantly shifting. In principle, to separate a group of individuals into two species, the variability of genotypes or phenotypes between species should be larger than between and within subpopulations within a species. However, answers to such questions have changed over time, and the nomenclature therefore also sometimes changes with the emergence of new knowledge. For example, major shifts in taxonomic units, also at the levels of families or orders, took place following the adoption of molecular techniques. Thus, species names are primarily a hypothesis, which can change if new data become available.

While early definitions of species were mostly based on similarities in morphological or other observable traits (**morphological** or **phenetic species concept**), the **biological species concept** defines a species as "groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups" (Mayr 1942). This concept works well in most cases, especially for sexually reproducing organisms. However, for plants, the biological species concept is somewhat problematic because of hybridisation between species, rarely also between genera (e.g. *Triticale*), and in the case of asexually reproducing organisms, for example, in apomictic plants (e.g. *Rubus*). More than 20 different species concepts have been proposed, including an **ecological species concept** (emphasising the occupation of ecological niches) and **evolutionary** or **phylogenetic concepts**. In particular, the use of modern molecular techniques opened the door to distinguishing taxonomic units based on genetic distances. All these definitions are based on distinct biological properties, which are acquired by lineages during the course of divergence (e.g. phenetically distinguishable, reproductively isolated, monophyletic) (de Queiroz 2007). Some concepts are partially incompatible with each other (often referred to as the "species problem"), and the adoption of different concepts allows for the occurrence of different species boundaries and, thus, different numbers of species. Nevertheless, the biological species concept is still the most often used species concept.

A proposed solution to the species problem suggests that the only necessary property of a species is the **existence of a separately evolving metapopulation lineage** (i.e. an ancestral–descendant sequence of sets of subpopulations connected through the exchange of genes; such groups of connected subpopulations are termed **metapopulations**). This property is inherent to all contemporary species concepts (de Queiroz 2005). It is a further development of Darwin's revolutionary idea to see species as branches in the line of descent, that is, the evolutionary basis for the concept of species. All other proposed properties to qualify being a species, such as being phenetically distinguishable, monophyletic (i.e. a group of species with an ancestral species and all its descendants), reproductively isolated or ecologically divergent, are considered as secondary, contingent properties of a species. These properties may (or may not) be acquired during the course of species existence and can be seen as different operational criteria to assess lineage separation and, hence, as evidence for the existence of a species. This general and unified species concept also works for asexually reproducing species if they form metapopulations as the result of some processes other than the exchange of genetic material or interbreeding, for example, by natural selection.

Estimates of the total number of all species on Earth vary greatly. Because many regions are not well sampled, we do not have a direct quantification of the global number of species. Instead, several indirect estimates have been put forth, all of which rely on particular assumptions and, therefore, have limitations. Current estimates range between three and ten million species, but

Fig. 20.4 Management and biodiversity. High species diversity is often found in traditionally cultivated landscapes, irrespective of climatic conditions. **a** Large number of cultivated rice varieties in a rural Indonesian market (Palu, Sulawesi). **b** A home garden in southern Chile (Puerto Montt). In both cultivated areas agrochemicals and modern agronomic techniques have little impact. (Photos: K. Müller-Hohenstein)

the actual figure may be higher by a factor of ten. Approximately 225,000 vascular plant species have been taxonomically described, but the total number could be around 315,000 (Mora et al. 2011).

Biodiversity cannot be described reasonably without considering **spatial** and **temporal scales** (Chaps. 17 and 18). The spatial characteristics of biodiversity are patterns of distribution of individuals, species, genera, communities and ecosystems. Recognition of these patterns depends on the scope of the research. Of course, to quantify species diversity in a cushion of epiphytic living mosses on a tree trunk in the rain forest involves different spatial scales than recording communities in a landscape where spatial patterns depend on the heterogeneity of site conditions and of human management (Fig. 20.4). The latter resulted in maximum species diversity in the traditionally managed landscapes of central Europe up to the middle of the last century, but thereafter it decreased owing to intensification of land use (Sect. 17.2).

Staying at the species level, compositional diversity encompasses not only species numbers but also the frequency and abundance of different species, that is, **species composition**. Obviously, two plant communities may have the same species number but harbour very different species in different abundances. Such differences in species composition can be either documented in phytosociological tables (full information retained), or by visualising **species abundance distributions**, for example, as rank-dominance curves (moderate retention of information), or by calculating indices of similarity (easy to understand but high loss of information, for example, Jaccard or Sørensen coefficients, Box 20.1). Multivariate statistical tools can also help to visualise differences in species composition (e.g. showing the range of species composition along environmental gradients). Species composition has big consequences for the diversity of other organismic groups, such as pollinators, herbivores or pathogens, since many higher trophic groups are to varying degrees specialised for certain plant species (Sect. 19.4). In addition, species composition also has large effects on ecological processes, such as nutrient cycling, because species differ in their morphological, physiological and chemical properties or traits (Sect. 20.2.3).

Table 20.3 Categories of plants by life form

Humboldt (1806)	Drude (1887)	Raunkiaer (1908)	Monsi (1960) and Walter (1973)	Schmithüsen (1968)
Palms	Woody plants with leaves	Phanerophytes	Herbaceous plants	Trees with crowns
Banana form	Trees	Chamaephytes	Annuals	Trees with apical bunched leaves
Mallow form	Bushes	Hemicryptophytes	Biennials	Giant grasses
Mimosa form	Lianas	Cryptophytes	Deciduous perennial	Strangler figs
Heathers	Mangroves	Therophytes	Evergreen perennial	Lianas
Cactus form	Parasites on woody plants			Shrubs
Orchids	Leafless woody plants	Subdivided after		Dwarf trees
Casuarinas	Stem succulents	Leaf size	Woody plants	Stem succulents
Pines	Leafless bushes	Leaf duration	Deciduous	Herbaceous plants
Arum form	Small bushes	Vegetative reproduction	Evergreen	Epiphytes
Lianas	Perennial herbs			Dwarf shrubs
Aloes	Rosette plants			Small bushes
Grass form	Leaf succulents			Dwarf succulents
Ferns	Epiphytes			Chamaephytic perennial herbs
Lilies	Hapaxanthic plants			Hemicryptophytic woody plants
Willow form	Land plants			Hemicryptophytic perennial herbs
Myrtle form	Water plants			Winter annuals
Melastoma form	Lichens			Geophytic perennial herbs
Laurel form	Saprophytes/parasites			Therophytic herbs
				Floating leaf plants
				Submerged herbs

From various authors, after Schulze (1982)

20.2.2 Structural Diversity

Looking at a plant community it becomes obvious that the species present may build up different structures, that is, different physical patterns. Vegetation structure is not only an important driver of the diversity of an ecosystem; it is also the key aspect that couples plants to the atmosphere, especially for gas exchange, trace gas fluxes, atmospheric deposition and rainfall interception (Sects. 9.1, 16.1–16.3).

Important structural characteristics of a plant include architectural traits, for example, height and branching patterns, leaf form and root stratification. Several attempts were made by plant geographers, as well as by ecologically orientated botanists, to differentiate between life forms based predominantly on structural features. Even the Greek philosopher Theophrastus (ca. 371—287 BC) already thought about criteria by which to categorise plants according to their physiognomy, that is, the outer appearance of living things. He came up with a tree, shrub, perennial herb and "useful" plant categorisation. These attempts show that it is very difficult to cope with the great diversity of structural features in the plant kingdom (Table 20.3). In closed stands, the presence of strata of different heights caused by different life forms, intertwining with lianas, as well as standing or lying dead woody debris, increases structural diversity (Fig. 20.5). In addition, the architecture of the canopy can differ widely depending on the different growth forms of the plants. Such structures, in turn, provide habitat for many other organisms like birds, insects, epiphytes and lichens. According to the

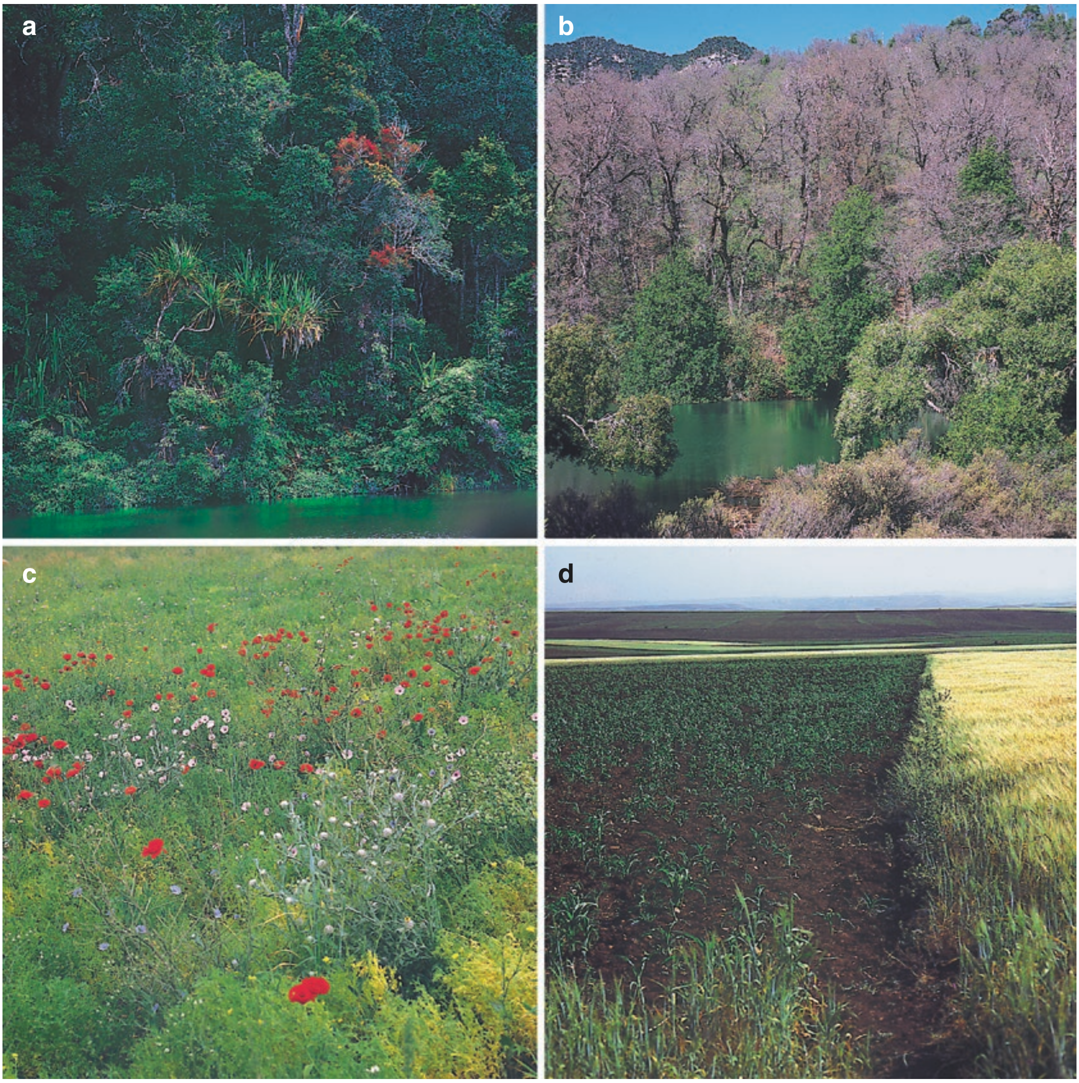


Fig. 20.5 Structural diversity and species richness. A tropical rain forest in Indonesia **a**, rich in species and in structures, has a structural diversity that is similar to that of an extra-tropical rain forest **b**, poor in species but rich in structure. However, the number of higher plant species differs ten-fold between both forest types. Cultivated cereal fields are single layered and as such poorer in structure than forests. Nevertheless, there are large differences in species richness among differently cultivated fields: a species-rich but structure-poor fallow **c** and a species- and structure-poor cereal field **d**, both located in Mediterranean areas of Morocco. (Photos: K. Müller-Hohenstein)

resource heterogeneity hypothesis and **niche theory** (Huston 1979) (Sect. 19.3), a larger variety of resources provide niches for other organisms with distinct requirements for habitat, food or environmental conditions. Hence, the structural heterogeneity or diversity of plant communities is often positively related to the biodiversity of other taxonomic groups, as shown by the classic example by MacArthur and MacArthur (1961) from temperate, deciduous forests of north-eastern North America (Fig. 20.6, also Fig. 20.14). Therefore, maintaining or enhancing certain aspects of structural diversity is relevant for many aspects of nature conservation and management. For example, in **retention forestry**, single trees, decaying logs or small patches of trees are left at

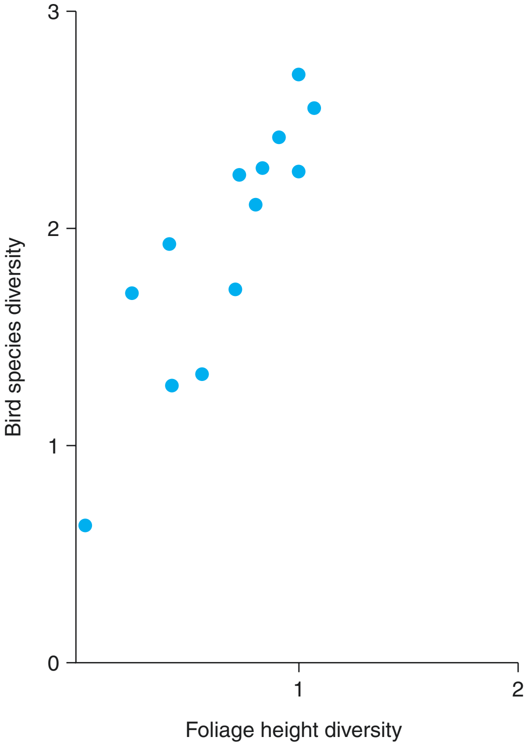


Fig. 20.6 Structural diversity in plant communities often begets biodiversity of other organisms. Bird diversity in temperate, deciduous forests of north-eastern North America is positively correlated with the structural diversity of the tree canopy. Foliage height diversity is a measure of habitat structural complexity and has been calculated as Shannon's diversity index with the proportion of the total foliage in several horizontal layers. Bird species diversity is Shannon's diversity index of breeding bird species territories recorded per 5 acres (approx. 2 ha). Two data points from a tropical savanna and from a pure spruce forest are also included. (MacArthur and MacArthur 1961). Reproduced with permission from John Wiley & Sons

the time of harvest and are not removed in future management operations. The aim is to promote the maintenance of biodiversity and ecological functions, based on the rationale that biological structures and complexity beget niches and habitats and, thus, biodiversity.

The structure of a plant community is also very relevant for the coupling between the biosphere and the atmosphere: the roughness of a canopy largely determines the exchange of water vapour and CO_2 (Sects. 16.1 and 16.2) and strongly influences the microclimate (Sect. 9.2). For example, the daytime surface temperature of a forest near the alpine tree line is much lower than that of adjacent alpine grassland because the tall trees are coupled to the lower atmospheric layer, causing a transport of convective heat (Sect. 9.1). In contrast, small grasses and herbs are decoupled from atmospheric conditions, leading to a strong warming of the grassland canopy and top soil during periods of high radiation (Körner 2003).

In landscape ecology, where the **importance of scale** is in focus, biodiversity and the diversity of abiotic conditions or environmental heterogeneity are summarised as **landscape diversity**. Abiotic features of landscapes and the spatial heterogeneity and arrangement of structures are very important for biodiversity, and landscapes differ in biodiversity. It can be assumed that landscapes with spatially heterogeneous abiotic conditions may provide a larger variety of potential niches than those with more homogeneous conditions. For example, Schulze et al. (1996) showed that the richness and diversity of trees and shrubs were significantly higher at sites with high geomorphological heterogeneity than at sites that exhibited little change in terrain or soil conditions in deciduous forest ecosystems. At the landscape scale, human-created structures must also be considered, for example, fragments of almost natural stands or linear elements such as hedgerows and windbreaks. At this level it is clear that structural heterogeneity contributes to high diversity and that diversity changes greatly in transitional areas of different ecosystems (ecotones), for species as well as for structures.

20.2.3 Functional Diversity

"In the quest to understand species coexistence and community assembly, and to address the ecological consequences of anthropogenic changes, ecologists have moved from *counting species* to *accounting for species*" (Cadotte et al. 2013, p. 1234, italics added). This insight derives from the fact that species largely differ ecologically and play different roles or functions in ecosystems. That is, besides species richness, evenness and composition, the **ecological dissimilarity** or functional differences among species cover an important aspect of biodiversity. To describe the dissimilarity among biological entities with respect to their functional roles in ecosystems, different measures of **functional diversity** have been developed. Functional diversity relates to "those components of biodiversity that influence how an ecosystem operates or functions" (Tilman 2001). It has increasingly been used to study the consequences of biodiversity change for ecosystem functioning and the delivery of ecosystem services (for a definition of these terms, Box 20.4) because it includes information on species characteristics—or traits—that are assumed to control ecological processes (Sect. 20.4).

In essence, any measure of functional diversity will summarise the value, range, distribution and relative abundance of traits in a community. In other words, indices of functional diversity capture the amount of variation in a multivariate **trait space** or hypervolume represented by the species (or other biological entities) within a community. This trait hypervolume thus characterises the phenotypic space occupied by a set of species. Therefore, it is important to get a clear understanding of the meaning of **functional traits**. Traits are characteristics of plants at the scale of cells, tissues and up to the whole organism that reflect their evolutionary history and that shape their performance. Hence, traits are rather broadly defined and encompass heritable quantitative morphological, anatomical, biochemical, physiological or phenological properties of organisms (Garnier et al. 2015). These properties must be measurable at the individual level. Traits can be continuous (e.g. specific leaf area, seed size) or categorical (e.g. life form, leaf habit). They have a direct or indirect impact on the fitness of an individual plant through their effects on growth, reproduction and survival, which constitute the three components of **plant performance**. Thus, traits offer insights into questions such as (Reich 2014): How and why does a plant "behave" as it does? Where does a plant grow and where does it not grow? How does a plant interact with other plants or other organisms, such as herbivores? How does it influence the abiotic and biotic environment around it? Analysing such questions from the perspective of plant attributes has therefore been called a **trait-based approach to plant ecology**, based on the work of Humboldt, Schimper, Larcher and many others.

Many traits are often correlated or covary across species or are similar in their functional consequences. These **trait syndromes** capture fundamental trade-offs along several important axes of plant strategy and function. Three dimensions of plant ecological strategies are considered fundamental for understanding plant functioning: the acquisition and use of resources, the stature of the plant and the capacity for sexual reproduction. For above-ground parts, these dimensions are represented by the **leaf economics**, **canopy size** and **seed size spectrum** (leaf–height–seed scheme) (Westoby 1998). For example, plants may have "cheaply constructed" leaves, with low leaf mass per area (LMA) (kg m^{-2}) resp. high specific leaf area (SLA) (m^2 kg^{-1}), that have a short lifespan but high N and P concentrations and gas exchange rates (Sect. 12.3). Among trees, European aspen (*Populus tremula*) would be an example. At the other extreme of this range, plants invest more biomass per leaf area (high LMA, low SLA), resulting in leaves with long lifespans, often associated with high concentrations of secondary metabolic compounds but low N and P concentrations and gas exchange rates. Norway spruce (*Picea abies*) would be an example for this strategy. Plant stature is related to the competitive ability of species: being larger than neighbours confers a competitive advantage in light capture and is therefore an important characteristic of a carbon acquisition strategy (Sect. 12.5). European beech (*Fagus sylvatica*), for instance, can grow in the shade of neighbouring trees for a long time, but it ultimately outcompetes other species owing to its large maximum height at maturity. The seed-size trade-off involves plants with large individual seed sizes but a low number of seeds or seed output per canopy area; such plants tend to have higher seedling survival under intense competition or low resource availability. An example would be sweet chestnut (*Castanea sativa*). Such species follow a so-called K strategy, living in densities close to carrying capacity (K) and producing fewer seeds (Sects. 17.3 and 19.3). In contrast, plants with small seeds can produce many more seeds with the same relative investment, enhancing dispersal to sites with low competition or high resource availability (Sect. 18.2). An example of such a species with high growth rates (r) and high seed output (r strategy) would be silver birch (*Betula pendula*).

In addition to these three major axes of ecological strategy, other trait dimensions with large variation are also important for plant functioning, including **xylem hydraulic and mechanical property trade-offs** of stems or wood, which is especially important for tree performance (Westoby and Wright 2006). In trees, the xylem is mainly responsible for the transport of water and nutrients, but also for mechanical stiffness. Therefore, a trade-off between conductive efficiency and mechanical strength can be found. In addition, conductance also trades off with resistance to embolism (i.e. the formation of gas bubbles in vessels, blocking the movement of water) because larger vessels or wider pit pores have a higher risk of embolism (Sect. 10.2).

More recently, the idea of a general whole-plant **fast–slow or acquisition–conservatism spectrum of plant economics** has been developed. It states that rates of resource acquisition and processing are converging for roots, stems or leaves owing to strong selective pressure along resource axes (Reich 2014). In other words, plant species that are fast in acquiring carbon (leaves), water or nutrients (roots) must also have characteristics enabling fast rates or use at other organs. For example, species that are capable of moving water rapidly also have low tissue density, short tissue lifespans and high rates of resource acquisition and flux at organ and individual scales. The converse is generally found for species with a slow or "conservatism" strategy. The fast–slow spectrum of traits also scales up to the ecosystem level, where the dominance of species with a fast strategy is associated with faster rates of ecosystem processes such as productivity or decomposition of organic matter, and vice versa (Sects. 12.5 and 16.2).

Root traits have been investigated less, but they are of course essential for water and nutrient uptake, anchoring, storage and competitive ability. Interestingly, some below-ground traits seem to covary with above-ground traits in some species, such as rooting depth and maximum height or specific root length (SRL) and SLA. However, for other species, coordination between above- and below-ground traits has not been found, which can be explained by the very different nature of the above- vs. below-ground environment and the different functions of roots, stems and leaves: roots must acquire water and nutrients from the soil solution, stems must provide mechanical strength for height growth and transport, and leaves must capture light and allow gas exchange for photosynthesis. In addition, the presence of mycorrhizae in most plants also changes many root traits, which makes trait coordination between above- and below-ground traits even less likely (Sect. 7.4).

Traits strongly determine the ecological role of plants within a community through two different means. First, they can explain individual plant responses to environmental factors, thereby influencing occurrence, community structure and diversity. Such properties have been called **response traits**; plant tolerance to frost would be an example, which strongly determines survival and, thus, altitudinal patterns of species occurrence. In addition, traits also determine how plants affect other trophic levels or influence ecosystem processes, that is, they are linked to the capture, use and release of resources. These properties are called **effect traits**; an example would be the concentration of aromatic substances in leaves, which affects herbivory or decomposition. These two "roles" of traits are also illustrated in a conceptual graph that structures the entire Chap. 20 (Fig. 20.1). It also depicts the central role of plant traits in linking the environment to plant diversity and to ecosystem function. It must be noted that response traits and effect traits may have varying degrees of overlap: for instance, SLA is usually high in nutrient-rich habitats (response trait), and it positively affects whole-plant relative growth rate (RGR) and, thus, also community productivity and biogeochemical cycles (effect trait) (Sect. 12.3, Table 20.4). Species' tolerance to environmental

Table 20.4 Association of selected traits with plant responses to environmental changes, plant competitive strength and protection against herbivores and pathogens, and effects on biogeochemical cycles and disturbance regimes

	Climate response	CO_2 response	Soil resource response	Disturbance response	Competitive strength	Plant defence/ protection	Effects on biogeochemical cycles	Effects on disturbance regime
Whole-plant traits								
Growth form	●	●	●	●	●	●	●	●
Life form	●	●	●	●	●		●	●
Plant height	●	●	●	●	●	●	●	●
Clonality	●	?	●	●	●			?
Spinescence	●	?			●	●		?
Flammability		?			●	?	●	●
Leaf traits								
Specific leaf area	●	●	●		●	●	●	
Leaf size	●	?	●		●	●	●	
Leaf dry matter content	●	?	●			●	●	●
Leaf N and P concentration	●	●	●	●	●	●	●	
Physical strength of leaves	●	?	●	●		●	●	
Leaf lifespan	●	●	●	●	●	●	●	●
Leaf phenology	●		●		●		●	●
Photosynthetic pathway	●	●			●			
Leaf frost resistance	●				●	●		
Stem traits								
Stem specific density	●	?	?	●		●	●	●
Twig dry matter content	●	?	?	?		●	●	●
Twig drying time	●	?	?				?	●
Bark thickness			●	●		●		?
Root traits								
Specific root length	●	?	●		●	●		?
Diameter of fine root	●	?	●					
Distribution of rooting depth	●	●	●	●	●		●	●
95% rooting depth	●	?	●		●			●
Nutrient uptake strategy	●	●	●	●	●		●	
Regenerative traits								
Dispersal mode				●				
Dispersal shape and size				●				
Seed mass			●	●	●	●		
Resprouting capacity		●	●	●			●	

Soil resources include water and nutrient availability. Disturbance includes any process that destroys major plant biomass. *Dots* indicate documented evidence of associations, *?* indicate lack of information, empty fields show no assumed associations. Reproduced from Cornelissen et al. (2003), with permission from CSIRO Publishing

Table 20.5 Predicting ecosystem properties by plant traits

	Biomass-weighted mean traits		
	SLA	LDMC	LNC
NPP_{SA}	0.78**	−0.71**	0.87***
Litter mass $Loss_{SM}$	0.78**	−0.81**	0.74*
C_{Soil}	−0.88***	0.84***	−0.96***
N_{Soil}	−0.84***	0.83***	−0.93***

Pearson correlation coefficients between SLA, that is, the ratio of water-saturated leaf area to leaf dry mass (m^2 kg^{-1}), leaf dry matter content (LDMC), that is, the ratio of leaf dry mass to water-saturated fresh mass (mg g^{-1}), or leaf nitrogen concentration (LNC) (mg g^{-1}), with specific above-ground net primary productivity (NPP_{SA}), that is, net primary production expressed on a per gram green biomass basis (g kg^{-1} day^{-1}), specific rate of litter mass loss (Litter Mass $Loss_{SM}$, that is, decomposition rate expressed per unit biomass (g kg^{-1} day^{-1}), total soil organic carbon concentration (C_{Soil}) (g kg^{-1}) and total soil nitrogen concentration (N_{Soil}) (g kg^{-1}). Biomass-weighted mean traits were calculated as aggregated on a community level. *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$ (Garnier et al. 2004)

factors, stressors or disturbances and their contributions to ecosystem functions and services will often not only depend on single traits, but on a combination of traits and often show a phylogenetic signal (Díaz et al. 2013).

Is it possible to predict certain properties of an ecosystem by the dominance of species with specific traits or by the **mean trait value** of the co-occurring species (Sect. 20.4.1)? To evaluate this hypothesis, **community-weighted means** (CWM) of single traits are calculated based on measured trait values, weighted by the abundance or biomass of the species. Community net primary productivity, litter decomposition rates or the accumulation of carbon and nitrogen in the soil, for instance, can be highly predicted by few leaf traits only, for instance (Table 20.5), which are of course correlated with other traits (e.g. root traits) that may have more direct effects on the processes studied. Mean trait values do not represent a measure of functional diversity but are a useful and widely used indicator of the functional structure of a community.

Plants are immobile, meaning they cannot physically escape predators and pathogens, search for pollinators or hide from approaching extreme climatic situations. Obviously, plants as sessile organisms must continuously cope with changing environmental conditions—from minute-by-minute, daily, seasonal to decadal fluctuations in temperature and light, changes in nutrient and water availability, or herbivore pressure, pathogen load or loss of mutualistic partners. Plants have therefore evolved a variety of mechanisms that enable them to tolerate and withstand environmental change, and to re-achieve internal homeostasis: plants are highly plastic and resilient to cope with a highly dynamic environment. This **phenotypic plasticity**, or the capacity of a given genotype to produce different physiological or morphological phenotypes in response to different environmental conditions, is also reflected in plant traits. Traits are usually quantified comparatively across species and are highly context-dependent. This means that traits are not only genetically fixed and heritable properties, but are also plastic. They can change over time (e.g. seasonal or ontogenetic variations) and can depend on environmental conditions, the presence of competitors or herbivores and pathogens. Examples of this phenotypic plasticity of traits are the development of sun and shade leaves within a single crown (Sect. 3.2) or the increase in defensive metabolites after herbivore attack (Sect. 8.3). In fact, plasticity can be considered a trait of its own, given its large variability across species and habitats. Trait plasticity, however, is also limited by multiple ecological factors, for example, extreme levels in a given abiotic factor can reduce plasticity to another factor (Valladares et al. 2007).

The traits present in a plant community also reflect the interplay between evolutionary and assembly processes and the physical environment (Sect. 20.3.2). Thus, understanding how and why plant traits vary among species and sites is a critical step towards understanding ecosystem properties and their functioning. Hence, **trait-based ecology** has received much attention over the last decade to acquire a better understanding of how traits influence species distribution, interactions and functions (e.g. Garnier et al. 2015 for a recent synopsis with extensive literature). Global data sets covering hundreds of traits and thousands of species are available

(Kattge et al. 2011), and handbooks about measurements of traits are useful for standardisation and cross-study comparisons (e.g. Pérez-Harguindeguy et al. 2013).

Once traits and their respective associations with ecological responses or effects have been clarified, different measures of functional diversity can be determined. A very critical aspect for its determination is the need to select those traits that are relevant for the process or function of interest, which thus must be defined explicitly. In general, measures of functional diversity fall into two main classes: (1) discontinuous measures, that is, categorising species into plant functional groups or types, and (2) continuous measures, that is, measuring the spread of species in an *n*-dimensional trait space.

20.2.3.1 Plant Functional Groups

A rather broad measure of functional richness is that of the number of **plant functional groups**, also often referred to as **plant functional types**. Plant functional types are groups of species with similar suites of co-occurring functional attributes, such as comparable physiological behaviour (e.g. C_3 and C_4 plants) (Sect. 12.1), similar morphology or growth forms (e.g. stem succulents, lianas) (Table 20.3), temporal niches (e.g. spring geophytes, pluviotherophytes, early or late seasonal species) or similar dispersal syndromes (e.g. anemochory, zoochory) (Sect. 18.2). In addition, **functional response groups** and **functional effect groups** are respectively species that show a similar response to a particular environmental factor (e.g. sprouters, being plants that are able to resprout after fire) (Sect. 13.5) or that have similar effects on ecosystem processes (e.g. nitrogen fixers, which exert a significant influence on biogeochemistry). One major reason for reducing the huge variety of different organisms into such functional groups is the need to simplify floristic complexity for global vegetation models (Sect. 22.4), for vegetation mapping, and for monitoring purposes. Methodologically, such functional groups are identified via *a priori* knowledge about functional attributes of species (e.g. C_3 and C_4 pathways) or by cluster analyses of trait values.

An important categorisation of functional groups in ecological and agronomic studies of grasslands is that of grasses—herbs—legumes, combining phylogenetic and above-ground architectural traits (grasses versus herbs and legumes) with physiological traits (nitrogen-fixing legumes versus non-fixing grasses and herbs). In forest ecology, the broadleaved/deciduous vs. evergreen/coniferous dichotomy is widely used. A generally applicable classification, however, is obviously not possible. Depending on the questions being posed, the same species may be classified into different groups. Many plants may belong to several functional groups; at the same time they may be “evergreen”, “zoochoric”, “deep rooting”, “nitrate storing”, and so forth, to name just a few (Fig. 20.7). Problematic is the categorisation into functional groups when considering traits with high phenotypic plasticity, because the same species may then fall into different groups, depending on the specific trait expression. Another problem with classifications into functional groups is that the ecological roles of plants are not always fully understood. It is easy to understand the function of the group Leguminosae, for example, because of its members’ ability to symbiotically fix atmospheric nitrogen, which causes disproportionate effects on ecosystem biogeochemistry (Fig. 20.8) (Sect. 16.3), but note that the degree of N-fixation is also highly plastic and depends on soil N availability, among other factors (Sect. 7.4). However, for groups such as “grasses” or “herbaceous plants”, this applies only partially (e.g. position of leaves and meristems, capacity to form fine roots). It is thus questionable whether such *a priori* subdivision of plants is justified for understanding the ecological role of species within the plant community. Classification of species according to functional groups is thus rather difficult for general purposes but might be useful for specific research questions. For example, if one is interested in whether a leaf habit in temperate mixed forests affects litter decomposition rates, the two functional groups “deciduous” versus “evergreen” tree species may already explain a large proportion of the data variability, and it may make a difference whether only one or two of these groups are present.

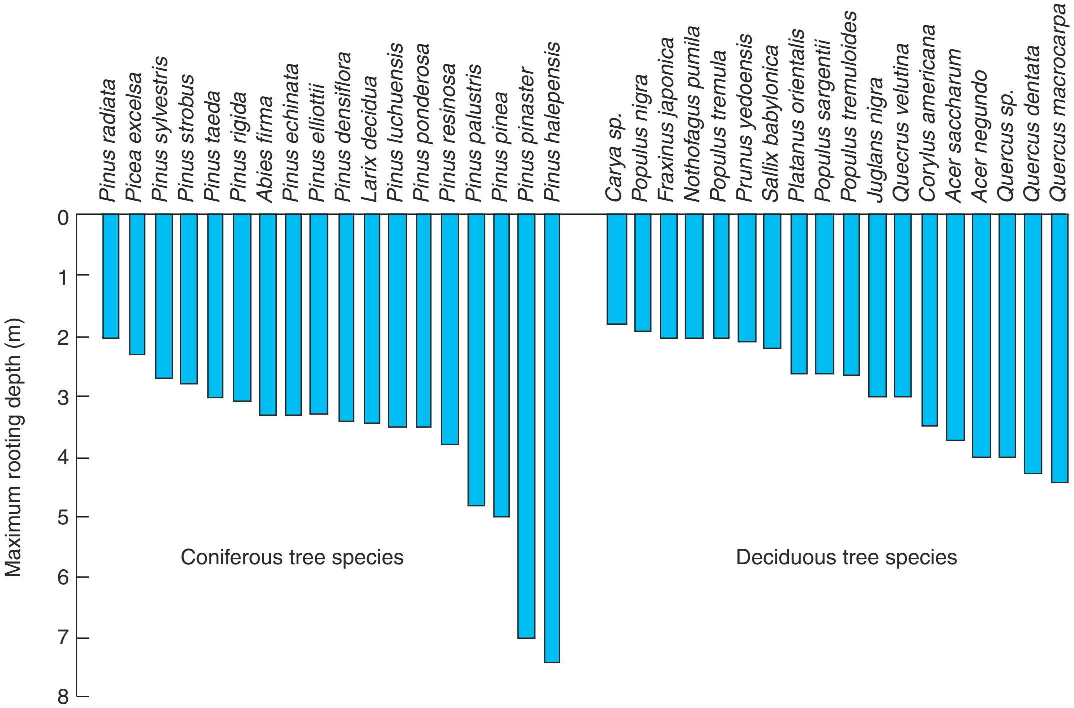


Fig. 20.7 Maximum rooting depth of temperate coniferous and deciduous tree species. Species within functional groups largely vary in trait expression, resulting in substantial overlap between both groups. (Körner 2005; based on data in Canadell et al. 1996)

20.2.3.2 Continuous Indices of Functional Diversity

Much information is lost by any classification procedure because many traits are not categorical but continuous and plastic. In addition, using functional groups implies that species within those groups might be exchangeable or redundant when it comes to determining the effects of diversity on ecosystems (Sect. 20.4). Continuous measures of functional diversity, in contrast, capture the heterogeneity and variability of traits within a community. These measures can be calculated for single traits (e.g. asking the question whether the variability of leaf N concentration can better explain primary production than its mean value) or for multiple traits together (e.g. whether a higher or lower variability of leaf N concentration, cuticula thickness and LDMC better explains herbivory rates).

More than a dozen such continuous indices of functional diversity have been suggested that are based on slightly different assumptions and mathematical approaches. There are guidelines on how to select the most suitable index for specific questions (Schleuter et al. 2010; Petchey et al. 2009), and software solutions are available to calculate them (e.g. several online R scripts, FDiversity) (Pla et al. 2012). In principle, these indices can be divided into three groups that represent different aspects of functional diversity: functional richness, functional evenness and functional divergence (Fig. 20.9) (Mason et al. 2005). The first two are derived from indices to describe taxonomic diversity (Box 20.1). The latter two indices may also contain information about species' abundances by weighting the contribution of each species based on cover or biomass, for example.

Functional richness represents the volume of the functional trait space that is occupied by the species present in a community (Fig. 20.9a, a′). It therefore reflects the potentially used niche space by a community, that is, the hypervolume of a Hutchinsonian multidimensional niche. It can be

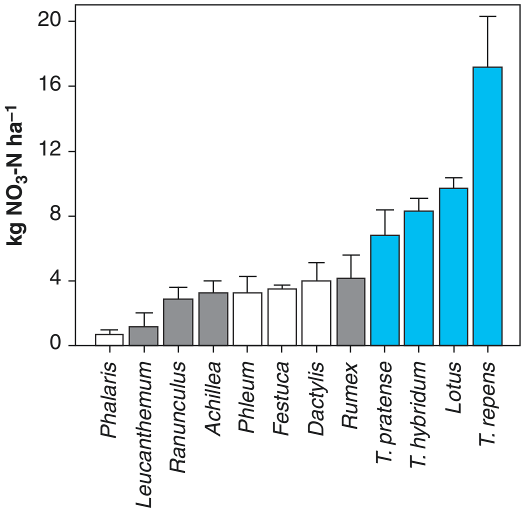


Fig. 20.8 Effects of different species on soil nitrate availability. Species were grown in monocultures under identical environmental conditions, so that differences in soil nitrate availability are only due to ecological differences among species. Legumes (blue) fix nitrogen, but to varying degrees, resulting in higher nitrate values than under forbs (grey) and grasses (white). *Phalaris*: *P. arundinacea*, *Leucanthemum*: *L. vulgare*, *Ranunculus*: *R. acris*, *Achillea*: *A. millefolium*, *Phleum*: *P. pratense*, *Festuca*: *F. ovina*, *Dactylis*: *D. glomerata*, *Rumex*: *R. acetosa*, *Lotus*: *L. corniculatus*, *T.*: *Trifolium*. (Palmborg et al. 2005)

used to test the hypothesis whether ecosystem properties depend on the size of the functional space covered. For example, it could be hypothesised that a community composed of species with very different rooting depths and plant heights (i.e. high functional richness) can take up more nutrients from the entire soil profile and capture more light, and hence produce more biomass, than a community composed of flat rooting species and small statured plants only (Fig. 20.38). The index is positively correlated with species richness, but communities with the same number of species may differ in functional richness if the traits are more similar in one community than in others.

Functional evenness measures the regularity in the distribution of species abundances in the occupied trait space, with high values representing a rather regular distribution of traits (Fig. 20.9b, b′). Functional evenness can also be linked to the utilisation of resources. Staying with the aforementioned example, it could be tested whether a community with an even distribution of rooting depths and plant heights (i.e. high functional evenness) is more productive than a community dominated by flat rooting small plants because the soil profile and the above-ground space are more evenly occupied and utilised, which could lead to higher nutrient uptake and light capture.

Functional divergence estimates the position of species within the trait space, for example, by quantifying how species abundances diverge from the centre of the functional space (Fig. 20.9c, c′). A high value means that very abundant species are very far from the centre of the trait space. In our example, it can be tested whether communities with large differences in rooting depths and heights (i.e. high functional divergence) may have a high degree of niche differentiation and low competition for resources (Sect. 20.4.9), potentially resulting in increased productivity, in comparison with communities dominated by species with small differences in these two traits.

20.2.4 Phylogenetic Diversity

Next to the use of functional, trait-based indices, the quantification of **phylogenetic diversity** is the second approach to measuring biodiversity based on species ecological differences. The concept relies on the simple assumption that the more time that has passed since two species shared a common ancestor, the higher the probability that they have ecologically and functionally diverged. Thus, this measure of biodiversity takes evolutionary history into account. For the calculation of phylogenetic diversity, the phylogenetic trees of the organisms occurring in a community must exist, and **phylogenies** of many different taxa have become increasingly available in recent decades owing predominantly to genome-sequencing efforts. In principle, community phylogenetic diversity is then calculated as the sum of the phylogenetic branch lengths connecting all taxa in a community and is thus a measure of the total amount of phylogenetic distance or evolutionary divergence in a community (Fig. 20.10). Because traits are the product of evolution,

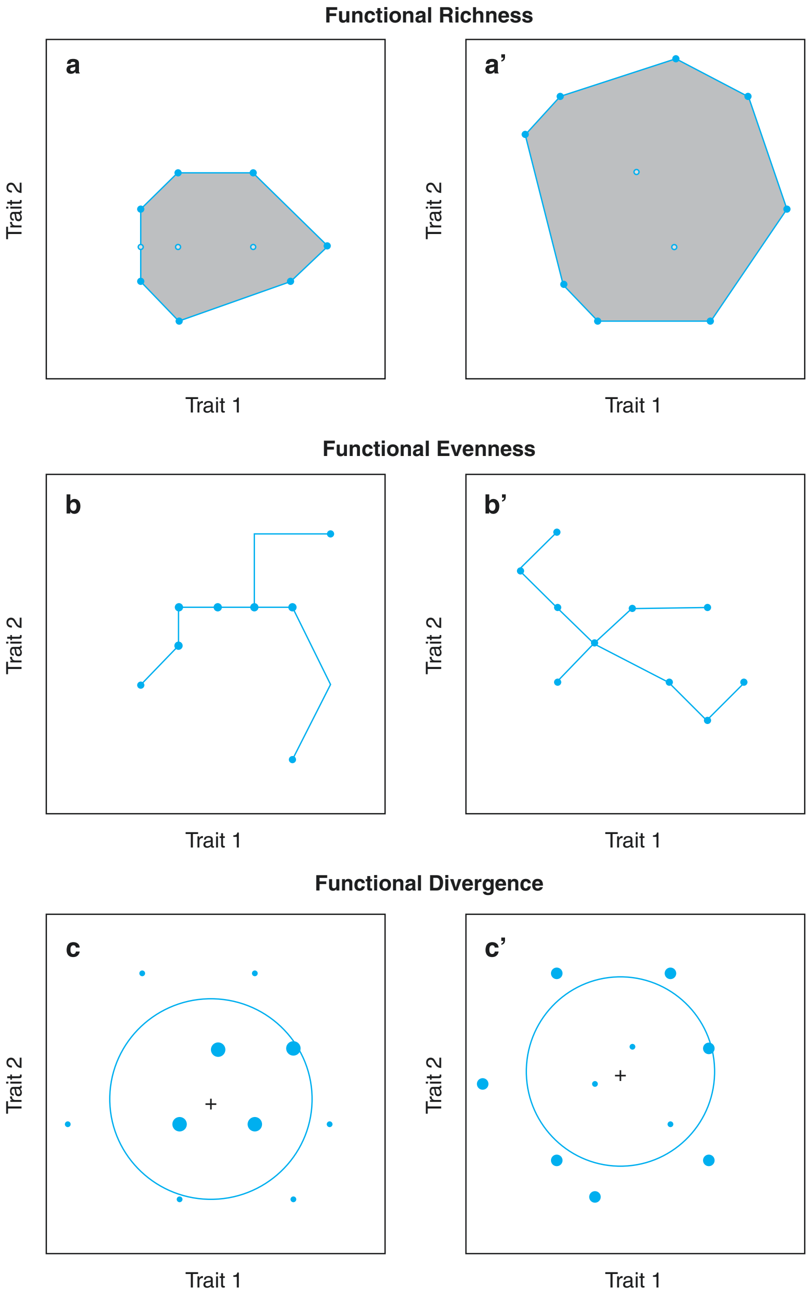


Fig. 20.9 Geometrical presentation of functional diversity indices. Two traits define a two-dimensional functional space for a local community of ten species (dots). Species are plotted in this space according to their respective trait values, with symbol size proportional to their abundances. The functional diversity of a community is thus the distribution of species and of their abundances in this functional space. For each component of functional diversity, two contrasting communities are represented, with low **a**, **b**, **c** and high **a′**, **b′**, **c′** index values. Functional richness **a** and **a′** is the functional space occupied by the community, functional evenness **b** and **b′** is the regularity in the distribution of species abundances in the functional space, and functional divergence **c** and **c′** quantifies how species abundances diverge from the centre of the functional space (Mouillot et al. 2011)

phylogenetic diversity encapsulates the entire evolved trait space of a community. In consequence, it can thus be used as a surrogate for trait diversity, for example, in cases where trait information is limited (Cadotte et al. 2010).

Phylogenetic diversity is an important aspect in studying the evolutionary processes that produce patterns of biodiversity and to understand the ecological interactions that determine species assemblage (Sect. 20.3). Being a surrogate of the functional structure of communities, it is also used to test hypotheses about the relationship between plant diversity and ecosystem functioning (Sect. 20.4). In addition, it is an important measure to define conservation priorities because communities with a high phylogenetic diversity

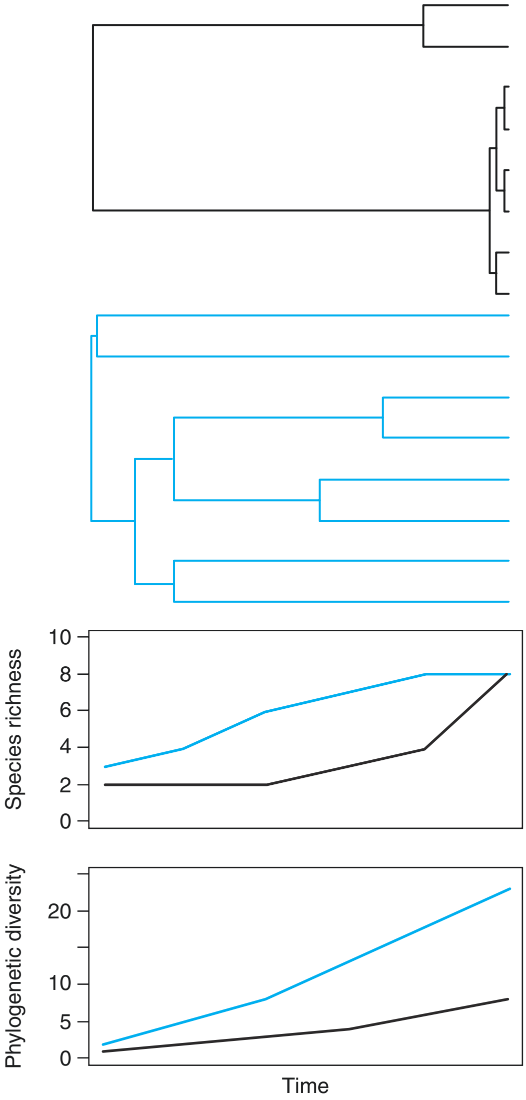


Fig. 20.10 Development of species richness and phylogenetic diversity through time. The black phylogeny represents a community or region with recent speciation events, and the blue phylogeny represents a situation with older speciation events. Both phylogenies ultimately produce the same number of species, but the accumulated branch lengths (i.e. phylogenetic diversity) in the blue phylogeny is much higher because of early diversification (Swenson 2011). Reproduced with permission from the Botanical Society of America

represent a larger store of genetic diversity, available for adaptation and innovation. Conserving such communities with a higher priority than those with low phylogenetic diversity would therefore maximise future evolutionary options.

20.3 Environmental Controls of Biodiversity

Plant species have evolved in certain areas and are adapted to specific environmental conditions. Hence, they are not evenly distributed across the globe or within their range. There are hostile regions, such as high alpine summits or extreme deserts, but also favourable regions, such as tropical rain forests. In consequence, plant diversity shows striking spatial patterns at various spatial scales, that is, at the global level (Fig. 20.11), but also within regions, landscapes or sites. Describing and understanding the causes of such differences in species distribution and diversity (**biogeography**) has a long tradition, with Alexander von Humboldt being the first to analyse the environmental constraints of plant distribution (von Humboldt 1808), followed by the seminal work of Andreas Franz Wilhelm Schimper (1898). In the preface of his book, Schimper wrote (the following quotes are taken from the authorised English translation by W. R. Fisher: Schimper 1903): “The delimitation of separate floral districts and their grouping into more comprehensive combinations are nearly completed, and the time is not far distant when all species of plants and their geographical distribution will be well known. The objectives of geographical botany will not, however, then be attained, as is often assumed, but a foundation merely will have been laid on which science can construct a larger edifice. The essential aim of geographical botany will then be an inquiry into the causes of differences existing among the various floras” (p. v). Further, he already acknowledged the intimate connections between natural history and experimental sciences needed to disentangle the underlying causes of biodiversity patterns: “The oecology of plant distribution will succeed in opening out new paths on condition only that it leans closely on experimental physiology, for it presupposes an accurate knowledge of the conditions of the life of plants which experiment alone can bestow” (p. vi).

The following sections mainly describe patterns of plant species richness across environmental gradients and their underlying mechanisms.

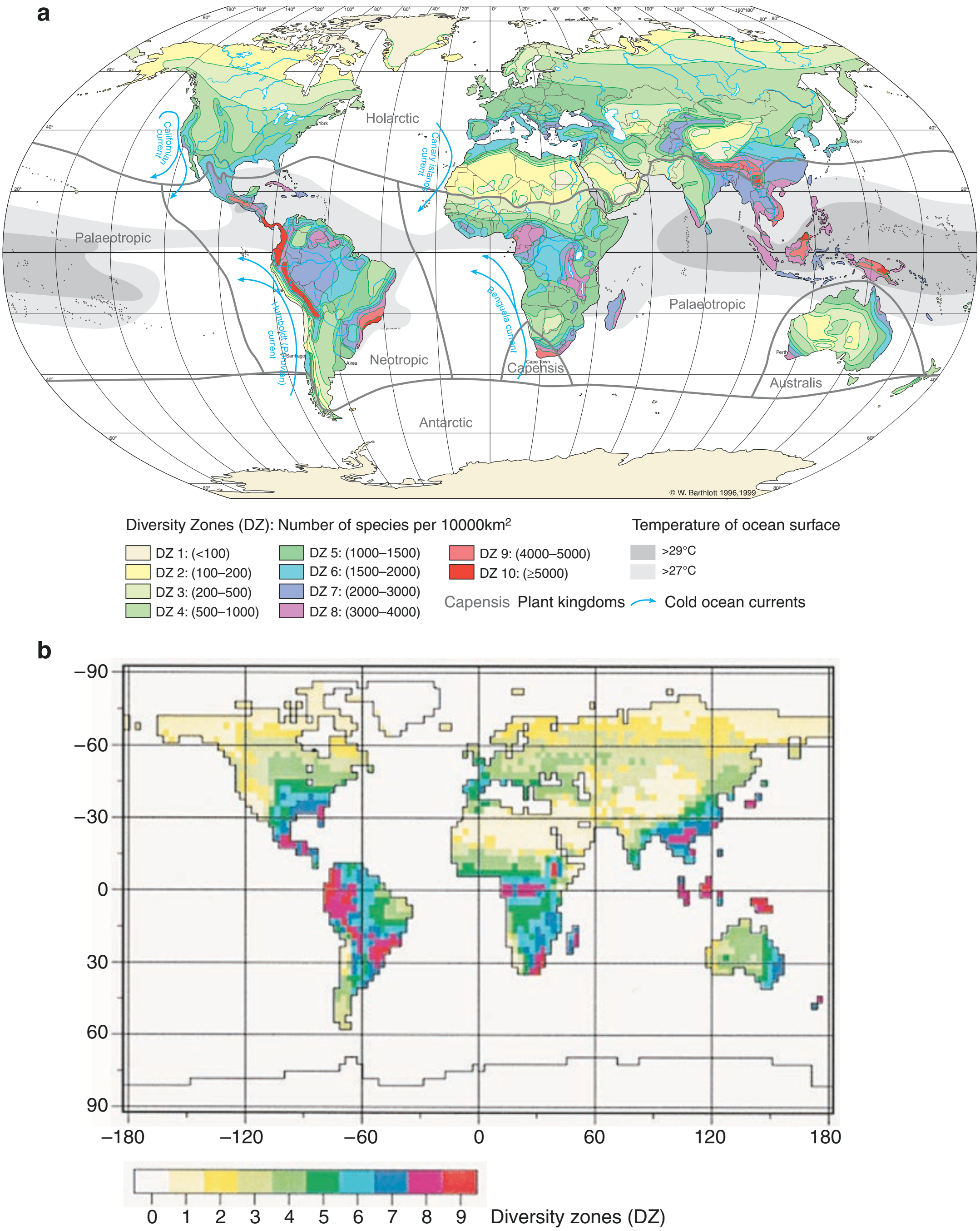


Fig. 20.11 Maps of global plant species richness. **a** Species richness based on empirical data from inventories and data on abiotic factors, including climate. The diversity zones (DZs) are grouped according to species numbers per 10,000 km^2 (Barthlott et al. 2005). Reproduced with permission from the Deutsche Akademie der Naturforscher Leopoldina - Nationale Akademie der Wissenschaften. **b** Species richness derived from simulations based on growth-limiting climatic scenarios only. The values are categorised into nine groups: (1) <2%, (2) 2–4%, (3) 4–10%, (4) 10–20%, (5) 20–30%, (6) 30–40%, (7) 40–60%, (8) 60–80%, and (9) 80% of the maximum diversity value simulated. (Kleidon and Mooney 2000)

Clearly, biodiversity today is greatly changed by humans, for example, through land-use change and management, eutrophication or, increasingly, also by climate change. These aspects are described in more detail in Part V.

20.3.1 Latitudinal Gradients

Barthlott et al. (2005) presented a detailed world map of **phytodiversity** (of vascular plants) that shows the large spatial gradients in plant species richness on a global scale. Such maps can be produced by overlying information about the spatial distribution of single species, which is derived from herbarium records, taxon revisions or range maps. An alternative to such a taxon-based approach is the inventory-based approach where species richness values from thousands of floras, local checklists and regional species accounts are used to calculate species richness at a specific spatial grid resolution. Since the sampled areas differ in size, the richness values for this spatial pixel have to be standardised using an empirical species–area relationship (Sect. 18.4). Finally, non-sampled areas are interpolated using data on climate, vegetation types and geodiversity. In the map shown here (Fig. 20.11a), which uses a 100 × 100 km grid, 10 **diversity zones** are graded according to the number of species, from fewer than 100 to more than 5,000 per grid cell. The zones of lowest plant diversity are located in the Arctic tundra, the driest deserts (e.g. parts of the Sahara) and high alpine deserts (e.g. Tibetan upland). These regions are characterised by a lack of available ambient energy or humidity, limiting plant growth. An exception to this rule is the Namib Desert in southern Africa, which has a very long evolutionary history, high heterogeneity in topography and soils, and highly predictable rainfalls from fog in winter. The centres of highest phytodiversity are located in the humid tropics, including the Tropical East Andes, North Borneo and New Guinea, but also on the Atlantic coast of Brazil. Interestingly, not all tropical regions outnumber non-tropical ones: for instance, plant species richness in the Congo basin, where large areas are still rather undisturbed by humans, is comparable to that in Central European regions, which have been under long-term human influence. Other extra-tropical regions of high diversity are located at the Maritime Alps in France, the Caucasus or the Cape of South Africa.

Are these patterns similar for different plant life forms? Trees, being important structural components of forest ecosystems and delivering many ecosystem goods and services, such as timber and non-timber products, are relatively well known in terms of their taxonomy and distribution. In addition, the increasing number of permanent forest inventory plots also allows for an upscaling of tree species richness to continental scales, assuming a relation between the number of species and the number of individuals of a defined region. Using standardised species lists with abundance data in such inventory plots in wet, moist and dry tropical forests, a recent study could show that the number of tropical tree species ranges between 40,000 and 53,000 in total, in contrast to only 124 tree species in temperate Europe (Slik et al. 2015)! The Neotropics and the Indo-Pacific region have very similar tree species richness (between approx. 18,600 and 24,800 species), while tropical forests of Africa are rather species poor, with only between 4,600 and 6,000 species. Thus, at least tropical trees indeed show spatial patterns similar to those shown for all vascular plants (Fig. 20.11).

So what factors are responsible for these spatial patterns? Kleidon and Mooney (2000) compared the map by Barthlott et al. (2005) with a map in which the global diversity of vascular plants was reconstructed on the basis of a climate model. Despite the different resolutions, both maps agree to a large extent (Fig. 20.11b). Obviously, climatic conditions can explain biodiversity at the global scale to a substantial degree. Climatic factors mostly constrain plant survival at the time of germination and during the development of young plants, and sufficient precipitation during those stages appears as a decisive factor: the smaller the number of days with favourable conditions for plant growth, the greater the constraints for growth and the less the diversity of species.

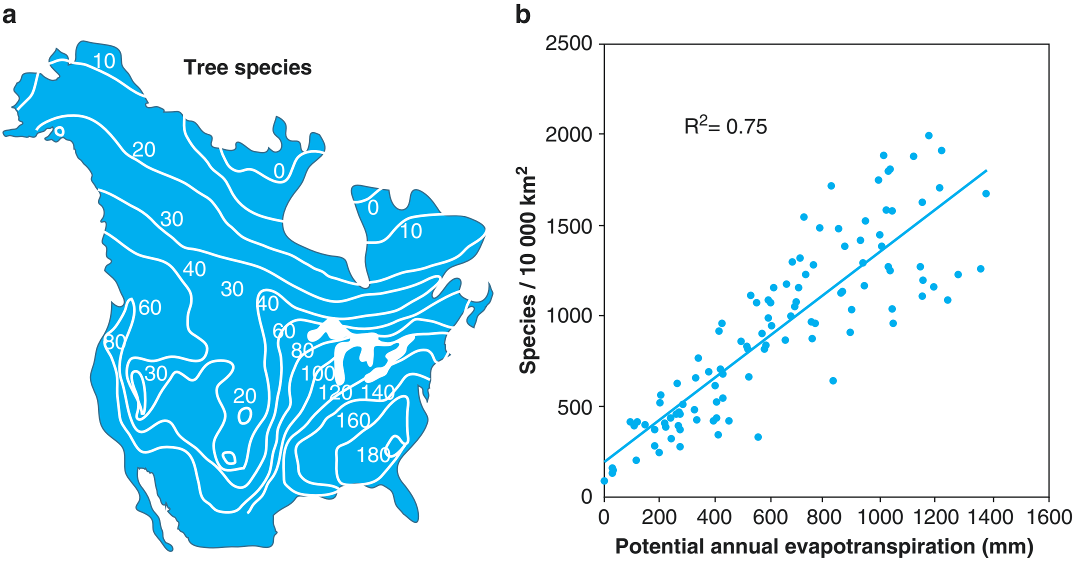


Fig. 20.12 Patterns of plant diversity along latitudinal and climatic gradients. **a** geographical distribution of tree species in North America. The isolines connect points with rather similar species numbers (Currie 1991). Reproduced with permission from University of Chicago Press. **b** Species diversity correlates well with climatic factors, such as evapotranspiration, that change along the latitudinal gradient, as shown for all vascular plant species of North America. The number of vascular plant species is based on grid cells of 100 × 100 km. Modified from Mutke and Barthlott (2005). Reproduced with permission from The Royal Danish Academy

Also, at higher taxonomic levels, climatic factors are well correlated with diversity. Woodward (1987) found a linear relation between the number of plant families and the absolute minimum temperature (for land surfaces along a 15°N latitude). In absolutely frost-free areas, the number of plant families exceeds 250; below a minimum of 10 °C, the number is less than 100. Another, well-known example of changes in plant diversity along environmental gradients relates to the geographical distribution of tree species in North America. As shown in Fig. 20.12a, the number of tree species correlates rather negatively with increasing latitude, that is, fewer tree species are found towards the boreal zone. Climatic factors, such as mean annual temperature, annual solar radiation and precipitation, as well as actual evapotranspiration (Sects. 10.1 and 16.1), are positively related to tree species richness. Evapotranspiration is also strongly related to species richness of all vascular plants of North America (Fig. 20.12b). At lower latitudes between 30° and 40°N, the higher variability is also due to climatic factors: precipitation and, thus, water availability strongly decrease from east to west in this region.

But is climate indeed the only driver of global, large-scale patterns in plant diversity? What other factors might also play a role? Such questions fall within the purview of **macro-ecology**. Several, not mutually exclusive, hypotheses have been formulated to explain the high plant diversity in the tropics and the decrease of diversity towards higher latitudes (see overviews by, for example, Huston 1994; Rosenzweig 1995; Hillebrand 2004; Clarke and Gaston 2006). Due to lower climatic fluctuations during the ice ages in the inner tropics, long-lasting favourable climatic conditions enabled long and undisturbed **adaptation and specialisation**. This can be illustrated by looking at the tree diversity data: as shown earlier, Africa harbours only approx. one-fourth of the diversity found in North America or the Indo-Pacific region, which cannot be explained solely by its smaller size and lower environmental variability. Rather, African forests were shrinking to small refugia areas during the Pleistocene, resulting in large species losses. Expanding to the current area, these forests must be repopulated from a depleted species pool, while forest area in the other two regions has not experienced similar shrinkages (Slik et al. 2015). Similarly, geologically old regions of the Earth are generally particularly rich in species because of their long history of evolution compared to geologically younger parts. Higher solar radiation and higher soil water availability at the equator, leading to increased evapotranspiration, result in increased annual productivity, which is the basis for many other organisms that can exploit this resource. A comparison between global maps of net primary production (Sect. 21.2, Fig. 21.4) with that of plant diversity (Fig. 20.11) intuitively shows that there might be underlying factors that positively influence both productivity and diversity. This climate-driven "**energy–diversity hypothesis**" has attracted substantial interest and is now considered one of the most important drivers of those latitudinal gradients (Fig. 20.12). In addition, higher predation and pathogen load all year round in tropical regions can reduce the dominance of single species, enabling the coexistence of other species with lower abundance. Finally, the tropical regions also have a higher land-to-sea ratio than regions at high latitudes, so that terrestrial diversity should be higher based on the species–area relationship (Sect. 18.4). In contrast, climatic regions requiring specialised adaptation by organisms to harsh conditions, such as boreal forest or tundra biomes, are often relatively poor in plant species owing to strong environmental filtering (Sect. 20.3.4). For the same reasons, the number of plant species generally declines with altitude in high mountains, although the diversity in mountainous areas is higher than in lowlands if based on the available area for plant growth (Körner 2003). This has been explained by their geographical isolation and the high degree of topographic complexity and strong climatic gradients, leading to a high number of small-scale structures (habitats) in a given space, which allows many specialised species to coexist. In addition, lower human impacts and low-intensity management regimes may have led to high levels of biodiversity in mountainous areas.

20.3.2 Environmental Heterogeneity

The relation between **environmental heterogeneity** and species richness, as mentioned earlier in connection with alpine regions, has for a long time attracted many ecologists in the search for mechanisms driving gradients in species diversity. Almost 100 years ago, Thienemann (1920) formulated two "biocoenotic laws" stating that the more diverse the environmental conditions and the closer they correspond to the "biological optimum", the larger the number of species, and vice versa. It has been argued that spatial environmental heterogeneity could promote species richness through three major mechanisms (Stein et al. 2014). The first mechanism is based on classical niche theory (Sect. 19.3): the available niche space (in a Hutchinsonian sense, defined as an *n*-dimensional hypervolume, with the dimensions being environmental conditions, resources and biotic factors) should become larger if environmental gradients become steeper, if the amount of habitat types and the number of resources available increases, or if the physical structure of habitats becomes more complex. More species can be packed into a larger niche space.

The second mechanism is related to the ability of species to persist against adverse conditions: environmentally heterogeneous areas should provide more possibilities for shelter and refuge. This has nicely been demonstrated in topographically highly structured alpine communities. Temperature variability on the same slope of alpine grassland varies substantially at very short distances. Plant species adapted to cool habitats (Sects. 4.2 and 9.4), with low indicator values for temperature, grow in significantly colder micro-habitats than plants with higher indicator values found on the same slope (Fig. 20.13). Thus, species may find suitable conditions matching their thermal niche within short distances to compensate for climate warming.

As a third mechanism, evolutionary processes leading to diversification are accounted for: opportunities for isolation and divergent adaptation to diverse environmental conditions should increase with increasing environmental heteroge-

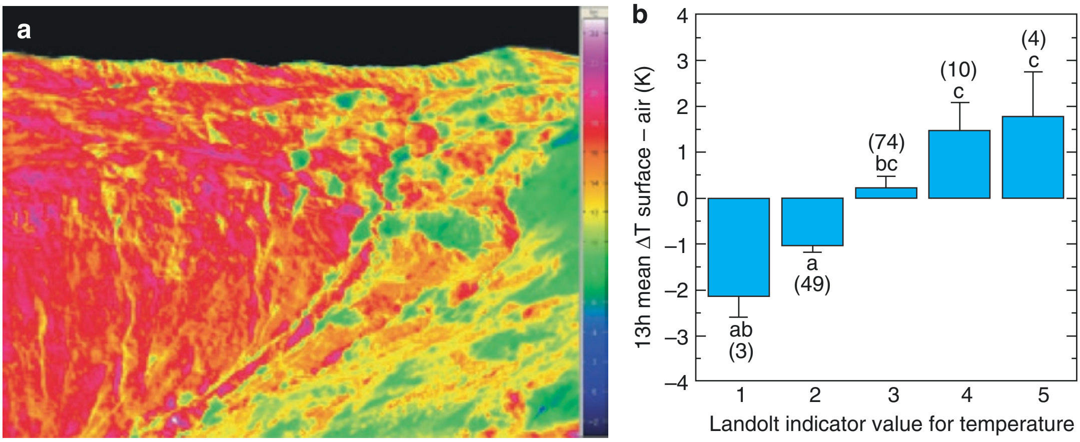


Fig. 20.13 Small-scale temperature heterogeneity in alpine grasslands. **a** False colour image based on infrared thermography of surface temperatures on a NNW exposed slope at the Furka Pass in the Swiss Alps under full direct solar radiation (12–18 h, August). Dark blue represents cold (2 °C) and magenta hot (24 °C) surface temperature (Scherrer and Körner 2010). Reproduced with permission from John Wiley & Sons. **b** Seasonal temperature differences between surface and air temperature during daytime hours per group of temperature indicator values. The numbers in brackets indicate the number of plant species within the different indicator groups; significant differences are denoted by different letters (Scherrer and Körner 2011). Reproduced with permission from John Wiley & Sons

neity, resulting in a higher probability of speciation events. A number of studies have tested these different mechanisms and found general support of the heterogeneity–diversity hypothesis, though generalisations are difficult owing to the different research approaches, terminology and spatial scales studied. Recently, a worldwide meta-analysis that used data from 190 independent studies found general support for the environmental heterogeneity hypothesis (Stein et al. 2014). Different measures of environmental heterogeneity, including those related to land cover, vegetation diversity and structure, climate, soil variables and topography, were all positively related to species richness of plants, invertebrates and vertebrates (Fig. 20.14).

Closely related to the heterogeneity–diversity hypothesis is the **intermediate disturbance hypothesis** (Huston 1979), which postulates that the highest species richness will be found at intermediate levels of disturbance: at very low levels of disturbance, competitive species dominate the community and diversity is low (competitive exclusion); increasing levels of disturbance intensity or frequency may result in a disproportional mortality of the dominant species and larger environmental heterogeneity, resulting in postponed competitive exclusion, coexistence and, thus, higher diversity; very intensive disturbance events may lead to a failure of populations to recover from mortality and to a homogenisation of environmental conditions (Sects. 13.5 and 17.3). Thus, there should be a trade-off between the ability of a species to compete with others and their ability to tolerate disturbance. Despite being a well-recognised hypothesis, the literature shows a variety of disturbance–diversity patterns, not a consistent peak as predicted by the intermediate disturbance hypothesis (Mackey and Currie 2001). Nevertheless, disturbance is an essential feature for ecosystem dynamics and affects biodiversity to a large degree. It is a natural component in all ecosystems, working at different spatial and temporal scales. For example, soil disturbance by ants or moles creates sites free of competitors for the germination and growth of seedlings; strong crown fires

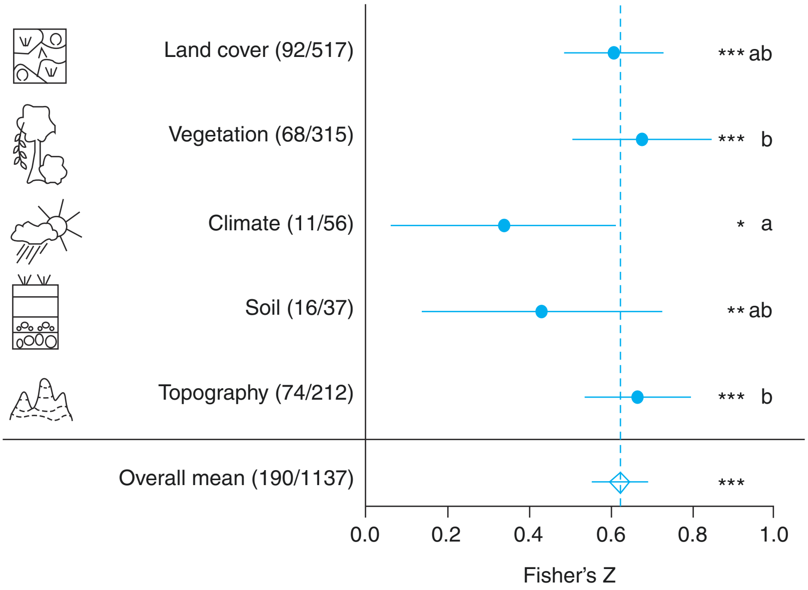


Fig. 20.14 Positive relationship between environmental heterogeneity and species richness. Effects of environmental heterogeneity were analysed separately for different categories (land cover, vegetation, climate, soil, topography). Mean effect sizes (Fisher's z) that are significantly larger than zero indicate positive relationships; lines show 95% confidence intervals. Different letters indicate significant differences among categories. Diamond and dashed lines represent the overall weighted mean effect. Numbers in parentheses give the respective numbers of studies/data points. All coefficients are different from zero at significance levels: $***p < 0.001$, $**p < 0.01$, $*p < 0.05$. Modified from Stein et al. (2014). Reproduced with permission from John Wiley & Sons

eliminate dominant tree species, reducing competition for light and soil resources and allowing the establishment of other species (Fig. 20.15); ground fires destroy thick layers of litter that otherwise cannot be penetrated by seedlings and increase mineralisation of litter-sequestered nutrients (Sect. 13.5). If such disturbances additionally act as barriers between populations, mutations that may lead to new species will have a better chance of getting established, leading to diversification over time (Sect. 17.2), as in the Mediterranean flora of the South African Cape region or the tropical Andes, for example.

In the examples presented in the previous sections, plant diversity is statistically treated as the **response variable**, while abiotic and biotic site factors (e.g. availability of light, water and nutri-

Fig. 20.15 Disturbances create "windows of opportunities" for species establishment. Species previously absent from a plant community are able to colonise a site after disturbances, such as fire. *Saponaria ocymoides* (pink flowers) and *Isatis tinctoria* (yellow) 4 years after a stand-replacing fire in the Swiss Alps (Leuk). (Photo: M. Scherer-Lorenzen)

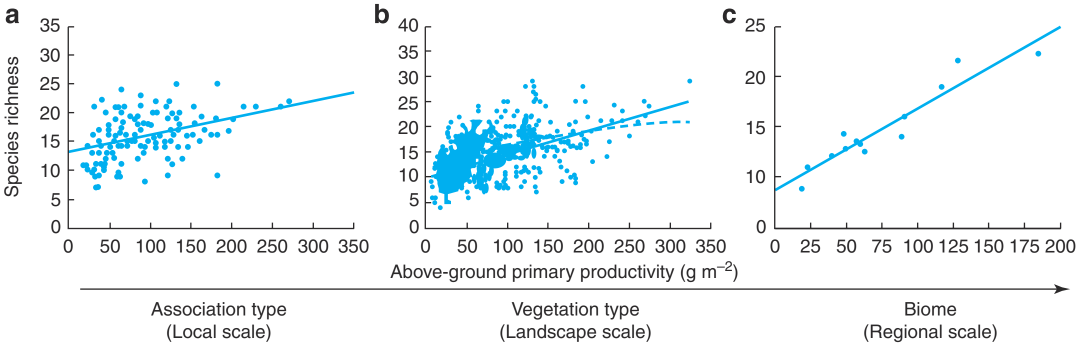


Fig. 20.16 Positive linear relationship between above-ground primary productivity and plant species richness. This example comes from the Inner Mongolia region of the Eurasian steppe and shows the productivity–diversity relationship across different spatial scales, **a** at the level of the plant community (*Stipa grandis* association), **b** at the level of the vegetation type (typical steppe), and **c** at the level of the entire biome (by association type). The fitted lines represent statistically significant linear (solid line) and quadratic (dashed line) relationships between productivity and species richness (Bai et al. 2007). Reproduced with permission from John Wiley & Sons

ents; disturbance regimes; herbivory) or modulators (e.g. temperature, pH) represent the independent variables that determine or explain the distribution of plant species and their diversity (Fig. 20.1). In the following section, we want to present in more detail one example of such biodiversity research, which is important to understand when we later discuss the functional importance of plant diversity (Sect. 20.4).

20.3.3 Productivity—Species Richness Relationships

There are striking biogeographical patterns of plant species diversity and several hypotheses exist to explain those patterns (Sect. 20.3.1). According to the energy–diversity hypothesis, plant diversity correlates well with measures of productivity along latitudinal gradients. Is this relationship ubiquitous and observable at various spatial scales?

Indeed, several studies have found relationships between some measures of productivity and plant species richness. It must be noted that productivity, defined as the net flux of carbon from the atmosphere into green plants per unit area and time (e.g. g m^{-2} $year^{-1}$) is difficult to measure directly in the field (Sects. 12.5 and 14.1). Instead, often indirect measures that correlate to varying degrees with the potential or actual productivity of a site are used, such as actual evapotranspiration (Sects. 10.1 and 16.1), rainfall, peak above-ground biomass or annual biomass production. For example, in the Mongolian steppe biome, Bai et al. (2007) observed a **positive linear relationship** between above-ground biomass and plant species richness at various spatial scales and grazing intensities (Fig. 20.16). However, other empirical studies reported unimodal or **hump-shaped relationships** (also referred to as humped-back model), with a peak of species richness at intermediate productivity levels and a decrease at very low or high productivity (Fig. 20.17). Such a decrease at high productivity—usually associated with high nutrient availability (Sect. 11.1)—was observed in natural situations or with modified levels of productivity, for example, through fertilisation. A famous example of reduction in plant species diversity by increasing nutrient levels and associated productivity comes from the Park Grass Experiment in Rothamsted, England, where grassland plots have been treated with different fertilisers since 1859. This decrease of diversity has been compared with the **paradox of enrichment** of predator–prey models (i.e. that increasing availability of resources may destabilise populations, which eventually can crash) (Rosenzweig 1971). Eutrophication, via high input of fertilisers or atmospheric deposition, therefore usually leads to severe declines in plant diversity (Sect. 23.5).

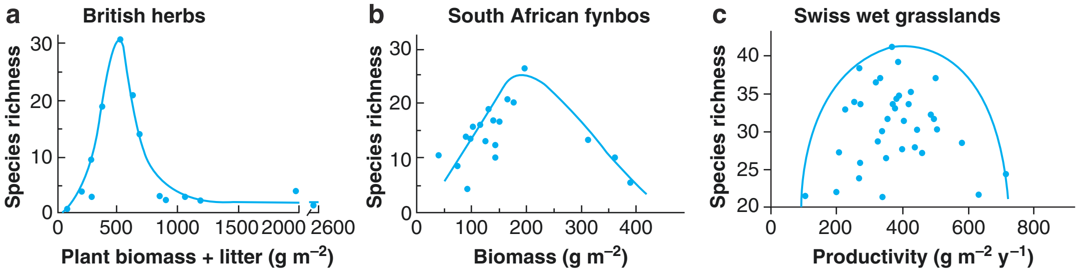
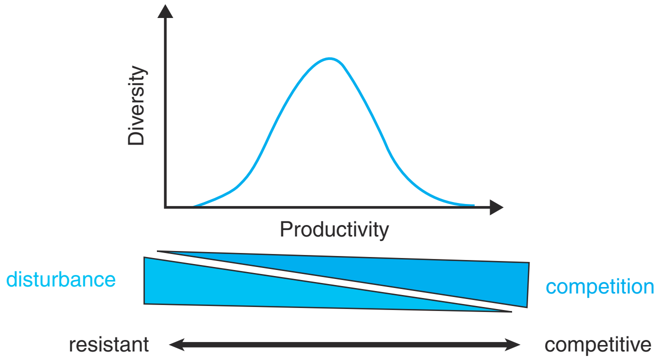


Fig. 20.17 Examples of hump-shaped relationship between productivity and plant species richness: **a** in British herb-dominated communities (Al-Mufti et al. 1977). Reproduced with permission from Blackwell Publishing Ltd.; **b** in South African Fynbos communities (Bond 1983); **c** in pre-alpine wet grasslands in Switzerland (Schmid 2002). Reproduced with permission from Elsevier Science Ltd.

Is the hump-shaped relationship ubiquitous? A meta-analysis by Mittelbach et al. (2001) showed that for vascular plants, hump-shaped relationships indeed dominate the observed patterns, especially at local scales or in studies that crossed community boundaries, that is, that included data from several different communities. A positive linear relationship was the second most observed pattern and has been reported mostly at continental to global scales. Interestingly, several studies showed that the area below the hump-shaped relationship is often filled with data points so that the hump-shaped line may be regarded as an upper envelope curve or border line, rather than a line of fitted average values (Fig. 20.17).

What could be the underlying mechanisms producing a hump-backed productivity–diversity relationship? Several different, not mutually exclusive, mechanisms have been proposed for the increasing and decreasing part of the hump and for the peak (Fig. 20.18). In short, the hump may be the result of varying levels of resource availability and heterogeneity and of disturbance (Grime 2001). Low productivity is a result of low resource availability, as well as of low resource heterogeneity and high disturbance. These conditions allow only for small population sizes of plant species, which are therefore prone to local extinction. Only few specialised species are adapted to such conditions. Examples are the first primary successional stages, for example, in glacier forefields or rock fans (Sect. 17.3). With increasing levels of resources and lowering levels of disturbance, more and more species are able to establish and to build up stable population sizes, and more biomass can be produced. Nutrient availability is still rather low at the increasing and plateau part of the hump, and plants mainly size-symmetrically compete for soil resources (i.e. species with larger root systems acquire more resources than those with smaller ones), which does not lead to competitive exclusion (Cahill 1999). At high levels of resource availability, coupled with low disturbance frequency and intensity, tall and highly competitive species produce closed canopies, diminishing light availability in the understorey. Competition for light is now more important than that for soil resources, and less competitive species are excluded, so diversity declines. This pre-emption of light is a good example of size-asymmetric competition for a resource of directional supply (Sect. 19.3).

This proposed mechanism explaining the decreasing part of the hump has been supported by a somehow simple, but clever, experiment. Hautier, Niklaus and Hector (2009) assembled grassland communities in a glasshouse, fertilised them and added light to the understorey (Fig. 20.19). As expected, fertilisation increased biomass production and canopy height and decreased light levels in the understorey. In consequence, this resulted in a loss of low-statured perennial grasses and herb species. Adding light to the understorey in the fertilised plots, however, reduced competition for light and maintained plant diversity. Thus, by combining fertilisation with light addition in a full factorial design, the researchers could show that competition for light did indeed result in a loss of plant species in the



Increasing part	Intermediate part	Decreasing part
• Low levels of resources allow only small population sizes with high risk of extinction	• Intermediate levels of resources allow good-sized populations	• High levels of resources lead to dominance of few competitive species
• Low resource heterogeneity	• Intermediate resource heterogeneity	• Low resource heterogeneity
• High disturbance rates	• Intermediate disturbance rates	• Low disturbance rates
• Very low resource competition	• Size-symmetric competition for soil resources	• Strong size-asymmetric competition for light
• Few species can tolerate these conditions	• Many species adapted to these conditions	• Few species are good competitors

Fig. 20.18 Conceptual model to explain the hump-shaped productivity–diversity relationship. The table summarises the main postulated mechanisms leading to the hump-shaped curve. The photos show some examples that are typical for the three parts of the hump. **a** *Linaria alpina*, a pioneer species colonising a heavily disturbed rock fan with minor amounts of mineral soil in the Swiss Alps. **b** Highly diverse, extensively managed subalpine meadow in the Swiss Alps, with intermediate levels of soil resource availability (low fertiliser input) and disturbance (cutting, grazing). **c** *Rumex alpinus* (foreground) dominates a patch in an alpine pasture, with high inputs of nutrients from resting livestock ("Lägerflur"). (Photos: M. Scherer-Lorenzen)

face of eutrophication and related increases in productivity. From an applied perspective, this experiment gives clear arguments to prevent or reduce eutrophication owing to a surplus of fertilisers or atmospheric deposition if biodiversity is to be protected or restored, especially in nutrient-limited, species-rich ecosystems (Fig. 20.18).

Despite the fact that the humped-shaped relationship between productivity and diversity has been documented often, controversy remains about the generality of this pattern, its dependence on spatial scale, the history of community assembly, measures of productivity or other methodological inconsistencies. For example, two large-scale, global studies that applied standardised sampling designs found either general support for the humped-shaped relationship in grassland communities (Fraser et al. 2015) or no significant relationship between peak aboveground live biomass and fine-scale plant species richness (Adler et al. 2011). The differences between both studies might be due to different statistical approaches or to the inclusion/exclusion of highly productive sites, which were found to be very low in species richness, thus strongly influencing the decreasing part of the hump in the Fraser et al. (2015) study. But despite these differences, both studies showed that the humped-back model has quite low explanatory power, even if the relationship as such remains significant. Rather, it seems that productivity and richness are both influenced by a multitude of factors and processes, such as nutrient supply rates, disturbance, habitat het-

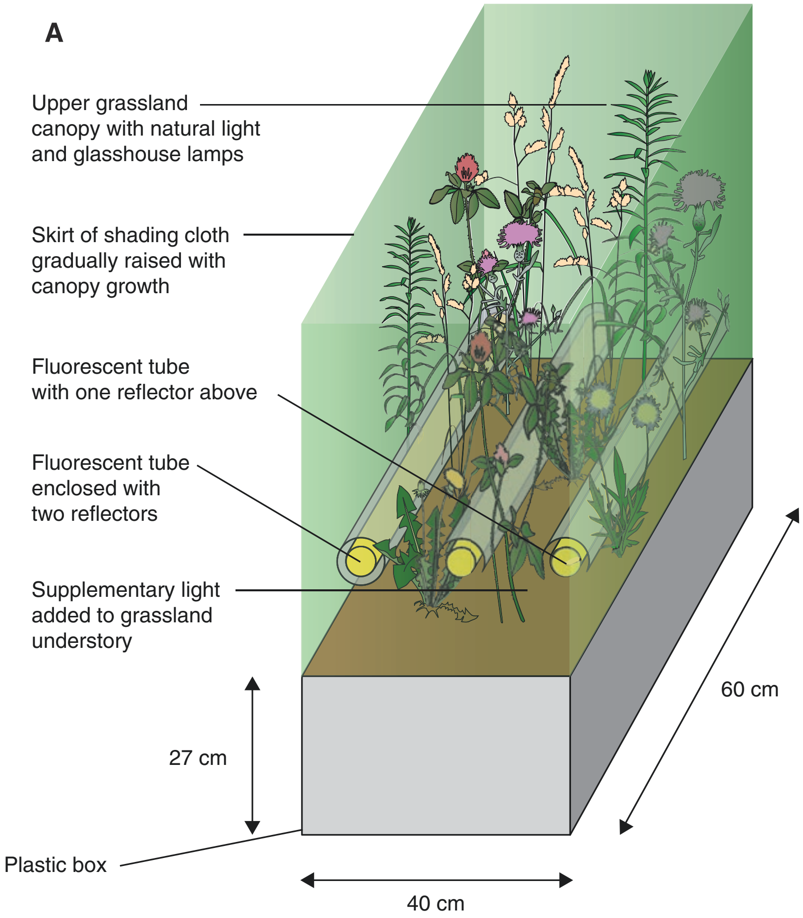


Fig. 20.19 Experimentally testing the decrease of species richness under high productivity levels. The experiment involved manipulation of soil nutrient levels and understorey light conditions in grassland model ecosystems. The four treatment combinations were "control" (unfertilised, closed lights), "fertilisation" (fertilised, closed lights), "light" (unfertilised, open lights) and "fertilisation + light" (fertilised, open lights). **A** Experimental set-up; for illustration purposes only, two open lights and one closed light are shown in the same experimental unit, but they were installed in different treatments. **B** Aboveground biomass production **a**, light availability in the understorey **b**, and change in plant species richness **c** in response to the experimental treatments. Points denote treatment means, and the intervals show least significant differences (treatments with non-overlapping intervals are significantly different at $p = 0.05$). PAR: photosynthetically active radiation (Hautier et al. 2009). Reproduced with permission from AAAS

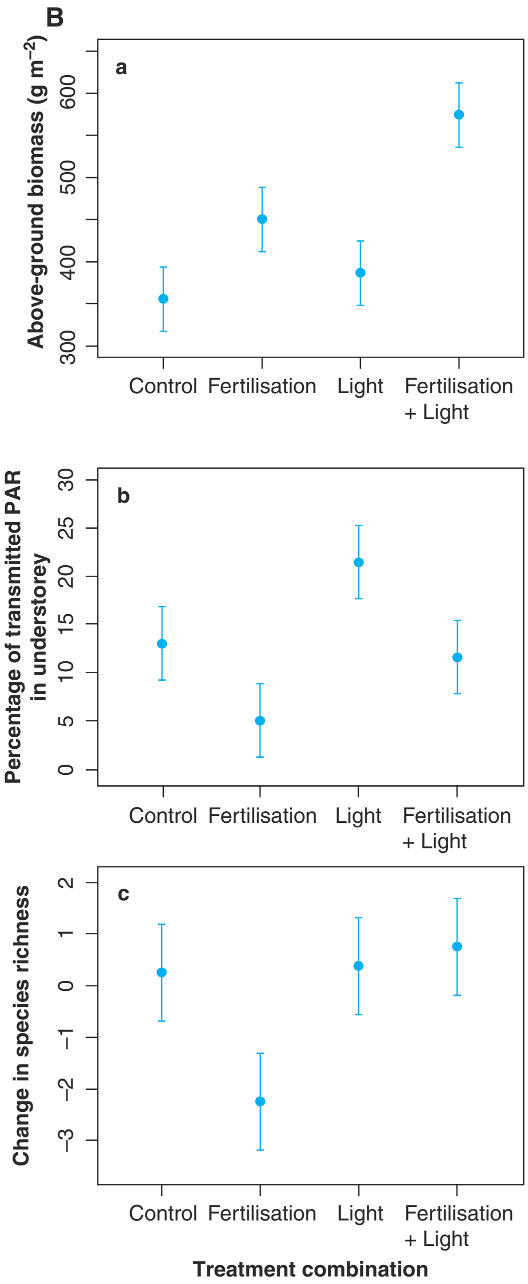


Fig. 20.19 (continued)

erogeneity, assembly history or management. Thus, instead of focusing too narrowly on bivariate patterns such as the hump-shaped curve, future investigations should look into multivariate mechanisms controlling plant diversity.

20.3.4 Biodiversity, Assembly Rules and Environmental Filters

The species composition of ecological communities is largely determined by environmental conditions, modulated by biotic interactions (Sects. 19.3 and 19.4) and stochastic effects, along with speciation and extinction events. Can these insights be used to predict community composition at a given location? Co-occurrence of the same species at different locations, but with similar environmental conditions, has been used in vegetation science to develop a hierarchical system of plant communities, similar to the Linnaean taxonomy of species. For example, in the system initiated by Josias Braun-Blanquet for Central Europe, vegetation is grouped according to floristic similarity into classes (e.g. European deciduous forests: Querco-Fagetea), orders (e.g. those growing on soils with good water availability: Fagetalia sylvaticae), alliances (e.g. beech and mixed beech forests: Fagion sylvaticae) and associations (e.g. those growing on poor, acidic soils: Luzulo-Fagetum). Working on North American successional trajectories, Frederick E. Clements developed the organismic concept of communities (“superorganism”), where co-occurring species are strongly linked together by interactions and a common evolutionary history (Clements 1916). This results in a deterministic development and similar final community composition at the end of successional series (monoclimax concept) (Sect. 17.3). Among other observations, such reiterating patterns of species composition have inspired ecologists to formulate **assembly rules**. The concept goes back to Jared Diamond, working on bird communities on islands, who formulated empirically derived rules of community composition (Diamond 1975). This concept initiated a long and lively debate among ecologists. In principle, assembly rules aim “to specify which traits (and therefore which subset of species) will occur in a particular environment. Because the problem primarily involves traits and environments, answers should be generaliz-

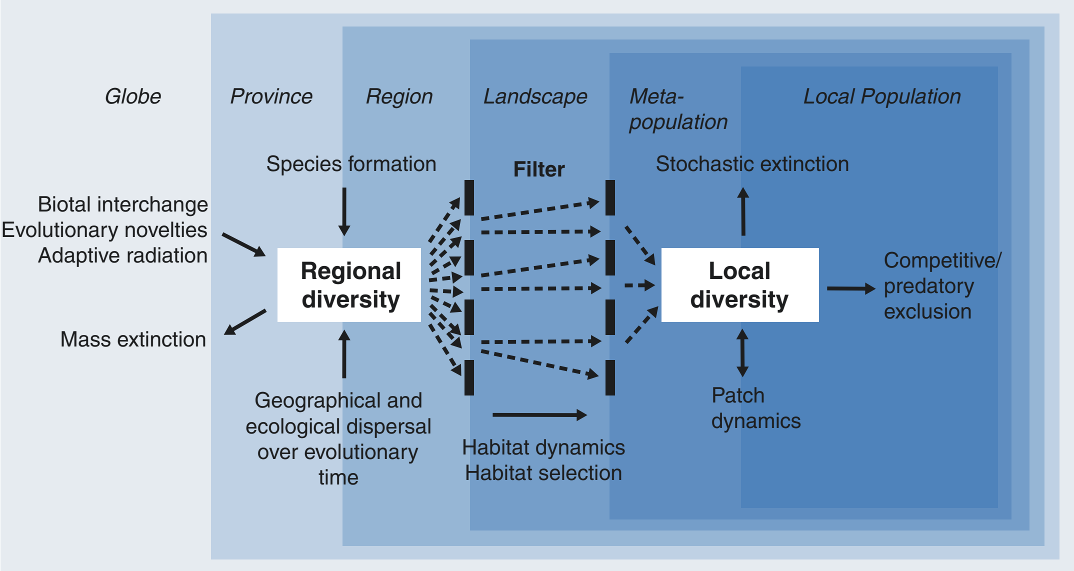


Fig. 20.20 Processes influencing species diversity. These processes range over different nested spatial and temporal scales. Environmental filters occur at several scales, but two are shown here for simplicity. (Ricklefs and Schluter 1993)

able to systems with very different taxonomic composition. In this context, the environment functions like a filter (or sieve) removing all species lacking specified combinations of traits. In this way, assembly rules are a community level analogue of natural selection" (Keddy 1992, p. 157). **Environmental filters** are recognised as one underlying cause of why not all species of the total species pool are actually found in a local community because of abiotic constraints, thus strongly determining the composition, structure and function of a community (Fig. 20.20). Those species that are actually absent from a community but part of the regional species pool comprise a so-called "**dark diversity**" (Pärtel et al. 2011). Several factors can act as filters that lead to environmental sorting of species (Gravel 2013; Ricklefs and Schluter 1993):

- Distance of sink (local community) from source (regional species pool) and the size of the sink ecosystem. These aspects have also been integrated into the equilibrium theory of island biogeography (Sect. 18.4)
- The structure and characteristics of the habitat (e.g. disturbance regime, nutrient status, water availability, resource heterogeneity) (Sect. 20.3)

In addition, diversity and community composition are further influenced by additional factors and processes that act at different spatial and temporal scales (Fig. 20.20):

- Species morphology and their adaptations, affecting habitat selection and survival (Sect. 2.1)
- Biotic interactions, such as competition, predation, facilitation, mutualism (Sects. 19.3 and 19.4)
- Population dynamics, including dispersal and biotal interchange, that is, the flow of species between adjacent regions (Sect. 18.2)
- Evolutionary processes, including selection, genetic drift and speciation (Sect. 17.2)
- Mass and stochastic extinctions

Environmental filters thus determine the trait spectrum of communities, and certain traits determine whether a species may pass through

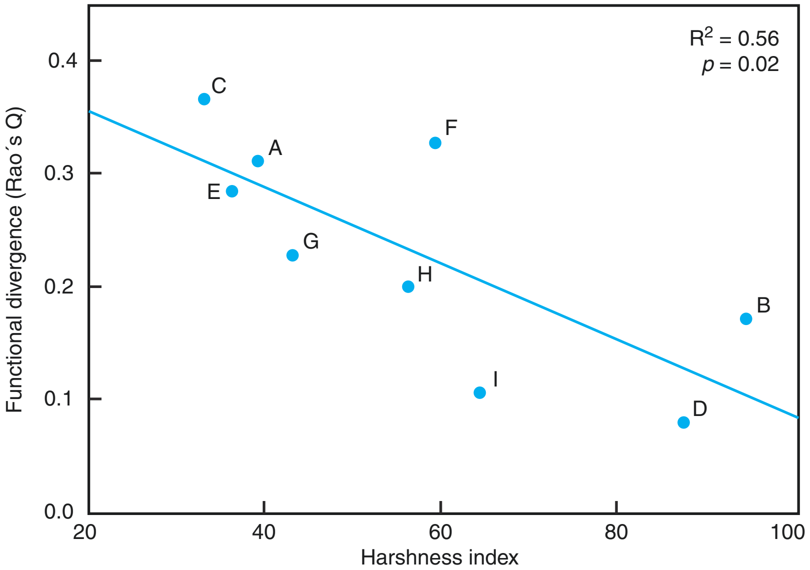


Fig. 20.21 Community assembly through environmental filtering. Plant trait convergence with increasing harshness results in decreasing functional diversity in different alpine plant communities in the Swiss Alps, at Albula Pass (*A*: subalpine rock vegetation, *B*: alpine-subnival rock vegetation, *C*: subalpine scree vegetation, *D*: alpine-subnival scree vegetation, *E*: *Carex firma* grassland, *F*: *Elyna myosuroides* grassland, *G*: snowbeds, *H*: fountain vegetation, *I*: fen). The harshness index was calculated based on on-site measurements of microclimate (wind speed, air and soil temperatures) and soil variables (soil vs. stone content, soil moisture), as well as altitude (to represent other factors that correlate with altitude). Functional divergence (Sect. 20.2.3) was calculated with 16 traits (4 growth-form-related traits, 9 leaf traits, and 3 shoot traits). (Schmid 2007)

the filter or not. Communities with a rather similar trait composition (**trait convergence** or **trait similarity**) are indicative of the presence of environmental filters because the coexisting species share ecological preferences for a specific set of environmental conditions. For example, soil fertility strongly impacts traits associated with basic physiological processes related to growth and biomass production. This "productivity filter" therefore leads to trait syndromes that reflect transitions from unproductive to productive environments (Fig. 20.23), such as those present along the leaf economics spectrum (Sect. 20.2.3). This view, also known as "weaker competitor hypothesis" (Grime 2006), states that trait convergence is the result of the competitive exclusion of species with traits associated with low competitive ability. Another example of trait convergence can be observed along gradients of environmental harshness: Communities at very unfavourable locations in terms of microclimate or soil fertility are often composed of few species that can cope with these conditions. In consequence, functional diversity decreases with increasing harshness (Fig. 20.21).

In contrast, high **trait divergence** (or **trait dissimilarity**) indicates that other ecological mechanisms are present that limit trait similarity, such as biotic filters imposed by competition. The concepts of limiting similarity and competitive exclusion and the related resource-ratio hypothesis (Sects. 17.3 and 19.3) state that two species that compete for the same resources—presumably due to the same trait combination—cannot coexist. That is, locally coexisting species should be functionally dissimilar to promote niche differentiation, which is one major mechanism allowing coexistence based on classical niche theory (Sect. 19.3). Thus, other factors may still allow for coexistence, such as local disturbances that diminish the competitive dominance of few species and promote regenerative mechanisms to exploit recruitment opportunities.

The study of factors driving plant community composition, their diversity and the patterns and mechanisms of trait divergence and convergence is a lively field of research. It shows that the driving factors, such as niche-related factors, environmental conditions and their heterogeneity, change along spatial scales: at small scales, niche- and soil-related variables more strongly determine community composition, while heterogeneity and disturbance-associated parameters as well as climatic factors prevail at larger scales. In general, trait convergence or divergence depends on a variety of factors, including the selection of traits or trait combinations, the spatial scale at which environmental filtering takes place, productivity or species richness.

20.4 Biodiversity and Ecosystem Functioning

Does biodiversity matter for the functioning of ecosystems? In other words, does it make any difference to the processes within an ecosystem if there are many or only a few species? These are central questions that arise when looking at ecosystems that differ significantly in their biological richness but that have a similar basic set of energy, matter, and information fluxes (Sect. 13.2). For example, both tropical forests, with their overwhelming richness in their flora and fauna, and extremely species-poor systems, such as lichen communities in Antarctica (Box 20.3), fix carbon through photosynthesis of the plant compartment, and organic matter is decomposed by microorganisms into mineral components, which are partly taken up by the primary producers again. Although admittedly simple, this example shows that processes that are central to the functioning of ecosystems might be maintained by many or very few organisms, which prompts the question whether there is any relationship between biodiversity and ecosystem functioning. Related to our conceptual framework (Fig. 20.1), we are now dealing with the links between biodiversity and ecosystem properties and processes. The field of ecology related to that question has been termed **functional biodiversity research**, also sometimes called biodiversity-ecosystem function (BEF) research, to contrast it with classical approaches that study the factors and processes that determine species coexistence and dominance and, thus, the diversity of ecosystems (Sect. 20.3). One motivation behind this work is the search for fundamental ecological mechanisms that determine the properties and processes of ecosystems mediated by interactions among a diverse array of organisms. However, the answers to these questions are not only of pure academic interest but are relevant for human well-being: the accelerating loss of biodiversity (Sect. 23.5) may have profound effects on the way ecosystems operate ("ecosystem functioning"; Box 20.4 for definitions of relevant terms) and on the delivery of ecosystem services, that is, the benefits humans derive from ecosystems (Sect. 21.1).

Box 20.3: How Many Species Are Required for a Functional Ecosystem?

From what is known about natural ecosystems, the answer is six. For millions of years, completely self-sustaining and stable ecosystems consisting of two algae, one lichen fungus, one parasitic fungus, one cyanobacterium and one non-photosynthetically active bacterium have existed in the Antarctic dry deserts (Friedmann 1982). The lichen and algal zones are formed by filamentous fungi and unicellular green algae (Chlorophyceae). Carbon is assimilated by the green algae and the cyanobacteria. Water is taken up after snow melt or as water vapour; nitrogen enters the system either as atmospheric deposition of ammonium and nitrate or via biological N_2-fixation by the cyanobacterium. Other inorganic nutrients are mobilised from rock, for example, by solubilisation of iron. Organic matter is decomposed and mineralised by the colourless, non-photosynthetic bacteria. Fungi can be regarded as consumers (Fig. 20.22).

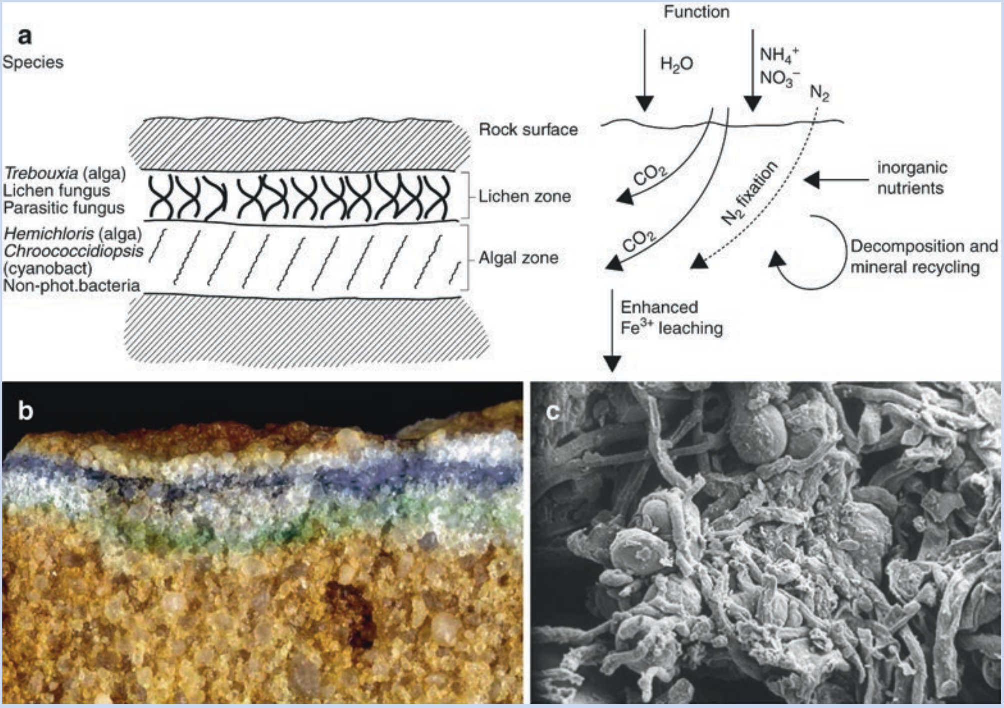


Fig. 20.22 Crypto-endolithic ecosystems in arid valleys in Antarctica. **a** Schematic representation of this ecosystem and the important ecosystem functions and matter fluxes (Woodward 1993). **b** Photograph of fractured sandstone, showing black (masses of fungal/mycobiont hyphae with enclosed groups of algal/phycobiont cells), white (loose web of mycobiont filaments) and green (algal cells) zones of this ecosystem. Each zone is only about 1–4 mm. Southern Victoria Land in Antarctica, Linnaeus Terrace, Asgard Range. **c** Electron microscope image of phycobiont cells and mycobiont filaments growing in airspaces of rock, ×1000. (Photos with courtesy by E. I. Friedmann)

Box 20.4: Terms and Definitions Used in Functional Biodiversity Research

The terms ecosystem (or ecological) processes and properties, functions or functioning, and services are central to the concepts of functional biodiversity research. They are used in the following sense (compiled from Naeem 2002; Hooper et al. 2005; Millennium Ecosystem Assessment 2005; de Groot et al. 2010; Díaz and Cabido 2001; Hillebrand and Matthiessen 2009; Stachowicz 2001); Chap. 13.

Ecosystem processes: the physical, chemical and biological actions or events that link organisms and their environment, for example, primary production, water dynamics, nutrient cycling.

Ecosystem properties: the size of compartments; for example, pools of material such as standing biomass or soil organic matter.

Ecosystem functions: the capacity of ecosystems to provide services—directly and indirectly—underpinned by biophysical structures and processes. They can be seen as intermediates between processes and services. Often used in the same sense as ecosystem processes.

Ecosystem functioning: flow of energy and materials through the arrangement of biotic and abiotic components of an ecosystem, that is, including many ecosystem processes.

Ecosystem services: benefits people obtain from ecosystems, including provisioning services (e.g. food, fibre, biological resources), regulating services (e.g. erosion control, climate regulation, pollination) and cultural services (e.g. spiritual and religious, recreational, educational). In addition, supporting services enable the production of other services (e.g. soil formation, primary production, nutrient cycling). Sect. 21.1.

20.4.1 Species Identity and Dominance Effects on Ecosystem Processes

Species differ in their physical structure and biomass produced, as well as in the amounts and combinations of resources they use and in their chemical composition. Hence, different species can have largely divergent effects on ecosystem properties and processes (Sect. 19.2). Therefore, biodiversity effects on ecosystem functioning cannot be understood without proper acknowledgement of the identity of species and their specific physiological and morphological characteristics, that is, their functional effect traits (Sect. 20.2.3). Identity effects are due to the presence/absence of particular species within mixtures and are distinct from species composition effects, which distinguish the effects of different species combinations. Examples of species identity effects are numerous. Tree species, for instance, differ widely in their effects on soil development and nutrient supply. In a replicated experiment with 14 gymnosperm and angiosperm tree species, Reich et al. (2005) observed that 30 years after the establishment of single-species plots, differences in litter calcium concentrations resulted in profound changes in soil chemistry and fertility on initially the same soils. In addition, earthworm abundance and diversity were higher in those stands where tree species rich in calcium were grown.

Interestingly, species with similar effects on ecosystem processes often coexist in plant communities, and they share similar life histories and morphological and physiological traits. This phenomenon of trait convergence (Sect. 20.3.4) can often be observed by comparing plant communities of fertile/productive and infertile/unproductive sites. On fertile sites, resource dynamics usually follow the acquisitive path of plant strategy (“fast and leaky”), with plants having high nutrient concentrations in leaves, high photosynthetic rates, high relative growth rates, and palatable and short-lived leaves with low investment in herbivore defence and that decompose fast. In contrast, unproductive sites are dominated by plants with the opposite trait characteristics and whose resource dynamics are rather retentive, that is, “slow and tight” (whole-plant fast–slow or acquisition–conservatism spectrum of plant economics, Sect. 20.2.3). Associated with such opposing trait syndromes of plants are profound differences in soil food webs and processes that are determined by the plant traits and related differences in the quality and quantity of organic matter that enters the soil (Fig. 20.23). In fertile, productive systems with acquisitive resource dynamics, litter decomposition is often mainly driven by bacteria, earthworms occur at high density, causing high bioturbation of the soil, and microarthropod density is rather low (Sect. 16.2). As a consequence, litter decay and mineralisation rates are high, leading to high nutrient supply rates and low accumulation of necromass (i.e. dead organic matter) on the forest floor (“mull-type” humus). A lot of labile decomposition products enter the soil and are processed by microbes, resulting in high long-term stabilisation and accumulation of soil organic matter and C sequestration, especially in soils with high clay content. In infertile, unproductive systems, soil energy is mainly channelled through fungi, and soil fauna composition differs strongly from that on fertile sites. Litter decay and mineralisation are slow with low nutrient supply rates, resulting in high accumulation of necromass on the forest floor (“raw

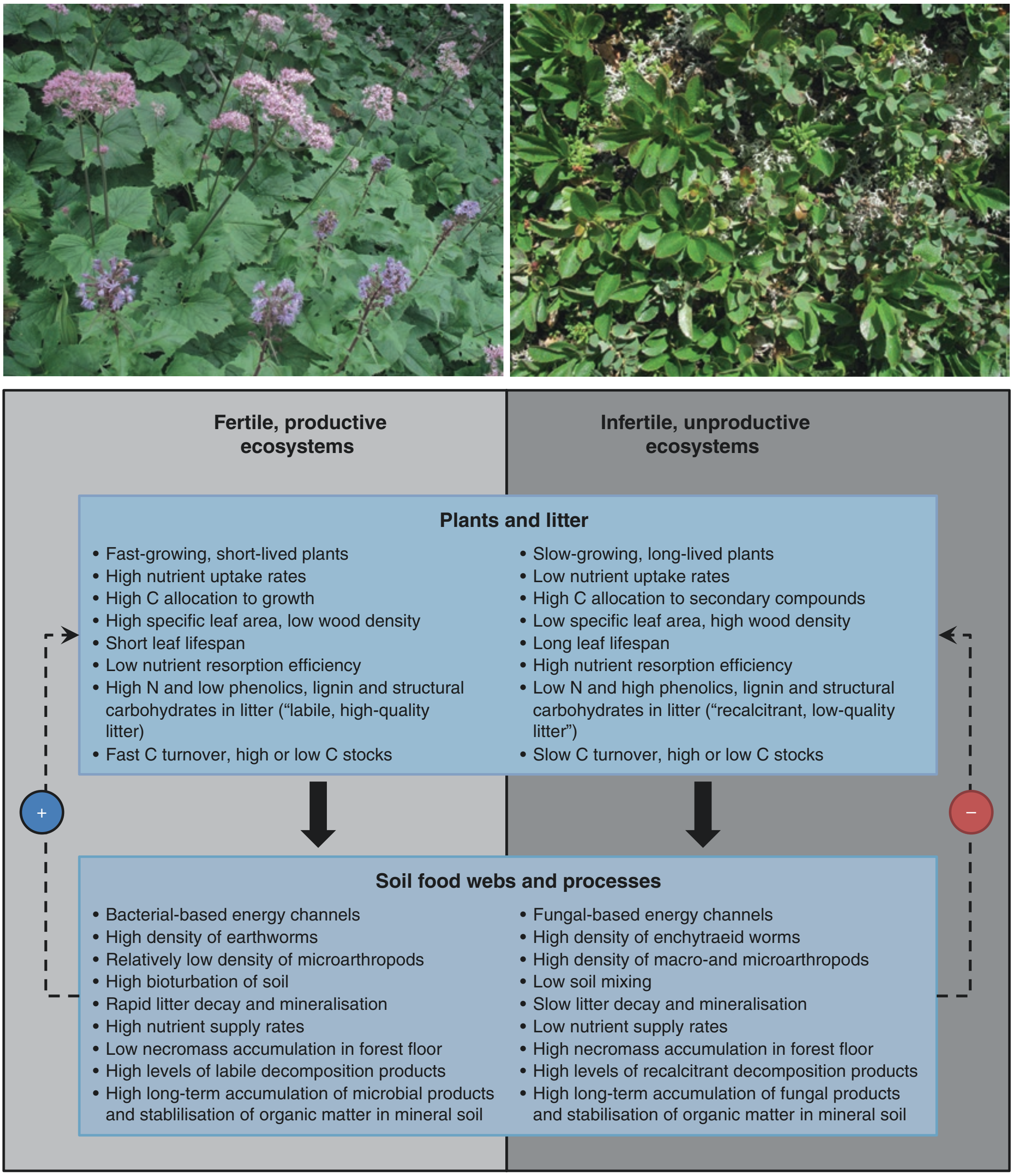


Fig. 20.23 Effects of morphological, physiological and life history traits on soil food webs and ecosystem processes. Positive feedbacks between the below-ground and above-ground systems in fertile ecosystems and negative ones in infertile systems (dashed arrows) result in strongly differing resource dynamics and species compositions (Modified from Díaz et al. 2009; Wardle et al. 2004; Cotrufo et al. 2013). The photographs show typical examples from productive (left) and unproductive (right) plant communities in the subalpine zone of the inner Alps of Switzerland (Simplon Pass). Both communities occur at the same altitude (2000 m a.s.l.) but strongly differ in water and nutrient supplies. The productive community dominated by large and fast-growing herbaceous species (*Cicerbita alpina*, bottom, and *Adenostyles alliariae*, top) obtains water surplus and high nutrient inputs from adjacent slopes. The unproductive community is situated on wind-exposed hilltops with flat soils and is composed of tiny dwarf shrubs from the Ericaceae family with small, often evergreen leaves (here mainly *Arctostaphylus alpinus*). Reproduced with permission from Oxford University Press and AAAS. (Photos: M. Scherer-Lorenzen)

humus”). Fewer labile microbial products but more recalcitrant fungal residues will remain in the mineral soil, which also can result in the stabilisation of organic matter and high long-term accumulation of soil organic matter. Depending on the location, some of the organismic groups mentioned earlier may be absent, such as earthworms in northern North America, and their introduction will thus result in alterations of ecosystem processes, such as litter decomposition. A change of the dominance structure of a plant community, for example, due to management or changing climate, will therefore have cascading effects on soil fauna and ecosystem processes and will feed back on the plant community composition owing to the linkages between the above-ground and below-ground systems.

What is the relevance of such species identity effects for the biodiversity–ecosystem functioning relationship? Changes in land use and anthropogenic alterations of climate, nutrient cycles or consumer presence alter not only the number of species but also their relative abundance and, thus, dominance or evenness (Box 20.1). The English plant ecologist Phil Grime included the knowledge of strong identity effects in his formulation of the “**mass ratio hypothesis**” (Grime 1998), which states that resource dynamics and other aggregate processes in communities and ecosystems should be strongly controlled by the structural and functional traits of the most abundant, that is, most dominant, primary producer (Sect. 20.2.3). In many cases, ecosystems are indeed dominated by one or a few species, with other species having rather low abundances (“subordinate” species) or occurring infrequently and in very low abundances (“transient” species). Hence, he argued that dominant species should have the highest impact on ecological processes such as biomass production, carbon sequestration or nutrient cycling, while subordinate species will impact these processes only to a certain degree, and transient species will have only very minor effects. Thus, the effect of dominance comprises both an effect of the degree of dominance (i.e. abundance) and the identity (i.e. presence and value of functional traits) of the dominant species. According to this hypothesis, diversity should have rather additive effects weighted by the biomass of the species present, with mixtures intermediate in performance between the corresponding monocultures. For example, Rothe and Binkley (2001) reviewed the empirical evidence on the nutritional interactions of tree species grown in monoculture and in two-species mixtures, focusing on foliar nutrition, soil nutrient supply, rates of nutrient input and patterns of root distribution. They showed that additive effects were most common, with few antagonistic and synergistic effects. Antagonistic effects are found if mixture performance is lower than expected based on monoculture performance, indicating interference competition. Correspondingly, synergistic effects could arise from positive interactions among species, such as niche partitioning and resource-use complementarity, or facilitation, for example, by nitrogen fixation of some species that increase the overall N availability for the entire plant community (Sect. 20.4.9 and Box 20.5).

20.4.2 Biodiversity Effects on Biomass Production

If single species have clear effects on ecosystems, then the next obvious question is whether adding different species to a system will result in changes in ecosystem processes and properties. In addition, it would be interesting to know whether such changes were purely additive or whether communities with more species showed some emergent properties, which can only be explained by some antagonistic or synergist interactions among species (Sect. 20.4.9). The number of studies testing the hypothesis that biodiversity affects ecosystem functioning has increased enormously in the last 20 years, so we will only be able to present a few classical and some key guiding examples. The first experiments were designed to test early hypotheses on how a change of plant species richness may affect ecosystem processes, while later experiments focused more on disentangling the underlying mechanisms of diversity effects on

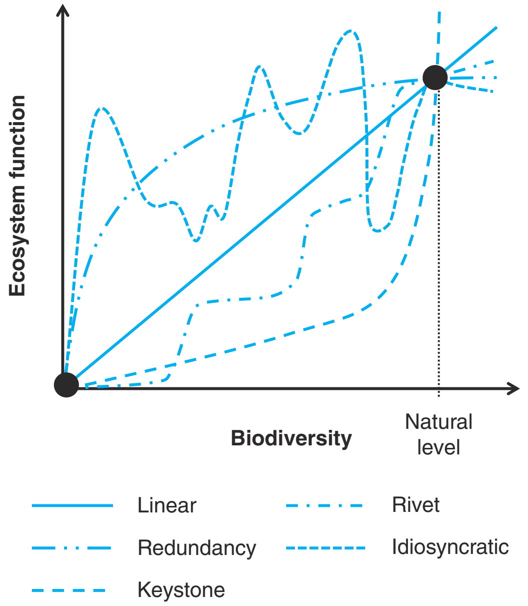


Fig. 20.24 Early hypotheses on the relationship between biodiversity and ecosystem functions. "Natural level" indicates the maximum level of diversity typical for the ecosystem under study; positions to the left of this point refer to biodiversity loss. The terminology of these early hypotheses is rarely used in current publications, but it has been important for the discussions and improvements of biodiversity–ecosystem functioning research

ecosystems. These early hypotheses (Fig. 20.24) predicted that diversity shows (1) no effect ("null hypothesis"), (2) a linear relationship between diversity and ecosystem processes, that is, loss of species causes proportional declines in ecosystem functions, or (3) an asymptotic relationship where species at higher levels of diversity might be redundant in their function ("**redundancy hypothesis**"). With further impoverishment of plant diversity, ecosystem functioning rapidly declines because functions cannot be maintained owing to incomplete niche occupation; very much like the loss of too many rivets leads to the failure of a machine ("**rivet hypothesis**"). Species could also be primarily singular (4), and their loss or addition would have disproportionate impacts on ecosystem functioning. Cases of singular species with extreme impacts are "**keystone species**" or "**ecosystem engineers**", with the former being species with disproportionate effects on ecosystems relative to their abundance (e.g. predators controlling dominance of other species) and the latter being species that modify the resource availability for other members of the community through modification of the habitat (e.g. dam-building beavers) (Lawton 1994). Finally, (5) the effects of species losses (or gains) might be totally dependent on the environmental context and are thus "**idiosyncratic**". Interestingly, the early graphical representation of these hypotheses never showed cases, where ecosystem functions declined with increasing diversity, that is, where monocultures had higher function levels (e.g. biomass production) than mixtures. It is now clear that such negative relationships can of course also occur, and some examples are given throughout the following sections.

This overview is organised according to the scientific approaches that were adopted in the respective studies, that is, observational and experimental studies (Sects. 14.1 and 14.2), as well as modelling exercises. It focuses on plant species richness as the measure of biodiversity and on biomass production as an important ecological process. Effects on other ecosystem functions are presented in Sect. 20.4.3.

20.4.2.1 Observational Studies

Observational studies in natural plant communities to quantify the effects of plant diversity on ecosystem functioning can be divided into **comparative studies** and **monitoring** or **sample surveys**. These approaches are described in detail in Sect. 14.1.

Here, we illustrate the use of such observational approaches with examples from forests. For instance, Baruffol et al. (2013) found in a comparative study that stand basal area (which is a measure of the area occupied by trees) and its increment over the course of 2 years (which is a proxy for stand growth) increased with the number of canopy tree species in different successional tree communities in subtropical China, even when accounting for the partial confounding of diversity and age (Fig. 20.25a). A detailed analysis of the underlying mechanisms revealed that, besides direct influences of tree diversity (which was quantified by tree species richness, functional and phylogenetic diversity), effects were driven by a combination of increased indi-

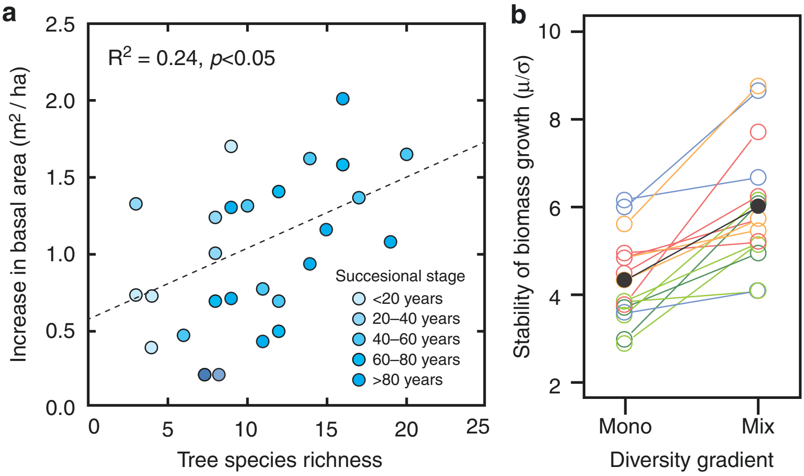


Fig. 20.25 Relationship between tree species richness and growth, and stability of growth, quantified in comparative studies. **a** Increase in basal area from 2008 to 2010 in relation to tree species richness of canopy trees and successional age in subtropical forests of China. Stand basal area is the total sum of the cross-sectional area of tree stems per hectare (Baruffol et al. 2013). **b** Stability of biomass growth from 1992 to 2011, quantified by measuring tree ring increments, in pure (Mono) and mixed (Mix) forest stands in Europe. Each open circle represents an individual species, while the filled circle represents the average stability across all species and regions. Red: Mediterranean-mixed forests in Spain; orange: thermophilous deciduous forests in Italy; dark green: beech forests in Germany; light green: mountainous beech forests in Romania; light blue: hemiboreal, mixed coniferous–deciduous forests in Poland; dark blue: boreal forests in Finland (Jucker et al. 2014). Reproduced with permission from John Wiley & Sons

vidual size of large canopy trees and increased density of smaller understorey trees at higher diversity.

Especially under a more applied aspect of timber production, a related question is whether tree diversity could also influence the stability of growth (Sect. 20.4.8). Also adopting a comparative approach, it has been shown that wood production can be more stable through time in mixed than in pure stands of very different forest types in Europe, ranging from boreal to Mediterranean forests (Fig. 20.25b). If growing in mixture, the different tree species reacted more differently to variable climatic conditions throughout the past 20 years of growth (asynchrony) and showed less temporal variation in growth through time, which resulted in overall higher stability with increasing tree species richness (Jucker et al. 2014).

National forest inventories and other permanent forest monitoring networks offer extremely data-rich and valuable tools to analyse large-scale correlations between tree species richness and ecosystem processes. Since forest inventories mainly follow silvicultural aims, some measure of tree growth prevails in those studies. A recent review showed that in nine out of ten studies, a positive association between tree species richness and biomass or wood production has been found (such as that shown in Fig. 20.26a), irrespective of forest type and biome (Scherer-Lorenzen 2014). Thus, mixtures of multiple species usually produce more biomass than the corresponding monocultures (Fig. 20.26b). However, once the confounding effects of environmental variables are accounted for, the positive diversity–productivity correlation gets weaker, and the variability of wood production explained by diversity is usually lower than that of abiotic variables, such as climate. Nevertheless, these results suggest that mixing tree species might be a silvicultural option to enhance wood production and its stability over time.

These examples show that trees growing together with many other different species are less negatively affected by interspecific competition than by intraspecific competition, presumably because of niche differentiation and resource-use complementarity, or facilitation

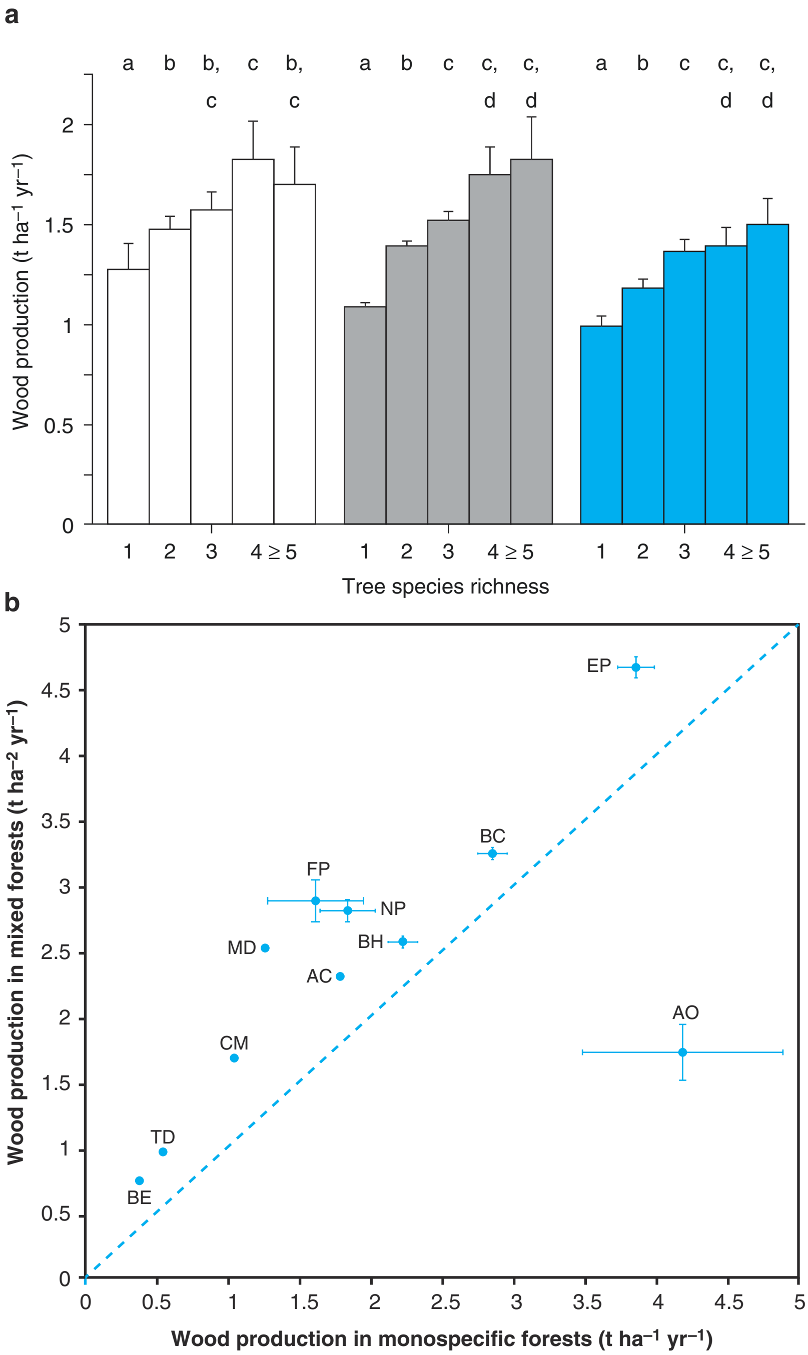


Fig. 20.26 Associations between tree species richness and biomass production form monitoring and sample surveys. **a** Forest Inventory data set from Mediterranean forests in Catalonia, Spain, with wood production (mean + SE) plotted against number of tree species per plot in deciduous (white bars), coniferous (grey) and sclerophyllous (blue) forests; total number of plots: $n = 5069$ (Vilà et al. 2007). Reproduced with permission from John Wiley & Sons. **b** Forest Inventory data sets from several countries, showing tree wood production (mean ± SE) in pairs of monospecific and mixed forests for different European forest types. The dashed line represents the line of unity, that is, values above this line indicate higher wood production in mixed than in pure stands, for each forest type. *BE* broadleaved evergreen ($n = 10{,}399$), *TD* thermophilous deciduous ($n = 1{,}580$), *CM* coniferous Mediterranean ($n = 13{,}921$), *MD* mesophytic deciduous ($n = 6{,}548$), *FP* floodplain ($n = 205$), *AC* alpine coniferous ($n = 12{,}719$), *BH*: boreal-hemiboreal ($n = 3{,}019$), *NP* non-riverine pioneer ($n = 754$), *BC* beech ($n = 2{,}389$), *AO* acidophilous oak ($n = 119$), *EP* exotic plantations ($n = 3{,}612$). After Vilà et al. (2013)

among species, and can thus have larger growth. Such highly favourable conditions for growth in mixture may also increase resistance and resilience to perturbations or environmental fluctuations, so that trees may be able to remain productive under less optimal conditions. We will come back to these mechanisms of positive diversity effects in Sect. 20.4.9. However, there are also examples from other comparative studies that do not support these positive tree diversity effects on growth and stability and that rather suggest increased competition in mixtures than in monocultures. These contrasting views may depend on the forest type and its management; for example, silvicultural thinning to reach an optimised tree density for timber may mask any potential diversity effects on growth. Opposite patterns of the diversity–productivity relationship found in natural ecosystems may also be due to different environmental contexts, which is discussed in detail in Sect. 20.4.7. In addition, processes that favour species similarity through strong environmental filtering (e.g. harsh climatic conditions, enabling only few species with similar adaptations to persist) (Sect. 20.3.4) should result in rather low or even absent effects of plant species on ecosystem functions because diversity effects are essentially based on differences among species in functional effect traits (Sect. 20.2.3 and Fig. 20.1). However, processes that limit similarity (e.g. competition for the same resources, effects of shared pathogens) and that enable species coexistence may result in strong diversity effects, which should thus be rather frequent in natural ecosystems.

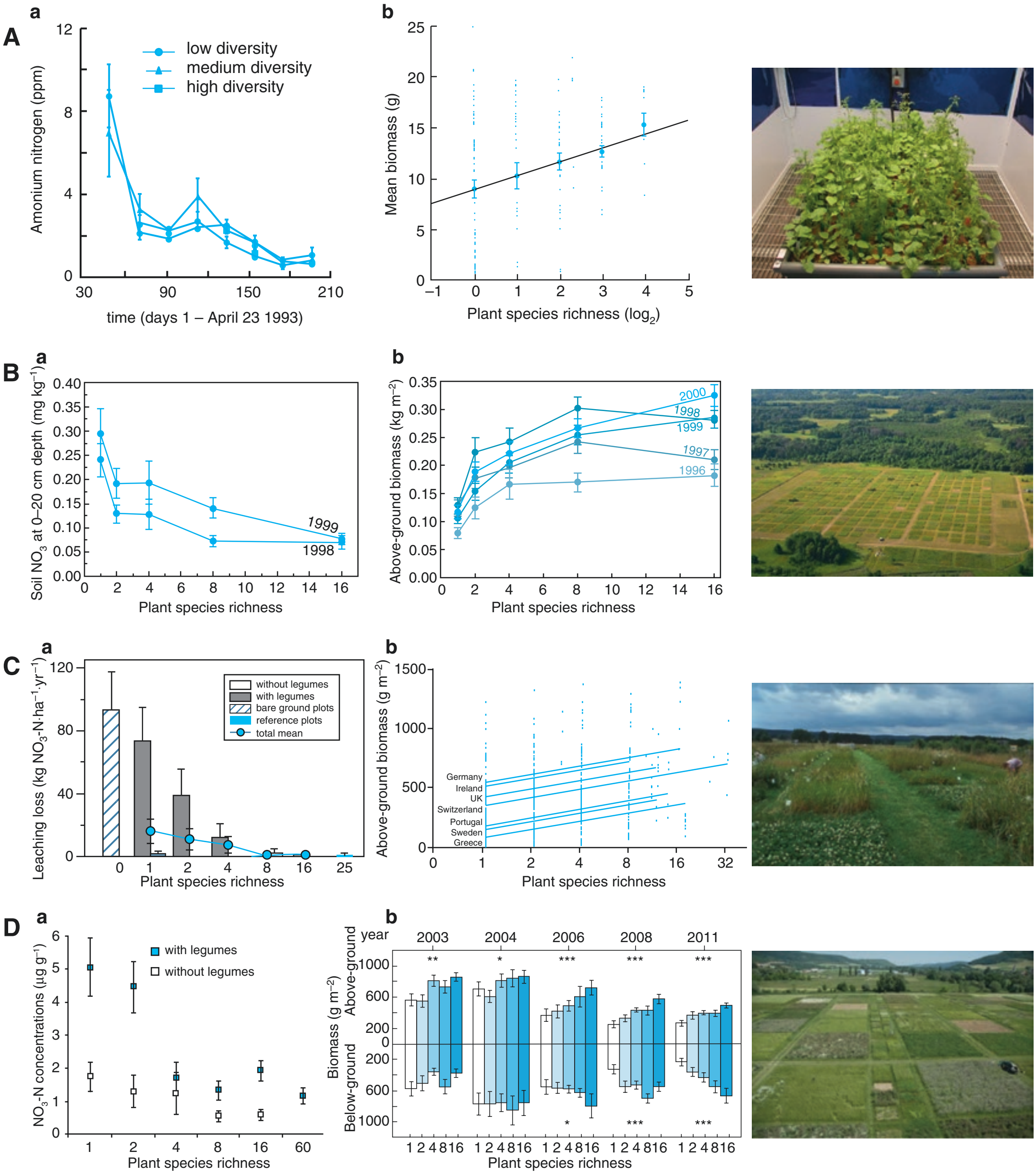
Despite these opposing views and the inherent limitations concerning causality of observed associations between diversity and function in observational studies (because both diversity and functions can be influenced by the same environmental factor) (Sect. 14.2), there is now increasing evidence that suggests that plant species richness is an important predictor of ecosystem functioning in natural plant communities, at least in forests. The scatter in the shown data sets nicely demonstrates that additional abiotic and biotic factors influence ecosystem functions, such as climatic or soil variables, and management. In addition, identity effects are usually very prominent in observational studies, that is, ecosystem functions are often strongly determined by the dominant species (Sect. 20.4.1). Thus, ecosystem ecology and the search for biodiversity effects on ecological functions cannot be tackled as univariate problems, but a multitude of abiotic and biotic factors need to be taken into account that interact in complex ways. Another way to reduce the effects of confounding factors is the use of experimental approaches.

20.4.2.2 Experimental Studies

Experimental studies in biodiversity–ecosystem functioning research aim to decouple biodiversity from environmental conditions in order to identify causality and mechanisms of diversity effects. Thus, the level of plant diversity is manipulated experimentally by researchers. These experiments can be done in natural communities (**removal experiments**) or with artificially created communities (**synthetic assemblage experiments** or simply **biodiversity experiments**). These approaches are described in detail in Sect. 14.2.

Of the two experimental approaches to studying biodiversity–functioning relations, removal experiments are highly underrepresented, although they can be useful to understand the ecosystem consequences of local, non-random extinctions, changes in natural abundance and complex interspecific interactions. For example, Wardle and Zackrisson (2005) removed plant species and entire plant functional groups from the understorey vegetation of 30 forested islands in northern Sweden. These islands differed in size, leading to a successional gradient from early successional, highly productive to late successional, less productive systems. Losses of functional groups and species decreased key ecosystem processes such as biomass production, litter decomposition and soil respiration. However, removals had strong effects on some islands but not on others, depending on island size and thus successional status and resource dynamics. This example therefore nicely highlights the importance of the specific context of study systems and shows that results cannot necessarily be generalised to other systems until properly tested.

The current thriving of functional biodiversity research and the wealth of information on the pattern of biodiversity effects as well as on their underlying mechanisms is clearly based on the use of biodiversity experiments with “synthetic assemblages”. Since environmental conditions are kept as constant as possible, disentangling diversity effects from those of the environment on ecosystem processes is possible. Several hundred such experiments have been conducted since the 1990s, and several reviews and meta-analyses have synthesised their outcomes (e.g. Cardinale et al. 2011, 2012; Tilman et al. 2014). Figure 20.27 shows results on biomass production and soil nutrient concentrations from selected grassland experiments, which can now be regarded as classical, since they spurred this field of research and also stimulated much debate about the interpretation and relevance of functional biodiversity research.



- Naeem et al. (1994, 1995) designed artificial ecosystems ("Ecotrons") with varying species richness levels of plants, herbivores and decomposers in climate chambers. The medium- and low-diversity communities were a subset of high-diversity communities, resembling functionally depauperate descendants. Only identical species mixtures were replicated at each level of diversity. Thus, the effect of the presence of highly productive species only occurring at higher diversity levels could not be separated from richness effects. Towards the end of the experiment, high-diversity communities had lower soil nutrient concentrations and were consistently more productive than medium- and low-diversity treatments
- Tilman and colleagues conducted several large-scale experiments at Cedar Creek, Minnesota, that showed that soil nitrate concentrations within and below the rooting zone decreased with increasing numbers of plant species, while biomass production increased (Tilman et al. 1997a, 2001). Interestingly, many mixtures had higher biomass than the single best performing monoculture ("transgressive overyielding"), refuting the sampling hypothesis as the sole explanation of the results and indicating complementarity effects (Sect. 20.4.9). On average, the diversity effects became stronger over time, due to increasing use of the available niche space (i.e. complementarity among co-occurring species). This resulted in a shift from asymptotic diversity–productivity relationships in young, developing communities to more linear relationships in mature, fully developed communities (Reich et al. 2012)
- Within the pan-European project BIODEPTH, the same basic design with manipulation of plant species richness and number of functional groups was replicated at eight different sites across Europe (Sweden to Greece). Across all sites, soil mineral nitrogen concentrations decreased with the number of functional groups (but not with plant species richness) (Spehn et al. 2005), and at the German site nitrate leaching also decreased significantly with both measures of diversity in the presence of N-fixing legumes (Scherer-Lorenzen et al. 2003). Above-ground biomass production increased with species and functional group richness (Hector et al. 1999). This effect got stronger over time and was mainly driven by complementarity, although sampling effects also contributed to the observed results. Unfortunately, not all species were grown as monocultures at some

Fig. 20.27 Results from selected classical biodiversity experiments adopting the "synthetic assemblage" approach. Data showing plant diversity effects on the efficiency by which communities take up limiting resources (light and nutrients) and convert these into biomass (productivity). **A**: Naeem et al.'s (1994) experiment in the climate chamber Ecotron facility at Imperial College, UK. Shown are **a** the temporal evolution of ammonium concentrations in the soil, which showed no clear pattern with diversity levels, and **b** the standing above-ground biomass (circles: means and standard errors by diversity level; points: values for each experimental assemblage (Naeem et al. 1995). Reproduced with permission from the Royal Society of London. (Photo P. Manning) **B**: The Biodiversity II field experiment at Cedar Creek, Minnesota, USA, with plant species richness effects on **a** soil nitrate concentrations (Tilman et al. 2002) and **b** standing above-ground biomass (Tilman et al. 2001). Reproduced with permission from AAAS. A variety of differently designed biodiversity experiments have been established at that site. (Photo J. Miller) **C**: The BIODEPTH experiment replicated at eight European sites. Shown are **a** values for nitrate loss to the groundwater at the German site (Scherer-Lorenzen et al. 2003; reproduced with permission from John Wiley & Sons) and **b** biomass production across all sites (Hector et al. 1999; reproduced with permission from AAAS) in relation to plant species richness. (Photo M. Scherer-Lorenzen) **D**: The Jena experiment in Germany, with plant species richness effects on **a** soil nitrate pool sizes (Oelmann et al. 2007; reproduced with permission from the Soil Science Society of America) and **b** biomass production (Ravenek et al. 2014). (Photo: Forschergruppe Jena Experiment)

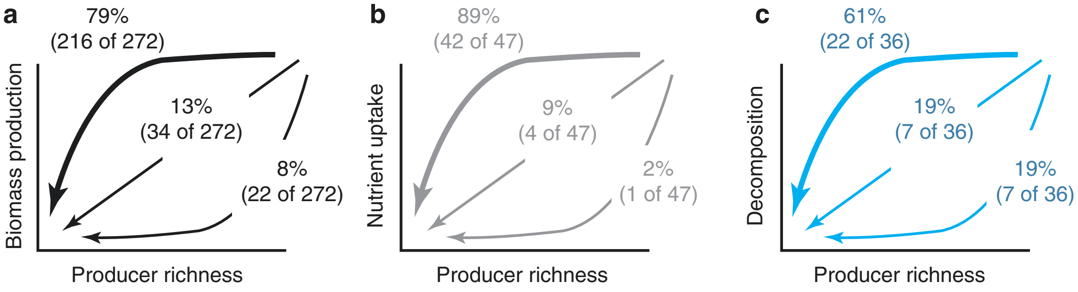


Fig. 20.28 Summary of results from several biodiversity experiments on key ecosystem functions. Of those studies that have shown significant plant diversity effects on ecosystems, most have found an asymptotic relationship between the number of plant species (producer richness) and three important ecosystem processes **a**: plant biomass production, **b**: plant nutrient uptake, **c**: plant litter decomposition). Fewer studies reported linear relationships or those that correspond to the loss of keystone species, where such losses lead to large declines in functioning. Given are the number and percentages of the studies analysed by Cardinale et al. (2011). Reproduced with permission from the Botanical Society of America

sites, which is necessary to unambiguously test for sampling effects. The biomass results also strongly differed among sites, with very large positive effects in Germany, Switzerland, Sweden, Portugal and the UK (Sheffield), unimodal or idiosyncratic relationships in Ireland and UK (Silwood) and no effects in Greece

- The Jena Experiment in Germany yielded results very similar to those described earlier: soil nutrient concentrations decreased with increasing plant species richness, or number of functional groups (grasses, small and tall herbs, and N-fixing legumes) (Oelmann et al. 2007). In parallel, biomass production increased with increasing diversity, both above and below-ground. The slopes of these relationships increased over the years, suggesting stronger and sustainable diversity effects with time. Again, complementarity effects prevailed, and the diversity-driven increase of biomass was a result of increasing plant density rather than plant size (Marquard et al. 2009)

Similar biodiversity experiments have also been established using model systems other than grasslands, including freshwater and marine ecosystems, freshwater and estuarine wetlands, intensively used agricultural systems and tundra, or tree communities. These experiments range across several magnitudes of the size of the organisms manipulated (from bacteria, algae, herbaceous plants to trees) and the size of experimental units (from glass vials, few square metre plots to 4 ha plots). In general, very similar results were obtained with such diverging systems: in more than 85% of all experiments, diversity effects on producer biomass or resource use were significantly positive, with producer biomass being 1.4 times higher in diverse mixtures than in monocultures and inorganic nutrient concentrations in soil or water being reduced by 48% relative to the monocultures (Cardinale et al. 2011). In most cases, positive diversity effects followed the redundancy hypothesis, that is, an initial loss of species has only minor impacts on ecosystem functioning because species are rather redundant in their effects on ecological processes and can replace each other. At lower diversity levels, loss of species cannot be compensated by other species. Thus, although different model ecosystems with different designs were used and the experiments were conducted by different research groups, many of the diversity–ecosystem function relationships were quite robust (Fig. 20.28).

20.4.2.3 Modelling Studies

Biodiversity–ecosystem functioning research can also be done solely on the computer, that is, in **modelling studies**, permitting the examination of specific mechanisms or the extension to larger spatial scales and longer time durations than empirical work. Models have been used in functional biodiversity research since early on and helped greatly in sharpening the hypotheses of underlying mechanisms. The first modelling exercises that explicitly dealt with biodiversity effects on ecosystem functioning mainly confirmed the observed positive diversity effects on productivity or nutrient retention found in experimental studies. For example, Tilman et al. (1997b) used models of interspecific competition for nutrients and randomly assembled communities with different species numbers. All species were identical, except that they differed in their **R*** values, that is, the concentration to which a resource is reduced by an equilibrial monoculture of that species (Sect. 17.3 and Box 19.2). They could show that, on average, productivity increases asymptotically with plant species richness, irrespective of the model complexity (with competition for one or two resources or with a generalised niche model). At the same time, nutrient retention also increased, which corresponds well to experimental results. This suggests lower nutrient losses at higher levels of diversity, for example, through soil nitrate leaching. In summary, the study showed that variation in species traits (R*, and the size of the niche spaced covered by each species) is sufficient to establish a positive richness–productivity relationship based on fundamental mechanisms of interspecific competition. Greater variation in species traits is magnified by interspecific interactions, which cause the average response of multispecies communities to differ from the response of the average monoculture. Both complementarity and selection effects (Sect. 20.4.9 and Fig. 20.37) contribute to this effect. Other models also confirmed the hypothesis that plant diversity can exert effects on ecosystem functions, for example, mechanistic models in spatially structured ecosystems in which plants compete for a limiting soil nutrient (Loreau 1998) or models of recruitment limitation in heterogeneous habitats or competition–colonisation trade-off models (Mouquet et al. 2002). However, these models also reveal situations where no diversity–function relationship should be expected, for instance, when species are redundant in their functional role (e.g. occupying the same spatial niche) and when the average resource-use intensity of the species is not affected by species diversity (which can hardly be found in real situations). These models also show that the slope of the diversity–function relationship depends on the mechanisms of species coexistence and on the causes of species richness gradients.

Besides the use of such models from theoretical ecology, which define species performance based on a theoretical trait space, models can also be parameterised by specific autecological traits and life-history trade-offs from real species. We present one example in more detail that nicely demonstrates how a modelling framework can be used to formulate hypotheses about mechanisms underlying diversity effects on ecosystem functioning (Fig. 20.29), which can then be tested in the field (Fig. 20.39). Using a forest succession model that was originally developed to simulate forest growth and dynamics, it has been shown that tree species richness promotes productivity in European temperate forests across a large climatic gradient (Morin et al. 2011). Interestingly, considering competition for light as the single form of species interaction and implementing real species-specific growth responses to light availability were sufficient to detect strong complementarity effects. Two underlying mechanisms could explain this, via diversity effects on mean values of forest canopy characteristics and their variability. First, higher species richness is associated with higher diversity in species traits (maximum height, growth rates, shade tolerance), leading, on average, to a higher leaf area index (LAI) of the canopy (1). Thus, functional diversity promotes light interception, which translates into higher productivity beyond that expected from monoculture performance (2). At the same time, higher light interception also means higher shading, which increases the mortality rates of smaller trees and the amount of dead biomass in the stand (3). Second, higher functional diversity in light-related traits reduces the temporal variability of LAI (4), so that incoming radiation can be better exploited, which also results in higher productivity in the model (5). Diversity also increases the heterogeneity in tree heights (and thus of light) within the canopy (6),

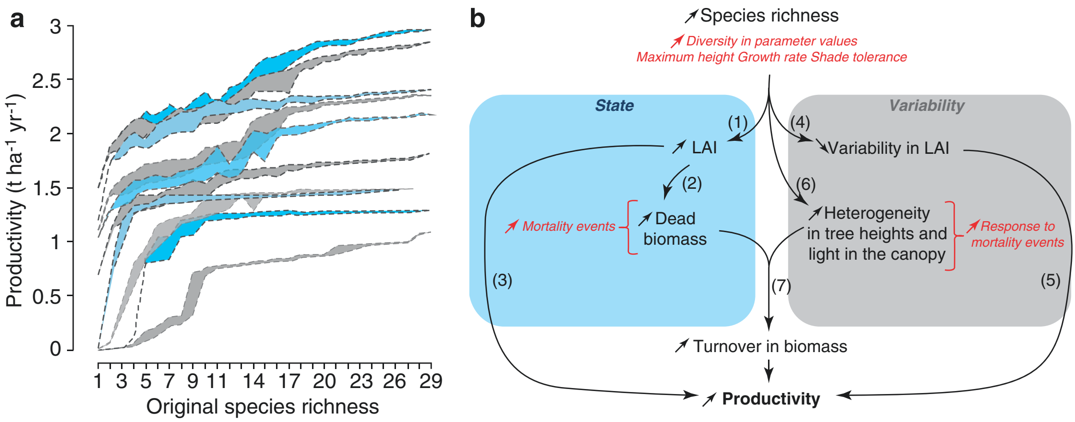


Fig. 20.29 Modelled productivity responses to changing tree species richness. **a** Estimates of productivity against original species richness for 11 different sites in Switzerland, for which the model has been parameterised. Shaded areas between dashed lines represent a 95% confidence interval of the true median of productivity. Similar results were obtained with realised species richness after 2000 years of simulated forest dynamics. **b** Hypothetical mechanisms underlying the observed positive diversity effect on productivity, which can be divided into two categories: those affecting the mean values of some forest characteristics (*state*) and those affecting the variability of these characteristics (*variability*). The numbers in brackets refer to the detailed explanations in the text (Morin et al. 2011). Reproduced with permission from John Wiley & Sons

that is, the vertical structure of the canopy is getting more complex through interspecific competition compared to intraspecific competition (monoculture). This change in structural complexity allows forests with varying traits to respond faster to small-scale mortality events, that is, they show a higher turnover in biomass (7). In sum, these main processes involved in the simulated dynamics together could explain the positive productivity response to increasing tree species richness and functional diversity.

20.4.3 Biodiversity Effects on Other Ecosystem Functions

The first experiments quantified biodiversity effects on the basis of a few ecosystem functions only—mainly measures of productivity and of resource uptake, as exemplified in the previous section. Later experiments often simultaneously measured a large variety of ecological properties and functions, including, for example, litter decomposition, carbon sequestration, soil water and nutrient dynamics, or greenhouse gas emissions. Several of these response variables are also affected by plant species composition and diversity, and some examples are presented here.

Soil physical characteristics (e.g. porosity, aggregate stability), chemical characteristics (e.g. pH, nutrient concentrations, carbon pools) and biological aspects (e.g. litter decomposition, fauna, microbial communities) (Fig. 20.30) have been found to depend on plant community composition and diversity. A large proportion of experimental work on the diversity–function relationship has been done with litter mixtures and decomposition trials, mainly owing to the rather easy possibilities for experimental manipulation of litter diversity. Several aspects of the decomposition process and the turnover of labile soil organic matter are sensitive to diversity-mediated changes in both abiotic and biotic conditions (Sect. 16.2), including microclimatic conditions or the abundance and composition of soil fauna and microbes. In fact, there are numerous examples of mixture effects on leaf litter decomposition. In three reviews of **litter decomposition** studies across different vegetation types (Gartner and Cardon 2004; Hättenschwiler 2005; Hättenschwiler et al. 2005), it was shown that synergistic diversity effects are known for roughly half of all litter mixtures studied, that is, decomposition rates of litter mixtures are higher than expected based on rates of single-species litter. Purely additive effects (i.e. no biodiversity effect,

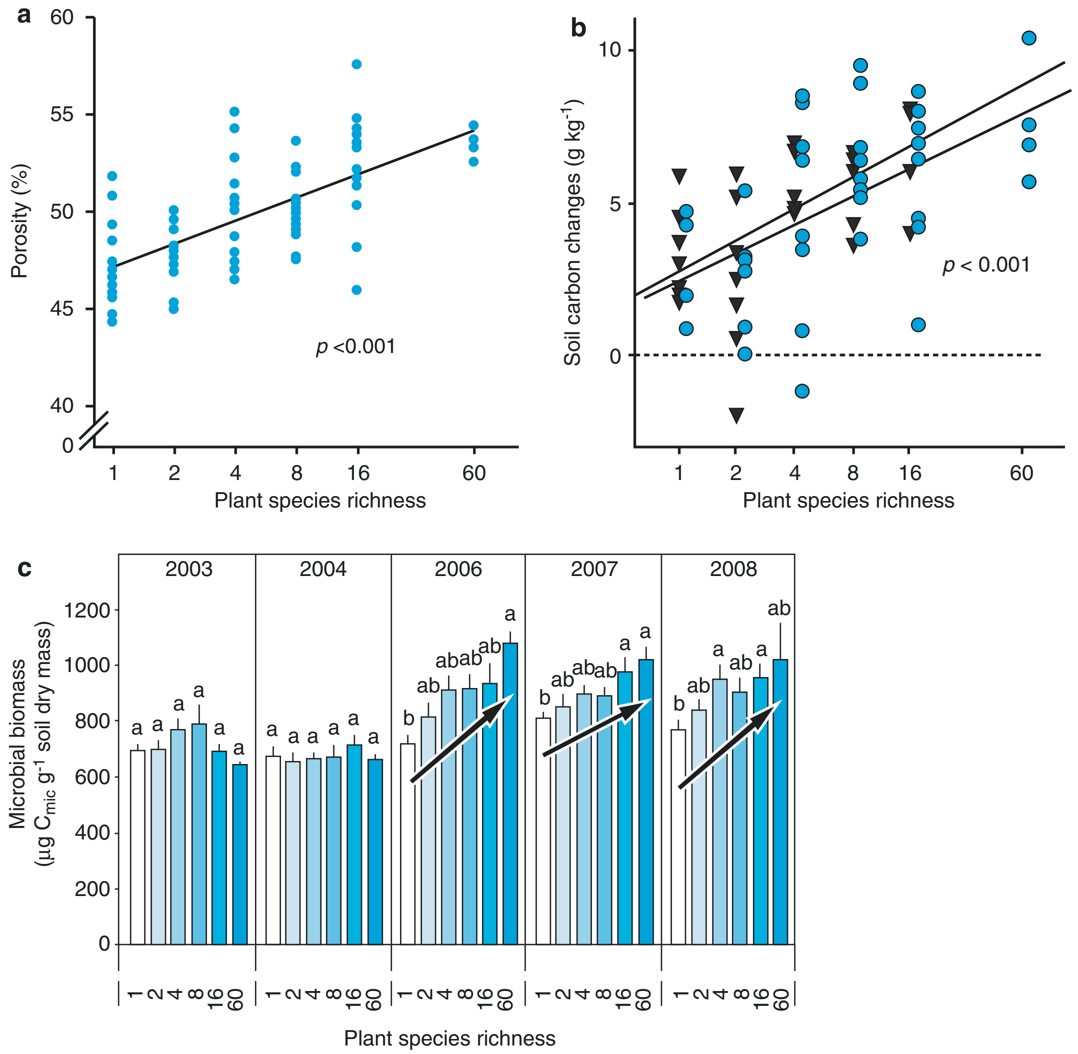


Fig. 20.30 Examples of plant species richness effects on soil ecosystem functions. All examples are from the Jena Experiment, Germany. **a** Porosity or infiltration capacity increases significantly with plant diversity, suggesting improved soil hydrological properties in mixtures (Fischer et al. 2015). **b** Changes in soil carbon stocks (calculated as the product of soil bulk density and its carbon concentration) between the beginning of the Jena Experiment (2002) and 9 years later (2011) significantly increase with plant species richness, in communities both with legumes (triangles) and without legumes (circles), implying greater carbon storage with increasing plant diversity (Lange et al. 2015). Since soil bulk density decreases with increasing diversity in this experiment (inverse pattern of porosity, see panel **a**, the rise in carbon storage is largely driven by changes in carbon concentrations, for example, through increased root exudation and microbial biomass. **c** Microbial biomass significantly increases with plant species richness only after some years after the establishment of new plant communities. Different letters indicate significant differences (Eisenhauer et al. 2010). Reproduced with permission from John Wiley & Sons

meaning that the decomposition of mixed litter can be predicted by the decomposition rates of the corresponding pure litter types) are reported for a third of all cases, and antagonistic effects (i.e. slower decomposition in mixed than in pure litter) can be observed in the remaining 20% of mixtures (Box 20.5 for explanation of the terms antagonistic, synergistic and additive). The positive or negative diversity effects on litter decomposition can be direct, for example, by providing different litter qualities and quantities, or by different timing of litter inputs in highly diverse communities, which may influence litter decomposition rates. Diversity effects can also be indirect by affecting the microenvironment, for example, through different canopy closures that feed back on soil moisture and temperature, which in turn affects litter decomposition. Experimentally, such direct and indirect effects can be disentangled by deploying different kinds of litter bags, with mass loss of the litter inside the bags as a measure of decay rate: bags with a standard material (e.g. wheat straw, cotton strips) will measure biodiversity effects that are driven by changes in the microenvironment (e.g. soil moisture, temperature, humidity, UV radiation); bags with community-specific litter employed in a homogeneous, similar vegetation type, but outside the target communities (common garden approach), will measure biodiversity effects through changes in litter composition and quality; bags with community-specific litter deployed in their corresponding community will measure the combined influences of biodiversity through litter quality and through changes in the microenvironment. Under such an approach, it has been shown that litter decomposition rates increased with functional diversity of the plant community, via both such direct and indirect effects (Scherer-Lorenzen 2008).

In biodiversity experiments, soil-related functions often react with some **time lag** after the initiation of the experiments in comparison with those above-ground, as seen for microbial biomass, for instance (Fig. 20.30c). Most plant diversity experiments following the synthetic community approach involve some land-use change and pretreatments or soil disturbances, such as ploughing, harrowing or herbicide application, before new communities are established. Many soil organisms therefore suffer a decline in abundance. Only with ongoing succession and recolonisation by soil organisms may differences in plant community composition and diversity finally manifest in specific soil communities and functions (Eisenhauer et al. 2010; Sects. 13.4 and 14.2). Such findings also highlight the need to run biodiversity experiments for prolonged periods of time.

20.4.4 Biodiversity Effects on Other Trophic Levels

Changes in plant biodiversity may have cascading effects on other organismic groups and multitrophic interactions and, thus, on herbivore damage, pathogen infection, pollination success and food web structure (Sect. 19.4). The abundance and diversity of above- and below-ground organisms, which are associated with the plant community, are often positively related to increasing plant species richness, with few exceptions (Fig. 20.31). Obviously, **diversity begets diversity**, at least in studies that manipulate plant diversity. In contrast, other plant species that initially do not belong to the plant community have less establishment success with an increasing number of species present. This **resistance to invading species** at high diversity levels can be due to lower levels of unconsumed resources left by the established species, as also predicted by resource-use models (Sect. 20.4.2), or due to fewer vacant niches. A higher degree of niche overlap between resident and invader species should also decrease invader success, and resident species having similar trait combinations (i.e. belonging to the same functional group) as invaders are often found to exert strong negative effects on invading species. In contrast, large-scale comparative studies most often find that resident species diversity is positively correlated with invader species diversity (Sect. 23.5). The factors that determine the diversity and coexistence of resident species, such as resource supply, levels of disturbance and habitat heterogeneity, probably also influence the success of invasive species. However, the two findings are not necessarily contradictory: while the positive effect of diversity on invasion resistance operates at the neighbourhood scale, other factors that covary with diversity may be more important in determining invasion success at larger scales.

Despite such a generally positive association between plant diversity and diversity of other organisms sometimes different organismic groups have opposing responses, even within the same study, which can be explained by the degree of feeding or host specialisation, foraging patterns or

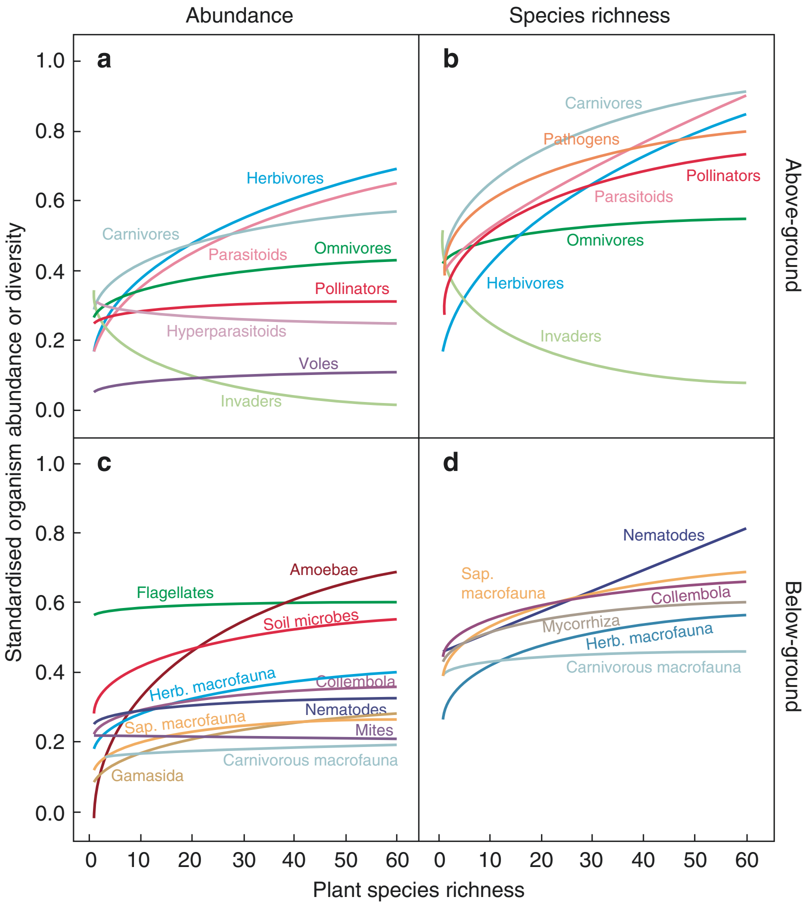


Fig. 20.31 Plant diversity begets diversity of other organismic groups. All response variables are scaled to [0, 1], and every curve is fitted using a power function with covariates. Identical colours in each horizontal pair of panels indicate identical groups of organisms. Invaders are non-sown plant species (Scherber et al. 2010)

movement mobility. This might become clear by looking at herbivores and pathogens that are often related to the presence of certain host species (Fig. 20.32a). Usually, generalist animal species profit from plant diversity as diets get broader, leading to higher herbivore damage in mixed plant communities. Such responses are termed—from a plant perspective—**associational susceptibility**. In contrast, a reduction of herbivore or pathogen damage with increasing diversity can be observed mostly for specialist animal or fungal species, a phenomenon called **associational resistance**. Clearly, such results are highly relevant for applied aspects, such as agriculture or forestry, where herbivores and pathogens are often seen as pests. Some meta-analyses suggest that in the majority of cases plant diversity exerts positive effects on the resistance against such pests (e.g. Jactel and Brockerhoff 2007; Castagneyrol et al. 2014), which opens the possibility of using plant biodiversity as a tool for controlling or regulating these organisms (Sect. 20.4.10).

20.4.5 Biodiversity and Multifunctionality

The quantification of many ecosystem functions within biodiversity studies opens the opportunity to quantify ecosystem **multifunctionality**. This term describes the fact that ecosystems simultaneously provide a multitude of ecosystem functions and services and are also often managed or valued in this respect. For example, mountain forests provide timber, protection against avalanches and landslides, continuous groundwater recharge, mushrooms and berries (so-called non-timber forest products) and recreation opportunities for hikers and mountain bikers, among other uses. It is therefore also of high practical and

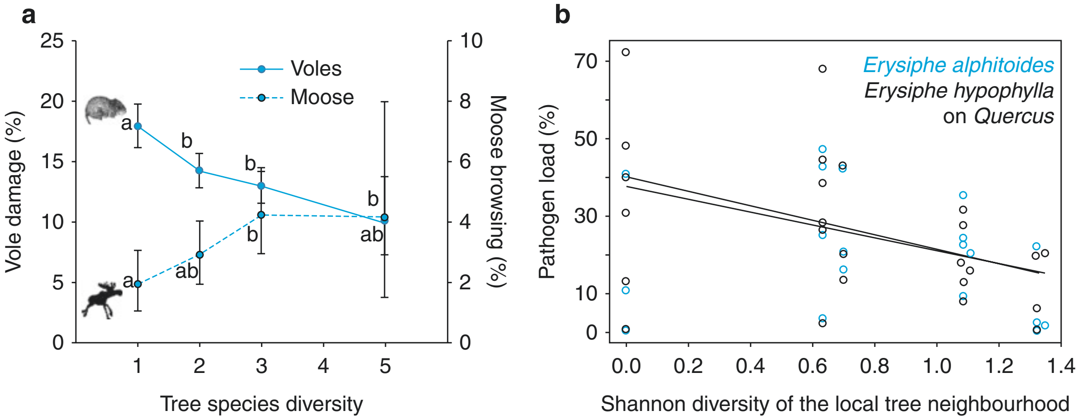


Fig. 20.32 Associational resistance and susceptibility. **a** Vole damage and moose browsing in a Finnish tree diversity experiment. Voles restricted their feeding to only the most palatable tree species, supporting the associational resistance hypothesis. In contrast, moose feed on more varied tree species, suggesting associational susceptibility (Vehviläinen and Koricheva 2006). **b** Pathogen load by mildew species growing on oaks decreases with the diversity of local tree neighbourhoods, that is, the number and abundance of tree species surrounding a target tree, representing a case for associational resistance. (Hantsch et al. 2013)

applied value to know whether plant diversity influences multiple ecosystem functions and services. This challenge has been tackled in several, complementary steps, and an overview of the different ways to quantify multifunctionality is presented by Byrnes et al. (2014). First, if single functions are considered that are measured at one place at one time and under one environmental change scenario (i.e. under a single setting of functional interactions or a single context), then many species, but not all, promote ecosystem functioning (Cardinale et al. 2011). Enlarging these analyses to more settings or to another context often shows that even more species are needed to ensure a certain threshold of ecosystem functioning because different species promote functioning, for example, in different years or at different places (e.g. different sites or different patches within a site) or under different global change scenarios. Second, more species are needed to provide several functions simultaneously because different species promote different functions. On average, this means that an index of multifunctionality responds positively to increasing biodiversity, as has been shown for very different terrestrial and aquatic communities (Lefcheck et al. 2015). One study combined all these different aspects and found that the proportion of species that promote ecosystem functioning increases with increasing numbers of years, places, ecosystem functions and environmental changes (Fig. 20.33) (Isbell et al. 2011). In other words, many different species are needed to maintain multiple functions at multiple times and places under changing environments, that is, biodiversity begets ecosystem multifunctionality under multiple contexts. These findings also put the concept of “redundancy” (Sect. 20.4.2) into another perspective: although species may appear to be functionally redundant when one function is considered under one set of environmental conditions, many species are needed to ensure ecosystem functioning and the delivery of ecosystem services if multiple contexts are considered simultaneously; thus, functional redundancy is not given.

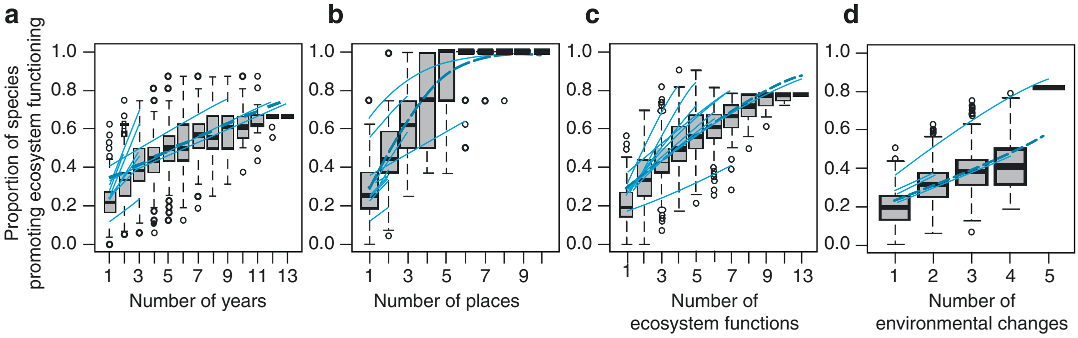


Fig. 20.33 Proportion of species needed to support ecosystem functioning. If multiple contexts are considered, more species are needed to promote ecosystem functioning, for example, when more years **a**, places **b**, ecosystem functions **c** or environmental change scenarios **d** are taken into account. The "proportion of species promoting ecosystem functioning" results from modelled ecosystem functioning response variables (e.g. productivity, litter decomposition) as a function of the presence or absence of each study species at the plot level and is a relative measure of the number of species needed. The dashed blue line represents the grand mean fitted across all studies; the solid blue lines represent the response found in single studies; box plots summarise observed data from the 17 grassland biodiversity experiments included in the study. (Isbell et al. 2011)

20.4.6 Different Metrics of Biodiversity Affecting Ecosystem Functioning

As exemplified by the selection of the studies discussed earlier, there is now substantial evidence that biomass production and many other ecosystem functions increase with increasing plant species richness, that is, taxonomic diversity. Does this pattern also hold true if other metrics (evenness) or facets of biodiversity (genetic, phylogenetic, functional or structural) are considered?

Increasing **evenness** of plant communities, that is, how evenly the abundance or biomass is distributed among species, commonly results in higher levels of biomass production. Starting with the experiments of Wilsey and Potvin (2000) in oldfields of Quebec, Canada, several studies have now confirmed their results, while others reported increased productivity with increasing dominance of species (Hillebrand et al. 2008). These contrasting results can be explained theoretically by the prevalence of species interactions influencing ecosystem processes: in the case of synergistic interactions, such as complementarity or facilitation (based on niche differentiation among species) (Sect. 20.4.9), increasing evenness should result in higher process rates, and increasing dominance to lower rates. In contrast, if species identity (i.e. the dominant trait) predetermines processes (corresponding to selection or sampling effects) (Sect. 20.4.9), these processes should be largely influenced by increasing dominance. In addition, under longer time scales with fluctuating environmental conditions, a higher evenness should allow communities to adapt to new ecological conditions and sustain ecosystem process rates due to higher trait variance. In contrast, under stable conditions, a certain optimal trait configuration should result in the highest process rates, and any deviation from this trait configuration through increasing evenness would reduce process rates.

Experiments that created a gradient of **plant genetic diversity** within species, for example, by planting communities with different numbers and combinations of genotypes (e.g. of seagrass (*Zostera marina*), wheat (*Triticum aestivum*), wall cress (*Arabidopsis thaliana*), evening primrose (*Oenothera biennis*) or different grassland species) also showed positive diversity–productivity relationships, often in the same magnitude as those found with species diversity (e.g. Zeller et al. 2012). Genetic diversity seems to be especially important for the temporal stability of biomass production (Prieto et al. 2015). As mechanisms, complementarity in resource use and facilitation (Sect. 20.4.9) in those mixtures of genotypes that differ in functional traits have been suggested.

Manipulating **phylogenetic diversity**, that is, planting communities differing in the evolutionary relatedness of the constituting species (Sect. 20.2.3), also often leads to similar results; for instance, Cadotte (2013) showed that if species were grown together with close relatives (low phylogenetic diversity) the biomass production was similar to that in monoculture. If they were grown with distantly related species (i.e. high phylogenetic diversity), they produced more biomass than expected from their monocultures. Thus, distantly related species differ more strongly in their niche requirements than closely related species, leading to an occupation of different niches that allows resource-use complementarity (Sect. 20.4.9).

Since plant functional traits may control ecological processes to a large degree, building the mechanistic bridge between species richness and its effects on ecosystems, many biodiversity experiments not only included a gradient of species richness in their design, but also one of **functional diversity**. In many cases, the number of functional groups (e.g. grasses, legumes, other forbs) has been varied. Quite often, but not always, such measures of functional diversity were even stronger predictors of ecosystem processes than species richness. This finding can be attributed to the fact that any diversity effect must be based on some functional differences among co-occurring species, which are better captured by measures of functional than taxonomic diversity. However, in those experiments, the gradients of species richness and of functional diversity cannot be completely orthogonal to each other (e.g. because there cannot be more functional groups than species), so that it is not possible to fully separate both factors, making the interpretation of their relative effects difficult. Building on such experiences, some newer biodiversity experiments now focus on manipulating functional trait diversity *a priori* while keeping species diversity constant. Including functional traits in the design may therefore allow for a better understanding of the mechanisms underlying the effects of altered biodiversity. In such approaches, a measure of functional diversity (Sect. 20.2.3) is calculated for all possible combinations of species mixtures at a given level of species richness, and the mixtures to be planted are drawn at random, resulting in a gradient from low to high functional diversity (Fig. 20.34). Alternatively, principal component analyses can be used to separate trait axes that describe gradients in trait similarity, from which mixtures differing in functional diversity can be selected. If the traits considered are related to resource-use complementarity, for instance, then mixtures with different levels of complementarity can be designed (Ebeling et al. 2014).

In analogy to the experimental manipulation of compositional or functional diversity, one might also think of biodiversity experiments that create a gradient of **structural diversity**, **β-diversity** or even **landscape diversity** directly, but this has not been done so far. It would be worth doing if we wish to understand the multiple effects that different facets of biodiversity may have on ecosystem multifunctionality, and across multiple spatial scales. Indeed, data from observational studies indicate that growth can be positively affected by increasing structural diversity in forest stands (Lei et al. 2009).

Although it has often been claimed that one biodiversity metric (e.g. functional diversity) should be better suited to explain diversity effects on ecosystems than others (e.g. species richness), the choice of the metric will certainly depend on the research question and on the taxa to be investigated.

20.4.7 Context Dependency of Biodiversity Effects on Ecosystems

Despite the overwhelming evidence for plant diversity effects on a multitude of ecological processes and functions, it is important to note that

Fig. 20.34 Aerial view of a trait-based tree diversity experiment (BIOTREE-FD). The experiment consists of stands differing in functional diversity, with the number of species kept constant at a level of four per plot. The species pool consists of 16 European temperate tree species. Within each hexagonally shaped plot, species were planted in round monospecific patches to delay outcompetition of slow-growing species in the early years (Scherer-Lorenzen et al. 2007). (Photo: K. Kovach)

ecosystem functions greatly differ in their response to changes in plant diversity: some functions increase with increasing diversity, others decrease, and others hardly respond at all. In addition, the same function, say productivity, also shows divergent responses to changes in diversity in different environments or at different successional stages. Thus, biodiversity–ecosystem process relationships are highly **context-dependent**. In other words, the form and cause of the relationship are likely to change as the environment alters the relative contributions of species to ecological processes (Cardinale et al. 2000). This can be illustrated by comparing the slopes of these relationships under different environmental situations. In principle, two scenarios are possible, and there is evidence for both of them:

- The values of ecosystem processes could increase or decrease with changing environmental conditions, but similarly across the entire range of diversity. In statistical terms, the slope of the relation does not change, only its intercept, and the interaction term between diversity and environmental conditions will be non-significant (Fig. 20.35a). As an example, drought stress reduced biomass production at all levels of plant species richness by the same absolute value in the Jena Experiment (Vogel et al. 2012).
- The values of ecosystem processes change under different environmental conditions, but the magnitude of this change depends on plant diversity, leading to changing slopes of the diversity–function relationship, and a significant diversity by environment interaction. If the slope increases, that is, when diversity effects become stronger under a changed environment relative to a control situation, two possibilities exist (Fig. 20.35b):

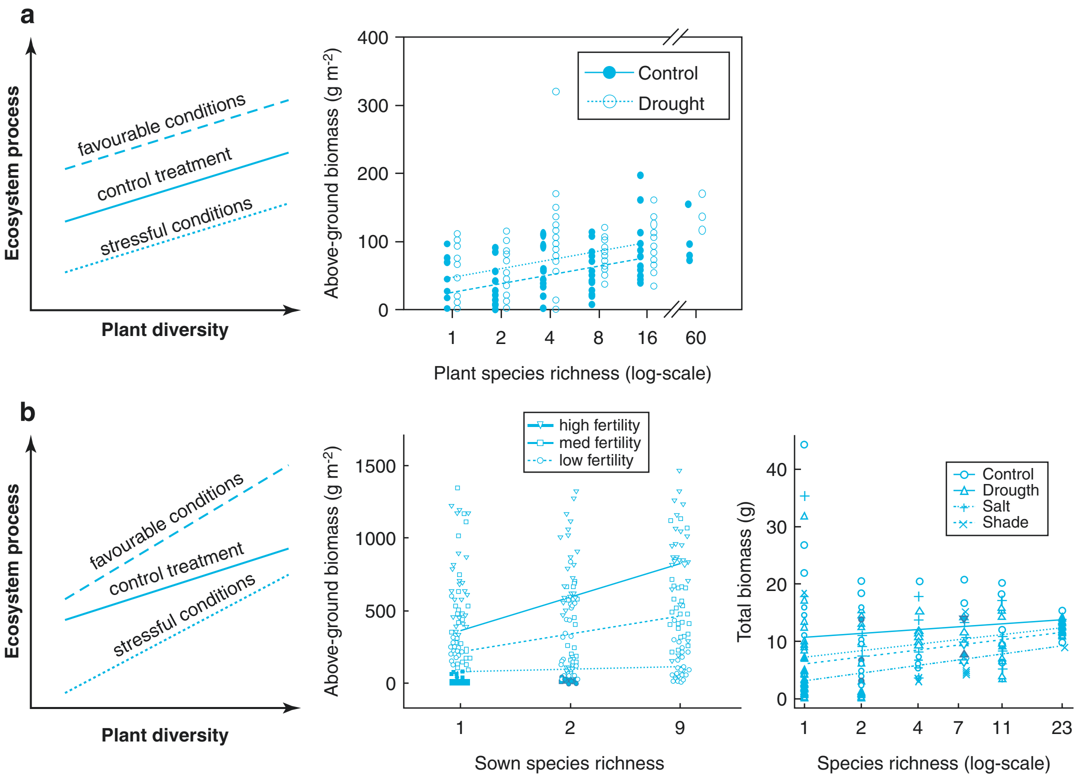


Fig. 20.35 Context dependency of biodiversity–ecosystem function relationships. **a** The slope of the relationship between plant diversity and ecosystem function stays constant with environmental context, but the absolute values of the response variable are different depending on environmental conditions. The example shows plant diversity effects on above-ground biomass under control conditions (black circles, solid line) and under drought, simulated with rainout shelters (open circles, dotted regression line) (Vogel et al. 2012). **b** The slope of the relationship between plant diversity and ecosystem function changes with environmental context, with stronger diversity effects under either favourable conditions (left example: diversity effects on above-ground biomass under different soil fertility levels, Fridley 2002) or stressful conditions (right example: diversity effects under control and drought, salt, or shade treatments) (Steudel et al. 2011). Reproduced with permission from John Wiley & Sons

- Plant diversity effects are stronger under more favourable conditions, that is, when resources are plentiful; examples include a larger soil volume that can be exploited or higher nutrient availability after fertilisation. This **biotope-space hypothesis** postulates that the niche space of individual species can expand into a larger biotope space and that more species with different niche requirements can be "packed" into the niche space under more favourable conditions (Dimitrakopoulos and Schmid 2004). Therefore, resource-use complementarity can be greater and beneficial biodiversity effects should increase under favourable conditions, where high soil resource availability is hardly limiting growth. For example, diversity effects increased with fertility of the soil in an experiment with annual plant communities and NPK fertilisation (Fridley 2002).
- Plant diversity effects are stronger under harsh environmental conditions because they often rely on facilitation or positive interactions among species (Sect. 20.4.9), which are more pronounced under harsh

conditions: according to the **stress-gradient hypothesis**, interactions among coexisting species shift from negative (competition) to positive (facilitation) as environmental stress increases from favourable to harsh conditions (Callaway 2007). For example, in a study with freshwater marsh plants, the absolute values of biomass production decreased in more stressful environments (drought, salt, shade) relative to a control treatment, but diversity effects increased (Steudel et al. 2011). Comparative studies from natural and semi-natural ecosystems, for example, forests, mostly support the view that diversity effects become stronger under harsh conditions.

Support for both scenarios has been documented, so it is not possible to say whether diversity effects should generally be stronger under harsh or favourable conditions. Presumably, the type of environmental conditions, that is, which resources limit plant growth most, and the nature of species interactions might both be crucial for the slope of the diversity–function relationship under different ecological contexts. For example, imagine a gradient of growing conditions, ranging from low supply of soil resources, where nutrient or water availability limits plant growth, to high soil resource availability, where light is the major growth-limiting factor. If species interactions result in improved light absorption, for example, through canopy stratification, or higher light-use efficiency, then the diversity effects should be stronger under more favourable conditions, in line with the biotope-space hypothesis. In contrast, if species interactions result in greater soil resource availability, for example, through N-fixation or accelerated rates of nutrient cycling, the diversity effects should increase with decreasing growing conditions, based on the stress-gradient hypothesis. Thus, the strength of positive interactions among species (complementarity, facilitation) will change along the gradient of growing conditions (Forrester 2014).

20.4.8 Plant Biodiversity and the Stability of Ecosystem Functioning

A long-standing hypothesis in ecology is that species diversity is positively related to ecosystem stability, which dates back to the seminal work of Charles S. Elton (1958) and which has fascinated ecologists ever since. An exhaustive overview of this "**diversity-stability hypothesis**" can be found in Griffin et al. (2009), Loreau and Mazancourt (2013) and Oliver et al. (2015). Interestingly, this field of ecology has been largely theory-driven. Early theory predicted that more diverse communities and food webs were more stable and more resistant to invasion by other species (e.g. MacArthur 1955). Later, Lotka-Volterra models of interspecific competition showed that communities became less stable as the number of interacting species increased (May 1973). In contrast, future statistical models showed that diversity may buffer environmental fluctuations through the scaling relationship between the mean and the variance (statistical averaging, or the so-called "**portfolio effect**"), even without interactions among species (Doak et al. 1998). This portfolio effect compares the temporal stability of ecosystem functions with that of financial assets, which show lower fluctuations and, thus, higher stability when partitioned across multiple stocks. Statistical averaging can also result in a positive diversity–stability relationship in the presence of species-specific responses to changing environmental conditions and functional redundancy within groups of species ("**insurance hypothesis**") (Yachi and Loreau 1999). Imagine that species differ in their requirements for abiotic or biotic environmental factors (e.g. temperature, soil moisture, nutrient availability), that is, in their fundamental niches. These species will respond to environmental fluctuations not similarly, but asynchronically, and declines in some species or populations will be compensated by increases in others, resulting in less variation in process rates at the aggregate community or ecosystem levels or in no net change of ecosystem functioning, a phenomenon called **compensatory dynamics**. Thus, a high diversity of species' responses within

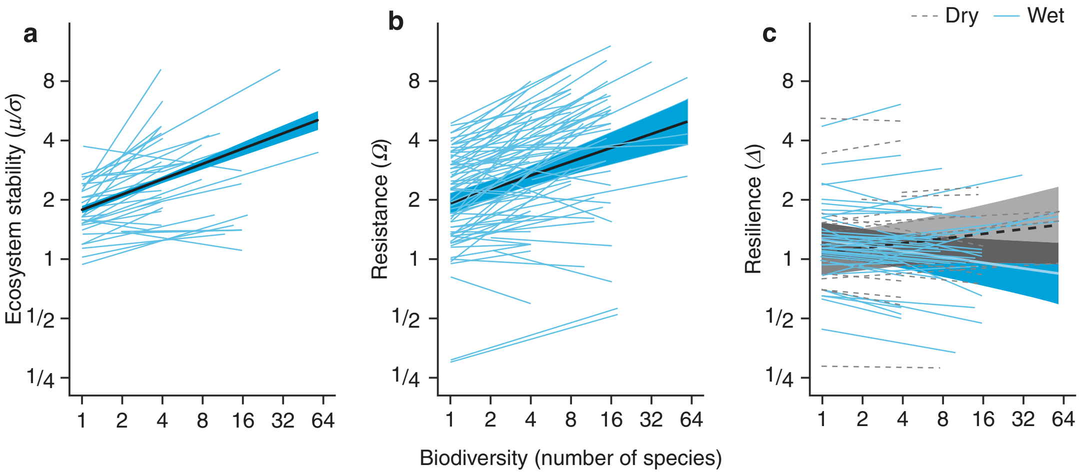


Fig. 20.36 Plant biodiversity effects on different aspects of ecosystem stability. Ecosystem stability is defined as low temporal variability **a**, resistance **b** or resilience **c** of biomass production. As perturbations, severe dry or wet years were considered across 46 plant diversity experiments. Thin lines represent mixed-effect model fits for each study **a** or a climatic event within each study **b**, **c**. Thick lines are model fits across climatic events and studies with 95% confidence interval bands. Axes are logarithmic. (Isbell et al. 2015)

functional groups further stabilises ecosystem functions through the **asynchrony of species responses** to environmental fluctuations. This mechanism can be seen as a form of temporal complementarity between coexisting species. Plant diversity can also increase the temporal stability of biomass production if mixed communities produce more biomass than monocultures (“overyielding”) (Sect. 20.4.9) while keeping temporal variability constant.

The effects of biodiversity on stability may differ depending on the different aspects of stability. For example, **temporal stability** refers to a low variation of an ecosystem function over time quantified as the reciprocal of the coefficient of variation. Tree growth, for instance, is more stable over time in mixed vs. pure forest stands (Fig. 20.25). There are also many cases from experimental studies where an increase of plant species richness leads to increased temporal stability in the face of climatic fluctuations (Fig. 20.36a). **Resistance** describes the ability of a system to maintain its original state in the face of an external perturbation. For example, highly diverse communities are often more resistant to invading plant species (Sect. 20.4.5) or maintain ecosystem functions against climatic fluctuation (Fig. 20.36b). Finally, **resilience** defines the speed at which a system recovers after a perturbation (Sects. 13.4 and 17.4), which often is unrelated to diversity (Fig. 20.36c). These results suggest that biodiversity stabilises ecosystem functions, such as productivity, during but not after perturbations.

20.4.9 Mechanisms Underlying Biodiversity–Ecosystem Functioning Relationships

Based on hundreds of observational and experimental studies, there is now broad consensus that plant diversity affects many ecosystem properties and processes, irrespective of the metric of biodiversity used. More diverse systems consistently have higher biomass production, higher nutrient uptake and, consequently, lower leaching losses to groundwater, among other effects. What are the underlying mechanisms that could explain such biodiversity–ecosystem function relationships?

In general, **trait differences among species are the underlying causes of any biodiversity**

effects on ecosystem functioning. In the debate about the relevance of results from manipulative experiments, often a distinction was made between the effects of species numbers and of species identities (i.e. their functional traits). Many studies have shown that the identity of species within a mixture is more important than the number of species. However, because no two species are identical in their characteristics (e.g. growth rate, size, nutrient use efficiency, leaf lifespan), it is impossible to manipulate species richness without selecting species with different characteristics. Thus, it becomes clear that there is **no magic effect of numbers of species per se** and that any effect will arise from functional differences between species and from species interactions. There can not be any relationship between species richness and ecosystem processes without these functional differences between species. All theoretical models of diversity–functioning relationships also include assumptions concerning differences in species' traits, and there is no theoretical mechanism that would produce any relationship between species richness and ecosystem processes with identical species. Therefore, the characteristic traits of species and, thus, the diversity of functions these species perform are important determinants of ecosystem processes.

Various mechanisms can result in diversity effects on ecosystem processes, and they have been grouped into several categories:

- Sampling and selection effects.
- Niche differentiation and resource-use complementarity.
- Facilitation and mutualisms.
- Trophic interactions and negative density-dependent effects.

20.4.9.1 Sampling and Selection Effects

The **sampling effect** is related to the statistical chance of a species being present in a mixed community. Consider a community assembled randomly from a fixed pool of species. The probability of the presence of a species increases with increasing species richness. For example, if the pool consists of ten different species, the probability of having species A in a monoculture is 0.1. In a five-species mixture, this probability is 0.5, and it is 1.0 at the ten-species level (where species A is always present). Thus, it is more likely for that species to have been "sampled" from the pool at higher diversity. Consider further that this species has a high performance in monoculture, that is, it influences ecosystem processes to a great extent, for example, because it is a very high-yielding species or because it has high values of other functional traits. If this particular species dominates the community (i.e. "selected"), the system should—on average—tend to take the functioning imposed by that species, which is then termed **selection effect** (Tilman et al. 1997b; Loreau and Hector 2001). In that case, a graph showing ecosystem process rates against number of plant species will have a flat upper bound of data variation, which indicates that the ecosystem process of highly diverse mixtures is not higher than the single best monoculture. Further, the mean rate of ecosystem processes will increase as the number of species increases (e.g. increasing productivity) (Fig. 20.37a). Similarly, the level of unconsumed resources will decrease with diversity if the sampled species is able to extract soil resources very effectively. A positive selection effect therefore indicates that a species with high monoculture performance dominates the mixed-species community and its functioning, leading to a positive relationship between plant diversity and ecosystem function. The selection effect can also be negative if communities are dominated by a species with low—and not high—values of functional traits or rates of ecosystem processes in monoculture, resulting in a negative biodiversity–ecosystem function relationship. The selection effect was initially viewed as an experimental artefact, but it is a simple possible mechanism linking diversity and ecosystem functioning, which involves species interactions—leading to the dominance of one species over others.

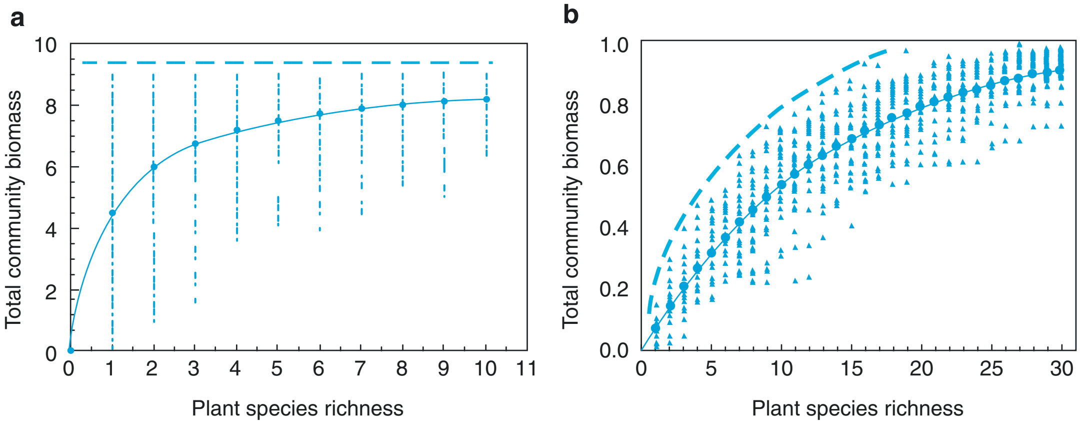


Fig. 20.37 Theoretical models of selection and complementarity effect. **a** Selection effect. Note the upper flat bound of the point cloud (dashed line), which indicates that the productivity of highly diverse mixtures is not higher than the single best monoculture. **b** Complementarity effect. Note the increasing upper bound of the point cloud (dashed line), which indicates that the productivity of highly diverse mixtures is higher than the single best monoculture. Triangles denote results from different simulation runs with different species compositions; lines and large dots show the means (Modified from Tilman et al. 1997b). Reproduced with permission of the National Academy of Sciences, USA

20.4.9.2 Niche Differentiation and Resource-Use Partitioning: The Complementarity Effect

Resource-based competition theory predicts the coexistence of species if *inter*specific competition is lower than *intra*specific competition. This could be achieved by differences in species' requirements for abiotic or biotic resources, habitat or environmental conditions, and, hence, in their niche space. Niche differentiation allows more species to coexist, that is, it promotes diversity (Sect. 19.3). Since plants depend on a small and common set of abiotic (water, light, CO_2, mineral nutrients) or biotic resources (pollinators, mycorrhiza, among others), partitioning of resource niches in plant communities is less obvious than in animal communities. One way in which plants could differ in resource niches is by partitioning a common resource in space (e.g. access to nutrients in different soil layers due to differences in rooting depths), time (e.g. different nutrient uptake phenology), chemical form (e.g. nitrogen nutrition via nitrate, ammonium or organic N) or a combination thereof.

Such partitioning of the available resource pool among the coexisting species allows them to use resources in a complementary way. Hence, a combination of species could obtain more resources than could any species living by itself, that is, the *per capita* performance of species in species-rich communities is higher than in species-poor ones. Thus, **niche differentiation** or **resource partitioning** and the resulting **resource-use complementarity** can lead to increased yield in mixtures compared to those of the corresponding monocultures due to a larger available total resource pool.

The principle of resource complementarity has been known for a long time. The German silviculturalist Heinrich Cotta (1763–1844) argued against large-scale afforestation with fast-growing species in monoculture, which were established on the recently developed concept of sustainability by von Carlowitz (1713): "Endeavours to establish pure stands everywhere are based on an old and highly detrimental prejudice. […] Since not all tree species utilise resources in the same manner, growth is more lively in mixed stands and neither insects nor storms can do as much damage; also, a wider range of timber will be available everywhere to satisfy different demands…" (Cotta 1828, p. 115; translation by Pretzsch 2005). He thus recognised the fact that different tree species occupy different resource niches and that this results in higher yields and even greater stability against biotic or abiotic perturbations; he also somehow anticipated the concept of ecosystem services by relating this ecological principle to human demands. Later, Charles Darwin in *The Origin of Species* used the term "ecological division of labour" to describe ecological niche differences that will result in higher productivity in mixed plant communities (Hector and Hooper 2002): "It has been experimentally proved that if a plot of ground be sown with one species of grass, and a similar plot be sown with several distinct genera of grasses, a greater number of plants and a greater weight of dry herbage can thus be raised" (Darwin 1872, p. 113). Since then, the concept of resource complementarity has already been successfully used for a long time in intercropping or agroforestry to increase yields per unit land area, for instance. In these cases, species with markedly distinct functional properties are chosen to produce higher yields in mixtures than in monoculture, a phenomenon known as "**overyielding**".

To illustrate this important ecological principle, consider a habitat with spatial or temporal heterogeneity of two factors that limit plant growth, such as light intensity (decreasing from the top to the bottom of a plant canopy) and soil nitrogen availability (decreasing with soil depth). Each species would occupy a certain region within this two-dimensional **niche space** owing to differences in plant height and rooting depth (Fig. 20.38a). It would perform best at a certain combination of light and soil N, and it would be the superior competitor with this combination. By adding more and more species (Fig. 20.38b), the heterogeneous habitat or the available niche space would be covered more completely (Fig. 20.38c). Since there would be some overlap in the fundamental niches of the species present, they would adjust their niche requirements (realised niche) to reduce niche overlap and competition (Fig. 20.38d, Box 19.3, Hohenheimer Groundwater Experiment). At the species level, niche breadth and niche overlap between species would decrease with increasing diversity. At the community level, the niche space occupied by the species present (or **total niche breadth**) and, hence, resource use would increase with species richness (Fig. 20.38e), allowing a higher biomass production. It must be noted that total niche breadth at the community level would also increase with diversity if the fundamental niches of the species did not overlap at all, that is, the effect would be purely additive and without the need to adjust the niche space with coexisting species. If different, randomly chosen species combinations are present at each level of species richness in a mathematical model, the resulting graph would thus show an asymptotic increase of mean total community biomass with increasing species richness until the resource pool is used up completely (Fig. 20.37b). The upper bound of the data cloud would also increase, indicating that some mixtures perform better than the monocultures, which cannot be explained by selection effects but only by complementarity or positive interactions among species in mixture. Hence, spatial, temporal or chemical resource complementarity has been suggested as an important mechanism underlying the often observed positive relationship between plant diversity and productivity or nutrient cycling. These different forms of complementarity are not mutually exclusive but can occur simultaneously in a mixed community.

Typical examples of resource-use complementarity are mixtures of small and large statured plants, of plants with shallow and deep roots, of sun-adapted trees in the overstorey and shade-tolerant species in the understorey, of early successional and late successional species, of warm-season and cold-season grasses, or of nitrate- vs. ammonium-preferring species. In agroforestry and intercropping, such species have also been called species with good "ecological combining abilities" because they face less competition in combination with other species than when growing only with conspecific neighbours.

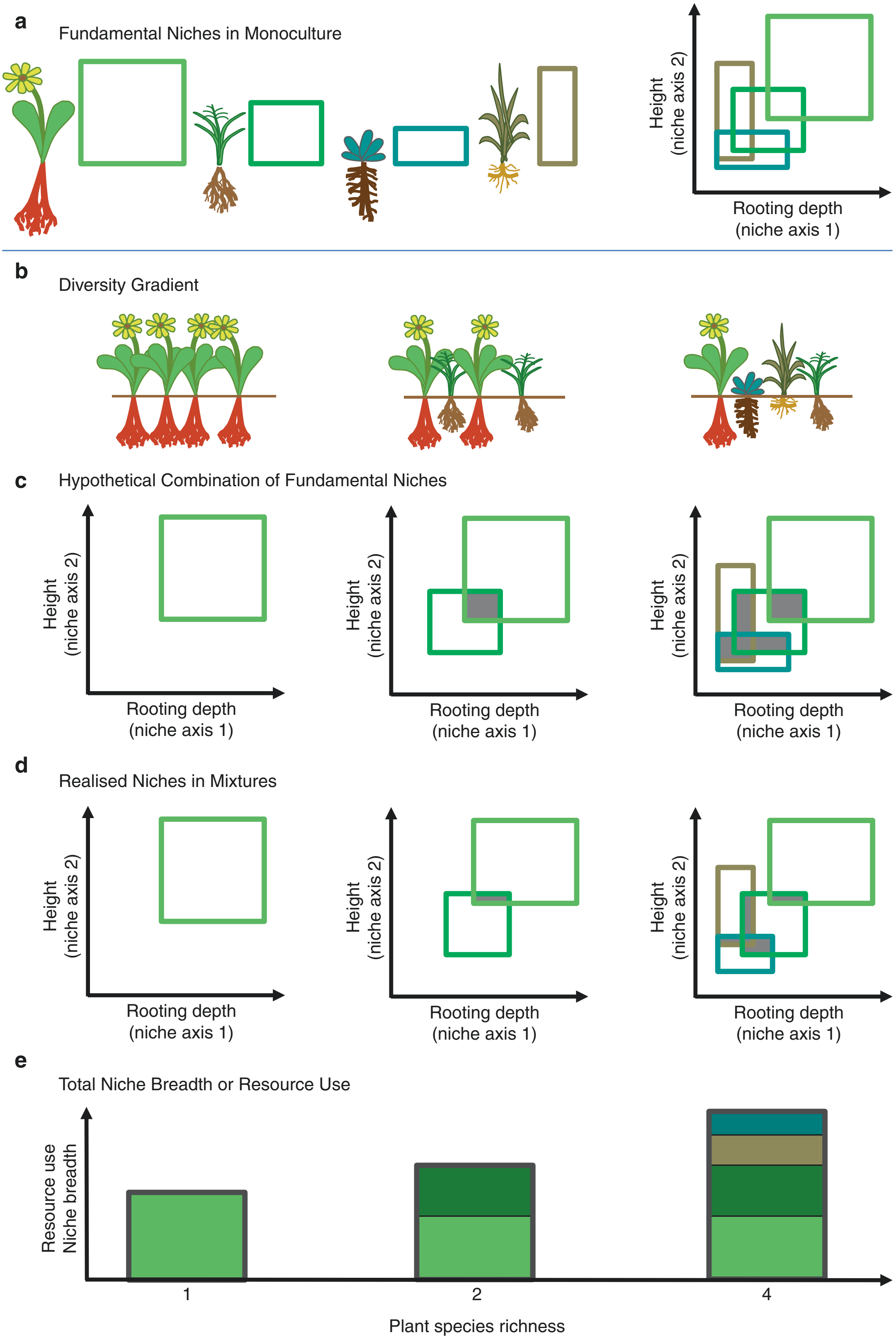

a
Fundamental Niches in Monoculture
Height
(niche axis 2)
Rooting depth
(niche axis 1)
b
Diversity Gradient
c
Hypothetical Combination of Fundamental Niches
Height
(niche axis 2)
Rooting depth
(niche axis 1)
d
Realised Niches in Mixtures
Height
(niche axis 2)
Rooting depth
(niche axis 1)
e
Total Niche Breadth or Resource Use
Resource use
Niche breadth
1
2
4
Plant species richness

Fig. 20.38 Niche occupation and resource complementarity. The complementarity effect is conceptually related to niche differentiation along different resource axes (e.g. above- and below-ground space), with diverging consequences for species' niche breadth, niche overlap among coexisting species and total niche breadth of the community (von Felten et al. 2009). **a** Species exhibit their fundamental niche (coloured boxes) if growing in monoculture, which are spread over the multidimensional niche space. **b** A gradient of plant species richness, for which the consequences are depicted for niche overlap and niche breadth **c**–**e**. Note that plant density remains constant, which is realised in biodiversity experiments using a replacement series or substitutive design (Box 19.1). **c** If one would combine the fundamental niche of several species along a gradient of plant diversity, niche overlap between species (grey areas) would be large. **d** Plants growing in mixtures are adjusting their niche space to avoid competition (realised niche), resulting in a smaller niche space of each individual species (cf. size of coloured boxes in **c** and **d** or of light green box in monoculture and in mixtures) and in lower niche overlap (compare grey areas in **c** and **d**). The lower niche overlap among species allows them to partition resources. **e** The total niche breadth, that is, the total volume occupied by coexisting species in the n-dimensional niche space, increases with the number of species present (total bar size). Each species contributes to total resource use (coloured stacked bars)

Box 20.5: Distinguishing Between Selection and Complementarity Effects

Discussions about the interpretation of early biodiversity experiments mainly centred on the question whether the observed patterns could be explained by niche complementarity or by the selection effect. It is now clear that these two classes of mechanisms are not mutually exclusive and that they can occur simultaneously. In addition, in most experiments, selection effects prevail during the early phases owing to the exponential growth of species that develop quickly and dominate mixed plots initially. Later in the course of the experiment, competitive dynamics take over and niche complementarity effects become stronger (Reich et al. 2012).

But how can one distinguish between these two classes of mechanisms? First, the visual inspection of the diversity–functioning patterns and their upper bounds can indicate the prevalence of selection or complementarity effects if all species are present at all diversity levels (flat in the case of selection effects, increasing in the case of complementarity effects, Fig. 20.37a, b respectively). However, since both complementarity and selection effects can produce similar patterns in a graphical representation and because both effects can occur at the same time, the underlying mechanisms cannot be inferred from patterns alone. Thus, mathematical approaches have been developed that are based on comparisons of plant community performance (e.g. biomass production, nutrient uptake) in monoculture and in mixtures. A very often used method is the additive partitioning approach, developed by Loreau and Hector (2001), which is a further development of approaches used in agronomic studies that calculate the relative yield (RY) of a species, that is, the yield of a species in mixture related to its yield in monoculture, and the relative yield total (RYT) of the entire community. The additive partitioning method calculates a **net biodiversity effect** (NE) and partitions it into two additive constituents: the **complementarity effect** (CE) and the **selection effect** (SE), with NE = CE + SE. If biomass production (or yield) is used as a response variable, the net effect is the difference between observed yield in mixture and the average of the monoculture yields, with a value NE = 0 being indicative of equal growth of plants in mixture and in monoculture ("additive" effect) (Fig. 20.39). The complementarity effect is the difference between observed relative yields (i.e. yield of a species in mixture expressed as a proportion of its yield in monoculture) and the expected relative yield (i.e. null-expectation values or the proportion of the species seeded or planted in mixture).

Values of CE > 0 indicate positive or "synergistic" biodiversity effects by resource complementarity or facilitation, while CE < 0 indicates "antagonistic" effects due to competition by physical or chemical interference. The selection effect occurs when relative yields of species in mixture are related to their monoculture biomass, calculated with a covariance function. NE, CE and SE are usually expressed in dimensions of yield but can be adapted to any ecosystem property measurable at the species level. As shown in several single studies and meta-analyses, NE and CE increase with increasing numbers of plant species and with time, while SE usually fluctuates around zero in most biodiversity experiments, which indicates that niche differences and positive interactions mainly drive biodiversity effects on ecosystems (e.g. Cardinale et al. 2007).

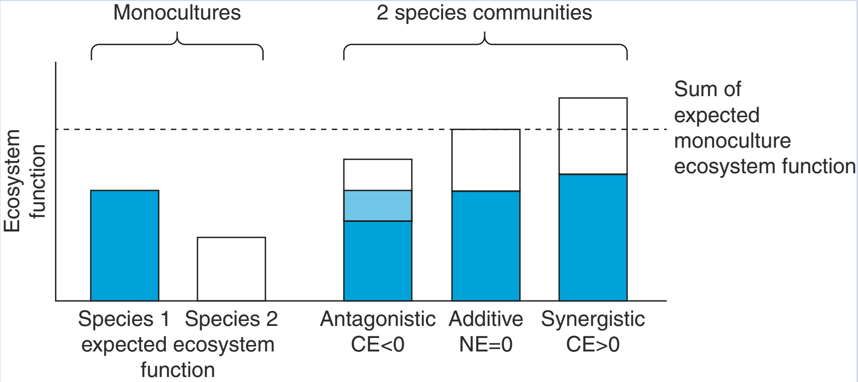
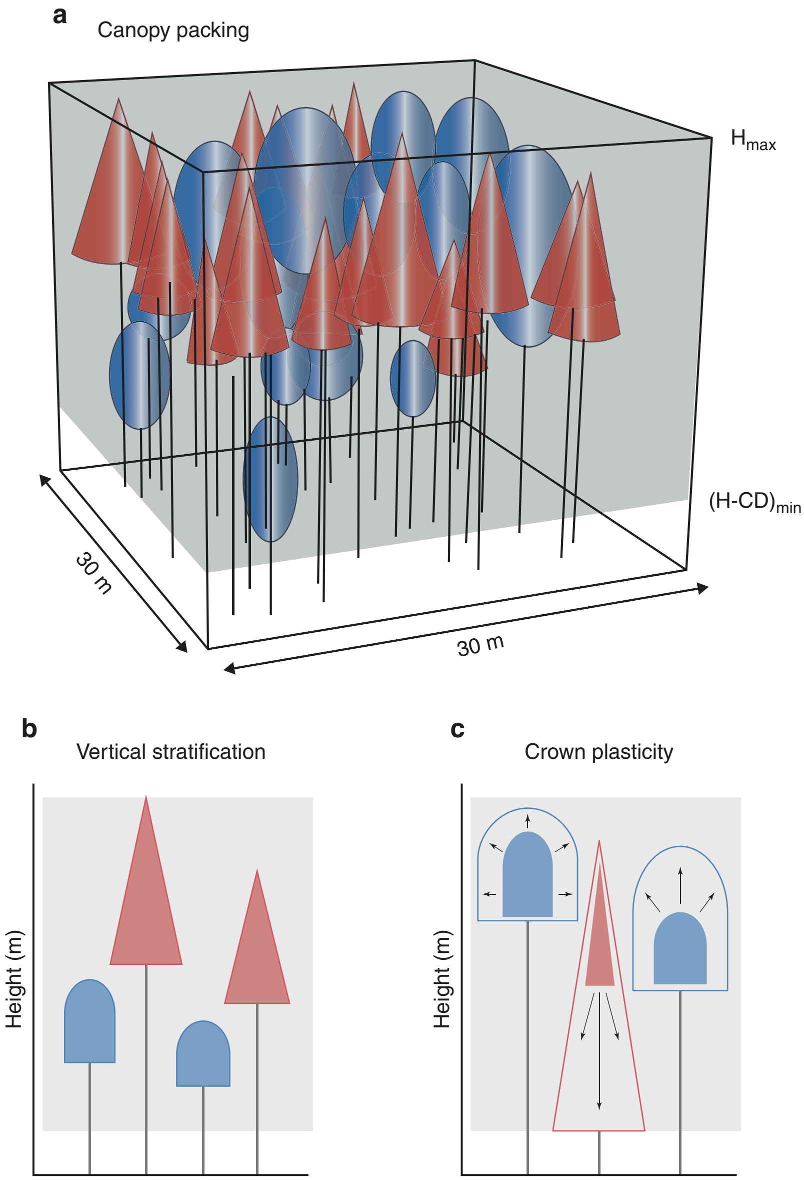


Fig. 20.39 Net effects of species interactions. Depending on the type of species interactions, community-level ecosystem functions, such as biomass production, can be lower, similar or higher than expected based on the performance of the constituent species in monoculture. Antagonistic or negative interactions, such as interference competition for shared and limited resources, result in community growth being worse than the sum of the expected species yields. Additive mixing effects correspond to the sum of the expected monoculture yields (dashed line) and occur if species use non-overlapping resources and do not interact otherwise. Synergistic effects result in higher than expected biomass production and occur if one or both species benefit in mixtures due to complementarity or facilitation. (Modified from Fiegna et al. 2015)

Mathematical approaches are helpful to detect complementarity effects and to distinguish them from selection effects (Box 20.5), but they do not indicate a specific biological process responsible for the observed effects. Thus, other approaches are needed to obtain a more mechanistic understanding of the role of plant diversity in ecosystems. For instance, below-ground resource complementarity can be quantified by determining the species-specific root distribution within the soil or by injecting nutrient or water tracers (e.g. distinct isotopes of nitrogen or water) at different soil depths, at different times of the year or in different chemical forms and measuring their uptake by plants. Aboveground, niche differentiation and complementarity for light can be related to the surface of light-absorbing tissues (mainly LAI) and community light capture (light attenuation within the canopy) or to detailed measures of **canopy packing** or space filling. Values of the LAI and other measures of plant canopy complexity often increase with increasing diversity, as well as with densities of the vertical stand profiles and community heights, all being indicative of higher canopy packing. Optimised canopy packing, which fills the available space more completely with photosynthetic active tissue in both

Fig. 20.40 Potential tree species richness effects on canopy packing. **a** 3D illustration of canopy packing within a 30 × 30 m plot, with maximum tree height (H_{max}), the lowest crown base (defined as the difference between tree height (H) and crown depth (CD) $(H\text{-}CD)_{min}$) and the volume of individual tree crowns (blue and red shapes). The grey shaded region depicts the potentially available space to grow in. **b** Canopy packing can be increased by mixing species that occupy different vertical strata. **c** Alternatively, canopy packing can also be optimised by plastic expansion of crowns to reduce competition with neighbours (Jucker et al. 2015). Reproduced with permission from John Wiley & Sons



space and time (e.g. through phenological niche differentiation), can thus be an important mechanism of above-ground resource complementarity to increase total light interception and canopy photosynthesis.

The role of complementary architectural traits in optimising canopy packing of mixed communities and the relevance of **vertical stratification** and **crown plasticity** can be illustrated nicely with tree stands, where the individual crown dimension can be rather easily quantified (Fig. 20.40). Vertical stratification occurs if tree species with different crown architectures and adaptations to shade coexist, thereby displaying leaves in distinct height strata. Such multilayered canopies develop, for example, during succession, when shade-tolerant, late successional species regenerate and grow under the canopy of light-demanding pioneer species. Crown architecture is additionally highly plastic, as trees adjust their height growth and branching patterns in response to neighbours: alteration of light intensity and of red/far red ratios, that is, light quality, will result in shade-avoidance reactions such as increased height growth (Sect. 3.2).

For example, using a network of 209 permanent forest plots across Europe, spreading a gradient of tree species richness at each of six sites, Jucker et al. (2015) were able to show that canopy packing increased significantly with the number of tree species within a stand. This positive diversity–canopy packing relationship was partly driven by differences in vertical crown stratification between different species (i.e. by mixing species with different canopy heights) (Fig. 20.40b). In addition, species increased crown volume (i.e. developing longer lateral branches and deeper crowns) in mixture compared to monocultures (+38%), thereby showing phenotypic plasticity in response to heterospecific neighbours (Fig. 20.40c).

Increased canopy packing by mixing species will enhance light interception, may increase litter production and alter microclimatic conditions and offers higher structural complexity. These changes will further affect productivity, biogeochemical fluxes and the diversity of other organisms. Thus, managing forests with the goal of safeguarding these functions may be achieved by increasing canopy packing and its structural complexity through mixing of tree species. However, there might be trade-offs between different management goals. For example, increased canopy packing may offer more structural heterogeneity and, thus, more habitats for canopy-living organisms, such as insects or birds (Fig. 20.6). But it may also result in higher light absorption in the tree canopy, and thus lower light availability at the forest floor for understorey vegetation, as well as cooler and dryer soil conditions that also negatively affect nutrient cycling. This highlights the need for local, site-specific management decisions, which might include a weighted valuation of different ecosystem functions or services (e.g. higher value for birds than for understorey plants) or which might include additional silvicultural interventions (e.g. reducing stand density to allow greater light penetration to the understorey).

20.4.9.3 Facilitation and Mutualism

Plants living in close proximity to each other commonly have demands for the same resources and therefore compete with each other. However, plants may also benefit from their neighbours through the amelioration of the physical and biotic environment. If such positive interactions among different species enhance the availability and, hence, capture of resources, then this can also generate a positive relationship between biodiversity and ecosystem processes. For example, **symbiotic fixation of atmospheric nitrogen** by some plant groups, such as legumes, increases the overall availability of nitrogen to the whole community through decomposition of the legume residues rich in N and through reduced competition for soil N (Sects. 7.4 and 16.3). Thus, more biomass can be produced than in the absence of legumes. This N-fertilisation effect is commonly applied in managed grasslands and in intercropping to increase yields, for example, by mixing grasses with clover species or corn with beans, respectively. Hence, positive plant diversity effects on productivity are observed not only in natural or low-intensity grasslands but also in intensively managed grass–clover leys (e.g. Kirwan et al. 2007). **Hydraulic redistribution** or **lift** is another example of facilitation, where deep-rooting species (e.g. trees) take up water from deeper soil layers and release some parts of that water through their roots in upper, drier layers. This water can then be taken up by other, more shallow-rooting species, such as grasses, which therefore benefit from the presence of the trees (Sect. 10.2). Because it is difficult to distinguish facilitative or mutualistic interactions from niche differentiation—in fact, there are many transitions between them—both aspects are often included in a general concept of complementarity.

20.4.9.4 Trophic Interactions and Negative Density-Dependent Effects

Negative density-dependent effects mediated by other trophic levels, in particular seed predators, pathogens and herbivores, may also lead to a positive diversity–productivity relation. Janzen

(1970) and Connell (1971) proposed that specialised seed predators would lead to a negative feedback on tree population growth that depends on the density and distance distribution of host trees (Sect. 19.3). While such **Janzen–Connell effects** have been proposed as an explanation of the high diversity of coexisting trees, they could also explain higher productivity in species-rich communities. In fact, the proportionally low productivity in plant monocultures compared to mixtures can be increased by (partial) soil sterilisation, which destroys fungi, bacteria, nematodes and other pathogenic organisms. These host-specific pathogens and herbivores induce large losses in plant biomass or cause more photosynthates to be diverted to defence mechanisms, leaving less carbon for growth (Sects. 8.1–8.3). Thus, the accumulation of host-specific pathogens over time produces strong negative effects, especially in monocultures or low-diversity mixtures owing to the large abundance of the host species, which facilitates the fast spread of pathogens. This effect have been known for a long time to farmers ("soil fatigue"), who avoid planting the same crop species in consecutive years. Yearly crop rotations are a means to avoid these negative **plant–soil feedback effects**. In mixed communities, such negative feedback will be diluted owing to the lower abundance of specific host species, thereby promoting a positive biodiversity–biomass relationship (van der Putten et al. 2013). In addition, there might also be facilitative, beneficial soil organisms for plants (e.g. microbes in the rhizosphere enhancing mineralisation rates, N-fixing bacteria, mycorrhizal species) (Sects. 7.4 and 19.4) that could accumulate over time, an effect that would be stronger in plant mixtures because different plant species attract different mutualists. Over longer stretches of time, the stronger effects of negative plant–soil feedbacks in monocultures, together with positive interactions that lead to an increasing *per capita* performance in mixtures, contribute to the observation that the slope of the plant diversity–ecosystem functioning relationship often becomes steeper over time (Eisenhauer et al. 2012).

20.4.10 Value of Biodiversity–Ecosystem Functioning Research

After almost two decades of intensive research, biodiversity–ecosystem functioning science has come into a phase of synthesis, fostered by several reviews (Kinzig et al. 2002; Loreau et al. 2002; Naeem et al. 2009; Weisser and Siemann 2004; Scherer-Lorenzen et al. 2005; Hooper et al. 2005; Tilman et al. 2014) and meta-analyses (Balvanera et al. 2006; Cardinale et al. 2006, 2007, 2011). The insights gained are all highly relevant for our fundamental understanding of how ecosystems work and how plant diversity controls ecosystem processes. However, how reliable are results from biodiversity–ecosystem functioning research, which is still largely based on some "artificial" experimental manipulation? Are biodiversity experiments suitable to predict the consequences of species changes in real ecosystems? Can the results from biodiversity–ecosystem functioning studies guide us in developing effective nature conservation or ecosystem management strategies? Can we design sustainable production systems based on the insights obtained from knowledge of biodiversity–ecosystem functioning? Especially for experimental approaches, these questions have generated controversy, despite the fact that they focus on general patterns and ecological mechanisms and less on applied problems of nature conservation (for an overview, see Duffy 2009).

20.4.10.1 Critical Views on Biodiversity–Ecosystem Functioning Experiments

The effects of plant diversity on ecosystem functions often reach an asymptote at rather low levels of diversity in experiments, suggesting redundancy among species at higher diversity levels, while natural ecosystems are often composed of many more species at similar spatial scales. This is only true for short-term experiments, and redundancy has been shown to decrease with the duration of experiments. Redundancy also mostly applies to single functions and is less plausible for multiple functions (Fig. 20.33). In addition, several studies that compared ecosystem functions across gradients in plant diversity in natural ecosystems also found similar diversity effects (e.g. Fig. 20.26). Finally, well-documented species–area relationships (Sect. 18.4) suggest that maintaining a given level of diversity at the local scale requires the conservation of species at regional scales.

Diversity effects are often a result of statistical sampling or selection effects (Sect. 20.4.9), which, unlike resource complementarity, has not been considered to be a "true" diversity effect (Huston 1997). However, sampling or selection effects mostly fade out with the duration of experiments, with complementarity becoming stronger over time. The sampling effect also focuses on single response variables. The maintenance of a variety of ecosystem functions and services provided by real, complex ecosystems requires a large number of species because there is no "super-species" that could provide such different functions at high rates and in several different contexts (Fig. 20.33).

Biodiversity experiments usually involve a substantial effort to maintain the gradient in species richness, for example, by weeding out colonising species, which usually is higher at low than at high diversity. They also often include species that are unlikely to occur in monoculture under the environmental conditions of the site or include species combinations rarely found growing together in nature. These aspects can result in rather low cover of the target species in monoculture or low-diversity mixtures, which would decrease the mean rates of ecosystem functions, such as biomass production, and hence introduce some potential artefacts in biodiversity–ecosystem function relationships. Several studies have now shown that weeding is actually not as detrimental as suspected and that the poor performance of species in monoculture is rather the result of an attack by various pathogens. Thus, higher weeding effort in monocultures could be largely the consequence—and not the cause—of poor monoculture performance.

One major critique is related to the predominant use of random extinction scenarios to create a gradient of plant diversity in experiments, while species loss in real ecosystems is usually not random but is based on species abundance, rarity and vulnerability. One might postulate that loss of less abundant, rare species should have fewer effects than a random scenario because the remaining and dominant species could compensate for the loss. However, theoretical studies, simulations and experiments that applied non-random extinction scenarios also found diversity effects on several ecosystem processes, sometimes even stronger than those based on random-loss designs. One could also argue that applying a random-loss order is a good starting point to study the consequences of diversity changes because future causes of species extinctions might be different than current ones. In fact, studying the effects of diversity change in experiments has produced an astonishing wealth of knowledge about the **general nature** of the relationship between biodiversity and ecosystem functioning (Schmid and Hector 2004). Nevertheless, the scientific evidence for consequences of realistic, non-random extinction scenarios is still much weaker than that of random scenarios, leaving room for further investigations.

Confusion often arises owing to the fact that plant diversity often declines as productivity increases at high levels of resource supply ("paradox of enrichment") (Sect. 20.3.3), while the "opposite" is mostly found in studies examining the ecosystem effects of changing diversity (Sect. 20.4.2). However, these views are not contradictory but rather focus on two different angles on the bidirectional relationship between species diversity and productivity: the former illustrates the response of species diversity to changing resource availability **across** ecosystems, which determines the potential for biomass production and diversity. In contrast, biodiversity experiments study the consequences of diversity changes for productivity (and other functions) **within** ecosystems in which resource levels are held constant. Thus, at any given level along a resource gradient, the availability of resources will determine the number and composition of species, while a reduction of species at this resource level will mostly result in reduced biomass production.

20.4.10.2 Relevance of Biodiversity–Ecosystem Function Research for Sustainable Production Systems, Nature Conservation and Ecosystem Management

Based on the assumption that diversity effects are generally robust (and there is now substantial evidence for it, at least from experiments directly manipulating diversity), we can suggest that **biodiversity can be used as a tool** to enhance productivity, stability and other ecosystem functions in production systems while at the same time reducing the input of agrochemicals and fertilisers. Starting from performance and trait expression in monocultures, it is possible to design optimal species combinations for the delivery of single or multiple ecosystem functions or services (e.g. Storkey et al. 2015). However, it must be taken into account that performance may change in mixtures owing to phenotypic plasticity, which will also lead to different observed levels of ecosystem function in mixtures than what would be expected based on monoculture performance (Sect. 20.4.9). In fact, there are several examples showing that high-diversity mixtures of plant species utilised in intensively used grasslands, forests or bioenergy production systems produce equivalent or sometimes even greater quantities of biomass than monoculture-based systems (e.g. Dickson and Gross 2015; Finn et al. 2013), often at lower levels of herbivory and inputs of fertilisers or other agrochemicals and with lower losses of nutrients or trace gases. Such **low-input**, **high-diversity systems** may thus be a sustainable option for biomass production, such as for forage, biofuels or biomaterials, which can combine conservation and greenhouse gas mitigation goals with production orientated goals (Tilman et al. 2006; Weigelt et al. 2009). Such production systems should have substantial advantages over high-input, low-diversity systems, especially in conditions of high environmental heterogeneity, as illustrated in Fig. 20.41. The upper solid curve shows the diversity–yield relationship under conditions of low environmental variability, for example, constrained by high fertiliser and pesticide input or irrigation. In this case, a single, very highly productive species grown in monoculture can achieve yields higher than or comparable to those of polycultures (blue dots). Farmers and foresters have selected such high-yielding or fast-growing species to maximise yields in short time spans, supporting them by excluding competing species or adding soil resources. Examples include corn (*Zea mays*), switchgrass (*Panicum virgatum*), Douglas fir (*Pseudotsuga menziesii*) or eucalypts (*Eucalyptus* spp.). In contrast, the lower dashed line shows the same relationship under conditions of large spatial or temporal environmental heterogeneity, for example, where it is too costly or impossible to homogenise the environment via agrochemicals, fertilisers or irrigation. In that case, polycultures of complementary species (due to niche differentiation) will produce higher yields than single species.

Finally, it can be questioned whether changes in biodiversity can have effects comparable to those of other drivers of global change, such as eutrophication, climate change or land-use change, which have significant impacts on ecosystems (Chap. 23). At least for biomass production, there is accumulating evidence that the effects of species loss are on the same order of magnitude as those of eutrophication in the form of nitrogen deposition or nutrient fertilisation, drought stress, fire, herbivory or elevated CO_2 (Hooper et al. 2012; Tilman et al. 2012). Thus, the global loss of biodiversity we are facing today is certainly one of the major drivers of changes in ecosystem functioning and, thus, is also strongly affecting the delivery of ecosystem services for humanity. Hence, besides ethical considerations, the strong control that biodiversity has on ecosystem multifunctionality and stability should be another, utilitarian argument for conservation and restoration of biological diversity in the era of human dominance of almost all global ecosystems.

Nevertheless, we close this chapter with a **note of caution**: high biodiversity or high levels of ecosystem functioning are often a reasonable goal for nature conservation or ecosystem management, but they are not always “good” or “desired”: for

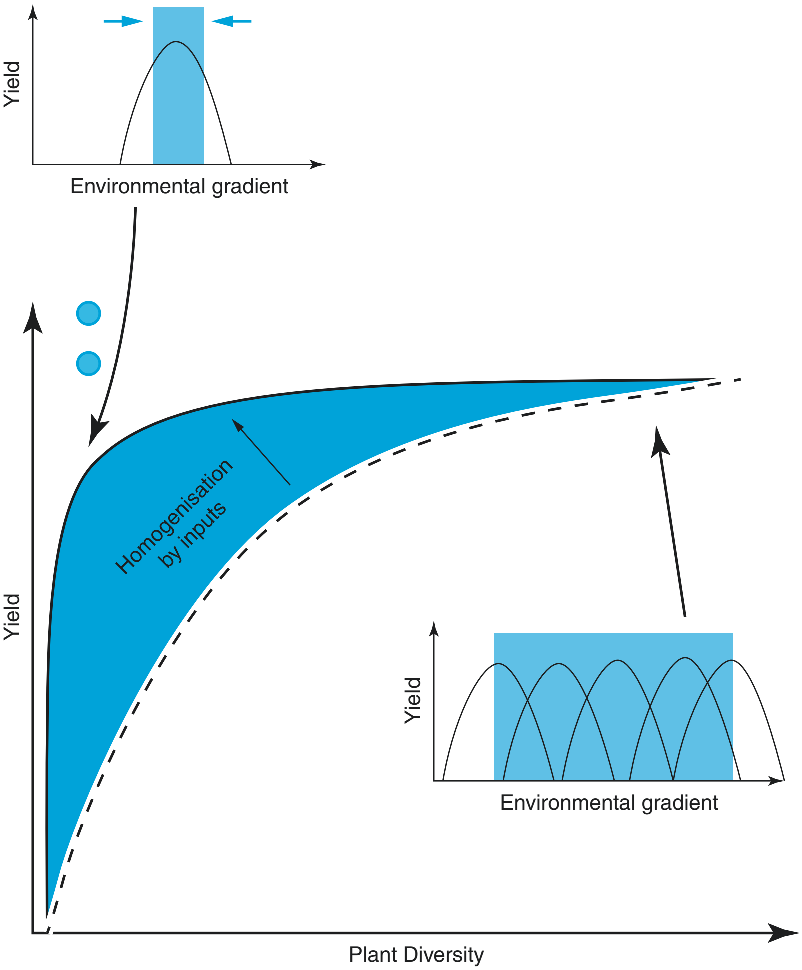


Fig. 20.41 Conceptual graph showing the potential of using high crop diversity to achieve high yields. The upper solid curve shows the diversity–yield relationship under conditions of low environmental variability (e.g. constrained by management interventions). The lower dashed line shows the same relationship under conditions of large spatial or temporal environmental heterogeneity (e.g. where it is too costly or impossible to homogenise the environment). Blue dots represent single, very high productive species. The insets show yield responses of single species along environmental gradients, and the blue shaded region represents the range of environmental conditions exhibited overs space and time (Modified from Isbell et al. 2017)

example, an increase of plant diversity in naturally species-poor ecosystems, such as raised bogs, is often indicative of substantial changes in site conditions, for example, through drainage. Similarly, an increase in productivity in oligotrophic ecosystems, such as acidic grasslands, is also often due to human-induced changes in resource availability, for example, through fertilisation or atmospheric nitrogen deposition. We should therefore base conservation efforts not only on general biodiversity–ecosystem functioning relationships, but on ecosystem- and site-specific targets of biodiversity (e.g. rare species, keystone and umbrella species, representative communities, natural seral communities) and ecological processes (e.g. predator–prey interactions, pollination, soil stabilisation, carbon sequestration).

Summary

- Biodiversity—or biological diversity—encompasses the variability of biological entities from all sources, including, *inter alia*, terrestrial, marine and other aquatic ecosystems, and the ecological complexes of which they are part, across all levels of biological hierarchies. This includes diversity within and between species and of ecosystems.
- Biodiversity can be categorised into compositional, structural and functional diversity, focusing on the elements that account for biodiversity and the resulting physical structures and functional consequences for ecosystems.
- Plant (functional) traits encompass morphological, anatomical, biochemical, physiological and phenological properties of organisms

that reflect their evolutionary history and shape their performance. They have a direct or indirect impact on the fitness of plant individuals through their effects on growth, reproduction and survival. Traits strongly determine the ecological role of plants within a community through their responses to environmental factors and their effects on other trophic levels or ecosystem processes.

- Plant species have evolved in certain areas and are adapted to specific environmental conditions. Hence, plant diversity shows striking spatial patterns at various spatial scales, reflecting the role of environmental filters that control species presence and absence. The availability of energy and water and environmental heterogeneity and disturbance regimes are major factors affecting diversity patterns. Human land use and management has strongly modified these patterns.
- Plant species richness sometimes peaks at intermediate levels along gradients of site productivity (humped-back productivity–diversity model). However, both productivity and richness are influenced by a multitude of factors and processes, making multivariate controls of plant diversity more relevant than simple bivariate relationships.
- Loss of biodiversity and alterations in plant species composition can influence ecological processes and functions within ecosystems, resulting in “biodiversity–ecosystem functioning” relationships. These can be driven either by the degree of dominance (i.e. abundance) and the identity (i.e. presence and value of functional traits) of the dominant species or by antagonistic or synergistic interactions among co-occurring species.
- There is often a positive relationship between plant diversity and multiple ecosystem processes. More diverse systems consistently have higher biomass production, higher nutrient uptake and, consequently, lower leaching losses to the groundwater, and they are more resistant to pathogens or invasion by other species than the corresponding monocultures. However, polycultures often produce less biomass than the highest yielding species grown in monoculture and retain lower amounts of soil resources than the most efficient monoculture. Loss of biodiversity usually increases temporal stability and the resistance of ecosystems in the face of disturbances.
- Mechanisms underlying the observed biodiversity–ecosystem functioning relationship include sampling and selection effects, resource complementarity among species due to niche differentiation, facilitation and mutualisms, or trophic interactions.
- Biodiversity–ecosystem functioning research has greatly improved our general understanding of community and ecosystem ecology, but it also has consequences for ecosystem management and the design of sustainable production systems in agriculture or forestry.

References

Adler PB, Seabloom EW, Borer ET, Hillebrand H, Hautier Y, Hector A, Harpole WS, O’Halloran LR, Grace JB, Anderson TM, Bakker JD, Biederman LA, Brown CS, Buckley YM, Calabrese LB, Chu C-J, Cleland EE, Collins SL, Cottingham KL, Crawley MJ, Damschen EI, Davies KF, DeCrappeo NM, Fay PA, Firn J, Frater P, Gasarch EI, Gruner DS, Hagenah N, Hille Ris Lambers J, Humphries H, Jin VL, Kay AD, Kirkman KP, Klein JA, Knops JMH, La Pierre KJ, Lambrinos JG, Li W, MacDougall AS, McCulley RL, Melbourne BA, Mitchell CE, Moore JL, Morgan JW, Mortensen B, Orrock JL, Prober SM, Pyke DA, Risch AC, Schuetz M, Smith MD, Stevens CJ, Sullivan LL, Wang G, Wragg PD, Wright JP, Yang LH (2011) Productivity is a poor predictor of plant species richness. Science 333(6050):1750–1753

Al-Mufti MM, Sydes CL, Furness SB, Grime JP, Band SR (1977) Quantitative analysis of shoot phenology and dominance in herbaceous vegetation. J Ecol 65:759–791

Bai Y, Wu J, Pan Q, Huang J, Wang Q, Li F, Buyantuyev A, Han X (2007) Positive linear relationship between productivity and diversity: evidence from the Eurasian Steppe. J Appl Ecol 44(5):1023–1034

Balvanera P, Pfisterer AB, Buchmann N, He J-S, Nakashizuka T, Raffaelli D, Schmid B (2006) Quantifying the evidence for biodiversity effects on ecosystem functioning and services. Ecol Lett 9(10):1146–1156

Barthlott W, Mutke J, Rafiqpoor MD, Kier G, Kreft H (2005) Global centres of vascular plant diversity. Nova Acta Leopoldina 92:61–83

Baruffol M, Schmid B, Bruelheide H, Chi X, Hector A, Ma K, Michalski S, Tang Z, Niklaus PA (2013) Biodiversity promotes tree growth during succession in subtropical forest. PLoS One 8(11):e81246

Bond W (1983) On alpha diversity and the richness of the Cape flora: a study in southern Cape Fynbos. In: Kruger FJ, Mitchell DT, Jarvis JUM (eds) Mediterranean type ecosystems: the role of nutrients. Springer, New York, pp 337–356

Bray JR, Curtis JT (1957) An ordination of upland forest communities of southern Wisconsin. Ecol Monogr 27:325–349

Byrnes JEK, Gamfeldt L, Isbell F, Lefcheck JS, Griffin JN, Hector A, Cardinale BJ, Hooper DU, Dee LE, Duffy JE (2014) Investigating the relationship between biodiversity and ecosystem multifunctionality: challenges and solutions. Methods Ecol Evol 5:111–124

Cadotte M, Albert CH, Walker SC (2013) The ecology of differences: assessing community assembly with trait and evolutionary distances. Ecol Lett 16(10):1234–1244

Cadotte MW (2013) Experimental evidence that evolutionarily diverse assemblages result in higher productivity. Proc Natl Acad Sci USA 110(22):8996–9000

Cadotte MW, Davies TJ, Regetz J, Kembel SW, Cleland E, Oakley TH (2010) Phylogenetic diversity metrics for ecological communities: integrating species richness, abundance and evolutionary history. Ecol Lett 13:96–105

Cahill JF (1999) Fertilization effects on interactions between above- and belowground competition in an old field. Ecology 80:466–480

Callaway RM (2007) Positive interactions and interdependence in plant communities. Springer, Dordrecht

Canadell J, Jackson RB, Ehleringer JB, Mooney HA, Sala OE, Schulze E-D (1996) Maximum rooting depth of vegetation types at the global scale. Oecologia 108(4):583–595

Cardinale BJ, Duffy JE, Gonzalez A, Hooper DU, Perrings C, Venail P, Narwani A, Mace GM, Tilman D, Wardle DA, Kinzig AP, Daily GC, Loreau M, Grace JB, Larigauderie A, Srivastava DS, Naeem S (2012) Biodiversity loss and its impact on humanity. Nature 486(7401):59–67

Cardinale BJ, Matulich KL, Hooper DU, Byrnes JE, Duffy E, Gamfeldt L, Balvanera P, O'Connor MI, Gonzalez A (2011) The functional role of producer diversity in ecosystems. Am J Bot 98(3):572–592

Cardinale BJ, Nelson K, Palmer MA (2000) Linking species diversity to the functioning of ecosystems: on the importance of the environmental context. Oikos 91:175–183

Cardinale BJ, Srivastava DS, Duffy EJ, Wright JP, Downing AL, Sankaran M, Jouseau C (2006) Effects of biodiversity on the functioning of trophic groups and ecosystems. Nature 443(7114):989–992

Cardinale BJ, Wright JP, Cadotte MW, Carroll IT, Hector A, Srivastava DS, Loreau M, Weis JJ (2007) Impacts of plant diversity on biomass production increase through time because of species complementarity. Proc Natl Acad Sci 104(46):18123–18128

Castagneyrol B, Jactel H, Vacher C, Brockerhoff EG, Koricheva J (2014) Effects of plant phylogenetic diversity on herbivory depend on herbivore specialization. J Appl Ecol 51:134–141

Clarke A, Gaston KJ (2006) Climate, energy and diversity. Proc R Soc B-Biol Sci 273(1599):2257–2266

Clements FE (1916) Plant succession: an analysis of the development of vegetation, vol Publication 242. Carnegie Institution of Washington, Washington, DC

Connell JH (1971) On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. In: den Boer PJ, Gradwell GR (eds) Dynamics of populations. Centre for Agricultural Publishing and Documentation, Wageningen, pp 298–312

Cornelissen JHC, Lavorel S, Garnier E, Diaz S, Buchmann N, Gurvich DE, Reich PB, ter Steege H, Morgan HD, van der Heijden MGA, Pausas JG, Poorter H (2003) A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. Aust J Bot 51(4):335–380

Cotrufo MF, Wallenstein MD, Boot CM, Denef K, Paul E (2013) The Microbial Efficiency-Matrix Stabilization (MEMS) framework integrates plant litter decomposition with soil organic matter stabilization: do labile plant inputs form stable soil organic matter? Glob Change Biol 19(4):988–995

Cotta JH (1828) Anweisung zum Waldbau. Arnoldische Buchhandlung, Dresden, Leipzig

Currie DJ (1991) Energy and large-scale biogeographical patterns of animal and plant species richness. Am Nat 137:27–49

Darwin C (1872) On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life. John Murray, London

de Groot RS, Alkemadeb R, Braatc L, Heina L, Willemen L (2010) Challenges in integrating the concept of ecosystem services and values in landscape planning, management and decision making. Ecol Complex 7(3):260–272

de Queiroz K (2005) Ernst Mayr and the modern concept of species. Proc Natl Acad Sci 102(Suppl 1): 6600–6607

de Queiroz K (2007) Species concepts and species delimitation. Syst Biol 56(6):879–886

Diamond J (1975) Assembly of species communities. In: Cody ML, Diamond J (eds) Ecology and evolution of communities. Cambridge, MA, Belknap, pp 342–444

Díaz S, Cabido M (2001) Vive la différence: plant functional diversity matters to ecosystem processes. Trends Ecol Evol 16(11):646–655

Díaz S, Purvis A, Cornelissen JHC, Mace GM, Donoghue MJ, Ewers RM, Jordano P, Pearse WD (2013) Functional traits, the phylogeny of function, and ecosystem service vulnerability. Ecol Evol 3(9):2958–2975

Díaz S, Wardle DA, Hector A (2009) Incorporating biodiversity in climate change mitigation initiatives. In: Naeem S, Bunker DE, Hector A, Loreau M, Perrings C (eds) Biodiversity, ecosystem functioning, and human wellbeing: an ecological and economic perspective. Oxford University Press, Oxford, pp 149–166

Dice LR (1945) Measures of the amount of ecologic association between species. Ecology 26(3):297–302

Dickson TL, Gross KL (2015) Can the results of biodiversity-ecosystem productivity studies be translated to bioenergy production? PLoS One 10(9):e0135253

Dimitrakopoulos PG, Schmid B (2004) Biodiversity effects increase linearly with biotope space. Ecol Lett 7:574–583

Doak DF, Bigger D, Harding EK, Marviesr MA, O'Malley RE, Thomson D (1998) The statistical inevitability of stability-diversity relationships in community ecology. Am Nat 151(3):264–276

Duffy JE (2009) Why biodiversity is important to the functioning of real-world ecosystems. Front Ecol Environ 7(8):437–444

Drude O (1887) Die systematische und geographische Anordnung der Phanerogamen. In: Schenk A (ed) Handbuch der Botanik, vol III/2. Trewendt, Breslau, pp 175–496

Ebeling A, Pompe S, Baade J, Eisenhauer N, Hillebrand H, Proulx R, Roscher C, Schmid B, Wirth C, Weisser WW (2014) A trait-based experimental approach to understand the mechanisms underlying biodiversity-ecosystem functioning relationships. Basic Appl Ecol 15:229–240

Eisenhauer N, Bessler H, Engels C, Gleixner G, Habekost M, Milcu A, Partsch S, Sabais ACW, Scherber C, Steinbeiss S, Weigelt A, Weisser WW, Scheu S (2010) Plant diversity effects on soil microorganisms support the singular hypothesis. Ecology 91(2):485–496

Eisenhauer N, Reich PB, Scheu S (2012) Increasing plant diversity effects on productivity with time due to delayed soil biota effects on plants. Basic Appl Ecol 13:571–578

Elton CS (1958) The ecology of invasions by animals and plants. Methuen, London

Fiegna F, Moreno-Letelier A, Bell T, Barraclough TG (2015) Evolution of species interactions determines microbial community productivity in new environments. ISME J 9(5):1235–1245

Finn JA, Kirwan L, Connolly J, Sebastià MT, Helgadottir A, Baadshaug OH, Bélanger G, Black A, Brophy C, Collins RP, Čop J, Dalmannsdóttir S, Delgado I, Elgersma A, Fothergill M, Frankow-Lindberg BE, Ghesquiere A, Golinska B, Golinski P, Grieu P, Gustavsson A-M, Höglind M, Huguenin-Elie O, Jørgensen M, Kadziuliene Z, Kurki P, Llurba R, Lunnan T, Porqueddu C, Suter M, Thumm U, Lüscher A (2013) Ecosystem function enhanced by combining four functional types of plant species in intensively managed grassland mixtures: a 3-year continental-scale field experiment. J Appl Ecol 50(2):365–375

Fischer C, Tischer J, Roscher C, Eisenhauer N, Ravenek J, Gleixner G, Attinger S, Jensen B, de Kroon H, Mommer L, Scheu S, Hildebrandt A (2015) Plant species diversity affects infiltration capacity in an experimental grassland through changes in soil properties. Plant Soil 397(1–2):1–16

Forrester DI (2014) The spatial and temporal dynamics of species interactions in mixed-species forests: from pattern to process. Forest Ecol Manag 312:282–292

Fraser LH, Pither J, Jentsch A, Sternberg M, Zobel M, Askarizadeh D, Bartha S, Beierkuhnlein C, Bennett JA, Bittel A, Boldgiv B, Boldrini II, Bork E, Brown L, Cabido M, Cahill J, Carlyle CN, Campetella G, Chelli S, Cohen O, Csergo A-M, Díaz S, Enrico L, Ensing D, Fidelis A, Fridley JD, Foster B, Garris H, Goheen JR, Henry HAL, Hohn M, Jouri MH, Klironomos J, Koorem K, Lawrence-Lodge R, Long R, Manning P, Mitchell R, Moora M, Müller SC, Nabinger C, Naseri K, Overbeck GE, Palmer TM, Parsons S, Pesek M, Pillar VD, Pringle RM, Roccaforte K, Schmidt A, Shang Z, Stahlmann R, Stotz GC, Sugiyama S-I, Szentes S, Thompson D, Tungalag R, Undrakhbold S, van Rooyen M, Wellstein C, Wilson JB, Zupo T (2015) Worldwide evidence of a unimodal relationship between productivity and plant species richness. Science 349(6245):302–305

Fridley JD (2002) Resource availability dominates and alters the relationship between species diversity and ecosystem productivity in experimental plant communities. Oecologia 132:271–277

Friedmann EI (1982) Endolithic microorganisms in the Antarctic cold desert. Science 215:1045–1053

Fromm E (1964) The heart of man. Harper & Row, New York

Garnier E, Cortez J, Billes G, Navas ML, Roumet C, Debussche M, Laurent G, Blanchard A, Aubry D, Bellmann A, Neill C, Toussaint JP (2004) Plant functional markers capture ecosystem properties during secondary succession. Ecology 85(9):2630–2637

Garnier E, Navas ML, Grigulis K (2015) Plant functional diversity. Organism traits, community structure, and ecosystem properties. Oxford University Press, Oxford

Gartner TB, Cardon ZG (2004) Decomposition dynamics in mixed-species leaf litter. Oikos 104:230–246

Gaston KJ, Spicer JI (1998) Biodiversity: an introduction. Blackwell Science, Oxford, London, Edinburgh

Gaston KJ, Spicer JI (2004) Biodiversity: An introduction. Wiley-Blackwell, Malden, Oxford, Carlton

Gravel D (2013) Assembly models. Ecology, Oxford Bibliographies Online

Griffin JN, O'Gorman EJ, Mmerson MC, Jenkins SR, Klein A-M, Loreau M, Symstad A (2009) Biodiversity and the stability of ecosystem functioning. In: Naeem S, Bunker DE, Hector A, Loreau M, Perrings C (eds) Biodiversity, ecosystem functioning, and human wellbeing. Oxford University Press, Oxford, New York, pp 78–93

Grime JP (1998) Benefits of plant diversity to ecosystems: immediate, filter and founder effects. J Ecol 86:902–910

Grime JP (2001) Plant strategies and vegetation processes, 2nd edn. John Wiley and Sons, Chichester

Grime JP (2006) Trait convergence and trait divergence in herbaceous plant communities: mechanisms and consequences. J Veg Sci 17(2):255–260

Hantsch L, Braun U, Scherer-Lorenzen M, Bruelheide H (2013) Species richness and species identity effects on occurrence of foliar fungal pathogens in a tree diversity experiment. Ecosphere 4(7):Article 81

Hättenschwiler S (2005) Effects of tree species diversity on litter quality and decomposition. In: Scherer-Lorenzen M, Körner C, Schulze E-D (eds) Forest diversity and function: temperate and boreal systems, Ecological studies, vol 176. Springer, Berlin, Heidelberg, New York, pp 149–164

Hättenschwiler S, Tiunov AV, Scheu S (2005) Biodiversity and litter decomposition in terrestrial ecosystems. Annu Rev Ecol Evol Syst 36(1):191–218

Hautier Y, Niklaus PA, Hector A (2009) Competition for light causes plant biodiversity loss after eutrophication. Science 324:636–638

Hector A, Hooper R (2002) Darwin and the first ecological experiment. Science 295:639–640

Hector A, Schmid B, Beierkuhnlein C, Caldeira MC, Diemer M, Dimitrakopoulos PG, Finn J, Freitas H, Giller PS, Good J, Harris R, Högberg P, Huss-Danell K, Joshi J, Jumpponen A, Körner C, Leadley PW, Loreau M, Minns A, Mulder CPH, O'Donovan G, Otway SJ, Pereira JS, Prinz A, Read DJ, Scherer-Lorenzen M, Schulze E-D, Siamantziouras A-SD, Spehn E, Terry AC, Troumbis AY, Woodward FI, Yachi S, Lawton JH (1999) Plant diversity and productivity experiments in European grasslands. Science 286:1123–1127

Heywood VH, Watson RT (eds) (1995) Global biodiversity assessment. Cambridge University Press, Cambridge

Hillebrand H (2004) On the generality of the latitudinal diversity gradient. Am Nat 163(2):192–211

Hillebrand H, Bennett DM, Cadotte MW (2008) Consequences of dominance: a review of evenness effects on local and regional ecosystem processes. Ecology 89(6):1510–1520

Hillebrand H, Matthiessen B (2009) Biodiversity in a complex world: consolidation and progress in functional biodiversity research. Ecol Lett 12:1405–1419

Hooper DU, Adair EC, Cardinale BJ, Byrnes JEK, Hungate BA, Matulich KL, Gonzalez A, Duffy JE, Gamfeldt L, O'Connor MI (2012) A global synthesis reveals biodiversity loss as a major driver of ecosystem change. Nature 486(7401):105–108

Hooper DU, Chapin FSI, Ewel JJ, Hector A, Inchausti P, Lavorel S, Lawton JH, Lodge D, Loreau M, Naeem S, Schmid B, Setälä H, Symstad AJ, Vandermeer J, Wardle DA (2005) Effects of biodiversity on ecosystem functioning: a consensus of current knowledge and needs for future research. Ecol Monogr 75(1):3–36

Huston MA (1979) A general hypothesis of species diversity. Am Nat 113:81–101

Huston MA (1994) Biological diversity. Cambridge University Press, Cambridge

Huston MA (1997) Hidden treatments in ecological experiments: re-evaluating the ecosystem function of biodiversity. Oecologia 110:449–460

Isbell F, Adler PB, Eisenhauer N, Fornara DA, Kimmel K, Kremen C, Letourneau DK, Liebmna M, Polley HW, Quijas S, Scherer-Lorenzen M (2017) Benefits of increasing plant diversity in sustainable agroecosystems. J Ecol 105:871–879

Isbell F, Calcagno V, Hector A, Connolly J, Harpole WS, Reich PB, Scherer-Lorenzen M, Schmid B, Tilman D, van Ruijven J, Weigelt A, Wilsey BJ, Zavaleta ES, Loreau M (2011) High plant diversity is needed to maintain ecosystem services. Nature 477:199–202

Isbell F, Craven D, Connolly J, Loreau M, Schmid B, Beierkuhnlein C, Bezemer TM, Bonin C, Bruelheide H, de Luca E, Ebeling A, Griffin JN, Guo Q, Hautier Y, Hector A, Jentsch A, Kreyling J, Lanta V, Manning P, Meyer ST, Mori AS, Naeem S, Niklaus PA, Polley HW, Reich PB, Roscher C, Seabloom EW, Smith MD, Thakur MP, Tilman D, Tracy BF, van der Putten WH, van Ruijven J, Weigelt A, Weisser WW, Wilsey B, Eisenhauer N (2015) Biodiversity increases the resistance of ecosystem productivity to climate extremes. Nature 526:574–577

Jaccard P (1912) The distribution of the flora of the alpine zone. New Phytol 11:37–50

Jactel H, Brockerhoff EG (2007) Tree diversity reduces herbivory by forest insects. Ecol Lett 10:835–848

Janzen DH (1970) Herbivores and the number of tree species in tropical forests. Am Nat 104:501–528

Jucker T, Bouriaud O, Avacaritei D, Coomes DA (2014) Stabilizing effects of diversity on aboveground wood production in forest ecosystems: linking patterns and processes. Ecol Lett 17(12):1560–1569

Jucker T, Bouriaud O, Coomes DA (2015) Crown plasticity enables trees to optimize canopy packing in mixed-species forests. Funct Ecol 29(8):1078–1086

Kattge J, Díaz S, Lavorel S, Prentice IC, Leadley P, Bönisch G, Garnier E, Westoby M, Reich PB, Wright IJ, Cornelissen JHC, Violle C, Harrison SP, Van Bodegom PM, Reichstein M, Enquist BJ, Soudzilovskaia NA, Ackerly DD, Anand M, Atkin O, Bahn M, Baker TR, Baldocchi D, Bekker R, Blanco CC, Blonder B, Bond WJ, Bradstock R, Bunker DE, Casanoves F, Cavender-Bares J, Chambers JQ, Chapin FS III, Chave J, Coomes D, Cornwell WK, Craine JM, Dobrin BH, Duarte L, Durka W, Elser J, Esser G, Estiarte M, Fagan WF, Fang J, Fernández-Méndez F, Fidelis A, Finegan B, Flores O, Ford H, Frank D, Freschet GT, Fyllas NM, Gallagher RV, Green WA, Gutierrez AG, Hickler T, Higgins SI, Hodgson JG, Jalili A, Jansen S, Joly CA, Kerkhoff AJ, Kirkup D, Kitajima K, Kleyer M, Klotz S, Knops JMH, Kramer K, Kühn I, Kurokawa H, Laughlin D, Lee TD, Leishman M, Lens F, Lenz T, Lewis SL, Lloyd J, LlusiÀ J, Louault F, Ma S, Mahecha MD, Manning P, Massad T, Medlyn BE, Messier J, Moles AT, Müller SC, Nadrowski K, Naeem S, Niinemets Ü, Nöllert S, Nüske A, Ogaya R, Oleksyn J, Onipchenko VG, Onoda Y, Ordonez J, Overbeck G, Ozinga WA, Patiño S, Paula S, Pausas JG, Penuelas J, Phillips OL, Pillar V, Poorter H, Poorter L, Poschlod P, Prinzing A, Proulx R, Rammig A, Reinsch S, Reu B, Sack L, Salgado-Negret B, Sardans J, Shiodera S, Shipley B, Siefert A, Sosinski E, Soussana JF, Swaine E, Swenson N, Thompson K, Thornton P, Waldram M, Weiher E, White M, White S, Wright SJ, Yguel B, Zaehle S, Zanne AE, Wirth C (2011) TRY – a global database of plant traits. Glob Change Biol 17(9):2905–2935

Keddy PA (1992) Assembly and response rules - 2 goals for predictive community ecology. J Veg Sci 3(2):157–164

Kinzig AP, Pacala SW, Tilman D (eds) (2002) The functional consequences of biodiversity: empirical progress and theoretical extensions, Monographs in population biology, vol 33. Princeton University Press, Princeton, Oxford

Kirwan L, Lüscher A, Sebastia MT, Finn JA, Collins RP, Porqueddu C, Helgadottir A, Baadshaug OH, Brophy C, Coran C, Dalmannsdottir S, Delgado I, Elgersma A, Fothergill M, Frankow-Lindberg BE, Golinski P, Grieu P, Gustavsson AM, Hoglind M, Huguenin-Elie O, Iliadis C, Jorgensen M, Kadziuliene Z, Karyotis T, Lunnan T, Malengier M, Maltoni S, Meyer V, Nyfeler D, Nykanen-Kurki P, Parente J, Smit HJ, Thumm U, Connolly J (2007) Evenness drives consistent diversity effects in intensive grassland systems across 28 European sites. J Ecol 95(3):530–539

Kleidon A, Mooney HA (2000) A global distribution of biodiversity inferred from climatic constraints: results from a process-based modelling study. Glob Change Biol 6(5):507–523

Körner C (2003) Alpine plant life. Functional plant ecology of high mountain ecosystems, 2nd edn. Springer, Berlin, Heidelberg, New York

Körner C (2005) An introduction to the functional diversity of temperate forest trees. In: Scherer-Lorenzen M, Körner C, Schulze E-D (eds) Forest diversity and function: temperate and boreal systems, Ecological studies, vol 176. Springer, Berlin, Heidelberg, New York, pp 13–38

Lange M, Eisenhauer N, Sierra CA, Bessler H, Engels C, Griffiths RI, Mellado-Vazquez PG, Malik AA, Roy J, Scheu S, Steinbeiss S, Thomson BC, Trumbore SE, Gleixner G (2015) Plant diversity increases soil microbial activity and soil carbon storage. Nat Commun 6:6707

Lawton JH (1994) What do species do in ecosystems? Oikos 71:367–374

Lefcheck JS, Byrnes JEK, Isbell F, Gamfeldt L, Griffin JN, Eisenhauer N, Hensel MJS, Hector A, Cardinale BJ, Duffy JE (2015) Biodiversity enhances ecosystem multifunctionality across trophic levels and habitats. Nat Commun 6:6936

Legendre P, Legendre LFC (2012) Numerical ecology, 3rd edn. Elsevier, Amsterdam

Lei X, Wang W, Peng C (2009) Relationships between stand growth and structural diversity in spruce-dominated forests in New Brunswick, Canada. Can J For Res 39(10):1835–1847

Loreau M (1998) Biodiversity and ecosystem function: a mechanistic model. Proc Natl Acad Sci 95:5632–5636

Loreau M, Hector A (2001) Partitioning selection and complementarity in biodiversity experiments. Nature 412:72–76

Loreau M, Mazancourt CD (2013) Biodiversity and ecosystem stability: a synthesis of underlying mechanisms. Ecol Lett 16:106–115

Loreau M, Naeem S, Inchausti P (eds) (2002) Biodiversity and ecosystem functioning. Oxford University Press, New York

MacArthur R (1955) Fluctuations of animal populations, and a measure of community stability. Ecology 36:533–536

MacArthur RH, MacArthur J (1961) On bird species diversity. Ecology 42:594–598

Mackey RL, Currie DJ (2001) The diversity-disturbance relationship: is it generally strong and peaked? Ecology 82(12):3479–3492

Marquard E, Weigelt A, Temperton VM, Roscher C, Schumacher J, Buchmann N, Fischer M, Weisser WW, Schmid B (2009) Plant species richness and functional composition drive overyielding in a 6-year grassland experiment. Ecology 90(12):3290–3302

Mason NWH, Mouillot D, Lee WG, Wilson JB (2005) Functional richness, functional evenness and functional divergence: the primary components of functional diversity. Oikos 111(1):112–118

May RM (1973) Stability and complexity in model ecosystems. Princeton University Press, Princeton

Mayr E (1942) Systematics and the origin of species. Columbia University Press, New York

Millennium Ecosystem Assessment (2005) Ecosystems and human well-being: biodiversity synthesis. World Resources Institute, Washington

Mittelbach GG, Steiner CF, Scheiner SM, Gross KL, Reynolds HL, Waide RB, Willig MR, Dodson SI, Gough L (2001) What is the observed relationship between species richness and productivity? Ecology 82(9):2381–2396

Monsi M (1960) Dry-matter reproduction in plants. I. Schemata of dry-matter reproduction. Bot Mag 73:81–90

Mora C, Tittensor DP, Adl S, Simpson AGB, Worm B (2011) How many species are there on earth and in the ocean? PLoS Biol 9(8):e1001127

Morin X, Fahse L, Scherer-Lorenzen M, Bugmann H (2011) Tree species richness promotes productivity in temperate forests through strong complementarity between species. Ecol Lett 14(12):1211–1219

Mouillot D, Villéger S, Scherer-Lorenzen M, Mason NWH (2011) Functional structure of biological communities predicts ecosystem multifunctionality. PLoS One 6(3):e17476

Mouquet N, Moore JL, Loreau M (2002) Plant species richness and community productivity: why the mechanism that promotes coexistence matters. Ecol Lett 5(1):56–65

Mutke J, Barthlott W (2005) Patterns of vascular plant diversity at continental to global scales. Biologiske Skrifter 55:521–531

Myers JP (1997) Perspectives on nature's services. In: Daily GC (ed) Nature's services. Societal dependence on natural ecosystems. Island Press, Washington, DC. Covelo, pp xvii–xviii

Naeem S (2002) Ecosystem consequences of biodiversity loss: the evolution of a paradigm. Ecology 83(6):1537–1552

Naeem S, Bunker DE, Hector A, Loreau M, Perrings C (eds) (2009) Biodiversity, ecosystem functioning, & human wellbeing: an ecological and economic perspective. Oxford University Press, Oxford

Naeem S, Thompson JT, Lawler SP, Lawton JH, Woodfin RM (1995) Empirical evidence that declining species diversity may alter the performance of terrestrial ecosystems. Philos Trans R Soc Lond 347(Series B):249–262

Naeem S, Thompson LJ, Lawler SP, Lawton JH, Woodfin RM (1994) Declining biodiversity can alter the performance of ecosystems. Nature 368:734–737

Noss RF (1990) Indicators for monitoring biodiversity: a hierarchical approach. Conserv Biol 4(4):355–364

Oelmann Y, Wilcke W, Temperton VM, Buchmann N, Roscher C, Schumacher J, Schulze ED, Weisser WW (2007) Soil and plant nitrogen pools as related to plant diversity in an experimental grassland. Soil Sci Soc Am J 71(3):720–729

Oliver TH, Heard MS, Isaac NJB, Roy DB, Procter D, Eigenbrod F, Freckleton R, Hector A, Orme CDL, Petchey OL, Proença V, Raffaelli D, Suttle KB, Mace GM, Martín-López B, Woodcock BA, Bullock JM (2015) Biodiversity and resilience of ecosystem functions. Trends Ecol Evol 30(11):673–684

Palmborg C, Scherer-Lorenzen M, Jumpponen A, Carlsson G, Huss-Danell K, Högberg P (2005) Inorganic soil nitrogen under grassland plant communities of different species composition and diversity. Oikos 110:271–282

Pärtel M, Szava-Kovats R, Zobel M (2011) Dark diversity: shedding light on absent species. Trends Ecol Evol 26(3):124–128

Pérez-Harguindeguy N, Díaz S, Garnier E, Lavorel S, Poorter H, Jaureguiberry P, Bret-Harte MS, Cornwell WK, Craine JM, Gurvich DE, Urcelay C, Veneklaas EJ, Reich PB, Poorter L, Wright IJ, Ray P, Enrico L, Pausas JG, de Vos AC, Buchmann N, Funes G, Quétier F, Hodgson JG, Thompson K, Morgan HD, ter Steege H, van der Heijden MGA, Sack L, Blonder B, Poschlod P, Vaieretti MV, Conti G, Staver AC, Aquino S, Cornelissen JHC (2013) New handbook for standardised measurement of plant functional traits worldwide. Aust J Bot 61(3):167–234

Petchey OL, ÓGorman EJ, Flynn DFB (2009) A functional guide to functional diversity measures. In: Naeem S, Bunker DE, Hector A, Loreau M, Perrings C (eds) Biodiversity, ecosystem functioning, and human wellbeing. Oxford University Press, Oxford, pp 49–59

Pielou EC (1966) Species-diversity and pattern-diversity in the study of biological collections. J Theor Biol 10:370–383

Pla L, Casanoves F, di Rienzo J (2012) Quantifying functional diversity. springer briefs in environmental science. Springer, Dordrecht

Pretzsch H (2005) Diversity and productivity in forests: evidence from long-term experimental plots. In: Scherer-Lorenzen M, Körner C, Schulze E-D (eds) Forest diversity and function: temperate and boreal systems, Ecological studies, vol 176. Springer, Berlin, Heidelberg, New York, pp 41–64

Prieto IN, Violle C, Barre P, Durand J-L, Ghesquiere M, Litrico I (2015) Complementary effects of species and genetic diversity on productivity and stability of sown grasslands. Nat Plants 1:15033

Raunkiaer C (1908) Livsformernes Statistik som Grundlag for biologisk Plantegeografi. Bot Tidsskr 29:42–83. Translation by G. Tobler in Beih. Bot. Centralbl., 27, Abt. 42, 1910, pp 1171–1206

Ravenek JM, Bessler H, Engels C, Scherer-Lorenzen M, Gessler A, Gockele A, De Luca E, Temperton VM, Ebeling A, Roscher C, Schmid B, Weisser WW, Wirth C, de Kroon H, Weigelt A, Mommer L (2014) Long-term study of root biomass in a biodiversity experiment reveals shifts in diversity effects over time. Oikos 123:1528–1536

Reich PB (2014) The world-wide 'fast–slow' plant economics spectrum: a traits manifesto. J Ecol 102(2):275–301

Reich PB, Oleksyn J, Modrzynski J, Mrozinski P, Hobbie SE, Eissenstat DM, Chorover J, Chadwick OA, Hale CM, Tjoelker MG (2005) Linking litter calcium, earthworms and soil properties: a common garden test with 14 tree species. Ecol Lett 8(8):811–818

Reich PB, Tilman D, Isbell F, Mueller K, Hobbie SE, Flynn DFB, Eisenhauer N (2012) Impacts of biodiversity loss escalate through time as redundancy fades. Science 336(6081):589–592

Ricklefs RE, Schluter D (1993) Species diversity: regional and historical influences. In: Ricklefs RE, Schluter D (eds) Species diversity in ecological communities. Historical and geographical perspectives. The University of Chicago Press, Chicago, London, pp 350–363

Rosenzweig ML (1971) The paradox of enrichment. Science 171:385–387

Rosenzweig ML (1995) Species diversity in space and time. Cambridge University Press, Cambridge

Rothe A, Binkley D (2001) Nutritional interactions in mixed species forests: a synthesis. Can J For Res 31:1855–1870

Scherber C, Eisenhauer N, Weisser WW, Schmid B, Voigt W, Fischer M, Schulze E-D, Roscher C, Weigelt A, Allan E, Beszler H, Bonkowski M, Buchmann N, Buscot F, Clement LW, Ebeling A, Engels C, Halle S, Kertscher I, Klein A-M, Koller R, Konig S, Kowalski E, Kummer V, Kuu A, Lange M, Lauterbach D, Middelhoff C, Migunova VD, Milcu A, Muller R, Partsch S, Petermann JS, Renker C, Rottstock T, Sabais A, Scheu S, Schumacher J, Temperton VM, Tscharntke T (2010) Bottom-up effects of plant diversity on multitrophic interactions in a biodiversity experiment. Nature 468(7323):553–556

Scherer-Lorenzen M (2005) Biodiversity and ecosystem functioning: basic principles. In: Barthlott W, Linsenmair KE, Porembski S (eds) Biodiversity: structure and function. In Encyclopedia of Life Support Systems (EOLSS), Developed under the auspices of the UNESCO. EOLSS Publisher, Oxford

Scherer-Lorenzen M (2008) Functional diversity affects decomposition processes in experimental grasslands. Funct Ecol 22(3):547–555

Scherer-Lorenzen M (2014) The functional role of biodiversity in the context of global change. In: Burslem D, Coomes D, Simonson W (eds) Forests and global change. Cambridge University Press, Cambridge, pp 195–238

Scherer-Lorenzen M, Körner C, Schulze E-D (eds) (2005) Forest diversity and function: temperate and boreal systems, Ecological studies, vol 176. Springer, Berlin, Heidelberg, New York

Scherer-Lorenzen M, Palmborg C, Prinz A, Schulze ED (2003) The role of plant diversity and composition for nitrate leaching in grasslands. Ecology 84(6):1539–1552

Scherer-Lorenzen M, Schulze E-D, Don A, Schumacher J, Weller E (2007) Exploring the functional significance of forest diversity: a new long-term experiment with temperate tree species (BIOTREE). Perspect Plant Ecol Evol Syst 9:53–70

Scherrer D, Körner C (2010) Infra-red thermometry of alpine landscapes challenges climatic warming projections. Glob Change Biol 16:2602–2613

Scherrer D, Körner C (2011) Topographically controlled thermal-habitat differentiation buffers alpine plant diversity against climate warming. J Biogeogr 38(2):406–416

Schimper AFW (1898) Pflanzengeographie auf physiologischer Grundlage. G. Fischer, Jena

Schimper AFW (1903) Plant-geography upon a physiological basis. Clarendon Press, Oxford

Schleuter D, Daufresne M, Massol F, Argillier C (2010) A user's guide to functional diversity indices. Ecol Monogr 80(3):469–484

Schmid B (2002) The species richness-productivity controversy. Trends Ecol Evol 17(3):113–114

Schmid B, Hector A (2004) The value of biodiversity experiments. Basic Appl Ecol 5(6):535–542

Schmid S (2007) Funktionelle und pflanzensoziologische Charakterisierung der alpin-subnivalen Vegetation im Gebiet der ETH-Forschungsstation Alp Weissenstein am Albulapass (GR, Schweiz). ETH Zürich, Zürich

Schmithüsen J (1968) Allgemeine Vegetationsgeographie, 3rd edn. Walter de Gryter, Berlin

Schulze E-D (1982) Plant life forms and their carbon, water and nutrient relations. In: Lange OL, Nobel PS, Osmond CB, Ziegler H (eds) Physiological plant ecology II, water relations and carbon assimilation, Encyclopedia of plant physiology, vol 12 B. Springer-Verlag, Berlin, Heidelberg, pp 616–676

Schulze E-D, Bazzaz FA, Nadelhoffer KJ, Koike T, Takatsuki S (1996) Biodiversity and ecosystem function of temperate deciduous broad-leaved forests. In: Mooney HA, Cushman JH, Medina E, Sala OE, Schulze E-D (eds) Functional roles of biodiversity: a global perspective, vol Scope 55. John Wiley & Sons, Chichester, New York, Brisbane, pp 71–98

Shannon CE, Weaver W (1949) The mathematical theory of communication. University of Illinois Press, Urbana

Simpson EH (1949) Measurement of diversity. Nature 163:688

Slik JWF, Arroyo-Rodríguez V, Aiba S-I, Alvarez-Loayza P, Alves LF, Ashton P, Balvanera P, Bastian ML, Bellingham PJ, van den Berg E, Bernacci L, da Conceicao Bispo P, Blanc L, Böhning-Gaese K, Boeckx P, Bongers F, Boyle B, Bradford M, Brearley FQ, Breuer-Ndoundou Hockemba M, Bunyavejchewin S, Calderado Leal Matos D, Castillo-Santiago M, Catharino ELM, Chai S-L, Chen Y, Colwell RK, Chazdon RL, Clark C, Clark DB, Clark DA, Culmsee H, Damas K, Dattaraja HS, Dauby G, Davidar P, DeWalt SJ, Doucet J-L, Duque A, Durigan G, Eichhorn KAO, Eisenlohr PV, Eler E, Ewango C, Farwig N, Feeley KJ, Ferreira L, Field R, de Oliveira Filho AT, Fletcher C, Forshed O, Franco G, Fredriksson G, Gillespie T, Gillet J-F, Amarnath G, Griffith DM, Grogan J, Gunatilleke N, Harris D, Harrison R, Hector A, Homeier J, Imai N, Itoh A, Jansen PA, Joly CA, de Jong BHJ, Kartawinata K, Kearsley E, Kelly DL, Kenfack D, Kessler M, Kitayama K, Kooyman R, Larney E, Laumonier Y, Laurance S, Laurance WF, Lawes MJ, Amaral IL, Letcher SG, Lindsell J, Lu X, Mansor A, Marjokorpi A, Martin EH, Meilby H, Melo FPL, Metcalfe DJ, Medjibe VP, Metzger JP, Millet J, Mohandass D, Montero JC, de Morisson Valeriano M, Mugerwa B, Nagamasu H, Nilus R, Ochoa-Gaona S, Onrizal PN, Parolin P, Parren M, Parthasarathy N, Paudel E, Permana A, Piedade MTF, Pitman NCA, Poorter L, Poulsen AD, Poulsen J, Powers J, Prasad RC, Puyravaud J-P, Razafimahaimodison J-C, Reitsma J, dos Santos JR, Roberto Spironello W, Romero-Saltos H, Rovero F, Rozak AH, Ruokolainen K, Rutishauser E, Saiter F, Saner P, Santos BA, Santos F, Sarker SK, Satdichanh M, Schmitt CB, Schöngart J, Schulze M, Suganuma MS, Sheil D, da Silva Pinheiro E, Sist P, Stevart T, Sukumar R, Sun I-F, Sunderland T, Suresh HS, Suzuki E, Tabarelli M, Tang J, Targhetta NL, Theilade I, Thomas DW, Tchouto P, Hurtado J, Valencia R, van Valkenburg JLCH, Van Do T, Vasquez R, Verbeeck H, Adekunle V, Vieira SA, Webb CO, Whitfeld T, Wich SA, Williams J, Wittmann F, Wöll H, Yang X, Adou Yao CY, Yap SL, Yoneda T, Zahawi RA, Zakaria R, Zang R, de Assis RL, Garcia Luize B, Venticinque EM (2015) An estimate of the number of tropical tree species. Proc Natl Acad Sci 112(24):7472–7477

Smith B, Wilson JB (1996) A consumer's guide to evenness indices. Oikos 76:70–82

Sørensen T (1948) A method of establishing groups of equal amplitude in plant sociology based on similarity of species and its application to analyses of the vegetation on Danish commons. Kongelige Danske Videnskabernes Selskab 5(4):1–34

Spehn EM, Hector A, Joshi J, Scherer-Lorenzen M, Schmid B, Bazeley-White E, Beierkuhnlein C, Caldeira MC, Diemer M, Dimitrakopoulos PG, Finn J, Freitas H, Giller PS, Good J, Harris R, Högberg P, Huss-Danell K, Jumpponen A, Koricheva J, Leadley PW, Loreau M, Minns A, Mulder CPH, O'Donovan G, Otway SJ, Palmborg C, Pereira JS, Pfisterer AB, Prinz A, Read DJ, Schulze E-D, Siamantziouras A-SD, Terry AC, Troumbis AY, Woodward FI, Yachi S, Lawton JH (2005) Ecosystem effects of the manipulation of plant diversity in European grasslands. Ecol Monogr 75(1):37–63

Stachowicz JJ (2001) Mutualism, facilitation, and the structure of ecological communities. Bioscience 51(3):235–246

Stein A, Gerstner K, Kreft H (2014) Environmental heterogeneity as a universal driver of species richness across taxa, biomes and spatial scales. Ecol Lett 17(7):866–880

Steudel B, Hautier Y, Hector A, Kessler M (2011) Diverse marsh plant communities are more consistently productive across a range of different environmental conditions through functional complementarity. J Appl Ecol 48(5):1117–1124

Storkey J, Döring T, Baddeley J, Collins R, Roderick S, Jones H, Watson C (2015) Engineering a plant community to deliver multiple ecosystem services. Ecol Appl 25(4):1034–1043

Swenson N (2011) The role of evolutionary processes in producing biodiversity patterns, and the interrelationships between taxonomic, functional and phylogenetic biodiversity. Am J Bot 98(3):472–480

Taberlet P, Zimmermann NE, Englisch T, Tribsch A, Holderegger R, Alvarez N, Niklfeld H, Coldea G, Mirek Z, Moilanen A, Ahlmer W, Marsan PA, Bona E, Bovio M, Choler P, Cieslak E, Colli L, Cristea V, Dalmas JP, Frajman B, Garraud L, Gaudeul M, Gielly L, Gutermann W, Jogan N, Kagalo AA, Korbecka G, Kupfer P, Lequette B, Letz DR, Manel S, Mansion G, Marhold K, Martini F, Negrini R, Nino F, Paun O, Pellecchia M, Perico G, Piekos-Mirkowa H, Prosser F, Puscas M, Ronikier M, Scheuerer M, Schneeweiss GM, Schonswetter P, Schratt-Ehrendorfer L, Schupfer F, Selvaggi A, Steinmann K, Thiel-Egenter C, van Loo M, Winkler M, Wohlgemuth T, Wraber T, Gugerli F, IntraBioDiv C (2012) Genetic diversity in widespread species is not congruent with species richness in alpine plant communities. Ecol Lett 15(12):1439–1448

Thienemann A (1920) Die Grundlagen der Biozönotik und Monards faunistische Prinzipien. Festschr. f. Zschokke 4:1–14

Tilman D (2001) Functional diversity. In: Levin SA (ed) Encyclopaedia of biodiversity. Academic Press, San Diego, pp 109–120

Tilman D, Hill J, Lehman C (2006) Carbon-negative biofuels from low-input high-diversity grassland biomass. Science 314:1598–1600

Tilman D, Isbell F, Cowles JM (2014) Biodiversity and ecosystem functioning. Annu Rev Ecol Evol Syst 45(1):471–493

Tilman D, Knops J, Wedin D, Reich P (2002) Plant diversity and composition: effects on productivity and nutrient dynamics of experimental grasslands. In: Loreau M, Naeem S, Inchausti P (eds) Biodiversity and ecosystem functioning: synthesis and perspectives. Oxford University Press, Oxford, pp 21–35

Tilman D, Knops J, Wedin D, Reich P, Ritchie M, Siemann E (1997a) The influence of functional diversity and composition on ecosystem processes. Science 277:1300–1302

Tilman D, Lehman C, Thomson K (1997b) Plant diversity and ecosystem productivity: theoretical considerations. Proc Natl Acad Sci U S A 94:1857–1861

Tilman D, Reich PB, Isbell F (2012) Biodiversity impacts ecosystem productivity as much as resources, disturbance, or herbivory. Proc Natl Acad Sci 109(26):10394–10397

Tilman D, Reich PB, Knops J, Wedin D, Mielke T, Lehmann C (2001) Diversity and productivity in a long-term grassland experiment. Science 294:843–845

Valladares F, Gianoli E, Gómez JM (2007) Ecological limits to plant phenotypic plasticity. New Phytol 176(4):749–763

van der Putten WH, Bardgett RD, Bever JD, Bezemer TM, Casper BB, Fukami T, Kardol P, Klironomos JN, Kulmatiski A, Schweitzer JA, Suding KN, Van de Voorde TFJ, Wardle DA (2013) Plant–soil feedbacks: the past, the present and future challenges. J Ecol 101(2):265–276

Vehviläinen H, Koricheva J (2006) Moose and vole browsing patterns in experimentally assembled pure and mixed forest stands. Ecography 29(4):497–506

Vilá M, Carrillo-Gavilán A, Vayreda J, Bugmann H, Fridman J, Grodzki W, Haase J, Kunstler G, Schelhaas M, Trasobares A (2013) Disentangling biodiversity and climatic determinants of wood production. PLoS One 8(2):e53530

Vilà M, Vayreda J, Comas L, Ibáñez JJ, Mata T, Obón B (2007) Species richness and wood production: a positive association in Mediterranean forests. Ecol Lett 10:241–250

Vogel A, Scherer-Lorenzen M, Weigelt A (2012) Grassland resistance and resilience after drought depends on management intensity and species richness. PLoS One 7(5):e36992

von Carlowitz HC (1713) Sylvicultura oeconomica, oder haußwirthliche Nachricht und Naturmäßige Anweisung zur wilden Baum-Zucht Braun, Leipzig

von Felten S, Hector A, Buchmann N, Niklaus PA, Schmid B, Scherer-Lorenzen M (2009) Belowground nitrogen partitioning in experimental grassland plant communities of varying species richness. Ecology 90(5):1389–1399

von Humboldt A (1808) Ansichten der Natur mit wissenschaftlichen Erläuterungen. J. G. Cotta'scher Verlag, Tübingen

Wardle DA, Bardgett RD, Klironomos JN, Setälä H, Van der Putten WH, Wall DH (2004) Ecological linkages between aboveground and belowground biota. Science 304:1629–1633

Wardle DA, Zackrisson O (2005) Effects of species and functional group loss on island ecosystem properties. Nature 435:806–810 von Humboldt A (1806) Ideen einer Physiognomik der Gewächse. Cotta´sche Buchhandlung, Tübingen

Walter H (1973) Die Vegetation der Erde. I. Tropische und subtropische Zonen, 3rd edn. Fischer, Jena, Stuttgart

Weigelt A, Weisser WW, Buchmann N, Scherer-Lorenzen M (2009) Biodiversity for multifunctional grasslands: equal productivity in high-diversity low-input and low-diversity high-input systems. Biogeosciences 6:1695–1706

Weisser WW, Siemann E (eds) (2004) Insects and ecosystem function, Ecological studies, vol 173. Springer, Berlin, Heidelberg, New York

Westoby M (1998) A leaf–height–seed (LHS) plant ecology strategy scheme. Plant Soil 199:213–227

Westoby M, Wright IJ (2006) Land-plant ecology and the basis of functional traits. Trends Ecol Evol 21:261–268

Whittaker RH (1960) Vegetation of the Siskiyou Mountains, Oregon and California. Ecol Monogr 30:279–338

Wilsey BJ, Potvin C (2000) Biodiversity and ecosystem functioning: importance of species evenness in an old field. Ecology 81(4):887–892

Wilson EO (1984) Biophilia. Harvard University Press, Cambridge

Wilson EO (1992) The diversity of life. Harvard University Press, Cambridge, MA

Woodward FI (1987) Climate and plant distribution. Cambridge University Press, Cambridge

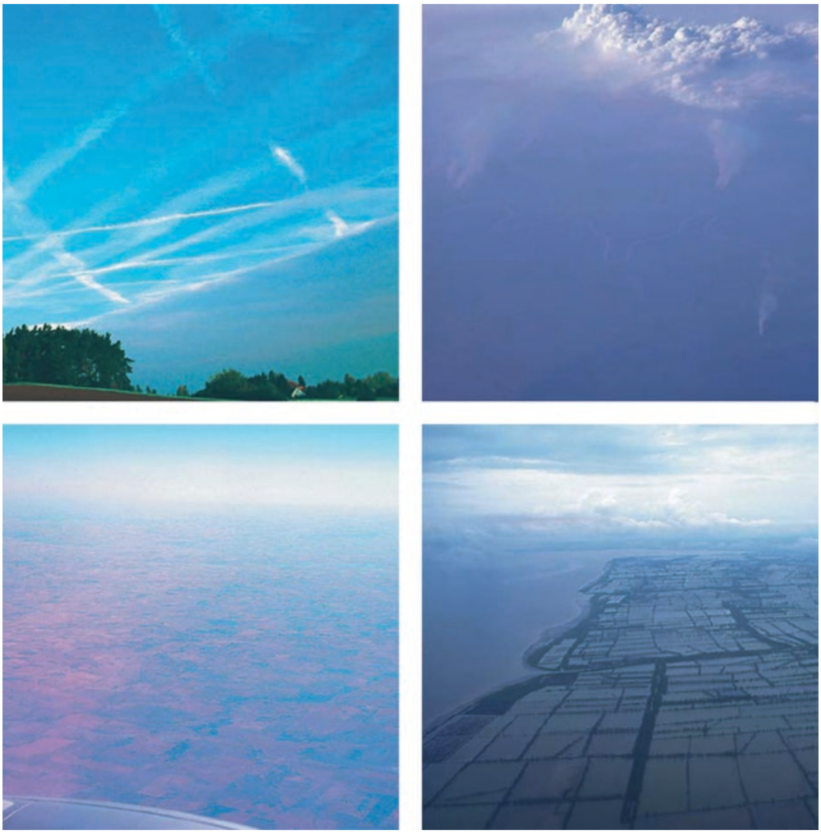
Woodward FI (1993) How many species re required for a functional ecosystem? In: Schulze E-D, Mooney HA (eds) Biodiversity and ecosystem function, Ecological studies, vol 99. Springer-Verlag, Berlin, Heidelberg, New York, pp 271–292

Yachi S, Loreau M (1999) Biodiversity and ecosystem productivity in a fluctuating environment: the Insurance Hypothesis. Proc Natl Acad Sci USA 96:57–64

Zeller SL, Kalinina O, Flynn DFB, Schmid B (2012) Mixtures of genetically modified wheat lines outperform monocultures. Ecol Appl 22(6):1817–1826

Part V

Global Ecology



Top left: Vapour trails from aeroplanes in the sky above the city of Bayreuth, Upper Franconia, Germany. The vapour trails impact the radiation budget of the Earth ("global dimming") and atmospheric chemical processes. Bottom left: Agricultural uses in the American Midwest, an area that was originally an open oak woodland and grassland. Top right: Thunderstorms caused by convection from forest fires, which are used to clear land in Malaysia. Bottom right: Fish farms, used to rear crabs, on the north coast of Java, where originally mangrove swamps were growing; owing to the spread of diseases, only a small proportion of this area is still useable. (Photos: E.-D. Schulze)

The **surface of the Earth** has an area of about 510 million km^2, of which about 361 million km^2 are oceans, i.e. 71% of the Earth's surface is covered by oceans. The continental area is about 149 million km^2, but only about 134 million km^2 (90% of continents) are ice-free. At present, virtually the entire ice-free surface of the Earth is **used by humans** for food and feed production, raw material extraction and processing, settlements, infrastructure or tourism. According to Running (2008), original vegetation has been entirely displaced by humans from about 50% of the Earth's surface, and the other half is used for grazing, hunting, gathering and tourism. About 3.5% of the land area is under conservation. Globally, about 70% of freshwater withdrawal by humans is used for **irrigation** (WWAP 2014). In 2010, 3.5 million tonnes of waste were produced worldwide every day, which is estimated to increase to more than 6 million tonnes by 2025 (Hoornweg et al. 2013). Invading plants replaced 20% of original plants in ecosystems (up to 50% in some vegetation types), but this process appears to have been initiated by human activities (Pearce 2015). About 20% of the known bird species are extinct, and 60% of fish stocks are overused by humans for food or to provide fishmeal as feed for farmed fish (Naylor et al. 2000) or animal husbandry. This list could be easily continued and extended.

Plants and ecosystems play a key role in many aspects of global change. Plants are Earth's primary producers, source of atmospheric oxygen, sink for atmospheric carbon dioxide and the basis for global food security. From an economic point of view, plants are an important resource for clothing (e.g. cotton, hemp, flax), medical drugs, furniture and timber. Plant biomass has also become an increasingly important alternative to fossil fuel and it is used as biofuel for the continuously growing energy requirements of modern societies. In addition, ecosystems provide many services that are important to humankind, for example, filtration and purification of air and water, storage of carbon dioxide, aesthetic services and tourism (Chap. 21: Global Biogeochemical Cycles).

The growing demands on Earth's land surface for food and feed production, biodiversity conservation, protection of terrestrial carbon sinks and urbanisation conflict with each other and are even sometimes mutually exclusive. A **sustainable use** of Earth's terrestrial ecosystems requires a deep understanding and ability to model (Chap. 22: Dynamic Global Vegetation Models) plant ecology at a global scale under changing environmental, socioeconomic and political boundary conditions (Chap. 23: Global Change and Terrestrial Ecosystems).

References

Hoornweg D, Bhada-Tata P, Kennedy C (2013) Waste production must peak this century. Nature 502:615–617

Naylor RL, Goldburg RJ, Primavera JH, Kautsky N, Beveridge MCM, Clay J, Folke C, Lubchenko J, Mooney H, Troell M (2000) Effect of aquaculture on world fish supply. Nature 405:1017–1025

Pearce F (2015) The new wild: why invasive species will be Nature's salvation. Beacon Press, Boston

Running SW (2008) Ecosystem disturbance, carbon, and climate. Science 321:652–657

WWAP (2014) The United Nations World Water Development Report 2014: Water and Energy. Paris, UNESCO

Global Biogeochemical Cycles

21

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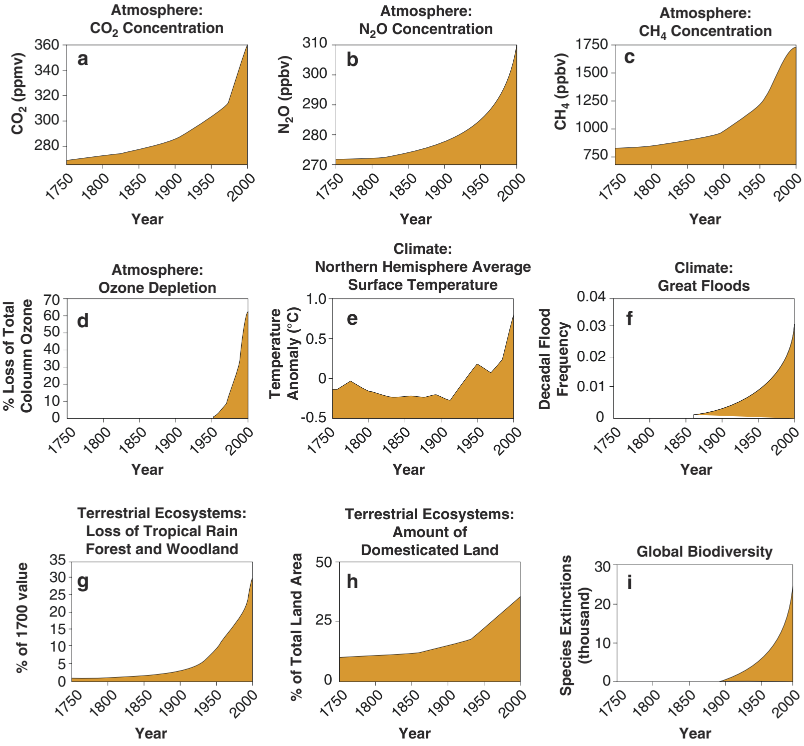

Changes in many characteristics of the Earth system as a result of human activities since 1750. Changes in atmospheric composition, **a**–**d** in surface temperature anomalies, **e** in decadal flood frequency, **f** in tropical rain forest and woodland area, **g** in land conversion to pastures and croplands, **h** in species extinction rates, **i.** (after Steffen et al. 2004)

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21.1 Distribution of Global Terrestrial Ecosystems

The **potential natural vegetation** of the Earth describes the distribution of global vegetation based on environmental conditions (i.e. soils, geomorphology, climate), but without consideration of any human influences, even though anthropogenic pollutants have changed soils (e.g. soil acidification) and thus affected the potential vegetation under present-day soil conditions. However, these effects are regarded as being still small on a global scale. Thus, the potential natural vegetation map (Fig. 21.1) basically follows the pattern of global climates and the Köppen climatic regions, which in turn also determine plant diversity (Sect. 20.3, Chap. 20) and affect soil formation and the occurrence of fire (Chap. 10). Bond et al. (2004) showed with models that global forest cover would double in a world without fire, mainly increasing in areas presently covered by C_4 grasslands.

The Northern Hemisphere has a clear zonation of potential vegetation across Africa and Asia with tropical rainforests at the equator, followed by seasonal forests with summer rainfall, savannas, tropical arid grasslands and arid regions along the Tropic of Cancer (Chap. 18). Further north, the vegetation consists of evergreen vegetation under Mediterranean winter rain climates, followed by summer-green deciduous forests and by a circumpolar belt of boreal forest and tundra. The same zonation exists also in the Southern Hemisphere, but it is not as clearly expressed owing to the effects of oceans and high mountains on climate over smaller landmasses. Also, the Southern Hemisphere has a larger component of evergreen broadleaved vegetation.

This mainly climate-driven zonation of vegetation (**land cover**, LC) has been fundamentally changed by human **land use** (**LU**), including agriculture, forest use and settlements (Fig. 21.2). This process is also called **land use and land-use change (LULUC)** (Chap. 23). For example, in large areas of the Amazon, the land-cover class *forests* has been replaced by the land-cover class *grasslands* or *herbaceous vegetation*, maybe even partly replacing C_3 vegetation (forests) with C_4 vegetation (grassland). This change in LC is linked to a change in LU, from collecting fruits and nuts or harvesting wood in a forest to grazing on grassland or soybean cropping on arable land. While remote sensing techniques can easily determine LC and LU, LU intensity can still not be detected from space (Chap. 14). Moreover, no area on Earth is “**pristine**” today since atmospheric pollution reaches also the most remote areas.

At present, 60–70% of potential vegetation has been converted into agricultural land in temperate and Mediterranean forests, and further changes are expected until 2050. At present, 40–50% of tropical dry forests and savannas has been already converted into agricultural land, and it is expected that this will increase to 70% by 2050, as in temperate forests. Furthermore, 20–30% of deserts and montane cloud forests has been converted into agriculture, and this will most likely change to 30–40% area of LU change by 2050. The only regions where LU change has been small (less than 10%) are boreal forests and tundra. However, these regions are used heavily for wood and grazing even today (MA 2005). Thus, Canadell and Schulze (2014) concluded that all of the terrestrial surface of the globe will be used by humans by 2050. Even ice-covered regions are presently used for tourism and science.

21.2 Global Biogeochemical Cycles

On a global scale, **biogeochemical cycles** are strongly tied to global environmental factors, the distribution and composition of terrestrial ecosystems, and human LU. Biogeochemical cycles (Fig. 21.3) (Schulze 2000) of carbon, water, nitrogen and sulphur are characterised by (1) accumulations of these in the atmosphere, in oceans and on continents; (2) the exchange processes between these compartments, the so-called **fluxes** (Chap. 16); and (3) the turnover within compartments. The fluxes between the Earth’s surface and the atmosphere are essentially controlled by organisms and anthropogenic activities, while the processes in the atmo-

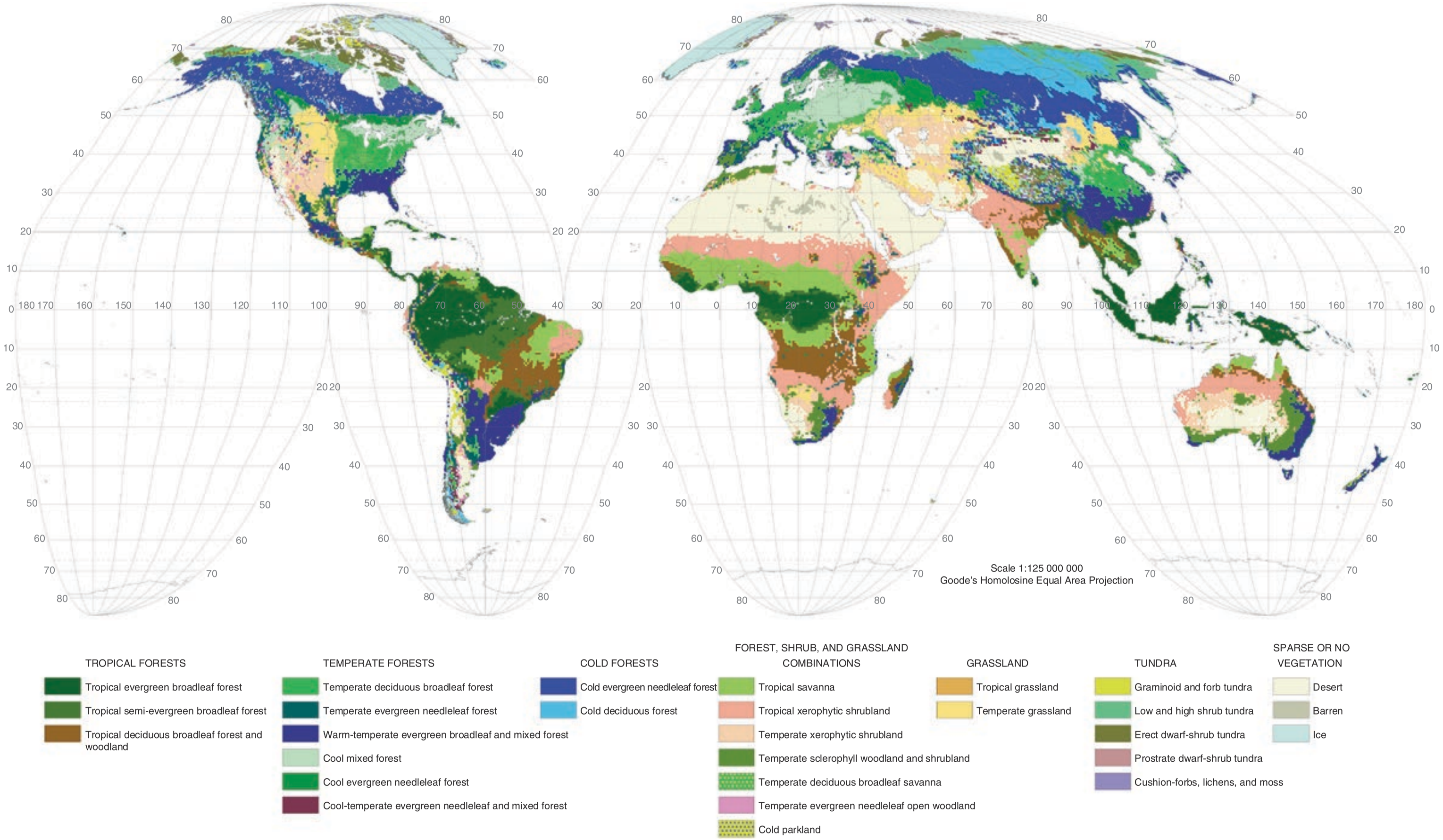

Fig. 21.1 Zonation of potential natural vegetation on Earth as determined by remote sensing and modeling. (Kaplan 2001)

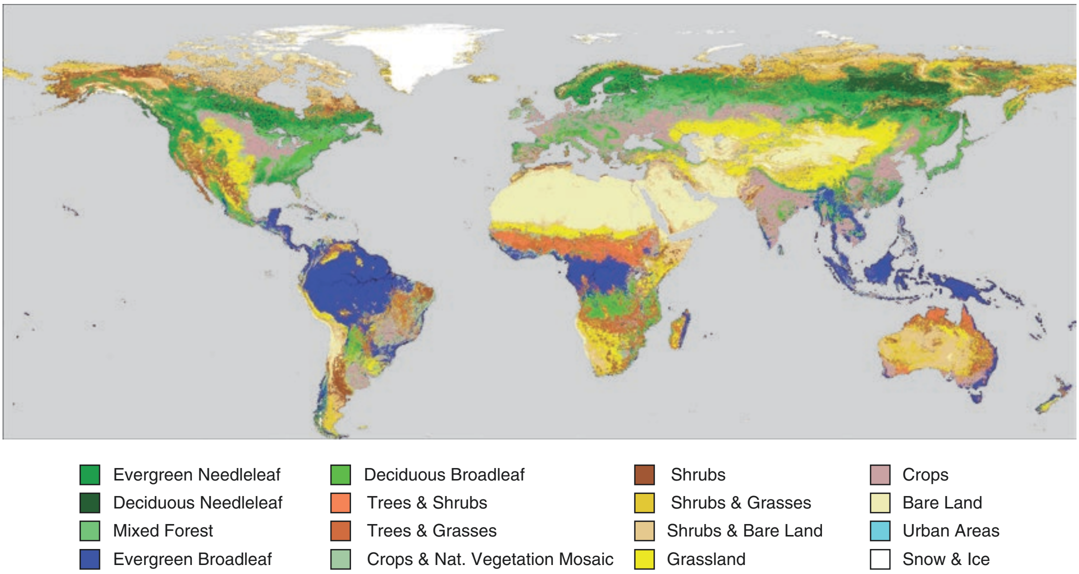

Fig. 21.2 Current global land use by humans as determined by remote sensing. (Jung et al. 2006)

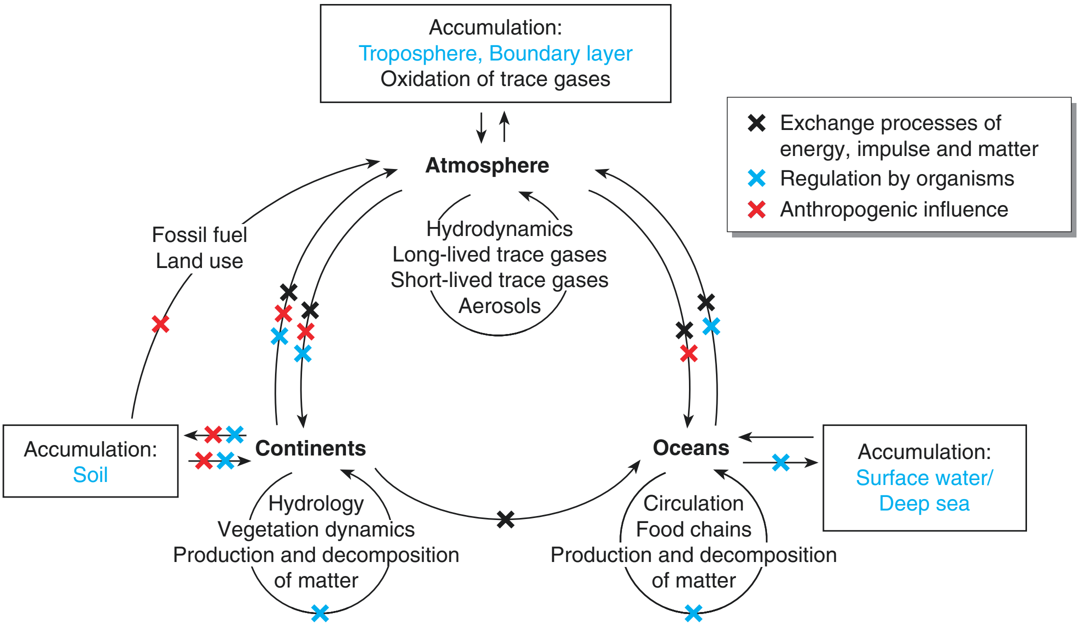

Fig. 21.3 Schematic presentation of global cycling of energy and matter between continents, oceans and atmosphere. Arrows: mass flows (mass per unit area per time), black crosses: physical processes, blue crosses: flows controlled by organisms, red crosses: processes affected by anthropogenic activities. (Schulze 2000)

sphere are strongly dependent on energy input from solar radiation. Plants play a crucial role in global biogeochemical cycles as they take up nutrients from the soil, release water to the atmosphere via transpiration, respire and photosynthesise, and bind atmospheric N_2 via symbiosis with rhizobia (legume species). Moreover, plants interfere with these cycles by providing the primary substrate for herbivores as well as the substrate for feeding soil organisms with organic matter via root exudates and litter

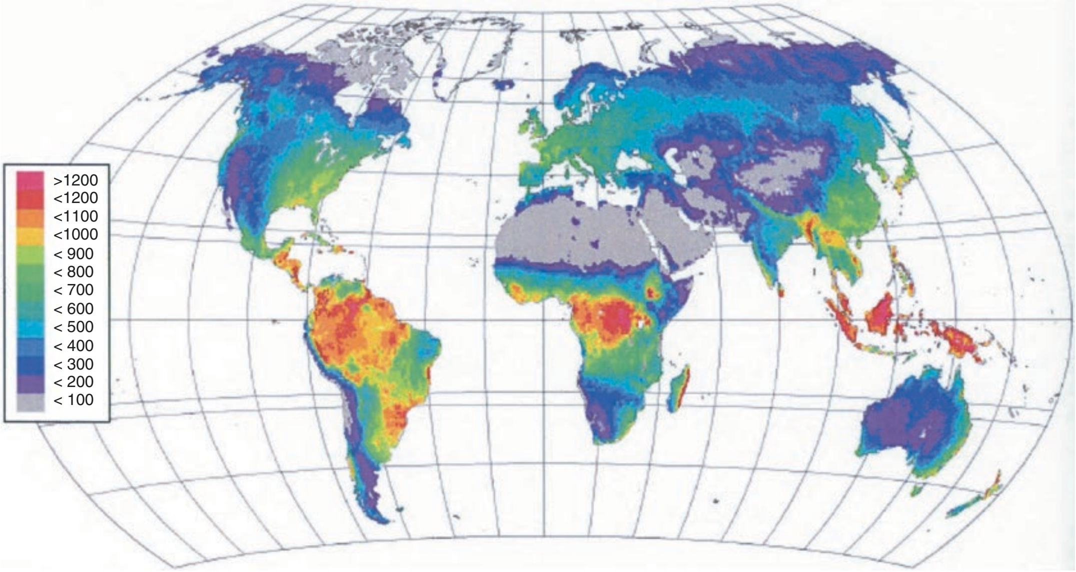

Fig. 21.4 Global map of actual net primary production (NPP) (g C m^{-2} $year^{-1}$) as modelled with six dynamic global vegetation models. (data from Cramer et al. 2001)

fall. The mineralisation of plant and soil organic matter by soil microorganisms (**heterotrophic soil respiration**) together with root respiration (**autotrophic soil respiration**) accounts for one of the biggest natural fluxes of CO_2. Moreover, soil organisms are also responsible for the release of CH_4, N_2 and N_2O from the soil to the atmosphere.

Owing to the burning of fossil fuels, deforestation and intensive agriculture, i.e. LU change, humankind has massively interfered with these natural biogeochemical cycles of carbon, water, nitrogen and sulphur, leading to climate change, eutrophication and changes in biodiversity. These impacts will be discussed in the following sections.

21.2.1 Global Carbon Cycle

The biological **carbon cycle** is characterised by very high rates of CO_2 uptake and release. Besides being released as a result of respiration of plants and heterotrophic organisms, CO_2 is also lost from burning vegetation and the burning of fossil fuels. The net gain from gross photosynthesis and respiration by plants (autotrophic respiration) is the production of organic material by plant cover; this is known as **net primary production** (**NPP**; Chap. 12). Thus, NPP quantifies the amount of plant material produced that may be available for other organisms, unless it is not harvested for human use, used for bioenergy or burned by vegetation fires. Owing to the methods used to determine annual NPP (sampling, drying, weighing; modelling; deduction from remote sensing proxies), one should be aware that published NPP does not account for root exudates, the export of carbohydrates to mycorrhizae, rhizobia or the rhizosphere, interannual leaf and root turnover, or herbivory. Despite these shortcomings, NPP has remained an important quantity in global carbon cycle studies for estimating yield potentials or assessing impacts of pollution.

The global map of NPP (Fig. 21.4) shows higher biomass production rates in the tropics than in the lower latitudes. This is mainly due to the period of time for production (growing season length), which is either limited by water surplus or shortage or by temperatures at higher latitudes (Schulze 1982). But even at low latitudes, NPP is often limited by sunlight due to frequent cloud cover in tropical regions (Nemani et al. 2003). These global patterns of NPP are strikingly similar to those of plant biodiversity (Sect. 20.3, Chap. 20, Fig. 20.11).

Owing to their increased demand for energy and land, humans have strongly interfered with

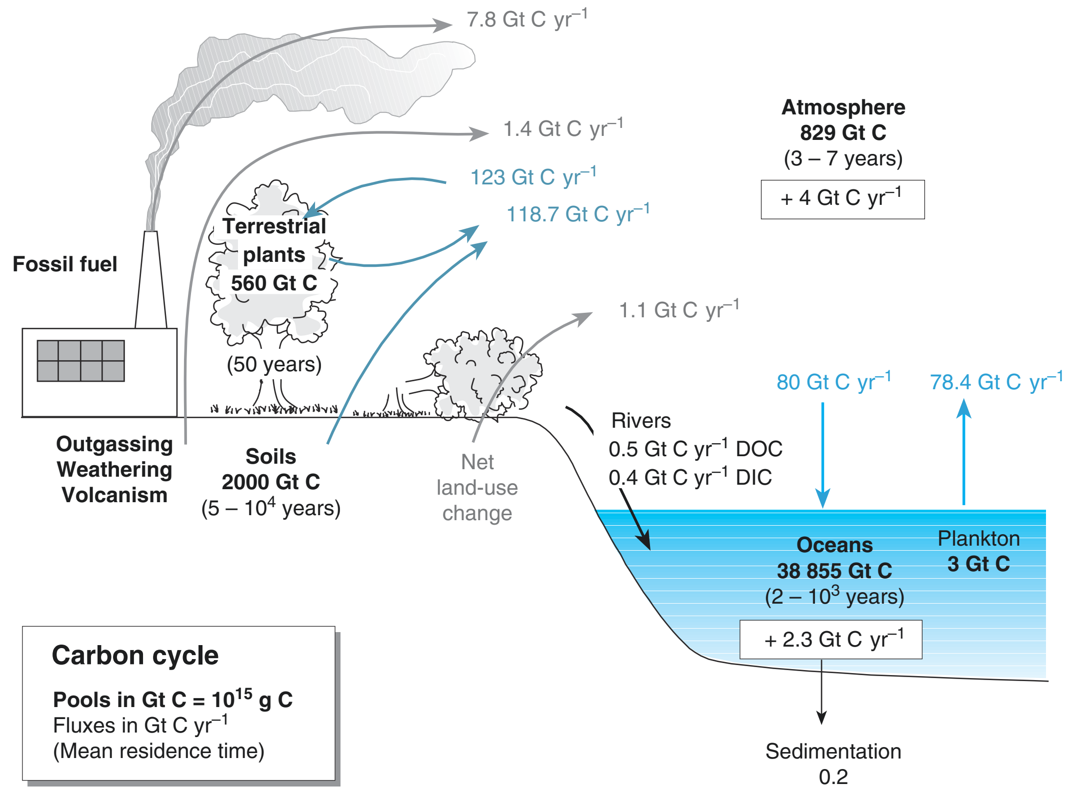

Fig. 21.5 Schematic presentation of global carbon cycle. Shown are the reservoirs (pool sizes), fluxes and mean residence times of a molecule in each compartment. *DOC* dissolved organic carbon; *DIC* dissolved inorganic carbon. (after Schlesinger and Bernhardt 2013; IPCC 2013)

the natural carbon cycle (Fig. 21.5). Since industrialisation in the nineteenth century, large quantities of CO_2 have been and are still being released into the atmosphere, mainly due to emissions from **fossil fuel burning**, cement production and release of CO_2 by changes in natural vegetation during LULUC. These anthropogenic fluxes are larger than the natural budget of gross photosynthesis and respiration of the biosphere. The human signal thus significantly perturbs the natural carbon cycle, causing a massive increase in atmospheric CO_2 concentrations, which drive **global warming**. The year 2016 was the first year in which atmospheric CO_2 concentrations at **Mauna Loa** (Hawaii) stayed above 400 ppm year round (www.esrl.noaa.gov/gmd/ccgg/trends/). Within the past two decades, a large amount of research has been carried out to understand the natural carbon source and sink capacities of terrestrial ecosystems and the oceans.

At the global scale, the carbon cycle has large reservoirs of C in the ocean and in soils (Fig. 21.5). Carbon in **atmospheric CO_2** is about 2% of the amount of C in the oceans. However, it compares well with the amount of C bound in the biomass of plants, but is only half of the C stored in soils.

The **mean residence time** (MRT) (defined as C pool over flux) of a CO_2 molecule in the atmosphere is about 3–7 years. However, because atmospheric CO_2 concentrations are determined not only by assimilation but also by respiration (Fig. 21.5), the overall residence time of CO_2 cannot be given by just one value but rather needs to be given for a certain process. For the period between 2000 and 2014, CO_2 in the atmosphere increased by 1.2–2.5% per year, but by around 3% per year in 2015 and 2016 (www.esrl.noaa.gov/). During this time, anthropogenic CO_2 emissions continuously increased by about 3.5% per year between 2000 and 2005 and by 1.8% per year between 2006 and 2015 (Le Quéré et al. 2016). Overall, the terrestrial biosphere has been a carbon sink at highly varying magnitudes over time. This **terrestrial carbon sink** accounted for about 31% of the anthropogenic CO_2 emissions between 2006 and 2015 (Le Quéré et al. 2016). The reasons for this C sink include CO_2 fertilisation effects on plant growth, increasing N deposition and a lengthening of the growing season, particularly in boreal and temperate regions.

The carbon cycle depicted in Fig. 21.5 does not consider other C-containing trace gases, such as **methane** (Chap. 16), which can have an even greater effect on climate than CO_2 (Fig. 21.6). Methane emissions, produced in wetlands around the globe, such as Siberia, are of a magnitude similar to that of methane emissions originating from waste management and agriculture, that is, from rice cultivation and ruminants (www.globalcarbonproject.org). However, most parts of the terrestrial biosphere also act as (small) sinks for methane, that is, their uptake of methane by soil microorganisms exceeds emissions (Fig. 21.6).

21.2.2 Global Water Cycle

The **water cycle** (Fig. 21.7) (Schlesinger and Bernhardt 2013; Chap. 10) is characterised by the large water reservoir of salt water in the oceans, accounting for about 96.5% of the Earth's water pools. Only 2.5% of water on Earth is **freshwater**, of which about 70% is locked up in glaciers on Antarctica and Greenland (Gleick and Palaniappan 2010). Thus, only a very small fraction, in fact less than 1%, of water on Earth can potentially be used by terrestrial ecosystems and for human life. Nevertheless, the terrestrial biosphere has a strong impact on the Earth's water cycle, being responsible for large water vapour fluxes, that is, **evapotranspiration** (ET, also called latent heat flux λE) (Chaps. 10 and 16). Ecosystem ET returns about 60% of total terrestrial precipitation back to the atmosphere. This large flux is highly variable spatially and temporally, depending on incident solar radiation, environmental conditions and ecosystem type (Chap. 16). Furthermore, a H_2O molecule has a MRT (calculated as reservoir/flux) in soil of only about 300 days; the MRT in the atmosphere is much smaller (MRT: 9 days). In contrast, the

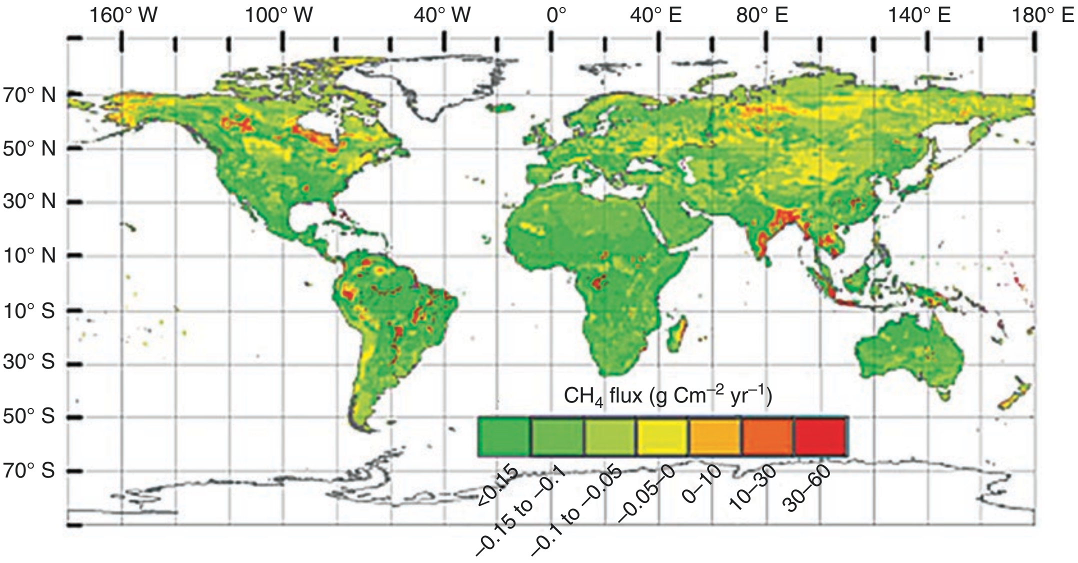

Fig. 21.6 Global distribution of methane emissions. The data result from a modelling study based on the most sensitive environmental variables causing methane emissions. Negative fluxes represent CH_4 uptake, positive fluxes represent CH_4 emissions. (Tian et al. 2015)

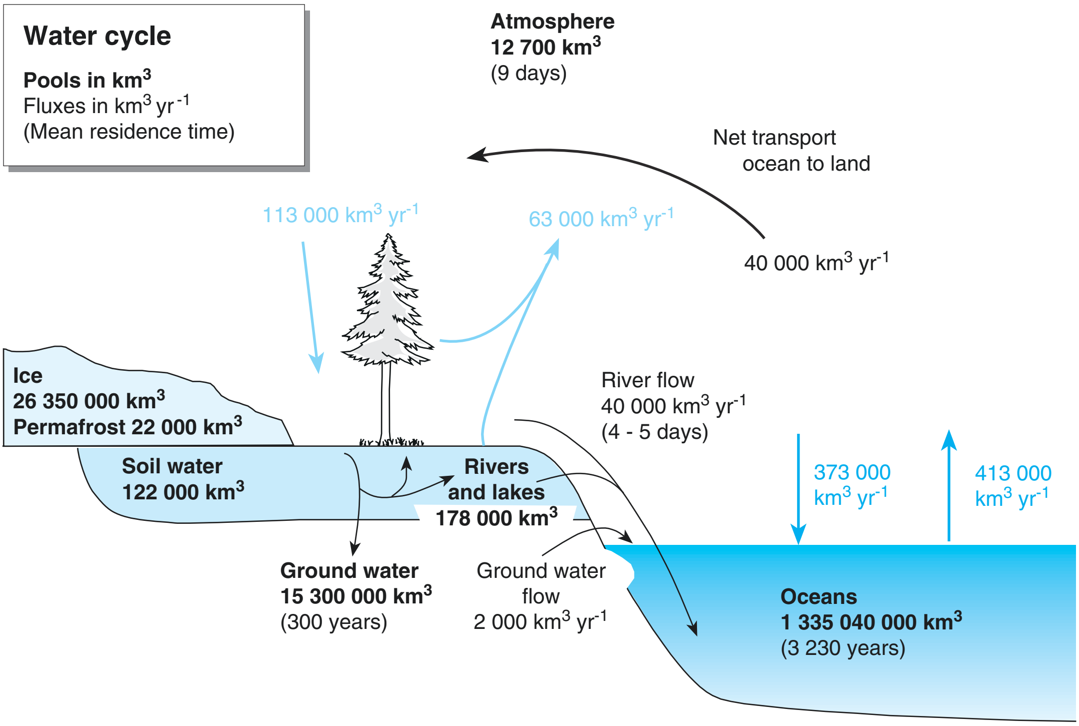

Fig. 21.7 Global hydrological pools and fluxes. (after Schlesinger and Bernhardt 2013)

MRT for water in the ocean is about 3200 years. The MTR in continental groundwater is 300 years.

The net transport of water vapour from the ocean to land is smaller than the fluxes above the oceans or landmasses. **Precipitation** evaporates in coastal regions, and this evaporated water is then precipitated over the interior of the landmasses again. A "wave" of rain, with evaporation and condensation events, "rolls" across the continents. In the case of the Eurosiberian region, it has been calculated that the same water molecule undergoes five to seven evaporation and condensation cycles before it reaches the Pacific Ocean. During these processes, losses by surface run-off and seepage occur, so that precipitation of about 1000 mm in the montane regions of Central Europe is reduced to 300 mm in Central Siberia and 150 mm in Eastern Siberia (Schulze et al. 2002). As a consequence of these precipitation patterns, vegetation changes accordingly: in the very dry (and cold) areas in Eastern Siberia, larch replaces pine and spruce, mainly owing to drought-associated fires.

With the large amounts of water vapour and precipitation that are converted globally, it may appear unlikely that humans can alter this cycle, particularly since they predominantly use surface freshwater, that is, the excess of the hydrological balance (Chap. 16). However, some effects of human activities are visible on regional and global scales (WBGU 1999), particularly:

- Changes in **river discharge** due to changes in LU and water diversion for urban settlements. These start with LC changes from forest to agriculture and continue with intensive mechanical management practices, fertilisation, irrigation and use of pesticides, potentially leading to soil degradation and erosion on agricultural land, and end with the redistribution of water via pipelines for drinking water and wastewater of cities. Water withdrawals from groundwater have already lowered regional groundwater levels, affecting plant water uptake and leading to drastic changes in species composition, but also facilitating saltwater intrusion into groundwater aquifers in coastal regions.
- Changes in **run-off** caused by dam building and irrigation (partially from fossil groundwa-

ter storage) and city water supplies. Well-known examples of such effects are the drastically reduced flow of the Colorado River in Arizona, the drying out of the Aral Sea and changes in water levels of the Nile River as caused by the Aswan Dam in Egypt.

- Changes in the **distribution of precipitation** due to the release of aerosols from combustion to the atmosphere (Fig. 21.8). Aerosols create additional condensation nuclei while the water vapour remains constant. Since there are more condensation nuclei, droplet size decreases, which delays precipitation. As a result, the vapour remains in the atmosphere as a haze, which does not develop into rain (Toon 2000). This explains the statistically established periodicity in weekly precipitation (Cerveny and Balling 1998) in the Eastern USA, where aerosol concentration increases rapidly at the beginning of the week and reaches a maximum on Wednesday/Thursday. This delays rainfall from the atmosphere. Precipitation in the first half of the week is low, increases only in the second half of the week, and reaches its statistical maximum on Saturday. Statistically, the least amount of precipitation falls on Monday. With ongoing climate change, it is also predicted that precipitation patterns across the globe will shift, causing floods in some parts and droughts in other parts (IPCC 2012). The current and predicted changes in precipitation patterns might have tremendous implications for terrestrial ecosystems and the distribution of species.

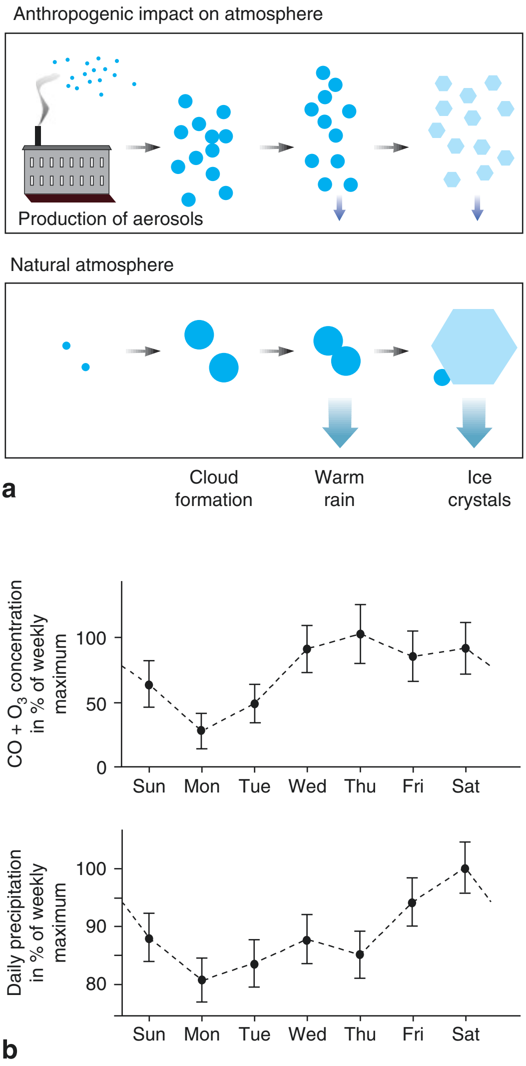

Fig. 21.8 Rain formation as influenced by aerosols. **a** In the presence of aerosols, the number of condensation nuclei rises and thus decreases the size of droplets and rainfall (after Toon 2000). **b** Statistical distribution of anthropogenic trace gases as indicators of aerosols and of rainfall during a week in the Northeastern USA. (Cerveny and Balling 1998)

Life on Earth is not possible without water. Plant life in particular is always exposed to a trade-off between starvation and withering. Once stomata open to assimilate CO$_2$ during leaf photosynthesis, water is lost simultaneously owing to transpiration. Thus, global water and carbon cycles are tightly connected by plants. The ratio between photosynthesis (carbon gain) and transpiration (water loss) is called **water use efficiency** (Chap. 10), an ecosystem function that plays a central role in connecting global water and carbon cycles. Recently it was shown that the fertilisation effect of increased atmospheric CO$_2$ during the last 20 years increased the water use efficiency of Northern Hemisphere boreal forests (Keenan et al. 2013), but it has emerged that the increase in photosynthesis is in fact caused by nitrogen deposition. An increase in water use efficiency in forests has also been observed during spring droughts in Switzerland, but not in grasslands (Wolf et al. 2013). Such contrasting ecosystem responses reflect different adaptive strategies between vegetation types, which are in turn important to biosphere–atmosphere feedbacks in the climate system (Chaps. 10 and 16). Currently, one third of global terrestrial evapotranspiration is lost from cropland and grazing land (Oki and Kanae 2006). One of the highest priorities in agricultural research is breeding for high water use efficiency since 70% of current world's water use is for irrigation (Condon et al. 2004).

21.2.3 Global Nitrogen Cycle

The largest amount of nitrogen (Fig. 21.9) (Schlesinger and Bernhardt 2013) is stored in gaseous form in the atmosphere (4×10^{15} t, with a MRT of 10^7 years). Storage in other compartments is negligible by comparison, even though flux rates are high. **Biological N_2 fixation** (Chap. 11) is the starting point of biological N processes on continents and in oceans within the **global nitrogen cycle**, with higher rates in oceans than on land. Also, denitrification is higher in oceans than on land. The N cycle is particularly affected by **industrial N_2 fixation** (Haber-Bosch process), resulting in NH_3 production, and by NO_x production during fossil fuel burning. The present rate of industrial N_2 fixation exceeds biological N_2 fixation. Also, total nitrogen fixation (biological + industrial) of 453×10^6 t N exceeds the global rate of denitrification (409×10^6 t N), apparently leading to a net N accumulation in terrestrial and aquatic ecosystems. Internal gross fluxes of organically and inorganically bound N in ecosystems exceed the net fluxes by about a factor of ten. Figure 21.9 does not depict the fate of reactive nitrogen and the processes of chemical transformation of reduced and oxidised nitrogen in the atmosphere and in the biosphere. Part of the fixed nitrogen is emitted again into the

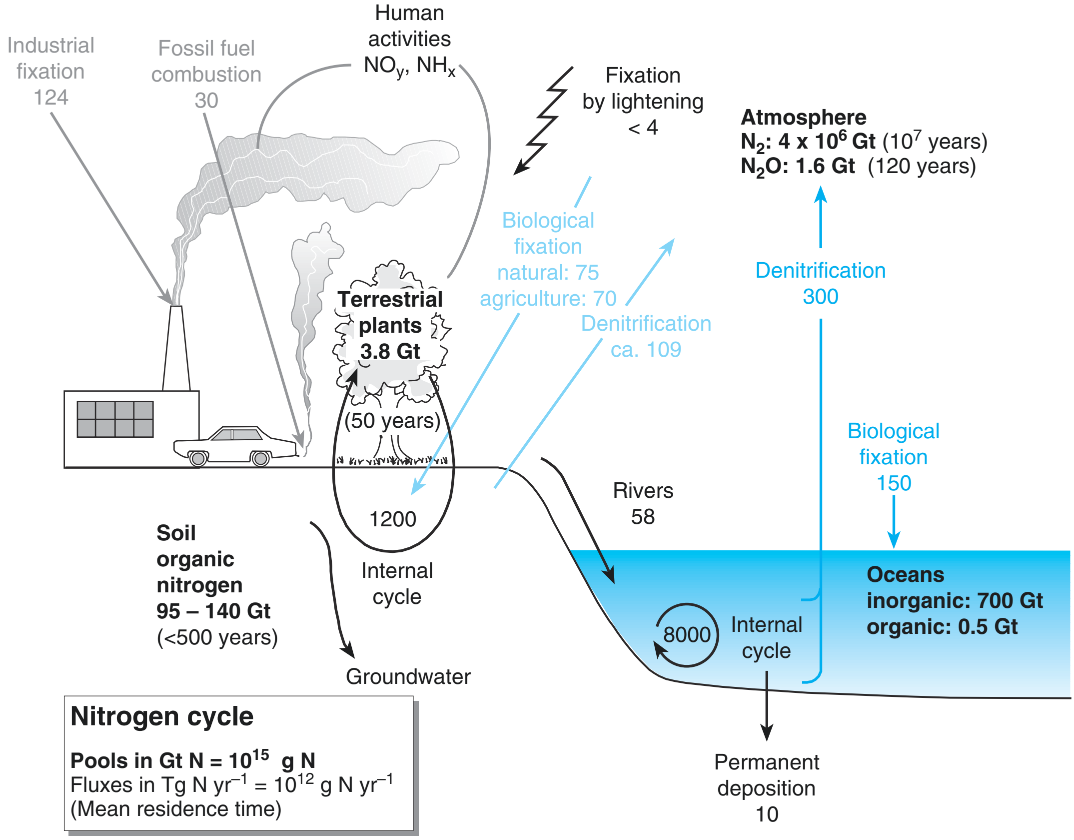

Fig. 21.9 Global nitrogen pools and fluxes. The uncertainty of each of these fluxes remains high and the fate of oxidised, and reduced volatile N compounds contains numerous subfluxes and compartments. (Gruber and Galloway 2008; Schlesinger and Bernhardt 2013)

atmosphere and returns to the biosphere via nitrogen deposition. These processes are shown in Schlesinger and Bernhardt (2013).

Figure 21.9 shows the flux of N_2 by denitrification but does not specifically consider the flux of N_2O generated by anoxic incomplete **denitrification** (Fig. 21.10). The **N_2O flux** is important in view of its slow turnover (lifetime of 114 years) and due to its global warming potential over a 100-year period, which is about 298 times larger than that of CO_2. N_2O fluxes are highest in the tropics and in regions with intensive agriculture such as Europe, India and China, mainly due to mineral fertilisation. However, very large N_2O fluxes can also be found following the restoration of permanent grassland, when fertiliser is added after ploughing, harrowing and resowing. N_2O fluxes were on average 2.9 g N m^{-2} $year^{-1}$ (Merbold et al. 2014), representing 51% of the CO_{2eq} fluxes from the site (i.e. equivalents of CO_2, meaning CO_2, CH_4 and N_2O). Fluxes were driven by N inputs, environmental factors such as soil water content and temperature, and by (a lack of) plant productivity.

An additional important N-containing trace gas is NO_x, which contributes to the formation of ozone in the atmosphere. **NO_x formation** is clearly associated with high industrial activities in the USA, Europe and East Asia and caused by car traffic. In the Southern Hemisphere, only South Africa contributes to NO_x production. NO_x acts initially as fertiliser for terrestrial vegetation, up to a point where negative impacts prevail. During the 1980s and 1990s, high N deposition in Europe and North America caused significant stress on forests, particularly for those on acidic, nutrient-poor soils, resulting in imbalanced nutrition, impairing mycorrhizal and, root growth, up to tree death (Chap. 11). Chronic N deposition also strongly affects plant species composition in many ecosystems worldwide, for example by favouring grass encroachment in forest understorey or enabling tree invasions into bogs.

21.2.4 Global Sulphur Cycle

The **global sulphur cycle** is important because of its effects on global aerosol production, which in turn affects the water cycle. Also, SO_2 emissions from coal burning significantly changed the cation balance in soils of the Northern Hemisphere, and soils in Europe have not recov-

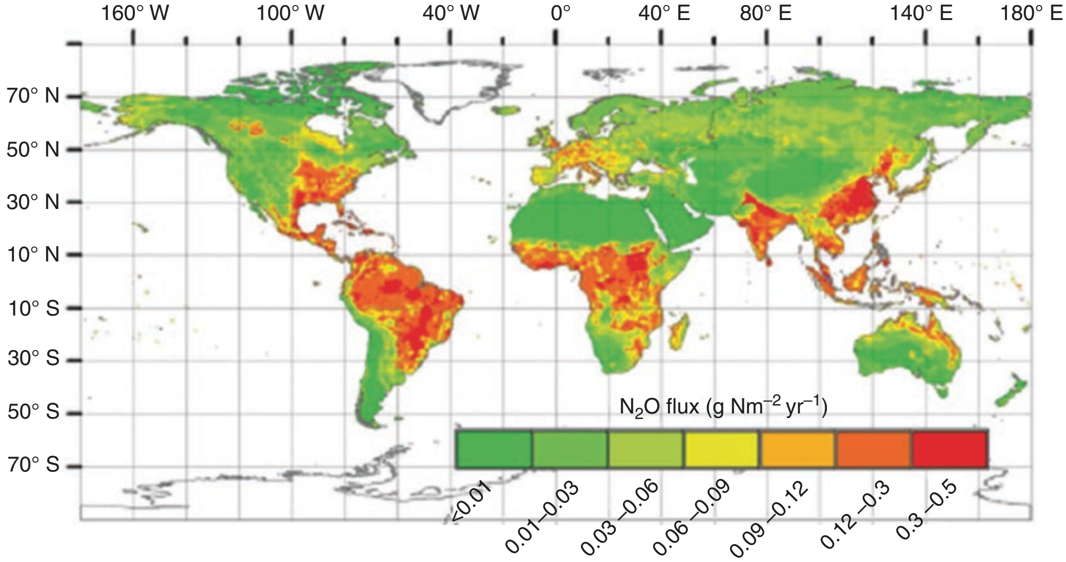

Fig. 21.10 Global fluxes of nitrous oxide. The global map is a modelling study based on the most sensitive environmental parameters causing methane emissions. (Tian et al. 2015)

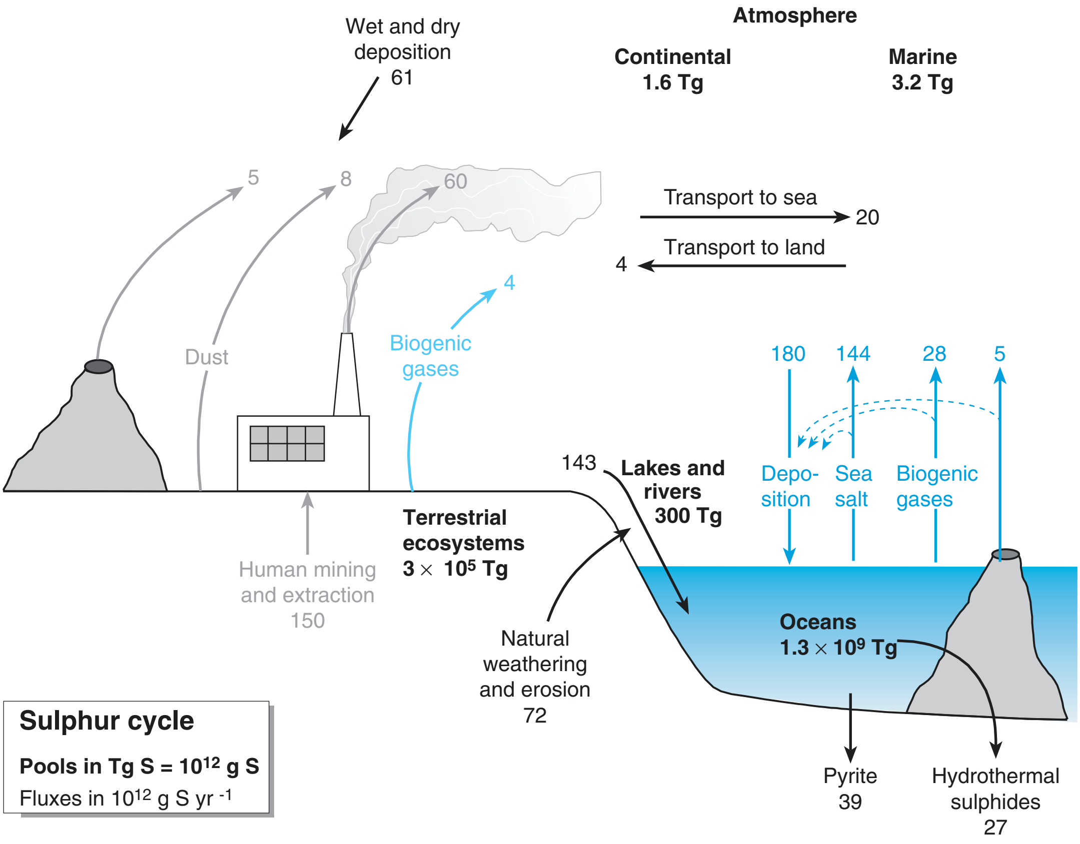

Fig. 21.11 Global pools and fluxes of sulphur. (after Schlesinger 1997; Schlesinger and Bernhardt 2013; Charlson et al. 1992)

ered despite large-scale liming. S deposition in combination with N deposition was responsible for **forest decline** in Europe and North America in the 1980s (Chap. 11). Present SO_2 emissions have decreased to pre-industrial levels over Europe but remain very high over East Asia (Piao 2009; Li et al. 2016).

The S cycle (Fig. 21.11) is characterised by high exchange rates across oceans caused by the release of **dimethyl sulphide** (**DMS**) from marine algae that contain chlorophyll a and c (dinoflagellates, green algae, diatoms and red algae). The MRT of DMS is about 1 day as it is oxidised to sulphate, which returns to the ocean by rain. The flux of sulphate is lower on land, where anthropogenic sources of S predominate, contributing to the formation of aerosols (ammonium-sulphate). During scrubbing of smoke from power plants sulphur is bound to Ca, forming gypsum, to be used in construction.

21.3 Ecosystem Services

The concept of **ecosystem services** (originally also called ecosystem goods and services) was introduced by Daily in 1997. In her book, ecosystem services were defined as "*the conditions and processes through which natural ecosystems, and the species that make them up, sustain and fulfil human life. They maintain biodiversity and the production of ecosystem goods […]. In addition to the production of goods, ecosystem services are the actual life-support functions, […] and they confer many intangible aesthetic and cultural benefits as well.*" Thus, the concept of ecosystem services is clearly human-centred. It states that there is a human demand for the processes and functions occurring in ecosystems because their products support human life (Daily 1997). An economic assessment estimated global ecosystem services to be worth USD 33 trillion per year, and this is considered a minimum estimate owing to high uncertainties (Costanza et al. 1997). For comparison, the global gross national product at that time was USD 18 trillion per year.

This concept was then advanced by the United Nations in the **Millennium Ecosystem Assessment** (MA 2005). Initiated in 2000, the MA goals were

- To assess the consequences of any change in global ecosystems for humankind and its well-being.
- To create the scientific basis needed to act, for example in nature conservation or to develop strategies for sustainable use of ecosystems.

Here, the definition of ecosystem services was sharpened, and they were defined as benefits people obtain from ecosystems. Thus, the human-centric focus enhanced.

More recently, the economic and social values of ecosystem services have been quantified in more detail, with the aim of raising awareness about the societal consequences of ongoing ecosystem change and degradation. **The Economics of Ecosystems and Biodiversity** study (TEEB, www.teebweb.org/) is a milestone in this respect (TEEB 2010). It focused on making nature's values visible and capturing those values in decision-making.

The **Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services** (IPBES), an intergovernmental body administered by the United Nations Environment Programme, is currently assessing the state of biodiversity and the ecosystem services it provides to society. More than 1000 scientists from all over the world contribute to strengthening the **science–policy interface** for biodiversity and ecosystem services for the conservation and sustainable use of biodiversity, long-term human well-being and sustainable development (www.ipbes.net). However, one should be aware that ecosystem services represent a very anthropocentric view of the world.

Ecosystem services are fundamentally based on biodiversity (Fig. 21.12, Sect. 20.1 in

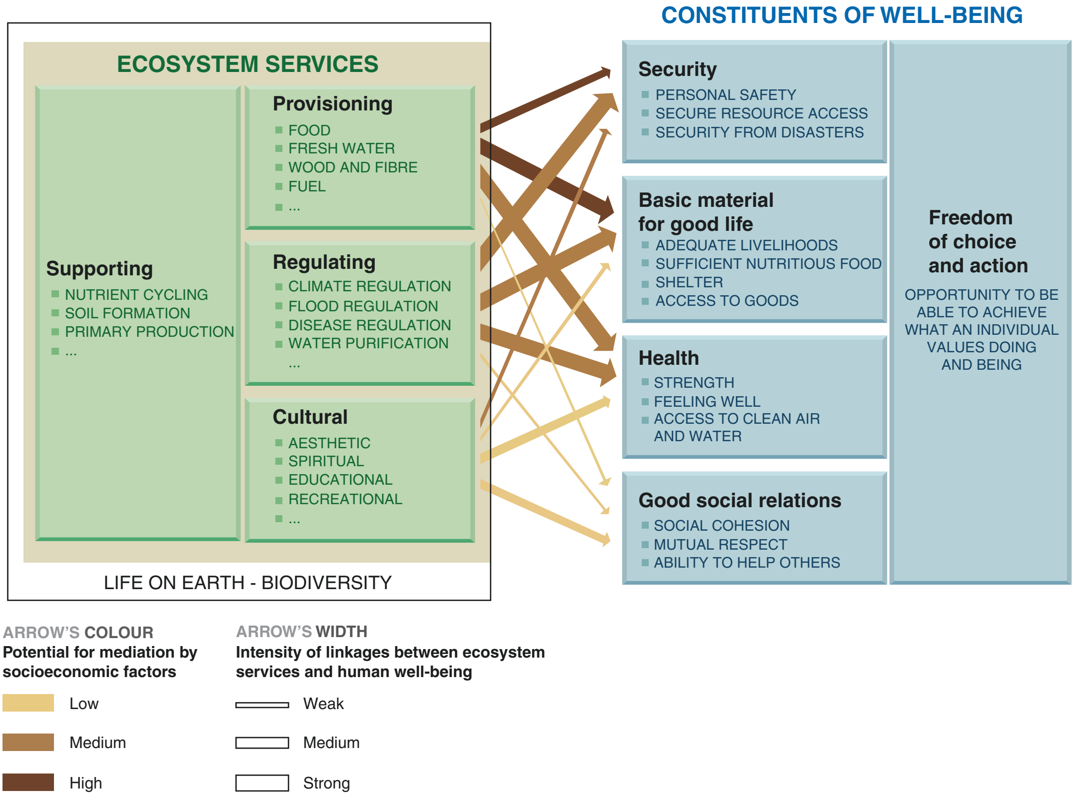

Fig. 21.12 Ecosystem services as a basis for human well-being. (MA 2005)

Chap. 20, Fig. 20.1, and Sect. 20.4, Box 20.4) and include supporting services (earlier called ecosystem functions), provisioning services, regulating services and cultural services. Plants and their diversity play a fundamental role in controlling ecosystem functions and services. Only when ecosystems are functioning properly can human well-being be achieved. Thus, with the concept of ecosystem services, a direct link was established scientifically but also politically (e.g. at the UN level) between ecosystems and global societies.

Summary

- Global biogeochemical cycles integrate fluxes of plants, animals, microorganisms and humans at different spatio-temporal scales and can be used as main indicators of anthropogenic impacts on terrestrial ecosystems. Although some numbers presented here still have high uncertainties, flux magnitudes are highly consistent across various measurement approaches and model simulations.
- Vegetation on Earth has been changed by LULUC from potential natural vegetation towards a vegetation cover that is influenced by humans across the terrestrial biosphere. By now, 60–70% of potential vegetation has been already converted into agricultural land.
- The global carbon cycle is dominated by CO_2 fixation and respiration, the two largest global CO_2 fluxes. CO_2 fixation on land and in oceans exceeds respiration. Changes in the carbon cycle are triggered by emissions from the burning of fossil fuels, which exceed emissions from LU change by almost a factor of 8 and from emissions of outgassing, weathering and volcanism by a factor of 7.
- The global water balance is dominated by the oceans. On land, water maintains life across the continents. About 60% of precipitation on land is returned to the atmosphere by evapotranspiration. The water cycle on land has been significantly altered by humans, mainly by irrigation, infrastructure (settlements, dams) and the release of aerosols.
- The global nitrogen cycle is dominated by anthropogenic N_2 fixation, which exceeds even natural N_2 fixation. The formation of N_2O during microbial processes, particularly under intensive agricultural LU, leads to large N_2O emissions. N_2O has a larger effect (per mass) on the global radiation budget compared to CO_2.
- The global sulphur cycle had been a major factor in the global radiation balance in the twentieth century, but industrial emissions have decreased to pre-industrial levels owing to the implementation of environmental legislation (e.g. scrubbing of smoke in power plants). SO_2 emissions are still a major concern in East Asia. The natural sulphur cycle is dominated by emissions of marine algae.
- Since all ecosystems on Earth are strongly affected by human activities and all are used in one way or another, the concept of ecosystem services has been developed to link ecosystem functions to society. One distinguishes between supporting services (e.g. nutrient cycling), provisioning services (e.g. food and feed), regulating services (e.g. climate regulation) and cultural services (e.g. aesthetics), which all contribute to the well-being of human populations.

References

Bond WJ, Woodward FI, Midgley GF (2004) The global distribution of ecosystems in a world without fire. New Phytol 165:525–538

Canadell JG, Schulze E-D (2014) Global potential of biospheric carbon management for climate mitigation. Nat Commun 5:5282

Cerveny RS, Balling RC (1998) Weekly cycles of air pollutants, precipitation and tropical cyclones in the coastal NW Atlantic region. Nature 394:561–563

Charlson RJ, Anderson TL, and McDuff RE (1992) The sulfur cycle. In: Butcher SS, Charlson RJ, Orians GH, and Wolfe GV (eds.) Global biogeochemical cycles. Academic Press: London, pp 285–300

Condon AG, Richards RA, Rebetzke GJ, Farquhar GD (2004) Breeding for high water-use efficiency. J Exp Bot 55:2447–2460

Costanza R, D'Arge R, De Groot R, Farber S, Grasso M, Hannon B, Limburg K, Naeem S, O'Neill RV, Paruelo J, Raskin RG, Sutton P, Van den Bel M (1997) The value of the world's ecosystem services and natural capital. Nature 387:253–260

Cramer W, Bondeau A, Woodward FI, Prentice IC, Betts RA, Brovkin V, Cox PM, Fisher V, Foley JA, Friend

AD, Kucharik C, Lomas MR, Ramankutty N, Sitch S, Smith B, White A, Young-Molling C (2001) Global response of terrestrial ecosystem structure and function to CO_2 and climate change: results from six dynamic global vegetation models. Glob Change Biol 7:357–373

Daily G (1997) Nature's services. Island Press, Washington, DC

Gleick PH, Palaniappan M (2010) Peak water limits to freshwater withdrawal and use. Proceedings of the National Academy of Sciences 107:11155–11162

Gruber N, Galloway JN (2008) An earth-system perspective of the global nitrogen cycle. Nature 451:293–296

IPCC (2012) Managing the risks of extreme events and disasters to advance climate change adaptation: a special report of working groups I and II of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge

IPCC (2013) Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Stocker TF, Qin D, Plattner GK, Tignor M, Allen SK, Boschung J, Nauels A, Xia Y, Bex V, Midgley PM (eds.)]. Cambridge University Press, Cambridge

Jung M, Henkel K, Herold M, Churkina G (2006) Exploiting synergies of global land cover products for carbon cycle modeling. Remote Sens Environ 101:534–553

Kaplan JO (2001) Geophysical applications of vegetation modeling. Ph.D. thesis. Lund University, Lund. https://doi.org/10.5281/zenodo.1492908

Keenan TF, Hollinger DY, Bohrer G, Dragoni D, Munger JW, Schmid HP, Richardson AD (2013) Increase in forest water-use efficiency as atmospheric carbon dioxide concentrations rise. Nature 499:324–328

Le Quéré C, Andrew RM, Canadell JG, Sitch S, Korsbakken JI, Peters GP, Manning AC, Boden TA, Tans PP, Houghton RA, Keeling RF, Alin S, Andrews OD, Anthoni P, Barbero L, Bopp L, Chevallier F, Chini LP, Ciais P, Currie K, Delire C, Doney SC, Friedlingstein P, Gkritzalis T, Harris I, Hauck J, Haverd V, Hoppema M, Klein Goldewijk K, Jain AK, Kato E, Körtzinger A, Landschützer P, Lefèvre N, Lenton A, Lienert S, Lombardozzi D, Melton JR, Metzl N, Millero F, Monteiro PMS, Munro DR, Nabel JEMS, Nakaoka S, O'Brien K, Olsen A, Omar AM, Ono T, Pierrot D, Poulter B, Rödenbeck C, Salisbury J, Schuster U, Schwinger J, Séférian R, Skjelvan I, Stocker BD, Sutton AJ, Takahashi T, Tian H, Tilbrook B, van der Laan-Luijkx IT, van der Werf GR, Viovy N, Walker AP, Wiltshire AJ, Zaehle S (2016) Global carbon budget 2016. Earth Syst Sci Data 8:605–649

Li B, Gasser T, Ciais P, Piao S, Tao S, Balkanski Y, Hauglustaine D, Boisier J-P, Chen Z, Huang M, Li LZ, Li Y, Liu H, Liu J, Peng S, Shen Z, Sun Z, Wang R, Wang T, Yin G, Yin Y, Zeng H, Zeng Z, Zhou F (2016) The contribution of China's emissions to global climate forcing. Nature 531:357–361

Merbold L, Eugster W, Stieger J, Zahniser M, Nelson D, Buchmann N (2014) Greenhouse gas budget (CO_2, CH_4 and N_2O) of intensively managed grassland following restoration. Glob Change Biol 20:1913–1928

Millennium Ecosystem Assessment (MA) (2005) Ecosystems and human well-being: current state and trends. Island Press, Washington, DC

Nemani RR, Keeling CD, Hashimoto H, Jolly WM, Piper SC, Tucker CJ, Myneni RB, Running SW (2003) Climate-driven increases in global terrestrial net primary production from 1982 to 1999. Science 300:1560–1563

Oki R, Kanae S (2006) Global hydrological cycles and world water resources. Science 313:1068–1072

Piao S (2009) The carbon balance of terrestrial ecosystems in China. Nature 458:1009–1013

Schlesinger WH (1997) Biogeochemistry: an analysis of global change. Academic Press, San Diego

Schlesinger WH, Bernhardt E (2013) Biogeochemistry: an analysis of global change. Academic Press, San Diego

Schulze E-D (1982) Plant life forms and their carbon, water and nutrient relations. In: Lange OL, Nobel PS, Osmond CB, Ziegler H (eds) Encyclopedia of plant physiology, Physiological plant ecology II, vol 12B. Water Relations and Photosynthetic Productivity, Springer, Berlin

Schulze E-D (2000) Der Einfluss des Menschen auf die biogeochemischen Kreisläufe der Erde. Max-Planck-Gesellschaft Jahrbuch 2000:39–58

Schulze E-D, Vygodskaya NN, Tchebakova NM, Czimczik CI, Kozlov DN, Lloyd J, Mollicone D, Parfenova E, Siderov KN, Varlagin AV, Wirth C (2002) The European transect: an introduction to the experimental design. Tellus 54B:421–428

Steffen W, Sanderson A, Tyson P, Jäger J, Matson P, Moore III B, Oldfield F, Richardson K, Schellnhuber HJ, Turner II BL, Wasson RJ (2004) Global change and the Earth system: a planet under pressure. Springer, Berlin

TEEB (2010) The economics of ecosystems and biodiversity: ecological and economic foundations. [Kumar P (ed.)] Earthscan, London

Tian H, Chen G, Lu C, Xu X, Ren W, Zang B, Banger K, Tao B, Pan S, Liu M, Zhang C, Bruhwiler L, Eofsy S (2015) Global methane and nitrous oxide emissions from terrestrial ecosystems due to multiple environmental changes. Ecosyst Health Sustain 1:1–20

Toon OB (2000) How pollution suppresses rain. Science 287:1763–1765

WBGU (1999) World in transition: ways towards sustainable management of fresh water. Springer, Berlin pp 392

Wolf S, Eugster W, Ammann C, Häni M, Zielis S, Hiller R, Stieger J, Imer D, Merbold L, Buchmann N (2013) Contrasting response of grassland versus forest carbon and water fluxes to spring drought in Switzerland. Environ Res Lett 8:035007

22

Dynamic Global Vegetation Models

Contribution by S. Zaehle

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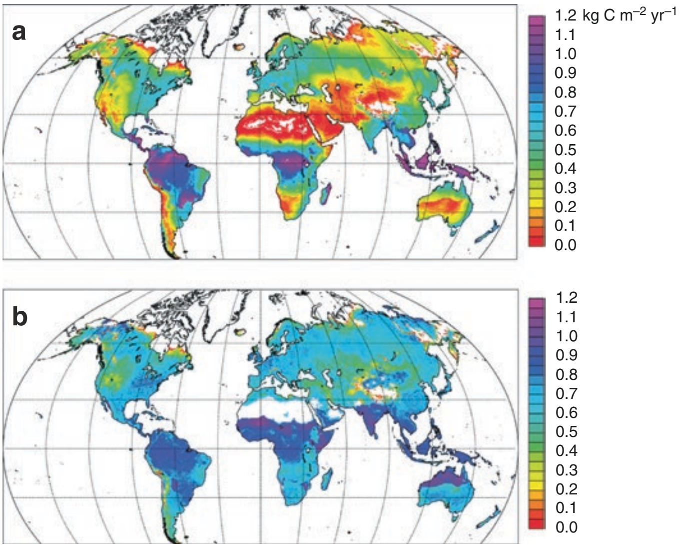

Dynamic Global Vegetation Models (DGVMs) are continuously developed to better represent terrestrial ecosystems. More processes, pools and interactions are considered, their representation in the models further improved, new model versions being validated against earlier versions of the same model but also against other models. Here, N cycling and N limitations of net primary production (NPP) have been included (Smith et al. 2014). The top panel shows NPP estimates modelled with N being considered, while the bottom panel shows the N limitation of NPP. Values close to one indicate no N limitation. Values approaching zero indicate increasing N limitation

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The class of **Dynamic Global Vegetation Models** (**DGVMs**) (Prentice and Cowling 2012) was conceived in the early 1990s as a fusion of four research fields: plant geography, plant physiology and biogeochemistry, vegetation dynamics, and biogeophysics (see Prentice et al. 2007 for a brief history). The development of DGVMs followed mainly two scientific challenges: On a fundamental level, uncertainty in the understanding of past **Earth system dynamics** originates to a large extent from the incomplete understanding of the multiple and likely non-linear feedbacks between the terrestrial biosphere and the physical climate (Prentice et al. 2007). On a more pragmatic level, the likely future land-use and rapid climatic changes will require an enhanced understanding of the **transient dynamics of vegetation** to predict the consequences of these changes for terrestrial ecosystems and their functioning. To respond to these challenges, DGVMs bridge the gap between (1) processes operating at the level of an individual plant (or even a plant organ), such as carbon (C) assimilation, nutrient and water uptake, and plant growth (Part II), and (2) processes operating at the community or ecosystem level, such as land–atmosphere gas exchange and vegetation dynamics (Chap. 16) affecting the structure and composition of ecosystems (Chap. 20).

This chapter provides an overview of the processes represented in the current generation of DGVMs and outlines current shortcomings and challenges in developing a predictive understanding of the terrestrial biosphere.

22.1 Anatomy of a DGVM

Despite a large diversity in the detailed representation of particular processes (Table 22.1), DGVMs share a common **modular structure** (Fig. 22.1) (Prentice et al. 2007). Fundamentally, they are similar to the wider class of models known as **terrestrial biosphere** models (Heimann et al. 1998; McGuire et al. 2001), with the unique feature of being able to simulate the transient development of vegetation composition and structure, hereafter referred to as **vegetation dynamics**.

DGVMs represent the globe as being divided into **grid cells** with a typical **spatial resolution** between approximately 50 × 50 km and 250 × 250 km. The resolution is defined primarily by the spatial resolution of the model forcing data (e.g. meteorology, soil) and available computing power. The grid cells are assumed to be homogenous in terms of their abiotic environment, for example soil properties and climate. Within a grid cell, vegetation may be represented as fractions or tiles occupied by different types of vegetation (i.e. plant species composition). Each vegetation type is typically described by a range of **state variables** describing physical properties that may change during the course of the simulation (Fig. 22.1). In the first generation of DGVMs, these state variables typically included characteristics of the population, such as average plant density, plant height, plant carbon and plant nitrogen content of different biomass compartments of the plant (e.g. leaves, fine roots, woody biomass), their respective allometry and factors affecting resource uptake (e.g. leaf area index, rooting density).

DGVMs include processes operating at different **time scales**, which are reflected as a series of nested time loops (Fig. 22.1). Fast processes acting on a diurnal time scale include the energy and gas exchange of the canopy and the soil surface with the atmosphere. Processes acting on daily and seasonal time scales include the phenology of leaves (leaf-out, growth and senescence), the growth of plant organs and the decomposition of dead organic material. Vegetation dynamics processes, for example recruitment and mortality, typically act on annual and longer time scales. While diurnal processes are considered explicitly at an hourly time scale in DGVMs developed from the land surface modules of comprehensive **Earth System Models**, some DGVMs integrate these processes implicitly over the diurnal time course. The latter strategy provides a computational advantage and likely has little effect on the seasonal time courses of ecosystem gas exchange and longer-term vegetation dynamics. However, this strategy precludes full exploitation of micrometeorological measurements for model evaluation (Sect. 22.4.1).

Table 22.1 Current Dynamic Global Vegetation Models (DGVMs). Non-exhaustive list of current DGVMs and some of their key characteristics related to vegetation dynamics

	Shortest time-step	Canopy scaling	Vegetation structure	Competition/ limiting resources	Establishment	Mortality	Disturbance	Land-surface scheme	References
TRIFFID	2 h	Beer's law with big-leaf assumption	Population average	Lotka-Volterra	Minimum seed	Constant turnover	No	Yes	Cox (2001)
JSBACH	30 min	2-stream approximation with 3 canopy layers	Population average	Light, water	NPP and density dependent	Constant turnover	Fire, windthrow	Yes	Brovkin et al. (2009)
IBIS	1 h	2-stream approximation with multiple canopy layers	Population average	Light (shading), water	Uniform	Constant turnover	No	No	Kucharik et al. (2000)
SDGVM	1 d	Beer's law with big-leaf assumption	Population represented by average individual	Light, water	Density dependent	Dependent on C balance	Fire, windthrow	No	Woodward et al. (1995)
LPJ	1 d	Beer's law with big-leaf assumption	Population represented by average individual	Light, water	Density dependent	Depending on growth efficiency and self-thinning	Fire	No	Sitch et al. (2003)
ORCHIDEE	30 min	Beer's law with multiple canopy layers	Population represented by average individual	Light, water	Density dependent	Depending on growth efficiency and self-thinning	Fire	Yes	Krinner et al. (2005)
CLM	30 min	2-stream approximation with multiple canopy layers	Population represented by average individual	Light, water	Density dependent	Depending on growth efficiency and self-thinning	Fire	Yes	Bonan and Levis (2006)
LPJ-Guess	1 d	Beer's law with multiple canopy layers	Individuals or cohorts	Light, water, nitrogen	Light in lowest vegetation layer	Depending on growth efficiency and self-thinning	Fire	No	Smith et al. (2014)

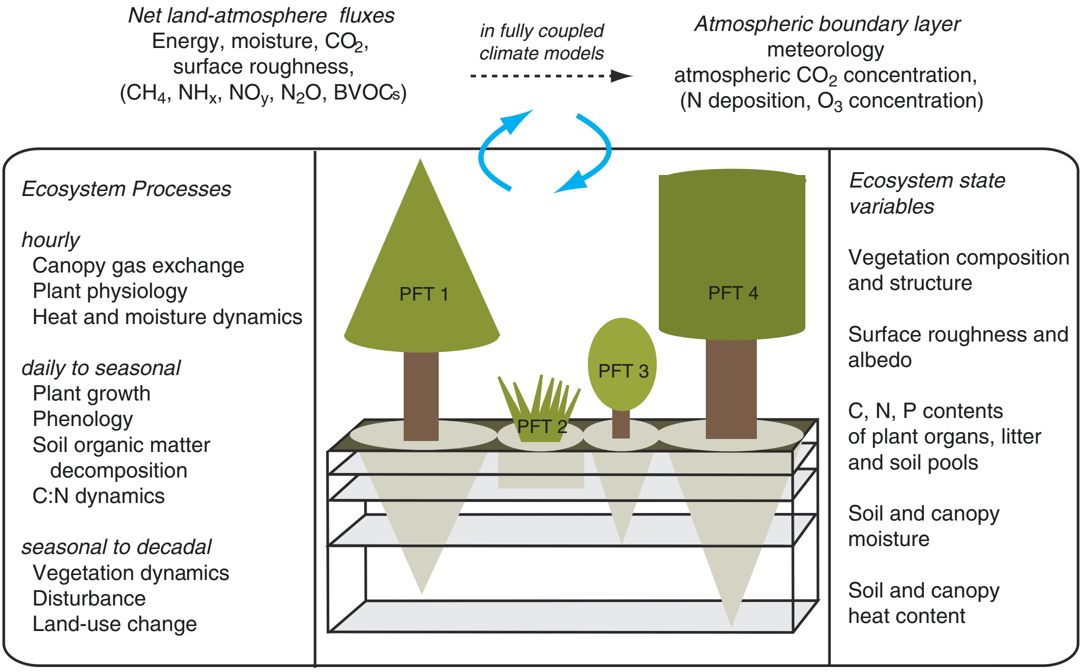

Fig. 22.1 Conceptual diagram of a Dynamic Global Vegetation Model (DGVM). The diagram illustrates the most important ecosystem processes and state variables

22.2 Biogeochemical Cycling

The primary currency for which plants compete in DGVMs is carbon, which is required to build biomass and to reproduce. Therefore, DGVMs focus on modelling plant carbon acquisition (and the carbon cycle) as well as all relevant factors that might limit carbon acquisition, that is light, water and nutrient availability (Part II).

22.2.1 Plant Carbon Assimilation

The carbon budget of vegetation is typically calculated at the level of a representative plant and then scaled to the grid cell, making assumptions about the population structure (Sect. 22.4). Gross primary production (GPP) is typically estimated based on the process-based photosynthesis model by Farquhar et al. (1980) (Sect. 12.2) or variants thereof. The earlier DGVMs applied a "**big-leaf**" assumption (Friend 2001). In these models, the amount of radiation intercepted by the canopy is calculated from Beer's law (Sect. 16.1). The total amount of intercepted radiation is subsequently used to calculate GPP with the Farquhar model, assuming the canopy was a single, big leaf. This makes it possible to efficiently calculate daily gross production, which is sufficient to capture the observed seasonal course of GPP. However, big-leaf models do not accurately capture the diurnal cycle of canopy gas exchange (Friend 2001). Consequently, models operating on diurnal time scales frequently employ a **multilayered canopy** (Table 22.1). In these models, the Farquhar model is applied for separate layers of the canopy with varying light levels, given the solution of a more complex light extinction calculation, considering the effects of leaf and solar angles and backscattering of radiation, as well as direct and diffuse sources of light (e.g. Sellers 1985; Spitters et al. 1986).

22.2.2 Plant Growth

The carbon available for plant growth depends on the plant's net assimilation (Sect. 22.2.1) and the plant's carbon-use efficiency (the ratio of net to gross primary production) (Fig. 22.2). The latter is determined by the partitioning of assimilated carbon to growth and respiration and is typically modelled in a much less process-based manner (Sects. 12.1 and 16.2 for leaf and ecosystem scales, respectively). The manifold **respiration** processes are typically lumped together into (1) respiration associated with the construction of new tissue ("growth respiration"), which is assumed to be proportional to NPP (~25%), and (2) respiration associated with maintenance processes of existing tissue ("maintenance respiration"), which is typically related to biomass (or nitrogen content of the plant tissue) as a surrogate for biochemical energy consumption (Thornley and Cannell 2000). Few models account for substrate (i.e. carbon) limitation of maintenance respiration, either by scaling maintenance respiration to GPP (Knorr 2000) or explicitly constraining maintenance respiration to the available non-structural hydrocarbon reserve (Zaehle and Friend 2010).

There is no fundamental theory of carbon allocation (Franklin et al. 2012), and therefore the **allocation** of NPP to plant organs follows empirical approaches in DGVMs. The simplest approach used by DGVMs is to allocate NPP to plant compartments given fixed fractions empirically derived from growth and biomass inventories. However, these fractions vary as plants grow (Lloyd 1999), and therefore a more advanced approach respects the functional relationship of plant compartments based on allometric relationships. An example of this approach is the "pipe model" (Shinozaki et al. 1964), which links the hydraulic transport capacity of the stem to the transpiring foliar area. This approach has the advantage of linking allocation strategies to plant traits, enabling the evaluation of trade-offs in terms of growth versus security of the foliar water supply (Hickler et al. 2006) (Sect. 22.2.5). Various frameworks have been proposed to model allocation in a more advanced manner, including growth maximising strategies and game-theoretic considerations, but these have not yet matured into a parameterisation applicable to DGVMs (Franklin et al. 2012).

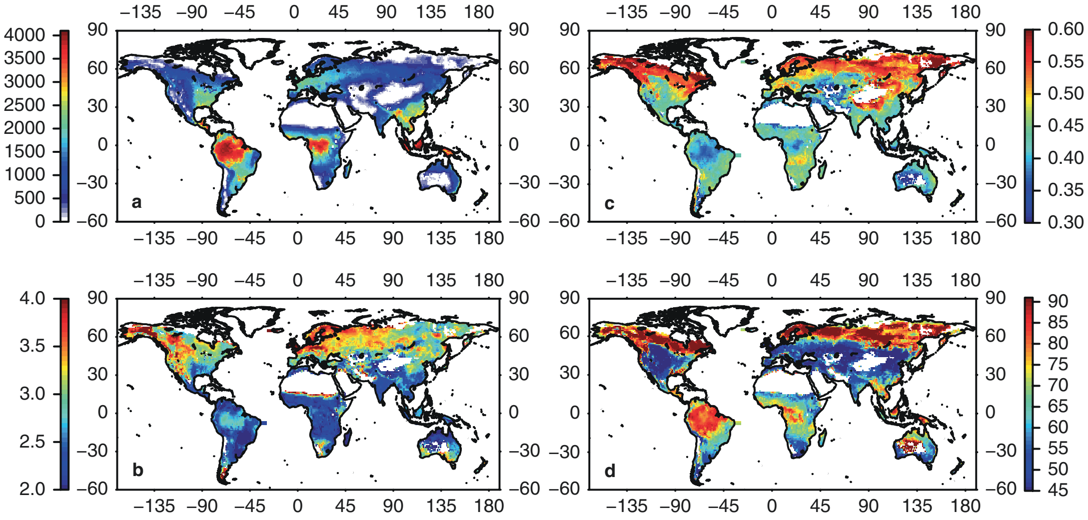

Fig. 22.2 Coupling of terrestrial carbon, nitrogen and water cycles. **a** GPP in g C m^{-2} year^{-1}; **b** water-use efficiency (g C kg^{-1} H$_2$O); **c** carbon-use efficiency (unitless); **d** nitrogen-use efficiency (g C g^{-1} N). All values refer to the 2000–2010 mean across all vegetation types present in a particular grid cell. Simulations were performed with the O–CN DGVM. (Zaehle and Friend 2010)

22.2.3 Decay of Litter and Soil Organic Matter

Senescent tissues and woody debris enter pools of fresh, non-decomposed litter of varying turnover times given their chemical composition (Sect. 16.2). DGVMs almost exclusively apply first-order kinetics to simulate the **decomposition** of fresh litter, considering rate-modifiers from soil temperature and soil moisture (Parton et al. 1993). A prescribed fraction of the decomposed litter is assumed to be respired by microorganisms and lost to the atmosphere as CO_2, while the remainder is incorporated into microbial biomass and then allocated to soil organic matter pools with differing turnover times, which represent the varying degrees of recalcitrance of organic residue. Implicit in this approach is the assumption that the microbial biomass is in equilibrium with the amount of material to be decomposed. While this may be an appropriate assumption on annual to decadal time scales, tree-girdling studies (e.g. Högberg et al. 2001) and free-air CO_2 enrichment experiments (e.g. Drake et al. 2011) have demonstrated that altered labile C inputs into the soil may stimulate microbial activity (i.e. *priming*) and thereby also modify the rate at which more recalcitrant soil organic matter is decomposed. The first models were proposed to incorporate these effects (Manzoni et al. 2012). However, their merit and effect on long-term dynamics still need to be established (Wieder et al. 2013).

22.2.4 Hydrological Cycle

The link of the **water balance** to the carbon cycle is an important feature of DGVMs because it represents the fundamental trade-off between plant carbon gain and water loss, which can be described by the **water-use efficiency** of carbon assimilation (gross carbon assimilation per unit transpiration) (Fig. 22.2). This trade-off occurs at the leaf level through the plants' control of stomatal conductance, regulating at the same time water loss and CO_2 uptake (Sect. 12.1). Through their stomatal regulation, plants exert strong control over the terrestrial water balance.

DGVMs that explicitly simulate the land–atmosphere coupling at an hourly time scale typically employ variants of the Ball–Berry model (Ball et al. 1987) at the leaf level, which is subsequently integrated into the canopy level (Sect. 16.1). This empirical model directly links photosynthesis and transpiration and makes predictions about the response of water-use efficiency to atmospheric drought (slight decreases) and atmospheric CO_2 (increases), which can be interpreted as optimal in terms of maximizing carbon gain for a given water-use strategy (Medlyn et al. 2013; Prentice et al. 2014). An alternative approach is to constrain canopy conductance by the maximum supported transpiration rate, which is a function of a plant's hydraulic properties such as minimum leaf water potential and xylem conductivity, thereby mimicking the mechanisms that control leaf water potential and stomatal closure without explicitly simulating plant water transport (Hickler et al. 2006).

The remainder of the hydraulic balance of DGVMs is generally treated in simple terms (Gerten et al. 2004). The top surface soil water bucket receives water input from precipitation (or snow) reduced by interception loss. A fraction of this water percolates to deeper soil layers, given a gradient of volumetric water content until it leaves the lowest layer, from where it is assumed to be lost to the ecosystem. The top layer loses water to evaporation, and the entire profile is subject to water loss by plant transpiration. The number of soil layers, as well as the detail with which soil physical processes are represented, varies widely from one model to the next.

22.2.5 Nutrient Cycles

Most early DGVMs focused on the relationship of vegetation with the combined water and carbon cycles and did not account explicitly for the bioavailability of macronutrients like nitrogen (N) and phosphorus (P), although this situation is gradually changing. Nutrient cycling provides feedback between the biological processes in vegetation and soils, and their incorporation provides a further step in the evolution of DGVMs towards dynamic global ecosystem models. One important reason for the hesitation in including nutrients was the challenge intrinsic to modelling nutrient cycles (Chaps. 11 and 16 for leaf and ecosystem scales, respectively).

The terrestrial N cycle provides a tight coupling between the growth and decay of plants and soil organisms. The N-related efficiency of plant growth (**nitrogen-use efficiency:** the ratio of net primary production and net nitrogen uptake) (Fig. 22.2) is the emergent outcome of the N available for plant uptake and the stoichiometric requirements (i.e. ratio of C and N) to support the growth of new tissue. The detail with which this N constraint on growth is represented in DGVM varies widely (see Zaehle and Dalmonech 2011 for a review): Simpler models adjust GPP or NPP such that it matches the stoichiometric constraint and the plant's N uptake at any given time, thereby letting plants make ad hoc adjustments to their carbon-use efficiency (e.g. Thornton et al. 2007). More complex models (e.g. Zaehle and Friend 2010) allow for the acclimation of the plant's stoichiometry and thereby a wider range of feedbacks by changing the tissue's photosynthetic and respiration rates and litter quality. The latter feedback is important to model plant–soil interactions because the amount of net N mineralisation (and thus N availability for plant growth) depends on the arrangement of stoichiometry between high C:N litter and low C:N soil organic matter.

Large, but geographically strongly varying, inputs from natural atmospheric N deposition and biological N_2 fixation, as well as substantial losses to leaching and gaseous emissions lead to varying degrees of the stoichiometric constraints on growth globally (Zaehle 2013) (Sect. 21.2). None of these terms can be measured with sufficient accuracy on a larger scale, nor is the regulation of these processes completely understood. Therefore, there is considerable uncertainty in any long-term projection of the terrestrial N cycle (Zaehle and Dalmonech 2011). Nevertheless, current results show that considering nitrogen constraints leads to attenuated responses of the terrestrial carbon cycle to perturbations of climate and atmospheric CO_2 (Zaehle et al. 2010). Regionally anthropogenic nitrogen deposition plays a strong role in fertilizing ecosystems, with side effects of this eutrophication in terms of rising N leaching and N_2O emissions (Zaehle et al. 2011) (Sect. 16.3 for ecosystem scale).

The terrestrial **P cycle** is strongly dependent on the P content of the original rock material upon which soil development is based, which is only poorly constrained by available data (Yang et al. 2013) (Chap. 11). Bioavailable P is derived from the weathering of the soil's parent material, reduced by P losses due to soil erosion (Buendía et al. 2010), and affected by deposition of P associated with the atmospheric transport of dust (Okin et al. 2004). At the time scales considered by current DGVMs (decades to centuries), ecosystem P availability is commonly assumed to be constant. The few DGVMs attempting to simulate P dynamics focus on representing the redistribution of ecosystem available P between the plant, soil organic and sorbed soil phases (Wang et al. 2010).

22.3 Biogeography

22.3.1 Concept of Plant Functional Types in Models

A fundamental challenge to modelling global vegetation distribution is to represent floristic and functional biodiversity (Chap. 20). It is impossible to represent all known species in a DGVM because of the lack of data to describe the species and the differences among them, as well as the computational costs of representing such a large number of plants in a model. Therefore, DGVMs represent vegetation based on **plant functional types** (also called **plant functional groups**) (Sect. 20.2), which are assumed to be representative of plants with similar ecology and ecophysiology (Lavorel et al. 2007).

The functional classification of the first-generation DGVMs was primarily based on stature (trees, herbaceous and sometimes shrub types), leaf physiognomy (needle-leaved versus broad-leaved), phenology (evergreen, rain green, summer green) and photosynthetic pathway

(C_3 and C_4). Some DGVMs further separated these functional types into bioclimatic groups (tropical, temperate and boreal) and defined common temperature and water-stress tolerances for these types based on bioclimatic limits (Woodward et al. 1995; Sitch et al. 2003). Physiological differences of the plant functional types are described by **plant traits**, which define ecophysiological trade-offs. An example is the so-called leaf-economic spectrum (Wright et al. 2004), which describes the commonly observed concurrent increase of the plant traits "leaf mass per unit leaf area" and "leaf-life span" across different vegetation types.

The ability of DGVMs to reproduce the global biome distribution of **potential natural vegetation** with a minimal reliance on ecological data in a computationally efficient manner is one reason for the wide application of DGVMs in terrestrial biosphere modelling to date. Land surface modules of the current generation of Earth system models frequently rely on this concept of a few plant functional types as a pragmatic and efficient way to represent vegetation. However, the lack of a detailed representation of biodiversity has often been criticised by ecologists. The focus on a few very distinct types is thought to cause artificially large gradients in ecosystem functioning at the transition zones of biomes. In addition, it is also thought to be one cause of rapid biome boundary shifts under climate change (Sect. 23.3), such as the dieback of the southern fringe of the boreal forest with climate warming (Sitch et al. 2008) or the savannisation of the Amazon basin under future increases in drought (Huntingford et al. 2013) (Sect. 22.6).

However, increasing the number of plant functional types is challenging, for the following reasons: (1) It typically requires the incorporation of more ecophysiological processes into DGVMs to explicitly simulate the emergent trade-off between different ecophysiological strategies. Uncertainties as to the precise ecophysiological mechanisms causing such trade-offs frequently limit further refinement of DGVMs. Nevertheless, some studies successfully added additional **functional trade-offs**, for instance by considering the plant hydraulic architecture (trading off security of water transport to leaves versus investment costs to support the hydraulic transport system) (Hickler et al. 2006), the investment in structural reserves as a means of stress tolerance (Fisher et al. 2010), trade-offs related to fire and shade tolerance of trees (Scheiter et al. 2012) or traits related to the nitrogen cycle (trade-offs between N_2-fixing and non-N_2-fixing species; Gerber et al. 2010). (2) Even if additional trade-offs can be represented in DGVMs, data to parameterise the plant traits associated with these trade-offs are often scarce and ambiguous (Sect. 20.2). Compared to the beginning of the development of DGVMs in the mid-1990s, when hardly any data were available, the ever-increasing body of literature describing plant traits now provides a wealth of information to define parameter values in DGVMs (Kattge et al. 2011). However, data gaps, geographically biased sampling and the large variation in plant traits within clusters of supposedly homogeneous species groups pose challenges to the consistent estimation of parameters in DGVMs (Hartig et al. 2012).

To resolve this situation, a new class of DGVMs has emerged, in which vegetation is no longer represented by plant functional types. Rather, **hypothetical plant species** are generated with random combinations of plants traits considered by the DGVM (Pavlick et al. 2013). First attempts have also been made to extend this concept to imitate community assembly by simulating the inheritance of plant traits between generations of plants (Scheiter et al. 2013). For a given location with a prescribed climate and pedographic setting, these hypothetical plants compete with each other given the trade-offs incorporated into the DGVM. In such a model, the diversity of prevailing plant trait combinations is an **emergent property** of the DGVM, rather than a prescribed input.

22.3.2 Scaling from Plant to Community

In early DGVMs, vegetation was represented by the properties and fluxes of a representative individual for each plant functional type. While some DGVMs do not consider vegetation structure (in terms of vegetation height, plant density) explicitly ("**green-slime approach**"), others scale the properties of the representative individual to the grid cell by means of an average population density (Table 22.1). In these models, the population density changes owing to recruitment and mortality processes, which in turn affect the properties of the average individual. The product of the average individual's size and the average population density is used as a measure to estimate plant functional types' access to resources (such as light, water and nutrients) and therefore determines a plant's competitive strength for resources and, thus, growth.

Most of the early models did not account for vertical competition for light, even though, for example, tree types can outcompete herbaceous types owing to shading. Despite differences in the details, **recruitment** and **mortality** processes are typically based on a plant's carbon balance and the relative contribution of plant functional types to the grid cell's plant density (Table 22.1). This high level of aggregation requires a lumped representation of vegetation dynamics processes. An example is the representation of shading competition based on the self-thinning rule (Westoby 1984), which describes the empirical, emergent relationship between tree density and tree size as the outcome of density (shading) competition of trees (Sect. 13.3). The simplicity of the approach causes a plant's net carbon balance to drive the competition to such an extent that most DGVMs have difficulty simulating the co-existence of plant functional types within one grid cell.

To circumvent the pitfalls of this lumped representation, a small number of DGVMs (e.g. Friend et al. 1997; Smith et al. 2001) represent all individual members of a plant community for representative "**patches**" within a grid cell by adopting the principles of a forest gap model (Table 22.1; Sect. 15.1). Patches are subdivisions of a grid cell of the size of a canopy-tree crown. Many patches are simulated at all stages of succession to represent the average state of the grid cell, such that the patch age distribution reflects the average (commonly prescribed and not dynamically simulated) disturbance rate (Sect. 22.3.3). The individual plants within a patch share common plant traits (Sect. 22.3.1) and differ only in their size. This makes it possible to explicitly simulate the vertical competition for light within a community (and theoretically also other resources) and allows for the introduction of, for instance, shade-tolerant versus shade-intolerant functional types. Arguably, this approach leads to a more realistic representation of vegetation structure and succession dynamics (Smith et al. 2001; Sato et al. 2007) (Chap. 17).

The high computational costs of this individual-based approach to represent vegetation structure has spurred the development of landscape-scale vegetation models, which simulate the size-related competition of plants within and across plant functional types, and is based on individuals representing size classes (Fisher et al. 2018). In the simplest case, these classes may be age classes (Smith et al. 2001), but more advanced schemes of averaging across size classes have also been developed (Medvigy et al. 2009). Purves et al. (2008) showed that the pertinent features of such models may be replicated by models representing an **over- and understorey** composed of representatives of the present plant functional types.

Common to all current DGVMs, with a few regional exceptions (e.g. Lischke et al. 2006), is that they ignore possible obstacles to **migration** of plant functional types between grid cells. Instead, they assume that new seedlings of any plant functional type can become established anywhere on the globe if bioclimatic conditions are favourable, and the vegetation density allows for the establishment of new individuals.

22.3.3 Disturbances

An essential component of the representation of vegetation dynamics in DGVMs are processes generally classified as "disturbance", such as fire, herbivory, strong winds or pests (Sect. 13.5 and Chap. 14). This definition is widely used in the literature, although the term "disturbance" is confusing, as these processes are intrinsic parts of the ecosystem processes that shape ecosystem composition and structure. The stochastic nature of disturbances makes them difficult to represent in DGVMs (Chap. 15). Some DGVMs therefore do not explicitly include disturbances. Instead, they are included implicitly in the turnover times of vegetation carbon (e.g. Friend et al. 1997; Krinner et al. 2005).

Fire is the main type of natural disturbance affecting ecosystems worldwide. Therefore, it is represented to some degree by most DGVMs (Table 22.1). The processes controlling the frequency of fires (ranging from every year to centuries) include the frequency of ignition (e.g. from lightning) and the amount, moisture and flammability of the biomass fuels (mostly the litter layer and near-surface biomass). These controls depend on climate and vegetation state and give rise to feedbacks between vegetation structure and fire frequency and intensity. Early semi-empirical models assumed that—given that grid cells of a DGVM were sufficiently large—the fraction of a grid cell affected by fire in a given year was equal to the probability of a fire to occur at a random location within the grid cell (Thonicke et al. 2001). This probability is based on the fuel load and moisture, factoring in the different levels of fire resistance across plant functional types. More complex models distinguished surface and crown fires and further effects of stand structure and meteorological conditions (e.g. wind speed) (Bachelet et al. 2003; Thonicke et al. 2010), as well as the occurrence of man-made ignitions (Venevsky et al. 2002).

22.3.4 Anthropogenic Land Use and Disturbance

While the earlier DGVMs only simulated processes related to natural potential vegetation, the scope of DGVMs has become enlarged in recent years to include the disturbances of natural vegetation and biogeochemical cycles due to anthropogenic **land use** (Sect. 23.2). These developments include the representation of **generic crop types** (in particular their phenology and carbon allocation strategy) (e.g. Bondeau et al. 2007; Smith et al. 2010) and the representation of forest disturbance by **harvesting** and **thinning** activities (Zaehle et al. 2006; Bellassen et al. 2011). These developments allow for a more accurate simulation of the seasonal to long-term carbon balance of specific ecosystems (Friend et al. 2007). Notwithstanding, the representation of land management is for the most part still in its infancy. One important consequence of these developments is that they contribute to a better understanding of the importance of land-use change for the regional and global carbon balance (McGuire et al. 2001; Hurtt et al. 2006; Shevliakova et al. 2009) (Sects. 16.2 and 21.2).

22.4 Evaluating DGVMs

The multi-faceted nature of DGVMs requires that model testing and evaluation be performed on scales ranging from the site level to global and from hours to decades. Multiple methodologies, including ground-based measurements across networks of monitoring stations (e.g. ecosystem gas exchange using the eddy covariance technique, inventories of biomass or community assembly), satellite-based remote sensing and monitoring of atmospheric greenhouse gases provide observations of terrestrial ecosystems, their structure and their energy and gas exchange on various temporal and spatial scales (Chap. 14). Each method measures a particular facet of the complexity of ecosystems and their relation to climate. Listing all available data sets and the virtues and challenges in using those would easily fill a book on its own (Luo et al. 2012 for an overview). In what follows, only the main features of DGVM evaluation are described.

22.4.1 Ecosystem Gas Exchange Measurements

High-frequency measurements of the **ecosystem–atmosphere exchange** of energy, H_2O vapour and CO_2 with the eddy covariance technique together with meteorological measurements provide a powerful tool for model evaluation (Baldocchi 2003; Friend et al. 2007). The FLUXNET initiative (http://fluxnet.ornl.gov/) provides an umbrella for the continuously growing network of towers equipped with the eddy covariance technique and gathers data of far over 850 sites, albeit very unevenly distributed across the world's major biomes (Sects. 14.1 and 16.3). These data can be used to explore the relationship between meteorological drivers, ecosystem state and ecosystem fluxes on diurnal, seasonal and interannual scales (Fig. 22.3). The challenge in using these data is that the time series are sometimes incomplete

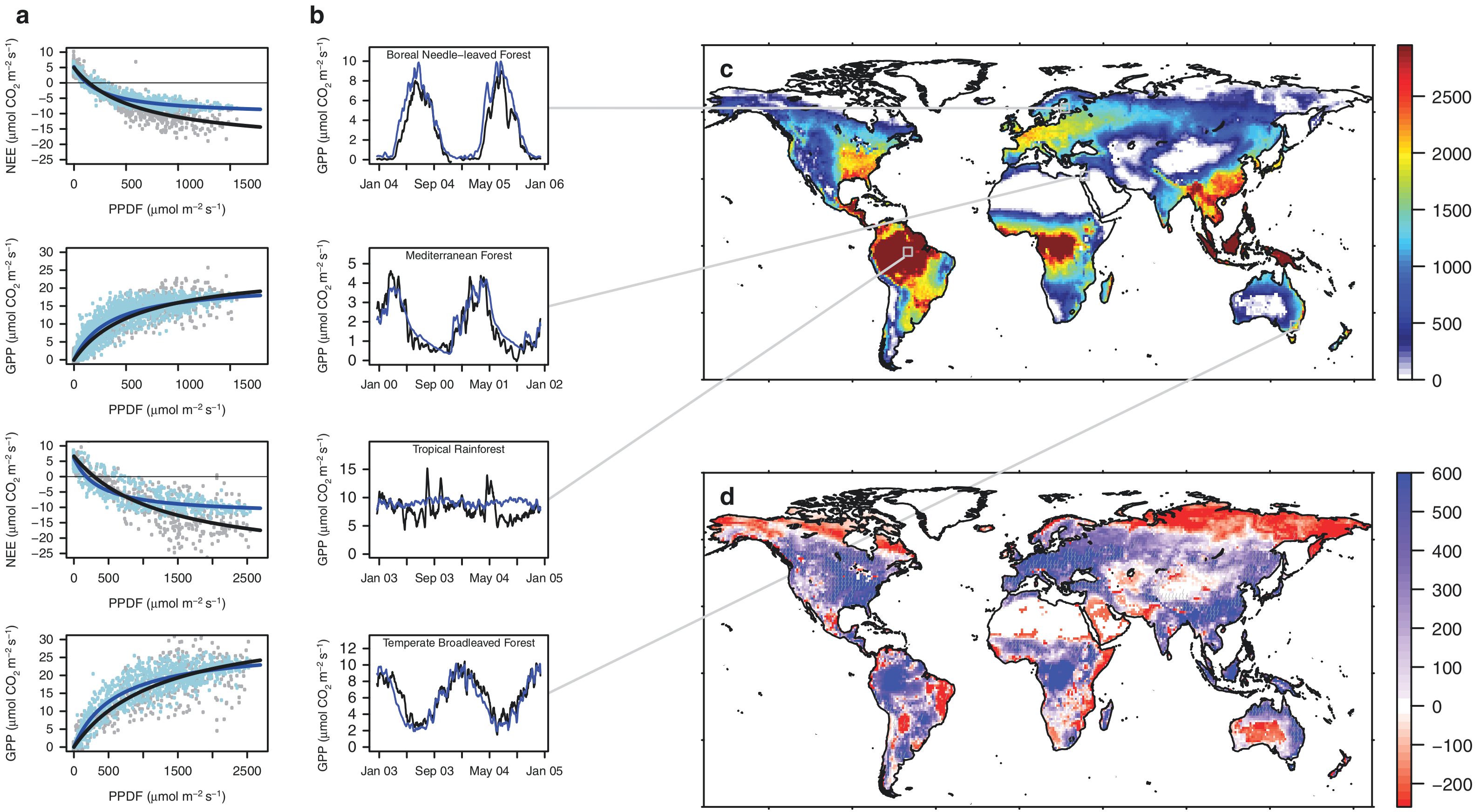

Fig. 22.3 Multi-scale evaluation of a Dynamic Global Vegetation Model (DGVM) (*blue lines*) with eddy covariance data (*black lines*). **a** Evaluation of ecosystem responses: Light response of half-hourly net ecosystem carbon exchange (NEE) and gross primary production (GPP; calculated as NEE = Reco − GPP, where Reco was estimated from night-time data). The upper two panels show data from boreal forests, the lower two from temperate deciduous forests. **b** Evaluation of seasonal cycles of GPP across boreal, temperate, Mediterranean and tropical ecosystems at the site level, facilitating a direct comparison of modelled and simulated values. Global evaluation: **c** average 1982–2011 annual GPP and **d** difference to estimates based on empirical upscaling of tower data (Jung et al. 2009, 2011). All simulations were performed with the O–CN model (Zaehle and Friend 2010). The stipplings in panel **d** mark grid cells, where the difference between model and data is larger than the observational uncertainty

(for reasons discussed by Moffat et al. 2007) and refer to a highly dynamic area (i.e. the footprint; from <100 × 100 m to >500 × 500 m, depending on atmospheric stability and measurement height), for which local soil conditions and disturbance history may be very important, but are not readily specified and considered in DGVMs. Recent advances in synthesising the FLUXNET database using observations from many sites and multivariate statistics provide regionally integrated estimates of ecosystem gas exchange and therefore allow for a comparison of observation-based and modelled fluxes on the same spatial and temporal scale (Fig. 22.3) (e.g. Jung et al. 2009; Guanter et al. 2014).

22.4.2 NPP and Inventories

Biometric measurements in specific ecosystems make it possible to quantify the annual NPP and sometimes also to partition them into foliar, woody and below-ground components of individual plots (Sects. 14.1 and 16.2). The high labour intensity implies that there are few, high-quality data sets that have also not been as effectively synthesised as FLUXNET data (Luyssaert et al. 2007; Olson et al. 2013). The same caveat concerning the imprint of local soil and disturbance history applies here as well, rendering it a challenge to use these data for model evaluation (e.g. Zaehle et al. 2010). Forest inventories, which are designed to gather growth and stock estimates representative of larger regions, provide complementary, regional-scale information (e.g. Pan et al. 2011; Saatchi et al. 2011). However, these data intrinsically combine growth and mortality information, providing only an indirect means of evaluation (Zaehle et al. 2006).

22.4.3 Remotely Sensed Vegetation Greenness

Satellite measurements of the spectral reflectance of surface radiation provide a way to assess the seasonal and interannually varying fraction of absorbed photosynthetically active radiation (fAPAR) globally with high spatial resolution (Sect. 14.1). fAPAR is a quantity modelled by DGVMs, and these data can therefore be used to evaluate the timing of seasonal **phenology** (e.g. bud burst or leaf shedding), as well as its sensitivity to meteorological parameters such as temperature or precipitation (e.g. Dalmonech and Zaehle 2013). Together with ancillary data, this seasonal information can also be used to evaluate the spatial distribution of phenology types predicted by DGVMs (e.g. Sitch et al. 2003). Earlier satellite measurements with lesser spectral coverage (Tucker et al. 2005) still provide evidence for the trends in vegetation greenness over the last three decades. These data provide an opportunity to evaluate longer-term trends in vegetation greenness or activity such as GPP (e.g. Forkel et al. 2013; Verma et al. 2014; Xia et al. 2015).

22.4.4 Atmospheric CO_2 Monitoring

A **top-down constraint** for the modelled net land–atmosphere carbon flux at seasonal and longer time scales can be derived from high-precision monitoring of atmospheric CO_2 concentrations (Heimann et al. 1998; Prentice et al. 2000). By means of an atmospheric transport model, the local terrestrial sources and sinks are advected to **CO_2 monitoring stations** (e.g. tall towers, stations on mountain tops, remote stations), where they can be directly compared to CO_2 concentration measurements. This approach is now widely used to evaluate terrestrial biosphere models (Dalmonech and Zaehle 2013; Kelley et al. 2013), despite the uncertainties that remain, in particular related to the vertical component of atmospheric transport (Gurney et al. 2004).

The concentration measurements show a distinct seasonal cycle with strongly geographically varying amplitude and phasing (Sect. 23.3). This variation reflects different seasonal patterns of carbon assimilation and release, predominantly from terrestrial ecosystems. The amplitude of the **seasonal cycle** increases from the South to the North Pole because of the large share of vegetated land in the Northern Hemisphere and the seasonal offset of production and decay (Heimann et al. 1998). The interannual variability of the growth rate of atmospheric CO_2 has been shown to correlate with the **ENSO cycle** and, thus, interannual anomalies in tropical land temperatures. Some, but not all, DGVMs are capable of reproducing the main features of the seasonal and interannual variations of atmospheric CO_2 (Fig. 22.4) (Dargaville et al. 2002; Peylin et al. 2005). Recent studies analysing the few existing long-term records (1960s until present) showed an increase of the seasonal cycle in the Northern Hemisphere (Sect. 21.2) (Graven et al. 2013) and a change in the association of the annual variations of the growth rate of CO_2 with land temperature (Wang et al. 2014). The land ecosystem processes behind these trends are currently not well understood.

22.4.5 Ecosystem Manipulation Experiments

The foregoing observations record the response of ecosystems to diurnal, seasonal and interannual variations of climate. They cannot evaluate the capacity of DGVMs to predict the consequences of future environmental changes, which depart from the envelope of current variability. Dedicated **ecosystem experiments** (Sect. 14.2) provide a unique

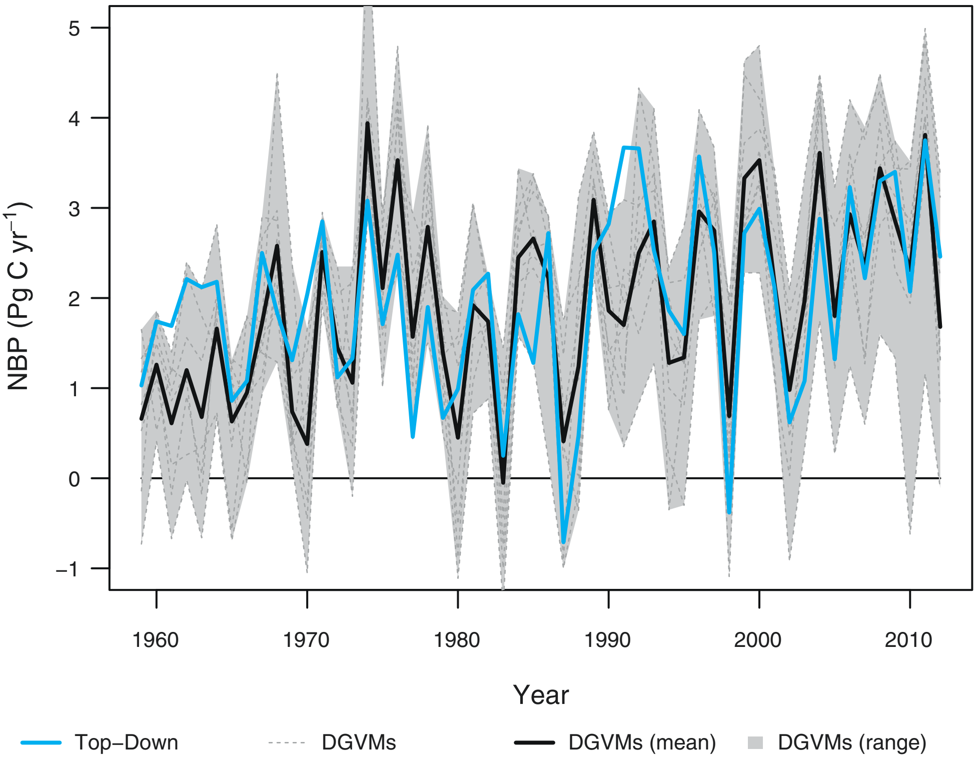

Fig. 22.4 Prediction of global terrestrial net land–atmosphere carbon exchange by an ensemble of Dynamic Global Vegetation Models (DGVMs). Simulated net biome production (NBP; net land–atmosphere C flux) across seven DGVMs compared to top-down estimate based on residual of anthropogenic CO_2 emissions from fossil fuel burning and land-use change, net ocean–atmosphere CO_2 flux and growth rate of atmospheric CO_2. The error bar corresponds to the 68% confidence interval of the top-down estimate. (Data from Le Quéré et al. 2013)

resource to test a model's sensitivity to altered temperature (Melillo et al. 2011), precipitation (Vicca et al. 2012), nutrient inputs (Thomas et al. 2013) or atmospheric CO_2 concentrations (Norby et al. 2005). Problems common to using these data for **model evaluation** are that most experiments follow a step-change, which may create artificially large responses, and that the response to a perturbation is often dependent on the ecosystem's initial state (and thus soil conditions and site history), which can only be crudely approximated by DGVMs. Nevertheless, the process understanding derived from these experiments are invaluable to elucidate the (in-)validity of model concepts (De Kauwe et al. 2013; Zaehle et al. 2014).

22.5 Applications of DGVMs

The first generation of DGVMs successfully simulated contemporary, global-scale observed patterns of vegetation distribution and functioning, as well as the terrestrial carbon and water cycles driven by observed meteorology and atmospheric CO_2 concentrations and with prescribed boundary conditions, such as physical soil properties and land use. One example of the application of DGVMs to predict contemporary biosphere dynamics is the global terrestrial **net land–atmosphere carbon exchange**, predicted by an ensemble of DGVMs (Fig. 22.4) (Le Quéré et al. 2013, 2016). This figure compares the DGVM simulations against the terrestrial carbon budget inferred as the residual of the other components of the global C budgets, which are relatively better constrained (anthropogenic emissions, net ocean C uptake and atmospheric CO_2 content) (Sects. 21.2 and 23.2).

Another important type of application for DGVMs is to elucidate the impact of past climates on the terrestrial biosphere. Such studies can be used, for instance, to analyse the consequences of past climates and climate variability for the distribution of vegetation types and, thereby, help to explain biome shifts recorded in palaeo-vegetation records (Ni et al. 2006). The importance of DGVMs in understanding **past Earth system dynamics** has recently been demonstrated by Prentice et al. (2011), who showed that a DGVM could reproduce records of terrestrial carbon storage and vegetation distribution at the last glacial maximum and the pre-industrial Holocene. The fact that this study provided evidence that the main processes controlling present-day terrestrial biosphere dynamics also operated in the past, such as during the last glacial maximum, may also be seen as an indication of the applicability of DGVMs for future climates.

Figure 22.5 shows an ensemble of such a **future scenario:** the mean prediction (across four DGVMs) of changes in vegetation cover in 2100 under the A2 climate change scenario as simulated by the Hadley Centre General Circulation Model (Sitch et al. 2008). The study showed that increases in forest cover in boreal regions (a consequence of warmer temperatures) as well as in savannas (a consequence of reduced water stress due to CO_2 fertilisation and associated increases in water-use efficiency) are robust predictions across models. Nevertheless, the magnitude and rates of change differ across DGVMs. Less robust projections of vegetation dynamics are associated with the dieback of forest vegetation, for instance in the Amazon basin and the southern fringe of the Eurasian boreal forest. Turnover of vegetation is a prime uncertainty in future projection (Friend et al. 2013). This uncertainty results from ambiguities in the representation of tree mortality (McDowell et al. 2013 for a review) and the response of trees to strong increases in temperature (and associated increases in drought stress and extreme temperatures).

A more comprehensive understanding of likely future trajectories can be obtained when DGVMs are run coupled with climate models to form so-called **Earth system models**, such that the **feedbacks** between the land surface gas and energy exchanges and climate can be assessed (Sect. 23.2 for more details). The latest generation of Earth system models used for the assessment of future climate change resulting from anthropogenic greenhouse gas emissions (Table 22.1) (Friedlingstein et al. 2006; Taylor et al. 2012; Arora et al. 2013) have revealed that these feedbacks are equally important to climate feedback mechanisms within the climate system (e.g. cloud feedbacks).

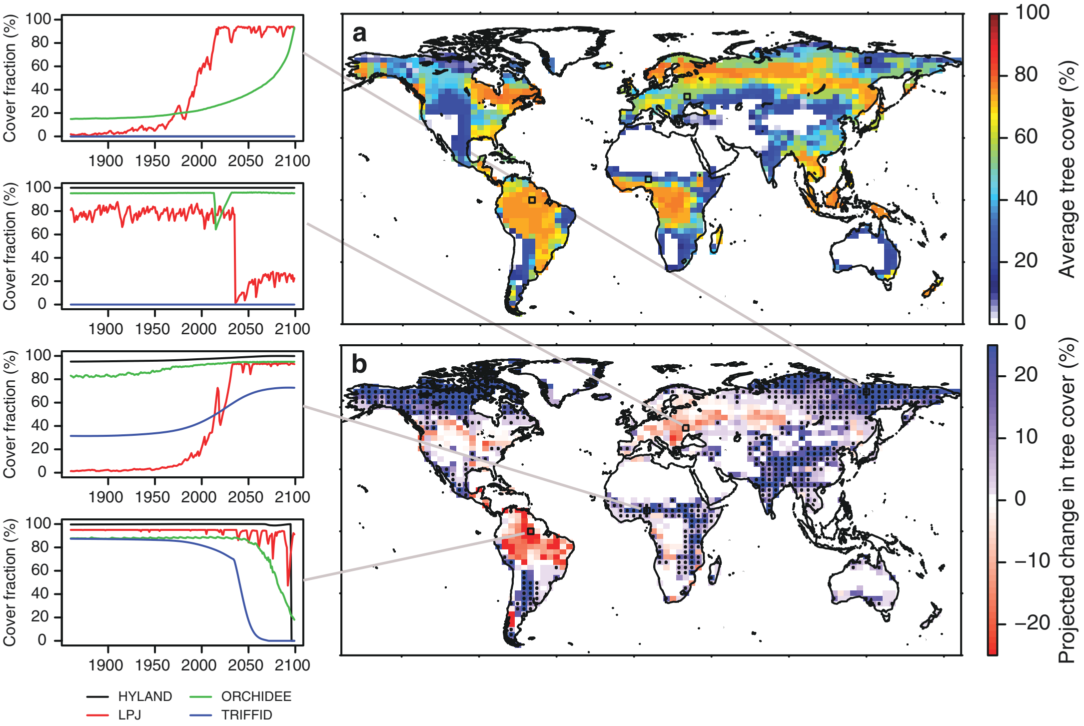

Fig. 22.5 Changes in vegetation cover in 2100 under the A2 climate change scenario. **a** Average tree cover in the year 2000. **b** Projected change in tree cover (2100 minus 1860) as simulated by four DGVMs, driven by the Hadley Centre Global Circulation Model climate projection under the A2 scenario (Sitch et al. 2008). The insets show time series of the forest cover in selected biomes. The stipplings in panel **b** mark grid cells, where at least three out of four DGVMs agreed on the trend

22.6 Conclusions and Outlook

DGVMs are a versatile tool for investigating past, present and future vegetation dynamics and their effects on biogeochemical cycling and biogeophysical land properties such as albedo. DGVMs have contributed to an improved understanding of (1) the global distribution of the major vegetation types, (2) ecosystem functioning, which is closely related to ecosystem services such as biomass production, habitat provision for biodiversity and water availability, and (3) the feedbacks between land biosphere and climate. Nonetheless, their long-term dynamics remain poorly understood and constrained, and consequently, these uncertain long-term dynamics contribute strongly to uncertainty in future projections of these comprehensive Earth system models.

The fundamental future challenge in the further development of DGVMs is to improve the capacity of predicting biome boundary shifts (also called **range shifts**). This requires increased realism concerning key processes related to the migration, establishment and mortality of plants, a better representation of the coexistence of vegetation types, a better understanding of the ecological diversity of plant functioning (such as acclimation to given environmental conditions) and a better representation of disturbances. Relating ecosystem functions simulated by DGVMs more closely to relevant ecosystem services will be important to future assessments of the impacts of climate and land-use change on ecosystems and humans (Sect. 23.1) (Schröter et al. 2005). Accounting for a larger set of potential **feedback mechanisms** with which the terrestrial ecosystems may affect the climate system, including wetland CH_4 emissions, soil N_2O emissions and the emission of biogenic volatile compounds, will also be important (Sect. 16.2) (Arneth et al. 2010). It cannot be stressed enough, however, that progress in predictive global vegetation and ecosystem models will only be possible with intensive model evaluation and scientific work to corroborate the database with which to evaluate these global models.

Summary

- DGVMs integrate knowledge from plant geography, plant physiology and biogeochemistry, vegetation dynamics and biogeophysics. Incorporating processes working at very different scales (e.g. leaf, community, ecosystem), this class of models helps to better understand biosphere–atmosphere feedbacks and transient vegetation dynamics in response to global change.
- The structure of DGVMs is modular, and the globe is represented as grid cells of 50 × 50 km to 250 × 250 km, depending on the spatial resolution of the data used to run the model. Abiotic conditions are homogenous in grid cells, while vegetation and vegetation characteristics can vary. Processes included in the models can function at very different time scales.
- DGVMs describe many biogeochemical processes, most importantly the carbon cycle. This includes carbon assimilation, plant growth and C allocation, as well as litter decomposition and environmental controls thereof. The models also describe the water cycle using water-use efficiency and land–atmosphere coupling, and nutrient cycles, particularly those of nitrogen and phosphorus.
- Vegetation is represented as plant functional types with similar characteristics, which also allows DGVMs to reproduce potential natural vegetation. The reduction of biodiversity to functional types can cause too large gradients or rapid biome shifts in models. However, including more functional types is challenging because this requires incorporating more ecophysiological processes and functional tradeoffs. By including recruitment and mortality processes, DGVMs scale from plants to the community. To correctly depict vegetation dynamics, DGVMs also include disturbances like fire or land use.
- Models need to be tested and evaluated to assure proper representation of processes and vegetation dynamics. This is done using measurement data from satellites, eddy covariance flux sites, inventories or ecosystem experiments.

References

Arneth A, Sitch SA, Bondeau A, Butterbach-Bahl K, Foster P, Gedney N, de Noblet-Ducoudré N, Prentice IC, Sanderson M, Thonicke K, Wania R, Zaehle S (2010) From biota to chemistry and climate: towards a comprehensive description of trace gas exchange between the biosphere and atmosphere. Biogeosciences 7:121–149

Arora VK, Boer GJ, Freidlingstein P, Eby M, Jones CD, Christian JR, Bonan G, Bopp L, Brovkin V, Cadule P, Hajima T, Ilyina T, Lindsay K, Tjiputra JF, Wu T (2013) Carbon-concentration and carbon-climate feedbacks in CMIP5 Earth system models. J Clim 26:5289–5214

Bachelet D, Neilson RP, Thomas H, Drapek RJ, Lenihan JM, Sykes MT, Smith B, Sitch S, Thonicke K (2003) Simulating past and future dynamics of natural ecosystems in the United States. Glob Biogeochem Cycles 17:1045

Baldocchi DD (2003) Assessing the eddy covariance technique for evaluating carbon dioxide exchange rates of ecosystems: past, present and future. Glob Change Biol 9:479–492

Ball J, Wooddrow I, Berry JA (1987) A model predicting stomatal conductance and its contribution to the control of photosynthesis under different environmental conditions. In: Biggens J (ed) Progress in photosynthesis research, vol 4. Springer, Dordrecht, The Netherlands, pp 221–224

Bellassen V, Viovy N, Luyssaert S, Maire G, Schelhaas M-J, Ciais P (2011) Reconstruction and attribution of the carbon sink of European forests between 1950 and 2000. Glob Change Biol 17:3274–3292

Bonan GB, Levis S (2006) Evaluating aspects of the community and atmosphere models (CLM3 and CAM3) using a dynamic global vegetation model. J Clim 10:2290–2301

Bondeau A, Smith PC, Zaehle S, Schaphoff S, Lucht W, Cramer W, Gerten D (2007) Modelling the role of agriculture for the 20th century global terrestrial carbon balance. Glob Change Biol 13:679–706

Brovkin V, Raddatz T, Reick CH, Claussen M, Gayler V (2009) Global biogeophysical interactions between forest and climate. Geophys Res Lett 36:L07405

Buendía C, Kleidon A, Porporato A (2010) The role of tectonic uplift, climate, and vegetation in the long-term terrestrial phosphorous cycle. Biogeosciences 7:2025–2038

Cox PM (2001) Description of the TRIFFID dynamic global vegetation model. In: Hadley Centre technical note, vol 24. Met Office, UK

Dalmonech D, Zaehle S (2013) Towards a more objective evaluation of modelled land-carbon trends using atmospheric CO_2 and satellite-based vegetation activity observations. Biogeosciences 10:4189–4210

Dargaville RJ, Heimann M, McGuire AD, Prentice IC, Kicklighter DW, Joos F, Clein JS, Esser G, Foley J, Kaplan J, Meier RA, Melillo JM, Moore B III, Ramankutty N, Reichenau T, Schloss A, Sitch S, Tian H, Williams LJ, Wittenberg U (2002) Evaluation of terrestrial carbon cycle models with atmospheric CO_2 measurements: results from transient simulations considering increasing CO_2, climate, and land-use effects. Glob Biogeochem Cycles 16:1092

De Kauwe M, Medlyn BE, Zaehle S, Walker AP, Dietze MC, Hickler T, Jain AK, Luo Y, Parton WJ, Prentice IC, Smith BLU, Thornton PE, Wang S, Wang Y-P, Wårlind DLU, Weng E, Crous KY, Ellsworth DS, Hanson PJ, Seok H-K, Warren JM, Oren R, Norby RJ (2013) Forest water use and water use efficiency at elevated CO_2: a model-data intercomparison at two contrasting temperate forest FACE sites. Glob Change Biol 19:1759–1779

Drake JE, Gallet-Budynek A, Hofmockel KS, Bernhardt ES, Billings SA, Jackson RB, Johnsen KS, Lichter J, McCarthy HR, McCormack ML, Moore DJ, Oren R, Palmroth S, Phillips RP, Pippen JS, Pritchard SG, Treseder KK, Schlesinger WH, Delucia EH, Finzi AC (2011) Increases in the flux of carbon belowground stimulate nitrogen uptake and sustain the long-term enhancement of forest productivity under elevated CO_2. Ecol Lett 14:349–357

Farquhar GD, von Caemmerer S, Berry JA (1980) A biochemical model of photosynthetic CO_2 assimilation in leaves of C_3 species. Planta 149:78–90

Fisher R, McDowell N, Purves D, Moorcroft P, Sitch S, Cox P, Huntingford C, Meir P, Woodward FI (2010) Assessing uncertainties in a second-generation dynamic vegetation model caused by ecological scale limitations. New Phytol 187:666–681

Fisher RA, Koven CD, Anderegg WRL, Christoffersen BO, Dietze MC, Farrior CE, Holm JA, Hurtt GC, Knox RG, Lawrence PJ, Lichstein JW, Longo M, Matheny AM, Medvigy D, Muller-Landau HC, Powell TL, Serbin SP, Sato H, Shuman JK, Smith B, Trugman A, Viskari T, Verbeeck H, Weng E, Xu C, Xu X, Zhang T, Moorcroft PR (2018) Vegetation demographics in Earth System Models: a review of progress and priorities. Global Change Biol 24:35–54

Forkel M, Carvalhais N, Verbesselt J, Mahecha M, Neigh C, Reichstein M (2013) Trend change detection in NDVI time series: effects of inter-annual variability and methodology. Remote Sens 5:2113–2144

Franklin O, Johansson J, Dewar RC, Dieckmann U, McMurtrie RE, Brannstrom A, Dybzinski R (2012) Modeling carbon allocation in trees: a search for principles. Tree Physiol 32:648–666

Friedlingstein P, Cox PM, Betts R, Bopp L, von Bloh W, Brovkin V, Cadule P, Doney S, Eby M, Fung I, Bala G, John J, Jones C, Joos F, Kato T, Kawamiya M, Knorr W, Lindsay K, Matthews HD, Raddatz T, Rayner P, Reick C, Roeckner E, Schnitzler K-G, Schnur R, Strassmann K, Weaver AJ, Yoshikawa C, Zeng N (2006) Climate-carbon cycle feedback analysis: results from the C4MIP model intercomparison. J Clim 19:3337–33504

Friend AD (2001) Modelling canopy CO_2 fluxes: are "big-leaf" simplifications justified? Glob Ecol Biogeogr 10:603–619

Friend AD, Stevens AK, Knox RG, Cannell MGR (1997) A process-based, terrestrial biosphere model of ecosystem dynamics (Hybrid v3.0). Ecol Model 95:249–287

Friend AD, Arneth A, Kiang NY, Lomas M, Ogée J, Rödenbeck C, Running SW, Santaren J-D, Sitch S, Viovy N, Woodward FI, Zaehle S (2007) FLUXNET and modelling the global carbon cycle. Glob Change Biol 13:610–633

Friend AD, Lucht W, Rademacher TT, Keribin R, Betts R, Cadule P, Ciais P, Clark DB, Dankers R, Falloon PD, Ito A, Kahana R, Kleidon A, Lomas MR, Nishina K, Ostberg S, Pavlick R, Peylin P, Schaphoff S, Vuichard N, Warszawski L, Wiltshire A, Woodward FI (2013) Carbon residence time dominates uncertainty in terrestrial vegetation responses to future climate and atmospheric CO_2. Proc Natl Acad Sci 111:3280–3285

Gerber S, Hedin LO, Oppenheimer M, Pacala SW, Shevliakova E (2010) Nitrogen cycling and feedbacks in a global dynamic land model. Glob Biogeochem Cycles 24:GB1001

Gerten D, Schaphoff S, Haberlandt U, Lucht W, Sitch SA (2004) Terrestrial vegetation and water balance – hydrological evaluation of a dynamic global vegetation model. J Hydrol 286:249–270

Graven HD, Keeling RF, Piper SC, Patra PK, Stephens BB, Wofsy SC, Welp LR, Sweeney C, Tans PP, Kelley JJ, Daube C, Kort EA, Santoni GW, Bent JD (2013) Enhanced seasonal exchange of CO_2 by northern ecosystems since 1960. Science 341:1085–1089

Guanter L, Zhang Y, Jung M, Joiner J, Voigt M, Berry JA, Frankenberg C, Huete A, Zarco-Tejada P, Lee J-E, Moran S, Ponce-Campos G, Beer C, Camps-Valls G, Buchmann N, Gianelle D, Klumpp K, Cescatti A, Baker JM, Griffis TJ (2014) Global and time-resolved monitoring of crop photosynthesis with chlorophyll fluorescence. Proc Natl Acad Sci 111:E1327–E1333

Gurney KR, Law RM, Denning AS, Rayner PJ, Pak BC, Baker D, Bousquet P, Bruhwiler L, Chen Y-H, Ciais P, Fung IY, Heimann M, John J, Maki T, Maksyutov S, Peylin P, Prather M, Taguchi S (2004) Transcom 3 inversion intercomparison: model mean results for the estimation of seasonal carbon sources and sinks. Glob Biogeochem Cycles 18:GB1010

Hartig F, Dyke J, Thomas H, Higgins SI, O'Hara RB, Scheiter S, Huth A (2012) Connecting dynamic vegetation models to data – an inverse perspective. J Biogeogr 39:2240–2252

Heimann M, Esser G, Haxeltine A, Kaduk J, Kicklighter DW, Knorr W, Kohlmaier GH, McGuire AD, Melillo J, Moore B III, Ottofi RD, Prentice IC, Sauf W, Schloss A, Sitch S, Wittenberg U, Würth G (1998) Evaluation of terrestrial carbon cycle models through simulations of the seasonal cycle of atmospheric CO_2: first results of a model intercomparison study. Glob Biogeochem Cycles 12:1–24

Hickler T, Prentice IC, Smith B, Sykes MT, Zaehle S (2006) Implementing plant hydraulic architecture within the LPJ dynamic global vegetation model. Glob Ecol Biogeogr 15:567–577

Högberg P, Nordgren A, Buchmann N, Taylor AFS, Ekblad A, Högberg MN, Nyberg G, Ottosson-Löfvenius M, Read DJ (2001) Large-scale forest girdling shows that current photosynthesis drives soil respiration. Nature 411:789–792

Huntingford C, Zelazowski P, Galbraith D, Mercado LM, Sitch S, Rosie Fisher R, Lomas M, Walker AP, Jones CD, Booth BBB, Malhi Y, Hemming D, Kay G, Good P, Lewis SL, Phillips OL, Atkin OK, Lloyd J, Gloor E, Zaragoza-Castells J, Meir P, Betts R, Harris PP, Nobre C, Marengo J, Cox PM (2013) Simulated resilience of tropical rainforests to CO_2-induced climate change. Nat Geosci 6:268–273

Hurtt GC, Frolking S, Fearon MG, Moore B, Shevliakova E, Malyshev S, Pacala SW, Houghton RA (2006) The underpinnings of land-use history: three centuries of global gridded land-use transitions, wood-harvest activity, and resulting secondary lands. Glob Change Biol 12:1208–1229

Jung M, Reichstein M, Bondeau A (2009) Towards global empirical upscaling of FLUXNET eddy covariance observations: validation of a model tree ensemble approach using a biosphere model. Biogeosciences 6:2001–2013

Jung M, Reichstein M, Margolis HA, Cescatti A, Richardson AD, Arain MA, Arneth A, Bernhofer C, Bonal D, Chen J, Gianelle D, Gobron N, Kiely G, Kutsch W, Lasslop G, Law BE, Lindroth A, Merbold L, Montagnani L, Moors EJ, Papale D, Sottocornola M, Vaccari F, Williams C (2011) Global patterns of land-atmosphere fluxes of carbon dioxide, latent heat, and sensible heat derived from eddy covariance, satellite, and meteorological observations. J Geophys Res 116:G00J07

Kattge J, Díaz S, Lavorel S, Prentice IC, Leadley P, Bönisch G, Garnier E, Westoby M, Reich PB, Wright IJ, Cornelissen JHC, Violle C, Harrison SP, van Bodegom PM, Reichstein M, Enquist BJ, Soudzilovskaia NA, Ackerly D, Bekker R, Blanco CC, Bloder B, Bond WJ, Bradstock R, Bunker DE, Casanoves F, Covender-Bares J, Chambers JQ, Chapin FS III, Chave J, Coomes D, Cornwell WK, Craine JM, Dobrin BH, Duarte L, Durka W, Elser J, Esser G, Estiarte M, Fagan WF, Fang J, Fernàndez-Méndez F, Fidelis A, Finegan B, Flore O, Ford H, Frank D, Freschet GR, Fyllas NM, Gallagher RV, Green WA, Gutierrez AG, Hickler T, Higgins SI, Hodgson JG, Jalili A, Jansen S, Joly CA, Kerkhoff AJ, Kirkup D, Kitajima K, Kleyer M, Klotz S, Knops JMH, Kramer K, Kühn I, Kurokawa H, Laughlin D, Lee TD, Leishman M, Lens F, Lenz T, Lewis SL, Lloyd J, Llusìa J, Louault F, Ma S, Mahecha MD, Manning P, Massad T, Medlyn BE, Messier J, Moles AT, Müller SC, Nadrowski K, Naeem S, Niinemets Ü, Nöllert S, Nüske A, Ogaya R, Oleksyn J, Onipchenko VG, Onoda Y, Ordoñez J, Overbeck G, Ozinga WA, Patiño S, Paula S, Pausas JG, Peñulas J, Phillips OL, Pillar V, Poorter H, Poorter L, Poschlod P, Prinzing A, Proulx R, Rammig A, Reinsch S, Reu B, Sack L, Sagado-Negret B, Sardans J, Shiodera S, Shipley B, Siefert A, Sosinski E, Soussana J-F, Swaine E, Swenson N, Thompson K, Thornton P, Waldram M, Weiher E, White M, White S, Wright SJ, Yguel B, Zaehle S, Zanne AE, Wirth C (2011) TRY – a global database of plant traits. Glob Change Biol 17:2905–2935

Kelley DI, Prentice IC, Harrison SP, Wang H, Simard M, Fisher JB, Willis KO (2013) A comprehensive benchmarking system for evaluating global vegetation models. Biogeosciences 10:3313–3340

Knorr W (2000) Annual and interannual CO_2 exchanges of the terrestrial biosphere: process-based simulations and uncertainty. Glob Ecol Biogeogr 9:225–252

Krinner G, Viovy N, de Noblet-Ducoudré N, Ogée J, Polcher J, Friedlingstein P, Ciais P, Sitch S, Prentice IC (2005) A dynamic global vegetation model for studies of the coupled atmosphere-biosphere system. Glob Biogeochem Cycles 19:GB1015

Kucharik CJ, Foley JA, Delire C, Fisher VA, Coe MT, Lenters JD, Young-Molling C, Ramank N (2000) Testing the performance of a Dynamic Global Ecosystem Model: water balance, carbon balance, and vegetation structure. Glob Biogeochem Cycles 14:795–825

Lavorel S, Díaz S, Cornelissen H, Garnier HSP, McIntyrE S, Pausas JG, Pérez-Harguindeguy N, Roumet C, Urcelay C (2007) Plant functional types: are we getting any closer to the Holy Grail? In: Canadell JG, Pataki D, Pitelka L (eds) Terrestrial ecosystems in a changing world. Springer, Berlin, pp 149–164

Le Quéré C, Andres RJ, Boden T, Conway T, Houghton RA, House JI, Marland G, Peters GP, van der Werf GR, Ahlström A, Andrew RM, Bopp L, Canadell JG, Ciais P, Doney SC, Enright C, Friedlingstein P, Huntingford C, Jain AK, Jourdain C, Kato E, Keeling RF, Klein Goldewijk K, Levis S, Levy P, Lomas M, Poulter B, Raupach MR, Schwinger J, Sitch S, Stocker BD, Viovy N, Zaehle S, Zeng N (2013) The global carbon budget 1959–2011. Earth Syst Sci Data 5:165–185

Le Quéré C, Andrew RM, Canadell JG, Sitch S, Korsbakken JI, Peters GP, Manning AC, Boden TA, Tans PP, Houghton RA, Keeling RF, Alin S, Andrews OD, Anthoni P, Barbero L, Bopp L, Chevallier F, Chini LP, Ciais P, Currie K, Delire C, Doney SC, Friedlingstein P, Gkritzalis T, Harris I, Hauck J, Haverd V, Hoppema M, Klein Goldewijk K, Jain AK, Kato E, Körtzinger A, Landschützer P, Lefèvre N, Lenton A, Lienert S, Lombardozzi D, Melton JR, Metzl N, Millero F, Monteiro PMS, Munro DR, Nabel JEMS, Nakaoka S, O'Brien K, Olsen A, Omar AM, Ono T, Pierrot D, Poulter B, Rödenbeck C, Salisbury J, Schuster U, Schwinger J, Séférian R, Skjelvan I, Stocker BD, Sutton AJ, Takahashi T, Tian H, Tilbrook B, van der Laan-Luijkx IT, van der Werf GR, Viovy N, Walker AP, Wiltshire AJ, Zaehle S (2016) Global carbon budget 2016. Earth Syst Sci Data 8:605–649

Lischke H, Zimmermann NE, Bolliger J, Rickebusch S, Löffler TJ (2006) TreeMig: a forest-landscape model for simulating spatio-temporal patterns from stand to landscape scale. Ecol Model 199:409–420

Lloyd J (1999) The CO_2 dependence of photosynthesis, plant growth responses to elevated CO_2 concentrations and their interaction with soil nutrient status, II. Temperate and boreal forest productivity and the combined effects of increasing CO_2 concentrations and increased nitrogen deposition at a global scale. Funct Ecol 13:439–459

Luo YQ, Randerson JT, Abramowitz G, Bacour C, Blyth E, Carvalhais N, Ciais P, Dalmonech D, Fisher JB, Fisher R, Friedlingstein P, Hibbard K, Hoffman F, Huntzinger D, Jones CD, Koven C, Lawrence D, Li DJ, Mahecha M, Niu SL, Norby R, Piao SL, Qi X, Peylin P, Prentice IC, Riley W, Reichstein M, Schwalm C, Wang YP, Xia JY, Zaehle S, Zhou XH (2012) A framework for benchmarking land models. Biogeosciences 9:3857–3874

Luyssaert S, Inglima I, Jung M, Richardson AD, Reichstein M, Papale D, Piao SL, Schulze ED, Wingate L, Matteucci G, Aragao LEOC, Aubinet M, Beers C, Bernhofer C, Black GK, Bonal D, Bonnefond JM, Chambers J, Ciais P, Cook B, Davis KS, Dolman AJ, Gielen B, Goulden M, Grace J, Granier A, Grelle A, Griffis T, Grünwald T, Guidolotti G, Hanson PJ, Harding R, Hollinger DY, Hutyra LR, Kolari P, Kruijt B, Kutsch WL, Lagergren F, Laurila T, Law B, Le Maire G, Lindroth A, Loustau D, Malhi Y, Mateu J, Migliavacca M, Misson L, Montagnani L, Moncrieff J, Moors EJ, Munger JW, Nikinmaa E, Ollinger SV, Pita G, Rebmann C, Roupsard O (2007) CO_2 balance of boreal, temperate, and tropical forests derived from a global database. Glob Change Biol 13:2509–2537

Manzoni S, Taylor P, Richter A, Porporato A, Agren GI (2012) Environmental and stoichiometric controls on microbial carbon-use efficiency in soils. New Phytol 196:79–91

McDowell NG, Fisher RA, Xu C, Domec JC, Hölttä T, Mackay DS, Sperry JS, Boutz A, Dickman L, Gehres N, Limousin JM, Macalady A, Martínez-Vilalta J, Mencuccini M, Plaut JA, Ogée J, Pangle RE, Rasse DP, Ryan MG, Sevanto S, Waring RH, Williams AP, Yepez EA, Pockman WT (2013) Evaluating theories of drought-induced vegetation mortality using a multimodel-experiment framework. New Phytol 200:304–321

McGuire AD, Sitch SA, Clein JS, Dargaville R, Esser G, Foley J, Heimann M, Joos F, Kaplan J, Kicklighter DW, Meier RA, Melillo JM, Moore B, Prentice IC, Ramankutty N, Reichenau T, Schloss A, Tian H, Williams LJ, Wittenberg U (2001) Carbon balance of the terrestrial biosphere in the twentieth century: analyses of CO_2, climate and land use effects with four process-based ecosystem models. Glob Biogeochem Cycles 15:183–206

Medlyn BE, Duursmara RA, De Kauwe MG, Prentice IC (2013) The optimal stomatal response to atmospheric CO_2 concentration: alternative solutions, alternative interpretations. Agric For Meteorol 182–183:200–203

Medvigy D, Wofsy SC, Munger JW, Hollinger DY, Moorcroft PR (2009) Mechanistic scaling of ecosystem function and dynamics in space and time: ecosystem demography model version 2. J Geophys Res 114:G01002

Melillo JM, Butler S, Johnson J, Mohan J, Steudler P, Lux H, Burrows E, Bowles F, Smith R, Scott L, Vario C, Hill T, Burton A, Zhou YM, Tang J (2011) Soil warming, carbon-nitrogen interactions, and forest carbon budgets. Proc Natl Acad Sci 108:9508–9512

Moffat AM, Papale D, Reichstein M, Hollinger DY, Richardson AD, Barr AG, Beckstein C, Braswell BH, Churkina G, Desai AR, Falge E, Gove JH, Heimann M, Hui DF, Jarvis AJ, Kattge J, Noormets A, Stauch VJ (2007) Comprehensive comparison of gap-filling techniques for eddy covariance net carbon fluxes. Agric For Meteorol 147:209–232

Ni J, Harrison SP, Prentice IC, Kutzbach JE, Sitch SA (2006) Impact of climate variability on present and Holocene vegetation: a model-based study. Ecol Model 191:469–486

Norby RJ, DeLucia EH, Gielen B, Calfapietra C, Giardina CP, King JS, Ledford J, McCarthy HR, Moore DJP, Ceulemans R, De Angelis P, Finzi AC, Karnosky DF, Kubiske ME, Lukac M, Pregitzer KS, Scarascia-Mugnozza GE, Schlesinger WH, Oren R (2005) Forest response to elevated CO_2 is conserved across a broad range of productivity. Proc Natl Acad Sci 102:18052–18056

Okin GS, Mahowald N, Chadwick OA, Artaxo P (2004) Impact of desert dust on the biogeochemistry of phosphorus in terrestrial ecosystems. Glob Biogeochem Cycles 18:GB2005

Olson JR, Scurlock J, Prince SD, Zheng DL, Johnson KR (2013) NPP Multi-Biome: NPP and driver data for ecosystem model-data intercomparison, R2. ORNL DAAC, Oak Ridge, TN. Data set

Pan Y, Birdsey RA, Fang J, Houghton R, Kauppi PE, Kurz WA, Phillips OL, Shvidenko A, Lewis SL, Canadell JG, Ciais P, Jackson RB, Pacala SW, McGuire AD, Piao SL, Rautiainen A, Sitch S, Hayes D (2011) A large and persistent carbon sink in the world's forests. Science 333:988–993

Parton WJ, Scurlock JMO, Ojima DS, Gilmanov TG, Scholes RJ, Schimel DS, Kirchner T, Menaut JC, Seastedt T, Moya EG, Kamnalrut A, Kinyamario JI (1993) Observations and modelling of biomass and soil organic matter dynamics for the grassland biome worldwide. Glob Biogeochem Cycles 7:785–809

Pavlick R, Drewry DT, Bohn K, Reu B, Kleidon A (2013) The Jena Diversity-Dynamic Global Vegetation Model (JeDi-DGVM): a diverse approach to representing terrestrial biogeography and biogeochemistry based on plant functional trade-offs. Biogeosciences 10:4137–4177

Peylin P, Bousquet P, Le Quéré C, Sitch S, Friedlingstein P, McKinley G, Gruber N, Rayner P, Ciais P (2005) Multiple constraints on regional CO_2 flux variations over land and oceans. Glob Biogeochem Cycles 19:GB1011

Prentice IC, Cowling SA (2012) Dynamic global vegetation models. In: Levin S (ed) Encyclopedia of biodiversity. Elsevier Publishing, New York, pp 670–689

Prentice IC, Heimann M, Sitch SA (2000) The carbon balance of the terrestrial biosphere: ecosystem models and atmospheric observations. Ecol Appl 10:1553–1573

Prentice IC, Bondeau A, Cramer W, Harrison SP, Hickler T, Lucht W, Sitch S, Smith B, Sykes MT (2007) Dynamic global vegetation modelling: quantifying terrestrial ecosystem responses to large-scale environmental change. In: Canadell JG, Pataki DE, Pitelka L (eds) Terrestrial ecosystems in a changing world. Springer, Berlin, pp 175–192

Prentice IC, Harrison SP, Bartlein PJ (2011) Global vegetation and terrestrial carbon cycle changes after the last ice age. New Phytol 189:988–998

Prentice IC, Dong N, Gleason SM, Maire V, Wright IJ (2014) Balancing the costs of carbon gain and water transport: testing a new theoretical framework for plant functional ecology. Ecol Lett 17:82–91

Purves DW, Lichstein JW, Strigul N, Pacala SW (2008) Predicting and understanding forest dynamics using a simple tractable model. Proc Natl Acad Sci 105:17018–17022

Saatchi SS, Harris NL, Brown S, Lefsky M, Mitchard ETA, Salas W, Zutta BR, Buermann W, Lewis SL, Hagen S, Petrova S, White L, Silman M, Morel A (2011) Benchmark map of forest carbon stocks in tropical regions across three continents. Proc Natl Acad Sci 108:9899–9925

Sato H, Itoh A, Kohyama T (2007) SEIB–DGVM: a new Dynamic Global Vegetation Model using a spatially explicit individual-based approach. Ecol Model 200:279–307

Scheiter S, Higgins SI, Osborne CP, Bradshaw C, Lunt D, Ripley BS, Taylor LL, Beerling DJ (2012) Fire and fire-adapted vegetation promoted C_4 expansion in the late Miocene. New Phytol 195:653–666

Scheiter S, Langan L, Higgins SI (2013) Next-generation dynamic global vegetation models: learning from community ecology. New Phytol 198:957–969

Schröter D, Cramer W, Leemans R, Prentice IC, Araujo MB, Arnell NW, Bondeau A, Bugmann H, Carter TR, Gracia CA, de la Vega-Leinert AC, Erhard M, Ewert F, Glendining M, House JI, Kankaanpaa S, Klein RJT, Lavorel S, Lindner M, Metzger MJ, Meyer J, Mitchell TD, Reginster I, Rounsevell M, Sabate S, Sitch S, Smith B, Smith J, Smith P, Sykes MT, Thonicke K, Thuiller W, Tuck G, Zaehle S, Zierl B (2005) Ecosystem service supply and vulnerability to global change in Europe. Science 310:1333–1337

Sellers PJ (1985) Canopy reflectance, photosynthesis and transpiration. Int J Remote Sens 6:1335–1372

Shevliakova E, Pacala SW, Malyshev S, Hurtt GC, Milly PCD, Caspersen JP, Sentman LT, Fisk JP, Wirth C, Crevoisier C (2009) Carbon cycling under 300 years of land use change: importance of the secondary vegetation sink. Glob Biogeochem Cycles 23:GB2022

Shinozaki K, Yoda K, Hozumi K, Kira T (1964) A quantitative analysis of the plant form – the pipe model theory. Jpn J Ecol 14:98–104

Sitch S, Smith B, Prentice IC, Arneth A, Bondeau A, Cramer W, Kaplan JO, Levis S, Lucht W, Sykes MT, Thonicke K, Venevsky S (2003) Evaluation of ecosystem dynamics, plant geography and terrestrial carbon cycling in the LPJ Dynamic Global Vegetation Model. Glob Change Biol 9:161–185

Sitch S, Huntingford C, Gedney N, Levy PE, Lomas M, Piao SL, Betts R, Ciais P, Cox P, Friedlingstein P, Jones CD, Prentice IC, Woodward FI (2008) Evaluation of the terrestrial carbon cycle, future plant geography and climate-carbon cycle feedbacks using five Dynamic Global Vegetation Models (DGVMs). Glob Change Biol 14:2015–2039

Smith B, Prentice IC, Sykes MT (2001) Representation of vegetation dynamics in the modelling of terrestrial ecosystems: comparing two contrasting approaches within European climate space. Glob Ecol Biogeogr 10:621–637

Smith PC, de Noblet-Ducoudre N, CIais P, Peylin P, Viovy N, Meurdesoif Y, Bondeau A (2010) European-wide simulations of croplands using an improved terrestrial biosphere model: phenology and productivity. J Geophys Res 115:G01014

Smith B, Wårlind D, Arneth A, Thomas H, Leadley P, Siltberg J, Zaehle S (2014) Implications of incorporating N cycling and N limitations on primary production in an individual-based dynamic vegetation model. Biogeosciences 11:2027–2054

Spitters CJT, Toussaint H, Goudriaan JD (1986) Separating the diffuse and direct component of global radiation and its implications for modeling canopy photosynthesis. 1. Components of incoming radiation. Agric For Meteorol 38:217–229

Taylor KE, Stouffer RJ, Meehl GA (2012) An overview of CMIP5 and the experiment design. Bull Am Meteorol Soc 93:485–498

Thomas RQ, Zaehle S, Templer PH, Goodale CL (2013) Global patterns of nitrogen limitation: confronting two global biogeochemical models with observations. Glob Change Biol 19:2986–2998

Thonicke K, Venevsky S, Sitch SA, Cramer W (2001) The role of fire disturbance for global vegetation dynamics: coupling fire into a Dynamic Global Vegetation Model. Glob Ecol Biogeogr 10:661–677

Thonicke K, Spessa A, Prentice IC, Harrison SP, Dong L, Carmona-Moreno C (2010) The influence of vegetation, fire spread and fire behaviour on biomass burning and trace gas emissions: results from a process-based model. Biogeosciences 7:1991–2011

Thornley J, Cannell MGR (2000) Modelling the components of plant respiration: representation and realism. Ann Bot 85:55–67

Thornton PE, Lamarque J-F, Rosenbloom NA, Mahowald NM (2007) Influence of carbon-nitrogen cycle coupling on land model response to CO_2 fertilization and climate variability. Glob Biogeochem Cycles 21:GB4018

Tucker C, Pinzon J, Brown M, Slayback DA, Pak EW, Mahoney R, Vermote EF, El Saleous N (2005) An extended AVHRR 8-km NDVI dataset compatible with MODIS and SPOT vegetation NDVI data. Int J Remote Sens 26:4485–4498

Venevsky S, Thonicke K, Sitch SA, Cramer W (2002) Simulating fire regimes in human-dominated ecosystems: Iberian Peninsula case study. Glob Change Biol 8:984–998

Verma M, Friedl MA, Richardson AD, Kiely G, Cescatti A, Law BE, Wohlfahrt G, Gielen B, Roupsard O, Moors EJ, Toscano P, Vaccari FP, Gianelle D, Bohrer G, Varlagin A, Buchmann N, van Gorsel E, Montagnani L, Propastin P (2014) Remote sensing of annual terrestrial gross primary productivity from MODIS: an assessment using the FLUXNET La Thuile dataset. Biogeosciences 11:2185–2200

Vicca S, Gilgen AK, Serrano MC, Dreesen FE, Dukes JS, Estiarte M, Gray SB, Guidolotti G, Hoeppner SS, Leakey ADB, Ogaya R, Ort DR, Ostrogovic MZ, Rambal S, Sardans J, Schmitt M, Siebers M, van der Linden L, van Straaten O, Granier A (2012) Urgent need for a common metric to make precipitation manipulation experiments comparable. New Phytol 195:518–522

Wang YP, Law RM, Pak B (2010) A global model of carbon, nitrogen and phosphorus cycles for the terrestrial biosphere. Biogeosciences 7:2261–2282

Wang X, Piao SL, Ciais P, Friedlingstein P, Myneni RB, Cox P, Heimann M, Miller J, Peng SS, Wang T, Yang H, Chen AP (2014) A two-fold increase of carbon cycle sensitivity to tropical temperature variations. Nature 506:212–215

Westoby M (1984) The self-thinning rule. Adv Ecol Res 14:167–225

Wieder WR, Bonan GB, Allison SD (2013) Global soil carbon projections are improved by modelling microbial processes. Nat Clim Chang 3:1–4

Woodward FI, Smith TM, Emanuel WR (1995) A global land primary productivity and phytogeography model. Glob Biogeochem Cycles 9:471–490

Wright IJ, Reich PB, Westoby M, Ackerly DD, Baruch Z, Bongers F, Cavender-Bares J, Chapin T, Cornelissen JHC, Diemer M, Flexas J, Garnier E, Groom PK, Gulias J, Hikosaka K, Lamont BB, Lee T, Lee W, Lusk C, Midgley JJ, Navas ML, Niinemets U, Oleksyn J, Osada N, Poorter H, Poot P, Prior L, Pyankov VI, Roumet C, Thomas SC, Tjoelker MG, Veneklaas EJ, Villar R (2004) The worldwide leaf economics spectrum. Nature 428:821–827

Xia J, Luo Y, Niu S, Ciais P, Janssens I, Chen J, Ammann C, Blanken PD, Cescatti A, Bonal D, Buchmann N, Curtis PS, Chen S, Dong J, Flanagan LB, Frankenberg C, Georgiadis T, Gough CM, Hui D, Kiely G, Li J, Lund M, Magliulo V, Marcolla B, Merbold L, Montagnani L, Moors E, Olesen JE, Piao S, Raschi A, Roupsard O, Suyker A, Urbaniak M, Vaccari F, Varlagi A, Vesala T, Wilkinson M, Weng E, Wohlfahrt G, Yan L (2015) Joint control of terrestrial gross primary productivity by plant phenology and physiology. Proc Natl Acad Sci 112:2788–2793

Yang X, Post WM, Thornton PE, Jain A (2013) The distribution of soil phosphorus for global biogeochemical modeling. Biogeosciences 10:2525–2537

Zaehle S (2013) Terrestrial nitrogen-carbon cycle interactions at the global scale. Philos Trans R Soc London Ser B 368:20130125

Zaehle S, Dalmonech D (2011) Carbon–nitrogen interactions on land at global scales: current understanding in modelling climate biosphere feedbacks. Curr Opin Environ Sustain 3:311–320

Zaehle S, Friend AD (2010) Carbon and nitrogen cycle dynamics in the O─CN land surface model: 1. Model description, site-scale evaluation, and sensitivity to parameter estimates. Glob Biogeochem Cycles 24:GB1005

Zaehle S, Sitch SA, Prentice IC, Liski J, Cramer W, Erhard M, Hickler T, Smith B (2006) The importance of age-related decline in forest NPP for modeling regional carbon balances. Ecol Appl 16:1555–1574

Zaehle S, Friend AD, Friedlingstein P, Dentener F, Peylin P, Schulz M (2010) Carbon and nitrogen cycle dynamics in the O─CN land surface model: 2. Role of the nitrogen cycle in the historical terrestrial carbon balance. Glob Biogeochem Cycles 24:GB1005

Zaehle S, Ciais P, Friend AD, Prieur V (2011) Carbon benefits of anthropogenic reactive nitrogen offset by nitrous oxide emissions. Nat Geosci 4:601–605

Zaehle S, Medlyn BE, De Kauwe MG, Walker AP, Dietze MC, Hickler T, Luo YQ, Wang YP, El-Masri B, Thornton P, Jain A, Wang SS, Warlind D, Weng ES, Parton W, Iversen CM, Gallet-Budynek A, McCarthy H, Finzi AC, Hanson PJ, Prentice IC, Oren R, Norby RJ (2014) Evaluation of 11 terrestrial carbon-nitrogen cycle models against observations from two temperate Free-Air CO_2 Enrichment studies. New Phytol 202:803–822

23

Global Change and Terrestrial Ecosystems

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Effects of thousands of years of land use and soil erosion in a subarid climate. The Middle East is considered to be one of the oldest farming areas on Earth. Deforestation and agricultural use over centuries led to the erosion of soil from slopes and to a re-allocation of fine soil particles to the valley floor. The photo shows an agricultural area near Hebron, currently under Israeli administration. From traces of foot paths it can be seen that slopes were grazed. Small fields on slopes are used for cereal crops. Fruit trees can only grow on the valley floor, where stone walls prevent the loss of topsoil during heavy rain events. Barley and wheat are the predominant cereals, and almond, apricot, pomegranate, olives and peaches are the main fruit trees. (Photo: E.-D. Schulze)

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23.1 Global Change

Global change is a widely accepted term. According to an early definition by the International Geosphere-Biosphere Programme (IGBP), global change includes changes of "atmospheric circulation, ocean circulation, climate, the carbon cycle, the nitrogen cycle, the water cycle and other cycles, sea-ice changes, sea-level changes, food webs, biological diversity, pollution, health, fish stocks, […] population, the economy, resource use, energy, development, transport, communication, land use and land cover, urbanisation, globalisation" (http://www.igbp.net). Other definitions include global freshwater use, ocean acidification, stratospheric ozone depletion and atmospheric aerosol loading. Thus, global change encompasses all possible anthropogenic changes at the scale of the globe as a whole. In terms of plant ecology, global change refers mainly to changes in land use, climate and biodiversity.

During geological times, changes in the Earth's climate and vegetation have always occurred independently of human activities, and human influences on Earth are not restricted to the present time (Sect. 17.2). **Human appropriation** of nature started at the transition from the Pliocene to the Pleistocene about two million years ago in the savannas of East Africa, and 1.8 million years ago (Lower Pleistocene), early humans (*Homo erectus*) spread in several migration waves across the planet (e.g. Balter and Gibbons 2000). *H. sapiens* evolved from *H. erectus* about 200,000 years ago (Middle Pleistocene) in Africa. At about the same time, *H. neanderthalensis* evolved from *H. erectus* in Europe. The first evidence of *H. sapiens* in Europe dates to about 40,000 years ago (Cro-Magnon period). Intensive settlement in the Mediterranean region started about 30,000 years ago (before peak glaciation of the last glacial period), when *H. sapiens* lived together with *H. neanderthalensis* in Southern Europe (Gibbons 2001). North America was reached by humans only about 19,000 years ago, while Australia was reached already 50,000 years ago (Harcourt 2016).

The transition from hunting and gathering to agriculture and animal domestication occurred in East Africa and East Asia about 11,000 years ago. Since then, a steady but slow increase in human population has taken place, along with increased land-use change (mainly by deforestation) for space to graze animals and for agriculture. The invention of **agriculture** resulted in an increase of the world's human population from an estimated two million 5000 years ago to about one billion in 1800 (Klein Goldewijk et al. 2010) (Fig. 23.1). Since 1800, the global human population has increased by a factor of seven to reach seven billion in 2013 (Klein Goldewijk et al. 2010). However, Ellis et al. (2013) point out that even a relatively small human population had likely caused profound and widespread ecological changes as far back as 3000 years ago. Recent advances in medicine, chemistry, technology and molecular biology have caused an unprecedented increase in population at the expense of the natural environment. Therefore, Crutzen (2002) proposed a new epoch in Earth's history, the **Anthropocene**, starting with changes in the global atmospheric composition. However, since defining geological times by the stratification of specific geological layers is the responsibility of the science of geology, a discussion has arisen about which activity of humans could be identified as or in a geological layer millions of years from now (Lewis and Maslin 2015). In fact, the geological epoch of the "Holocene" was already defined as the period of increased human activity. Thus, the question of how to classify and separate the Holocene from the Anthropocene in geological terms remains unresolved. Currently, it has been proposed that nuclear bomb tests that led to a peak in radioactive isotopes by 1964 or the accumulation of plastic materials in oceans flood plains and soils after 1950 could serve as geological evidence for the start of such a new geological epoch.

Since human life is dependent on various ecosystem services (Sect. 21.3), specific

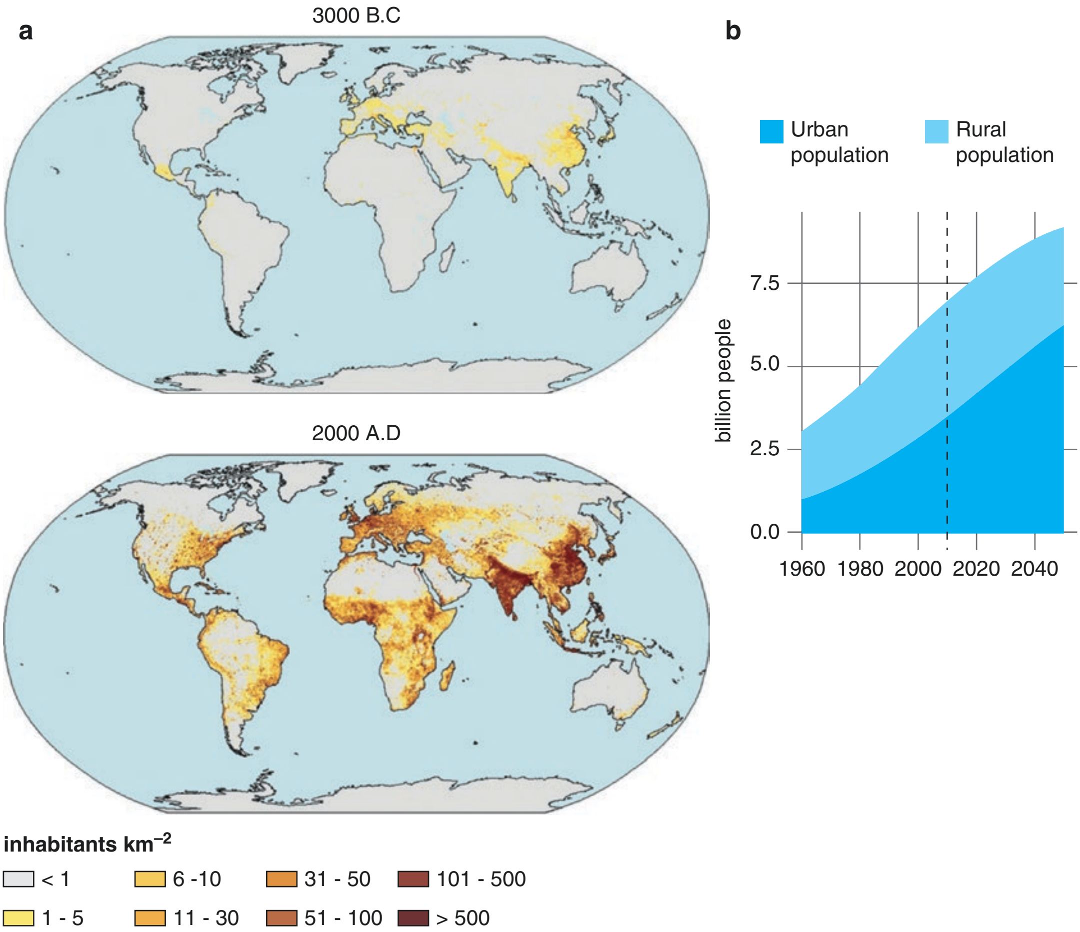


Fig. 23.1 Human population. **a** Global population density at 3000 BC and 2000 AD (after Klein Goldewijk et al. 2010). **b** Estimated world rural and urban population growth between 1960 and 2050. (FAO 2013)

questions about the role of plant ecology for global change arise:

- How do changes in climate, land use and biodiversity affect terrestrial ecosystems?.
- How do changes in terrestrial ecosystems feed back on ecosystem services?.

It has become clear (Fig. 23.2) that not only human population size, but also the intensity of **human activities** as carried out by a minority of the population has resulted in changes in land use, global biogeochemistry and biotic assemblages, which in turn result in climate change and in a loss of biological diversity. Both these changes will feed back on human activities as modulated by socio-economic conditions (Chap. 20, Fig. 20.1).

In particular, with increasing human populations and their growing demands, there is an increasing need for land that can be cultivated or managed for resources to meet human needs. It is expected that by 2050, remote regions and areas of low productivity will also be appropriated by humans for their own needs (Canadell and Schulze 2014).

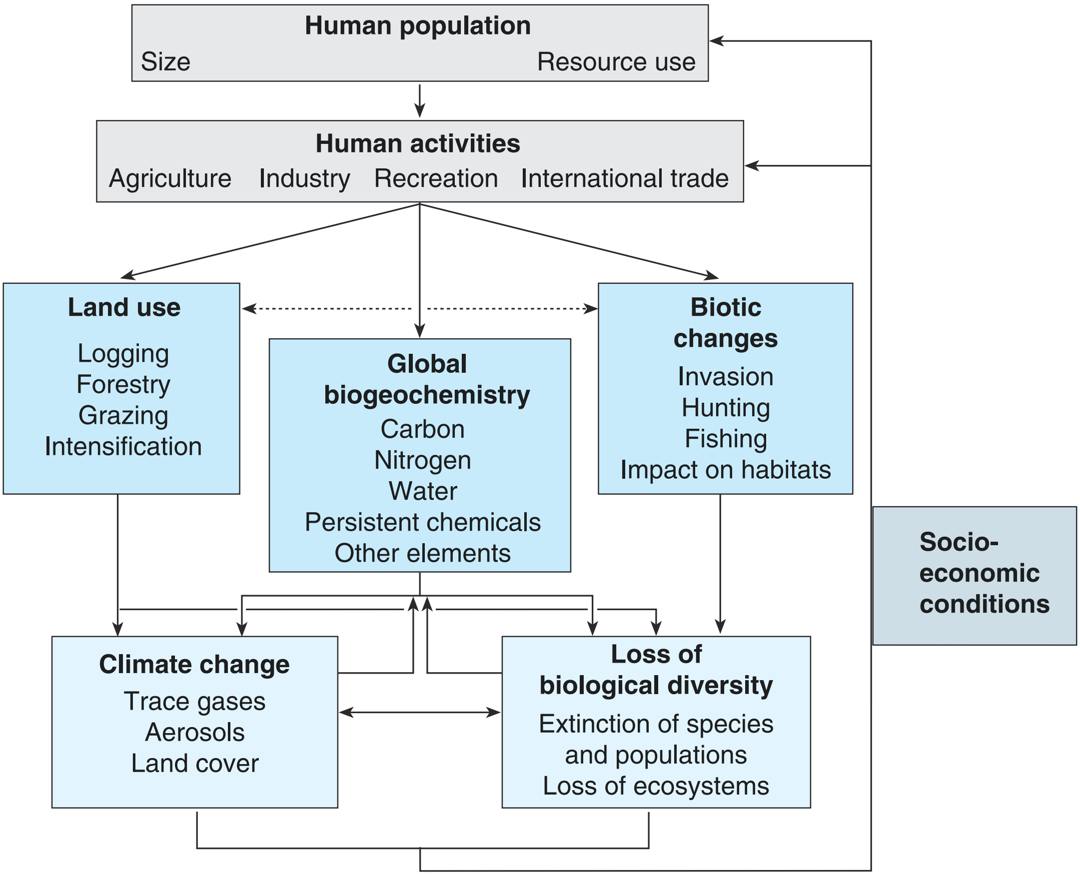


Fig. 23.2 Schematic illustration of interaction between human activity and global change. Human population size and use of resources via specific activities (agriculture, industry, recreation and trade) have effects on land use, global biogeochemical cycles and biodiversity. These effects initiate changes in climate and in biodiversity, and both in turn influence populations and resources used by people. How this feedback occurs, and how strong it is, depends on socio-economic parameters. Thus, it is difficult to predict scientifically how climate change will affect the situation in developed and in developing countries. (after Vitousek et al. 1997)

23.2 Land Use and Land-Use Change

The terms “land use” (LU) and “land-use change” (LUC) originated from the Kyoto Protocol (Sect. 23.5) and the intention to financially account for **afforestation, reforestation and deforestation (ARD)** activities. The definitions of LU and LUC were the focus of a special report of the Intergovernmental Panel on Climate Change (IPCC) under the title “Land Use, Land-Use Change, and Forestry” (Watson et al. 2000). In this report, **land use** was for the first time clearly defined as “a change affecting the amount of biomass in existing biomass stocks by management”, while **land-use change** is “a change in the way land is used” (e.g. change from forestry towards agriculture). **Land cover** is an additional term that partly overlaps with LULUC but also includes natural vegetation. It is “the physical and biological cover of the Earth’s land as vegetation or man-made feature”. However, it neglects the intensity of LU (Sect. 21.1).

Thus, **land use and land-use change** (**LULUC**) affect the vegetation by changing the vegetation cover as well as soils by erosion, salinity, desertification and eutrophication. This in turn changes the biogeochemical cycles of carbon, nutrients and water, causing additional emissions of greenhouse gases (GHGs) such as CO_2, N_2O and CH_4 (Chap. 21).

23.2.1 Agriculture and Forestry

According to the FAO, global agricultural production increased over the past decade by about 2% per year, although the cultivated area increased only by 1%. About 40% of our food production comes from irrigated land, although this only accounts for 20% of the cultivated land. The area of irrigated land doubled over the same period of time. **Irrigation** has therefore indirectly relieved the pressure on land expansion and thus helped in protecting natural vegetation (Sect. 23.5). However, the other side of the coin is a possible accumulation of salt (NaCl) by irrigation and an associated abandonment of land area due to salinity and erosion (Sect. 17.2). Further examples of **salinisation** following LUC come from Australia, where salt from deep soil layers was brought to the surface with changes in the rooting depth of agricultural plants compared to native *Eucalyptus* trees. Moreover, irrigation is often based on groundwater in many parts of the world (e.g. fossil, Pleistocene water below the Sahara) and not from renewable freshwater sources. These groundwater reservoirs are limited, and their recharge rates are slow and highly variable. Rates range from <10 mm year^{-1} in semi-arid rangeland to 580 mm year^{-1} in irrigation-dominated agriculture, overall accounting for about 22% of annual precipitation. Mean residence times are about 300 years (Sect. 21.2).

Forestry also has large impacts on LU, but agriculture dominates LUC. Forests cover about 30% of the global ice-free land area (about 40 million km^2), with about 7% of these forests being planted and 93% being natural or semi-natural with natural regeneration (FAO 2015). Presently, the increased requirements for animal feed, timber for construction, and palm oil still result in large-scale LUC, mainly in the tropics. Hot spots of tropical LUC are Brazil and Indonesia, with deforestation rates up to 40,000 km^2 year^{-1}. The global forest loss has recently been quantified for the period from 2000 to 2012 using Earth repeated observation data at a spatial resolution of 30 m. Hansen et al. (2013) estimated global forest loss at about 2.3 million km^2 over 12 years, mainly in tropical and boreal zones. During the same time, afforestation occurred over only 0.8 million km^2, mainly in subtropical and temperate regions (Fig. 23.3). In comparison, the FAO (2015) reported net for-

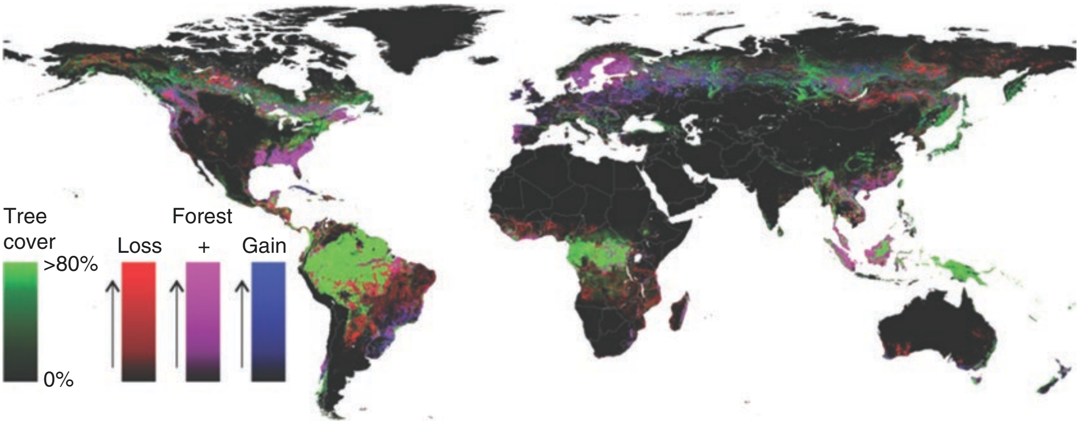


Fig. 23.3 Changes in tree cover and global forest loss and gain during the twenty-first century. Areas with forest loss are mainly used for agriculture. The map is based on remotely sensed data during 2000 and 2012 at a spatial resolution of 30 m (from Hansen et al. 2013). Green shows areas with increased tree cover, red shows areas with increasing forest loss, and blue shows areas with increasing forest gain. The magenta areas summarise losses and gains. The grey areas are regions without any change in forest area

est cover loss between 1990 and 2015 of 14.7 million km^2 (4 million km^2 between 2000 and 2010), which is larger than the estimate by Hansen et al. (2013) for approximately the same time period. This indicates the large uncertainties of any of these global estimates of forest gains and losses.

In surveying these changes from satellites it should be emphasised that land cover and related LUC can only be detected by repeated satellite observations because otherwise harvesting of forests would be recorded as deforestation under the category of LUC, even though it might be part of sustainable forest management that is followed by forest regeneration (Sect. 14.1). In contrast, clearings around infrastructures and the breakdown of fragmented forest remnants would add to observed deforestation, but this is generally not recorded (Laurance et al. 1997). Forest degradation due to fire and damage by selective logging of native forests are not included either (Nepstad et al. 1999). Thus, there remains a great deal of uncertainty when it comes to forest cover maps.

Deforestation and afforestation are asymmetric in their effects on **global climate**. Prentice et al. (2001) showed that afforesting all areas that have been cleared by humankind since the Industrial Revolution would decrease atmospheric CO_2 concentrations by only 40 ppm, while clearing the existing primary forests would lead to an increase by about 200–400 ppm. Thus, CO_2 emissions by LUC clearly increased anthropogenic CO_2 emissions. However, compared to emissions from fossil fuel burning (9.3 ± 0.5 Gt C year^{-1} in 2006 until 2015), emissions from LUC are relatively small but still increasing (1.0 ± 0.5 Gt C year^{-1}, Le Quéré et al. 2016).

It should be noted that the human appropriation of land by LUC mainly meets the demands of the industrialised world. Figure 23.4a shows the main agricultural cropping regions and agricultural grain yields of 175 crop types around the world. Additional land is needed for bioenergy (Fig. 23.4b, c), which shows a large trade flux of ethanol and biodiesel from South America and the USA to Europe (SRREN 2011).

The crop types with the largest **grain yield** globally are maize, rice and wheat (Table 23.1). Like maize, soybeans are produced for both human and animal use. Potatoes, sorghum and barley are produced much less. Global sugar production is mainly by sugar cane, but with large continental differences: while in the Americas sugar originates mainly from sugar cane (C_4 plant), in Europe sugar beet (C_3 plant) dominates. Additional large areas are needed for cattle grazing (Sect. 21.1). Nevertheless, meat production is as variable across the globe as crop production (Table 23.1). While pigs are mainly produced in Asia, chicken dominates in the Americas and Asia, while cattle clearly dominates in the Americas. As with pellets and biofuels, all these commodities are traded globally. Excellent statistics can be found at the FAO webpage (http://www.fao.org/faostat).

23.2.2 Consequences of Land Use on Biogeochemical Pools and Fluxes

The effects of LU on the water, nutrient and carbon fluxes in ecosystems are highly relevant. The impacts of LU start with forest **grazing** and collection of **fire-wood** and continue to intensive management (Table 23.2). Changes in resource availability for plants and microorganisms in managed (agriculture and forestry) and unmanaged systems (including conservation areas) are either by direct supply of resources (fertilisation, irrigation) or indirect via atmospheric deposition and run-off, or by expanding large herbivore populations, such as deer, following the extinction of predators. Many LU practices clearly affect soil structure and soil climate (e.g. soil temperature, soil moisture), but also competition among plants (increased resource supply, opening of stand structure with fire and grazing, leading to the selection of tolerant species).

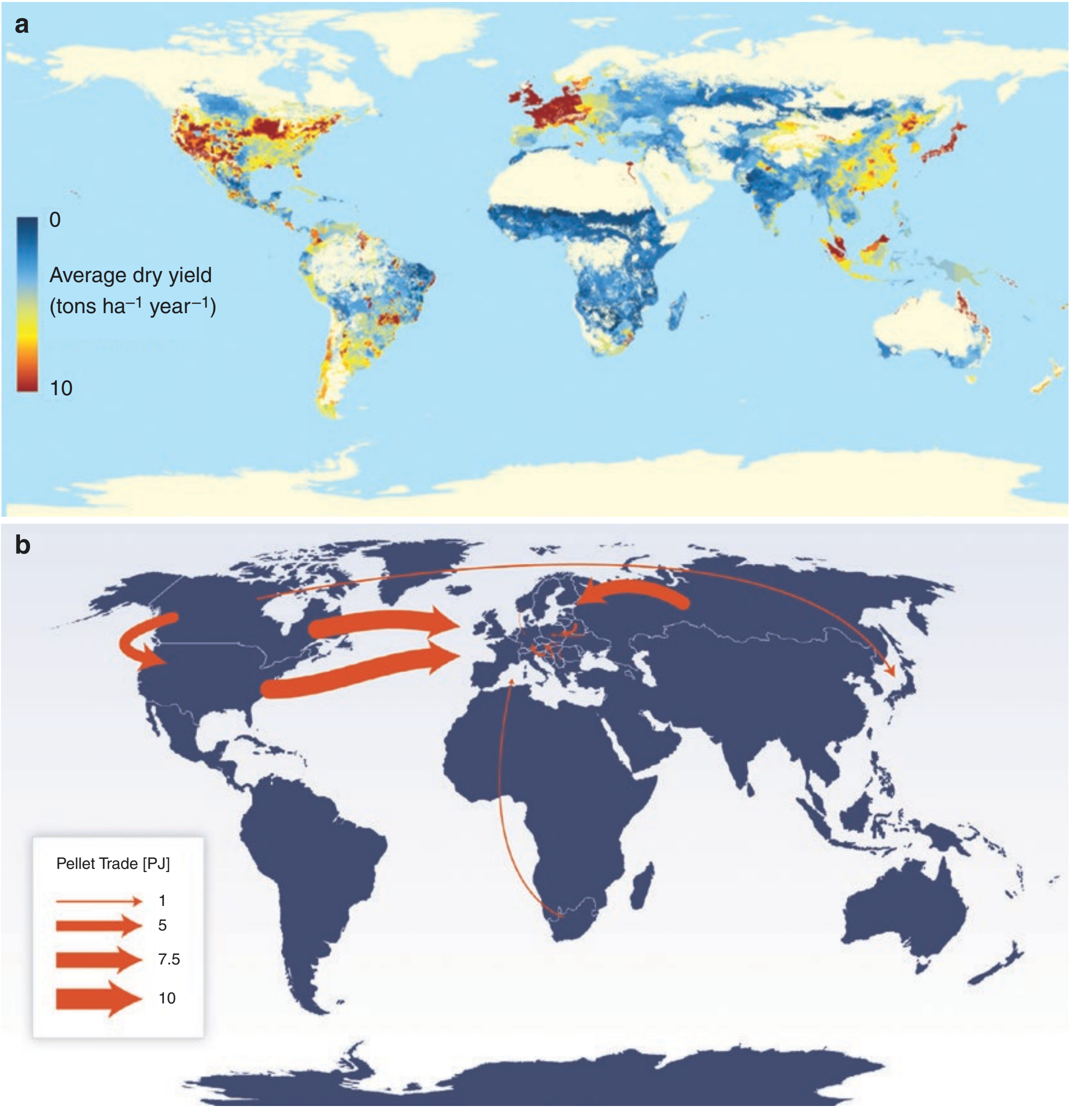


Fig. 23.4 Global maps of agricultural production and of trade for wood pellets and biofuels. **a** Global map of agricultural production for 175 crop types (West et al. 2010). **b** Global trade of wood pellets in 2009. Size of arrows increases with larger trade volume given in PJ. **c** Global biofuel production and trade. Histograms and flows in orange represent ethanol, in blue biodiesel. (from SRREN 2011)

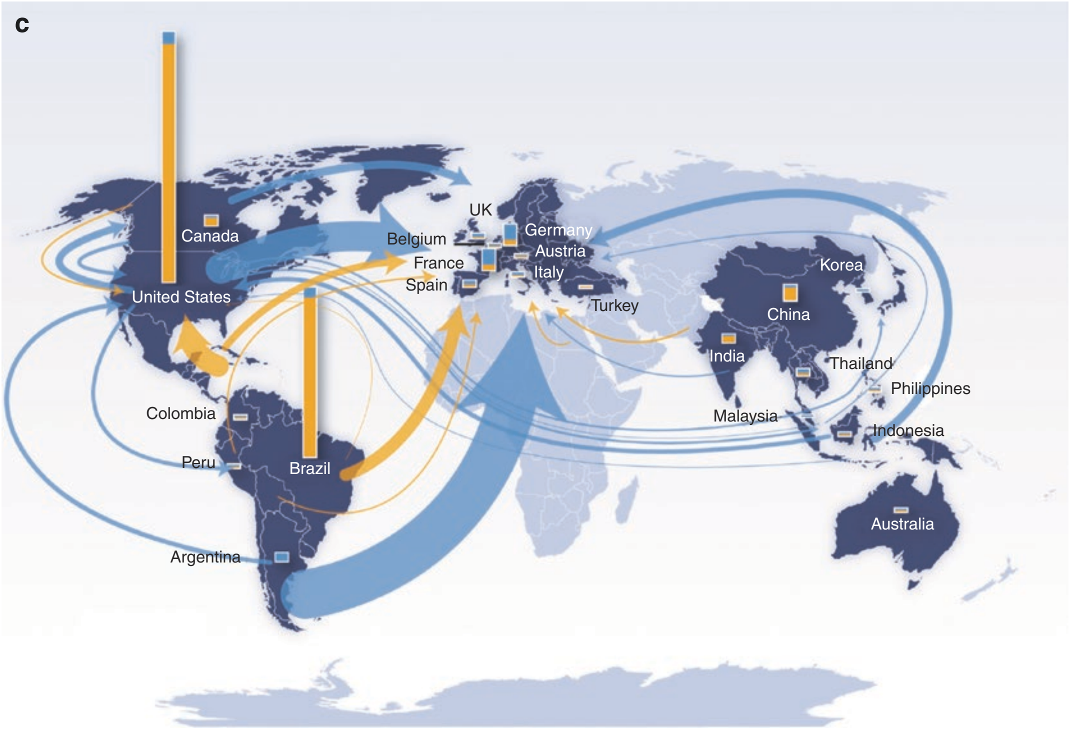


Fig. 23.4 (continued)

For example, the effects of **browsing** by wild ungulates in temperate forests resulted in the selection of browsing-tolerant species such as *Fagus* in Europe (Schulze et al. 2014). Structural responses were found in natural subtropical woodlands (Asner et al. 2009). Positive (increased growth, regeneration) as well as negative consequences (change in biodiversity, invasion, erosion) can follow. At the same time, all LU practices also trigger feedbacks of ecosystems under use to the atmosphere and, thus, climate (trace gas fluxes, changes in albedo and in evapotranspiration). Moreover, adjacent ecosystems can be impacted as well (run-off, erosion). Impacts on biodiversity will be discussed in more detail later (Sect. 23.4).

Over time, LU has changed even for the same ecosystem type (e.g. tropical forest or semi-arid rangeland) or land cover (e.g. forest or grassland) owing to changes in human needs (gathering of fruits vs. timber harvests in tropical forests) or LU practices (deep ploughing vs. no till). Moreover, some management practices are capable of restoring degraded systems, for example no or low tillage, conservation tillage, mulching and organic residue management. The effects of LUC on the C budget were analysed for the USA because historical changes in land acquisition by European immigrants could still be reconstructed (Fig. 23.5) (Houghton et al. 1999). About 27 10^9 t C were released by changing prairie grasslands into agricultural cropland and by the use of wood for energy and construction between 1770 and 1945. Maximum emissions occurred around 1880, but these emissions decreased after 1900, because there was no more land to be changed. Since 1945, the trend reversed as a result of fighting fires and forest succession on abandoned land. Soils started to accumulate C again, starting around 1970 owing to furrow cultivation (Matson et al. 1997). Thus, LU and LUC are very dynamic

Table 23.1 Production of crops and meat from primary livestock across global regions. Production for each region is given as a percentage of global production, averaged over the years 2010 to 2014. Maximum production is given in millions of tons per country, also averaged over 2010 to 2014. Top five producers are given. Maize production does not include green maize production. Data from FAOSTAT (http://www.fao.org/faostat)

Production	Maize *Zea mays*	Rice (paddy) *Oryza satica*	Wheat *Triticum aesticum*	Soybeans *Glycine max*	Potatoes *Solanum tuberosum*
Americas	50.4	5.0	16.2	86.4	11.3
Africa	7.5	3.9	3.6	0.7	7.5
Asia	30.5	90.4	44.7	10.6	48.3
Europe	11.6	0.6	31.8	2.3	32.4
Oceania	0.1	0.1	3.8	0	0.5
Max. production	323.2	202.2	120.3	91.2	90.8
Top 5 producers	USA, China, Brazil, Argentina, Ukraine	China, India, Indonesia, Bangladesh, Viet Nam	China, India, USA, Russian Federation, France	USA, Brazil, Argentina, China, India	China, India, Russian Federation, Ukraine, USA
Production	Sorghum *Sorghum bicolor*	Barley *Hordeum vulgare*	Sugar cane *Saccharum officinale*	Sugar beet *Beta vulgaris*	Banana *Musa paradisica*
Americas	37.5	13.2	54.1	12.2	25.2
Africa	41.5	4.7	5.1	4.5	17.9
Asia	16.3	14.7	39.1	13.7	55.1
Europe	1.6	61.1	0	69.6	0.4
Oceania	3.1	6.2	1.7	0	1.3
Max. production	83.0	15.0	735.4	37.6	28.4
Top 5 producers	USA, Mexico, Nigeria, India, Sudan	Russian Federation, France, Germany, Ukraine, Canada	Brazil, India, China, Thailand, Pakistan	Russian Federation, France, USA, Germany, Turkey	India, China, Philippines, Ecuador, Brazil
Primary livestock	Pigs	Chicken	Cattle		
Americas	17.3	45.9	48.0		
Africa	1.1	4.9	9.0		
Asia	56.5	32.4	21.9		
Europe	24.6	16.4	16.5		
Oceania	0.4	1.3	4.6		
Max. production	51.1	17.2	11.8		
Top 5 producers	China, USA, Germany, Spain, Brazil	USA, China, Brazil, Russian Federation, Mexico	USA, Brazil, China, Argentina, Mexico		

processes that can be managed in positive and negative ways (Table 23.2). This knowledge of **land management** is often the basis for international agreements, such as the Kyoto Protocol or Paris Agreement Protocol (Sect. 23.5), for future management of the Earth in a sustainable manner.

LULUC is not only restricted to agriculture and forestry but also includes **urban settlements** and establishing infrastructure for human activities, such as highways, reservoirs and dams. The water cycle is strongly affected by reservoirs and dams (Chaps. 16 and 21). This can result in regional **desertification**, that is, the degradation

Table 23.2 Factors contributing to agricultural and forest land use as well as consequences for terrestrial ecosystems and their feedbacks to the environment. The table will never be complete in terms of consequences and feedbacks to the environment, that is, adjacent ecosystems, the atmosphere and the hydrosphere, because impacts of LU vary with frequency and intensity of LU

Factors contributing to land use	Consequences for ecosystem	Feedbacks to environment
Land conversion	Loss of soil C and nutrient pools, erosion, loss of biodiversity	Change in water fluxes and evaporative cooling and in albedo, input of nutrients
Fire	Loss of C and nutrients, deposition of soot, changes in soil climate, increased microbial mineralisation, run-off, erosion, weed control, loss of vegetation, opportunity for regeneration	Change in albedo, change in water and nutrient fluxes, input of nutrients via run-off
Soil management	Change in soil structure and water-holding capacity, impacts on soil biota, change in weed pressure, danger of erosion	Change in nutrient inputs via run-off, trace gas fluxes
Irrigation	Increased water availability, salinisation, change in interspecific competition, increased growth	Increase in evapotranspiration and evaporative cooling, decrease in groundwater depth
Fertilisation	Increased nutrient availability, change in interspecific competition, increased growth	Leaching of nutrients, eutrophication, trace gas fluxes
Pesticide application	Change in interspecific competition, weed and pest control, increased growth	Lateral spread of pesticides
Harvest	Loss of vegetation, change in soil climate, impacts on soil biota, danger of erosion	Change in water fluxes and evaporative cooling, change in albedo, trace gas fluxes
Grazing/ browsing	Partial loss of vegetation, change in competition, impacts on soil biota, change in soil structure, danger of erosion	Change in water fluxes and evaporative cooling, change in albedo, trace gas fluxes, input of nutrients via run-off
Introduction of alien species	Change in competition, loss of biodiversity, impacts on soil biota, change in fire frequency	Change in nutrient and water fluxes, erosion

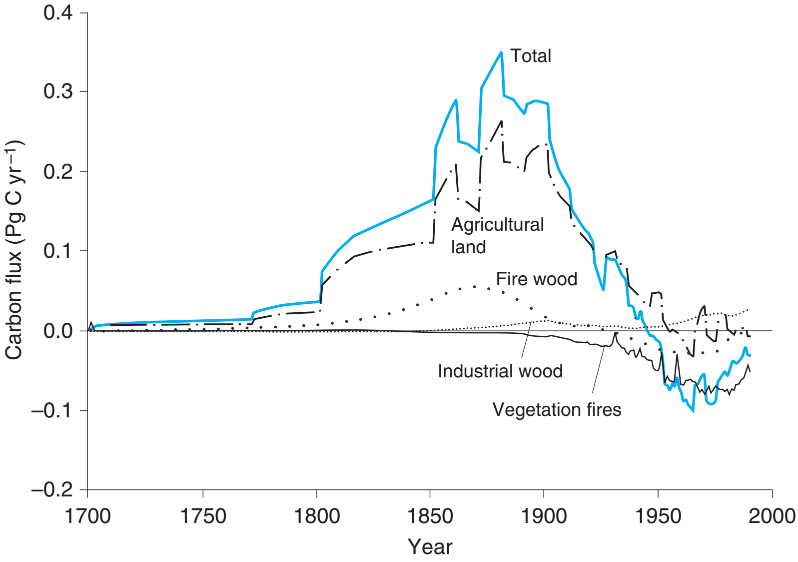


Fig. 23.5 Historic changes in C fluxes following land-use change in the USA. Annual CO_2 fluxes (C source depicted as positive value and C sink as negative value) of the USA from agricultural land, forests and fires. Emissions increased after 1750 owing to deforestation, reaching a maximum around 1900. Subsequently, emission fluxes decreased and the land became a C sink (negative values) around 1950. Recently, this C sink has decreased again, in part owing to changes in land use intensity. (Houghton et al. 1999)

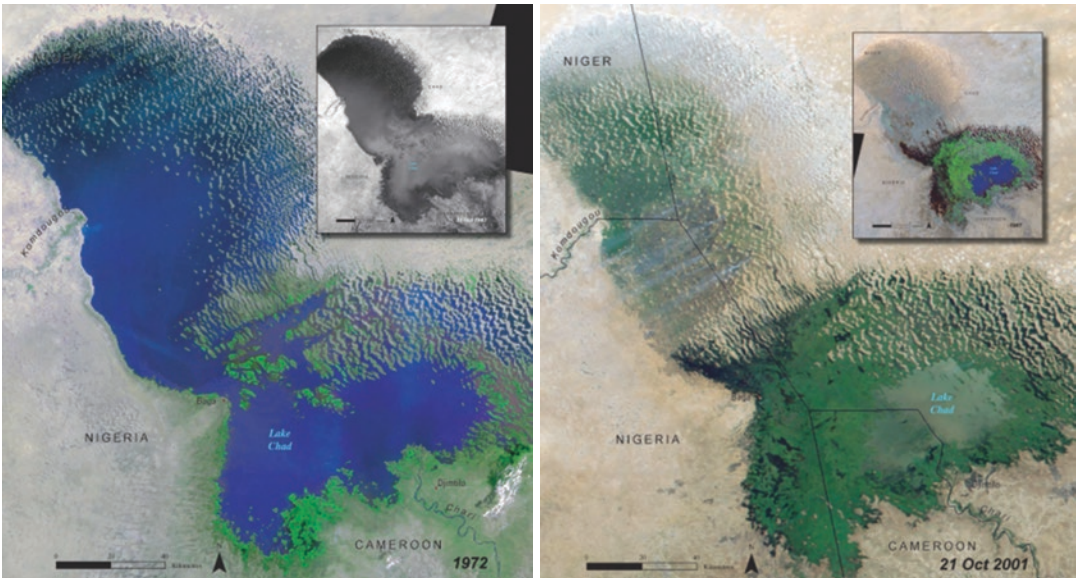


Fig. 23.6 Drying of Lake Chad between 1972 and 2001. (From UNEP 2006)

of land as defined by the **UN Convention to Combat Desertification** (Sects. 17.2 and 23.5). Examples include the reduced flow of the Colorado River in Arizona and the drying out of the Aral Sea in Russia and of Lake Chad in the Sahel (Fig. 23.6).

LUC influence not only the water balance but also water quality. **Eutrophication** from households and industry, inputs of organic materials, heavy metals, high salt loads, N deposition and — as the newcomer — nanoparticles and plastic waste contribute to water pollution. In particular, large N and phosphorus (P) fertiliser inputs to agricultural lands are still problematic. Globally, N fertiliser use by plants is still below 50%. Nitrate leaching, NH_3 volatilisation and N_2O emissions are thus large N fluxes to the environment from many agricultural areas (Table 23.2). About 1–7% of added N fertilisers are emitted as N_2O globally (Smith et al. 2016), making agricultural soils currently the major global source of N_2O (Reay et al. 2012). In contrast, agricultural sources of CH_4 originate from ruminants, rice cultivation, organic waste deposits and biomass burning (Kirschke et al. 2013).

In Germany, the nitrate content in groundwater correlated linearly with **nitrogen deposition** from the atmosphere and fertilisation in agriculture (Lehn et al. 1996). In south-western Germany, a total of 550 water sources (more than 20% of the total number) were taken out of the water supply networks between 1980 and 1992 because of anthropogenic pollution, making long-distance water supplies and mixing water from different sources necessary.

Management of water pollution can be very complex as shown by the reduction of **P contamination** in **lakes** (Finlay et al. 2013). A decrease of P deposition in lakes will increase water quality in terms of oxygen concentrations in the water column by avoiding algal blooms and associated eutrophication. However, the reduction of P inputs also affects other biogeochemical cycles, for example the N cycle in lakes. Decreasing the number of algae blooms also limits their "benefits". Algae incorporate (and thus remove) not only P and C from the water column but also reactive N. When algae die, their dead tissues sink to the lake sediments. Here, they fuel **denitrification** by anaerobic microbes (Bernhardt 2013), and nitrate is metabolised to N_2 and N_2O. However, in the absence of P, the process that converts reactive N into inert atmospheric N_2 is lacking since no algal blooms are initiated. The now algae-free, but nitrogen-polluted, freshwater lakes are stronger sources of N_2O than P-polluted waters (McCrackin and Elsener 2010). This example shows that the management of biogeochemical cycles can contain many surprises owing to the multiple interactions and feedbacks between organisms and biogeochemical processes.

23.3 Climate Change

23.3.1 Changes in Atmospheric Conditions

Climate change is strongly linked to the global carbon cycle since atmospheric CO_2 is one of the most important GHGs responsible for global warming. Trace gases or GHGs in the atmosphere reflect long-wave radiation back to the Earth's surface that would normally reach the cosmos (back-radiation) (Chap. 9). The resulting temperature change is called **global warming**. Climate change scepticism is often based on the argument that climate has always been changing during Earth's history, as has the concentration of GHGs. Indeed, ice core records do show that atmospheric CO_2 concentrations have been fluctuating between 172 and 300 ppm over the last 800,000 years (Lüthi et al. 2008). However, the CO_2 fluctuations caused by geological events were slow and associated with glacial and interglacial cycles of millennia caused by changes in the tilt of the Earth and the planetary circulation of the Earth around the Sun. The time scale during which past changes occurred is quite different from the time scale of present changes in the atmosphere, even though there had been fast events also in the past, such as the drainage of Lake Agassiz into the North Atlantic. Since the reference period 1850–1900, atmospheric CO_2 concentrations increased 120 ppm from 280 (so called pre-industrial) to 400 ppm (2016). This is equivalent to the magnitude of change that occurred during one glacial–interglacial cycle over about 100,000 years. The CO_2 concentration in the atmosphere has been increasing over the last decade on average by about 2.1 ppm per year (Chap. 21) (www.esrl.noaa.gov/).

The rise in **CO_2 concentration** has been measured continuously at Mauna Loa on Hawaii since 1958, with minima corresponding to the growing season in the Northern Hemisphere summer and maxima corresponding to the dormant phase in winter when anthropogenic CO_2 production is also very high (Fig. 23.7a). A decrease in the **oxygen concentration** was observed in parallel to this increase in CO_2 at La Jolla, California, USA (Fig. 23.7a) (Heimann 1997). With increasing CO_2 concentrations also the $\delta^{13}C$ in this CO_2 (i.e. atmospheric $^{13}C/^{12}C$ ratio compared to a standard) has been decreasing owing to the burning of fossil fuels, which are highly depleted in ^{13}C (negative $\delta^{13}C$) (Fig. 23.7b). In pre-industrial times, the $\delta^{13}C$ value was −6.5‰. Adding CO_2 from fossil fuel sources has decreased the $\delta^{13}C$ of atmospheric CO_2 by ca. 1.8‰ in the last 135 years, i.e. to about −8.3‰ in 2012. Plotting O_2 versus CO_2 concentration gives further evidence that the rise in CO_2 is caused by fossil fuel combustion and that it is not the consequence of natural CO_2 release, for example from volcanic activity or emissions by the oceans (Fig. 23.7c). When fossil fuels are burned, O_2 consumption is proportional to CO_2 release. However, since O_2 is also exchanged by the oceans (without releasing an equivalent amount of CO_2) and by photosynthesis (where CO_2 is simultaneously produced), measured CO_2 concentrations are lower than those postulated by fossil fuel burning alone (Keeling et al. 1996). This clearly indicates a global C sink. Thus, it has become clear from oxygen and stable carbon isotope measurements that the increased CO_2 concentrations in the atmosphere are a consequence of fossil fuel combustion.

For the decade 2006–2015, total **anthropogenic CO_2 emissions** were 10.3 Gt C year^{-1} (1.0 ± 0.5 Gt C year^{-1} from LUC plus 9.3 ± 0.5 Gt C year^{-1} from fossil fuels), but during 2015 alone, they increased

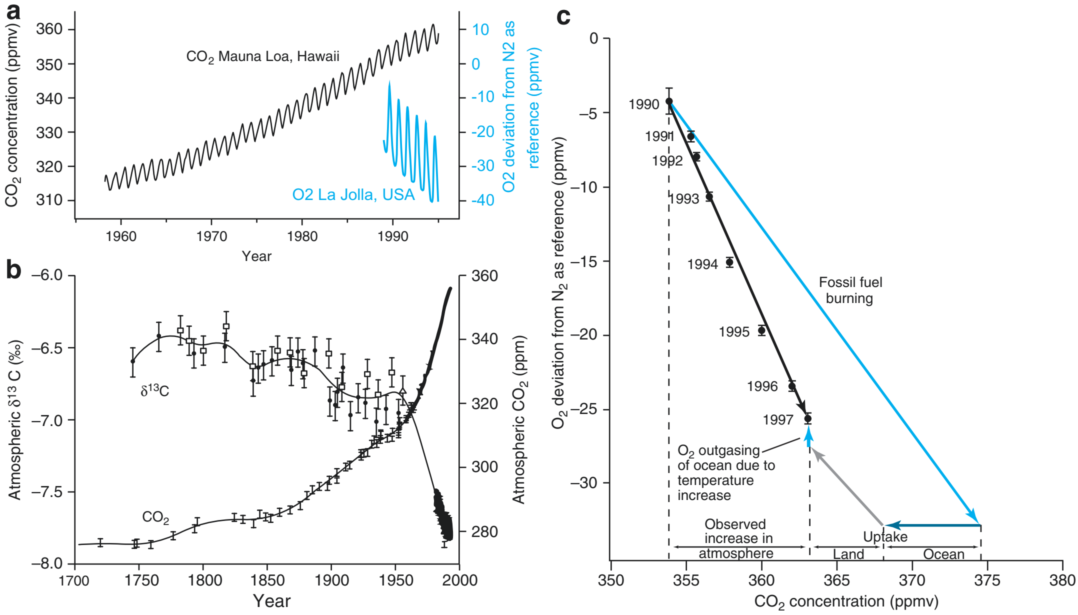
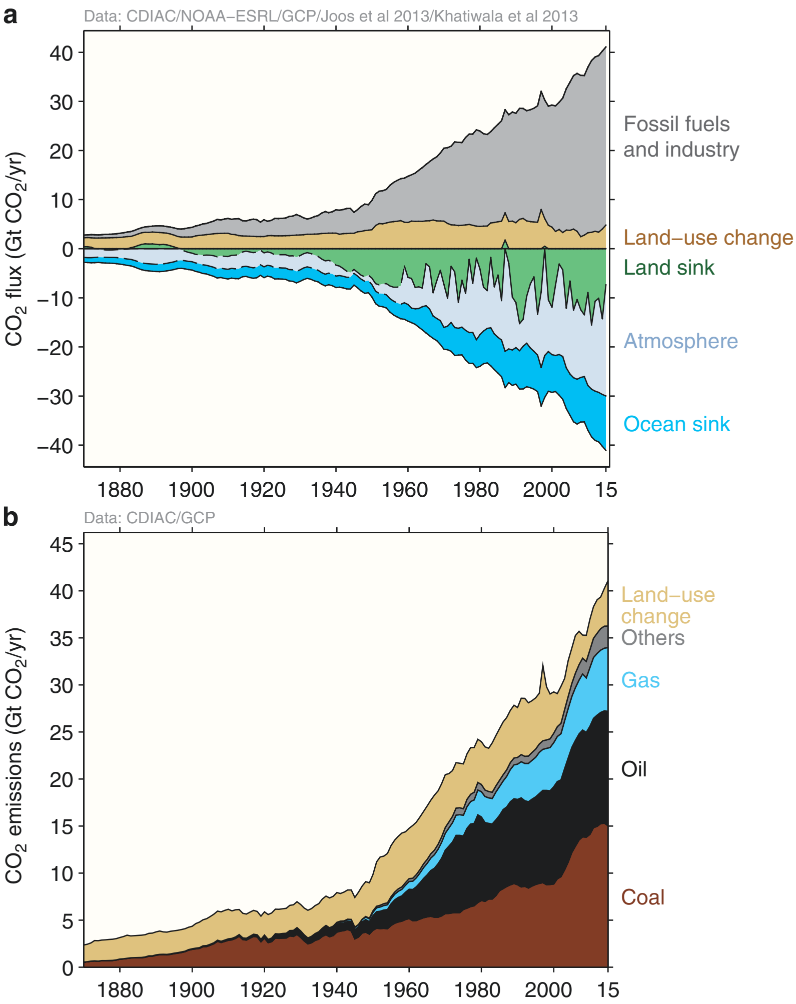


Fig. 23.7 Time series of CO$_2$ concentrations, δ^{13}C and O$_2$ concentrations as well as an analysis of the contribution of fossil fuel burning to atmospheric CO$_2$ concentrations. **a** CO$_2$ concentrations in the atmosphere have been measured at Mauna Loa on Hawaii since 1958. The simultaneous reduction in O$_2$ concentrations measured at La Jolla, California, is also shown. The O$_2$ concentrations show annual oscillations that are opposite to those of CO$_2$ (after Heimann 1997). **b** Changes in atmospheric CO$_2$ concentration and the δ^{13}C value since 1700. (**c**) Changes in O$_2$ concentrations and relationship to CO$_2$ concentrations. (After Keeling et al. 1996)

to 11.2 Gt C year^{-1} (1.3 ± 0.5 Gt C year^{-1} from LUC plus 9.9 ± 0.5 Gt C year^{-1} from fossil fuels) (Fig. 23.8a). The anthropogenic CO$_2$ emissions during 2006–2015 were partially balanced by uptake into the ocean (2.6 ± 0.5 Gt C year^{-1}) and the land (3.1 ± 0.9 Gt C year^{-1}, calculated as residual). However, for 2015 alone, the estimated terrestrial carbon uptake was only 1.9 ± 0.9 Gt C year^{-1}. This CO$_2$ uptake of oceans and the terrestrial surface is termed a **carbon sink** owing to the flux from the atmosphere to the land surface and into the oceans. The present sink (2006–2015) was about 55% of the emissions, i.e. almost half (45%) of the anthropogenic emissions remained in the atmosphere (4.5 ± 0.1 Gt C year^{-1}). Moreover, the temporal variability of these partitioned global fluxes is very high, as seen for years with considerable flux increases, closely followed by years with smaller increases (light blue and green spikes in Fig. 23.8a). These fluctuations can be caused by changes in the ratio of respiration to assimilation, that is, **net ecosystem production (NEP)** and **net biome production (NBP)** (Chap. 16), or fire occurrences. Years with El Niño events stand out (i.e. 1987, 1998, 2015) as years with very low terrestrial CO$_2$ sinks. For example, in 1998, the increase in atmospheric CO$_2$ concentrations approximately corresponded to the total release of CO$_2$ from fossil fuels and industry. The continents took up hardly any CO$_2$; only the oceans balanced the emissions from LUC. In contrast, in 1990, with no El Niño, the Earth's surface was a significant CO$_2$ sink. Overall, the contributions to the CO$_2$ emissions were mainly coal and, to a smaller extent, oil and gas. LUC contributed only about 9% of the emissions during 2006–2015 (Fig. 23.8b).

Thus, the present atmospheric CO$_2$ concentration is not just the result of a mass balance in a specific year but contains the history of sinks and sources of the past. The cumulative emissions

Fig. 23.8 Components of global carbon dioxide budget as a function of time. Land-use change was the main source of CO_2 emissions until about 1950. Since then, fossil fuel burning and industrial emissions have dominated. **a** Component fluxes of CO_2 sources and sinks. **b** Contribution of different sources to CO_2 emissions. (Le Quéré et al. 2016 and www.globalcarbonproject.org)



from 1870 to 2015 were caused by the burning of coal (35%), oil (26%), gas (10%), burning of cement (2%) and LUC (26%). These emissions, totalling 262 ppm, were balanced by terrestrial ecosystems (Chap. 16) as land sink (29%) and net uptake by the oceans (28%). Further, 43% of the total CO_2 emissions since 1870, totalling 112 ppm (288 ppm in 1870 vs. 400 ppm in 2015), remained in the atmosphere by 2015 (www.globalcarbonproject.org).

Total CO_2 emissions mainly originate from three regions of the world: Eastern USA, Europe and East Asia. The use of biofuel and other renewable energies did not change this pattern of emissions. Each region had a different pattern of emissions over time (Fig. 23.9a), but the increase of total CO_2 emissions from China since 2000 is most remarkable.

Industrial emissions of CO_2 are the result of major commercial flows of oil and of goods around the globe (Fig. 23.9b). The Near East is the main producer of oil that is transported mainly to Europe, East Asia and the USA. In addition, Europe receives as much fossil energy from oil as from gas originating from Russia (fossil fuel fluxes not shown in Fig. 23.9). Europe and the USA receive additional fossil fuel from Norway and Canada, respectively. The import of energy as oil to East Asia enables high industrial production of many goods, which are then exported. This results in a major net export of **embedded carbon** in the form of these exported

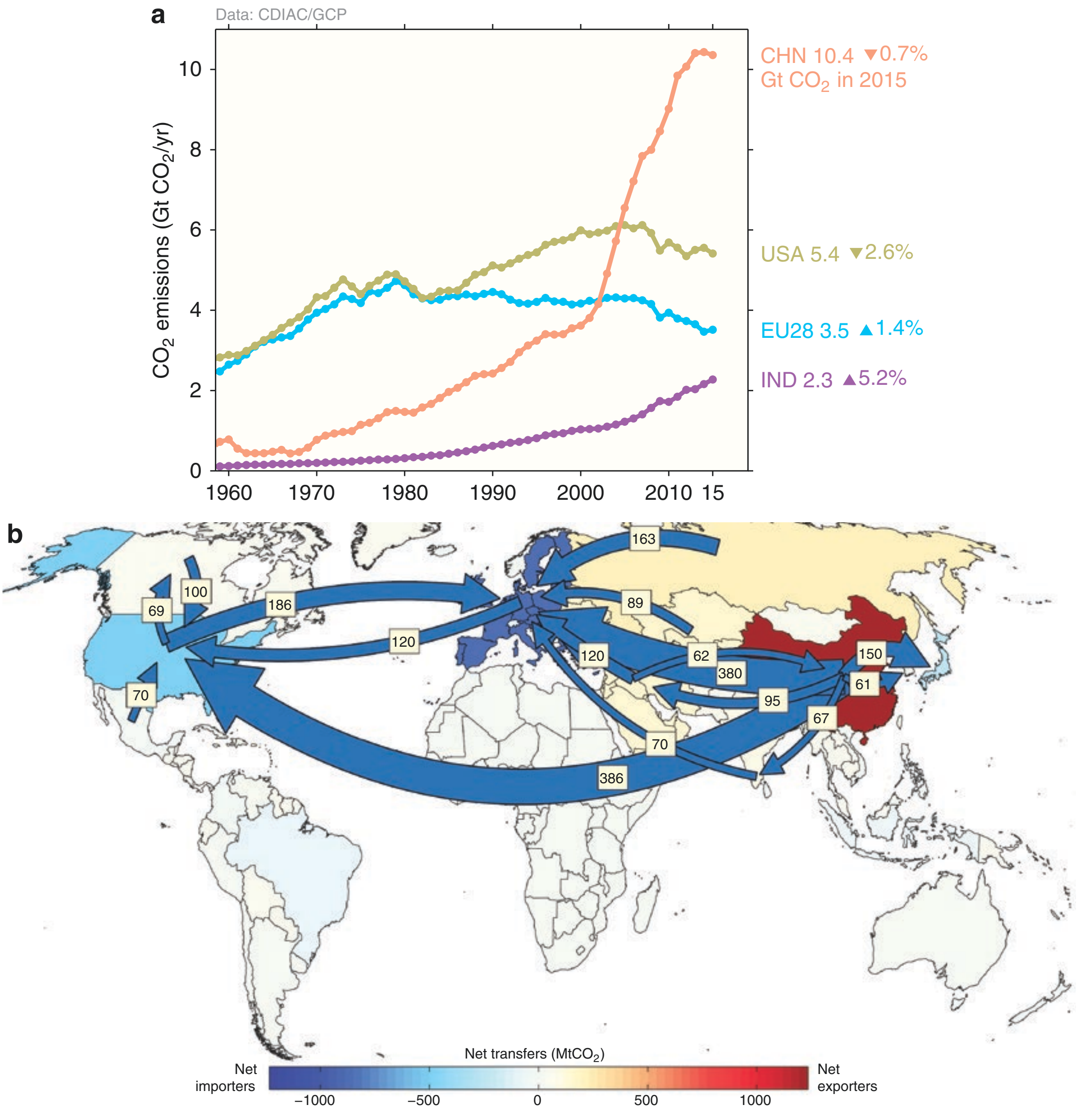


Fig. 23.9 Global distribution of CO$_2$ emissions and net flows of carbon embedded in commercial goods. **a** Total CO$_2$ emissions (Gt CO$_2$ year^{-1}) in different regions of the world for the year 2015. Red: China, green: USA; blue: Europe and magenta: India. **b** Flow of carbon embedded in commercial goods and services expressed in Mt CO$_2$ year^{-1} (www.globalcarbonproject.org). Top 16 global flows are shown

industrial goods from China, while Europe and the USA are net importers of embedded C. Thus, it is the demand for goods that caused the increased emissions of China, and it is under debate whether the associated emissions should be attributed to the countries of production (China) or those of consumption (Europe, USA). Over the past 60 years, the emissions per capita have been three times as high in the USA as in Europe and China. The decrease of the emissions per capita since about 2005 in Europe and the USA was not the result of environmental policy for renewable energy but resulted from imports of embedded carbon in products imported from China. Thus, the effective total emissions per capita have not changed in the Western world.

Parallel to the increase in CO_2 concentrations, the concentrations of **methane** (**CH_4**) and **nitrous oxide** (**N_2O**) also increased (Chap. 21). Despite relatively low concentrations in the atmosphere (in the parts per billion range), CH_4 and N_2O are very important drivers of global warming. Biological CH_4 emissions are caused by microbes under anaerobic conditions and incomplete fermentation, for example under conditions of flooded rice cultivation, and the digestive systems of ruminants and termites, and from organic waste, including landfills. CH_4 is also produced during biomass burning, fossil fuel burning and natural leaks (Kirschke et al. 2013). Previously it was assumed that 70% of global CH_4 emissions originated from biological sources and 30% from fossil fuel industry and natural geological leaks (IPCC 2013). A novel methane budget, based on stable isotopes of C and H, supports this percentage but also reveals that anthropogenic CH_4 emissions originating from geological sources, i.e. leakage and oil and gas industries, are much larger than originally thought (Schwietzke et al. 2016). N_2O emissions are mainly caused by nitrification and denitrification in soils and oceans owing to natural processes and fertilisation, fossil fuel burning and biomass burning.

In addition to these trace gases, other trace gases, such as stratospheric ozone-depleting **halocarbons** (CFCs, HCFCs), and short-lived gases like CO and NO_x contribute to the radiative forcing. Also, **aerosols** and their precursors (mineral dust, SO_2, NH_3, organic carbon, black carbon or soot) play an important role, although their impact on **radiative forcing** can be negative or positive. Negative effects on radiative forcing (i.e. cooling the atmosphere) result from the reflection of solar radiation by aerosols already high in the atmosphere, so radiation does not reach the ground in the first place. Positive effects on radiative forcing (i.e. warming the atmosphere) result from the absorption of radiation by aerosols and the albedo effects black carbon or soot have when deposited on surfaces, for example snow. Aerosols and their interactions with clouds are responsible for the largest uncertainty in the overall radiative budget estimate (IPCC 2013). One crucial aspect has been the occurrence of **global dimming**, observed in radiation measurements over several decades since 1950. The incoming solar radiation gradually decreased owing to aerosols from air pollution. However, after environmental regulations were put in place and air pollution and, thus, aerosol levels decreased, this trend reversed: **global brightening** has been observed since the 1990s (Wild et al. 2007). Global dimming probably reduced the effect of increasing GHG concentrations early on. Overall, GHGs contributed about 0.5–1.3 K (1951–2010) to the global mean surface warming, while aerosols and other anthropogenic forcing contributed about −0.6 to 0.1 K. These estimates support the observed warming of about 0.6–0.7 K during the same period.

The link between radiative forcing by trace gases and by aerosols and the resulting global temperature change is called **climate sensitivity**. It quantifies the change in Earth temperature with increasing radiative forcing that could be caused either by changes in solar radiation or by GHGs, which absorb in the infrared, and aerosols (Eq. 23.1):

$$\Delta T_s = \lambda \mathrm{RF}, \tag{23.1}$$

with ΔT_s indicating the change in global surface temperature, RF the radiative forcing, and λ climate sensitivity.

Based on geological evidence, the climate sensitivity is with high confidence 1.5–4.5 K per doubling of atmospheric CO_2 (IPCC 2013). The **global warming potential (GWP)** of gases is calculated based on a time-integrated radiative forcing for 1 kg of a gas relative to the RF of a reference gas. In the case of climate change, this is CO_2, which has a GWP of exactly 1. The GWP of all other gases is expressed in CO_2 equivalents (CO_2–C_{eq}), generally estimated on a 100-year time scale to account for the lifetime of different gases. The **IPCC** (Sect. 23.5) has slightly changed the GWP values over the course of its different reports and also introduced other metrics (IPCC 2013). For methane, the GWP (without accounting for climate–carbon feedbacks) is

28 g CO_2–C_{eq} per g CH_4, and for N_2O it is 265 g CO_2–C_{eq} per g N_2O (IPCC 2013).

One of the major tasks of the IPCC is to evaluate what effects different scenarios of increased trace gas and aerosol emissions, and thus atmospheric trace gas and aerosol concentrations, would have on global and regional climate in the future. The prediction of the future is difficult because the future is embedded in a socio-economic background of political and societal decisions, which are beyond any predictability. Thus, the IPCC decided to develop **Representative Concentration Pathways (RCPs)** (Nakicenovic and Swart 2000), which are the basis for science and fact-based predictions of how climate will develop if certain emissions are maintained or changed. A temperature increase of 2 K is regarded as a critical limit. This limit is exceeded with an increase of global CO_2 concentrations beyond 450 ppm. In the year 2016, the global CO_2 concentration already exceeded 400 ppm, which is about 120 ppm above the pre-industrial CO_2 concentration of 280 ppm. In 2014, the temperature increase was 1 K, exceeding the temperature maximum of the past 1000 years as confirmed by tree-ring analyses (LaMarche et al. 1984).

At the moment, a doubling or tripling of the pre-industrial CO_2 concentrations is predicted depending on the RCP, leading to a calculated **global temperature increase** of 3–4 K. There is a delay between increasing CO_2 concentrations and temperature because of the heat capacity of oceans (they act as a heat sink) (Levitus et al. 2000) and the melting of the polar ice caps (energy required for melting). The increase in temperature will not be constant across the globe; rather, it will affect the Northern Hemisphere more than the Southern Hemisphere, the Arctic and boreal regions more than the temperate and tropical zones (Fig. 23.10). Also, precipitation patterns, and thus soil moisture levels, are expected to change in the future (Fig. 23.10). There is an increasing likelihood of drought in the Mediterranean region, in the Amazon and in South-East Asia. Dry summers appear to move poleward and will affect Central Europe later this century. Moreover, the observed extreme events of the past, for example heavy precipitation, drought and heatwaves, may increase in frequency in the future. Observations confirm a general increase in heavy precipitation events globally, as expected from radiative forcing. There is medium confidence that anthropo-

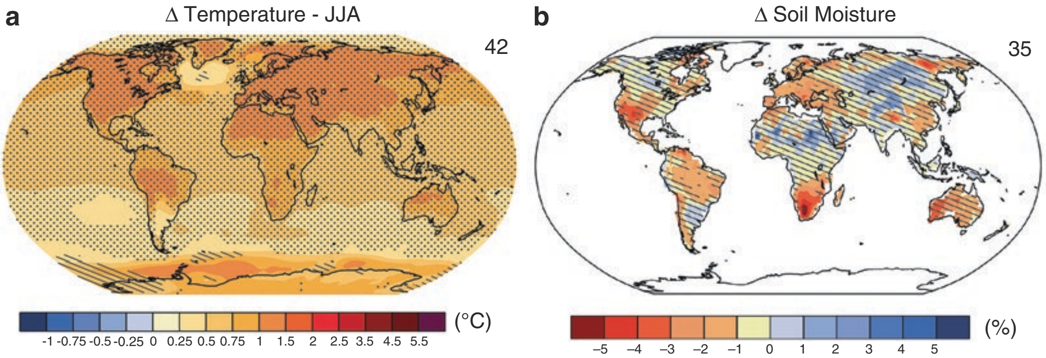


Fig. 23.10 Predicted changes in global temperature and global soil moisture. **a** Global temperature change in June, July and August comparing 2016–2035 relative to 1986–2005. **b** Associated changes in soil moisture. Hatched areas indicate regions where the projected changes are smaller than the internal variability by one standard deviation; stippling indicates regions where the multi-model mean projections deviate significantly from the simulated 1986 to 2005 period and where at least 90% of the models agree. Thus, these are the regions where significant changes took place over the past decade. The number of models considered in the analysis is listed at the top right-hand side of the graphs. (IPCC 2013)

genic influences have contributed to the occurrence of droughts globally, but not on a regional scale. Tropical storms appear to have moved poleward, but an increase in intensity could not be shown, even though observations suggest an increase in the intensity of tropical cyclones.

Since the future temperature rise will depend on the net budget of **historic emissions**, one can calculate the total amount of allowable future emissions to reach a certain climate goal. A 2 K temperature rise will be reached by 1000 Gt C emissions. Of this quota, 555 Gt C were already emitted by 2015, with 445 Gt C remaining, which could be used within 40 years at the present rate of global CO_2 emissions. This would mean in reality that by 2057, no fossil fuel can be used anymore to reach the 2 K temperature goal.

23.3.2 Responses of Terrestrial Ecosystems to Climate Change

Terrestrial ecosystems on Earth have already responded to the existing level of climate change in numerous ways, despite their capacity to resist and recover, that is, their **resilience** (Sects. 13.4 and 17.4). Thanks to their adaptive capacity, it is most likely that not all responses are evident yet. Furthermore, ecosystems respond to multiple factors contributing to climate change at the same time, for example increasing atmospheric CO_2 concentrations and air temperature (Table 23.3). Therefore, responses cannot be linked to one factor alone. This is only possible with dedicated experiments (Sect. 14.2). It is also expected that ecosystems can tolerate change until a threshold is crossed (e.g. temperature extremes). Beyond this threshold, they might not be able to withstand the impact and their **adaptive capacity** might not be capable of ensuring their existence. As a consequence, they might transform into another state, lose their functioning or change their species composition or both.

The factors of climate change to which ecosystems need to react include changes in atmospheric conditions (CO_2, O_3 and aerosol concentrations, temperature, precipitation, N deposition), but also extreme events (heatwave, drought, flood) (Table 23.3). Many of these factors and events directly affect ecosystem biogeochemical fluxes of water, carbon and nutrients, independently of whether these fluxes come from plants or microorganisms (Chap. 16), and therefore affect carbon and nutrient pools as well. This can lead to changes in ecosystem composition and biodiversity via changes in interspecific interactions, damage and death of vegetation, or loss of species (Chap. 20). The soil compartment plays a crucial role as well (Smith et al. 2016). However, the responses of ecosystems are not restricted to the local scale but also show effects on landscape or even larger scales. Any change in net ecosystem fluxes feeds back to the atmosphere and the hydrosphere. Changes in local species composition together with climate change can trigger species migration and larger-scale biodiversity changes. These **feedback** and **feedforward** effects make understanding and dealing with climate change effects difficult and complex. Some examples will illustrate this:

Changes in photosynthesis, biomass production and allocation: High atmospheric CO_2 concentrations have been shown to increase photosynthesis rates at the leaf level (Chap. 12) and in the short-term also at the stand level (Chap. 14). In the long-term or under resource limitations (either nutrients or water), the response to elevated CO_2 diminishes (Norby and Zak 2011). *Downregulation of photosynthesis* plays an important role since stomatal apertures are reduced at high ambient CO_2 concentrations to reduce transpirational losses (Chap. 10). Thus, the ratio of photosynthesis to transpiration increases. Moreover, leaf chemistry and, thus, litter quality changes with developing nutrient deficiencies under elevated CO_2, leading to lower decomposition rates and lower carbon sequestration potentials. On the other hand, forests use more photoassimilates for above-ground biomass production at higher nutrient availability than at low nutrient availability (58 vs. 42%) (Vicca et al. 2012). This difference in allocation of up to 16% is not due to increased autotrophic respiration under high nutrient supply but probably to higher investment below-ground for root growth

Table 23.3 Factors contributing to climate change as well as responses of terrestrial ecosystems and their feedbacks to the environment. The table will never be complete in terms of ecosystem responses and feedbacks to the environment, for example adjacent ecosystems, the atmosphere and the hydrosphere, because responses of ecosystems might be buffered and therefore delayed while at the same time affected by the magnitude of climate change

Factors contributing to climate change	Consequences for ecosystem	Feedbacks to environment
CO_2 concentration	Change in ratio of photosynthesis to transpiration and leaf area index (LAI), impact on carbon allocation, changes of litter composition and decomposition, change in competitive interactions between C3 and C4 plants, change in soil microbial community	Change in evaporative cooling, changes in soil C inputs and CO_2 fluxes, migration
Atmospheric N deposition, O_3	Impacts on plant growth and LAI, change in soil biogeochemistry, soil acidification, support but also damage and decline of vegetation (highly context-specific)	Change in biodiversity, change in soil leaching, effects on landscape albedo and hydrology
Temperature	Impacts on all biogeochemical and physiological processes, occurrence of stress, changes in competition and thus biodiversity, thawing of permafrost, release of CH_4	Change and loss of habitats, migration of species, changes in biospheric–atmospheric water and trace gas exchange
Heat wave	Decrease in most biogeochemical and physiological processes, stress, damage and death of vegetation, loss of C sequestration	Decrease in biospheric–atmospheric trace gas exchange, change in evaporative cooling
Growing season length	Impacts on plant growth and LAI, changes in competition and thus biodiversity, impact on C sequestration, change in trophic interactions	Change in albedo, changes in biospheric–atmospheric water and trace gas exchange
Precipitation	Change in ratio of photosynthesis to transpiration and LAI, impacts on plant growth and carbon allocation, changes in competition and thus biodiversity, impact on C sequestration	Changes in biospheric–atmospheric water and trace gas exchange, migration
Drought, flood	Decrease in most biogeochemical and physiological processes, stress, damage and death of vegetation, loss of C sequestration	Decrease in biospheric–atmospheric trace gas exchange, change in evaporative cooling, change in biodiversity
Aerosols	Impacts on photosynthesis and growth, impacts on nutrient cycling and C sequestration	Effects on landscape albedo and hydrology, change in soil leaching

and symbioses under conditions of low nutrient supply. Thus, increasing CO_2 concentrations will not necessarily lead to the assimilation of more CO_2. This can happen only if nitrogen and other resources are available in the long-term. However, the shift in allocation from below- towards above-ground parts makes these ecosystems more vulnerable to drought, in forests also to windthrow.

Change in C sequestration: Carbon sequestration in terrestrial ecosystems is affected in different ways. Climate change factors modulate gross primary production (GPP) and, thus, C inputs into the ecosystem but also autotrophic and heterotrophic respiration and, thus, C loss from ecosystems (Chap. 16). Based on ecosystem flux measurements, it has been shown that assimilation is more susceptible to drought than respiration at the ecosystem level (Schwalm et al. 2010). Thus, depending on the relation between gains and losses, the ecosystem CO_2 flux budget will change.

Forest decline, tree mortality and forest die-off: Forest decline was a major concern across the Northern Hemisphere in the 1970s and 1980s (Chaps. 11 and 16), and it has been recognised as an interaction of nutrient effects. Acid rain from SO_2 resulted in the acidification of soils and a decrease in cation availability, while nitrogen availability from wet and dry deposition increased and accelerated tree growth. Thus, trees died from a nutrient imbalance. This phenomenon disappeared with the scrubbing of smoke from power stations, with liming agricultural and forest soils in Europe and North America as well as thinning of declining forests. Since then, many forests have recovered.

In recent decades, decreased forest performance and increased forest death have been observed worldwide owing to the occurrence of **climate extremes** during the growing season. Examples range from direct effects, as during the heat wave across Central Europe in 2003 (Ciais et al. 2005), to combined effects, like tree mortality due to drought after beetle outbreaks and associated viral and fungal infections in North America. The simultaneous occurrence of heat and drought or drought and insect outbreaks results in complex interactions. During the heat wave in 2003, GPP and ecosystem respiration in forests were both negatively affected. Because GPP was more affected than respiration, the NEP of European forests changed and they turned from a C sink into a C source. The equivalent of 4 years of C sink was lost in a few weeks of an extreme weather event. Different ecosystem types react very differently to severe drought events. While grasslands keep up both GPP and ecosystem water vapour fluxes (ET) for quite some time into a drought period, forests react almost immediately to a drought by decreasing ET. This pattern changes when the drought lasts longer: grassland vegetation dies off, while the forests continue to photosynthesise and transpire (Sect. 16.1). Thus, evaporative cooling of the atmosphere by the biosphere is highly dynamic and strongly related to landscape heterogeneity, that is, the fraction of forest to grassland vegetation. The impact of drought and heat waves on forests can be aggravated when bark beetles carry viral and fungal infections. The beetles are specialised at attacking weakened tree individuals and are able to use a prolonged and warm growing season for several generations in 1 year (Sect. 13.5, Box 13.1). These beetle populations can then also attack healthy trees. Whole landscapes with forest vegetation may change into open woodlands within a couple of years (Allen et al. 2015). Also other extremes, such as the combination of heat and ozone, could affect ecosystem and human health.

Spring advancement and increased growing season length: Earlier unfolding of leaves (also called spring advancement), as well as earlier nesting of birds or arrival of migrant birds and butterflies, has been observed primarily in the Northern Hemisphere (Parmesan and Yohe 2003; Peñuelas et al. 2009). Globally, spring events advanced by 2.3 days per decade over the last 130 years, with considerable variation among ecosystem types (up to 14 days per decade for boreal ecosystems). **Range shifts** of about 6 km per decade northward or 6 m per decade upward have been reported (Parmesan and Yohe 2003). Leaf unfolding dates in Europe were negatively correlated across a large number of woody species with the pre-season temperature (−0.61 ± 0.61) (Fu et al. 2015). Not only woody species but also herbaceous plants respond with earlier leafing out. However, the advance of unfolding declined from 3.4 days K^{-1} during the period from 1980–1994 to 2.3 days K^{-1} during the period 1999–2013. This decline in response to spring warming could not be explained by chilling periods in early spring but was explained by the fact that other mechanisms may also be involved, such as the photoperiod. Even with further warming, leaves will not unfold in winter because of the shorter photoperiod. This would give an advantage to evergreen conifers or to wintergreen herbaceous crops (winter wheat), which assimilate CO_2 whenever temperatures are suitable. Richardson et al. (2013) reviewed the interactions of **phenology** and climate change, also focusing on feedback and feedforward processes. Increases in annual GPP with longer growing season length are well supported by eddy-covariance flux measurements (Chaps. 14 and 16). However, this does not necessarily increase overall NEP. With increasing autumn temperatures, respiratory losses also increase, at least in northern ecosystems (Piao et al. 2008), compensating higher spring or annual GPP. This seems to be due to enhanced soil respiration (Gonsamo et al. 2017).

The length of the growing season is determined not only by unfolding but also by leaf **senescence** in autumn. It emerges that also leaf fall is delayed, but the response is species-specific.

While some broad-leaved species show leaf senescence with a change in leaf colour in autumn (*Fagus, Acer*), other species (*Fraxinus, Alnus*) keep their green leaves until a first frost kills the leaves. Nevertheless, with warmer autumns, leaf fall has also been delayed. An increased growing season length of 2.1 to 42 days per decade has been reported for temperate forests in Europe and North America (Richardson et al. 2013). For crops, the frost-free days decreased from 1975 to 2010 at a rate of −0.8 to −0.4 days per year in Northern, Eastern and Central Europe but showed little or no change in the Mediterranean region (European Environmental Agency 2017).

23.3.3 Feedbacks of Terrestrial Ecosystems to Climate

Terrestrial ecosystems are affected not only by climate change and show multiple responses to changes in the atmosphere (Chap. 23); they also exhibit numerous feedbacks with which ecosystems affect the climate (Table 23.3). These feedbacks can also be considered emergent properties of ecosystems (defined in Chap. 13). Some examples will illustrate these feedbacks.

Temperature sensitivity of the carbon cycle: Any change in ecosystem C sequestration is related to changing proportions of assimilation to respiration. But these processes have feedbacks to the atmosphere, in particular with respect to decomposition and soil organic matter formation (Chap. 16). The decomposition of plant material is stimulated by increasing temperatures and litter fall (but decreased by low litter quality). A value of 7.7 ppm CO_2 per 1 K has recently been suggested as carbon cycle climate sensitivity for the Northern Hemisphere, that is, additional CO_2 emissions due to such a temperature feedback (Frank et al. 2010). However, it remains unclear whether respiration will acclimate and decline again in relation to the available substrate.

Net GHG *budgets*: The net uptake of carbon dioxide from the atmosphere and its sequestration in soils and woody biomass, but also the secondary use of products for bioenergy, are among the main processes considered for climate change mitigation. In addition, reductions of CH_4 and N_2O emissions, particularly from agriculture, have been discussed. Assessing full GHG budgets require not only flux measurements of these gases (Chaps. 14 and 16) but also the compilation of further data on C inputs and exports to calculate the NBP (Chap. 16). In addition, CH_4 and N_2O fluxes need to be considered to calculate the **net greenhouse gas budget (NGB)**. Using the European GHG budget as an example (Fig. 23.11) (Schulze et al. 2009, 2012), forests, grasslands and croplands are compared, which form the highly heterogeneous European landscape. At the level of GPP, the three LU types do not differ since the availability of light mainly limits this process. Differences in metabolic rates are compensated by differences in growing season length and plant structures. At the level of NPP, grasslands have higher flux rates than forests or croplands, but most of this production is either harvested for animal feed or grazed. Harvest removals are similarly high for croplands. But eventually forests are also harvested or fall to the ground after disturbances. Restricting the NBP calculation to biomass ($NBP_{Biomass}$ in Fig. 23.10) results in the highest accumulation of carbon in forests (here: negative NBP means C uptake), but this depends on the present age structure of forests in Europe. This large capacity of forests to accumulate carbon in (mainly woody) biomass of growing stands and in soils is the basis for promoting afforestation programmes in the context of climate change mitigation. Storage in products is also not yet included. Moreover, grasslands are mainly used as feed for ruminants, which emit CH_4, and both grasslands and croplands are fertilised and typically emit N_2O. Thus, fluxes of these other GHGs must be considered as well. The resultant total net greenhouse gas balance (NGB total) shows that forests remove more GHGs from the atmosphere (negative sign) than grasslands and croplands. The overall total NGB for all three European LU types is carbon neutral.

Fossil fuel substitution has been suggested as a major mechanism to support climate change mitigation. Biomass use for **bioenergy** (including methane production and liquid biofuels) has been state-supported, even though biofuel production

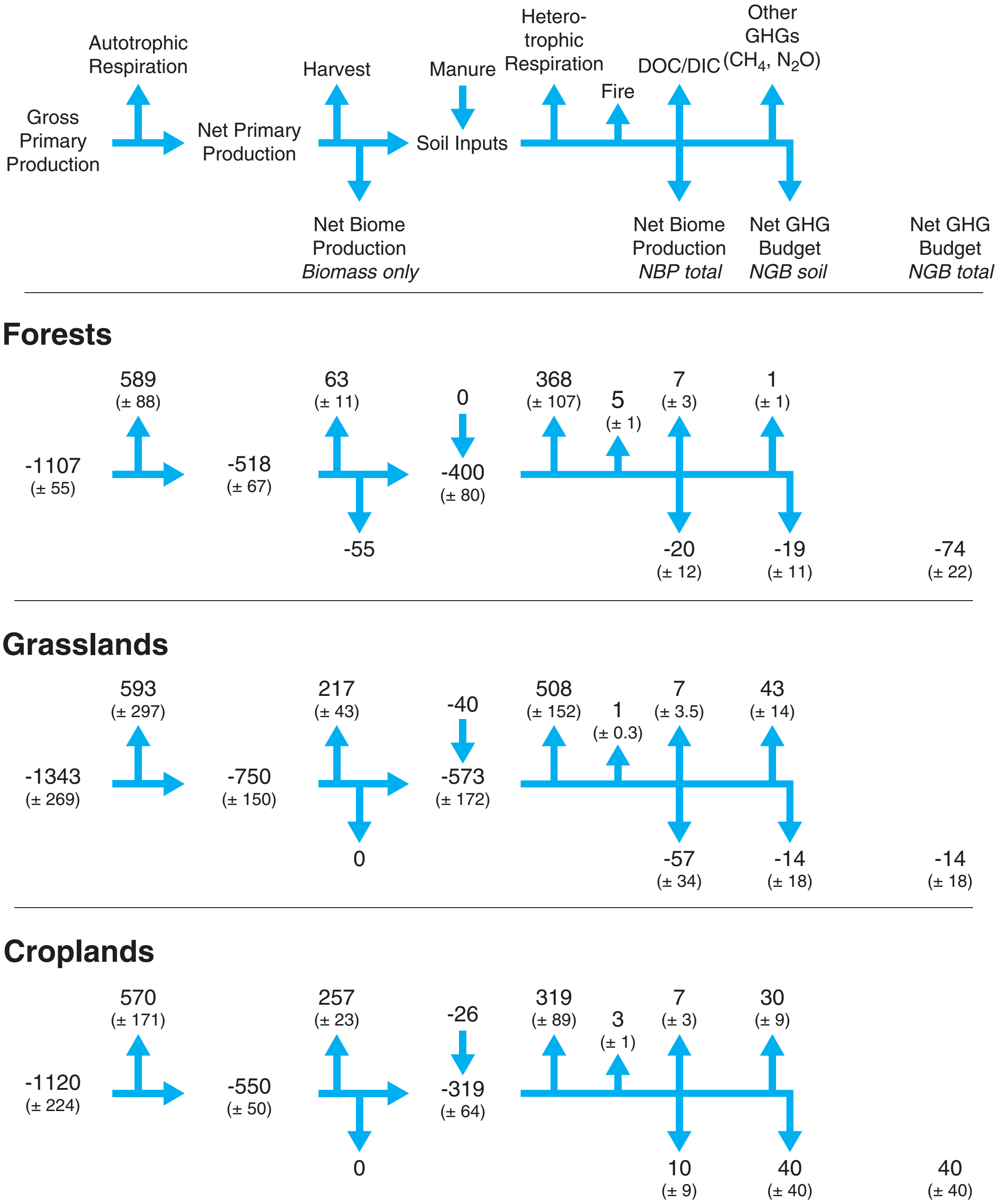


Fig. 23.11 Net greenhouse gas budgets (NGBs) for different land use types in Europe. All three GHGs, CO_2, CH_4 and N_2O, are considered as CO_2–C equivalents. NGBs are given for soils (NGB Soil) and for the entire ecosystem (NGB Total). Negative numbers give GHG sinks, positive numbers GHG sources. NGB total is composed of changes in NBP and NGB_{soil}. Numbers in brackets represent one standard deviation. GHG losses are depicted with arrows pointing upward, GHG gains with arrows pointing downward. DOC and DIC stand for dissolved organic and inorganic carbon, respectively. (after Schulze et al. 2009)

using agricultural crops competes with food and feed production. Also, fertilisation of bioenergy crops produces N_2O, and the land area for the production of oil, such as oil-palm or soybean, competes with natural vegetation (Haberl et al. 2012). The energy shortage in Europe in the nineteenth century before fossil-based energy (mainly coal) was available may be taken as an indication of the limitations of biomass production to mitigate fossil fuel use. Nevertheless, the use of biomass for energy after a chain of uses still appears to be an important contribution to climate change mitigation. **Bioeconomy** is an additional means to replace fossil fuels where all products for daily life shall be biomass-based (e.g. instead of plastics). This will increase the demand for biomass in the future, and it is not clear where this biomass will be produced (Canadell and Schulze 2014).

Evapotranspiration: Evapotranspiration of the land surface is an additional major factor contributing to the cooling of the atmosphere, as explained earlier (Sect. 16.1). It has thus been hypothesised that the destruction of the rainforest in the Amazon basin would result in a warmer and drier climate (Bonan et al. 1992). However, this remains a hypothesis. On the other hand, grasslands can have even higher rates of evapotranspiration than forests, particularly early into a drought (see example given above). This contributes to **atmospheric cooling** and can promote regional rainfall. This behaviour reverses with longer drought periods and after harvests. During longer droughts, forests remain the main source of water vapour fluxes (Sect. 16.1) (Teuling et al. 2010). Moreover, harvested fields have low evapotranspiration rates and dissipate a lot of sensible heat. When warm air masses move across heterogeneous landscapes (with agriculture, forest and urban LU), this increases the evapotranspiration from forests. The now hot and moist air masses contribute to convective thunderstorms and hail and may cause extreme events over cities that are heat islands in the landscape.

Albedo: These negative effects of forest evapotranspiration on the radiative forcing reverse in the boreal and arctic zones, where the northward progression of forests not only increases carbon storage but also changes the albedo of the landscape, especially in winter (Chap. 9). Dark tree crowns reduce the reflectivity of snow, from >0.5 over snow to <0.15 over forests. This leads to warmer winter temperatures (Bonan 2008). Thus, high-latitude afforestation will accelerate rather than mitigate climate change (Bala et al. 2007).

23.4 Changes in Biodiversity

Diversity of species is the main variable available for an assessment of changes in biodiversity at the global scale (Sect. 20.2). Most often, vascular plant species are used, and sometimes birds and certain insect groups are included. However, no information is available about the diversity of microorganisms at the global scale. Further indicators closely relate to species information, such as extinction risks, habitat extent or community composition. Considering the world map of plant distribution (Sect. 20.3, Fig. 20.11), there are 35 so-called **biodiversity hotspots** (Fig. 23.12), regions with very high plant diversity and high level of endemism (>1500 endemic species/hot spot), and where 70% of the habitat are already lost. In addition, there are genetic centres of crop species, also called **Vavilov centres**. Both regions overlap only partially. It has been estimated that species hotspots covered about 16% and the hotspots of crops about 8% of the Earth's surface in the past (Cincotta et al. 2000). Currently, about 1.1 billion people live within those biodiversity hotspots, covering about 2.5% of the Earth's surface. If it were possible to protect these hotspot areas from further LUC today, it would be possible to protect 50% of global plant species as well as 42% of birds, mammals, reptiles and amphibians (Myers et al. 2000).

Biodiversity loss is tightly linked to several aspects of human LU, resulting in direct removal of species or habitat degradation and loss. Currently, the "big killers" are over-exploitation (LUC, hunting, fishing), agricultural activities (crop and livestock farming, timber plantations) and urban development (housing, tourism, traffic). Other important drivers of biodiversity loss are **invasive**

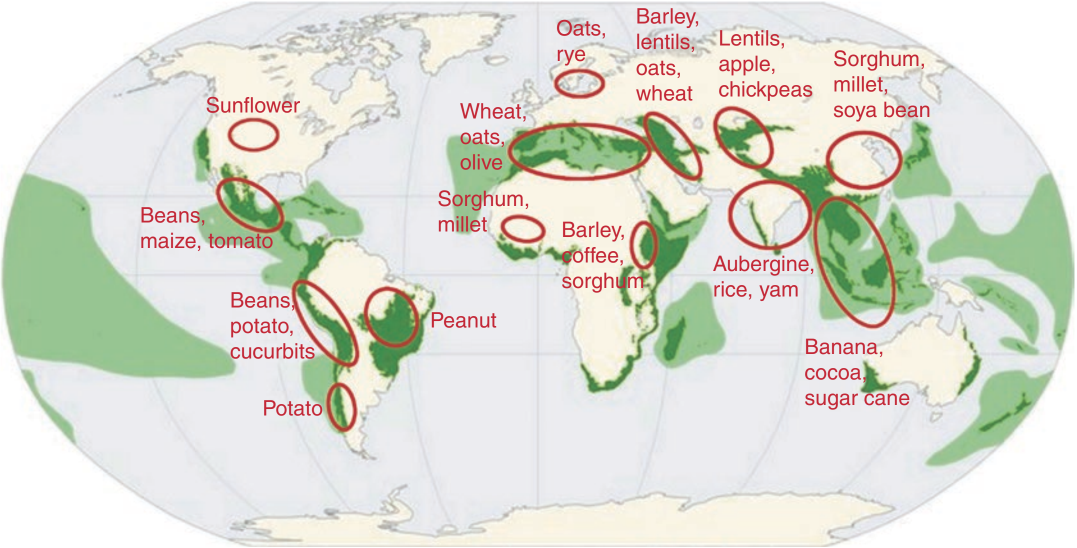


Fig. 23.12 Global distribution of diversity hotspots and the genetic origins of economically important species. (data from Myers et al. 2000 and Reid and Miller 1989)

species and diseases, pollution (pesticides, wastes, N deposition and eutrophication), climate change and system modifications, such as increasing fire frequency and dam constructions (Maxwell et al. 2016). Climate change is negatively affecting biodiversity through storms and flooding, habitat modification, extreme temperatures and drought (Table 23.2). Simulations suggest that with a 4 K increase in global temperatures by 2100, more than 500 plant species per 110 × 110 km grid cell could be lost, mainly in tropical and subtropical regions (Sommer et al. 2010). Climate change will cause **extinctions** if species cannot adapt to new environmental conditions or if their dispersal capacities do not allow them to migrate to sites with suitable conditions. Because the range of **dispersal** mechanisms is very large (Sect. 18.2), even within vegetation types, the distribution of plant species will change considerably: some species may keep pace with climate change, while others may lag behind, resulting in new combinations and associations of species. Such spatial shifts may occur over hundreds of kilometres, but also within very short distances: for example, the large spatial heterogeneity in growing conditions within alpine ecosystems allows species to migrate to suitable growing conditions within a few centimetres (Sect. 20.3, Fig. 20.13). Besides such range shifts, species may also respond by shifting their climatic niche through temporal changes (shifts in phenology) or internal plastic changes (shifts in physiology) (Bellard et al. 2012).

LUC is expected to remain the most important driver of biodiversity loss until the end of the century, followed by climate change, N deposition, biotic exchange and elevated CO_2 concentration (Sala et al. 2010). Most indicators used to evaluate the state of global biodiversity show decreasing trends, while many drivers of biodiversity, for example resource use, invasive alien species, N pollution, over-exploitation and climate change impacts, show increasing trends (Butchart et al. 2010). Concerning LULUC, the effect of intensified and extended agriculture on the diversity of species can be seen worldwide. It is a direct consequence of increasing human populations and of changes in diets, for example increased meat consumption, which requires more animal feed. With the current rise in the human population and human activities, the scope for reducing agricultural expansion or for stabilizing and protecting climate seems very limited.

Presently, about 50% of the terrestrial ice-free surface of the globe is intensively used by humans

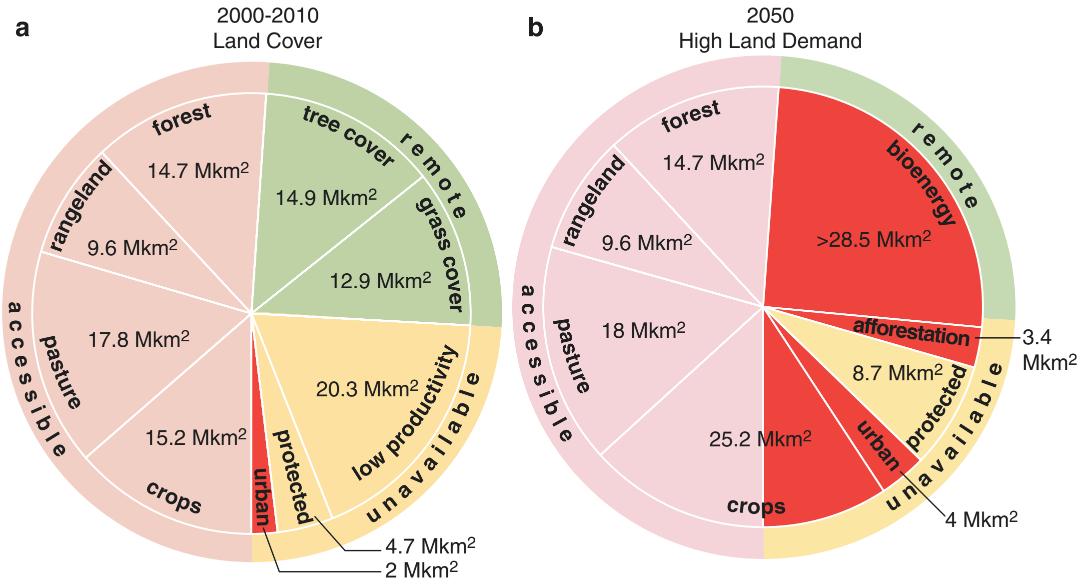


Fig. 23.13 Partitioning of global land area for human use and species protection. (from Canadell and Schulze 2014)

for crops, grazing, forestry and urban development (Fig. 23.13a) (Canadell and Schulze 2014). The remaining area is either too remote or of low productivity and thus only extensively used or unused. Currently, 4.7% of the land area is under protection. These numbers will change in the future (Fig. 23.13b). Assuming a high land demand, a scenario based on the implementation of a global bioeconomy and increasing living standards and unregulated LUC, the human appropriation of land for intensive use might increase to up to 90% of the land surface by 2050. The area of protected regions might even increase to about 8%. Nevertheless, such a scenario implies a major loss of species in the near future.

However, besides the negative perspectives for biodiversity, there are also positive aspects:

- Low diversity does not necessarily mean lower productivity. Generally, a rise of productivity is being observed with increasing species numbers under similar environmental conditions (Sect. 20.4). However, the deliberate selection of highly productive species may result in higher yields than in mixed communities. Most agricultural systems rely on this principle. In forestry, few managed species such as *Eucalyptus* and *Pseudotsuga menziesii* can have a productivity level that is a magnitude higher than that of other tree species or mixed forests (Fig. 23.14a), even though there is a higher risk of disturbance and a change of habitat function in mono-specific stands. Thus, potentially it would be possible to increase productivity in confined areas, which would release the pressure of LUC on other areas. For example, 73 Mio ha of well-managed plantations with a productivity of 25 m^3 ha^{-1} year^{-1} would ensure the current global need for industrial round timber, corresponding to only 2% of the global forest area (Seppälä 2007). With appropriate LU, the partitioning of global land could also make it possible to maintain a large fraction of protected and endangered habitats (Fig. 23.14b).
- Extensive LU can actually create large heterogeneity in environmental conditions, sometimes allowing more species to coexist than in the pristine ecosystems that have been replaced. An example of traditional agricultural landscapes with high plant species diversity was already discussed in Sect. 17.2. Several species, which rely on human disturbances, for example the segetal flora (species

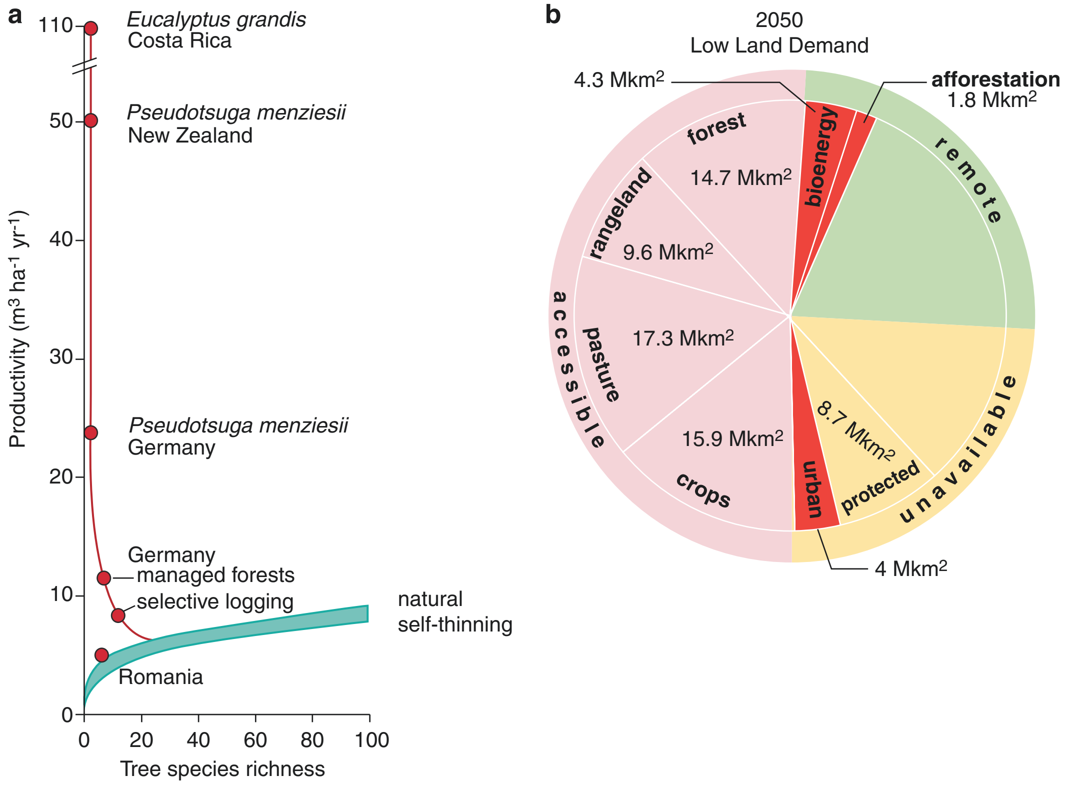


Fig. 23.14 Productivity–diversity relationship for forests, including managed species and the partitioning of land with appropriate management. **a** Productivity of natural forests, under conditions of self-thinning, as related to tree species richness (blue band) (from Liang et al. 2016), and productivity of managed forests (red line) in various locations and with associated species (from Liang et al. 2016, supplement). **b** Predicted LU in 2050 at low land demand, assuming high-intensity management on productive land (from Canadell and Schulze 2014). The remaining unmanaged unavailable lands are mainly alpine and Arctic regions and bogs. The unmanaged remote lands are mainly remote boreal forests

growing in cultivated fields), are now considered endangered and are protected. Sustainably managed forests do not necessarily differ from protected forests in their species composition (Paillet et al. 2009).

- Intensive LU creates a larger number of newly evolving species, such as apomictic or pesticide-resistant species (e.g. Anthony et al. 1998). The genus of *Rubus* is a well-investigated example (Sochor et al. 2015).
- Nature conservation efforts can result in the successful protection of populations and species if the driver of endangerment can effectively be stopped, for example by changing management or by protecting large or small areas, even though the protection of geographically confined sites may not be a solution under conditions of climate change and species migration. The so-called blue species lists in Switzerland (Gigon et al. 1998), for instance, compile such examples of positive developments of endangered species population sizes.

There are numerous additional interactions of global change and biodiversity, such as changes in **pollination** (e.g. Klein et al. 2007; Potts et al. 2010) and **invasions** of new species (Mooney and Hobbs 2000; Pearce 2015), where the combined effects of LU and climate change drivers can result in a weakening of the resilience of existing plant communities and ecosystems (Sect. 17.4). This in turn opens up opportunities for invasion by **pests** and **diseases** and by **alien plant species**. About 20% of the 64

Central European tree species are affected by modern diseases and by old, but increasingly aggressive, diseases. This can even lead to some species facing extinction (*Ulmus*, *Fraxinus*). Thus, there is room for new species invading from outside (e.g. Mooney and Hobbs 2000). Therefore, alien and invasive species are often regarded as a kind of "pest" that needs to be eliminated, for example *Pseudotsuga* in *Fagus* forests of Europe. But one can also take the opposite view, namely that alien species occupy niches in communities that were opened up by human management or by global climate change (Pearce 2015). Thus, the invaders in fact complement the species assembly and maintain ecosystem functioning, creating so-called **novel ecosystems** (Hobbs et al. 2009).

Thus, with global changes in climate and biodiversity, the future world will be different from the present one. What the net effect will be between loss of species and the evolution of novel species, only time will tell. However, although current estimates of future biodiversity changes are still variable, the majority of models predict substantial negative consequences for global biodiversity, leading to extinction of species (Bellard et al. 2012).

23.5 Global Agreements to Address Global Ecological Challenges

It is clear from the foregoing chapters that it is beyond the scope of a single nation to solve the problems of climate change, loss of biodiversity, degradation of soil and so forth. Therefore, these global issues were discussed at the United Nations Conference on Environment and Development (UNCED) in 1992 in Rio de Janeiro, Brazil, also called the **Earth Summit**. Three important conventions were signed:

- Framework Convention on Climate Change (UNFCCC).
- Convention on Biological Diversity (UNCBD).
- Convention to Combat Desertification (UNCCD).

An international agreement to protect forests was not ratified because of conflicting interests, and this remains an unresolved issue to the present day.

23.5.1 Biological Diversity

The UNCBD (www.cbd.int), a result of the 1992 Earth Summit in Rio and in the meantime signed by 196 member states, has nearly global coverage, the USA being the most prominent non-member. Administratively hosted by the United Nations Environment Programme (UNEP), it is acknowledged as the leading treaty in the field of biodiversity, with other treaties taking over specific tasks, like the **Ramsar Convention** for the conservation of wetlands or the **Convention on International Trade in Endangered Species (CITES)** for trade-related issues. The UNCBD defines biological diversity as the diversity of ecosystems, the diversity of species and genetic diversity within species. It pursues three overarching goals:

- The conservation of biological diversity.
- The sustainable use of the components of biological diversity.
- The fair and equitable sharing of benefits resulting from the use of genetic diversity.

Member states are obliged to develop national biodiversity strategies and action plans, setting their own national targets and priorities, and 185 states out of the 196 members have done so as of 2017. This in itself represents a major success, considering the situation in 1992 when the UNCBD was signed, when no state had such a strategy, and most states did not even have a ministry for the environment.

To structure its work, the UNCBD has developed a set of thematic work programmes for certain types of ecosystems (e.g. marine and coastal ecosystems, mountain ecosystems, forests) and cross-cutting work programmes for issues like, for example, sustainable use, invasive alien species and protected areas. Furthermore, two internationally binding protocols have been developed by the UNCBD, ratified and signed by member states, which now are obliged to implement them:

- Since 2003, the **Cartagena Protocol on Biosafety** (170 member states), which regulates the safe handling, transport and use of living genetically modified organisms (LMOs).
- Since 2014, the **Nagoya Protocol** on Access to Genetic Resources and the Fair and Equitable Sharing of Benefits Arising from their Utilisation (96 member states).

The UNCBD is an "agreement under international law" whose Article 3 declares that "States have, in accordance with the Charter of the United Nations and the principles of international law, the sovereign right to exploit their own resources pursuant to their own environmental policies …" (United Nations 1992). This means that all organisms that naturally live in a country are now the property of that country and cannot be taken away or used without permission by the state. This holds also for research, which is defined as the use of biological materials, termed "genetic resources" (GRs). The Nagoya Protocol, determining the framework for the third aim of the UNCBD, i.e. "Access and Benefit Sharing", under Article 8 encourages member states to support biodiversity research on their GRs and in particular for non-commercially motivated, basic research. However, it falls within states' sovereignty to follow that guideline or not. One of the major efforts implicitly expressed in the Nagoya Protocol is the endeavour to act against **biopiracy** and to share commercial gains between a country and the producer of a commodity. For basic research, other benefits can be envisaged such as capacity building or the development of biological collections and databases. Following the rules and standards of the Nagoya Protocol in projects even of basic research takes more preparatory time and administrative expenditure.

The UNCBD had set itself the goal of significantly reducing by 2010 the rate of loss of biodiversity. However, in a stock-taking exercise (Secretariat of the Convention on Biological Diversity 2010), the UNCBD had to acknowledge that this goal had not been reached and biodiversity loss in most ecosystems was ongoing. Therefore, in 2010, the UNCBD adopted a new strategic plan with 20 clearly defined targets to be reached by 2020, the so-called **Aichi Targets** (named after the province in Japan where the respective Conference of the Parties, called COP, took place). These targets, *inter alia*, specify that

- The rate of loss of all natural habitats, including forests, will be at least halved and where feasible brought close to zero, and degradation and fragmentation is significantly reduced (target 5).
- Areas under agriculture, aquaculture and forestry will be managed sustainably, ensuring conservation of biodiversity (target 7).
- Pollution, including excess nutrients, will have been brought to levels that are not detrimental to ecosystem function and biodiversity (target 8).
- Invasive alien species and pathways will be identified and prioritised, priority species controlled or eradicated, and measures be put in place to manage pathways to prevent their introduction and establishment (target 9).
- The extinction of known threatened species will have been prevented and their conservation status, particularly of those most in decline, improved and sustained (target 12).

An intermediate overview (Secretariat of the Convention on Biological Diversity 2014) in 2014 showed that progress is being made under most of the 20 targets, but that the current ambition and implementation speed shown by member states is not sufficient to reach the targets by 2020.

To strengthen relations between science and policy for biodiversity issues and ecosystem services an **Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES)** (www.ipbes.net) was founded in 2012 under the auspices of four United Nations entities: UNEP, UNESCO, FAO and the UN Development Programme. Its task is the ongoing assessment of the state of biodiversity and of ecosystem services, like that of the IPCC for climate (Sect. 23.2). One thousand scientists from all over the world currently contribute to the work of IPBES on a voluntary basis. The IPBES assessments shall be used by decision makers for the conservation and sustainable use of biodiversity, long-term human well-being and sustainable development. A first thematic assessment on pollinators, pollination and food production was published in 2016, including a summary for policy-makers with a set of key messages. It was the UNCBD that had requested IPBES to produce such assessments, and consequently these key messages were taken up by the UNCBD at the thirteenth COP in 2016. The COP is the convention's ultimate authority that meets every 2 years. The messages were transformed into a decision encouraging CBD member states to take steps to implement concrete measures accordingly.

Although the UNCBD is a legally binding international agreement, it allows member states to implement measures and programmes under national priorities and with respect to national circumstances, and there is no sanctioning mechanism in the UNCBD. In other words, the UNCBD cannot enforce implementation in its member states, but it is the responsibility of states themselves to take appropriate steps to reach the targets set on a global stage. Thus, the Aichi Targets aimed at halting biodiversity loss have a similar status as the 2 °C goal negotiated with the Paris Agreement of the UNFCCC (Sect. 23.5.2), and both these international targets depend on implementation by the individual member states.

23.5.2 Climate Change

The statement of the IPCC (1996) that “a recognisable influence of man on global climate” exists resulted in the so-called **Kyoto Protocol** as part of the United Nations (1998). This protocol anticipated a legally binding obligation to reduce the emissions of six GHGs (CO_2, CH_4, N_2O, CFCs, PFCs, SF_6) on average by 5.2% below the level of 1990 within the period from 2008 to 2012. The European Union (EU) as a whole promised a reduction of 8%, Germany a reduction of 21%. The obligation to reduce emissions was signed by the 30 so-called Annex I states, that is, industrial nations and states in transition to a market economy. The other 159 nations of the UN, including the USA and China, did not agree to such obligations, despite their large share of total global CO_2 emissions (Fig. 23.15).

To achieve the reduction commitment not only by industrial activities, the Kyoto Protocol, for the first time, also considered an enhancement of biological sinks. The idea was to incorporate biological processes into the calculations, based on the fact that the obligation for a 5.2% reduction was only a fraction of the natural CO_2 fluxes of assimilation and respiration and that a slight change in these fluxes

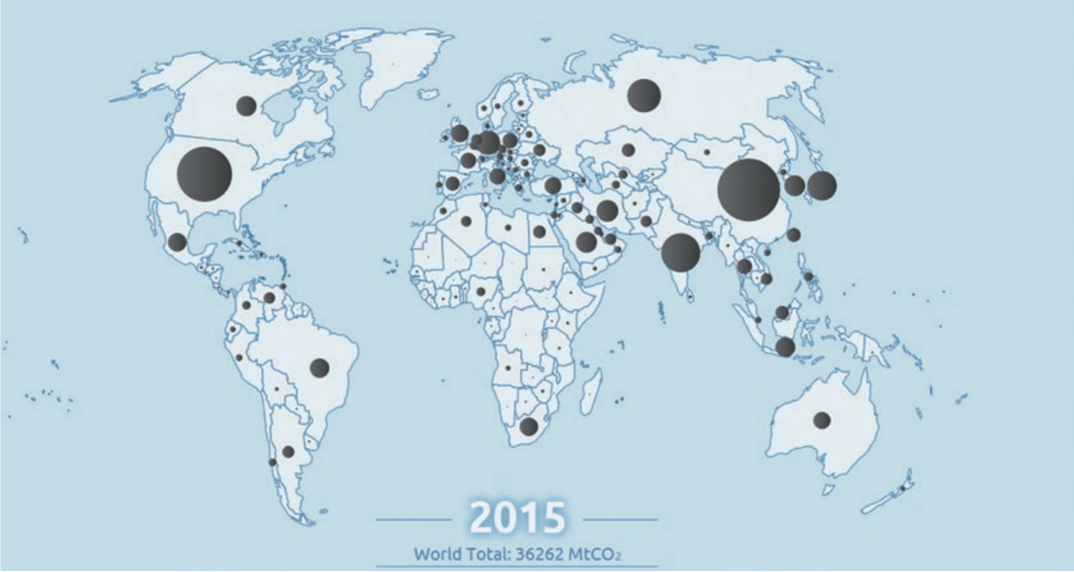


Fig. 23.15 Spatial distribution of CO_2 emissions across the globe in 2015. The size of the circles is proportional to the magnitude of CO_2 emissions. (http://globalcarbonatlas.org/en/CO2-emissions)

would compensate the obligations for reduction to a large extent.

The following measures were considered in the Kyoto Protocol:

- Enhance technical measures to reduce emissions.
- Increase biological sinks in forests by promoting afforestation and avoiding clearing.
- Establish emission-reducing measures, for example in agriculture.
- Trade with emission certificates between industrial nations.
- Establish projects in developing countries to increase sinks and to reduce emissions (Clean Development Mechanism).

The ecological effects of the Kyoto Protocol were discussed in the IPCC report on changes in LU and forestry (Watson et al. 2000). The problems were as follows:

- The definition of forest (forests are stands with trees greater than 0.5 ha, 2 m in height and with 10% cover) did not protect against degradation (over-use) of forests. Emissions resulting from degradation were not credited.
- There was no allowance to account for the protection of primary, natural forests. These were not regarded as “anthropogenic” sinks because they did not experience any management and thus would not be credited.
- Sustainable forest management, where the harvest corresponds to the increase of biomass in younger stands and replaces fossil fuel use, was considered “non-creditable”. Changing forests into other forms of use (deforestation) was treated as emissions, while harvesting prior to LUC was not taken into account.
- Support was given for forest plantations with fast-growing tree species, which very often are alien to natural flora (e.g. *Eucalyptus* plantations in Portugal, *Pinus radiata* plantations in Chile and New Zealand). In these plantations, only the increase in stem volume was accountable, but not the net ecosystem production (Sect. 16.2), thus not accounting for soil C losses from intensive cultivation.
- Food, feed and wood trade from developing to developed nations which simulataneously afforested and even increased forest conservation, resulting in a displacement of the problems into non-industrialised nations (called **leakage**). As the areas required in developing countries were often made available by clearing primary forests, this triggered emissions and not a global C sink. By not incorporating forestry and relocation of production to developing nations, many possibilities became available for crediting additional anthropogenic sinks, but without taking into account related emissions.

In view of these shortcomings, a new protocol for decreasing GHG emissions, adaptation and financing was discussed at the Paris meeting of the UNFCCC in 2015. A new agreement was formulated, the **Paris Agreement** (United Nations 2015), which was signed by most nations of the UN, including the USA and China. By March 2017, the agreement had been signed by 194 nations and ratified by 141. Thus, the Paris Agreement entered into force in November 2016. It was agreed that global temperatures should not increase more than 2 K and preferably not more than 1.5 K above pre-industrial levels, but no binding measures were included. Each nation is free to decide how to decrease emissions. One major change compared to the Kyoto Protocol was the inclusion of forest products in the mechanisms of mitigation. In addition, a regular “stocktaking” of global implementation mechanisms was agreed to. Emission reductions are to be achieved without threatening food production. It will be interesting to see whether this very free agreement will have any effect within the next decades.

Summary

- Global change is the sum of changes in LU and climate that affect not only biodiversity but also many other processes. The effects of *Homo sapiens* have reached a level where a new geological epoch, the “Anthropocene”, is under discussion. Humans affect the globe not

only by their population but mainly by the intensity of their activities.
- We distinguish LU of variable intensity, where the land cover is not changed, and LUC, which is a change in the way the land is used. In addition, land cover describes the cover of the Earth's land as natural or human-made features. LUC has mainly affected forests by transforming them into agricultural land (cropland, grassland).
- The production of food, feed and energy dominates LU. Only a small number of regions around the world (Europe, temperate North America and East Asia) supply the necessary food for nine billion people. In addition, there are major flows of biomass between continents, mainly to meet the needs of the developed world, and the flow of industrial goods, which contain "embedded carbon" due to the energy cost of production in the land that produced these goods.
- Climate change is a major component of global change. In the last decades, it was mainly caused by the burning of fossil fuels for energy. LUC contributed about 10% to the total emissions of 10 Gt C year^{-1}; 26% of the emissions were balanced by ocean uptake and 31% by the net uptake of terrestrial ecosystems, while 45% remained in the atmosphere. This resulted in a change in the physical properties of the atmosphere and, thus, in global warming. The physical properties of the atmosphere are additionally changed by emissions of N_2O, originating mainly from incomplete decomposition and from incomplete N_2 fixation, and by emissions of CH_4 resulting from mining fossil fuels and from anaerobic processes during decomposition and enteric fermentation. At present, all continents and all climatic regions of the world are affected by global climate change.
- The factors contributing to climate change are increased GHG concentrations, warmer temperatures and longer growing seasons, and the occurrence of climatic extremes (heat waves, droughts), as well as changes in precipitation patterns. Terrestrial ecosystems respond to these factors by changes in production and allocation, but also by decline and mortality. In addition, competition and species composition change along with biogeochemical processes.
- These changes in terrestrial ecosystems have profound feedbacks to neighbouring ecosystems and the atmosphere. These include changes in the rate of respiration, but they also affect other GHG emissions. Evapotranspiration as well as changes in albedo have profound effects on the energy budgets of the Earth's surface.
- The establishment of net GHG budgets is a grand task for science in order to ascertain that major processes that may affect climate are not overlooked. Despite its high ecosystem production, Europe is about C neutral due to its high emissions of CH_4 and N_2O. Mitigation of climate change is expected from the use of biomass for bioenergy and bioeconomy, which will replace fossil fuel–based products.
- Global change has resulted in major changes in biodiversity and the provisioning of ecosystem services. Biodiversity hotspots and genetic diversity centres are under threat. It is expected that with further LUC, these effects will increase in the future. One solution being discussed is the use of high yielding crops and forest species to alleviate the pressure placed on natural systems.
- Global agreements, such as the Convention on Biological Diversity (UNCBD), the Framework Convention on Climate Change (UNFCCC) and the Convention to Combat Desertification (UNCBD), have been negotiated internationally to address these problems. Although the pressures are high, progress remains rather slow. Major achievements are the Aichi Targets (UNCBD) and the Paris Agreement (UNFCCC).

References

Allen CD, Breshhears DD, McDowell NG (2015) On understanding of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. Ecosphere 6:129

Anthony RG, Waldin TR, Ray JA, Bright SW, Hussea BP (1998) Herbicide resistance caused by spontaneous mutation of the cytoskeletal protein tubulin. Nature 393:260–263

Asner GP, Levick SR, Kennedy-Bowdoin T, Knapp DE, Emerson R, Jacobson J, Colgan MS, Martin RE (2009) Large-scale impacts of herbivores on the structural diversity of African savannas. Proc Natl Acad Sci 106:4947–4952

Bala G, Caldeira K, Wickett M, Phillips TJ, Lobell DB, Delire C, Mirin A (2007) Combined climate and carbon-cycle effects of large-scale deforestation. Proc Natl Acad Sci 104:6550–6553

Balter M, Gibbons A (2000) A glimpse of human's first journey out of Africa. Science 288:948–950

Bellard C, Bertelsmeier C, Leadley P, Thuiller W, Courchamp F (2012) Impacts of climate change on the future of biodiversity. Ecol Lett 15:365–377

Bernhardt ES (2013) Cleaner lakes are dirtier lakes. Science 342:205–206

Bonan GB (2008) Forests and climate change: forcing, feedbacks, and the climate benefits of forests. Science 320:1444–1449

Bonan GB, Pollard D, Thompson SL (1992) Effects of boreal forest vegetation on global climate. Nature 359:716–718

Butchart SHM, Walpole M, Collen B, van Strien A, Scharlemann JPW, Almond REA, Baillie JEM, Bomhard B, Brown C, Bruno J, Carpenter KE, Carr GM, Chanson J, Chenery AM, Csirke J, Davidson NC, Dentener F, Foster M, Galli A, Galloway JN, Genovesi P, Gregory RD, Hockings M, Kapos V, Lamarque JF, Leverington F, Loh J, McGeoch MA, McRae L, Minasyan A, Hernández Morcillo M, Oldfield TEE, Pauly D, Quader S, Revenga C, Sauer JR, Skolnik B, Spear D, Stanwell-Smith D, Stuart SN, Symes A, Tierney M, Tyrrell TD, Vié JC, Watson R (2010) Global biodiversity: indicators of recent declines. Science 328:1164–1168

Canadell JG, Schulze ED (2014) Global potential of biospheric carbon management for climate mitigation. Nat Commun 5:5282

Ciais P, Reichstein M, Viovy N, Granier A, Ogee J, Allard V, Aubinet M, Buchmann N, Bernhofer C, Carrara A, Chevallier F, Noblet N, Friend AD, Friedlingstein P, Grünwald T, Heinesch B, Keronen P, Knohl A, Krinner G, Loustau D, Manca G, Matteucci G, Miglietta F, Ourcival JM, Papale D, Pilegaard K, Rambal S, Seufert G, Soussana J-F, Sanz MJ, Schulze E-D, Vesala T, Valentini R (2005) Europe-wide reduction in primary productivity caused by the heat and drought in 2003. Nature 437:529–533

Cincotta RP, Wisnewski J, Engelmann R (2000) Human populations in the biodiversity hotspots. Nature 404:990–992

Crutzen PJ (2002) Geology of mankind: the Anthropocene. Nature 415:23

Ellis EC, Kaplan JO, Fuller DQ, Vavrus S, Klein Goldewijk K, Verburg PH (2013) Used planet: a global history. Proc Natl Acad Sci 110:7978–7985

European Environmental Agency, EEA (2017) Climate change, impacts and vulnerability in Europe 2016. EEA, Copenhagen

FAO, Food and Agriculture Organization (2013) FAO Statistical Yearbook 2013: World food and agriculture. FAO, Rome

FAO, Food and Agriculture Organization (2015) Global forest resources. Assessment 2015. FAO, Rome

Finlay JC, Small GE, Sterner RW (2013) Human influences on nitrogen removal in lakes. Science 342:247–250

Frank DC, Esper J, Raible CC, Büntgen U, Trouet V, Stocker B, Joos F (2010) Ensemble reconstruction constraints on the global carbon cycle sensitivity to climate. Nature 463:527–532

Fu YH, Zhao H, Piao S, Peaucelle M, Peng S, Zhou G, Ciais P, Huang M, Menzel A, Penuelas J, Song Y, Vitasse Y, Zeng Z, Lanssens IA (2015) Declining global warming effects on the phenology of spring leaf unfolding. Nature 526:104–107

Gibbons A (2001) The riddle of coexistence. Science 291:1725–1172

Gigon A, Langenauer R, Meier C, Nievergelt B (1998) Blaue Listen der erfolgreich erhaltenen oder geförderten Tier- und Pflanzenarten der Roten Listen, Methodik und Anwendung in der nördlichen Schweiz, vol 129. Veröff. Geobot. Inst. ETH, Stiftung Rübel, Zürich

Gonsamo A, D'Odorico P, Chen JM, Wu C, Buchmann N (2017) Changes in vegetation phenology are not reflected in atmospheric CO_2 and $^{13}C/^{12}C$ seasonality. Glob Change Biol 23(10):4029–4044

Haberl H, Körner CH, Lauk CH, Schmid-Staiger U, Smetacek V, Schulze ED, Thauer R, Weiland P, Wilson K (2012) The availability and sustainability of biomass as an energy source. In: Leopoldina statement: bioenergy – chances and limits, pp 9–42

Hansen MC, Potapov PV, Moore R, Hancher M, Turubanova SA, Tyukavina A, Thau D, Stehman SV, Goetz SJ, Loveland TR, Kommareddy A, Egorov A, Chini L, Justice CO, Townshend JRG (2013) High-resolution global maps of 21st-century forest cover change. Science 342:850–853

Harcourt AH (2016) Human phylogeography and diversity. Proc Natl Acad Sci 113:8072–8078

Heimann H (1997) A review of the contemporary global carbon cycle and as seen a century ago by Arrhenius and Högbom. Ambio 26:17–24

Hobbs RJ, Higgs E, Harris JA (2009) Novel ecosystems: implications for conservation and restoration. Trends Ecol Evol 24:599–605

Houghton RA, Hackler JL, Lawrence KT (1999) The US carbon budget: contributions from land use change. Science 285:574–578

IPCC (1996) Climate change 1995. In: Second assessment report. Cambridge University Press, Cambridge

IPCC (2013) Climate change 2013. In: The physical science basis. Cambridge University Press, Cambridge

Keeling RF, Piper SC, Heimann M (1996) Global and hemispheric CO_2 sinks deduced from changes in atmospheric O_2 concentration. Nature 381:218–221

Kirschke S, Bousquet P, Ciais P, Saunois M, Canadell JG, Dlugokencky EJ, Bergamaschi P, Bergmann D, Blake DR, Bruhwiler L, Cameron-Smith P, Castaldi S, Chevallier F, Feng L, Fraser A, Heimann M, Hodson EL, Houweling S, Josse B, Fraser PJ, Krummel PB, Lamarque J-F, Langenfelds RL, Le Quéré C, Naik V, O'Doherty S, Palmer PI, Pison I, Plummer D, Poulter B, Prinn RG, Rigby M, Ringeval B, Santini M, Schmidt M, Shindell DT, Simpson IJ, Spahni R, Steele LP, Strode SA, Sudo K, Szopa S, van der Werf GR, Voulgarakis A, van Weele M, Weiss RF, Williams JE, Zeng G (2013) Three decades of global methane sources and sinks. Nat Geosci 6:813–823

Klein AM, Vaissière BE, Cane JH, Steffan-Dewenter I, Cunningham SA, Kremen C, Tscharntke T (2007) Importance of pollinators in changing landscapes for world crops. Proc R Soc B Biol Sci 274:303–313

Klein Goldewijk K, Beusen A, Janssen P (2010) Long-term dynamic modeling of global population and built-up area in a spatially explicit way: HYDE 3.1. The Holocene 20:565–573

LaMarche VC, Graybill DA, Fritts HC, Rose MR (1984) Increasing atmospheric carbon dioxide: tree ring evidence for growth enhancement in natural vegetation. Science 225:1019–1021

Laurance WF, Laurance SG, Ferreira LV, Rankin-de Merona JM, Gascon C, Lovejoy TE (1997) Biomass collapse in Amazonian forest fragments. Science 278:1117–1118

Lehn H, Steiner M, Mohr H (1996) Wasser – die elementare Ressource. In: Leitlinien einer nachhaltigen Nutzung. Springer, Berlin

Le Quéré C, Andrew RM, Canadell JG, Sitch S, Korsbakken JI, Peters GP, Manning AC, Boden TA, Tans PP, Houghton RA, Keeling RF, Alin S, Andrews OD, Anthoni P, Barbero L, Bopp L, Chevallier F, Chini LP, Ciais P, Currie K, Delire C, Doney SC, Friedlingstein P, Gkritzalis T, Harris I, Hauck J, Haverd V, Hoppema M, Klein Goldewijk K, Jain AK, Kato E, Körtzinger A, Landschützer P, Lefèvre N, Lenton A, Lienert S, Lombardozzi D, Melton JR, Metzl N, Millero F, Monteiro PMS, Munro DR, Nabel JEMS, Nakaoka S, O'Brien K, Olsen A, Omar AM, Ono T, Pierrot D, Poulter B, Rödenbeck C, Salisbury J, Schuster U, Schwinger J, Séférian R, Skjelvan I, Stocker BD, Sutton AJ, Takahashi T, Tian H, Tilbrook B, van der Laan-Luijkx IT, van der Werf GR, Viovy N, Walker AP, Wiltshire AJ, Zaehle S (2016) Global carbon budget 2016. Earth Syst Sci Data 8:605–649

Levitus S, Antonov JI, Boyer TP, Stephens C (2000) Warming of the world's oceans. Science 287:225–229

Lewis SL, Maslin MA (2015) Defining the Anthropocene. Nature 519:171–180

Liang J, Crowther TW, Picard N, Wiser S, Zhou M, Alberti G, Schulze ED, McGuire AD, Bozzato F, Pretzsch H, de-Miguel S, Paquette A, Hérault B, Scherer-Lorenzen M, Barrett CB, Glick HB, Hengeveld GM, Nabuurs G-J, Pfautsch S, Viana H, Vibrans AC, Ammer C, Schall P, Verbyla D, Tchebakova N, Fischer M, Watson JV, Chen HYH, Lei X, Schelhaas M-J, Lu H, Gianelle D, Parfenova EI, Sala C, Lee E, Lee B, Seok Kim H, Bruelheide H, Coomes DA, Piotto D, Sunderland T, Schmid B, Gourlet-Fleury S, Sonké B, Tavani R, Zhu J, Brandl S, Vayreda J, Kitahara F, Searle EB, Neldner VJ, Ngugi MR, Baraloto C, Frizzera L, Bałazy R, Oleksyn J, Zawiła-Niedźwiecki T, Bouriaud O, Bussotti F, Finér L, Jaroszewicz B, Jucker T, Valladares F, Jagodzinski AM, Peri PL, Gonmadje C, Marthy W, O'Brien T, Martin EH, Marshall AR, Rovero F, Bitariho R, Niklaus PA, Alvarez-Loayza P, Chamuya N, Valencia R, Mortier F, Wortel V, Engone-Obiang NL, Ferreira LV, Odeke DE, Vasquez RM, Lewis SL, Reich PB (2016) Positive biodiversity-productivity relationship predominant in global forests. Science 354:aaf8957

Lüthi D, Le Floch M, Bereiter B, Blunier T, Barnola JM, Siegenthaler U, Raynaud D, Jouzel J, Fischer H, Kawamura K, Stocker TF (2008) High-resolution carbon dioxide concentration record 650,000–800,000 years before present. Nature 453:379–382

Matson PA, Parton WJ, Power WJ, Swift MJ (1997) Agricultural intensification and ecosystem properties. Science 277:504–508

Maxwell S, Fuller RA, Brooks TM, Watson JEM (2016) The ravages of guns, nets and bulldozers. Nature 536:143–145

McCrackin ML, Elsener JJ (2010) Atmospheric nitrogen deposition influences denitrification and nitrous oxide production in lakes. Ecology 91:528–539

Mooney HA, Hobbs RJ (2000) Invasive species in a changing world. Island Press, Washington

Myers N, Mittermeier RA, Mittermeier CG, da Fonseca GAB, Kent J (2000) Biodiversity hotspots for conservation priorities. Nature 403:853–858

Nakicenovic N, Swart R (2000) IPCC special report on emission scenarios. Cambridge University Press, Cambridge

Nepstad DC, Verissimo A, Alencar A, Nobre C, Lima E, Lefebvre P, Schlesinger P, Potter C, Moutinho P, Mendoza E, Cochrane M, Brooks V (1999) Large-scale impoverishment of Amazonian forests by logging and fire. Nature 398:505–508

Norby RJ, Zak DR (2011) Ecological lessons from free-air CO_2 enrichment FACE experiments. Annu Rev Ecol Evol Syst 42:181–203

Paillet Y, Bergès L, Hjältèn J et al (2009) Biodiversity differences between managed and unmanaged forests: meta-analysis of species richness in Europe. Conserv Biol 24:101–112

Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. Nature 421:37–42

Pearce F (2015) The new wild: why invasive species will be Nature's salvation. Beacon Press, Boston

Peñuelas J, Rutishauser T, Filella I (2009) Phenology feedbacks on climate change. Science 324:887–888

Piao S, Ciais P, Friedlingstein P, Peylin P, Reichstein M, Luyssaert S, Margolis H, Fang J, Barr A, Chen A, Grelle A, Hollinger DY, Laurila T, Lindroth A, Richardson AD, Vesala T (2008) Net carbon dioxide losses of northern ecosystems in response to autumn warming. Nature 451:49–53

Potts SG, Biesmeijer JC, Kremen C, Neumann P, Schweiger O, Kunin WE (2010) Global pollinator declines: trends, impacts and drivers. Trends Ecol Evol 25:345–353

Prentice IC, Farquhar GD, Fasham MJR, Goulden ML, Heimann M, Jaramillo VJ, Kheshi HS, Le Quéré C, Scholes RJ, Wallace DWR (2001) The carbon cycle and atmospheric CO_2. In: IPCC-WG I third assessment report. Cambridge University Press, Cambridge

Reay DS, Davidson EA, Smith KA, Smith P, Melillo JM, Dentener R, Crutzen PJ (2012) Global agriculture and nitrous oxide emissions. Nat Clim Chang 2:410–416

Reid WV, Miller KR (1989) Keeping options alife: the scientific basis for conserving biodiversity. World Resource Institute, Washington

Richardson AD, Keenan TF, Migliavacca M, Ryu Y, Sonnentag O, Toomey M (2013) Climate change, phenology, and phenological control of vegetation feedbacks to the climate system. Agric For Meteorol 169:156–117

Sala OE, Chapin FS III, Armesto JJ, Berlow E, Bloomfield J, Dirzo R, Huber-Sanwald E, Huenneke LF, Jackson RB, Kinzig A, Leemans R, Lodge DM, Mooney HA, Oesterheld M, LeRoy PN, Sykes MT, Walker BH, Walker M, Wall DH (2010) Global biodiversity scenarios for the year 2100. Science 287:1770–1774

Schulze ED, Luyssaert S, Ciais P, Freibauer A, Janssens IA, Soussana JF, Smith P, Grace J, Levin I, Thiruchittampalam B, Heimann M, Dolman AJ, Valentini R, Bousquet P, Peylin P, Peters W, Rödenbeck C, Etiope G, Vuichard N, Wattenbach M, Nabuurs GJ, Poussi Z, Nieschulze J, Gash JH, CarboEurope Team (2009) Importance of methane and nitrous oxide for Europe's terrestrial greenhouse gas balance. Nat Geosci 2:842–850

Schulze ED, Bouriaud O, Wäldchen J, Eisenhauer N, Walentowski H, Seele C, Heinze E, Pruschitzki U, Dănilă G, Marin G, Hessenmöller D, Bouriaud L, Teodosiu M (2014) Ungulate browsing causes species loss in deciduous forests independent of community dynamics and silvicultural management in Central and Southeastern Europe. Ann For Res 57:267–288

Schulze ED, Körner CI, Law BE, Haberl H, Luyssaert S (2012) Large-scale bioenergy from additional harvest of forest biomass is neither sustainable nor greenhouse gas neutral. Glob Change Biol Bioenergy 4:611–616

Schwalm C, Williams C, Schaefer K, Arneth A, Bonal D, Buchmann N, Chen J, Law B, Lindroth A, Luyssaert S, Reichstein M, Richardson A (2010) Assimilation exceeds respiration sensitivity to drought: a FLUXNET synthesis. Glob Change Biol 16:657–670

Schwietzke S, Sherwood OA, Bruhwiler LM, Miller JB, Etiope G, Dlugokencky EJ, Michel SE, Arling VA, Vaughn BH, White JW, Tans PP (2016) Upward revision of global fossil fuel methane emissions based on isotope database. Nature 538:88–91

Secretariat of the Convention on Biological Diversity (2010) Global Biodiversity Outlook 3. Secretariat of the Convention on Biological Diversity, Montréal

Secretariat of the Convention on Biological Diversity (2014) Global Biodiversity Outlook 4. Secretariat of the Convention on Biological Diversity, Montréal

Seppälä R (2007) Global forest sector: trends, threats and opportunities. In: Freer-Smith PH, Broadmeadow MSJ, Lynch JM (eds) Forestry and climate change. CAB International, Wallingford. pp 25–30

Smith P, House JI, Bustamante M, Sobocka J, Harper R, Pan G, West PC, Calk JM, Adhya T, Rumpel C, Paustian K, Kuikman P, Cotrufo MF, Elliott JA, McDowell R, Griffiths RI, Asakawa S, Bondeau A, Jain AK, Meersmans J, Pugh TAM (2016) Global change pressures on soils from land use and management. Glob Change Biol 22:1008–1028

Sochor M, Vašut RJ, Sharbel TF, Trávníček B (2015) How just a few makes a lot: Speciation via reticulation and apomixis on example of European brambles (*Rubus* subgen. *rubus*, Rosaceae). Mol Phylogenet Evol 89:13–27

Sommer JH, Kreft H, Kier G, Jetz W, Mutke J, Barthlott W (2010) Projected impacts of climate change on regional capacities for global plant species richness. Proc R Soc B Biol Sci 277:2271–2280

SRREN (2011) Renewable energy sources and climate change mitigation. Special report of the intergovernmental panel on climate change. Cambridge University Press, Cambridge

Teuling AJ, Seneviratne SI, Stöckli R, Reichstein M, Moors E, Ciais P, Luyssaert S, van den Hurk B, Ammann C, Bernhofer C, Dellwik E, Gianelle D, Gielen B, Grünwald T, Klumpp K, Montagnani L, Moureaux C, Sottocornola M, Wohlfahrt G (2010) Contrasting response of European forest and grassland energy exchange to heatwaves. Nat Geosci 3:722–727

UNEP (2006) Africa's lakes: atlas of our changing environment. Nairobi, Kenya

United Nations (1992) Convention on biological diversity. United Nations

United Nations (1998) Kyoto protocol to the United Nations Framework Convention on Climate Change. UN Doc FCCC/CP/1997/7/Add.1, Dec. 10, 1997; 37 ILM 22

United Nations (2015) Paris agreement. United Nations

Vicca S, Luyssaert S, Penuelas J, Campioli M, Chapin FS III, Ciais P, Heinemeyer A, Högberg P, Kutsch WL, Law BE, Malhi Y, Papale D, Piao SL, Reichstein M, Schulze ED, Janssens IA (2012) Fertile forests produce biomass more efficiently. Ecol Lett 15:520–526

Vitousek PM, Mooney HA, Lubchenco J, Melillo JM (1997) Human domination of Earth ecosystems. Science 277:494–499

Watson RT, Noble IR, Bolin B, Ravindranath NH, Verardo DJ, Dokken DJ (eds) (2000) Land-use, land use change and forestry. Cambridge University Press, Cambridge

West PC, Gibbs HK, Monfreda C, Wagner J, Barford CC, Carpender SR, Foley JA (2010) Trading carbon for food: global comparison of carbon stocks vs crop yields on agricultural land. Proc Natl Acad Sci 107:19645–19648

Wild M, Ohmura A, Makowski K (2007) Impact of global dimming and brightening on global warming. Geophys Res Lett 34:L04702

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