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# PLANT COMPETITION UNDERGROUND

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## ABSTRACT

Belowground competition occurs when plants decrease the growth, survival, or fecundity of neighbors by reducing available soil resources. Competition belowground can be stronger and involve many more neighbors than aboveground competition. Physiological ecologists and population or community ecologists have traditionally studied belowground competition from different perspectives. Physiologically based studies often measure resource uptake without determining the integrated consequences for plant performance, while population or community level studies examine plant performance but fail to identify the resource intermediary or mechanism. Belowground competitive ability is correlated with such attributes as root density, surface area, and plasticity either in root growth or in the properties of enzymes involved in nutrient uptake. Unlike competition for light, in which larger plants have a disproportionate advantage by shading smaller ones, competition for soil resources is apparently more symmetric. Belowground competition often decreases with increases in nutrient levels, but it is premature to generalize about the relative importance of above- and belowground competition across resource gradients. Although shoot and root competition are often assumed to have additive effects on plant growth, some studies provide evidence to the contrary, and potential interactions between the two forms of competition should be considered in future investigations. Other research recommendations include the simultaneous study of root and shoot gaps, since their closures may not occur simultaneously, and improved estimates of the belowground neighborhood. Only

by combining the tools and perspectives from physiological ecology and population and community biology can we fully understand how soil characteristics, neighborhood structure, and global climate change influence or are influenced by plant competition belowground.

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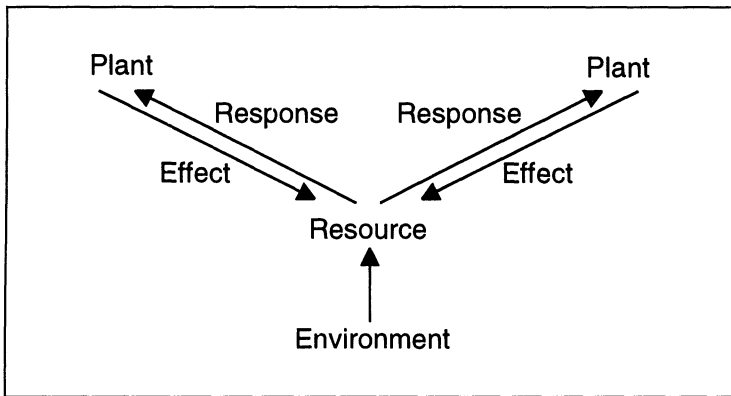
## INTRODUCTION

Much of the competition among plants takes place underground. In contrast to aboveground competition which primarily involves a single resource, light, plants compete for a broad range of soil resources, including water and at least 20 essential mineral nutrients that differ in molecular size, valence, oxidation state, and mobility within the soil. Belowground competition often reduces plant performance more than does aboveground competition (141), and it is the principal form of competition occurring in arid lands or other systems with extremely low plant densities (47).

We review the mechanisms and ecological importance of belowground competition, emphasizing the certainties and uncertainties that have made it a productive area of research. We begin by describing the processes by which soil resources reach roots and consider plant traits and soil properties likely to affect competition for those resources. We then discuss how belowground competition is measured, describing current methods and their limitations. Next, we consider several questions related to the roles of belowground plant competition in population structure, community organization, and vegetation dynamics. Finally, we suggest a number of research directions for the future. We attempt to combine the dual perspectives of physiological ecology and population or community ecology; one of our goals is to promote the merging of tools and perspectives from these disparate fields to foster progress in the future.

## DEFINITION OF BELOWGROUND COMPETITION

We apply Goldberg's definition of competition (50), which takes into account how plants affect the abundance of an intermediary and how other plants respond to the change in abundance (Figure 1). For resource-mediated competition to occur belowground, a plant must have a negative effect on the availability of some belowground resource to which another plant shows a positive response in growth, survival, or reproduction (50). In other words, the reduced level of the intermediary has a negative impact on the performance of competing plants measured per individual or per unit size. In reality, studies typically focus on only one aspect of the competitive interactions described in Figure 1.



*Figure 1* Plant competition as characterized by (50). In this framework plants must have an effect on the abundance of a resource and other plants must respond to the change. Both the effect and the response must be of appropriate sign for competition to occur.

Physiologically based studies commonly identify how resource uptake by one individual affects the quantity of resource taken up by another without determining the consequences for plant performance. Population or community level approaches rely on phenomenological responses of plants but usually fail to identify the intermediary resource.

Under our working definition of competition, the ability to take up soil resources and competitive ability are not necessarily correlated. For example, a plant may improve water uptake by growing a deeper root system and tapping a source of water unavailable to more shallow-rooted neighbors. Such habitat partitioning may not increase and could even decrease competition for water, although competition for mineral nutrients or light may increase as a consequence of more vigorous plant growth or increased plant densities. Likewise, drought may increase density-independent mortality of seedlings simply because their root systems are not well developed. Plants also differ in their ability to convert soil resources to biomass, referred to as water-use efficiency or nutrient-use efficiency (95), and these differences can affect relative plant growth rates across a soil resource gradient even in the absence of belowground interactions.

By limiting our discussion to resource-mediated plant competition, we ignore interference competition occurring through allelopathy (82), information-acquiring systems that allow plants to respond to neighbors prior to resource reduction (5a), and resource competition between plants and soil microbes (73). These are ecologically important but beyond the scope of this review.

## RESOURCE UPTAKE AND MECHANISMS OF COMPETITION

Soil resources reach the root surface through three general processes: 1. root interception, 2. mass flow of water and nutrients, and 3. diffusion (84). Root interception is the capture of water and nutrients as the root grows through the soil, physically displacing soil particles and clay surfaces. In general, root interception accounts for less than 10% of resource uptake by roots and is the least important of the three processes (84). Mass flow of water and dissolved mineral nutrients is driven by plant transpiration and is a function of the rate of water movement to the root and the concentration of dissolved nutrients in the soil solution. Diffusion of nutrients toward the root occurs when nutrient uptake exceeds the supply by mass flow, creating a local concentration gradient. Diffusion is especially important for nutrients with large fractions bound to the solid soil matrix, such as potassium and phosphate, whereas mass flow is often more important for nitrogen, particularly nitrate. Supply of the three major nutrients (N, P, and K) almost always depends on diffusion and mass flow working together (96), and the two processes are difficult, if not impossible, to separate experimentally in the field.

The size of the concentration gradient surrounding roots, referred to as the depletion zone, and the rate of ion diffusion depend on several factors (84). The effective diffusion coefficient ( $D_e$ ) is the term applied to the mobility of nutrient ions; it depends on the ion's rate of diffusion in water, the volumetric water content of the soil, the impedance of the soil structure to ion movement through the aqueous fraction, and the ability of the soil matrix to release nutrients into the soil solution. Both the diffusion coefficient and the width of the depletion zone increase with soil water content. The width of the depletion zone also increases with overall nutrient concentration and with the root's ability to depress the nutrient concentration at its surface.

Among mechanisms of root interactions, competition via diffusion has received the most attention. Neighboring roots reduce nutrient uptake when nutrient depletion zones overlap (6, 96). For a given interroot distance, the degree of competition increases as effective diffusion increases, resulting in potentially greater competition for nitrate ions than for potassium or the relatively immobile phosphate ions. The relationship between the width of the diffusion zone and overall soil nutrient levels may imply that competition occurs at lower root densities in high nutrient soils than in low nutrient soils. The concept of overlapping diffusion zones is less applicable to water and dissolved nutrients that are primarily supplied to the root by mass flow. For those nutrients, competition must depend both on nutrient uptake and water uptake, driven by transpiration. Aboveground attributes such as maximum transpiration or stomatal conductance will both affect and be affected by rates of water uptake (113a).

## TRAITS RELATED TO BELOWGROUND COMPETITIVE ABILITY

With a basic understanding of the processes involved in the acquisition of soil resources and the mechanisms by which competition for those resources takes place, we now consider morphological and physiological attributes likely to improve belowground competitive ability. Figure 2 provides a conceptual outline of important traits.

### *Root Surface Area and Rates of Resource Uptake*

Of primary importance in belowground competition is the occupation of soil space. The ability to occupy space depends on several root characters, including relative growth rate, biomass, fine root density, and total surface area. As an example, Aerts et al (1) grew two evergreen shrubs and a perennial grass in a replacement series in the field with four competition treatments: no competition, aboveground only, belowground only, and above- and belowground together. The superior competitor in the experiment was the grass *Molinia caerulea*, which allocated three times the proportion of biomass to its roots as did either of the shrubs and was the only species to extend roots into the soil compartment of competitors. The authors concluded that its success was due in large part to

### Belowground Competition In Plants

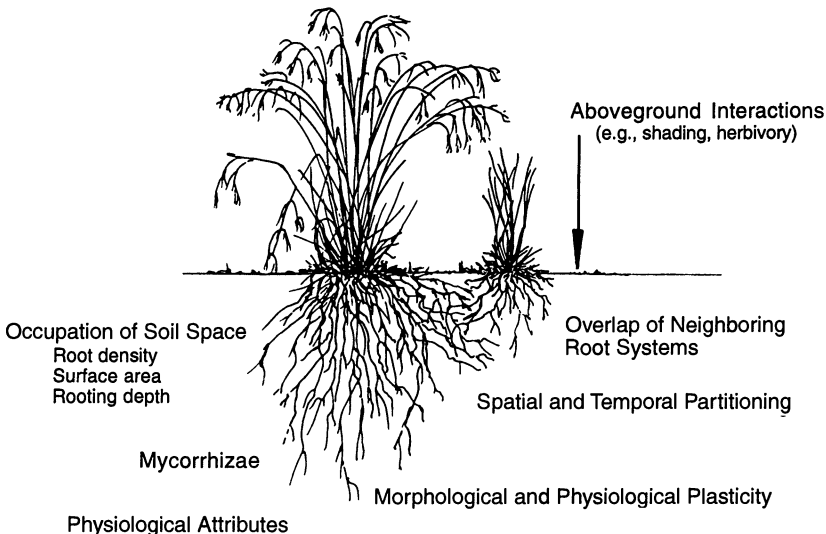


Figure 2 Plant traits that influence belowground competitive ability.

its high productivity and extensive root system. One of the only field experiments to measure root densities and nutrient uptake in competing root systems (20, 22) showed that root abundance alone was insufficient to explain relative nutrient uptake among three species in the sagebrush steppe. The non native tussock grass *Agropyron desertorum* had eight- to tenfold more roots in nutrient patches than did sagebrush, *Artemisia tridentata*, one week after the patches were created, and four- to sixfold more roots at three weeks. Despite this difference, the two species acquired the same amount of phosphate from the patches. The shrub also took up six to eight times more phosphate than did a native grass, *Pseudoroegneria spicata*, despite greater root densities for the grass.

Several factors may explain the lack of direct correspondence between root density and the outcome of belowground competition. First, competition may also occur among roots on the same plant, so the return per investment in new root growth may decline at higher root densities. Second, where and when roots are deployed may be just as important as average root density. A plant with much root surface area in one region of the soil might be poorly represented in a second region or less able to concentrate its roots in localized nutrient patches, or rooting density may vary temporally. Third, mycorrhizae play an important role but are frequently ignored in studies of nutrient acquisition, and fourth, physiological properties related to the rate of uptake are also crucial to competitive ability.

As a simplification, nutrient uptake by roots in most natural systems is governed by apparent Michaelis-Menten kinetics:

$$V = V_{\max} C_1 / (C_1 + K_m) \quad 1.$$

where  $V$  is the flux of ion into the root per unit time,  $V_{\max}$  is the maximum such influx rate,  $K_m$  is the soil solution concentration where influx is  $0.5 \times V_{\max}$ , and  $C_1$  is the soil solution concentration at the root surface (96). The equation is sometimes modified to include a  $C_{\min}$  term, the soil solution concentration at which net influx into the root is zero (7). A species with more enzymes per root surface area (greater  $V_{\max}$ ), a higher ion affinity of enzymes (smaller  $K_m$ ), or a greater ability to draw nutrients down to a low level (smaller  $C_{\min}$ ) will be at a competitive advantage, all else being equal.

### *Morphological and Physiological Plasticity*

The ability to make morphological or physiological adjustments to the local soil environment may be critical to a plant's belowground competitive success.

Advantages of plasticity must be viewed both in terms of how much additional resource is taken up and how quickly because increasing the rate of uptake could be very important in the presence of competitors. Many plants respond to

nutrient-enriched patches of soil by root proliferation (37, 38, 134). Proliferated roots tend to be smaller in diameter and greater in density than those found in the background soil, and consequently they have much greater surface area. In an experiment with eight British herbs, Campbell et al (25) showed that species with large rooting areas were less able to place roots selectively in high-nutrient patches, suggesting a trade-off between the ability to explore large soil volumes and that to exploit nutrient-rich patches. Beyond those experiments, we know little about scales of root foraging across broad groups of species. A factor rarely considered is fine root demography (59). When *in situ* root growth was examined for a hardwood forest in northern Michigan (100), roots were found to proliferate in response to localized water and nitrogen additions, and new roots in enriched patches lived significantly longer than new roots in control patches. Lengthening the lifespan of a root may be just as effective for a plant as growing a new cohort of roots and potentially less expensive (41).

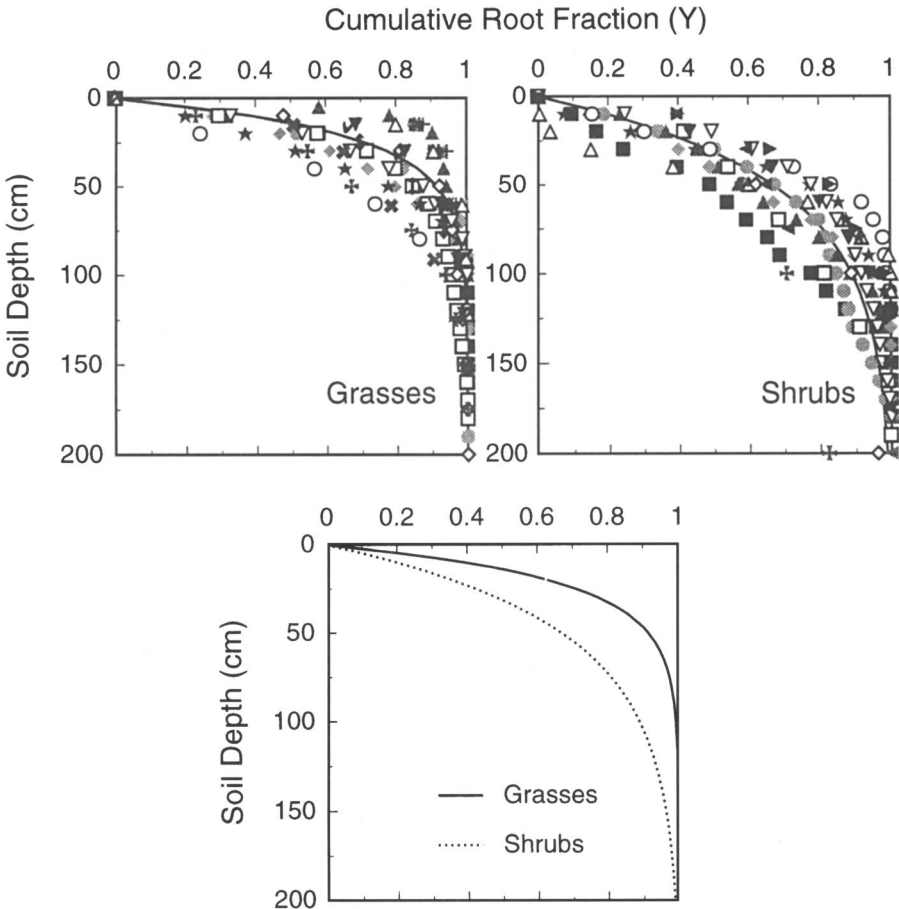
Architectural adjustment is another type of morphological plasticity with the potential to increase resource capture (44,45). While selective biomass allocation is architectural in a broad sense, we refer instead to local changes in topology, root length, or branching angles. Fitter (44) examined root architectural attributes of 11 herbaceous species. On average, roots in relatively high-nutrient patches had more of a herringbone branching pattern than did roots in low-nutrient patches. The herringbone pattern can increase the efficiency of nutrient uptake by concentrating higher order lateral roots in the enriched patch (45).

Physiological plasticity involves changes in uptake rates attributable to altered enzyme attributes or other physiological traits. In the case of mineral nutrients, plants in the laboratory and in the field both increase  $V_{\max}$  and decrease  $K_m$  in response to local increases in nutrient concentration (37, 71, 79). For water, osmoregulation can lower cell water potential and maintain net uptake in the face of drying soils (15, 117). To show that plants are able to increase uptake by selectively altering physiological attributes is different from predicting when and if it is beneficial to do so. Another factor not usually considered is the cost involved in constructing or operating additional enzymes (40). For mineral nutrients, mobility within the soil is also important (16). When competition occurs through overlapping depletion zones, physiological plasticity should increase the uptake of relatively mobile nutrients (e.g. nitrate) more than the uptake of less mobile ones (e.g. ammonium, phosphate). Conversely, root proliferation may be less beneficial for the uptake of relatively mobile nutrients, since a single root depletes a broader volume of soil (96, 109). For extensive overviews of morphological and physiological plasticity and resource capture, see (33, 66, 108).



### *Spatial and Temporal Soil Partitioning*

Some spatial and temporal rooting patterns seem to reduce belowground competition, thereby probably falling into the general category of niche separation. Although the majority of roots are found within the top 30 cm of soil, some reach great depths (70, 92, 106, 119). At least 50 species grow roots more than 5 m deep, 22 species reach below 10 m, and several desert species reach 50 m (26). These numbers almost certainly underestimate the importance and frequency of deep roots in many ecosystems because the study of deep soil



**Figure 3** The distribution of grass and shrub roots as a function of soil depth. The data are from deserts, temperate grasslands, and tropical grasslands where the two growth forms potentially co-occur. See (70) for a key to the symbols.

has been largely neglected. Whether deep roots are engaged in belowground competition depends on the rooting depth of neighboring plants.

The lack of secondary thickening in roots of grasses and many herbs places a morphological limit on their ability to grow deep roots and provides an *a priori* rationale for separating plants into different belowground functional groups. Walter (131) first proposed the two-layer model of deep- and shallow-water partitioning between grasses and shrubs/trees in subtropical savannas. This simple model remains a useful way of subdividing vegetation by resource use (78, 105, 112, 129), and a recent comprehensive analysis (70) showed distinctly different rooting profiles for plants of the two groups (Figure 3). Analyses of hydrogen isotope ratios in plant tissues verified that the two groups acquire water from different depths (39). Some spatial and functional root overlap does occur between grasses and woody plants, however. Some grass roots are more than 5 m deep (134), and many woody plants are capable of taking up resources from both shallow and deep layers (32).

Spatial and temporal partitioning of soil resources can be related. Deep roots may allow plants access to a water source available after upper soil layers have dried out, enabling them to decouple the timing of growth from rainfall events, persisting after neighboring species have died or become dormant. Examples of temporal partitioning include early and late season annuals in the Mediterranean climate of California (88), shrub species of the Great Basin (42), and various trees (80).

## MEASUREMENTS OF BELOWGROUND COMPETITION

Belowground competition is measured by quantifying the extent that root interactions reduce resource uptake, vegetative growth, or fecundity. Population or community level approaches generally estimate belowground competition from biomass increases when interactions with neighboring roots are prevented through the use of root exclusion tubes, trenching, or neighbor removal. Such methods often alter the soil environment and may even affect the availability of resources for which the plants are competing. Resource-based approaches usually involve less manipulation of the environment, but the integrated consequences of competition for plant performance are often unknown or require assumptions of scaling. Combining approaches is necessary to document both the resource intermediary and the ecological significance of belowground competition.

Root exclusion tubes (30, 103) are frequently employed in population or community level studies. Typically, these cylindrical steel or plastic partitions are inserted into the soil to separate the roots of target individuals, usually

transplanted seedlings, from those of neighboring plants. Root competition is determined by comparing the growth or survival of target plants inside the partitions with those having roots systems that can interact freely with neighboring vegetation. Neighbors within partitions are killed by a fast-degrading herbicide, severed at the soil surface to remove shoots, or removed completely by excavating, sieving, and replacing the soil. By varying the length of the tubes, some studies have determined the soil depths at which the belowground competitive interactions take place (30, 103). Two related methods are neighbor removal without using exclusion tubes and trenching, which severs the roots of potential competitors so they do not extend into the rooting area of target plants. Trenching is often used for woody species with extensive root systems (10); a good recent example shows strong root competition between alder and spruce (29). Both neighbor removal and trenching attempt to eliminate belowground interactions without using a physical barrier (though some trenching experiments insert a root-restriction fabric to impede regrowth) and without much physical disturbance of the soil.

These methods all suffer from the possibility that soil resources are altered by the experimental protocol. A major worry is that roots left to decompose may release bursts of nutrients (11, 101) or result in nutrients being sequestered by rapidly growing populations of soil microorganisms (34). A greenhouse bioassay experiment (87) addressed this issue by comparing growth of two target plant species over three months in undisturbed field soil, soil that had been sieved to remove roots, and sieved soil to which roots had been added back. Root removal did not affect the performance of either species, but for the mycorrhizal species, soil disturbance lowered mycorrhizal infection and shoot growth. The results suggest that shoot removal alone or the application of herbicides may be preferable to removing roots physically.

Two additional concerns are related to potential differences in root growth rates in empty versus root-occupied soil and the extent that exclusion tubes create undesirable side effects. Starting with empty soil in treatments where neighbors' roots are allowed access to the space (49) may be comparable to greenhouse pot experiments, which Grubb (60) suggested could give fundamentally different measures of competition than field experiments in which root systems are already in place. He proposed that differences in the rates that roots fill vacant soil space may explain why greenhouse experiments, more often than field experiments, show an increase in root competition with increasing nutrient levels. Undesirable side effects of root exclusion tubes include restricting lateral movement of water and nutrients. Newer, more sophisticated "tubes" employ modern fabrics with small pore sizes that permit passage of water but not nutrients and exclude roots but not mycorrhizal hyphae (81). Since soil space itself may be a resource (85, 86), consideration should also be given to

tube diameter and whether restricting lateral root spread has consequences for target plant biomass.

Physiologically based approaches identify the currency of the competition, examining the effect of belowground competitors on the acquisition of particular resources. In a study that documented interspecific differences in competitive ability, Caldwell et al (19) used a dual-labeling approach with  $^{32}\text{P}$  and  $^{33}\text{P}$  to examine competition in the sagebrush and grass system described earlier. By growing each grass species on opposite sides of the same sagebrush plants, and placing one label in the soil on each side of the shrub, they showed that the shrub took up 86% of its phosphate from the side shared with *P. spicata*. Although an elegant demonstration of interspecific effects on resource uptake, it is unclear how such short-term differences affect long-term plant performance.

## EFFECTS OF THE SOIL ENVIRONMENT

Ecologists use the above methods to examine the role of belowground competition in natural systems, a subject that can be separated into two broad topics. The first deals with the influence of the soil environment on belowground competitive interactions, and the second examines how characteristics of neighboring plants figure in the interactions.

### *Productivity Gradients*

One active line of research concerns whether the strength of belowground competition changes in a consistent way over gradients in habitat productivity. The research is motivated by two models with different predictions about the relationship between competition and soil resource levels. Grime (54, 55) suggested that more productive sites should exhibit greater overall importance in competition for both aboveground and belowground competition. Tilman's (120, 121) resource ratio model predicted no change in total competition as productivity increases but an increase in the ratio of aboveground to belowground components.

Experimental tests of these models require separating the effects of above- and belowground competition on plant growth. Root competition is measured as growth reduction in the presence of only neighboring roots, while total competition is measured as growth reduction in the presence of both roots and shoots of neighbors. Many studies do not measure shoot competition directly but calculate shoot competition as the difference between total competition and root competition. Most calculate competition as competitive intensity, where growth reduction is expressed on a percentage basis. This standardizes measurements to account for differences between sites in overall plant growth rates (51). Experimental systems include artificial productivity gradients created by

adding fertilizer, and natural productivity gradients, where biomass standing crop is often used as an indicator of soil resource levels.

Experimental studies assessing competition as a function of habitat productivity often show a decrease in the magnitude of belowground competition with increased soil resource levels. It is premature, however, to generalize about the relative importance of above- and belowground competition under various soil resource conditions. In a Minnesota old field, the terrestrial system where Tilman has tested his model, nitrogen addition resulted in decreased belowground competition but no change in total competition for most species (142–144). Another study using tree seedlings planted under shrubs in three abandoned agricultural fields obtained similar results (102). This study measured aboveground and belowground competition independently and found that competition was largely belowground in the most xeric, nutrient-poor site, whereas shoot competition was stronger than root competition in the most productive site. Root and shoot competition acted together to reduce plant growth at the intermediate site. In contrast, a study comparing competition in two wetland habitats differing in standing biomass found that both the forb *Lythrum salicaria* and the sedge *Carex crinita* experienced greater aboveground and total competition in the more productive site, but the gradient in belowground competition differed between species (124). Belowground competition increased with productivity for *C. crinita* but decreased for *L. salicaria*.

Since standing biomass is often used as a proxy for resource levels, it is important to understand the relationship between neighbor biomass and competitive intensity. For example, Belcher et al (9) recognized that the relationship may be nonlinear, their explanation for why total competitive intensity did not increase over a soil depth gradient in shallow limestone-derived soils in Ontario. In that system, standing biomass was positively correlated with soil depth, but neither total competition nor root competition was correlated with standing biomass or soil depth; aboveground competition was insignificant. They suggested that competition may increase with neighbor biomass until some asymptotic level of competition is reached; additional biomass would have no additional effect on competition. An asymptotic relationship would mean that the inclusion of sites with relatively low standing crop would be more likely to detect a correlation between biomass and competition.

Belowground competition is thought to be the main component of competition in arid systems because low plant densities often result in minimal shading by neighbors. While we know of no studies specifically examining relative changes in root and shoot competition over aridity gradients, total competition has been compared among sites differing in soil moisture in desert or semi-desert habitats (61, 72, 98). Results often point to competition increasing as water becomes more abundant and productivity increases. Rainfall patterns can result

in temporal soil moisture gradients, and the magnitude of density-dependent interactions also seems to decrease in dry years (8, 27, 46, 72). Without knowing the relative contributions of aboveground and belowground interactions, one cannot determine whether competition for water really increases with water availability—one explanation for these results. Under extreme aridity, shading can be beneficial by ameliorating temperatures and lowering evaporative water loss from plants and soil. These benefits may sometimes outweigh any detrimental effects of belowground or aboveground competition and result in facilitation between closely associated individuals (23, 53).

Belowground competition may not necessarily decrease with increasing levels of soil resources for at least two reasons. First, standing crop usually increases with soil resource levels, and many of the above studies found correlations between neighbor aboveground biomass and total competitive intensity. Of relevance to understanding the role of soil resources in affecting competition is whether the relationship between competition and standing biomass varies with soil resource levels; both water addition and nutrient addition have been found to change the slope of the regression relationship (72, 144). Second, understanding how nutrient levels affect the size of depletion zones leads to the prediction that competition will sometimes take place at lower root densities with increasing nutrients. Even though nutrient uptake per length of root may be greater under high nutrient conditions, the potential for uptake to be affected by neighboring roots may also be greater there. Some workers have argued that the development of depletion zones may result in strong competition even in fertile soils (24, 56, 57, 141), and the same could hold for water as well.

### *Heterogeneity in Soil Resources*

Competition for soil resources may also change with their spatial and temporal distribution. The practical difficulties such variation presents for predicting crop yields were recognized early this century (133), and natural systems are just as variable at both fine and coarse scales (107, 118). While heterogeneity at scales as large as or larger than the rooting area of a plant is likely to affect relative plant performance and contribute to the maintenance of species diversity (123), fine-scale heterogeneity, occurring where root systems overlap, should have the greatest direct impact on belowground interactions. Campbell et al (25) suggested that small-scale heterogeneity may be even more important than average soil nutrient levels in determining competitive outcome. Likewise, Gross et al (59) suggested that small-scale heterogeneity, which increases in old fields over time, may be a factor contributing to successional vegetation changes in that habitat.

Numerous studies have documented fine-scale variation in nature and the ecological importance of its occurrence. In a classic study of *Trifolium repens*,

Snaydon (118) showed substantial variation in soil pH, calcium, and phosphate at scales of less than a meter in a Welsh grassland; documenting this variation was critical for understanding the local distribution of the species. In a later study, Jackson & Caldwell (68) found on average that soil ammonium and nitrate varied more than ten-fold in the rooting zone of individual plants in the sagebrush steppe. Phosphate at the same site varied three-fold around single plants, and soil pH differed up to 1.3 units in samples less than half a meter apart. A more recent study in the same system has shown that such spatial variability in mineral nutrients and water does not remain constant (111); both spatial patterning and the scale of heterogeneity changed over a single growing season.

Understanding how heterogeneity influences competitive outcome is an area that would especially benefit from integrating resource-based and higher level approaches. Much is known about the ability of roots to respond morphologically and physiologically to nutrient patches, but less is understood about how patchiness influences competition. There are two general possibilities. If co-occurring species differ simply in ability to harvest soil resources from patches, then heterogeneity may affect their relative performance, independent of competition. A second possibility is that heterogeneity directly alters the dynamics of root interactions. Since roots can proliferate in nutrient-rich patches, heterogeneity may result in spatial aggregation of competing root systems, potentially intensifying belowground competition.

Most information regarding the consequences of heterogeneity on plant performance come from studies of isolated plants grown in pots or hydroponic media. Plant growth is often enhanced when nutrients are patchily distributed in space and time (11a, 108). In experiments varying the spatial distribution of phosphate to potted crop plants plant growth increased as the same amount of phosphate was applied to smaller fractions of the soil volume (5, 14). This is thought to occur because a localized, more concentrated application of phosphate increases the amount in the soil solution proportionately more than it does the amount bound to the solid phase in forms unavailable to plants (75). While there are no similar data from field studies, model simulations based on measurements of spatial nutrient variability and root plasticity in the sagebrush steppe showed that spatial heterogeneity should result in more uptake of nitrate and phosphate than when the same quantities of nutrients are uniformly distributed (69).

At the population level, heterogeneity in the form of alternating 640 cm<sup>3</sup> patches of high and low nutrients was nearly inconsequential for the population structure of *Abutilon theophrasti* when compared to populations growing on a homogeneous mixture of the same two soil types (28). Heterogeneity increased productivity only at an intermediate planting density and slightly lowered mortality overall. Heterogeneity also did not affect plant size variation within the

population, which would be expected if plants competed for patches, but did influence the ranking of plants within the population size hierarchy. Plants with stems located on high-nutrient patches were larger than individuals on low nutrient patches, probably because they grew faster as seedlings and gained dominance within the population. In populations of *Ocimum basilicum*, localization of nutrients within a thin horizontal layer increased local rooting densities, presumably increasing belowground competition, and lowered the intercept of the self-thinning line for both root biomass and shoot biomass (90). This occurred only when nutrients elsewhere were extremely limited.

Evidence that neighbors can affect access to resource patches is limited. Caldwell et al (21) removed frozen soil cores from interspaces between individuals of sagebrush and the same two grass species used in previous experiments and quantified the distribution and identity of fine roots within the cores. Roots of the sagebrush were more abundant when the soil space was shared with *P. spicata* than with *A. desertorum*. When nutrient patches were created between plants by fertilizing with a solution containing nitrate and phosphorus, both overall rooting densities and the proportionate representation of sagebrush roots increased. The proximate cause of these particular rooting distributions is not known. Other studies have found little evidence for species-specific root recognition among the same three species (65, 76). Species-specific root avoidance has been demonstrated, however, in at least one system (82).

## THE BELOWGROUND COMPETITIVE NEIGHBORHOOD

In this section we explore belowground competition within the context of population and community structure. We discuss interactions between aboveground and belowground competition, the relationship between plant size and belowground competitive ability, the structure of the belowground neighborhood, and the potential importance of root gaps in community dynamics.

### *Interactions Between Root and Shoot Competition*

The practice of calculating shoot competition from direct measurements of root competition and total competition is based on the assumption that aboveground competition and belowground competition are additive in their effects on plant growth. Some researchers acknowledge that an interaction between the two forms of competition is likely, that shoot competition may affect a plant's belowground competitive ability or vice versa, but they assume either that the interaction is not important or that the direction and magnitude of the interaction does not change over the resource gradients with which they work (9, 124, 142). Often cited is JB Wilson's review of root competition studies



(141), most conducted in the greenhouse, from which he concluded that non-additive interactions of root and shoot competition are rare.

Where the consequences for plant performance of root and shoot competition have been measured separately, results have suggested nonadditive effects of the two forms of competition for some species (35, 36, 48, 49, 102). In a study examining how interactions with two vine species affected saplings of *Liquidambar styraciflua*, clear nonadditive effects of aboveground and belowground competition were demonstrated for *Lonicera japonica* (35). Root interactions alone reduced sapling growth, but shoot interactions reduced growth only if root interactions were also present. A physiologically based study showed that shading reduced nutrient uptake in a perennial tussock grass (67); this is one way that above- and belowground competition could interact to affect plant growth, but there are others.

Field experiments have also provided evidence that interactions between root and shoot competition do not remain constant in different resource environments (102). JF Cahill (17a) measured separate effects of root and shoot competition and their combined effects on the growth of *Abutilon theophrasti* in an abandoned agricultural field. He found a strong interaction between below- and aboveground competition that changed in direction with the addition of nutrients. Where fertilizer had not been added, the sum of root competitive intensity and shoot competitive intensity measured separately was much greater than total competitive intensity measured as the combined effects of root and shoot interactions. With fertilizer addition, the sum of root competitive intensity and shoot competitive intensity was less than total competitive intensity. These results suggest that indirect measures of shoot competition may be inaccurate and that interactions between belowground and aboveground competition are physiologically complex.

### *The Symmetry of Belowground Competition*

The extent to which plant size confers a competitive advantage may be an important difference between belowground and aboveground competition. The disproportionate advantage of size in competing for light occurs because larger plants shade smaller ones (137). The suppression of smaller plants results in the development of size hierarchies that become more pronounced over time. Plants that are larger aboveground do not seem to enjoy a similar disproportionate advantage in competing for belowground resources (137). Data come mostly from pot experiments in which partitions are installed to prevent the interaction of neighbor shoots (93, 136, 138, 141). Belowground competitive ability appears to be size-symmetric; root interactions with neighbors reduce plant growth but do not increase size variation among competing individuals. A recent study examining nitrate and ammonium uptake as a function

of plant size provided corroborating physiological evidence. Within crowded populations of yellow birch seedlings were grown in tubs, individuals acquired  $^{15}\text{N}$  tracer in direct proportion to several measures of root system size (132).

Fewer data regarding the relationship between size and belowground competitive ability are available for plants in field situations in which roots are not confined to pots and soil resources are more spatially heterogeneous. One field study varied the size of transplanted seedlings for six species used as target plants and found growth response to belowground competition to be in direct proportion to size of transplant (48). In considering situations where root competition might become asymmetric, Schwinning & Weiner (115) suggested the possibility that larger root systems would have a disproportionate advantage in a patchy soil environment because they should be more likely to encounter a high-nutrient patch (114). These authors also recognized that the relationship between root system size and resource uptake could depend on the mobility of the limiting resource.

### *Size of the Belowground Neighborhood*

The amount of belowground competition experienced by an individual will be a function of both the sizes of neighbors and their numbers. How many plants make up the belowground neighborhood? Does root overlap and belowground competition primarily occur among nearest neighbors, or is lateral root spread so extensive that the belowground neighborhood includes many additional plants? Because of the difficulty of excavating roots, especially fine roots that are most involved in resource uptake, few realistic estimates of total rooting area or root system overlap exist.

When rooting area is larger or smaller than the spread of the canopy, aboveground neighborhoods and belowground neighborhoods may be different sizes. In arid and semiarid areas, the lateral spread of a plant belowground is almost always greater than the spread of the canopy aboveground (104). The belowground area occupied by dominant shrubs in a California chaparral, for example, was over 10 times the area occupied by their canopy (77). One study estimated the zone of nutrient uptake for the bunchgrass *Schizachyrium scoparium* in an old field habitat by killing all neighbors within a 2 m radius of target individuals and then measuring the distances over which target plants reduced soil nitrogen (122). A single clump of *S. scoparium* was found to forage for nitrogen over a 1–1.5 m<sup>2</sup> area, which is large enough to include hundreds of other plants.

Potential rooting area and the area occupied in the presence of neighbors are not necessarily the same, however. One population level study found the root systems of 32 excavated creosote shrubs to be shaped as irregular polygons,

which seemed to reflect growth away from the greatest competitive pressure of adjacent plants (17). The irregular geometry of the roots filled soil space more effectively than would circular rooting areas, and root overlap occurred among four or more neighbors in only a small portion of the population. The study ignored roots smaller than 2 mm diameter, a factor that may not have affected measurements of geometry but certainly affected estimates of root overlap. Similarly, root systems in stands of loblolly pine and sweetgum were not circular in area, and structural roots also seemed to avoid those of other individuals (91).

Another consideration is how the distribution of neighboring root systems changes with the spatial distribution of nutrients. We expect spatial heterogeneity to affect the distribution of neighboring root systems based on evidence of root morphological plasticity within nutrient patches. In the study of loblolly pine and sweetgum, fine-root densities increased with local soil resource levels so that, at the population level, fine-root biomass and aboveground biomass were not correlated (91). Another study examined distributions of roots of the palm *Borassus aethiopum* in relation to nutrient patches associated with termite mounds and clumps of other trees in a humid savanna (89). Although rooting densities were highest within 2–3 m of the palm trunk, some roots extended laterally an impressive 20 m in accessing a nutrient-rich patch.

### *Root Gaps*

Openings in the belowground neighborhood are likely to be important for plant establishment. The extent to which root gaps are associated with canopy openings and the role of root gaps in the dynamics of gap succession have only recently been considered. A series of studies have documented the importance of belowground gaps for seedling establishment in the shortgrass steppe (2, 3, 62, 63). Recruitment is apparently limited by water availability and is most successful in larger gaps, where rooting densities of neighboring adults are lowest. Root gaps formed by death of fine roots have also been documented in a hardwood forest (140); root death occurred after canopy openings were formed by felling trees to simulate bole breakage without disturbing the soil by forming tip-up mounds. Such gaps may be short-lived. Data from a similar study in a *Pinus menziesii* forest showed little evidence for the maintenance of fine root gaps six months after aboveground gaps as large as 50 m in diameter were formed (127). Fine roots were still lacking from mineral soil after that time, but they were found in other substrates such as buried pieces of dead wood, again suggesting that standing trees exploited nutrient-rich patches over great distances. Root competition is recognized as a potentially important factor limiting establishment of woody and herbaceous seedlings in forest communities (31, 64, 140). Root dynamics as well as nutrient dynamics (99, 125, 126) may be important determinants of the course of gap succession.

## FUTURE DIRECTIONS

A full understanding of when and how belowground competition takes place and its ecological importance requires input from many fields of biology. While much is known about how roots respond to their soil environment, we are far from linking the physiological and growth responses of roots to the ways that plants affect each other. Furthermore, we are inadequately prepared to predict when and how strongly belowground competition occurs. Progress would be helped by experiments integrating the resource emphasis of physiological ecology and measurements of plant performance at the population or community level (58). Successful integrative approaches should identify the resources for which plants are competing, the mechanisms involved, and the ecological impact of the competitive interactions.

### *Mycorrhizae in Belowground Competition*

In this review, we have given little consideration to mycorrhizae despite their obvious importance in the belowground community. The ways in which mycorrhizae alter root interactions are likely very complicated. Their presence can either increase competition (139) or cause nutrient sharing (94), and plants' reliance on mycorrhizae may be density-dependent (74). Mycorrhizae may also enable plants to capture quantities of nutrients that would otherwise be inaccessible (4), potentially increasing the pool of belowground resources available to competing individuals. Much is yet to be learned about these mechanisms and the role of mycorrhizae in affecting community composition and population structure (4).

### *Competition for Water*

Although thousands of published studies deal with manipulating water availability to plants, we still have a poor understanding of how and under what circumstances competition for water occurs. Paying greater attention to the mechanisms of competition for water and measuring the strength of belowground competitive interactions under different conditions of water availability should determine whether competition really does increase across spatial or temporal gradients in soil moisture and the extent to which the increase is explained by correlated changes in plant growth or biomass. It is important to separate the phenomenon of water availability from plant competition for water; that water limitations may be greatest in arid systems does not necessarily mean that competition for water is greatest there.

### *Understanding Interactions Between Root and Shoot Competition*

With the exception of arid systems, in which aboveground competition may be minimal, above- and belowground competition act together to affect plant

performance. It should no longer be assumed that these forms of competition cause additive reductions in plant growth, given empirical evidence for non-additive interactions between the two. Experimental approaches should also allow for the possibility that neighbors could have opposing effects above- and belowground. For example, at least one old field species benefits from root interactions with neighbors (144), and it is reasonable to expect that belowground facilitation may sometimes co-occur with competition for light. Until more is understood about the frequency and causes of interactions between above- and belowground competition, their relative importance cannot be evaluated comprehensively. Here, too, combined research approaches could usefully identify the physiological bases of important ecological phenomena.

The relative importance of the two forms of competition should especially be considered in the recovery of vegetation gaps. Because closure of root gaps and canopy gaps may not occur simultaneously, we suggest that succession within gaps should be examined separately above- and belowground. The degree that these processes occur independently and the degree to which root and shoot competition interact to affect plant growth have implications for the composition of successional vegetation.

### *Defining the Belowground Neighborhood*

Determining the size of plant root systems and the area over which they take up resources is important for constructing neighborhood models of plant competition (13, 116, 130, 135). Built with the assumption that most interactions occur among nearby plants, these models are commonly used to predict size distributions in populations, population dynamics, or the outcome of interspecific encounters. The approach has been extended to examine how competitive outcomes may change with abiotic factors such as spatial heterogeneity in soil resources (12, 97), but the models are designed without much information about the structure of populations belowground and how that structure may change with plant density or variation in the soil environment. The application of radioactive tracers or stable nutrient analogs, tools used extensively in physiological studies (18, 83), could help define the area of nutrient uptake and thus the size of the belowground neighborhood.

### *Belowground Competition and Global Change*

Whatever the current importance of belowground competition, it is likely to increase with predicted changes in the earth's atmosphere. The projected doubling in CO<sub>2</sub> by the end of the next century (113) should increase photosynthetic rates, at least for C<sub>3</sub> plants, and decrease carbon limitation for plants globally. Furthermore, root biomass generally increases in elevated CO<sub>2</sub> experiments (110), suggesting an increase in the importance of belowground competition for water and nutrients.

Progress in at least three belowground research areas would help in predicting vegetation responses to global change. First, no global rooting map exists for use by modelers, though recent progress has been made (26, 70, 119, 128). Such a map should provide a global description of total biomass, fine root biomass, and fine root surface area as a function of soil depth, as well as the maximum rooting depth for the dominant vegetation in each biome. This information is important if global models are to represent belowground phenomena in a realistic manner. Second, a better grasp of the interaction between aboveground and belowground competition would also improve predictions of community-level consequences of atmospheric changes (43). Third, progress is needed in the grouping of plants into meaningful belowground functional types and in determining their distribution worldwide. A better understanding of belowground competition is needed—now more than ever before—if we are to meet the challenge of predicting biotic responses to the altered environment.

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BBC dedicates this paper to the memory of her father, D Bowers, who passed away while it was being written.

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#### Literature Cited

1. Aerts R, Boot RGA, van der Aart PJM. 1991. The relation between above- and belowground biomass allocation patterns and competitive ability. *Oecologia* 87:551–59
2. Aguilera MO, Lauenroth WK. 1993. Seedling establishment in adult neighborhoods—intraspecific constraints in the regeneration of the bunchgrass *Bouteloua gracilis*. *J. Ecol.* 81:253–61
3. Aguilera MO, Lauenroth WK. 1995. Influence of gap disturbances and type of microsites on seedling establishment in *Bouteloua gracilis*. *J. Ecol.* 83:87–97
4. Allen EB, Allen MF. 1990. The mediation of competition by mycorrhizae in successional and patchy environments. See Ref. 52, pp. 367–89
5. Anghinoni I, Barber SA. 1980. Phosphorus application rate and distribution in the soil and phosphorus uptake by corn. *Am. J. Soil Sci. Soc.* 44:1041–44
- 5a. Aphalo PJ, Ballaré CL. 1995. On the importance of information-acquiring systems in plant interactions. *Funct. Ecol.* 9:5–14
6. Baldwin JP. 1976. Competition for plant nutrients in soil: a theoretical approach. *J. Agric. Sci.* 87:341–56
7. Barber SA. 1984. *Soil Nutrient Bioavailability*. New York: Wiley Intersci.
8. Bauder ET. 1989. Drought and competition effects on the local distribution of *Pogogyne abramsii*. *Ecology* 70:1083–89
9. Belcher JW, Keddy PA, Twolan-Strutt L.

1995. Root and shoot competition intensity along a soil depth gradient. *J. Ecol.* 83:673–82
10. Belsky AJ, Amundson RG, Duxbury JM, Riha SJ, Ali AR, Mwonga SM. 1989. The effects of trees on their physical, chemical, and biological environments in a semi-arid savanna in Kenya. *J. Appl. Ecol.* 26:1005–24
  11. Berendse F. 1983. Interspecific competition and niche differentiation between *Plantago lanceolata* and *Anthoxanthum odoratum* in a natural hayfield. *J. Ecol.* 71:379–90
  - 11a. Bilbrough CJ, Caldwell MM. 1997. Exploitation of springtime ephemeral N pulses by six Great Basin species. *Ecology* 78:231–43
  12. Biondini ME, Grygiel CE. 1994. Landscape distribution of organisms and the scaling of soil resources. *Am. Nat.* 143:1026–54
  13. Bonan GB. 1993. Analysis of neighborhood competition among annual plants: implications of a plant growth model. *Ecol. Model.* 65:123–36
  14. Borkert CM, Barber SA. 1985. Soybean shoot and root growth and phosphorus concentration as affected by phosphorus placement. *Am. J. Soil Sci. Soc.* 49:152–55
  15. Boyer JS. 1995. *Water Relations of Plants and Soils*. San Diego: Academic
  16. Bray RH. 1954. A nutrient mobility concept of soil-plant relationships. *Soil Sci.* 78:9–22
  17. Brisson J, Reynolds JF. 1994. The effect of neighbors on root distribution in a creotebush (*Larrea tridentata*) population. *Ecology* 75:1693–702
  - 17a. Cahill JF. 1997. *Symmetry, intensity, and additivity: belowground interactions in an early successional field*. PhD diss. Univ. Penn, PA
  18. Caldwell MM, Eissenstat DM. 1987. Coping with variability: examples of tracer use in root function studies. In *Plant Response to Stress—Functional Analysis in Mediterranean Ecosystems*, ed. JD Tenhunen, FM Catarino, OL Lange, WC Oechel, pp. 95–106. Berlin: Springer-Verlag
  19. Caldwell MM, Eissenstat DM, Richards JH, Allen MF. 1985. Competition for phosphorus: differential uptake from dual-isotope-labeled soil interspaces between shrub and grass. *Science* 229:384–86
  20. Caldwell MM, Manwaring JH, Durham SL. 1991. The microscale distribution of neighboring plant roots in fertile soil microsites. *Funct. Ecol.* 5:765–72
  21. Caldwell MM, Manwaring JH, Durham SL. 1996. Species interactions at the level of fine roots in the field: influence of soil nutrient heterogeneity and plant size. *Oecologia* 106:440–47
  22. Caldwell MM, Manwaring JH, Jackson RB. 1991. Exploitation of phosphate from fertile soil microsites by three Great Basin perennials when in competition. *Funct. Ecol.* 5:757–64
  23. Callaway RM. 1995. Positive interactions among plants. *Bot. Rev.* 61:306–49
  24. Campbell BD, Grime JP, Mackey JML, Jalili A. 1991. The quest of a mechanistic understanding of resource competition in plant communities: the role of experiments. *Funct. Ecol.* 5:241–53
  25. Campbell BD, Grime JP, Mackey JML, Jalili A. 1991. A trade-off between scale and precision in resource foraging. *Oecologia* 87:532–38
  26. Canadell J, Jackson RB, Ehleringer JR, Mooney HA, Sala OE, Schulze E-D. 1996. Maximum rooting depth for vegetation types at the global scale. *Oecologia* 108:583–95
  27. Casper BB. 1996. Demographic consequences of drought in the herbaceous perennial *Cryptantha flava*: effects of density, associations with shrubs, and plant size. *Oecologia* 106:144–52
  28. Casper BB, Cahill JF, Jr. 1996. Limited effects of soil nutrient heterogeneity on populations of *Abutilon theophrasti* (Malvaceae). *Am. J. Bot.* 83:333–41
  29. Chapin FSI, Walker LR, Fastie CL, Sharman LC. 1994. Mechanisms of primary succession following deglaciation at Glacier Bay, Alaska. *Ecol. Monogr.* 64:149–75
  30. Cook SJ, Ratcliff D. 1984. A study of the effects of root and shoot competition on the growth of green panic (*Panicum maximum* var. *trichoglume*) seedlings in an existing grassland using root exclusion tubes. *J. Appl. Ecol.* 21:971–82
  31. Cristy EJ. 1986. Effect of root competition and shading on growth of suppressed western hemlock (*Tsuga heterophylla*). *J. Veg. Sci.* 65:21–28
  32. Dawson TE, Pate JS. 1996. Seasonal water uptake and movement in root systems of Australian phraeatophytic plants of dimorphic root morphology: a stable isotope investigation. *Oecologia* 107:13–20
  33. de Kroon H, Hutchings MJ. 1995. Morphological plasticity in clonal plants: the foraging concept reconsidered. *J. Ecol.* 83:143–52

34. Diaz S, Grime JP, Harris J, McPherson E. 1993. Evidence of a feedback mechanism limiting plant response to elevated carbon dioxide. *Nature* 364:616–17
35. Dillenburg LR, Whigham DF, Teramura AH, Forseth IN. 1993. Effects of below- and aboveground competition from vines *Lonicera japonica* and *Parthenocissus quinquefolia* on the growth of the tree host *Liquidambar styraciflua*. *Oecologia* 93:48–54
36. Donald CM. 1958. The interaction of competition for light and for nutrients. *Aust. J. Agric. Res.* 9:421–35
37. Drew MC, Saker LR. 1975. Nutrient supply and the growth of the seminal root system in barley. II. Localized, compensatory increases in lateral root growth and rates of nitrate uptake when nitrate supply is restricted to only part of the root system. *J. Exp. Bot.* 26:79–90
38. Duncan WG, Ohlrogge AJ. 1958. Principles of nutrient uptake from fertilizer bands. II. Root development in the band. *Agric. J.* 50:605–08
39. Ehleringer JR, Phillips SL, Schuster WSF, Sandquist DR. 1991. Differential utilization of summer rains by desert plants. *Oecologia* 88:430–34
40. Eissenstat DM. 1992. Costs and benefits of constructing roots of small diameter. *J. Plant Nutri.* 15:763–82
41. Eissenstat DM, Yanai RD. 1997. The ecology of root lifespan. *Adv. Ecol. Res.* 27:1–60
42. Fernandez OA, Caldwell MM. 1975. Phenology and dynamics of root growth of three cool semi-desert shrubs under field conditions. *J. Ecol.* 63:703–14
43. Field CB, Chapin FSI, Matson PA, Mooney HA. 1992. Responses of terrestrial ecosystems to the changing atmosphere: a resource-based approach. *Annu. Rev. Ecol. Syst.* 23:201–35
44. Fitter AH. 1994. Architecture and biomass allocation as components of the plastic response of root systems to soil heterogeneity. In *Exploitation of Environmental Heterogeneity by Plants: Ecophysiological Processes Above- and Belowground*, ed. MM Caldwell, RW Pearcy, pp. 305–23. San Diego: Academic
45. Fitter AH, Strickland TR, Harvey ML, Wilson GW. 1991. Architectural analysis of plant root systems. I. Architectural correlates of exploitation efficiency. *New Phytol.* 119:383–89
46. Fowler NL. 1986. Density-dependent population regulation in a Texas grassland community. *Ecology* 67:545–54
47. Fowler NL. 1986. The role of competition in plant communities in arid and semiarid regions. *Annu. Rev. Ecol. Syst.* 17:89–110
48. Gerry AK, Wilson SD. 1995. The influence of initial size on the competitive responses of six plant species. *Ecology* 76:272–79
49. Gill DS, Marks PL. 1991. Tree and shrub seedling colonization of old fields in central New York. *Ecol. Mono.* 61:183–205
50. Goldberg DE. 1990. Components of resource competition in plant communities. See Ref. 52, pp. 27–65
51. Grace JB. 1993. The effects of habitat productivity on competition intensity. *Trends Evol. Ecol.* 8:229–30
52. Grace JB, Tilman D. 1990. *Perspectives on Plant Competition* San Diego: Academic
53. Greenlee JT, Callaway RM. 1996. Abiotic stress and the relative importance of interference and facilitation in montane bunchgrass communities in western Montana. *Am. Nat.* 148:386–96
54. Grime JP. 1974. Vegetation classification by reference to strategies. *Nature* 250:26–31
55. Grime JP. 1979. *Plant Strategies and Vegetation Processes*. London: Wiley
56. Grime JP. 1993. Ecology sans frontières. *Oikos* 68:385–92
57. Grime JP. 1994. The role of plasticity in exploiting environmental heterogeneity. In *Exploitation of Environmental Heterogeneity by Plants*, ed. MM Caldwell, RW Pearcy, pp. 1–19. San Diego, CA: Academic
58. Grime JP. 1994. Defining the scope and testing the validity of C-S-R theory: a response to Midgley, Laurie, and Le Maitre. *Bull. Southern Afr. Inst. Ecologists Environ. Scientists* 13:4–7
59. Gross K, Peters A, Pregitzer KS. 1993. Fine root growth and demographic responses to nutrient patches in four old-field plant species. *Oecologia* 95:61–64
60. Grubb PJ. 1994. Root competition in soils of different fertility: a paradox resolved? *Phytocoenologia* 24:495–505
61. Gurevitch J. 1986. Competition and the local distribution of the grass *Stipa neomexicana*. *Ecology* 67:46–57
62. Hook PB, Lauenroth WK. 1994. Root system response of a perennial bunchgrass to neighborhood-scale soil water heterogeneity. *Funct. Ecol.* 8:738–45
63. Hook PB, Lauenroth WK, Burke IC. 1994. Spatial patterns of roots in a semi-arid grassland: abundance of canopy



- openings and regeneration gaps. *J. Ecol.* 82:485–94
64. Horn JC. 1985. Responses of understory tree seedlings to trenching. *Am. Midl. Natur.* 114:252–58
  65. Huber-Sannwald E, Pyke DA, Caldwell MM. 1996. Morphological plasticity following species-specific recognition and competition in two perennial grasses. *Am. J. Bot.* 83:919–93
  66. Hutchings MJ, de Kroon H. 1994. Foraging in plants: the role of morphological plasticity in resource acquisition. *Adv. Ecol. Res.* 25:159–238
  67. Jackson RB, Caldwell MM. 1992. Shading and the capture of localized soil nutrients: nutrient contents, carbohydrates, and root uptake kinetics of a perennial tussock grass. *Oecologia* 91:457–62
  68. Jackson RB, Caldwell MM. 1993. The scale of nutrient heterogeneity around individual plants and its quantification with geostatistics. *Ecology* 74:612–14
  69. Jackson RB, Caldwell MM. 1996. Integrating resource heterogeneity and plant plasticity: modelling nitrate and phosphate uptake in a patchy soil environment. *J. Ecol.* 84:891–903
  70. Jackson RB, Canadell J, Ehleringer JR, Mooney HA, Sala OE, Schulze E-D. 1996. A global analysis of root distributions for terrestrial biomes. *Oecologia* 108:389–411
  71. Jackson RB, Manwaring JH, Caldwell MM. 1990. Rapid physiological adjustment of roots to localized soil enrichment. *Nature* 344:58–60
  72. Kadmon R. 1995. Plant competition along soil moisture gradients: a field experiment with the desert annual *Stipa capensis*. *J. Ecol.* 83:253–62
  73. Kaye JP, Hart SC. 1997. Competition for nitrogen between plants and soil microorganisms. *Trends Ecol. Evol.* 12:139–43
  74. Koide RT. 1991. Density-dependent response to mycorrhizal infection in *Abutilon theophrasti* Medic. *Oecologia* 85:389–95
  75. Kovar JL, Barber SA. 1988. Phosphorus supply characteristics of 33 soils as influenced by seven rates of phosphorus addition. *Am. J. Soil Sci. Soc.* 52:160–65
  76. Krannitz PG, Caldwell MM. 1995. Root growth responses of three Great Basin perennials to intra- and interspecific contact with other roots. *Flora* 190:161–67
  77. Kummerow J, Krause D, Jow W. 1977. Root systems of chaparral shrubs. *Oecologia* 29:163–77
  78. Le Roux X, Bariac T, Mariotti A. 1995. Spatial partitioning of the soil water resource between grass and shrub components in a West African humid savanna. *Oecologia* 104:147–55
  79. Lee RB. 1982. Selectivity and kinetics of ion uptake by barley plants following nutrient deficiency. *Ann. Bot.* 50:429–49
  80. Lyr H, Hoffmann G. 1967. Growth rates and growth periodicity of tree roots. *Inter. Rev. For. Res.* 1:181–236
  81. Mäder P, Vierheilig H, Alt M, Wiemken A. 1993. Boundaries between soil compartments formed by microporous hydrophobic membranes (GORE-TEX<sup>®</sup>) can be crossed by vesicular-arbuscular mycorrhizal fungi but not by ions in the soil solution. *Plant Soil* 152:201–06
  82. Mahall BE, Callaway RM. 1992. Root communication mechanisms and intra-community distributions of two Mojave desert shrubs. *Ecology* 73:2145–51
  83. Mamolos AP, Elisseeu GK, Veresoglou DS. 1995. Depth of root activity of co-existing grassland species in relation to N and P additions, measured using non-radioactive tracers. *J. Ecol.* 83:643–52
  84. Marschner H. 1995. *Mineral Nutrition of Higher Plants*. London: Academic. 2nd ed.
  85. McConnaughay KDM, Bazzaz FA. 1992. The occupation and fragmentation of space: consequences of neighboring roots. *Funct. Ecol.* 6:704–10
  86. McConnaughay KMD, Newman EI. 1991. Is physical space a soil resource? *Ecology* 72:94–103
  87. McLellan AJ, Fitter AH, Law R. 1995. On decaying roots, mycorrhizal colonization and the design of removal experiments. *J. Ecol.* 83:225–30
  88. Mooney HA, Hobbs RJ, Gorman J, Williams K. 1986. Biomass accumulation and resource utilization in co-occurring grassland annuals. *Oecologia* 70:555–58
  89. Mordelet P, Barot S, Abbadié L. 1996. Root foraging strategies and soil patchiness in a humid savanna. *Plant Soil* 182:171–76
  90. Morris EC. 1996. Effect of localized placement of nutrients on root competition in self-thinning populations. *Ann. Bot.* 78:353–64
  91. Mou P, Jones RH, Mitchell RJ, Zutter BR. 1995. Spatial distribution of roots in sweetgum and loblolly pine monocultures and relations with aboveground biomass and soil nutrients. *Funct. Ecol.* 9:689–99

92. Nepstad DC, de Carvalho CR, Davidson EA, Jipp PH, Lefebvre PA, et al. 1994. The role of deep roots in the hydrological and carbon cycles of Amazonian forests and pastures. *Nature* 372:666–69
93. Newberry DM, Newman EI. 1978. Competition between grassland plants of different sizes. *Oecologia* 33:361–80
94. Newman EI. 1988. Mycorrhizal links between plants: their functioning and ecological significance. *Adv. Ecol. Res.* 18:243–71
95. Nobel PS. 1991. *Physiochemical and Environmental Plant Physiology*. San Diego: Academic
96. Nye PH, Tinker PB. 1977. *Solute Movement in the Soil-Root System*. Berkeley: Blackwell
97. Pacala SW. 1987. Neighborhood models of plant population dynamics. 3. Models with spatial heterogeneity in the physical environment. *Theor. Pop. Biol.* 31:359–92
98. Pantastico-Caldas M, Venable DL. 1993. Competition in two species of desert annuals along a topographic gradient. *Ecology* 74:2192–203
99. Parsons WfJ, Knight DH, Miller SL. 1994. Root gap dynamics in lodgepole pine forest: nitrogen transformations in gaps of different sizes. *Ecol. Appl.* 4:354–62
100. Pregitzer KS, Hendrick RL, Fogel R. 1993. The demography of fine roots in response to patches of water and nitrogen. *New Phytol.* 125:575–80
101. Putwain PD, Harper JL. 1970. Studies in the dynamics of plant populations. III. The influence of associated species on populations of *Rumex acetosa* L. and *R. acetosella* L. in grassland. *J. Ecol.* 58:251–64
102. Putz FE, Canham CD. 1992. Mechanisms of arrested succession in shrublands: root and shoot competition between shrubs and tree seedlings. *For. Ecol. Manage.* 49:267–75
103. Reichenberger G, Pyke DA. 1990. Impact of early root competition on fitness components of four semiarid species. *Oecologia* 85:159–66
104. Richards J. 1986. Root form and depth distribution in several biomes. In *Mineral Exploration: Biological Systems and Organic Matter*, ed. D Carlisle, WL Berry, IR Kaplan, JR Watterson, pp. 82–96. Englewood Cliffs, NJ: Prentice-Hall
105. Richards JH, Caldwell MM. 1987. Hydraulic lift: substantial nocturnal water transport between soil layers by *Artemisia tridentata* roots. *Oecologia* 73:486–89
106. Richter DD, Markewitz D. 1995. How deep is soil? *BioScience* 45:600–09
107. Robertson GP, Klingensmith KM, Klug MJ, Paul EA, Crum JR, Ellis BG. 1997. Soil resources, microbial activity, and primary production across an agricultural ecosystem. *Ecol. Appl.* 7:158–70
108. Robinson D. 1994. The responses of plants to non-uniform supplies of nutrients. *New Phytol.* 127:635–74
109. Robinson D. 1996. Resource capture by localized root proliferation: Why do plants bother? *Ann. Bot.* 77:179–85
110. Rogers HH, Runion GB, Krupa SV. 1994. Plant response to CO<sub>2</sub> enrichment with emphasis on roots and the rhizosphere. *Environ. Pollut.* 83:155–89
111. Ryel RJ, Caldwell MM, Manwaring JH. 1996. Temporal dynamics of soil spatial heterogeneity in sagebrush-wheatgrass steppe during a growing season. *Plant Soil* 184:299–309
112. Sala OE, Golluscio RA, Lauenroth WK, Soriano A. 1989. Resource partitioning between shrubs and grasses in the Patagonian steppe. *Oecologia* 81:501–05
113. Schlesinger WH. 1991. *Biogeochemistry: an Analysis of Global Change*. San Diego: Academic
- 113a. Schulze E-D, Kelliher FM, Körner CH, Lloyd J, Leuning R. 1994. Relationships among maximum stomatal conductance, ecosystem surface conductance, carbon assimilation rate, and plant nitrogen nutrition: a global ecology scaling exercise. *Annu. Rev. Ecol. Syst.* 25:629–60
114. Schwinning S. 1996. Decomposition analysis of competitive symmetry and size structure. *Ann. Bot.* 77:47–57
115. Schwinning S, Weiner J. 1997. Mechanisms determining the degree of size-asymmetry in plant competition. *Oecologia*. In press
116. Silander JA, Jr., Pacala SW. 1985. Neighborhood predictors of plant performance. *Oecologia* 66:256–63
117. Slatyer RO. 1967. *Plant-Water Relationships*. London: Academic
118. Snaydon RW. 1962. Micro-distribution of *Trifolium repens* L. and its relation to soil factors. *J. Ecol.* 50:133–43
119. Stone E, Kalisz PJ. 1991. On the maximum extent of tree roots. *For. Ecol. Manage.* 46:59–102
120. Tilman D. 1982. *Resource Competition and Community Structure*. Princeton, NJ: Princeton Univ. Press
121. Tilman D. 1988. *Plant Strategies and the Dynamics and Structure of Plant*

- Communities*. Princeton, NJ: Princeton Univ. Press
122. Tilman D. 1989. Competition, nutrient reduction, and the competitive neighborhood of a bunchgrass. *Funct. Ecol.* 3:215–19
  123. Tilman D, Pacala S. The maintenance of species richness in plant communities. In *Species Diversity in Ecological Communities: Historical and Geographical Perspectives*, ed. RE Ricklefs, D Schulter, pp. 13–25. Chicago, IL: Univ. Chicago Press
  124. Twolan-Strutt L, Keddy PA. 1996. Above- and belowground competition intensity in two contrasting wetland plant communities. *Ecology* 77:259–70
  125. Vitousek PM, Denslow JS. 1986. Nitrogen and phosphorus availability in treefall gaps of lowland tropical rainforest. *Ecology* 74:1167–78
  126. Vitousek PM, Matson PA. 1985. Disturbance, nitrogen availability, and nitrogen losses in an intensively managed loblolly pine plantation. *Ecology* 66:1360–76
  127. Vogt KA, Vogt DJ, Asbjornsen H, Dahlgren RA. 1995. Roots, nutrients and their relationship to spatial patterns. *Plant Soil* 168/169:113–23
  128. Vogt KA, Vogt DJ, Boon P, O'Hara J, Asbjornsen H. 1996. Factors controlling the contribution of roots to ecosystem carbon cycles in boreal, temperate, and tropical forests. *Plant Soil* 187:159–219
  129. Walker BH, Ludwick D, Holling CS, Peterman RM. 1981. Stability of semi-arid savanna grazing systems. *J. Ecol.* 69:473–98
  130. Waller DM. 1981. Neighborhood competition in several violet populations. *Oecologia* 51:116–22
  131. Walter H. 1954. Die verbuschung, eine erscheinung der subtropischen savannengebiete, und ihre ökologischen ursachen. *Vegetatio* 5/6:6–10
  132. Wayne P, Berntson W. 1996. *Resource acquisition in crowded populations: linking mechanistic and phenomenological aspects of plant competition*. Presented at Ecol. Soc. Am. Ann. Comb. Meeting, 77th, Providence, RI
  133. Waynick DD, Sharp LT. 1919. Variability in soils and its significance to past and future soil investigations. II. Variation in nitrogen and carbon in field soils and their relation to the accuracy of field trials. *Univ. Calif. Publ. Agric. Sci.* 4:121–39
  134. Weaver JE. 1919. *The Ecological Relations of Roots*. Washington, DC: Carnegie Inst.
  135. Weiner J. 1982. A neighborhood model of annual-plant interference. *Ecology* 63:1237–41
  136. Weiner J. 1986. How competition for light and nutrients affects size variability in *Ipomoea tricolor* populations. *Ecology* 67:1425–27
  137. Weiner J. 1990. Asymmetric competition in plant populations. *Trends Ecol. Evol.* 5:360–64
  138. Weiner J, Wright DB, Castro S. 1997. Symmetry of below-ground competition between *Kochia scoparia* individuals. *Oikos* 79:85–91
  139. West HM. 1996. Influence of arbuscular mycorrhizal infection on competition between *Holcus lanatus* and *Dactylis glomera*. *J. Ecol.* 84:429–38
  140. Wilczynski CJ, Pickett STA. 1993. Fine root biomass within experimental canopy gaps: evidence for a below-ground gap. *J. Veg. Sci.* 4:571–74
  141. Wilson JB. 1988. Shoot competition and root competition. *J. Appl. Ecol.* 25:279–96
  142. Wilson SD, Tilman D. 1991. Components of plant competition along an experimental gradient of nitrogen availability. *Ecology* 72:1050–65
  143. Wilson SD, Tilman D. 1993. Plant competition and resource availability in response to disturbance and fertilization. *Ecology* 74:599–611
  144. Wilson SD, Tilman D. 1995. Competitive responses of eight old-field plant species in four environments. *Ecology* 76:1169–80