

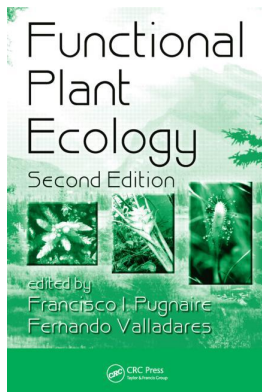
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15 Plant Interactions: Competition

Heather L. Reynolds and Tara K. Rajaniemi

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Not until we reach the extreme confines of life, in the arctic regions or on the borders of an udder desert, will competition cease. The land may be extremely cold or dry, yet there will be competition between some few species, or between the individuals of the same species, for the warmest or dampest spots.

—Darwin (1859)

INTRODUCTION

Organisms are said to compete when shared resource needs have mutual negative effects (–) on survival, growth, or reproduction. This happens when resources are limiting, that is, when organismal demand for resources exceeds the supply of resources from the environment. Resources are quantities of matter or energy whose consumption promotes positive per capita growth or reproduction of an organism over at least some range of resource availability (Tilman 1982). As autotrophs, plants require the inorganic resources carbon dioxide (CO₂), water, light, and mineral nutrients. The major mineral nutrients are nitrogen, phosphorus, potassium, iron, calcium, magnesium, and sulfur; the minor ones are molybdenum, copper, zinc, manganese, boron, chlorine, sodium (some Chenopodiaceae), aluminum (ferns), cobalt (legumes that symbiotically fix nitrogen), and silicon (diatoms) (Banister 1976). Because plants are sessile and do not exhibit behavior, the main mechanism of plant competition is exploitation; competitors interact solely by consuming (i.e., depleting or preempting) resources (Figure 15.1; see Weiner and Thomas 1986 and Thomas and Weiner 1989 for discussion of resource depletion vs. resource preemption). Conversely, interference competition involves direct interactions between competitors that prevent access to resources, such as fighting between animals. In plants, interference competition can occur by one individual overgrowing another. Allelopathy, or production of

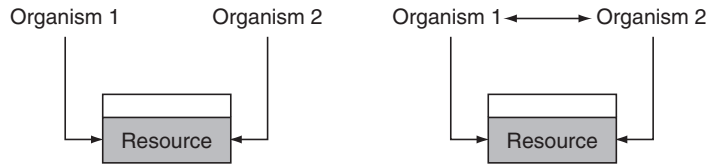


FIGURE 15.1 Mechanisms of competition. (*Left*) In exploitation competition, organisms interact only indirectly, via shared resource use. (*Right*) In interference competition, organisms interact directly for the shared resource. Interference competition is common in animals (e.g., fighting over mates or food), although plants can sometimes interfere by growing over one another, or via chemical production (allelopathy).

chemicals that inhibit plant function, may also be (but is not necessarily) an evolved mechanism of interference competition (Williamson 1990). Allelopathy has received renewed attention of late, particularly for its relevance to understanding exotic plant invasions (e.g., Wardle et al. 1998, Mallik and Pellissier 2000, Bais et al. 2003, Callaway and Ridenour 2004).

The relative importance of competition versus other biotic interactions (e.g., mutualism or facilitation, predation, herbivory) and abiotic factors (e.g., fire, pH, soil fertility) to the ecology and evolution of species and the structure of communities is an old debate in ecology (Roughgarden and Diamond 1986). Related issues concern whether the intensity of competition varies with environmental conditions and what traits are important to competitive ability. During about a 20 year period from the late 1970s to the mid-1990s, debate about these issues among plant ecologists crystallized in the contrasting perspectives of the competition–stress–ruderal (C–S–R) model of Grime (1977, 1979, 1988) and the resource competition model of Tilman (1982, 1988, 1990). After a number of stimulating exchanges and a substantial associated literature, the Grime–Tilman debate largely faded away, as attention turned to a number of new pressing issues, including the relationship between biodiversity and ecosystem functioning (Naeem et al. 2002, and see Chapter 10) and the causes and consequences of exotic species invasions (Levine et al. 2003, Hierro et al. 2005). Yet C–S–R and resource competition theory continue to be used as guiding frameworks in these and other areas of plant ecology (e.g., Wardle et al. 1997, Shea and Chesson 2002, MacDougall and Turkington 2005). This chapter reviews C–S–R and resource competition theory and the associated literature on competition intensity (CI) and competitive traits. We then turn to a relatively new area of focus for plant ecologists who study competition—soil heterogeneity, asking how current work in this area is informed by, and informs, C–S–R and resource competition theory. We conclude with a brief summary and suggestions for future research. The appendix to this chapter provides an overview of the various approaches to designing competition experiments and calculating competition indices.

C–S–R AND RESOURCE COMPETITION MODELS

It has sometimes been asserted that different definitions of competition are at the root of any disagreement between the C–S–R and resource competition models (Thompson 1987, Grace 1991a). However, both Grime and Tilman define competition in terms of exploitation (Tilman 1987): “Here, competition is defined as the tendency of neighboring plants to utilize the same quantum of light, ion of a mineral nutrient, molecule of water, or volume of space” (Grime 1973) and “The mechanism of competitive displacement is resource consumption” (Tilman 1988).

Competition can only occur for resources when they are limiting. Some resources required by plants (e.g., CO₂) are generally superabundant, and use by one organism has no effect on

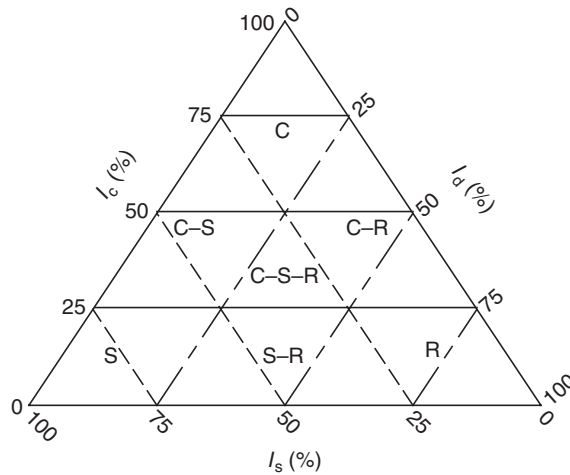


FIGURE 15.2 Model showing the various equilibria between competition (C), stress (S), and disturbance (d) in vegetation and the location of primary and secondary strategies. I_c , relative importance of competition (—); I_s , relative importance of stress (-----); I_d , relative importance of disturbance (— · — · —). (Source: Grime, J.P., *Am. Nat.*, 111, 1169, 1977. With permission.)

other organisms requiring the same resource. Resources become limiting when potential demands on resources by organisms exceed resource supply. The major source of disagreement between the C–S–R and resource competition models is when resource demand has the potential to exceed resource supply.

C–S–R

The C–S–R model is a conceptual model that categorizes vegetation into general strategies based on adaptation to combinations of two types of selection pressures: stress and disturbance (Figure 15.2). Stress is defined as any environmental condition that limits plant production (e.g., extremes of pH or temperature), and disturbance as any environmental condition that removes plant biomass (e.g., herbivory, pathogens, wind, fire, human activities) (Grime 1977). Low availability of mineral nutrients (low soil fertility) is most often associated with stress in this model. Stress and disturbance are thought to reduce competition by preventing development of a dense vegetation and thereby reducing demand for resources. Competition is hypothesized to be of highest intensity and greatest importance in highly productive vegetation, such as that which develops on fertile soil under relatively undisturbed conditions. Proponents of the C–S–R model (Grime 1977, Campbell et al. 1991) reason that dense, highly productive vegetation result in increased demand for both light and belowground resources (water, mineral nutrients). Therefore, traits important to the competitive strategy are considered to be those that maximize acquisition of all resources. These traits include high growth rates, large size and height, and high plasticity in roots and shoots to allow active foraging for undepleted resource pockets. Investment in resource acquisition comes at the expense of investment in traits important for adapting to stress and disturbance. Such trade-offs in allocation to competition, stress, and disturbance mean that each species cannot be adapted to the extremes of more than one strategy, although adaptation to intermediate intensities of competition, stress, and disturbance may occur (Grime 1977, 1988).

RESOURCE COMPETITION

The resource competition model is a mechanistic, mathematical model of plant population dynamics that considers essentially similar selection pressures (or environmental constraints):

Rate of biomass change = Growth – Loss

$$(a) \quad \frac{dB_i}{B_i dt} = f_i(R) - m_i$$

Rate of resource change = Supply rate – Sum of consumption rates

$$(b) \quad \frac{dR}{dt} = \gamma(R) - \sum_{i=1}^n [Q_i B_i f_i(R)]$$

FIGURE 15.3 Simple consumer-resource model of exploitative competition for a limiting soil nutrient. (a) Per-unit biomass rate of change of a population, where B_i is biomass of species i ; $f_i(R)$ is a function that describes the dependence of net growth for species i on the resource (R); and m_i is loss rate of species i . (b) Resource dynamics, where $\gamma(R)$ is a function that describes resource supply; Q_i is the nutrient content per unit biomass of species i , and n is the total number of consumer species. This simple model can be extended to include more than one limiting resource. (Source: Tilman, D., *Perspectives on Plant Competition*, J.B. Grace and D. Tilman, eds, Academic Press, San Diego, CA, 1990.)

soil resource supply rates and loss (disturbance, mortality) rates. The model consists of two types of coupled equations, one describing plant dynamics as a function of resource-dependent growth and loss and the other describing resource dynamics as a function of resource supply and plant consumption (Figure 15.3). The model is explicit about the fact that plants grow by consuming resources, and exploitative competition is an integral component of the model because the resources consumed (light, soil resources) are depletable (i.e., plant consumption affects availability) and can therefore become limiting.

Competition is not restricted mainly to dense vegetation of high productivity habitats, as in the C–S–R model, but occurs under every combination of resource supply and loss rate. The reason for this is that the model considers plant demand for resources relative to resource supply. It is the ratio of supply to demand that determines whether resources are limiting (and consequently whether competition occurs) (Taylor et al. 1990, see also a related discussion by Chesson and Huntly 1997). The absolute demand for soil resources may be high in high productivity sites, but soil resource supply rates are also high, and thus the ratio of supply to demand is not necessarily different from that in low productivity sites (in which absolute demand is lower, but so is supply).

In fact, the resource competition model predicts that competition is equally important at both low and high soil fertility (low and high plant productivity). Only the nature of the resources for which there is competition is predicted to change along fertility gradients, as the limiting resources change from soil nutrients at low soil resource supply rates (causing strong belowground competition) to light at high soil resource supply rates (causing strong aboveground competition). Loss rates can similarly influence the nature of competition (below- vs. aboveground) through their influence on availabilities of soil nutrients and light (Tilman 1988, Smith and Huston 1989).

Traits important to competitive ability are also predicted to vary with resource supply and loss rates. For example, at low soil resource supply rates, allocation to acquisition and retention of soil resources is predicted (e.g., traits such as high root to shoot ratio, long-lived tissues). At high soil resource supply rates, allocation to acquisition of light may become important (e.g., traits such as high stem allocation) (Tilman 1988). Investment in belowground resource acquisition and use necessarily comes at the expense of investment in traits important for acquisition and use of aboveground resources. Such trade-offs impose limits on the ability of any one organism to dominate in all habitat types (Tilman 1988, 1990, Smith and Huston 1989).

By acquiring depletable resources for itself, an individual reduces availability of those resources to other species. The level to which the individuals of a population deplete a given resource at equilibrium is known as R^* (Tilman 1982, 1988, 1990). Tilman (1990) and Reynolds and Pacala (1993) have shown analytically how traits can influence R^* s. Resource reduction is the mechanism of exploitation competition, and thus, the lower the R^* of a species, the more resource it has gained for itself and the better is its competitive ability for that resource. At equilibrium, the species with the lowest R^* (i.e., greatest ability to consume the resource) is predicted to displace all competitors (Tilman 1977, 1982, 1988, 1990).

It is important to note that the resource competition model can also be solved numerically to predict the competitive dominants under nonequilibrium conditions (Tilman 1987, 1988). However, these so-called transient dominants are not considered to be the true superior competitors for a given set of soil resource supply and loss rates. According to resource competition theory, the true superior competitor for a given set of soil resource supply and loss rates is defined as the species that dominates at equilibrium (Tilman 1987, 1988). For practical reasons, many competition experiments are of very short term, and thus the competitive outcomes may sometimes reflect transient dynamics rather than equilibrium conditions. Failure to distinguish transient from equilibrium outcomes has likely contributed to debate between the C–S–R and resource competition perspectives (Tilman 1987).

COMPETITION INTENSITY

In the 1980s and 1990s, experimental work on competition moved from demonstrating the existence of plant competition in the field (Connell 1983, Schoener 1983) toward a focus on testing theory, including the contrasting predictions of the C–S–R and resource competition models (Goldberg and Barton 1992, Gurevitch et al. 1992). Two questions are typically asked: (1) Does competition intensity (competitive ability) change along gradients of soil fertility and disturbance? (2) What physiological and morphological traits are important to competitive ability? No consensus has been reached on either of these questions. Especially for the first question, several issues have been raised that might lead to conflicting results and obscure a clear answer. These include:

1. *Choice of an appropriate competition index.* Competition intensity may be measured as absolute reduction in performance (physiological state, growth rate, fecundity, size, fitness) due to the presence of competition or as relative reduction in performance (Appendix 15.1). Absolute CI will almost inevitably be greater as plant biomass increases (e.g., with fertilization), simply because the maximum possible difference between monoculture and mixture performance increases as biomass increases (Campbell and Grime 1992, Grace 1993). Relative CI avoids this effect because it is standardized to maximum possible performance. Most recent competition studies employ relative measures of CI.
2. *Failure to clearly distinguish between the intensity of competition and its importance.* Intensity (CI, as earlier) measures the reduction below optimum in some measure of performance due to competition, whereas importance measures the relative degree that competition affects performance compared with other processes (e.g., herbivory, disturbance, direct abiotic effects, facilitation) (Weldon and Slauson 1986). Weldon and Slauson argue that high intensity of competition does not necessarily translate into high importance (or vice versa), as is typically assumed, and that the two concepts are often confused. Although it is sometimes argued that the predictions of the C–S–R model are for competition importance, and those of the resource competition model are for competition intensity, the vast majority of experiments measure only intensity

(Brooker et al. 2005, but see Welden et al. 1988, Mclellan et al. 1997, Sammul et al. 2000).

3. *Inattention to the selection regime commonly experienced by the study species.* A common expectation in competition experiments is that species act as phytometers of competition intensity that are dependent only on the experimental conditions (e.g., soil fertility) and independent of the environmental conditions to which the study species are adapted. This expectation is reasonable only if the C–S–R model holds, in which case species should experience greater competition intensity at high versus low soil fertility regardless of whether they are adapted to low- or high-fertility soil (Taylor et al. 1990). However, if the resource competition model holds, a species adapted to a lower-fertility soil (i.e., a good competitor for soil resources) should experience greater competition intensity when competing on a higher-fertility soil against better light competitors than when competing on its own soil type (Aarssen 1984, Tilman 1988, Smith and Huston 1989). The converse is true for a species adapted to high-fertility soil and similar reasoning can be applied to the relationship between competition intensity and other important environmental factors (e.g., disturbance).

This section discusses the experimental evidence from field studies on competition intensity across soil fertility (or productivity) and disturbance gradients in light of the selection regime-dependent predictions of the resource competition model. The focus is on field studies conducted in natural or partially natural soil because artificial soil mixes are likely to have depleted microbe communities compared with natural soils or natural soil mixes (Diaz et al. 1993). Only results based on relative CI are discussed here.

SOIL FERTILITY OR PRODUCTIVITY GRADIENTS

A number of studies measuring the interactions between target species and surrounding vegetation have found that competition was more intense at high compared with low soil fertility or productivity, as predicted by the C–S–R model. Some of these studies examined target species most common at (and presumably most adapted to) low-fertility environments (Wilson and Keddy 1986, Reader and Best 1989, Reader 1990, Bonser and Reader 1995). As previously argued, the resource competition model predicts higher competition intensity at high versus low soil fertility for species adapted to low-fertility soil when competing against species adapted to high-fertility soil. These results could therefore be consistent with either model. Other studies have examined target species most abundant at high fertility or productivity (Kadmon and Schmidha 1990, Kadmon 1995, Keddy et al. 2000) and calculated competition intensity by averaging across a range of target species (Wilson and Keddy 1986a, Twolan-Strutt and Keddy 1996). These studies tend to provide clearer support for the C–S–R model. A study by Sammul et al. (2000) found that both competition intensity and importance were greater at higher versus lower plant community productivity for a short-statured grass species (*Anthoxanthum odoratum*, whose pattern of abundance along the productivity gradient was unclear).

In contrast, other studies have found that competition intensity did not vary with soil fertility for at least some target species (Wilson and Keddy 1986a, Wilson and Shay 1990, Wilson and Tilman 1991, 1993, Reader et al. 1994, Belcher et al. 1995, Twolan-Strutt and Keddy 1996, Peltzer et al. 1998, Cahill 1999). Several studies that also measured below- versus aboveground competition found that belowground competition was stronger at low soil fertility, whereas aboveground competition was stronger at high soil fertility for these target species (Wilson and Tilman 1991, 1993, Twolan-Strutt and Keddy 1996, Peltzer et al. 1998, Cahill 1999, Belcher et al. 1995 found that aboveground competition was consistently insignificant). These results can be interpreted as support for the resource competition

model, with the caveat that some species can be plastic in their competitive abilities, such that they are able to compete well at both low and high soil fertility. Differences in plasticity among species could explain why some studies find that the relationship between competition intensity and soil fertility varies with target species (DiTommaso and Aarssen 1991, Reader 1992, Wilson and Tilman 1995).

A meta-analysis of target competition experiments (Goldberg et al. 1999) revealed unexpected patterns. Competition intensity was constant along productivity gradients, as predicted by the resource competition model, when competition was measured as the effect of surrounding vegetation on growth. When competition was measured as effects on final biomass or survival, on the other hand, competition intensity decreased with increasing productivity, which is consistent with neither model.

Results from studies examining competition within experimental mixtures of low and high fertility-adapted species tend to support the resource competition model. A number of these studies found the predicted reversals of competitive ability among low and high fertility-adapted species with increases in soil fertility (low fertility-adapted species favored on low-fertility soil, high fertility-adapted species favored on high-fertility soil) (Helgadóttir and Snaydon 1985, McGraw and Chapin 1989, Aerts et al. 1990; see also Aerts et al. 1991). Similarly, species common to the high-fertility end of a shoreline gradient were found to be stronger competitors at high fertility than those more common to the low-fertility end of the shoreline gradient (Wilson and Keddy 1986b). Two other studies again suggested the existence of plasticity in competitive ability, finding that for most study species, relative (although not absolute) competition intensity was constant over a range of soil fertilities (Campbell and Grime 1992, Turkington et al. 1993).

One of the most straightforward ways of addressing whether competition intensity varies with soil fertility is to compare the intensity of aboveground, belowground, and total competition among low fertility-adapted species growing on low-fertility soil with that among high fertility-adapted species growing on high-fertility soil (Taylor et al. 1990). The same approach could be used to examine competition intensity along disturbance or other environmental gradients. This type of experiment has hardly ever been conducted. A partial example is provided by Wilson (1993), who examined belowground competition intensity in forest (higher fertility) versus prairie (lower fertility). In support of resource competition theory, Wilson found that belowground competition was stronger where soil resources were the lowest. More recently, Callaway et al. (2002) examined competition intensity for a total of 115 target species at low versus high alpine elevation (higher vs. lower primary productivity, interpreted as a stress gradient) at 11 locations around the world. Although it is not clear whether aboveground or both above- and belowground competition were examined, Callaway et al. found that competition was strongest where productivity was highest and that plant interactions were in fact facilitative on balance at high elevations, providing support for the C-S-R model.

In conducting this type of experiment, it is important to consider the soil heterogeneity of the study sites. For example, a site may have a matrix of low soil fertility but contain patches of higher-nutrient soil (and the converse may be true for a site of mostly high soil fertility). We consider the role of soil heterogeneity later in this chapter.

DISTURBANCE GRADIENTS

Effects of disturbance on competition intensity have been examined using a variety of experimentally imposed treatments (fire, tilling, clipping, trampling) and natural gradients (herbivory). The study species used in such studies vary in the extent to which they are adapted to each disturbance. Annual species are presumably adapted to tilling; perennial prairie grasses to fire, grazing (clipping), and possibly trampling; and species typically found

where herbivory is intense are presumably adapted to herbivory. The C–S–R model (see also Taylor et al. 1990) predicts that species experience lower competition intensity in the presence of disturbance regardless of how well they or their competitors are adapted to the disturbance. In support of this, Reader (1992) found that exposure to herbivory appeared to decrease the intensity of competition (as measured by flower production) experienced by pasture species. In addition, annual tilling reduced the relative intensity of belowground (Wilson and Tilman 1995) and total competition (Wilson and Tilman 1993) for old-field species, regardless of whether they were annuals or perennials.

However, accounting for differences in species' adaptations to disturbance could be important in interpreting experimental results. Disturbance is thought to reduce competition intensity by reducing population density or biomass and so reducing demand for resources. But adaptation to disturbance (e.g., defense against herbivores) may require increased expenditures of energy and resources by organisms, that is, disturbance may result in fewer organisms that require more resources, so that the effective demand for resources may not really be changed at all by disturbance (see Holt 1985 and Chesson and Huntly 1997 for related discussion). Thus, whether disturbance reduces competition intensity may depend on whether the competing species are adapted to the disturbance (equivalently, on how novel the disturbance is). Competition intensity might be lower in the presence versus absence of a novel disturbance if the disturbance knocks species abundances far enough below the resource-supplying power of the environment. Alternatively, competition intensity among species similarly adapted to a disturbance may show no change in the presence versus absence of that disturbance. Competition among species similarly adapted to grazing (Turkington et al. 1993) and fire (Wilson and Shay 1990) may explain why no change in relative competition intensity with disturbance was typically observed in two studies of grassland species.

Of course, in the field, disturbance gradients may often be correlated with soil fertility or productivity gradients, with important consequences for understanding patterns in the intensity of plant competition. For example, degree of wave exposure along shorelines creates a gradient from nutrient-poor, disturbed (via wave action) conditions to nutrient-rich, undisturbed conditions (Wilson and Keddy 1986a). Patterns in competition intensity may reflect one or the other, or both of the underlying fertility and disturbance gradients. As another example, the exploitation ecosystem hypothesis (Fretwell 1977, Oksanen et al. 1981, Oksanen and Oksanen 2000) predicts that the degree of plant competition versus herbivory alternate along gradients of fertility or primary productivity, depending on whether conditions are productive enough to support carnivores that limit the impact of herbivores. Work in arctic-alpine plant communities has supported the exploitation ecosystem hypothesis, finding that plant competition is more intense and herbivory less intense at higher habitat fertilities and productivities (Olofsson et al. 2002, see also Sammul et al. 2006).

TRAITS

In most cases, it is not feasible to experimentally manipulate traits within any one species. The influence of traits on competitive ability must therefore be examined by correlating traits (e.g., R^* s, root to shoot ratio, height, seed size) across species with some measure of species performance in competition. Traits are usually measured on species grown in the absence of interspecific competition. Relatively few studies have examined the relationship between traits and competitive ability; therefore, this section includes greenhouse studies and studies conducted in artificial soils as well as field studies.

An approach that allows comparison of a large number of species is the neighborhood design of Gaudet and Keddy (1988). The competitive ability of different neighbor species is measured as relative ability to suppress the growth of a common target species, or phytometer. Multiple regression is used to determine which morphological and physiological traits

of each neighbor species correlate with competitive ability. The generality of results can be assessed by testing the neighbor species (or some subset of them) against different phytometer species. Thus far, this approach has been used to compare species of highly productive wetland communities growing in high-fertility soil (Gaudet and Keddy 1988). Results showed that competitive ability was most strongly correlated with aboveground biomass, followed by total and belowground biomass. Plant height, canopy diameter and area, and leaf shape were of secondary importance. These results could be interpreted as supporting either the C–S–R or resource competition model. The C–S–R model predicts that large size and height are among traits that allow acquisition of both above- and belowground resources at high soil fertility, whereas the resource competition model emphasizes large aboveground size as important for light acquisition at high soil fertility.

To date, relatively few traits and species have been evaluated in most other studies of plant competitive ability. As a group, however, these studies support resource competition theory in suggesting that traits related to acquisition of aboveground resources are important at high soil fertility, and traits related to acquisition of belowground resources are important at low soil fertility.

For example, size (biomass, seed size, height) is often a good predictor of competitive ability when light competition becomes important (i.e., conditions of high soil fertility and consequently high productivity) (Black 1958, Schoener 1983, Dolan 1984, Gross 1984, Stanton 1984, Weiner and Thomas 1986, Goldberg 1987, Miller and Werner 1987, Bazzaz et al. 1989, Reekie and Bazzaz 1989, Houssard and Escarré 1991, Wilson and Tilman 1991, Grace et al. 1992). A reason suggested for this is that light is a directional resource, and thus competition for light is asymmetric; large plants are often able to obtain proportionately more light than smaller plants (Weiner and Thomas 1986, Thomas and Weiner 1989). Asymmetric competition may explain the existence of competitive hierarchies and transitivity (i.e., consistent rankings of competitive ability; $A > B$, $B > C$, therefore $A > C$) in some competition studies (Keddy and Shipley 1989; but see Silvertown and Dale 1991 for a critique of these studies).

However, size is not always a good indicator of ability to preempt light. The degree to which biomass or productivity negatively correlates with light interception may, instead, depend on canopy architecture. For example, Tremmel and Bazzaz (1993) found that neighbor biomass was a poor predictor of the ability of neighbors to suppress targets, but that an index of neighbor light interception was a good predictor of neighbor competitive ability. In addition, Wilson (1994) found that size made no difference in seedling competitive ability when seedlings were competing against mature (larger) vegetation.

Conversely, when competition is mostly for soil resources (i.e., conditions of low soil fertility and consequently low productivity), root allocation, specific root length, and ability to retain or to efficiently use nutrients become good predictors of competitive success (Eissenstat and Caldwell 1988, McGraw and Chapin 1989, Tilman and Wedin 1991, Berendse et al. 1992, Wilson 1993a,b). R^2 s for soil resources also correspond with competitive success at low soil fertility (Tilman and Wedin 1991), and Tilman (1990) has shown analytically how R^2 summarizes the effects of these other traits on ability to acquire resources.

SOIL HETEROGENEITY

Resource heterogeneity is a feature of all natural environments, and its potential importance for plant competition and coexistence has been a recent focus of competition research. Soil resource availability differs at large scales of several meters or more (Lechowicz and Bell 1991, Jackson and Caldwell 1993a,b, Robertson et al. 1993, Gross et al. 1995, Ryel et al. 1996, Cain et al. 1999, Lister et al. 2000, Guo et al. 2002), and at small scales of less than a meter

(Ryel et al. 1996, Farley and Fitter 1999b). Soil resources also change temporally, within a growing season (Ryel et al. 1996, Cain et al. 1999, Farley and Fitter 1999b) or across successional time (Grace 1991b, Gross et al. 1995). Although large-scale, long-term resource variation contributes to patterns such as succession and gradients in species composition and diversity, small-scale heterogeneity detectable by individual plants has the potential to influence competitive interactions between individuals. Thus, this discussion focuses primarily on small-scale variation. It also focuses on heterogeneity of soil resources, rather than light, since most studies of heterogeneity at this scale address only soil resources.

The effects of temporal heterogeneity of resources on competitive interactions have largely been neglected. Goldberg and Novoplansky (1997) proposed a model of two-phase resource dynamics, in which the intensity of competition differs between periods of resource pulses (e.g., periods of rainfall in a water-limited system) and interpulse periods. This model attempts to reconcile the C–S–R and resource competition models. During pulses, competition is intense as plants attempt to preempt available resources (despite the influx of resources, pulse periods can thus be interpreted as times when resource demand by plants outweighs resource supply). During interpulse periods, tolerance of low resource levels determines survival. In productive environments, pulses are frequent and competition during pulses dominates. In unproductive environments, interpulse periods are longer. Competition may be the main influence on the community (as predicted by resource competition) if interpulse resource levels are determined primarily by plant uptake and if plant survival in inter-pulses depends on growth during pulses (i.e., resource demand on average outweighs resource supply). On the other hand, the community may be influenced mostly by stress tolerance (as predicted by C–S–R) if interpulse resource levels are determined more by physical processes such as drainage or leaching and if plant survival in inter-pulses is uncorrelated with competitive success during pulses (i.e., resource supply on average outweighs resource demand, which might occur when a species is better adapted to pulse than to interpulse periods, such that the onset of an interpulse period greatly reduces survival or growth, and thus demand for resources). To date, little data exist with which to test the two-phase resource dynamics hypothesis, and Goldberg and Novoplansky's (1997) call for more studies that focus on competition under pulsed resource regimes is well justified.

Most research on heterogeneity and plant competition has focused on effects of spatial heterogeneity. Predictions regarding the effects of spatial heterogeneity within a community depend on the size of resource patches, which may be smaller or larger than an individual plant's rooting zone.

For patches larger than (or equal to) an individual rooting zone, heterogeneity may generate diversity. In the resource competition model, heterogeneity promotes coexistence of species at any point along a soil fertility or productivity gradient because different patches represent areas where different species are the best competitors (Tilman 1982, Tilman and Pacala 1993). Although the C–S–R model does not explicitly address heterogeneity at this scale, it would presumably make a similar prediction, at least for productive environments where competition is predicted to be most intense. Several observational studies have reported positive correlations between environmental heterogeneity and species diversity (Harner and Harper 1976, Lundholm and Larson 2003, Davies et al. 2005). In addition, field studies have reported shifts in competitive abilities with naturally occurring local-scale soil heterogeneity (e.g., Reynolds et al. 1997). Experiments that have manipulated resource heterogeneity, on the other hand, find that increasing average soil resource levels (or decreasing light) reduces diversity, but heterogeneity has no effect (Collins and Wein 1998, Stevens and Carson 2002, Baer et al. 2004, Reynolds et al. in press, but see Vivian-Smith 1997). For instance, Stevens and Carson (2002) manipulated both average availability and heterogeneity of light in an old field community, and found that average light had a strong effect on diversity whereas degree of heterogeneity had no effect. Similarly, Reynolds et al. (submitted) found that spatial

heterogeneity of soil nutrients did not affect species diversity, and that species did not sort into areas of preferred nutrient availability. Instead, dominance of clonal species increased with both homogeneous and heterogeneous fertilizer applications. The authors suggest that, by foraging over areas larger than the patches created, clonal species may constrain the community response to heterogeneity.

Patches within a single plants' rooting zone may also affect the outcome of competition, although such patches are treated differently under C–S–R versus resource competition models. According to the resource competition model, these patches are not relevant. An individual plant uniformly depletes resources within its rooting zone, and the effects of varying resource levels on the plant are averaged out across the entire rooting zone (Tilman and Pacala 1993). In contrast, the C–S–R model predicts that morphological plasticity and active foraging for resource-rich patches are important traits contributing to competitive ability (Grime 1977, Grime et al. 1991). Therefore, ability to respond to fine-scale heterogeneity should be favored in productive environments, where both the resources available for growing new roots and the reserves they can tap into are high (but see Reynolds and D'Antonio 1996 for a different prediction). Furthermore, plasticity is predicted to be coarse-grained (altering root:shoot ratio, for example) for dominant species and fine-grained (altering within root allocation) for subordinate species (Campbell et al. 1991, Grime et al. 1991). There has been little work testing the prediction that foraging for resource patches is most adaptive in productive environments. However, many studies have addressed the C–S–R predictions that foraging influences competition and that species may employ different strategies for foraging.

Clearly, many species do exhibit plastic responses to resource-rich patches in the soil. Generally, both root growth and nutrient uptake rates increase in resource-rich patches, although the degree of increase varies greatly among species (Robinson 1994). In isolated plants, proliferation of roots does not appear to be adaptive at first: because nitrate is highly mobile in the soil, intense proliferation is not necessary to access nitrogen and does not in fact increase total nitrogen uptake (Robinson 1996, Robinson et al. 1999). However, proliferation does offer an advantage in a competitive situation: when plants of different species compete, the species with the greater proliferation response captures more nitrogen from a patch (Hodge et al. 1999, Robinson et al. 1999, Hodge 2003, Kembel and Cahill 2005).

Campbell et al. (1991) offered a framework for classifying species' morphological responses to heterogeneity by defining three aspects of foraging: scale (ability to explore a large soil volume), precision (ability to proliferate roots extensively in resource-rich patches), and rate (ability to reach patches quickly). They also proposed that there should be a trade-off between foraging scale and rate, with dominant species using high-scale foraging and subordinate species using high-precision foraging (Campbell et al. 1991). Several studies have measured foraging scale and precision for sets of species. These studies confirm that foraging traits are highly variable between species, although trade-offs have not always been found (Campbell et al. 1991, Einsmann et al. 1999, Farley and Fitter 1999a, Wijesinghe et al. 2001, Rajaniemi and Reynolds 2004, Kembel and Cahill 2005).

The effects of resource heterogeneity and species' foraging strategies on competition are inconsistent. The outcome of two-species competition sometimes differs between homogeneous and heterogeneous soils (Fransen et al. 2001, Bliss et al. 2002, Day et al. 2003b), and sometimes does not (Cahill and Casper 1999). In those pairwise experiments in which heterogeneity matters, the more precise forager tends to be the better competitor in patchy soils (Fransen et al. 2001, Bliss et al. 2002). However, in a study testing for correlations between competitive effect and foraging traits, competitive hierarchies were not affected by resource heterogeneity, and a species' foraging scale was a better predictor of its competitive ability than its foraging precision (Rajaniemi, in press). Any changes in competition in heterogeneous soils are also predicted to affect population and community structure

(Hutchings et al. 2003). For example, if large individuals can preempt resources, soil heterogeneity might lead to size-asymmetric competition (Schwinning and Weiner 1998), which would increase size inequality in populations. Again, some studies support this prediction, finding that size inequality is greater on patchy soils (Fransen et al. 2001, Facelli and Facelli 2002, Day et al. 2003a) whereas others do not (Casper and Cahill 1996, 1998, Blair 2001). Finally, effects of heterogeneity on competition might ultimately influence community structure. In the single study addressing this question, Wijeshinghe et al. (2005) showed that composition in an experimental community of herbaceous plants differed between homogeneous and heterogeneous soils, but species diversity did not.

Some of the inconsistencies described earlier might be resolved by considering the effects of patch characteristics. Patches may differ in size, contrast with background soil, spatial distribution, duration, and temporal predictability (Fitter 1994, Hutchings et al. 2003). The effects of heterogeneity on competitive interactions and population and community structure may depend on the nature of the patches (Hutchings et al. 2003), but researchers have only begun to address these factors. A few studies have failed to find effects of patch characteristics. Fransen et al. (2001) showed that the presence of patches influenced competition between two grass species, but that the size of patches had no effect. In this case, total nutrient levels were equal in all treatments, meaning that smaller patches also had greater nutrient concentration (and therefore greater contrast). Number of patches (also confounded with contrast) did not alter species' competitive effects in a target-neighbor experiment (Rajaniemi, submitted). On the other hand, a study of an experimental community provides intriguing evidence that patch characteristics may affect competitive outcomes. In this study, patch number did not affect diversity, but did affect species composition (Wijeshinghe et al. 2005). In addition, temporal predictability of patches had one subtle effect on community structure: the predictable treatment had a greater biomass of species considered colonists. The predictably low-nutrient patches may have served as refuges from competition for these species (Wijeshinghe et al. 2005). Future research on the importance of soil resource heterogeneity should further pursue the effects of patch characteristics, to unravel when and where we might expect strong effects of heterogeneity. Other issues still to be resolved include the importance of temporal resource pulses, the role of heterogeneity in promoting diversity in environments of differing productivity, and the adaptive value of foraging in environments of differing productivity.

CONCLUSIONS AND FUTURE DIRECTIONS

Plants compete when demands on resources (water, light, mineral nutrients, CO₂) exceed resource supply. Plant competition has been measured in a variety of habitats, from desert to temperate grassland, yet controversy remains about its significance for the ecology and evolution of species and the structure of communities, about whether the intensity of competition varies with environmental conditions, and about what traits are important to competitive ability. The need to understand these issues has only increased in the face of global changes, such as nitrogen enrichment, exotic invasions, and altered climate, that have the potential to alter competitive interactions and change community structure. By definition, exotic invasive species competitively exclude existing species in the communities to which they are introduced. Invasions are also generally associated with predator release, disturbance, and increased resource availability (Tilman 1999, Shea and Chesson 2002, Hierro et al. 2005). Invasions thus provide a particularly good opportunity to test competition theory as well as to assess the relative role of competition versus other factors, such as herbivory, in structuring plant communities.

Further progress in resolving controversy over the importance of plant competition, its intensity in different habitats, and the traits most important in predicting competitive

outcomes requires studies that (1) distinguish between importance and intensity, (2) examine a wide range of species (including native, noninvasive exotic, and invasive exotic species) and traits (including R^* , a potentially useful summary trait), (3) include as many environmental constraints (e.g., soil fertility, disturbance) as possible, including spatially heterogeneous and temporally pulsed resources, and (4) pay close attention to the extent to which each study species is adapted to the particular environmental constraints used. It may be useful to distinguish two aspects of the question of whether competition intensity changes along fertility (or disturbance) gradients: (1) Is competition equally intense among low fertility-adapted species growing on low-fertility soil and among high fertility-adapted species growing on high-fertility soil (low disturbance-adapted species growing in undisturbed environments vs. high disturbance-adapted species growing in disturbed environments)? and (2) Does competition play a role in maintaining community boundaries, for example, in preventing low fertility-adapted species from invading high-fertility soil and vice versa?

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APPENDIX 15.1: EXPERIMENTAL DESIGN AND COMPETITION INDICES

There are four main types of experimental designs for measuring competition between two species: (1) the replacement series (or substitutive design); (2) the additive design; (3) the bivariate factorial design; and (4) the neighborhood design. These designs have produced a variety of competition indices (Table 15.A1). In a replacement series (de Wit 1960), species are grown in pure stands and in mixtures, with one species at proportion p of its pure stand density and the other species at proportion $(1-p)$ of its pure stand density (Connolly 1986). The pure stand densities of each species need not be equal; however, the standard replacement design consists of one pure stand of each species grown at the same density, and a single 1:1 mixture of the two species, with each at half the pure stand density (Figure 15.A4a). The replacement approach thus attempts to measure interspecific competition relative to intraspecific competition.

The additive design also uses pure stands and mixtures of two species, but the density of each species is the same in pure and mixed stands. The standard additive design consists of pure stands of each species at the same density and a single 1:1 mixture of the two species, with each at its pure stand density (Figure 15.A4b). The additive approach thus attempts to measure the magnitudes of interspecific competition while holding intraspecific competition constant. Knowledge of the magnitudes of both types of competition is necessary for predicting the effects of competition on species distribution and abundance (Roughgarden 1979, Underwood 1986). Additive designs can easily be extended to measure absolute magnitudes of intraspecific competition (Underwood 1986).

For both designs, many indices of competition are based on performance of species in mixture compared with their performances in pure stand. Replacement designs have been criticized because this comparison confounds change in intraspecific density with change in interspecific density (Firbank and Watkinson 1985, Connolly 1986, Underwood 1986, Silvertown and Dale 1991, Snaydon 1991). Such confounding causes dependence of the competition indices on species densities in pure stands versus mixtures (Connolly 1986, Snaydon 1991), as well as on species' proportions and patterns of response to density (Snaydon 1991). Inherent differences in species' sizes can also cause dependence of competition indices

TABLE 15.A1

Common Indices of Competition for Replacement, Additive, Simplified Neighbor, Neighbor, and Bivariate Factorial Designs

Design ^a	Index	Abbreviation	Formula ^b		Reference
			Interspecific ^c	Intraspecific	
r, a	Relative yield total	RYT	$(Y_{ij}/Y_{ii}) + (Y_{ji}/Y_{jj})$	—	de Wit (1960)
r, a	Relative crowding coefficient ^d	RCC	$(Y_{ij}/Y_{ii})/(Y_{ii}/Y_{jj})$	—	Harper (1977)
r, a	Aggressivity	A	$1/2[(W_{ij}/W_{ii}) - (W_{ji}/W_{jj})](r)$ $(W_{ij}/W_{ii}) - (W_{ji}/W_{jj})(a)$ or $(Y_{ij}/Y_{ii}) - (Y_{ji}/Y_{jj})(r, a)$	—	McGilchrist and Trenbath (1971)
r, a	Absolute severity of competition	ASC	$\log_{10}(W_{40}/W_{ii})$	$\log_{10}(W_{40}/W_{ii})$	Snaydon (1991)
r, a	Relative severity of competition	RSC	$\log_{10}(W_{ii}/W_{ij})$	—	Snaydon (1991)
a, sn	Absolute competition intensity	Absolute CI	$Y_{ii} - Y_{ij}(a)$	$Y_{40} - Y_{ii}(a, sn)$	Campbell and Grime (1992)
a, sn	Relative competition intensity	Relative CI	$(Y_{ii} - Y_{ij})/Y_{ii}(a)$	$(Y_{40} - Y_{ii})/Y_{40}(a, sn)$	Campbell and Grime (1992)
a, sn	Relative neighbor effect	RNE	$Y_{40} - Y_{ij}/Y_{40}(a, sn)$	—	Wilson and Tilman (1991)
a, sn	Log response ratio	Ln(RR)	$\text{Ln}(Y_{40}/Y_{ij})$	—	Markham and Chanway (1996)
a, sn	Relative interaction index	RII	$Y_{ij} - Y_{40}/(Y_{ij} + Y_{40})$	—	Hedges et al. (1999)
n	Per-amount competitive effect	X	$W_i = W_{40}/(1 + XB_i)$	$W_i = W_{40}/(1 + XB_i)$	Armas et al. (2004)
a	Competition coefficient	α	$W_i = W_{40}[1 + \alpha_i(N_i + \alpha_{ij}N_j)]$	—	Goldberg (1987)
b	Competition coefficient	c	$W_i = W_{40}/(1 + N_i^c + N_j^c)$	—	Firbank and Watkinson (1990)
n	Interference coefficient ^e	c	$W_i = W_{40}/(1 + c_{ii}N_i + c_{ij}N_j)$	Same	Law and Watkinson (1987)
				Same	Silander and Pacala (1990)

a r, replacement design; a, additive design; sn, simplified neighbor design; n, neighbor design; b, bivariate factorial design.

b Variables: Y, yield per unit area; W, yield or weight per plant; B, total number of neighbors; a and b, fitted regression parameters. Subscripts: i, species i; j, species j; i0, species i grown with no competition; ii, species i grown in pure stand; ji, species j grown in pure stand; ij, species j grown in mixture with species i, whereas for α and c, refers to effect of species j on species i; ji, for Y and W, refers to species j when grown in mixture with species i, whereas for α and c, refers to effect of species i on species j.

c Note that interspecific formulas are given in terms of species i when grown with species j.

d For 1:1 ratios only (see Willey and Rao 1980, for application to other component ratios). Snaydon (1991) recommends \log_{10} or loge transformations to facilitate statistical and biological analysis.

e See Pacala and Silander (1985, 1990), and Silander and Pacala (1985, 1990), for methods of determining the best neighborhood size.

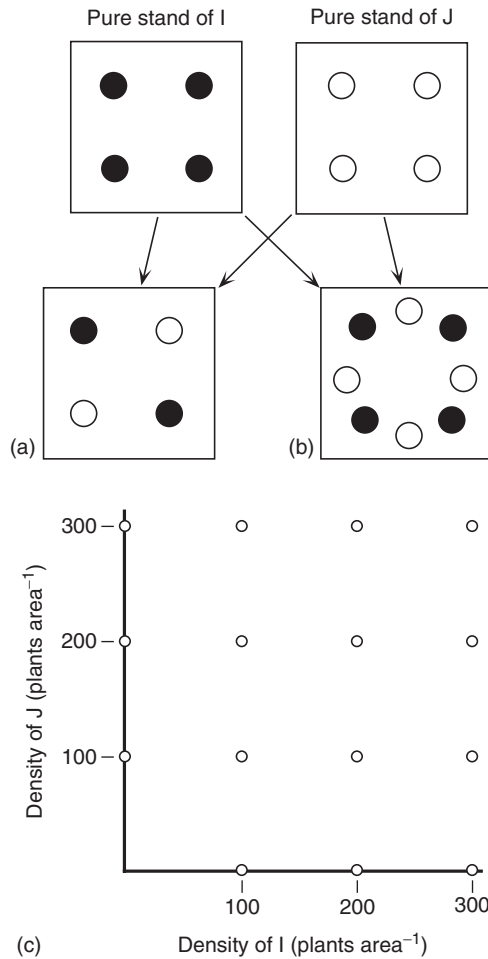


FIGURE 15.A4 Planting arrangements for pure stands of I (filled circle) and J (open circles) and for (a) replacement mixtures and (b) additive mixtures of I with J. (c) Diagrammatic representation of a bivariate factorial design, in which densities of the two species are varied independently. (Source: Snaydon, R.W., *J. Appl. Ecol.*, 28, 930, 1991. With permission.)

on species' densities (Connolly 1986, Grace et al. 1992). Sackville Hamilton (1994) defends replacement designs, but only for a restricted set of conditions (Snaydon 1994).

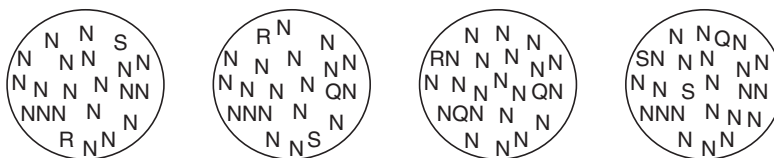
Because species' densities are the same in pure stands and mixtures in additive designs, competition indices are unaffected by pure stand densities or by species' patterns of response to density (Snaydon 1991). However, additive (and replacement) designs are, of course, sensitive to total density. If total densities are low enough, resources will not be limiting, and species will not compete even if they would experience strong competition at higher densities (Taylor and Aarssen 1989). Additive designs may also be sensitive to species proportions, that is, it is possible that relative competitive abilities change as species proportions in mixture change. To deal with these issues, additive designs may be repeated over a range of densities or proportions, yielding additive series (Snaydon 1991). When species' densities are varied factorially, producing a complete range of total densities and species' proportions, the resulting design has been termed both an addition series (Firbank and Watkinson 1985, 1990) and a bivariate factorial design (Snaydon 1991).

Additive series and bivariate factorial designs can be analyzed by regressing weight per plant in mixture on the density and proportion of each component species (Firbank and Watkinson 1985, 1990) or by calculating separate competition indices for each mixture (Snaydon 1991).

A modification of the additive design that has become popular is the neighborhood design, in which the density of a neighbor species around a single individual of a target species is varied (Goldberg and Werner 1983, Goldberg 1987) (Figure 15.A5). Performance (e.g., growth rate, survival) of the target species can be regressed on the amount (e.g., biomass, density) of neighbor species. The slope of this regression measures the per-amount competitive effect of the neighbor species on the target species (Goldberg and Werner 1983), and the coefficient of determination measures the importance of competition (the proportion of variation in performance that is explained by variation in neighbor amount) (Welden and Slauson 1986). The total competitive effect of a neighbor species is given by the product of its per-amount effect and its abundance. Per-biomass effects are indicative of physiological and morphological effects, whereas per-individual effects are often related to inherent size (Goldberg 1987). This approach has also been developed for populations of two species whose densities vary randomly, and can also be used to measure intraspecific competition, to compare the effects of different neighbor species on one target species or the responses of different target species to one neighbor species, and to account for the effects of neighbor distance or angular dispersion (Mack and Harper 1977, Weiner 1982, Pacala and Silander 1985, 1987, Silander and Pacala 1985). Gaudet and Keddy (1988) have used a simplified neighborhood approach to identify traits important to competitive ability (see “Conclusions and Future Directions”).

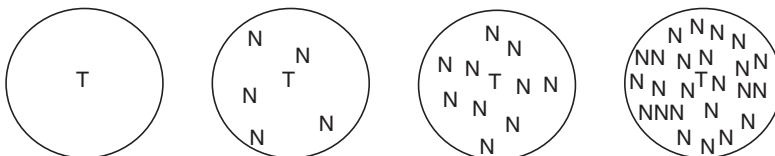
All of the designs mentioned earlier measure competition between only two species at a time, yet natural communities are typically composed of many more than two species. The number of experiments necessary to study all possible pairs of species in a multispecies assemblage quickly becomes unreasonably large—even without considering intraspecific interactions, different species’ densities or proportions, or the effect of environmental

Initial field conditions



(a)

After treatment



(b)

FIGURE 15.A5 Example of the experimental design for evaluating competitive effects of one neighbor species (N) on a target species (T). R, Q, and S represent individuals not belonging to the neighbor species selected for study. Only four steps of the neighbor density gradient (after treatment) are shown: the experiments must include a much wider range of densities to estimate accurately the slope of the regression of target performance on amount of neighbors. (Source: Goldberg, D.E. and Werner, P.A., *Am. J. Bot.*, 70, 1098, 1983. With permission.)

heterogeneity on competitive interactions (Keddy 1990, Tilman 1990). Ability to predict the outcome of competition in a community from pairwise competition experiments may also be complicated by indirect effects. Indirect interactions between two species arise via direct interactions with a third species (Connell 1990).

Many studies have used a simplified neighborhood approach to multispecies competition: comparing the performance of target individuals in the presence versus the absence of neighbor vegetation (Reader and Best 1989, Reader 1990, Reader et al. 1994, Wilson 1994), or in the presence versus absence of neighbor roots (Wilson 1993a), or roots and shoots (Aerts et al. 1991, Wilson and Tilman 1991, 1993, 1995, Wilson 1993b, Belcher et al. 1995, Gerry and Wilson 1995). This approach has been useful in examining changes in total, above- and belowground competition along environmental gradients (such as soil fertility gradients; [see the section on “Soil Heterogeneity”](#)).

Another approach to multispecies competition is to compare the performance of each species when grown in a single, multispecies community to that when grown in pure culture (additive design: Campbell and Grime 1992, replacement series design: Turkington et al. 1993). Alternatively, species can be removed from existing communities, and the performance of the remaining species can be compared with that in no-removal controls (Pinder 1975, Abul-Fatih and Bazzaz 1979, Fowler 1981, Silander and Antonovics 1982, Gurevitch and Unnasch 1989, Keddy 1989). Goldberg et al. (1995) suggested a design called the community density series that additionally varies neighbor abundance. In this design, community density is varied while initial relative abundances of component species are held constant. The slope of a regression of eventual relative abundance on initial community density for each species yields a measure of its community-context competitive ability. Although these multispecies approaches do not separate the effects of different neighbor species, or the effects of total neighbor biomass or density from per-amount effects of neighbors, they provide information about species' competitive performance under conditions more similar to that in the field.

Tilman (1990) suggested that a focus on the mechanism of competition—resource reduction ([see the section on “Competition Intensity”](#))—leads to the simplest and the most predictive approach to understanding multispecies competition. Theoretically, the species that reduces the limiting resource (e.g., available nitrogen, water, light) to the lowest level in monoculture is eventually able to displace all competitors (Tilman 1982, 1988). Many fewer experiments are required to determine the R^* (or R^* s, if more than one resource is limiting) of each species in a community than to run pairwise competition experiments (Tilman 1990). R^* s for soil nitrogen were found to predict the outcome of pairwise competition among four perennial grass species (Tilman and Wedin 1991). Similarly, greater rates of water extraction and greater depletion of available water were correlated with the superior competitive ability of one aridland tussock grass compared with another (Eissenstat and Caldwell 1988). This approach is yet to be applied to other terrestrial plant systems or to competition among multispecies assemblages.

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