1
Assumptions and Approaches

Introduction—History, Assumptions, and Approaches

1. What Is Ecophysiology?

Plant ecophysiology is an experimental science that seeks to describe the **physiological mechanisms** underlying ecological observations. In other words, ecophysiologists, or physiological ecologists, address ecological questions about the controls over the growth, reproduction, survival, abundance, and geographical distribution of plants, as these processes are affected by interactions of plants with their physical, chemical, and biotic environment. These ecophysiological patterns and mechanisms can help us understand the functional significance of specific plant traits and their evolutionary heritage.

The questions addressed by ecophysiologists are derived from a higher level of integration, i.e., from "ecology" in its broadest sense, including questions originating from agriculture, horticulture, forestry, and environmental sciences. However, the ecophysiological explanations often require mechanistic understanding at a lower level of integration (physiology, biochemistry, biophysics, molecular biology). It is, therefore, quintessential for an ecophysiologist to have an appreciation of both ecological questions and biophysical, biochemical, and molecular methods and processes. In addition, many societal issues, often pertaining to agriculture, environmental change, or nature conservation, benefit from an ecophysiological perspective. A modern ecophysiologist thus requires a good understanding of both the molecular aspects of plant processes and the functioning of the intact plant in its environmental context.

2. The Roots of Ecophysiology

Plant ecophysiology aims to provide causal, mechanistic explanations for ecological questions relating to survival, distribution, abundance, and interactions of plants with other organisms. Why does a particular species live where it does? How does it manage to grow there successfully, and why is it absent from other environments? These questions were initially asked by geographers who described the global distributions of plants (Schimper 1898, Walter 1974). They observed consistent patterns of morphology associated with different environments and concluded that these differences in morphology must be important in explaining plant distributions. Geographers, who know climatic patterns, could therefore predict the predominant life forms of plants (Holdridge 1947). For example, many desert plants have small, thick leaves that minimize the heat load and danger of overheating in hot environments, whereas shade plants often have large, thin leaves that maximize light interception. These observations of morphology provided the impetus to investigate the physiological traits of plants from contrasting physical environments (Blackman 1919, Pearsall 1938, Ellenberg 1953, Larcher 1976).

H. Lambers et al., *Plant Physiological Ecology*, Second edition, DOI: 10.1007/978-0-387-78341-3_1,

Although ecophysiologists initially emphasized physiological responses to the abiotic environment [e.g., to calcareous vs. acidic substrates (Clarkson 1966) or dry vs. flooded soils (Crawford 1978)], physiological interactions with other plants, animals, and microorganisms also benefit from an understanding of ecophysiology. As such, ecophysiology is an essential element of every ecologist's training.

A second impetus for the development of ecophysiology came from agriculture and physiology. Even today, agricultural production in industrialized nations is limited to 25% of its potential by drought, infertile soils, and other environmental stresses (Boyer 1985). A major objective of agricultural research has always been to develop crops that are less sensitive to environmental stress so they can withstand periods of unfavorable weather or be grown in less favorable habitats. For this reason agronomists and physiologists have studied the mechanisms by which plants respond to or resist environmental stresses. Because some plants grow naturally in extremely infertile, dry, or salty environments, ecophysiologists were curious to know the mechanisms by which this is accomplished.

Plant ecophysiology is the study of physiological responses to the environment. The field developed rapidly as a relatively unexplored interface between ecology and physiology. Ecology provided the questions, and physiology provided the tools to determine the mechanism. Techniques that measured the microenvironment of plants, their water relations, and their patterns of carbon exchange became typical tools of the trade in plant ecophysiology. With time, these studies have explored the mechanisms of physiological adaptation at ever finer levels of detail, from the level of the whole plant to its biochemical and molecular bases. For example, initially plant growth was described in terms of changes in plant mass. Development of portable equipment for measuring leaf gas exchange enabled ecologists to measure rates of carbon gain and loss by individual leaves (Reich et al. 1997). Growth analyses documented carbon and nutrient allocation to roots and leaves and rates of production and death of individual tissues. These processes together provide a more thorough explanation for differences in plant growth in different environments (Mooney 1972, Lambers & Poorter 1992). Studies of plant water relations and mineral nutrition provide additional insight into controls over rates of carbon exchange and tissue turnover. More recently, we have learned many details about the biochemical basis of photosynthesis and respiration in different environments and, finally, about the molecular basis for differences in key photosynthetic and respiratory proteins. This mainstream of ecophysiology has been highly successful in explaining why plants are able to grow where they do.

3. Physiological Ecology and the Distribution of Organisms

Although there are 270000 species of land plants (Hammond 1995), a series of **filters** eliminates most of these species from any given site and restricts the actual vegetation to a relatively small number of species (Fig. 1). Many species are absent from a given plant community for **historical reasons**. They may have evolved in a different region and never dispersed to the site under consideration. For example, the tropical alpine of South America has few species in common with the tropical alpine of Africa, despite similar environmental conditions, whereas eastern Russia and Alaska have very similar species composition because of extensive migration of species across a land bridge connecting these regions when Pleistocene glaciations lowered sea level 20000–100000 years ago.

Of those species that arrive at a site, many lack the appropriate physiological traits to survive the physical environment. For example, whalers inadvertently brought seeds of many weedy species to Svalbard, north of Norway, and to Barrow, in northern Alaska. However, in contrast to most temperate regions, there are currently no exotic weed species in these northern sites (Billings 1973). Clearly, the **physical environment** has filtered out many species that may have arrived but lacked the physiological traits to grow, survive, and reproduce in the Arctic.

Biotic interactions exert an additional filter that eliminates many species that may have arrived and are capable of surviving the physical environment. Most plant species that are transported to different continents as ornamental or food crops never spread beyond the areas where they were planted because they cannot compete with native species (a biotic filter). Sometimes, however, a plant species that is introduced to a new place without the diseases or herbivores that restricted its distribution in its native habitat becomes an aggressive invader, for example, *Opuntia ficus-indica* (prickly pear) in Australia, *Solidago canadensis* (golden rod) in Europe, *Cytisus scoparius* (Scotch broom) in North America, and *Acacia cyclops* (red-eyed wattle) and *A. saligna* (orange wattle) in South Africa. Because of biotic interactions, the actual distribution of a species (realized niche, as determined by **ecological amplitude**) is more restricted than the range of conditions

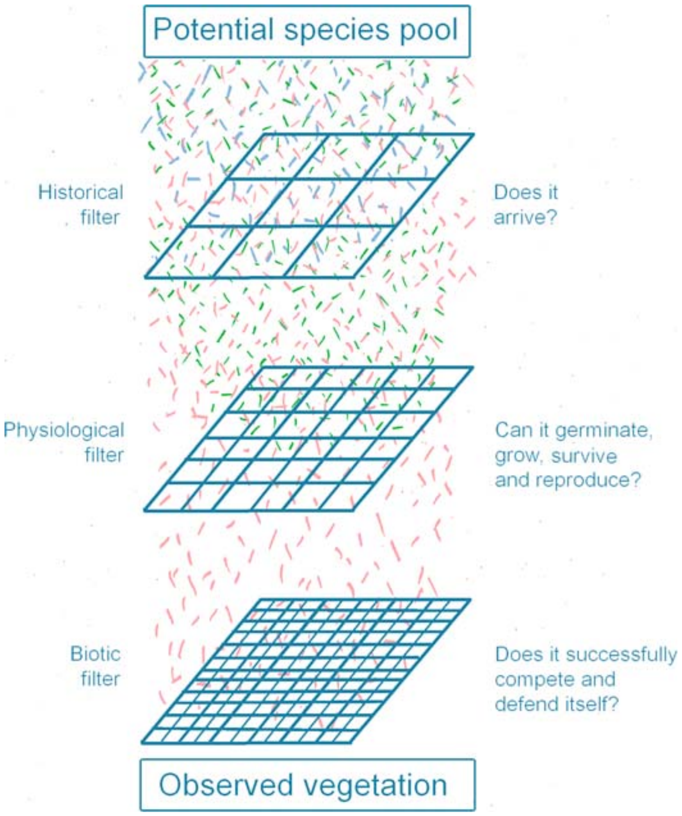

Figure 1. Historical, physiological, and biotic filters that determine the species composition of vegetation at a particular site.

where it can grow and reproduce (its fundamental niche, as determined by **physiological amplitude**) (Fig. 2).

Historical, physiological, and biotic filters are constantly changing and interacting. Human and natural introductions or extinctions of species, chance dispersal events, and extreme events such as volcanic eruptions or floods change the species pool present at a site. Changes in climate, weathering of soils, and introduction or extinction of species change the physical and biotic environment. Those plant species that can grow and reproduce under the new conditions or respond evolutionarily so that their physiology provides a better match to this environment will persist. Because of these interacting filters, the species present at a site are simply those that arrived and survived. There is no reason to assume that the species present at a site attain their maximal physiologically possible rates of growth and reproduction (Vrba & Gould 1986). In fact, controlled-environment studies typically demonstrate that a given species is most common under environmental conditions that are distinctly suboptimal for most physiological processes because biotic interactions prevent most species from occupying the most favorable habitats (Fig. 2).

Given the general principle that species that are present at any site reflect their arrival and survival, why does plant species diversity differ among sites that differ in soil fertility? Typically, this diversity increases with decreasing soil fertility, up to a maximum, and then declines again (Grime 1979, Huston 1994). To answer this question, we need detailed ecophysiological information on the various mechanisms that allow plants to compete and coexist in different environments. The information that is required will depend on which ecosystem is studied. In biodiverse (i.e., species-rich), nutrient-poor, tropical rainforests, with a wide variation in light climate, plant traits that enhance the conversion of light into biomass or conserve carbon are likely to be important for an understanding of plant diversity. In the biodiverse, nutrient-impoverished sandplains of South Africa and Australia, however, variation in root traits that are associated with nutrient acquisition offers clues to understanding plant species diversity.

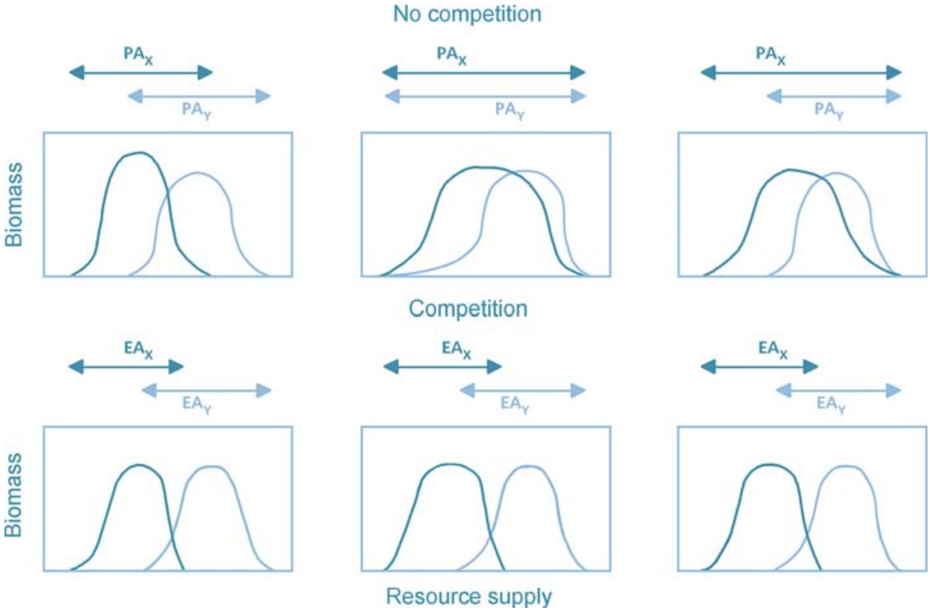

Figure 2. Biomass production of two hypothetical species (x and y) as a function of resource supply. In the absence of competition (*upper panels*), the physiological amplitude of species x and y (PA$_x$ and PA$_y$, respectively) defines the range of conditions over which each species can grow. In the presence of competition (*lower panels*), plants grow over a smaller range of conditions (their ecological amplitude, EA$_x$ and EA$_y$) that is constrained by competition from other species. A given pattern of species distribution (e.g., that shown in the bottom panels) can result from species that differ in their maximum biomass achieved (*left-hand* pair of graphs), shape of resource response curve (*center* pair of graphs), or physiological amplitude (*right-hand* pair of graphs). Adapted from Walter (1973).

4. Time Scale of Plant Response to Environment

We define **stress** as an environmental factor that reduces the rate of some physiological process (e.g., growth or photosynthesis) below the maximum rate that the plant could otherwise sustain. Stresses can be generated by abiotic and/or biotic processes. Examples of stress include low nitrogen availability, heavy metals, high salinity, and shading by neighboring plants. The immediate response of the plant to stress is a reduction in performance (Fig. 3). Plants compensate for the detrimental effects of stress through many mechanisms that operate over different time scales, depending on the nature of the stress and the physiological processes that are affected. Together, these compensatory responses enable the plant to maintain a relatively constant rate of physiological processes despite occurrence of stresses that periodically reduce performance. If a plant is going to be successful in a stressful environment, then there must be some degree of stress **resistance**. Mechanisms of stress resistance differ widely among species. They range from **avoidance** of the stress, e.g., in deep-rooting species growing in a low-rainfall area, to stress **tolerance**, e.g., in Mediterranean species that can cope with a low leaf water content.

Physiological processes differ in their sensitivity to stress. The most meaningful physiological processes to consider are growth and reproduction, which integrate the stress effects on fine-scale physiological processes as they relate to fitness, i.e., differential survival and reproduction in a competitive environment. To understand the mechanism of plant response, however, we must consider the response of individual processes at a finer scale (e.g., the response of photosynthesis or of light-harvesting pigments to a change in light intensity). We recognize at least three distinct time scales of plant response to stress:

1. The **stress response** is the immediate detrimental effect of a stress on a plant process. This generally occurs over a time scale of seconds to days, resulting in a decline in performance of the process.

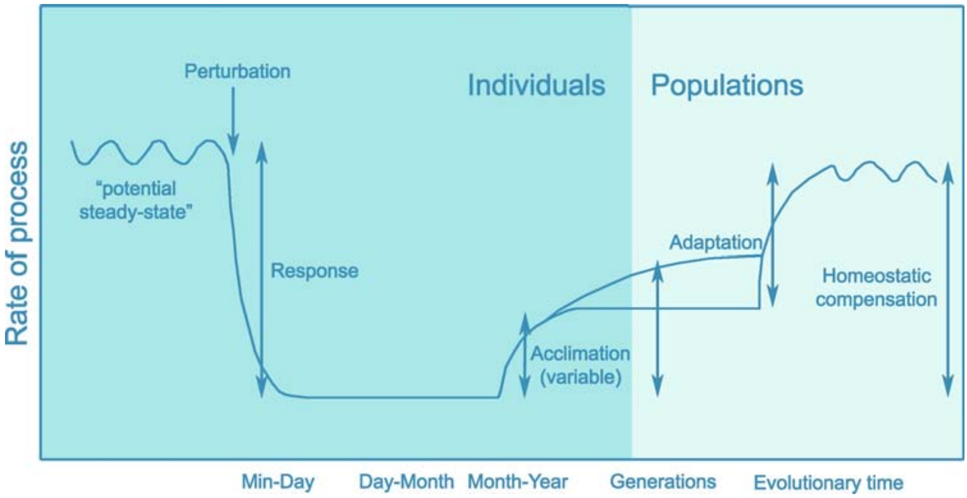

FIGURE 3. Typical time course of plant response to environmental stress. The immediate response to environmental stress is a reduction in physiological activity. Through *acclimation*, individual plants compensate for this stress such that activity returns toward the control level. Over evolutionary time, populations *adapt* to environmental stress, resulting in a further increase in activity level toward that of the unstressed unadapted plant. The total increase in activity resulting from acclimation and adaptation is the in situ activity observed in natural populations and represents the total homeostatic compensation in response to environmental stress.

2. **Acclimation** is the morphological and physiological adjustment by individual plants to compensate for the decline in performance following the initial stress response. Acclimation occurs in response to environmental change through changes in the activity or synthesis of new biochemical constituents such as enzymes, often associated with the production of new tissue. These biochemical changes then initiate a cascade of effects that are observed at other levels, such as changes in rate or environmental sensitivity of a specific process (e.g., photosynthesis), growth rate of whole plants, and morphology of organs or the entire plant. Acclimation to stress always occurs within the lifetime of an individual, usually within days to weeks. Acclimation can be demonstrated by comparing genetically similar plants that are growing in different environments.
3. **Adaptation** is the evolutionary response resulting from genetic changes in populations that compensate for the decline in performance caused by stress. The physiological mechanisms of response are often similar to those of acclimation, because both require changes in the activity or synthesis of biochemical constituents and cause changes in rates of individual physiological processes, growth rate, and morphology. In fact, adaptation may alter the potential of plants to acclimate to short-term environmental variation. Adaptation, as we define it, differs from acclimation in that it requires genetic changes in populations and therefore typically requires many generations to occur. We can study adaptation by comparing genetically distinct plants grown in a common environment.

Not all genetic differences among populations reflect adaptation. Evolutionary biologists have often criticized ecophysiologists for promoting the "Panglossian paradigm", i.e., the idea that just because a species exhibits certain traits in a particular environment, these traits must be beneficial and must have resulted from natural selection in that environment (Gould & Lewontin 1979). Plants may differ genetically because their ancestral species or populations were genetically distinct before they arrived in the habitat we are studying or other historical reasons may be responsible for the existence of the present genome. Such differences are not necessarily adaptive.

There are at least two additional processes that can cause particular traits to be associated with a given environment:

1. Through the quirks of history, the ancestral species or population that arrived at the site may

have been pre-adapted, i.e., exhibited traits that allowed continued persistence in these conditions. Natural selection for these traits may have occurred under very different environmental circumstances. For example, the tree species that currently occupy the mixed deciduous forests of Europe and North America were associated with very different species and environments during the Pleistocene, 100000 years ago. They co-occur now because they migrated to the same place some time in the past (the **historical filter**), can grow and reproduce under current environmental conditions (the **physiological filter**), and outcompeted other potential species in these communities and successfully defended themselves against past and present herbivores and pathogens (the **biotic filter**).

2. Once species arrive in a given geographic region, their distribution is fine-tuned by ecological sorting, in which each species tends to occupy those habitats where it most effectively competes with other plants and defends itself against natural enemies (Vrba & Gould 1986).

5. Conceptual and Experimental Approaches

Documentation of the correlation between plant traits and environmental conditions is the raw material for many ecophysiological questions. Plants in the high alpine of Africa are strikingly similar in morphology and physiology to those of the alpine of tropical South America and New Guinea, despite very different phylogenetic histories. The similarity of physiology and morphology of shrubs from Mediterranean regions of western parts of Spain, South Africa, Chile, Australia, and the United States suggests that the distinct floras of these regions have undergone **convergent evolution** in response to similar climatic regimes (Mooney & Dunn 1970). For example, evergreen shrubs are common in each of these regions. These shrubs have small, thick leaves, which continue to photosynthesize under conditions of low water availability during the warm, dry summers characteristic of Mediterranean climates. The shrubs of all Mediterranean regions effectively retain nutrients when leaves are shed, a trait that could be important on infertile soils, and often resprout after fire, which occurs commonly in these regions. Documentation of a correlation of traits with environment, however, can never determine the relative importance of adaptation to these conditions and other factors such as pre-adaptation of the ancestral floras and ecological sorting of ancestral species into appropriate habitats. Moreover, traits that are measured under field conditions reflect the combined effects of differences in magnitude and types of environmental stresses, genetic differences among populations in stress response, and acclimation of individuals to stress. Thus, documentation of correlations between physiology and environment in the field provides a basis for interesting ecophysiological hypotheses, but these hypotheses can rarely be tested without complementary approaches such as growth experiments or phylogenetic analyses.

Growth experiments allow one to separate the effects of **acclimation** by individuals and genetic differences among populations. Acclimation can be documented by measuring the physiology of genetically similar plants grown under different environmental conditions. Such experiments show, for example, that plants grown at low temperature generally have a lower optimum temperature for photosynthesis than warm-grown plants (Billings et al. 1971). By growing plants collected from alpine and low-elevation habitats under the same environmental conditions, we can demonstrate genetic differences: with the alpine plant generally having a lower temperature optimum for photosynthesis than the low-elevation population. Thus, many alpine plants photosynthesize just as rapidly as their low-elevation counterparts, due to both acclimation and **adaptation**. Controlled-environment experiments are an important complement to field observations. Conversely, field observations and experiments provide a context for interpreting the significance of laboratory experiments.

Both acclimation and adaptation reflect complex changes in many plant traits, making it difficult to evaluate the importance of changes in any particular trait. Ecological modeling and molecular modification of specific traits are two approaches to explore the ecological significance of specific traits. Ecological models can range from simple empirical relationships (e.g., the temperature response of photosynthesis) to complex mathematical models that incorporate many indirect effects, such as negative feedbacks of sugar accumulation to photosynthesis. A common assumption of these models is that there are both **costs** and **benefits** associated with a particular trait, such that no trait enables a plant to perform best in all environments (i.e., there are no “super-plants” or “Darwinian demons” that are superior in all components). That is presumably why there are so many interesting physiological differences among plants. These models seek to identify the conditions under which a particular trait allows superior performance or compare performance of two plants that differ in traits. The theme of **trade-offs** (i.e., the costs and benefits of particular traits) is one that will recur frequently in this book.

A second, more experimental approach to the question of optimality is **molecular modification** of the gene that encodes a trait, including the regulation of its expression. In this way we can explore the consequences of a change in photosynthetic capacity, sensitivity to a specific hormone, or response to shade. This molecular approach is an extension of comparative ecophysiological studies, in which plants from different environments that are as similar as possible except with respect to the trait of interest are grown in a common environment. Molecular modification of single genes allows evaluation of the physiological and ecological consequences of a trait, while holding constant the rest of the biology of the plants.

6. New Directions in Ecophysiology

Plant ecophysiology has several new and potentially important contributions to make to biology. The rapidly growing human population requires increasing supplies of food, fiber, and energy, at a time when the best agricultural land is already in production or being lost to urban development and land degradation. It is thus increasingly critical that we identify traits or suites of traits that maximize sustainable food and fiber production on both highly productive and less productive sites. The development of varieties that grow effectively with inadequate supplies of water and nutrients is particularly important in less developed countries that often lack the economic and transportation resources to support high-intensity agriculture. Molecular biology and traditional breeding programs provide the tools to develop new combinations of traits in plants, including GMOs (genetically modified organisms). Ecophysiology is perhaps the field that is best suited to determine the costs, benefits, and consequences of changes in these traits, as whole plants, including GMOs, interact with complex environments.

Past ecophysiological studies have described important physiological differences among plant species and have demonstrated many of the mechanisms by which plants can live where they occur. These same physiological processes, however, have important effects on the environment, shading the soil, removing nutrients that might otherwise be available to other plants or soil microorganisms, transporting water from the soil to the atmosphere, thus both drying the soil and increasing atmospheric moisture. These plant effects can be large and provide a mechanistic basis for understanding processes at larger scales, such as community, ecosystem, and climatic processes (Chapin 2003). For example, forests that differ only in species composition can differ substantially in productivity and rates of nutrient cycling. Simulation models suggest that species differences in stomatal conductance and rooting depth could significantly affect climate at regional and continental scales (Foley et al. 2003, Field et al. 2007). As human activities increasingly alter the species composition of large portions of the globe, it is critical that we understand the ecophysiological basis of community, ecosystem, and global processes.

7. The Structure of the Book

We assume that the reader already has a basic understanding of biochemical and physiological processes in plants. Chapters 2A–C in this book deal with the primary processes of carbon metabolism and transport. After introducing some biochemical and physiological aspects of photosynthesis (Chapter 2A), we discuss differences in photosynthetic traits among species and link these with the species' natural habitat. Trade-offs are discussed, like that between a high water-use efficiency and a high efficiency of nitrogen use in photosynthesis (Chapter 2A). In Chapter 2B we analyze carbon use in respiration and explore its significance for the plant's carbon balance in different species and environments. Species differences in the transport of photosynthates from the site of production to various sinks are discussed in Chapter 2C. For example, the phloem transport system in climbing plants involves an interesting trade-off between transport capacity and the risk of major damage to the system. A similar trade-off between capacity and safety is encountered in Chapter 3, which deals with plant water relations. Subsequently, the plant's energy balance (Chapter 4A) and the effects of radiation and temperature (Chapter 4B) are discussed. After these chapters that describe photosynthesis, water use, and energy balance in individual leaves and whole plants, we then scale the processes up to the level of an entire canopy, demonstrating that processes at the level of a canopy are not necessarily the sum of what happens in single leaves, due to the effects of the surrounding leaves (Chapter 5). Chapter 6 discusses mineral nutrition and the numerous ways in which plants cope with soils with low nutrient availability or toxic metal concentrations (e.g., sodium, aluminum, heavy metals). These first chapters emphasize those aspects that help us to analyze ecological problems. Moreover, they provide a sound basis for later chapters in the book that deal with a higher level of integration.

The following chapters deal with patterns of growth and allocation (Chapter 7), life-history traits (Chapter 8), and interactions of individual plants with other organisms: symbiotic microorganisms (Chapter 9A); ecological biochemistry, discussing allelopathy and defense against herbivores (Chapter 9B); microbial pathogens (Chapter 9C); parasitic plants (Chapter 9D); interactions among plants in communities (Chapter 9E); and animals used as prey by carnivorous plants (Chapter 9F). These chapters build on information provided in the initial chapters.

The final chapters deal with ecophysiological traits that affect decomposition of plant material in contrasting environments (Chapter 10A) and with the role of plants in ecosystem and global processes (Chapter 10B). Many topics in the first two series of chapters are again addressed in this broader context. For example, allocation patterns and defense compounds affect decomposition. Photosynthetic pathways and allocation patterns affect to what extent plant growth is enhanced at elevated levels of carbon dioxide in the atmosphere.

Throughout the text, "boxes" are used to elaborate on specific problems, without cluttering up the text. They are meant for students seeking a deeper understanding of problems discussed in the main text. A glossary provides quick access to the meaning of technical terms used in both this book and the plant ecophysiological literature. The references at the end of each chapter are an entry point to relevant literature in the field. We emphasize review papers that provide broad syntheses but also include key experimental papers in rapidly developing areas ("the cutting edge"). In general, this book aims at students who are already familiar with basic principles in ecology, physiology, and biochemistry. It should provide an invaluable text for both undergraduates and postgraduates and a reference for professionals.

References

Billings, W.D. 1973. Arctic and alpine vegetation: Similarities, differences, and susceptibility to disturbance. *BioScience* **23**: 697–704.

Billings, W.D., Godfrey, P.J., Chabot, B.F., & Bourque, D.P. 1971. Metabolic acclimation to temperature in arctic and alpine ecotypes of *Oxyria digyna*. *Arc. Alp. Res.* **3**: 277–289.

Blackman, V.H. 1919. The compound interest law and plant growth. *Ann. Bot.* **33**: 353–360.

Boyer, J.S. 1985. Water transport. *Annu. Rev. Plant Physiol.* **36**: 473–516.

Chapin III, F.S., 2003. Effects of plant traits on ecosystem and regional processes: A conceptual framework for predicting the consequences of global change. *Ann. Bot.* **91**: 455–463.

Clarkson, D.T. 1966. Aluminium tolerance in species within the genus *Agrostis*. *J. Ecol.* **54**: 167–178.

Crawford, R.M.M. 1978. Biochemical and ecological similarities in marsh plants and diving animals. *Naturwissenschaften* **65**: 194–201.

Ellenberg, H. 1953. Physiologisches und ökologisches Verhalten derselben Pflanzanarten. *Ber. Deutsch. Bot. Ges.* **65**: 351–361.

Field, C.B., Lobell, D.B., Peters, H.A., & Chiariello, N.R. 2007. Feedbacks of terrestrial ecosystems to climate change. *Annu. Rev. Env. Res.* **32**: 1–29.

Foley, J.A., Costa, M.H., Delire, C., Ramankutty, N., & Snyder, P. 2003. Green surprise? How terrestrial ecosystems could affect earth's climate. *Front. Ecol. Environ.* **1**: 38–44.

Gould, S.J. & Lewontin, R.C. 1979. The spandrels of San Marco and the Panglossian paradigm: A critique of the adaptationists programme. *Proc. R. Soc. Lond. B.* **205**: 581–598.

Grime, J.P. 1979. Plant strategies and vegetation processes. Wiley, Chichester.

Hammond, P.M. 1995. The current magnitude of biodiversity. In: Global biodiversity assessment, V.H. Heywood (ed.). Cambridge University Press, Cambridge, pp. 113–138.

Holdridge, L.R. 1947. Determination of world plant formations from simple climatic data. *Science* **105**: 367–368.

Huston, M.A. 1994. Biological diversity. Cambridge University Press, Cambridge.

Lambers, H. & Poorter, H. 1992. Inherent variation in growth rate between higher plants: A search for physiological causes and ecological consequences. *Adv. Ecol. Res.* **22**: 187–261.

Larcher, W. 1976. Ökologie der Pflanzen. Ulmer, Stuttgart.

Mooney, H.A. 1972. The carbon balance of plants. *Annu. Rev. Ecol. Syst.* **3**: 315–346.

Mooney, H.A. & Dunn, E.L. 1970. Convergent evolution of Mediterranean-climate sclerophyll shrubs. *Evolution* **24**: 292–303.

Pearsall, W.H. 1938. The soil complex in relation to plant communities. *J. Ecol.* **26**: 180–193.

Reich, P.B., Walters, M.B., & Ellsworth, D.S. 1997. From tropics to tundra: Global convergence in plant functioning. *Proc. Natl. Acad. Sci.* **94**: 13730–13734.

Schimper, A.F.W. 1898. Pflanzengeographie und physiologische Grundlage. Verlag von Gustav Fischer, Jena.

Vrba, E.S. & Gould, S.J. 1986. The hierarchical expansion of sorting and selection: Sorting and selection cannot be equated. *Paleobiology* **12**: 217–228.

Walter, H. 1973. Die Vegetation der Erde in ökophysiologischer Betrachtung. 3rd ed. Gutsav Fisher Verlag, Jena.

Walter, H. 1974. Die Vegetation der Erde. Gustav Fisher Verlag, Jena.