9E. Interactions Among Plants

1. Introduction

In previous chapters we dealt with many physical and chemical environmental factors that affect a plant's performance, and with the effects of microsymbionts, herbivores, pathogens, and parasites. For many plants, however, the most important factor shaping their environment is other plants. One of the most active debates in both ecology and agriculture focuses on the question of the mechanisms by which plants interact with one another. Plant–plant interactions range from positive (**facilitation**) to neutral to negative (**competition**) effects on the performance of neighbors (Bazzaz 1996, Li et al. 1999). Competition occurs most commonly when plants utilize the same pool of growth-limiting resources (**resource competition**). Competition may also occur when one individual produces chemicals that negatively affect their neighbors (**interference competition** or **allelopathy**). Competition between two individuals is often highly asymmetric, with one individual having much greater negative impact than the other.

The question of which species wins in competition also depends strongly on the time scale of study. Short-term outcomes of competition often depend on rates of resource acquisition and growth, whereas equilibrium persistence of a species in a community is affected by rates of resource acquisition, tolerance of ambient resource availability, efficiency of converting acquired resources into biomass, and retention of acquired resources (Goldberg 1990). Rare events, e.g., a severe drought, flood, fire, or frost, once in a decade, may be more important for the outcome of competition than mean conditions.

The **competitive ability** of a species depends on environment. There are no "super species" that are competitively superior in all environments; rather, there are **trade-offs** among traits that are beneficial in some environments, but which reduce competitive ability in other environments. For a plant to compete successfully in a particular environment, it must have specific ecophysiological traits that allow effective growth in that environment (the **physiological filter** discussed in Sect. 3 of Chapter 1 on assumptions and approaches). An extreme cold temperature represents an absolute boundary for survival of some *Rhododendron* species in a common garden experiment, whereas warm temperatures do not. These *Rhododendron* species may therefore survive **global warming** in situ because of high temperature tolerance, but temperature effects on reproduction are uncertain. There may also be a significant time lag between change in climate and transient species distribution which makes the effect of global warming on species distribution difficult to predict (Vetaas 2002).

We have provided many examples of physiological traits necessary for ecological success in dry, cold, hot, saline, flooded, or other harsh environments. Only those species that are adapted, or can acclimate to, such environmental conditions can survive, compete, and reproduce successfully in these environments. As the saying goes: "when the going gets tough, the tough get going". Other plants typically grow in more favorable conditions where abiotic stresses are moderate. Most species can survive in these conditions, but only a small proportion compete effectively (Sect. 3 of Chapter 1 on assumptions and approaches). We have already discussed many of the traits that enable plants to grow rapidly under these conditions. Although this brief introduction of "plant strategies" provides a context for the present discussion of ecophysiological traits that are important in competitive interactions, the situation is far more complicated (Box 9E.1). Traits that are important for **competitive success** at an early stage of succession may differ greatly from those that are pertinent in later stages. Similarly, plant characteristics that determine the outcome of competition in short-term experiments often differ from those that give a species a competitive edge in the long run (Sect. 4).

Box 9E.1
Plant Ecological Strategies

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Plant ecological strategy schemes arrange species in categories or along spectra, according to their ecological attributes. One aim is to express an understanding of the main opportunities and selective forces that shape the life histories, architectures, growth allocations, and physiologies of plants. Another is to describe vegetation in terms of a limited number of types, for practical convenience. A third is to position particular species within a wider comparative context.

Many schemes have been proposed. Some split up species on the basis of a single attribute thought to be important. For example Raunkiaer's life-form scheme is based on the location of the buds where regrowth arises after the unfavorable season of the year (Fig. 1). Other schemes have an overtly conceptual basis.

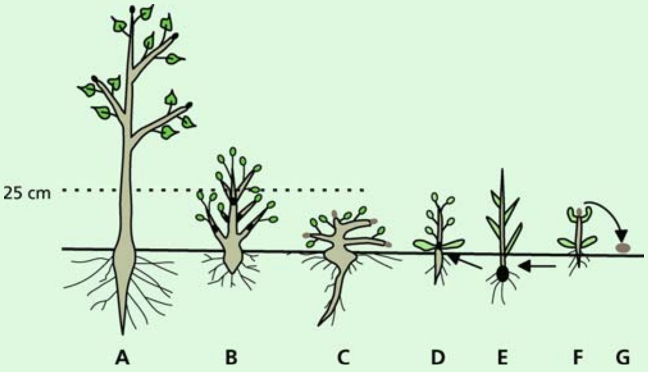

Figure 1. Plant life-forms of Raunkiaer (1907, English translation 1934). Perennating organs are shown in black, woody organs in pink, and deciduous organs green. (A) Phanerophyte (tree or tall shrub), with buds more than 25 cm above the ground. (B) Chamaephyte, semishrub, slightly woody at the base, with buds less than 25 cm above the ground. (C) Chamaephyte, semishrub, with buds less than 25 cm above the ground. (D) Hemicryptophyte, perennial herb with its bud at ground surface. (E) Geophyte, perennial herb with a bulb or other perennating organ below the ground surface. (F) Therophyte, annual plant surviving unfavorable periods only as seed. Barkman (1988) reviewed the wide range of life form and growth form systems.

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Box 9E.1 *Continued*

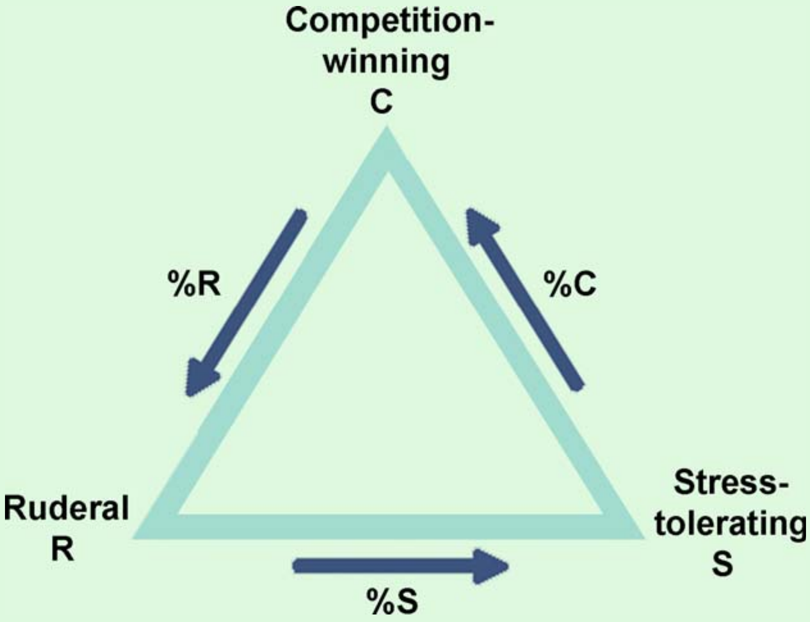

FIGURE 2. The C–S–R triangle model (Grime 1979). The strategies at the three corners are C, competition-winning species; S, stress-tolerating species; R, ruderal species. Particular species can engage in any mixture of these three primary strategies, and the mixture is described by their position within the triangle.

Grime's (1977) triangle (Fig. 2) (see also Sects. 6.1 and 6.3 of Chapter 7 on growth and allocation) is a two-dimensional scheme. A C–S axis (Competition-winning species to Stress-tolerating species) reflects adaptation to favorable vs. unfavorable sites for plant growth, and an R-axis (Ruderal species) reflects adaptation to disturbance.

Trait-Dimensions

A recent trend in plant strategy thinking has been trait-dimensions, that is, spectra of variation with respect to measurable traits. Compared with category schemes, such as Raunkiaer's, trait dimensions have the merit of capturing continuous variation in quantitative properties. Compared with the C–S–R scheme, trait dimensions have the advantage that the position of a species along the spectrum can be quantified straightforwardly and compared with other species worldwide. Trait-dimensions are a very active and open-ended research area (Westoby et al. 2002, McGill et al. 2006, Westoby & Wright 2006). Here I first summarize two dimensions that are quite well characterized and understood, then comment briefly on some other dimensions that are not yet so well understood.

Leaf Economics Spectrum

Five traits that are coordinated across species are leaf mass per area (LMA), leaf life-span, leaf N concentration, and potential photosynthesis and dark respiration on a mass basis. In the five-trait space, 79% of all variation worldwide lies along a single main axis (Fig. 33 of Chapter 2A on photosynthesis; Wright et al. 2004). Species with low LMA tend to have short leaf life-spans, high leaf nutrient concentrations, and high potential rates of mass-based photosynthesis. These species occur at the "quick-return" end of the leaf economics spectrum. The fast turnover of plant parts permits a more flexible response to the spatial patchiness of light and soil resources (Grime 1994). At the "slow-return" end of the spectrum are species with long leaf life-span, expensive leaf construction (high LMA), low nutrient concentrations, and lower photosynthetic rates.

continued

Box 9E.1 *Continued*

Seed-Size–Seed-Output Dimension

Species having smaller seeds can produce more seeds within a given mass devoted to reproduction. Seed mass varies 10^4- or 10^5-fold, even across co-existing species. It is therefore the strongest influence on seed output per square meter of canopy cover, and therefore on the chance that an occupied site will disperse a propagule to an establishment opportunity. Seed mass is also a good indicator of a cotyledon-stage seedling's ability to survive various hazards (Leishman et al. 2000, Westoby et al. 2002).

Some Other Dimensions

Canopy height at maturity is universally recognized as expressing important differences among species; height strategies also include the pace of height gain and the capacity of a stem to persist over time having reached a given height. The best traits to express these dimensions have not yet been clarified.

Leaf size is closely correlated with the size of terminal twigs and with branch spacing. It expresses scaling of the shoot architecture, but the ecological significance of leaf size remains poorly understood.

Sapwood density is potentially influenced by the proportion of the cross-section that is vessel lumen, and by the density of tissue outside lumens. Potential outcomes from low wood density therefore include higher hydraulic conductivity and capacitance, and faster shoot elongation from a given dry mass invested in stem. It is not yet clear whether there are one or more major dimensions of variation in wood properties.

Two species properties of high importance for plant geography and for modeling vegetation under global change are temperature preferences and the rooting depth from which water is extracted by transpiration. Up to now, however, no species traits have been found that capture these outcomes and that are readily measurable.

Plant Strategy Variation

Plant strategic traits are expected to vary consistently in relation to physical environment, e.g., mean seed mass is *ca.* 300-fold larger in the tropics than at 60° latitude (Moles et al. 2007). Nevertheless, it is striking that for the quantitative traits investigated so far, variation across species within a site is at least as important as variation across site averages worldwide. This means that plant strategy traits are as much about different styles of sustaining a population within sites, as they are about adaptation to physical environment.

The Future

Brisk progress is being made currently with plant strategy dimensions, especially because data for many traits are accumulating into worldwide datasets, giving a firm context for interpreting costs and benefits. At the same time, there remain many unresolved questions and a great deal of opportunity for future research.

In this text on physiological ecology we emphasize the physiological mechanisms rather than the community consequences of competition. An ecophysiologist attempts to explain competitive interactions in terms of the performance of individual plants that make up a community. The challenge then is to scale up from the knowledge that is available at the cell, organ, and whole-plant level to the processes that occur in natural and managed communities.

An important aspect of the functioning of a plant among surrounding competitors may well be to *avoid* potentially negative effects. That is, rather than producing leaves that are acclimated to shade, or roots that can access sparingly available nutrients, a plant might grow away from its neighbors and make leaves that are acclimated to a high level of irradiance and roots that can exploit a favorable nutrient supply. This requires mechanisms, however, that allow a plant to detect the proximity of its neighbors (Sect. 3).

2. Theories of Competitive Mechanisms

Several theoretical frameworks have been developed to predict the outcome of plant competition, each of which makes different assumptions about the mechanisms by which competition occurs. Grime (1977) suggested that species with high **relative growth rates** are effective competitors because rapid growth enables them to dominate available space and to acquire the most resources (Sect. 6.1 of Chapter 7 on growth and allocation). If correct, then traits that promote rapid resource acquisition and growth should be favored. On the other hand, Tilman (1988) suggested that the species that can draw a resource down to the lowest level (**R***) is the best competitor for that resource, because this enables a species to tap that resource at levels below those required by other species. These perspectives are not incompatible (Grace 1990). We expect that, in short-term growth experiments, especially in high-resource environments, traits that contribute to rapid growth contribute to competitive success. At equilibrium, however, especially in low-resource environments, when species effects on resource availability should be greatest, the potential of a species to extract scarce resources may be more important than maximum rates of resource acquisition.

If **resource competition** occurs by **depletion of a shared limiting resource**, then there are at least two ways in which a species might be an effective competitor: drawing down resources to a low level (low R*) and/or tolerating low levels of resources (Goldberg 1990). The physiological bases of these two facets of competition are quite different, as discussed later. Because of physiological trade-offs, however, traits that promote **resource draw-down** and **tolerance of low resource supply** may be correlated (Sect. 7).

Two major **physiological trade-offs** have been discussed as the basis of broad patterns of competitive ability in different environments. First, there is a trade-off between rapid growth to occupy space and maximize resource acquisition vs. resource conservation through reductions in tissue turnover (Grime 1977) (Sect. 4). Second, there is a trade-off between allocation to roots to acquire water and nutrients vs. allocation to shoots to capture light and CO_2 (Sect. 7; Tilman 1988). Because of these trade-offs, no species can be a superior competitor in all environments, but instead will specialize to grow and compete effectively in a certain restricted set of environments.

The effects of competition, as measured experimentally, are observed in both high-resource and low-resource environments (Goldberg & Barton 1992, Gurevitch et al. 1992). In low-resource environments, however, where growth rates are slow, competitive exclusion may take a very long time. Before there is any winner, environmental conditions (e.g., climate, fire) may change. This might account, in part, for the enormous richness of plant species on severely nutrient-impoverished sandplains in South Africa and Western Australia (Myers et al. 2000). On the other hand, the distribution of the Proteaceae along a transect on nutrient-impoverished soils supporting fynbos in South Africa appears to be determined by adaptations to local soil factors more than by competitive exclusion (Richards et al. 1997).

Competition is least likely to occur in recently disturbed sites where low plant biomass and/or high resource supply minimize resource limitation. In other cases, coexisting species may be limited by different factors, as when species have radically different phenology, height, or rooting depth. In order for plants to minimize competition, they must adjust growth to tap resources that are not utilized by neighbors.

3. How Do Plants Perceive the Presence of Neighbors?

Plants can perceive the proximity of neighbors, as described in discussing plant growth in shady conditions. First, a reduction in the level of photosynthetically active radiation reduces the concentration of soluble sugars, which can be sensed by plant cells (Sect. 6.3 of Chapter 2A on photosynthesis). Second, special pigments, **cryptochrome** and **phytochrome**, perceive both the level and the red/far-red ratio of radiation (Sect. 5.1.1 of Chapter 7 on growth and allocation). In *Populus* (poplar), for example, linear relationships exist between stem growth rate, plant spacing, and $P\text{fr}/P\text{t}$ calculated from radiation that is propagated vertically within the canopy. The dynamics of developing or regenerating canopies is partly based on phytochrome-mediated perception of the proximity of neighboring plants (Gilbert et al. 1995, Ritchie 1997). Through the phytochrome system, plants clearly sense cues that indicate current or future shading. Shade-avoiding species typically respond with enhanced stem elongation, whereas no such response is found for species naturally occurring under a dense canopy (Sect. 5.1.1 of Chapter 7 on growth and allocation; Fig. 1).

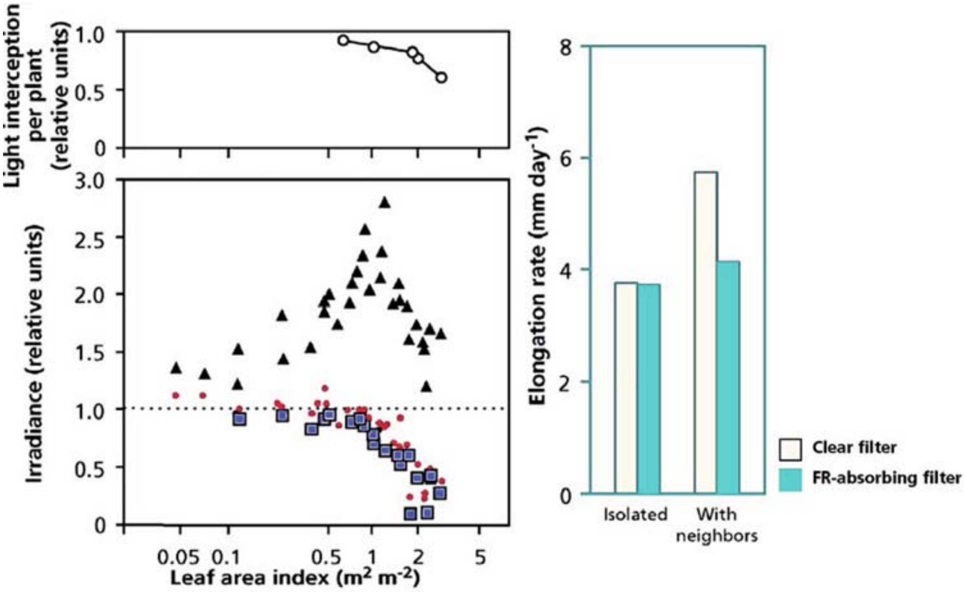

Figure 1. (*Left*) Effects of increasing the leaf area index [LAI, m^2 (leaf area) per m^2 (soil surface)] in even-height canopies of dicotyledonous seedlings on (top) light interception and (bottom) the light climate of the stem. Seedling stands of *Sinapis alba* (mustard) and *Datura ferox* (thorn apple) of differing densities and plant sizes were used to obtain a range for the leaf area index. The values are given relative to the measurements obtained for isolated plants (horizontal line). Triangles, far-red light; circles, red light; squares, blue light. (*Right*) Elongation response of the first internode of *Datura ferox* (thorn apple) seedlings to the proximity of neighboring plants. The seedlings were placed at the center of an even-height canopy with a leaf area index of approximately 0.9. During the 3-day experiment the seedlings are surrounded by cuvettes containing distilled water (clear filter) or a $CuSO_4$ solution (far-red-absorbing filter) that maintain the red/far-red radiation near 1.0 (Ballaré et al. 1995; reproduced with the author's permission from *HortScience* 30: 1172–1182).

Plants are also capable of "smelling" the presence of neighbors that release above-ground **chemical signals**, such as jasmonate or other volatiles (Sect. 2 of Chapter 9B on ecological biochemistry, Sect. 3 of Chapter 9C on effects of microbial pathogens). Contrary to common expectation, plants have highly sensitive **chemoperception** systems that play a central role in communication with surrounding organisms (Chapters 9A–9D). Physically touching surrounding plants is an additional way in which neighbors can be perceived (Sect. 5.7 of Chapter 7 on growth and allocation).

Plants can also perceive the presence of surrounding plants because of their neighbors' effect on above-ground **microclimate**, which is caused by differential heat exchange. This can have a tremendous effect on the outcome of competition (e.g., in frost-prone areas). Tree seedlings may grow well in forest clearings for the first few years, but once a grassy groundcover establishes, the growth of the young trees becomes retarded and more susceptible to frosts. Although some of these effects might be due to competition for nutrients and water, this cannot account for their greater frost sensitivity. When seedlings of *Eucalyptus pauciflora* (snow gum) are surrounded by grass, the minimum air temperature experienced by seedlings decreases by as much as 2°C, and they experience more frosts. These effects cause greater photoinhibition, reduced growth, and a shorter growing season for seedlings surrounded by grass compared with those in bare patches. Thus, the microclimate above grass adversely affects spring growth of juvenile trees and may account for much of the competitive inhibition of tree seedling growth by grass during spring (Fig. 2).

Plants can also sense the presence of neighbors below ground. For example, below-ground competition of *Lolium perenne* (perennial ryegrass) with *Plantago lanceolata* (snake plantain) markedly reduces root mass and root length of *Lolium perenne*, without any effect on shoot growth. Contrary to the effects of a limiting nutrient supply, competition with *Plantago lanceolata* does not affect the specific root length. This suggests the perception of the presence of *Plantago lanceolata* by the grass roots via an

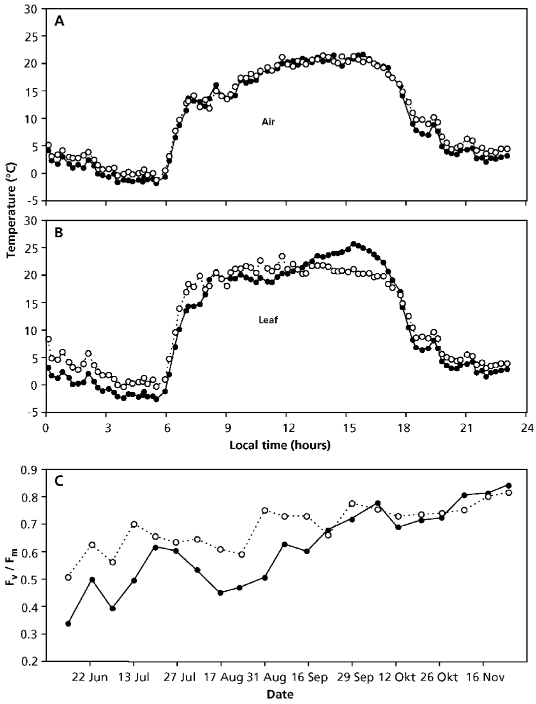

Figure 2. Diurnal variation in (A) air temperature and (B) the temperature of the leaves of *Eucalyptus pauciflora* (snow gum) above an open patch (open symbols) and above grass (filled symbols), measured from midnight to midnight on a day in September (early spring). Temperatures were measured 10 cm above ground level for one leaf of a seedling; seedlings were about 2 m apart. (C) Seasonal changes in average weekly midday values for the fluorescence characteristic F_v/F_m, which is an indicator of the quantum yield of photosynthesis, for seedlings of *Eucalyptus pauciflora* grown in an open habitat (open symbols) or above grass (filled symbols) (Ball et al. 1997). Copyright Blackwell Science Ltd.

allelochemical (Fitter 1976). Roots of two native California shrub species, *Haplopappus ericoides* (California goldenbush) and *Haplopappus venetus* (isocoma), similarly reduce overlap with the roots of an invasive introduced perennial succulent, *Carpobrotus edulis* (iceplant), by redistributing root growth further down in the soil profile (Fig. 3). Removal of *Carpobrotus edulis* from around the native shrubs also results in higher predawn xylem water potentials which suggest that the invasive succulent uses some water that would have been available for the native shrubs (D'Antonio & Mahall 1991). The change in rooting pattern could partly reflect differential root proliferation in zones of high availability of nutrients or water (Sect. 3.4 of Chapter 3 on plant water relations). The effect also occurs, however, when plants are well provided with water and nutrients which indicates a specific response to avoid the roots of neighbors (Mahall & Callaway 1991).

A chemical root interaction (i.e., the accumulation of **allelochemicals**) is a likely explanation for many of the patterns observed in the field (Sect. 2 of Chapter 9B on ecological biochemistry). When the roots of *Ambrosia dumosa* (white bursage), whose growth is normally inhibited by the presence of the roots of *Larrea divaricata* (creosote bush), are treated with activated charcoal that adsorbs allelochemicals, the inhibition is reduced. This is consistent with inhibition by a slowly diffusing allelochemical that is released by the roots of *Larrea divaricata*, and may account for the dispersed distribution of *Larrea divaricata* in the Mojave Desert in California, USA.

The intraspecific inhibition of root growth of *Ambrosia dumosa* (white bursage), however, is not affected by activated charcoal, indicating that it depends on **physical contact**. The nature of deterrence by direct contact with the roots of *Ambrosia dumosa* is not clear (Mahall & Callaway 1992), but it might involve **thigmomorphogenetic processes** (Sect. 5.8 of Chapter 7 on growth and allocation). Plants clearly differ in their response to surrounding plants of the same species just as they differ in their response to plants of a different species (Huber-Sannwald et al. 1996).

Climbing plants, which depend on neighboring plants for support, somehow perceive the presence of mechanical support. The elongation of tendrils is suppressed when they contact a supporting structure (Sect. 5.8 of Chapter 7 on growth and allocation). Provided with support other than a neighboring plant, climbing plants grow taller than unsupported individuals. Unsupported plants allocate more resources to their shoot branches, possibly increasing the chance of reaching a supportive structure, and allocate less to their roots. This indicates that it is the support itself, rather than any aspect of the neighboring plant's physiology that affects the allocation pattern of climbing plants (Putz 1984, Den Dubbelden & Oosterbeek 1995).

There are clearly many ways in which plants perceive their neighbors, both above and below ground. Plants may respond in such a way as to avoid competition or in a manner that makes them superior competitors. That is, plants that are sufficiently **plastic** for certain traits may well be able to avoid their neighbors and grow in such a way as to tap resources not utilized by neighbors (Sect. 6). In the following sections we explore what ecophysiological traits determine competitive success when

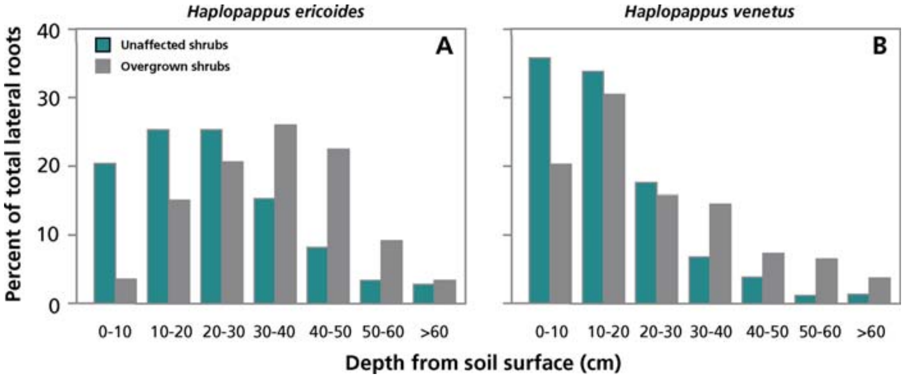

FIGURE 3. Percentage of total number of lateral roots of two shrubs, *Haplopappus ericoides* and *Haplopappus venetus* in each 10 cm depth increment below soil surface. Open bars: no competing invasive plants of *Carpobrotus edulis* (iceplant) present; filled bars: competing plants of *Carpobrotus edulis* present (D'Antonio & Mahall 1991). Copyright Botanical Society of America, Inc.

plants are forced to compete for the same pool of limiting resources.

4. Relationship of Plant Traits to Competitive Ability

4.1 Growth Rate and Tissue Turnover

Evidence from field studies, laboratory experiments, and ecological theory have converged on the conclusion that species from high-resource environments exhibit high **relative growth rate** (RGR**)**, whereas species from low-resource environments compete most effectively by minimizing tissue loss (greater **tissue longevity**) more than by maximizing resource gain (Sects. 3 and 6 of Chapter 7 on growth and allocation). The ecological advantage of a high potential RGR seems straightforward: fast growth results in the rapid occupation of a large space which leads to the preemption of limiting resources (Grime 1977). A high RGR may also facilitate rapid completion of the plant's life cycle which is essential for **ruderals**, whose habitat does not persist for a long time. In growth analyses and in short-term competition experiments carried out at a limiting nutrient supply, potentially fast-growing species grow faster and produce more biomass than do slow-growing ones (Lambers & Poorter 2004). Even when growing naturally in a nutrient-poor meadow, in competition with surrounding plants, the species with the highest RGR_{max} grows fastest and produces most biomass in relatively short experiments (Fig. 4). The greater competitive ability in these short-term experiments is associated with a higher leaf area ratio (LAR), due to a lower leaf mass density (Lambers & Poorter 2004); it is also associated with a higher specific root length (SRL), due to thinner roots (Eissenstat 1992) and a lower root mass density (Ryser & Lambers 1995).

Why do plants with a small root diameter and low tissue mass density (i.e., a high specific root length) and with thin leaves and a low tissue mass density (i.e., a high specific leaf area) fail to dominate on nutrient-poor sites? For widely different species, including evergreen and deciduous ones, the low **tissue mass density** of fast-growing species is associated with a more rapid turnover of their leaves and a shorter **mean residence time of nutrients** (Sect. 4 of Chapter 6 on mineral nutrition). In a comparison of ecologically contrasting grass species, slower-growing species from nutrient-poor habitats also tend to have a higher tissue mass density and slower turnover rates than do faster-growing ones from more productive sites (Ryser 1996). Turnover of plant parts inevitably causes loss of about half of the leaf nutrients from the plant and reduces the mean residence time of the nutrients (Sect. 4 of Chapter 6 on mineral nutrition). Although rapid growth may therefore lead to a competitive advantage in the short term, even when the nutrient supply is severely limiting, there is a penalty associated with this trait in the long run (Berendse & Aerts 1987, Tilman 1988). That is, the losses associated with tissue turnover become so large that they cannot be compensated for by uptake of nutrients from the nutrient-poor environment. As a result, the fast-growing species are outcompeted by the slower-growing ones, once the time scale of the experiment is long enough that differences in

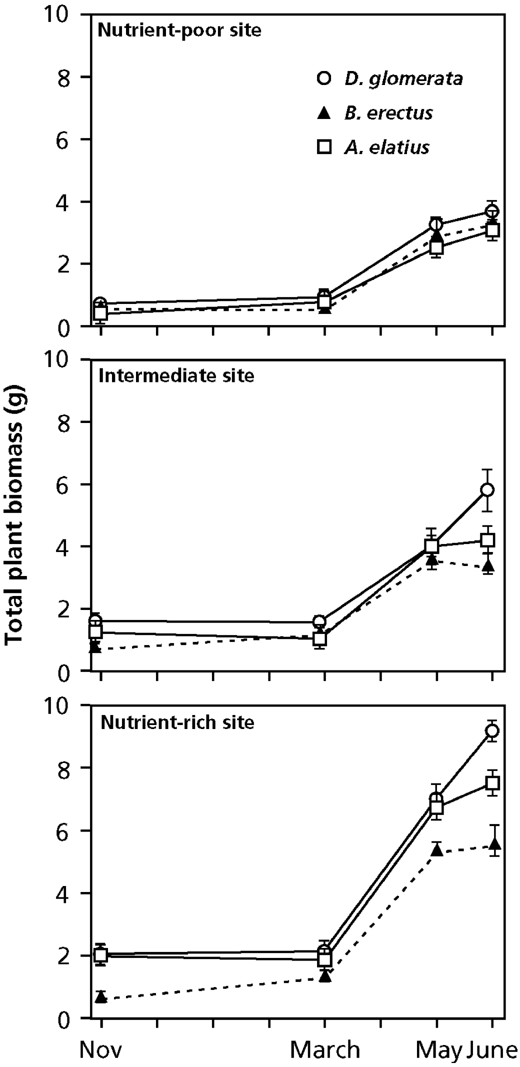

Figure 4. Total biomass of three tussock-forming grasses, growing in three meadows that differ in nutrient availability. The grasses differ in their RGR_{max}, with *Bromus erectus* (upright brome; filled triangles) having the lowest RGR_{max}, *Arrhenaterum elatius* (oatgrass; open squares) an intermediate RGR_{max}, and *Dactylis glomerata* (open circles) the highest (Schläpfer & Ryser 1996). Copyright Oikos.

tissue loss and mean residence time influence the outcome of competition (Aerts & Van der Peijl 1993).

Why should a low tissue mass density be associated with faster turnover and shorter residence times? Part of the answer is straightforward: a high tissue mass density reflects a large investment in cell walls, sclerenchyma, and fibers, which reduce the **palatability** and **digestibility** of the tissue and allow the tissue to withstand abiotic stresses and deter herbivores. Or, as expressed by Eeyore (Milne 1928): "Why do all plants which an animal likes, have the wrong sort of swallow or too many spikes" (Sect. 3.3 of Chapter 7 on growth and allocation).

Senescence is a highly programmed process of tissue death that also causes tissue turnover. The rate of tissue turnover is quite separate from tissue mass density, though correlating with it for reasons that will become clear in this section. This programming is obviously prolonged for leaves with a greater longevity, even though we understand very little of the mechanisms underlying these differences. If the programming, however, is such that the leaves last a long time, the leaves must be constructed in such a way that biotic and abiotic factors do not prevent longevity. In other words, natural selection for slow turnover and a large investment in defense should go together which explains the close correlation between the two, without there being a causal link.

There is a third reason for shorter nutrient residence times in faster-growing species at a low nutrient supply (Sect. 7 of Chapter 7 on growth and allocation). Species differ in the manner in which they respond to a limitation by nutrients in the environment: the typical response of a fast-growing species upon sensing nutrient shortage is to promote leaf senescence and so withdraw nutrients from older leaves and use these for its newly developing tissues. A slow-growing species that naturally occurs on nutrient-poor sites will slow down the production of new tissues, with less dramatic effects on leaf senescence and allocation pattern. In other words, the environmentally induced senescence is much stronger in faster-growing species than in slower-growing ones. We again understand too little of a plant's physiology to account fully for our ecological observations, but the result is clear: the environmentally induced senescence of the rapidly growing species causes them to lose more nutrients.

4.2 Allocation Pattern, Growth Form, and Tissue Mass Density

In nutrient-rich conditions, *Lychnis flos-cuculi* (ragged robin) genotypes with an inherently high **leaf mass ratio** (LMR) achieve higher yields in competition with *Anthoxanthum odoratum* (sweet vernalgrass) and *Taraxacum hollandicum* (dandelion) than do genotypes with a lower LMR. At a low nutrient supply, this allocation pattern confers no advantage; moreover, genotypes with an inherently high **specific leaf area** (SLA) tend to produce smaller rosettes

(Biere 1996). This information on the ecological significance of SLA is consistent with results on an African C_4 species that has been introduced into Venezuela. The introduced species with a high SLA outcompetes a native C_4 species that has a low SLA in relatively fertile places, but not in more infertile habitats (Baruch et al. 1985). On subantarctic islands the introduced grass *Agrostis stolonifera* (creeping bentgrass), with a high SLA, is similarly able to survive in the wind-sheltered places, but it is not found outside these shelters, whereas *Agrostis magellania*, which is characterized by a lower SLA due to more sclerenchyma, occurs in the windswept parts of these islands (Pammenter et al. 1986). A high LAR, due to a high SLA and/or a high LMR, which is associated with a high growth rate, is advantageous in productive environments. On the other hand, a low SLA, which is associated with a low growth rate, confers a selective advantage in relatively unfavorable environments (Sects. 3.7 and 6.3 of Chapter 7 on growth and allocation; Lambers & Poorter 2004).

Just as SLA is an important above-ground trait for a plant's competitive ability, the **specific root length** (SRL) is an important below-ground characteristic, determining a plant's ability to compete for nutrients and water. This can be illustrated using two tussock grasses, competing with *Artemisia tridentata* (sagebrush) as an indicator species (Eissenstat & Caldwell 1988). *Agropyron desertorum* (desert wheatgrass) is an introduced species, with a greater competitive ability than the native *Pseudoroegneria spicata* (formerly *Agropyron spicatum*; bluebunch wheatgrass). When *Artemisia tridentata* plants are planted among near-monospecific stands of one of the two tussock grasses, they show lower survival, less growth and reproduction, and a more negative water potential during part of the season when surrounded by *Agropyron desertorum* than they do when they compete with *Pseudoroegneria spicata*. *Agropyron desertorum* extracts water more rapidly from the soil profile, but it is remarkably similar in architecture, shoot phenology, root mass distribution in the soil profile, growth rate in various environments, and the efficiency of water and N use (Eissenstat & Caldwell 1987). Its roots are thinner, however, so that the length per unit mass (SRL) is about twice that of the less competitive *Pseudoroegneria spicata*. This higher SRL, in combination with more root growth in winter and early spring, allows the more competitive tussock grass to extract water more rapidly from the profile. These traits likely contribute to the observation that *Artemisia tridentata*, growing side by side with the two tussock grasses, acquires 86% of all its absorbed labeled P_i from the interspace shared with *Pseudoroegneria spicata*, and only 14% from the interspace with *Agropyron desertorum* (Fig. 5). Clipping of the tussock grasses enhances P_i uptake by sagebrush substantially, confirming that the grasses competed for resources from the soil before clipping (Caldwell et al. 1987). Because P_i is highly immobile in soil, roots of the competing plants or their associated mycorrhizal fungal hyphae must have been very close to each other.

To be a successful competitor above ground as well as below ground, plants would need a high SLA as well as a high SRL, both of which can be realized through a low tissue mass density. Competitive species naturally occurring in productive meadows do, indeed, have a low leaf mass density as well as a low root mass density (Ryser & Lambers 1996).

4.3 Plasticity

Previous chapters provided numerous examples of the acclimation of photosynthesis, respiration, and biomass allocation to environmental factors such as irradiance and nutrient supply. A high capacity to acclimate reflects a genotype's **phenotypic plasticity** for a specific trait; however, a relatively small plasticity for one trait may result from a large plasticity in other traits. For example, the low morphological plasticity (stem length) of an alpine *Stellaria longipes* (Sect. 5.7 of Chapter 7 on growth and allocation) is a consequence of a high physiological plasticity (ethylene production). Both traits are directly related to the same environmental cue (wind stress) and the expressed phenotype has a direct bearing on the plant's fitness (Emery et al. 1994). In addition, a large morphological plasticity in biomass allocation between roots and leaves in response to nutrient supply or irradiance results in a low plasticity of the plant's growth rate, so that this varies relatively little between different environments (Fig. 6).

It has been suggested that a high plasticity allows a genotype to maintain dominance in spatially or temporally variable environments by enabling them to continuously explore new patches that have not been depleted, thus sustaining resource capture and maintaining fitness (Grime et al. 1986). By contrast, in habitats of predictably low resource supply, plant production would be restricted to a continuously low level and a strategy of conservation of captured resources, associated with slow growth, would be favored. Such a contention is hard to verify, in view of the fact that greater plasticity for one trait is made possible by smaller plasticity for another.

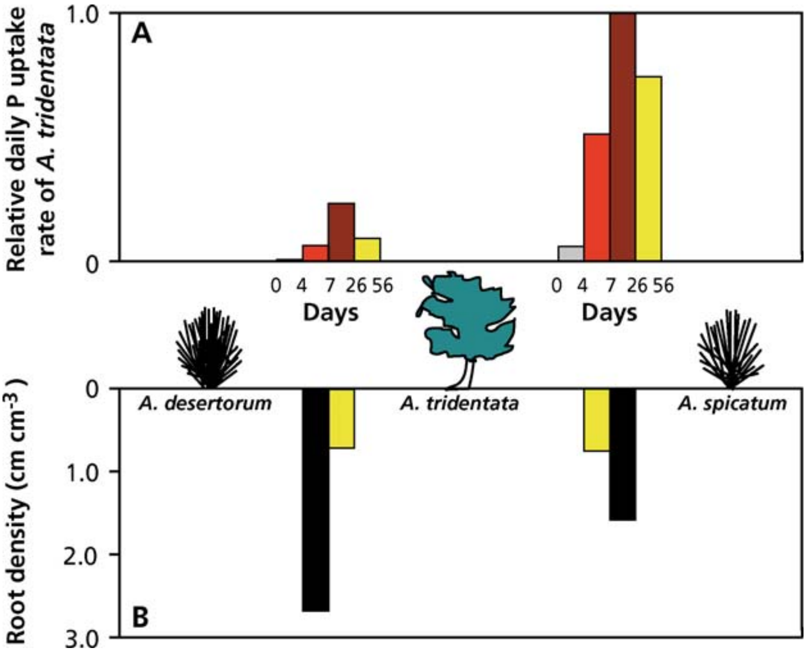

Figure 5. (A) The relative rate of P_i absorption. That is, the average daily uptake of P_i isotopes, ^{32}P and ^{33}P, by root tips of *Artemisia tridentata* (sagebrush) from soil interspaces shared with one of two tussock grasses, the native *Pseudoroegneria spicata* or the introduced *Agropyron desertorum* at various times after labeling. The separate labels were injected at either side of *Artemisia tridentata,* in the interspace shared with one of the two tussock grasses. This made it possible to assess from which interspace the label had been acquired. (B) Rooting density of the tussock grasses (filled bars) and of *Artemisia tridentata* (open bars). Rooting densities were not significantly different in the two interspaces or between the tussock grass species, but they were significantly less for *Artemisia tridentata* than they were for the tussock grasses. From Caldwell et al. (1985). Reprinted with permission from AAS.

There are certainly convincing examples of greater plasticity associated with competitive ability in a particular environment. **Late-successional species** tend to have a greater potential for adjustment of their photosynthetic characteristics to **shade** than do early-successional species (Küppers 1984). A classic case is the response of stem elongation to shade light (Sect. 5.1 of Chapter 7 on growth and allocation and Sect. 2). Shade light also suppresses branching in dicotyledonous species and enhances tillering in grasses like *Lolium perenne* (perennial ryegrass) and *Lolium multiflorum* (Italian ryegrass), and this plastic response is probably important in coping with neighbors (Deregibus et al. 1983). To confirm the importance of the **phytochrome system** for the perception of neighboring plants, Ballaré (1994) used transgenic plants of *Nicotiana tabacum* (tobacco), over-expressing a phytochrome gene. These transgenics show a dramatically smaller response to the red/far-red ratio of radiation and to neighboring plants. In a stand of such transgenics, the small plants of the population are rapidly suppressed by their neighbors. These results indicate that a high degree of plasticity in morphological parameters plays an important role in the competition with surrounding plants.

With respect to variation in nutrient supply, the present information is far from conclusive. Fast-growing species from high-resource environments often show less or a similar change in allocation parameters like root mass ratio and stem mass ratio compared with slow-growing ones from nutrient-poor environments (Poorter et al. 1995). A survey of a large number of species finds no correlation between relative growth rate and allocation (root mass ratio and stem mass ratio) (Reynolds & D'Antonio 1996).

In summary, it appears that fast-growing species from high-resource environments are more plastic for some traits, such as photosynthetic characteristics and the rate of stem elongation in response to shade, surrounding plants, and wind. When it comes to

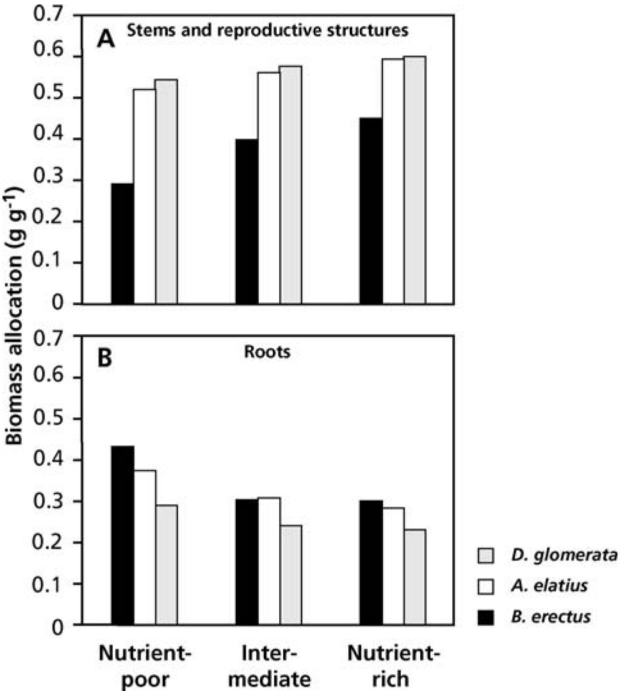

Figure 6. Biomass allocation to (A) stems and reproductive structures and (B) roots of three tussock grasses, growing in three meadows that differ in nutrient availability: nutrient-poor, intermediate and nutrient-rich. The grasses differ in their RGR_{max}, with *Bromus erectus* (upright brome; filled bars) having the lowest RGR_{max}, *Arrhenaterum elatius* (oatgrass; open bars) an intermediate RGR_{max}, and *Dactylis glomerata* (cocksfoot; shaded bars) the highest (after Schläpfer & Ryser 1996).

below-ground plant traits and morphological plasticity in response to the supply of nutrients, this conclusion is hard to substantiate, in part because plasticity in many traits (e.g., nutrient uptake, root growth, and nutrient storage) can influence the response of allocation to nutrient supply.

5. Traits Associated with Competition for Specific Resources

5.1 Nutrients

We have shown the physiological basis for the trade-off between rapid growth and tolerance of low nutrient supply (Sect. 4). What evidence is there that species growing on infertile soils draw down resources below levels used by potential competitors (i.e., low R*) and what might be the processes responsible for such **resource draw-down**? The most explicit test of the R* hypothesis is a field experiment in which several perennial prairie grasses that naturally occur on sites of different soil fertilities are planted in monoculture and in competition on several soils of differing fertility (Wedin & Tilman 1990, Tilman & Wedin 1991). Within 3 years, monocultures of the more slowly growing species reduce the concentration of extractable soil NO_3^- and NH_4^+ to lower levels than do monocultures of high-RGR species from more fertile sites (Fig. 7). In addition, soil NO_3^- concentrations are just as low in competition treatments between fast and slow-growing species as they are in monocultures of the slow-growing species. This coincides with elimination of the more rapidly growing species. The traits most consistently associated with competitive success in these experiments are a high **allocation to root biomass** and **low RGR**. High allocation to roots is the plant trait that correlates most strongly with the N draw-down. The low RGR reduces loss rates and enhances tolerance of low supply rates.

What other nutritional traits might be involved in competition for nutrients? The **uptake kinetics** of species from infertile soils are unlikely to result in low soil solution concentrations. These species typically have a lower I_{max} of nutrient uptake and do not differ consistently in K_m from species that occur on fertile soils (Sect. 2.2.3.1 of Chapter 6 on mineral nutrition). The influence of uptake kinetics on soil solution concentration should be greatest for mobile nutrients (e.g., NO_3^-) and least pronounced for cations (e.g., NH_4^+) and P_i (Sect. 2.1.2 of Chapter 6 on mineral nutrition).

Plants and their mycorrhizal partners from specific nutritional situations often have a capacity to tap sources of nutrients unavailable to other species,

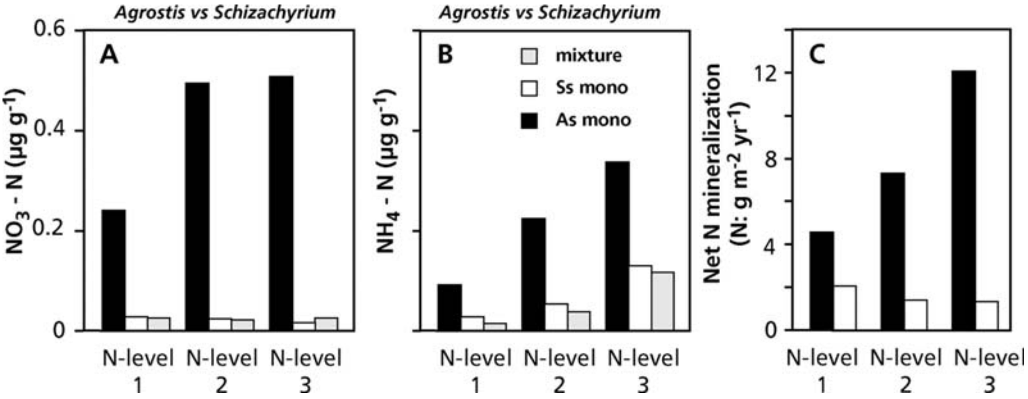

Figure 7. Extractable soil NO_3^- and NH_4^+ and net N mineralization in experimental monocultures of an early-successional, fast-growing prairie grass (*Agrostis scabra*) and a late-successional, slow-growing prairie grass (*Schizachyrium scoparium*) and of the two species growing together in mixture. Plants from a Minnesota prairie (United States) were grown for 3 years in soils that contain three levels of N, after which soil samples were extracted for measurement of NO_3^- and NH_4^+. Net N mineralization was measured monthly in the field (Tilman & Wedin 1991, Wedin & Tilman 1990). Copyright Ecological Society of America.

such as sorbed P or organic N (Sects. 2.2.4 and 2.2.5 of Chapter 6 on mineral nutrition). Traits of roots and their mycorrhizal partners that allow access to N that has been immobilized by tannins provide access to a N pool that is not available to species lacking these traits (Sect. 2.4 of Chapter 9A on symbiotic associations).

The most likely cause of **nutrient draw-down** by species in infertile soils is **immobilization** of nutrients due to the low nutrient and high tannin concentrations of the litter of species adapted to infertile soils (Sect. 4.3.2 of Chapter 6 on mineral nutrition and Sect. 3.1 of Chapter 9B on ecological biochemistry). Leaf litter from such plants decomposes very slowly, leading to slow net mineralization rates (Fig. 7). In addition, a large proportion of the litter is produced by roots, which typically have lower tissue nutrient concentrations than do leaves, and which are dispersed throughout the soil, so that the zone of immobilization coincides with the zone of uptake.

Nutrient-impoverished habitats, such as the heathlands of Western Australia and South Africa, are among the most species-rich habitats in the world. How do so many species coexist where strong competition for nutrients must be critical for survival? There are some specialized root traits (cluster roots) that enable certain species to tap sorbed P that is unavailable to other species (Sects. 2.2.4 and 2.2.5 of Chapter 6 on mineral nutrition). Although species differ in preference for forms of N, most species have the physiological capability to tap all forms of soluble N and to adjust their capacities for uptake and assimilation, depending on supply (Sect. 2.1.2 of Chapter 6 on mineral nutrition). Allelochemicals may inhibit **nitrification** (Sect. 2 of Chapter 9B on ecological biochemistry). Since NH_4^+ is far less mobile than NO_3^-, such inhibition may enhance the availability of N for plants whose roots release nitrification inhibitors. Ectomycorrhizas and ericoid mycorrhizas may break down **protein N** that would otherwise not be directly available to plants (Lambers et al. 2008).

Except in severely nutrient-impoverished soils (Lambers et al. 2006), competitive coexistence of multiple species in a community is not a simple function of capacity to tap a unique resource or capacity to draw down a single resource; rather, it involves a wide range of traits and subtle differences in resistance to different environmental circumstances.

5.2 Water

The mechanism by which **desiccation-resistant plants** draw down soil moisture is well established. The lower the **water potential** that a species can tolerate, the lower the level to which it can reduce soil moisture. When soil water potential falls below the minimum water potential tolerated by potential competitors, they can no longer withdraw water from the soil. The traits that enable a species to maintain activity at a low water potential include osmotic or elastic adjustment and a stomatal conductance that is relatively insensitive to signals associated with a low root or leaf water potential (Sects. 4.1 and 5.4.1 of

Chapter 3 on plant water relations). This highlights a stark contrast with the mechanisms involved in competing for nutrients (Sect. 5.1). Interestingly, water has not been explored within the context of R*, whereas it would appear to fit quite well within the concept based on nutrient acquisition.

Transpiration is the major avenue of water loss to the atmosphere and therefore of soil drying in dense vegetation. In general, the species with greatest **desiccation resistance** have a suite of morphological and biochemical traits that enable them to conserve water (e.g., CAM and C_4 photosynthesis, low stomatal conductance, low hydraulic conductance of the stem). When water is available, most plants maximize stomatal conductance and therefore water loss. In a mixed-species community, the species responsible for the greatest quantity of water loss are not those that are most resistant of water stress. The desiccation-resistant species are probably most important in the final stages of moisture draw-down, after less resistant species become dormant. The abundance of different life forms and physiological strategies in deserts indicates that there are many ways of competing effectively in dry environments, only some of which involve extreme resistance of low soil water potential. Other modes of competing effectively in deserts include phenological **avoidance** of drought and rapid growth when water is available.

Roots commonly pass through dry soil layers to deep horizons that contain more moisture. In the dry soil layers the soil matric potential may be more negative than the hydrostatic pressure in the xylem of the roots. Water may then move from the roots to the dry soil, and roots can form a bridge for water transport between soil layers (Sect. 5.2 of Chapter 3 on plant water relations). Stolon-connected plants in separate moist and dry soil compartments similarly may transport considerable quantities of water from one soil compartment to the other (Van Bavel & Baker 1985).

A low conductance between roots and soil or of the soil might preclude substantial efflux of water from roots. A nocturnal down-regulation of water-channel proteins (Sect. 5.2 of Chapter 3 on plant water relations) might reduce water loss to dry soil. Although water efflux from roots into soil might be viewed as undesirable, there is no metabolic cost to water movement, and the water released at night is available for reabsorption during the day. In addition, the moist soil may promote nutrient acquisition by roots and prolong the activity of symbiotic microorganisms such as mycorrhizal fungi in the upper soil layers. The moist soil may also prevent chemical signals that would otherwise originate from roots in contact with dry soil (Sect. 5.4.1 of Chapter 3 on plant water relations). Some of the hydraulically lifted water will probably be available for shallow-rooted competing plants. As much as 20–50% of the water used by a shallow-rooted tussock grass [*Agropyron desertorum* (desert wheatgrass)] comes from water that is hydraulically lifted by neighboring sage brush (*Artemisia tridentata*) in the Great Basin desert of western North America (Richards & Caldwell 1987). *Acer saccharum* (sugar maple) similarly provides by hydraulic lift 46–61% of the water used by *Fragaria virginiana* (Virginia strawberry) growing beneath the tree (Dawson 1993). Individuals that are large enough to be quantitatively important in **hydraulic redistribution** will have predictable access to water and will be taller than the shallow-rooted species; therefore, they may not be severely impacted by this competition.

5.3 Light

Strong **competition for light** seldom coincides with strong competition for below-ground resources for two reasons. First, high availability of below-ground resources is an essential prerequisite for the development of a leaf canopy dense enough to cause intense light competition, which is strongest under conditions where water and nutrients are not strongly limiting to plant growth. Second, tradeoffs between shoot and root competition constrain the amount of biomass that can be simultaneously allocated to acquisition of above- and below-ground resources (Tilman 1988). Those species that are effective competitors for light are trees with a high above-ground allocation.

As with water, the species that most strongly reduce light availability are not necessarily the species that are most tolerant of low light. Species that are tall and have a high **leaf area index** (LAI) have greatest impact on light availability, whereas understory plants and late-successional species are generally the most shade-tolerant. Because light is such a strongly directional resource, competition for light is generally quite asymmetric, with the taller species having greatest impact on the shorter species, with often little detectable effect of understory species on the overstory, at least with respect to light competition.

5.4 Carbon Dioxide

Carbon dioxide is relatively well mixed in the atmosphere; therefore, plant uptake creates less localized depletion of CO_2 than of nutrients, water, or light.

Nonetheless, photosynthesis is often CO_2-limited, especially in C_3 plants. Plants with contrasting photosynthetic pathways may therefore differ in their competitive ability in relation to atmospheric CO_2 concentration. For example, one might expect the growth of C_4 plants, whose rate of photosynthesis is virtually saturated at current CO_2 concentrations of 370 μmol mol^{-1}, to respond less to the global rise in atmospheric CO_2 concentration than that of C_3 plants. To test this hypothesis, Johnson et al. (1993) compared the growth of **C_3 and C_4 plants**, while growing in competition at CO_2 concentrations, ranging from pre-industrial levels to 350 μmol mol^{-1}, the prevalent CO_2 concentration at the time of the experiment. As expected, photosynthesis and growth were enhanced more by high levels of CO_2 in C_3 species than in C_4 species. Whereas the C_4 species outyielded the C_3 plants at low CO_2 concentrations, the C_3 plants were superior competitors at elevated [CO_2] (Fig. 8). How can we assess whether a change in competitive ability as suggested by the data in Fig. 9 has indeed occurred? To address this question, soil organic matter of known age was analyzed for ^{13}C to estimate changes in the relative abundance of C_3 and C_4 species between the Late Pleistocene and the Early Holocene in northern Mexico. This showed an increase in C_3 species about 9000 years ago, a time when Antarctic ice cores showed a rapid rise in atmospheric [CO_2]. Plant macrofossils from packrat middens show that this vegetation change coincided with an increase in aridity, which should have favored C_4 species. The vegetation change, therefore, was most likely caused by increased atmospheric CO_2 rather than by climatic change.

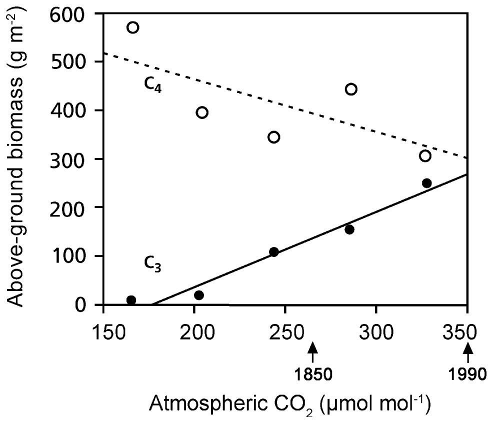

FIGURE 8. Above-ground biomass of C_3 and C_4 species that developed from the seed bank of a Texas savanna soil over a range of CO_2 concentrations from 150 to 350 μmol mol^{-1} over a period of 13 weeks (Johnson et al. 1993).

Further evidence that C_3 plants profit more from a rise in atmospheric [CO_2] than C_4 plants comes from work on a woody C_3 legume, *Prosopis glandulosa* (honey mesquite). This invasive species has increased in abundance in North American C_4-dominated grasslands over the past 150 years. When grown in monoculture, its below-ground biomass, rate of N_2 fixation, and water-use efficiency are increased at present-day levels of atmospheric CO_2, in comparison with historically lower levels. In competition with a C_4 grass, *Schizachyrium scoparium* (little bluestem), however, there is no effect on biomass. Rising levels of CO_2 may well have contributed to its success, but the shrub's strategy to avoid competition with neighboring grasses is probably more important (Polley et al. 1994).

Will C_3 species continue to conquer the world at the expense of C_4 species in years to come, while the concentration of CO_2 continues to rise? In experiments using around 340 and 620 μmol CO_2 mol^{-1} air, the competitive ability of *Festuca elatior* (tall fescue) or *Triticum aestivum* (wheat) (both C_3) is enhanced compared with that of *Sorghum halepense* (Johnsongrass) or *Echinochloa frumentacea* (Japanese millet) (both C_4), respectively (Carter & Peterson 1983, Wong & Osmond 1991). Drake and co-workers studied the effects of elevated [CO_2] on natural saltmarsh vegetation, consisting of both C_3 [predominantly *Scirpus olneyi* (olney threesquare)] and C_4 [mainly *Spartina patens* (salt hay grass)] sedges. After 4 years of exposure to elevated [CO_2], the biomass of *Scirpus olneyi* is greatly enhanced, both on sites where this species occurs as a pure stand and also where it grows in mixtures with *Spartina patens*. There is very little effect of elevated [CO_2] on the biomass of *Spartina patens* growing in a monospecific community, whereas it is reduced on sites where it grows in competition with the C_3 sedge (Arp et al. 1993).

The results show that **C_4 plants** decreased in **competitive ability** since the beginning of the industrial revolution. They may well continue to lose ground with a further rise in atmospheric CO_2 concentration. Elevated CO_2 concentrations interact with temperature, however, and affect plant growth in a manner that may be quite different from a plant's response to elevated [CO_2] alone. The climate change caused by elevated [CO_2] may well have an opposite effect on competition between C_3 and C_4 species. Increased temperatures and drier climates might favor C_4 grasses and lead to an expansion of the area occupied by C_4 species in Australia (Henderson et al. 1995).

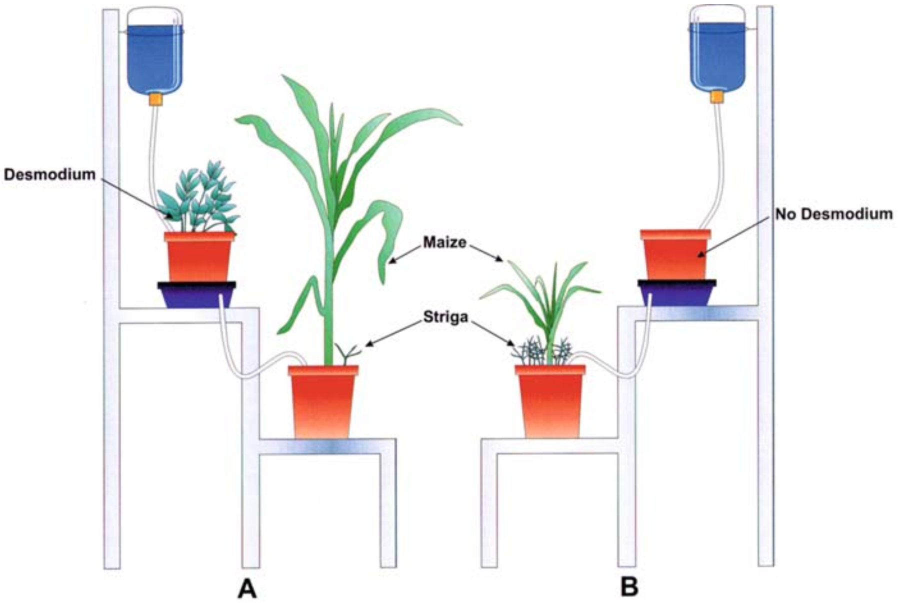

FIGURE 9. Diagram of an experiment to investigate the allelochemical mechanism of the fodder legume *Desmodium uncinatum* (silverleaf) in suppressing *Striga hermonthica* (witchweed) infestation of *Zea mays* (corn). A comparison was made between corn plants irrigated by root eluates of *Desmodium uncinatum* (A) with those irrigated by water passing through pots containing only autoclaved soil (B) (redrawn after Khan et al. 2002).

Elevated atmospheric CO_2 concentrations can alter availability of other environmental resources that can shift competitive balance in unpredictable ways. In a dry North American prairie, elevated [CO_2] causes an increase in soil moisture as a result of the reduction in stomatal conductance and transpiration. The improved soil moisture favors tall C_4 grasses over a subdominant C_3 grass which is opposite the result expected from direct photosynthetic response to CO_2 (Mo et al. 1992, Owensby et al. 1993).

Many of the published studies on competitive interactions of C_3 and C_4 species have been conducted in relatively fertile soils (Reynolds 1996), where we would expect photosynthetic performance to have the strongest connection to growth and competitive ability. Nutrient limitation reduces plant growth response to elevated CO_2 (Luo et al. 2004, Edwards et al. 2005, Reich et al. 2006), and there is no consistent competitive advantage of C_3 or C_4 species at low nutrient availability. Therefore, **nutrient limitation** could reduce any competitive advantage that C_3 species might have with future increases in atmospheric CO_2. In summary, despite the greater photosynthetic responsiveness of C_3 plants to elevated CO_2, compared with that of C_4 species, this may not translate into a future competitive advantage (Mooney et al. 1999).

The results on the outcome of competition between C_3 and C_4 plants as dependent on the CO_2 concentration in the atmosphere suggests photosynthesis has been a major factor in determining past competitive interactions, but is that also the case if we restrict our comparison to C_3 plants only? There is a wealth of information on the photosynthetic traits of "invasive" species as well as on early-succession woody species and the species that ultimately replace these. Succession is far more complicated than can be accounted for by competitive interactions alone. Competition in the succession following a fire or upon canopy destruction by a storm is a race without a single winner, unlike in a standard athletic contest. The entry in subsequent races may occur via vegetative regeneration, via a stored seed bank, or via dispersal to other locations, but the prerequisite for any of these is sufficient carbon and nutrient accumulation at some stage during vegetative growth. In succession, therefore, competition does play a role, and at later stages of succession the early-successional species are very poor competitors. Two exotic vines, *Pueraria lobata* (kudzu) and *Lonicera japonica* (Japanese honeysuckle), are major weed species in the south-eastern United States. In comparison with a number of native vines, *Rhus radicans* (poison ivy), *Parthenocissus quinquefolia* (Virginia creeper), *Vitis vulpina* (wild grape), and *Clematis virginiana* (virgin's bower), they have very similar rates of photosynthesis. Thus, the highly prolific growth of the two exotic weedy vines cannot be explained by higher rates of photosynthesis (Carter et al. 1989).

6. Positive Interactions Among Plants

Not all plant–plant interactions are competitive. Plants often ameliorate the environment of neighbors and increase their growth and survivorship (**facilitation**), particularly at the seedling stage and where the physical environment or water and nutrients strongly constrain growth (Callaway 2007).

6.1 Physical Benefits

In hot dry environments, seedlings often establish preferentially in the shade of other **nurse plants**. At the seedling stage, barrel cacti (*Ferocactus acanthodes*) suffer high mortality in deserts because of their small thermal mass. Seedlings in the shade of other plants are 11°C cooler than they are in full sun and only survive in shade (Turner et al. 1966, Nobel 1984). Facilitation due to shading also occurs in oak savannas by reducing desiccation and overheating, and in salt marshes by reducing soil evaporation and therefore salt accumulation (Callaway 1995). Hydraulic lift by deep-rooted plants may increase water potential and growth of adjacent plants (Sect. 7.2). Other facilitative effects of plants include oxygenation of soils, stabilization of soils, physical protection from herbivores, and attraction of pollinators (Callaway 1995).

6.2 Nutritional Benefits

A second general category of facilitation involves enhanced **nutrient availability**. The most dramatic examples of this are establishment of N_2-fixing species in early-successional and other low-N habitats (Vitousek et al. 1987, Chapin et al. 1994). Decomposition of high-N litter of N_2-fixing plants increases N availability in these environments. In other cases, organic matter enhances the nutrient and water status of understory plants (Callaway 1995).

When P is limiting and most of it is sorbed onto soil particles, plants that access sorbed P due to the release of carboxylates from their roots can benefit their neighbors that lack this ability (Sect. 2.2.5 of Chapter 6 on mineral nutrition; Cu et al. 2005). On calcareous soil, Fe uptake is restricted in calcifuge species, e.g., *Arachis hypogaea* (peanut). When peanut is intercropped with *Zea mays* (corn), which releases phytosiderophores, peanut does not show signs of Fe deficiency and yields much better (Sect. 2.2.6.2 of Chapter 6 on mineral nutrition; Zuo et al. 2000). These nutritional benefits can therefore be taken advantage of in **intercropping** systems in agriculture (Hauggaard-Nielsen & Jensen 2005).

In the real world, plant–plant interactions involve complex mixtures of competitive and facilitative effects, which often occur simultaneously. For example, at Glacier Bay, Alaska, *Alnus sinuata* (Sitka alder) is an early colonizer that has multiple effects on *Picea sitkensis* (Sitka spruce), which is the ultimate-successional dominant. Alder increases spruce growth by adding N and organic matter, but negatively affects spruce growth through shading and root competition. Alder increases seedling mortality as a result of seedling burial by litter and by providing habitat for seed predators (Chapin et al. 1994). Over the long term, the net effect of alder is to reduce stand density and increase the growth of individual spruce trees. Similar combinations of competitive and facilitative effects have been observed in many studies, with the net effect of one plant on another often changing with time, depending on variation in weather and successional stage (Aguiar et al. 1992, Callaway 1995).

6.3 Allelochemical Benefits

As discussed in Sect. 2 of Chapter 9B on ecological biochemistry, some plants release allelochemicals that affect herbivores. For example, *Eragrostis curvula* (weeping lovegrass) releases chemicals that have a **nematicidal** effect. Such species may be used to manage nematodes in agriculture (Katsvairo et al. 2006).

In subsistence farming in Kenya, intercropping of *Zea mays* (corn) with the fodder legumes silverleaf (*Desmodium uncinatum*) and greenleaf (*Desmodium intortum*) dramatically reduce the infestation of maize by **parasitic witchweeds** such as *Striga hermonthica*, due to allelochemicals released by the fodder legumes. Laboratory studies have shown that the allelochemical is a germination stimulant for *Striga hermonthica* as well as an inhibitor for haustorial development (Sects. 2.1 and 2.2 of Chapter 9D on parasitic association) (Fig. 9).

Certain plants release **stress signals** even when undamaged, and these can cause defense responses in intact neighbors. These discoveries provide the basis for new crop protection strategies, either through conventional intercropping with plants that release stress signals or by genetic modification of plants (Pickett et al. 2003). Similar signaling discoveries within the **rhizosphere** offer potential to extend these approaches into new ways of controlling weeds and pests, by exploiting the potential of allelochemicals through signaling rather than by direct physiological effects (Sect. 4.3 of Chapter 9B on ecological biochemistry). "**Push–pull strategies**" involve the behavioral manipulation of pests and their natural enemies via the integration of stimuli that act to make the protected resource unattractive or unsuitable to the pests (push) while luring them toward an attractive source (pull) from where the pests are subsequently removed (Cook et al. 2007). The push and pull components are usually integrated with methods for population reduction, preferably biological control. While the use of intercrops as part of the push–pull strategy reduces the area available for the actual crop to a small extent, it greatly enhances the yield of the crop per unit area. The strategy is a valuable tool for **integrated pest management** aiming to reducing pesticide input and has been used successfully in subsistence farming in Africa (Hassanali et al. 2008).

These are just a few of numerous examples of chemical interactions between plants involving other organisms. They reveal an exciting ecophysiological complexity that we are only just beginning to appreciate. Possibilities for applications in agriculture are numerous, as alluded to above and in several other chapters.

7. Plant–Microbial Symbiosis

Many woody species that appear in early phases of succession (e.g., after a fire) are **N_2-fixing legumes**. When the level of N in the soil increases, their rates of N_2 fixation decline (Sect. 3.9 of Chapter 9A on symbiotic associations). At later stages during succession, such pioneers may succumb to phytophagous arthropods [e.g., the pioneer *Acacia baileyana* (Cootamundra wattle), in Australia]. The competitive success of *Acacia saligna* (orange wattle), which was introduced into South Africa from Australia to stabilize sand dunes, is partly ascribed to its symbiotic association with rhizobia (Stock et al. 1995).

If competing plants are **mycorrhizal**, we also need to consider the ability of their external mycelium to capture nutrients. If they share a common external mycelium, then competition exists between the plants to acquire nutrients from that external mycelium. Can mycorrhizal infection alter the balance between different species? When seedlings of the grass *Festuca ovina* (sheep fescue) grow in nutrient-poor sand in competition with seedlings of other species, they grow less well in the presence of AM fungi than they do in their absence. Seedlings of many of their competitors, however, grow substantially better (with the exception of nonmycorrhizal species) in the presence of AM (Grime et al. 1987). The grass *Lolium perenne* (perennial ryegrass) and the dicot *Plantago lanceolata* (snake plantain) show similar values for RGR when the plants are grown separately, irrespective of their mycorrhizal status (Fig. 10). When grown in competition, however, the mycorrhizal *Planceolata lanceolata* has a higher mean RGR than *Lolium perenne*, whereas the opposite occurs when the plants are nonmycorrhizal. This suggests that the coexistence of *Plantago lanceolata* in grasslands may depend on mycorrhizas (Newman et al. 1992).

Competitive interactions may become complicated when species differ in their mycorrhizal dependency (Sect. 2.1.2 of Chapter 9A on symbiotic associations; Koide & Li 1991). For example, of two tallgrass prairie grasses, *Andropogon gerardii* (big bluestem) is 98% dependent on the symbiosis, vs. only 0.02% in *Koeleria pyranidata* (junegrass). When competing in pairs, *Andropogon gerardii* dominates in the presence of mycorrhizal fungi, whereas

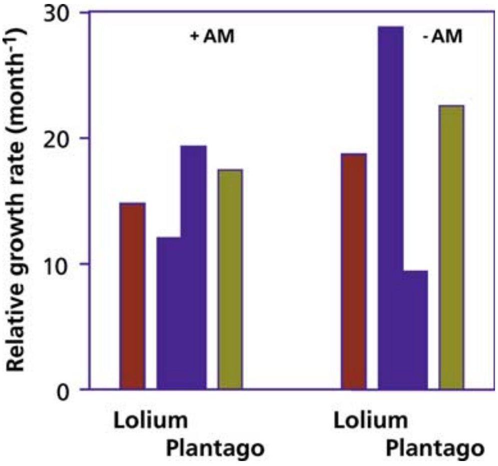

FIGURE 10. Relative growth rates of the grass *Lolium perenne* (perennial ryegrass) and the dicot *Plantago lanceolata* (snake plantain) grown in a glasshouse in heat-sterilized, nutrient-poor grassland soil that was originally free of mycorrhizal fungi. The plants were grown separately (open bars) or together (filled bars), either without AM fungi or inoculated at the time that the plants were competing, as judged from the size of the plants (Newman et al. 1992).

Koeleria pyranidata does in the absence of the fungus (Hetrick et al. 1989).

Some herbaceous pioneers are **nonmycorrhizal** (Sect. 2.2. of Chapter 9A on symbiotic associations). Some of these plants may grow well in the early phase of succession because of their special ability to release P_i from sparingly available sources (Sect. 2.2.5 of Chapter 6 on mineral nutrition) or because the P_i availability is high. At later stages, mycorrhizal species may arrive and replace nonmycorrhizal species. When growing in competition with the nonmycorrhizal *Brassica nigra* (black mustard), growth and nutrient uptake of the mycorrhizal *Panicum virgatum* (switchgrass) are reduced when plants are of equal size. The presence of collembola that graze mycorrhizal fungi enhances the competitive advantage of the nonmycorrhizal black mustard. When seedlings of the nonmycorrhizal *Brassica nigra* have to compete with the mycorrhizal plants of *Panicum virgatum* that germinated 3 weeks earlier, the situation is reversed: *Brassica nigra* is negatively affected by competition, whereas the larger and older grass plants are not (Boerner & Harris 1991). This may account, in part, for the gradual replacement of nonmycorrhizal annuals by mycorrhizal perennials.

Allelochemicals released by the mycorrhizal fungus may also be important in the replacement of nonmycorrhizal species (Sect. 2.2 of Chapter 9A on symbiotic associations). Germination and seedling growth of nonmycorrhizal species are inhibited by the presence of mycorrhizal hyphae in the rhizosphere (Fig. 11). When P fertilization suppresses the mycorrhizal microsymbiont, the deleterious effects on root growth and functioning of nonmycorrhizal species become less pronounced. This might lead us to the erroneous conclusion that the growth of the plants whose biomass increases most strongly with P fertilization is more limited by P than is that of the mycorrhizal plants. If we go to the root of the problem, however, intricate allelochemical interactions that involve mycorrhizal fungi may well account for our field observations (Francis & Read 1994).

Mycorrhizal fungi can harm nonmycorrhizal plants, but the reverse may also occur. When *Glycine max* (soybean) is grown in the vicinity of the nonmycorrhizal species *Urtica dioica* (stinging nettle), infection of the soybean roots by the mycorrhizal fungus *Glomus mosseae* is inhibited (Fig. 12A). A fungitoxic **lectin** (Sect. 2.2 of Chapter 9A on symbiotic associations) distinctly inhibits the growth of fungal hyphae (Fig. 12B) which suggests that the lectin might be partly responsible for the effect of the presence of nonmycorrhizal species on the performance of mycorrhizal plants. Other lectins [e.g., from mycorrhizal hosts like *Triticum aestivum* (wheat), *Solanum lycopersicum* (tomato), or *Solanum tuberosum* (potato)] that have a high affinity for chitin have no antifungal properties (Schlumbaum et al. 1986). It remains to be firmly established if the lectin from roots and rhizomes of stinging nettle is the major factor that accounts for the effect of this nonmycorrhizal plant on mycorrhizal neighbors.

Herbivory has equally strong effects on competitive interactions, with the effect depending on the selectivity of herbivores. Plants that are

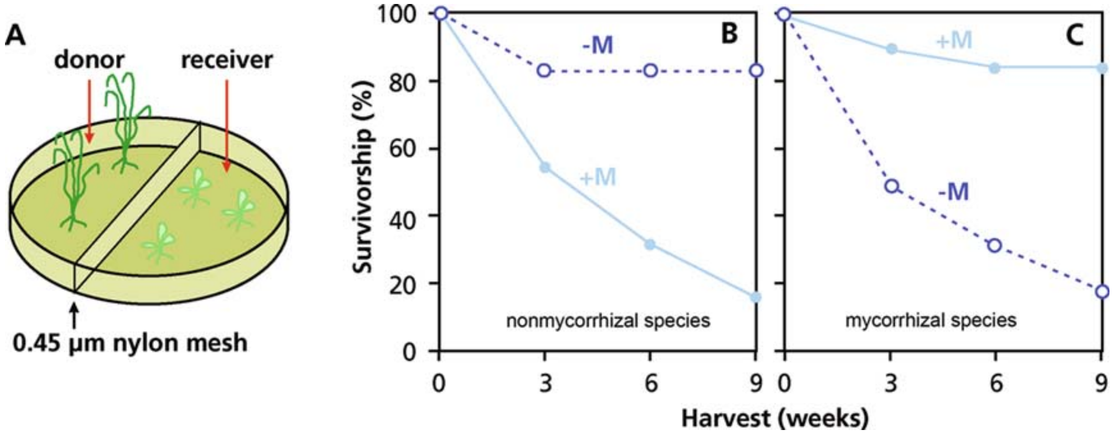

Figure 11. (A) Experimental design to assess the effect of the presence of mycorrhizal hyphae on the survival of seedlings of mycorrhizal and nonmycorrhizal species. (B) Effects of mycorrhizal fungi on seedling survival of the nonmycorrhizal *Arenaria serpyllifolia* (thyme-leaved sandwort). (C) Effects of mycorrhizal fungi on seedling survival of the mycorrhizal *Centaurium erythraea* (common centaury) (Francis & Read 1994).

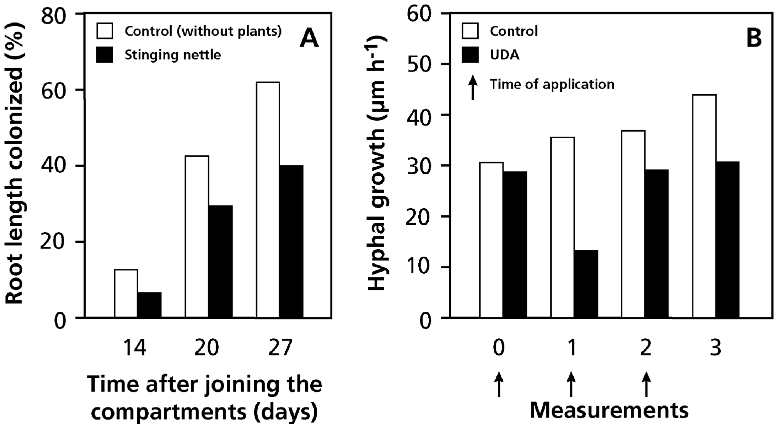

FIGURE 12. (A) Spread of the mycorrhizal fungus *Glomus mosseae* across the rhizosphere of *Urtica dioica* (stinging nettle) or control soil, without stinging nettle. Uncolonized *Glycine max* (soybean) plants were used as acceptor plants. They were separated from well-colonized soybean plants (donor plants) by a test container of soil planted with stinging nettle or a container of soil without plants. (B) Effect of agglutinin from *Urtica dioica* on the hyphal growth of *Glomus mosseae.* The growth of hyphae of germinated spores was measured after application of small droplets of purified agglutinin. Application was repeated at 1 hour intervals (arrows) (Vierheilig et al. 1996).

selectively grazed, due to low defensive investment or other reasons, always have a reduced competitive ability compared with ungrazed neighbors. In the presence of nonselective grazing (the "lawnmower effect"), however, species that lack well-developed defensive mechanisms are typically more tolerant of grazing (Bryant & Kuropat 1980, Rosenthal & Kotanen 1994).

8. Succession

Successional changes in species composition following disturbance are the net result of different rates of **colonization**, **growth**, and **mortality** of early and late-successional species (Egler 1954, Walker & del Moral 2003). Competition and facilitation both play strong roles in successional change, and the resulting change in species composition through succession is associated with predictable changes in ecophysiology. The physiology of initial colonizers differs strikingly between primary succession, when plants colonize an area for the first time, and secondary succession, when plants recolonize previously vegetated areas after disturbances such as fire or agriculture. Soils in primary succession typically have low N and organic matter content (Fig. 6.1A of Chapter 6 on mineral nutrition).

Primary-successional soils initially lack a buried seed pool, requiring colonizers to disperse to the site, whereas secondary-successional sites are colonized from the buried seed pool, resprouting individuals, and dispersal to the site. Propagules of early colonizers of primary succession have seeds that are as small as, or smaller than, those of species that colonize secondary succession, which, in turn, are smaller than seeds of late-successional species (Fig. 13), perhaps because colonizers of many primary-successional environments have further to travel than do secondary-successional colonizers. The larger **seed size** of late-successional species (see also Sect. 3.1 of Chapter 8 on life cycles) provides reserves to support growth in fully vegetated sites, where competition is likely to be more intense.

When grown under favorable laboratory conditions, early-successional species grow more rapidly than do late-successional species. A high **RGR** (Sect. 2) is a trait selected for, as pointed out by Grime (1977). A high RGR is associated with a high specific leaf area (SLA; Sect. 3.1 of Chapter 7 on growth and allocation). Colonizers of primary-successional habitats have lower RGR than do colonizers of more fertile secondary-successional disturbed sites (Fig. 14) which suggests that among colonizing species low soil fertility has selected for species with traits that cause low RGR. A low RGR is associated with a low SLA

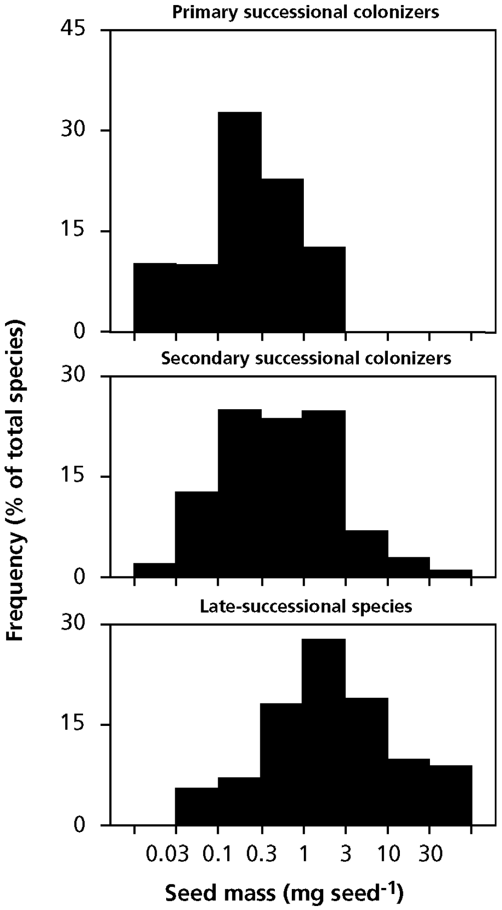

Figure 13. Frequency distribution of log (seed mass) for British species that are colonizers of primary-successional (skeletal, $n = 60$ species), secondary-successional (disturbed, $n = 88$ species), or late-successional (woodland, $n = 58$ species) habitats. Data calculated from Grime et al. (1981).

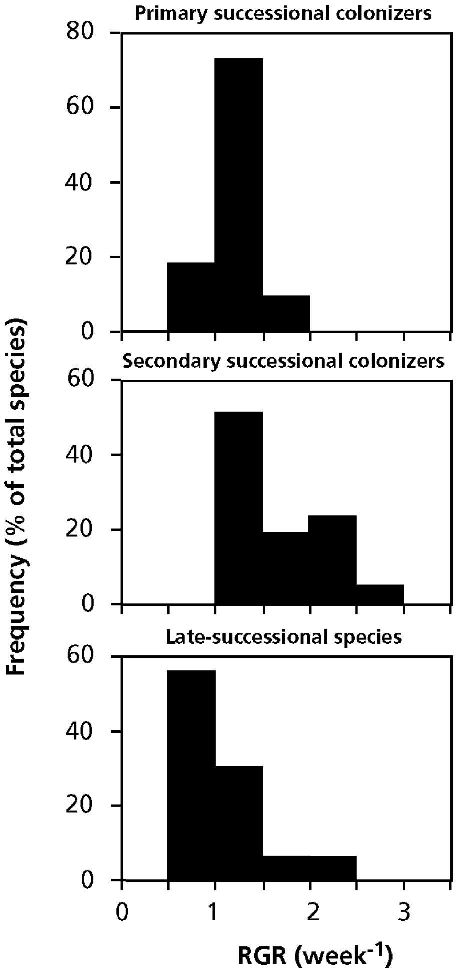

Figure 14. Frequency distribution of RGR for British species that are colonizers of primary-successional (skeletal), secondary-successional (disturbed), or late-successional (woodland) habitats. Calculated from Grime & Hunt (1975) after classifying species according to Grime et al. (1981).

(Sect. 3 in Chapter 7 on growth an allocation), which is accounted for by a large investment in quantitative defense (Sect. 3.2 in Chapter 9B on ecological biochemistry). Plants that occur at later-successional stages may also have nutrient-acquisition strategies that deplete the soil nutrients to a greater extent (Sect. 2), as pointed out by Tilman (1988, 1990).

Early-successional trees or shrubs invariably have higher rates of **photosynthesis** on an area basis than do those that appear later in succession (Table 1; Raaimakers et al. 1995, Owens 1996). When the light-saturated rates of photosynthesis of shrubs (Table 1) are compared with those of the final climax tree species, *Fagus sylvatica* (beech) which are only as low as 3–4 µmol m^{-2} s^{-1}, it is quite obvious that high rates of photosynthesis cannot explain the replacement of early-successional species by later ones. The late-successional and invasive species have a more positive carbon balance, due to their greater leaf area and better exposure of the leaves. The physiological mechanisms accounting for leaf expansion and leaf exposure are clearly far more important than are the photosynthetic capacity of individual leaves in explaining the outcome of competition.

As with photosynthesis, early- and mid-successional species typically have higher potential to absorb nutrients than do late-successional species

TABLE 1. Photosynthetic characteristics of a number of Central European woody species from a hedgerow.

Photosynthetic trait, units	Species, time of appearance during succession, and competitive ability				
	Rubus corylifolius (blackberry) early pioneer, low competitive ability	*Prunus spinosa* (blackthorn) later pioneer	*Crataegus macrocarpa* (hawthorn) late-successional	*Acer campestre* (field maple) late-successional	*Ribes uvacrispa* (gooseberry) later-successional shrubby undergrowth species
A_{max} (μmol m^{-2} s^{-1})	11–15	9–12	8–12	8–11	6–14
Stomatal conductance at A_{max} (mmol m^{-2} s^{-1})	150–250	350–450	350–500	150–200	150–350
Photosynthesis per unit leaf N [μmol g^{-1} (N) s^{-1}]	8.6–11.6	4.7–6.3	3.6–5.3	4.3–5.9	4.5–10.5
Photosynthesis per unit leaf [μmol g^{-1} (P) s^{-1}]	83–113	56–75	30–45	44–60	62–144

Source: Küppers et al. 1984.

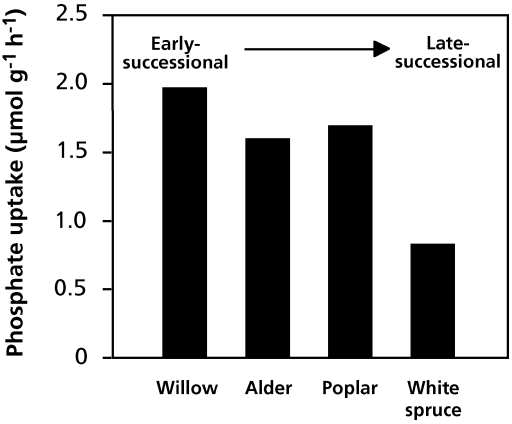

FIGURE 15. Rate of P_i uptake by excised roots of tree seedlings from an Alaskan primary-successional floodplain sequence grown in a glasshouse (after Walker & Chapin 1986).

(Fig. 15). This could reflect their high potential growth rate and, consequently, the high nutrient demands of colonizing species.

Herbivores are often a major cause of plant mortality during succession. Late-successional species, with their long-lived leaves have higher concentrations of defensive compounds and are therefore less palatable than early-successional species (Fig. 16).

In summary, the changes in ecophysiological traits through succession are identical to those described earlier in species that compete effectively in high- vs. low-resource sites, explaining the change in competitive balance that causes species replacement through succession.

9. What Do We Gain from This Chapter?

There is no single ecophysiological trait that gives a genotype competitive superiority. The outcome of competition may be due to the occurrence of an event, such as flooding, frost, fire, or drought, with which one genotype is better able to cope and therefore survive, whereas other genotypes may lose out. Superior traits in one environment (e.g., a low tissue mass density, which is associated with rapid growth when nutrients are plentiful) may be inferior traits in a different environment, when a low tissue density is associated with relatively large losses of nutrients when nutrients are scarce. These trade-offs among suites of physiological traits are critical to understanding patterns of competitive success in different environments.

Competitive advantage may depend on a plant's secondary metabolism (i.e., the exudation of allelochemicals that harm other plants, excretion of compounds that solubilize sparingly available nutrients or detoxify harmful soil components, production of chemicals that chelate Al or heavy metals, or the accumulation of defensive compounds that reduce the effects of herbivore attack and diseases). If plants did not produce such defense compounds, they might be able to grow faster in productive environments. In the longer term, however, such plants may succumb to pests or attack by a pathogenic bacterium, such as *Crataegus monogyna* (hawthorn) in Europe and many *Acacia* species in Australia. When released in a foreign environment, where such pests are absent, some species may become invasive [e.g., *Acacia saligna* (orange wattle) from

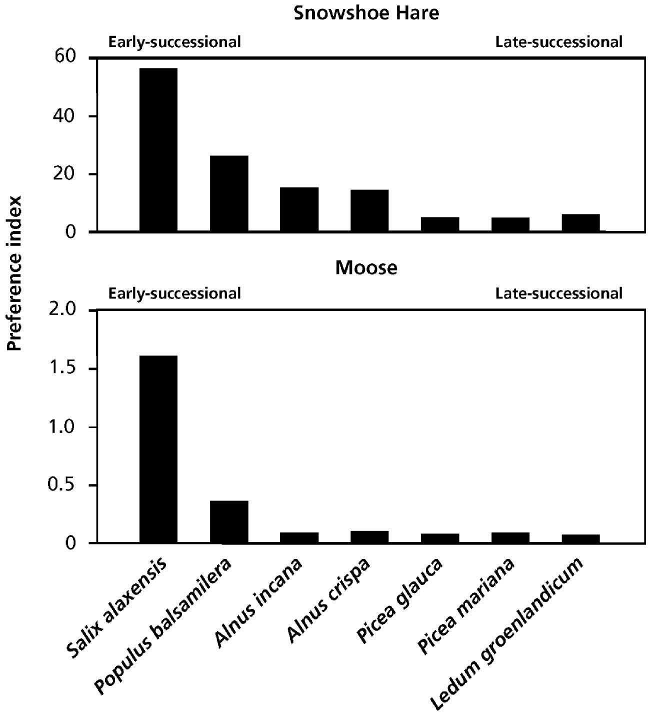

Figure 16. Preference by two species of herbivores for plant species from an Alaskan primary-successional floodplain sequence (after Bryant & Chapin 1986).

Australia, which was introduced in South Africa to stabilize sand dunes (New 1984)]. Other examples include *Prunus padus* (bird cherry) from North America which was introduced in Western Europe, and *Salix* species (weeping willow) from Asia and *Rubus corylifolius* (blackberry) from Europe, both of which now invade river valleys in Australia.

A large phenotypic plasticity for various plant traits (e.g., photosynthetic characteristics, nutrient acquisition, and stem elongation) may also contribute to competitive success. In addition, competitive advantage may be based on a profitable association with another organism, such as a symbiotic N_2-fixing microorganism, a mycorrhizal fungus, or a higher plant, that happens to be a suitable host to parasitize.

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