8: Mechanisms of Plant Competition

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8.1 Introduction

The presence of a plant species in a locality, its abundance and the number of other plant species with which it coexists are influenced by numerous biological and physical processes. Interspecific interactions such as competition, herbivory, seed predation, mutualism, parasitism and disease may greatly affect plant dynamics and community structure (e.g. Janzen 1970; Hubbell 1980; Fowler 1981; Tilman 1982; Schoener 1983, 1985; Crawley 1983; Berendse 1985; Coley et al. 1985; Brown et al. 1986; McNaughton 1986; Clay 1990; Huntly 1991). In addition, soil pH, temperature, rainfall and other physical factors, fire, trampling, burial, erosion, windfall, landslides and other disturbances, and seed or pathogen or herbivore dispersal and other spatial processes also greatly influence plant distribution, dynamics and diversity (e.g. Connell 1978; Sprugel & Bormann 1981; Goldberg 1985; Pickett & White 1985; Vitousek & Matson 1985; Whitney 1986; Clark 1989; Petraitis et al. 1989; Gilpin & Hanski 1991). Plant ecology is an exciting and intriguing area of study because of this multiplicity of interacting forces. This chapter focuses on one of these, competition among plant species. The basic mechanisms of plant competition are developed first, and then these mechanisms are integrated with some of the other potentially important forces to build more complete explanations for observed patterns.

8.2 Competition in natural plant communities

The ability of an individual of one species to inhibit the survival and/or growth of individuals of another species is called interspecific competition, i.e. competition between different species. Ecologists define interspecific competition as an interaction in which an increase in the population density or biomass of one species leads to a decrease in the population growth rate and the population density or biomass of another species. For plants, the strength of interspecific competition is measured in terms of the magnitude of growth suppression caused by each unit biomass of the neighbouring species. Interspecific competition can be a major force in natural plant communities. Numerous experimental studies have shown that the survival and growth of an
individual plant may be strongly influenced by competition with its neighbours (e.g. Connell 1983; Schoener 1983; Wilson & Keddy 1986a,b; Goldberg 1987; Gurevitch et al. 1990).

8.2.1 Competition in a grassland field

Wilson and Tilman (1991) studied competition in a Minnesota field that was dominated by native North American prairie species. To measure the strength of competition, they planted seedlings of three different grass species into existing vegetation (All in Fig. 8.1a) and determined how rapidly they grew during a growing season. They also inserted these seedlings into sites from which they had removed all neighbouring plants and excluded roots of other plants within 25-cm metal rings that had been driven into the soil (— All in Fig. 8.1a). At the end of the growing season, the seedlings of a native bunchgrass called little bluestem (*Schizachyrium scoparium*) weighed 8.5 g per plant without neighbours but weighed only 0.5 g per plant in the presence of neighbours (Fig. 8.1a). Thus, the neighbouring plants led to a 16-fold inhibition of growth of little bluestem. Similarly, the presence of neighbours caused an eightfold inhibition for Kentucky bluegrass (*Poa pratensis*) and a sixfold inhibition for quack grass (*Agropyron repens*). This inhibition indicates that all three of these grass species experience strong interspecific competition in this field.

Although this demonstrates strong interspecific competition, it does not specify the actual mechanisms whereby each species inhibits the other. For plants, at least, it seems unlikely that inhibition is a direct

![Fig. 8.1](image)

(a) Biomass of little bluestem plants at the end of one growing season for seedlings planted into a prairie field. Both roots and shoots of all plants were removed from some plots (— All, just shoots were held back to prevent shading in some plots (— Shoot) or all existing plants were left intact (All) for some plots. (Data from Wilson & Tilman 1991.) (b) Biomass of little bluestem plants in similar plots in the same field, except these plots were much more productive because they had been fertilized for the preceding 5 years.
result of changes in plant density or biomass. Rather, changes in the biomass or population density of one species are likely to affect the availabilities of various resources, which then influence the growth and possibly the survival of the other species. Thus, the most likely mode of competition among plants is competition for resources.

8.2.2 Limiting resources

All plants require light, water and the same set of approximately 15 inorganic nutrients (N, C, K, P, Ca, Mg, S, etc.; see Chapter 3). The growth rate of a plant population, which is often best measured in terms of the specific rate of biomass change (i.e. as $1/B\ dB/\text{d}t$, where $B$ is plant biomass per unit area), depends on the concentrations of these resources in that habitat. It is often the case that the growth rate of a species in a habitat is determined by the one resource in lowest availability relative to the plant’s requirements for all resources. This is called the limiting resource for that plant species in that habitat. In general, the specific rate of biomass change of a species is an increasing, but saturating, function of the environmental concentration of its limiting resource. The growth of an individual plant would be decreased by the presence of neighbouring plants if these plants consumed and thus reduced the environmental concentration of its limiting resource. This is the basic mechanism of resource competition.

What may have caused the observed interspecific competition among grass species at Cedar Creek Natural History Area? A variety of lines of evidence suggest that these plants were competing with each other for a single limiting resource, soil nitrogen. Nutrient addition experiments that have been performed in this field have shown that addition of inorganic nitrogen (as ammonium nitrate fertilizer) led to significant increases in plant biomass, but that addition of P, K, Ca, Mg, S, water and trace metals had no effect on plant biomass (Tilman 1987, 1988, 1990b). Measurements of the concentration of soil ammonium and nitrate in the Wilson and Tilman competition plots described above found that these concentrations were very low in the plots that had the normal complement of neighbouring plants living in this field, but that concentrations were much higher in plots from which all neighbouring plants had been removed. These higher concentrations may explain the higher growth rates of seedlings in these plots.

8.2.3 Competition for nitrogen and light

Moreover, Wilson and Tilman’s competition experiment included an additional treatment. Seedlings of all three grass species were also planted into plots that contained the roots of neighbouring plants, but the shoots (the above-ground parts of the plants) were kept from shading a seedling by clear nylon mesh that held them back from the
seedling (– Shoot in Fig. 8.1a). At the end of the growing season, there was no detectable difference in the biomass of the seedlings between those grown in the presence of both the roots and shoots of the neighbouring plants versus those grown just in the presence of the roots. Both treatments greatly inhibited seedling growth compared with plots from which all neighbours had been removed. This indicates that the three grass species were inhibited by the roots of their neighbours and unaffected by the shoots of the neighbours on this nitrogen-poor soil. This further suggests that these plants were competing for a soil resource but were not competing for light.

Identical treatments were performed in other replicated plots in this field that had been fertilized with ammonium nitrate for the preceding 5 years. These fertilized plots had much greater above-ground plant biomass and had markedly different species composition and species diversity than the unfertilized plots. In the fertilized plots, the higher plant biomass led to much greater interception of light, and thus to low intensity of light at the soil surface. Comparisons of seedling biomass at the end of the growing season in the various treatments in these highly productive plots showed that plants competed as strongly in productive plots as they had in unproductive plots (Wilson & Tilman 1991). However, there was a shift in the mechanism of competition. In the productive plots, there was a highly significant effect of shading by neighbours. Unshaded plants grew significantly faster than those experiencing the shoots and roots of neighbours, but not as rapidly as those without neighbours (Fig. 8.1b). Thus, in the productive plots, the three grass species were competing for both light and nitrogen, whereas they were competing mainly for nitrogen in the unproductive plots.

8.3 A single limiting resource

For the grassland habitat discussed above, the major limiting resource was nitrogen. Let us now consider a simple, general theoretical framework that should apply to and predict the outcome of competition for a limiting soil resource (O’Brien 1974; Tilman 1976, 1977, 1982; Hsu et al. 1977; Armstrong & McGehee 1980). One piece of information needed is the dependence of plant growth rate on resource availability. Figure 8.2 shows hypothetical resource-dependent growth curves for two species, species A and B. Note that the specific growth rate ($\frac{dB}{Bdt}$, which is also called the relative growth rate, or RGR) increases with resource concentration, but that each plant species has a maximal specific growth rate that is approached at high resource concentrations. Each plant population also experiences various sources of loss or mortality. For instance, herbivores or pathogens may consume leaves, roots or stems, seed may be consumed, physical processes such as wind or frost may damage plants, and various factors may lead to plant death. All such sources of loss reduce the effective growth rate of a plant
population. These losses can be expressed in terms of their effect on the specific rate of change of plant biomass, i.e. in the same $dB/Bdt$ currency as used for plant growth (Hubbell & Werner 1979). This then leads to a simple relationship:

$$\text{rate of biomass change} = \text{growth} - \text{loss}$$

or

$$dB/Bdt = f(R) - m$$  \hspace{1cm} (8.1)

where $f(R)$ is a function describing the resource dependence of the specific growth rate of a plant (as shown by the curves in Fig. 8.2) and $m$ is the total mortality and loss rate, again expressed on a specific biomass basis.

![Diagram](image)

Fig. 8.2 (a) Resource-dependent growth and loss for species A. The resource concentration at which growth equals loss is $R_A^*$. (b) Resource-dependent growth and loss for species B and its $R_B^*$. (c) Dynamics of resource competition between species A and B. Note that species B, which has the lower $R^*$, displaces species A and drives the resource concentration down to $R_B^*$. 
8.3.1 The $R^*$ concept (‘$R$ star’)

When $dB/Bdt = 0$, the biomass of the species is no longer changing, and is thus at equilibrium. The long-term outcome of resource-dependent growth is thus determined by setting $dB/Bdt = 0$. When $dB/Bdt = 0$, $f(R)$ must be equal to $m$, i.e. the resource-dependent growth of the species must equal its loss rate. The implication of this is immediately grasped by inspection of Fig. 8.2. Note that $dB/Bdt = 0$ at the resource concentration at which the line labeled $m$ intersects with the resource-dependent growth curve. The resource concentration at which this occurs is called $R^*$ (Fig. 8.2).

$R^*$ represents the environmental resource concentration required for the growth rate of a species to exactly balance its various sources of loss. A species will only be able to survive in a habitat if the habitat has a resource concentration of at least $R^*$. If the resource concentration of a habitat were held at a value less that $R^*$, the resource-dependent growth rate of the species would be less than its loss rate and the species would go extinct locally.

8.3.2 Resource dynamics

The concentration of the resource depends on the balance between the rate at which the resource is consumed by the species and the rate at which it is being resupplied within the habitat, i.e.

$$\text{rate of resource change} = \text{supply rate} - \text{consumption rate}$$

The consumption rate depends on the amount consumed per unit biomass in a given time interval multiplied by the biomass of the species. The supply rate, for a mineral nutrient like nitrogen, depends on microbial decomposition of organic matter, excretion of nitrogenous wastes by animals and various fixation processes.

Eventually an equilibrium will be reached at which neither the resource concentration (which would be at $R^*$) nor the biomass (per unit area) change. When this occurs, the biomass of the species will be such that it consumes the resource at the rate at which it is being supplied, and the growth rate of the species equals its loss rate. This equilibrium point is stable, i.e. the population biomass and the resource concentration will tend to return to this point if perturbed away from it (Tilman 1980). This is caused by adjustments in population biomass in response to resource concentrations and adjustments in resource concentrations in response to population biomass.

There are many different forms that can be used for $f(R)$. The simplest form is the Michaelis–Menten equation, which states that

$$f(R) = \frac{rR}{(R + k)}$$

(8.2)

where $r$ is the maximal specific growth rate of the species (also called its
RGR_{max}), R is the resource concentration and k is the half-saturation constant for growth (the resource concentration at which the species grows at half of its maximal growth rate, i.e. at r/2). This form of the model, when substituted into Equation 8.1, leads to

\[ R^* = \frac{mk}{(r - m)} \]  

(8.3)

Other, more complicated models have been proposed because the Michaelis–Menten formulation seems to exclude many of the interesting features of terrestrial plants, such as their production of leaves, roots, stems and seeds, the differences in the longevity of these structures and differences in nutrient conservation abilities (Tilman 1990a). Interestingly, even the most complex models lead to a rather simple conclusion. At equilibrium, all such models predict that a species will have a unique \( R^* \) value, and that this value will be determined by all the plant traits included in the model.

Thus, when a single species lives in a habitat, it reduces the concentration of its limiting resource down to its \( R^* \). \( R^* \) is the concentration of resource that a species requires to survive in a habitat. The \( R^* \) of a species is a summary variable that incorporates the effects of all types of nutrient and tissue loss, herbivory and mortality, as well as the effects of all traits that influence growth, including the nutrient dependence of photosynthesis and respiration, the plant pattern of allocation to root, leaf, stem and seed, and the nutrient conservation ability of the species.

\( R^* \) is a critical variable because it is the direct measure of the effect of one plant species on a potential competitor. Plants compete through their effects on environmental resource levels, and \( R^* \) quantifies these effects. It is the level to which each species can reduce the concentration of the limiting resource. There are two qualitatively different ways to determine the \( R^* \) of a species for a limiting resource. The simplest way is to observe it directly by allowing a single species to grow, in monoculture, in an environment in which a particular resource is known to be the only limiting resource. Once the biomass of the monoculture reaches an equilibrium, the level to which it has reduced the concentration of the limiting resource is the \( R^* \) of that species. The other way is to construct a realistic model of processes controlling growth and loss, determine the values of the parameters for a particular plant species and predict the \( R^* \) from the underlying model.

### 8.3.3 Competition for a limiting resource

If several different plants compete for the same single limiting resource, the single species with the lowest \( R^* \) should displace all other species from the habitat (Tilman 1976, 1977; Hsu et al. 1977). This displacement occurs because the species with the lowest \( R^* \) can continue increasing in abundance and reducing the resource concentration down to its \( R^* \). However, once the resource concentration falls below the \( R^* \)
values of other species, they are unable to survive in the habitat because their resource-dependent growth rates are held to a lower rate than their losses.

This is illustrated in Fig. 8.2b,c. Note that species A and B have different resource-dependent growth curves and different loss rates. Species B has a lower $R^*$ than species A. As the two species grow in the same habitat, they will compete for the limiting resource. Species B starts to displace species A when it first reduces the resource concentration below $R^*$. As equilibrium is approached, the resource concentration approaches $R^*$, the biomass of species B stops changing and the biomass of species A approaches 0.

8.3.4 Tests of the $R^*$ hypothesis

There have been numerous tests of resource competition theory, which has proven to be surprisingly robust. The first was an experimental study of competition between two species of freshwater algae, both diatoms (Tilman 1976). *Asterionella formosa* (Fragilariaceae) had a lower $R^*$ for phosphate than did *Cyclotella meneghiniana* (Bacillariophyceae). When they were grown together with phosphate as the only limiting nutrient, *Asterionella* displaced *Cyclotella*. *Cyclotella* had a lower $R^*$ for silicate (which diatoms require to make their frustule, which functions like a cell wall), and *Cyclotella* displaced *Asterionella* when they were silicate limited. Hansen and Hubbell (1980) showed, for several different cases, that the bacterial species with the lower $R^*$ for tryptophan, the limiting resource, competitively displaced the other species. Rothhaupt (1988) showed that $R^*$ successfully predicted the outcome of interactions among two zooplankton species that were consuming two different algal species. Tilman *et al.* (1981) found that the temperature dependence of $R^*$ could be used to predict the outcome of competition among diatoms for silicate along a temperature gradient. Other cases, reviewed in Tilman (1982), also show that $R^*$ can correctly predict the long-term outcome of competition among aquatic organisms for a single limiting resource.

However, there were questions about the applicability of resource competition theory to more complex organisms, such as terrestrial vascular plants. Indeed, the complexity of terrestrial plants may make it quite difficult to predict the $R^*$ of a species based on its underlying physiology, morphology and life history. However, does this mean that measured $R^*$ values would be unable to predict the outcome of resource competition?

We studied nitrogen competition among five grass species (Tilman 1990b; Tilman & Wedin 1991a,b; Wedin & Tilman 1993). Each of the five species was grown in replicated, long-term monocultures in garden plots with soils prepared such that nitrogen was the only limiting resource. By the third growing season, the above- and below-ground
living biomass of the five species has equilibrated, and the species differed significantly in levels to which they had reduced the concentration of nitrogen (nitrate and ammonium) in the soil solution (Fig. 8.3). Little bluestem (*Schizachyrium scoparium*) and big bluestem (*Andropogon gerardii*) had the lowest $R^*$ values for nitrogen of the five grass species. They also had the greatest allocation to root and the greatest belowground living biomass of the five species. In contrast, *Agrostis scabra* had the lowest allocation to root and the greatest $R^*$ of these species, and *Poa pratensis* and *Agropyron repens* had intermediate $R^*$ values. Thus species that allocated a greater proportion of their biomass to root drove soil ammonium and nitrate concentrations down to lower levels.

Various pairs of these species were also planted together in replicated garden plots in which soil nitrogen was the only limiting resource. Three qualitatively different starting conditions were used: seed competing against seed, seed competing against established plants, and established plants competing by invading into other established plants (Wedin & Tilman 1993). The long-term outcome of competition after 5 years was identical for all three types of experiments. In all cases, if a species had a significantly lower $R^*$ than another species, it displaced that other species. The results of competition between *Agrostis* and *Schizachyrium*, which differed greatly in their $R^*$ values, can be compared to that between *Agropyron* and *Poa*, which have quite similar $R^*$ values (Fig. 8.4a,b). *Agrostis*, which has an $R^*$ for nitrogen that is 5.5 times greater than the $R^*$ of *Schizachyrium*, was rapidly displaced by *Schizachyrium* from low nitrogen soils (Tilman & Wedin 1991b). In contrast, the $R^*$ of *Agropyron* was only 1.05 times that of *Poa*, and competitive displacement of *Agropyron* by *Poa* is much slower. Indeed, for the various pairs of species tested, the rate of competitive displacement was more rapid the greater the difference in the $R^*$ values, as is predicted by theory. This indicates that resource competition theory can correctly predict the outcome of competition between terrestrial plants.
Fig. 8.4 (a) The dynamics of competition for limiting nitrogen between *Agrostis* (solid symbols) and *Schizachyrium* (open symbols), for seeds planted into long-term garden plots. Each point is a mean of three replicates. Each line represents a different initial ratio of seeds of the two species. *Schizachyrium* has a lower $R^*$ for nitrogen and, as predicted, is the superior competitor. (Data from Tilman & Wedin 1991b.) (b) A similar case of competition, except between *Agrostis* (solid symbols) and *Agropyron* (open symbols). These species have more similar $R^*$ values. *Agropyron*, which has the lower $R^*$, is the predicted winner, and did come to dominate these plots.

### 8.4 Competition for two resources

In order to predict the outcome of plant competition for two or more resources, it is necessary to know the dependence of the growth of each species on the availability of all limiting resources. Plants require many different resources, most of which are essential for plant survival, i.e. plants cannot survive without them. Some species may be limited simultaneously by two or more resources and it is possible for different species to be limited by different resources in the same habitat. However, different forms of an essential resource, such as the ammonia and nitrate forms of nitrogen, can be substituted for each other. This chapter only considers competition for limiting, essential resources. A more complete development of theory can be found in Tilman (1982).

#### 8.4.1 Resource isoclines

Although the theory of competition for two resources is best expressed using differential equation models (Tilman 1977, 1985, 1990a), its major features can be understood graphically (Tilman, 1980). The curve shown in Fig. 8.5a is the resource-dependent zero net growth isocline for a plant species. This isocline shows the concentrations of two limiting resources ($R_1$ and $R_2$) for which the resource-dependent growth of this species exactly balances all its losses (i.e. $dB/dt = 0$). For any of the resource concentrations on this curve, the population biomass of this species will be constant. The two ‘ends’ of the curve give, in
their limits, the $R^*$ values of this species for $R_1$ and $R_2$. The shape of this curve means that these two resources are ‘interactive-essential’ for this species. This occurs if a plant can adjust its morphology or physiology in response to concentrations of two essential resources so as to acquire them in the proportion in which they are required. Plants that are not so plastic, such as single-celled algae, have an isocline that is closely approximated by a right-angled corner.

Population biomass will decrease ($dB/dt < 0$) if resource availabilities fall inside the isocline, and it will increase if an environment has resource availabilities that fall outside the isocline. On the horizontal portion of the isocline, far from the origin, the species is limited by $R_2$, and changes in $R_1$ do not affect its growth and vice versa. To see this, consider the extreme right-hand end of the isocline. At this point, addition of $R_2$ would lead to increased growth and its removal would lead to decreased growth, but there would be almost no effect on growth from changes in $R_1$, which would just lead to motion along the isocline.

8.4.2 Resource consumption vectors

Equilibrium will occur when resource consumption equals resource supply, and reproduction equals mortality. Reproduction equals mortal-
ity for any point on the growth isocline. The actual point on the isocline that will be the equilibrium point in a given habitat is determined by the rates of resource consumption and supply. Optimal foraging theory (Rapport 1971) predicts that a plant should consume nutritionally essential resources in the proportion in which the plant is equally limited by them. This is represented by a consumption vector, $C$ (Fig. 8.5a). The length of the consumption vector is the amount of the two resources consumed by this species. The slope of this consumption vector gives the ratio in which this species requires $R_2$ and $R_1$. This consumption vector can be empirically determined, or it can be approximated by assuming that it is parallel to a line from the origin through the 'corner' of the isocline. The slope of such a line should approximate the ratio in which the plant requires these resources.

### 8.4.3 Resource supply vectors

Let $S_1$ and $S_2$ be the maximal amounts of all forms of resources 1 and 2 in a given habitat. The point $(S_1, S_2)$ is called the resource supply point of that habitat. Each habitat is considered to have a particular resource supply point. A simple model of resource supply assumes that rate of supply of a resource should be proportional to the amount of the resource that is not already in the available form. This would give

$$dR_j/dt = a(S_j - R_j) \quad (8.4)$$

where $a$ is a rate constant and $j$ refers to resource $j$. This equation defines a resource supply vector, $U$, that always points toward the supply point. Thus, the resource supply point $(S_1, S_2)$ of Fig. 8.5a leads to the equilibrium point shown with a dot. At the equilibrium point, the population density of the species is such that its total rate of resource consumption of each resource equals the total rate of supply of each resource. This occurs because, at this point, the two vectors are equal in length and opposite in direction. Because this occurs at a point on the zero net growth isocline, the plant's reproductive rate equals its mortality rate.

### 8.4.4 Coexistence and displacement

To predict the outcome of competition between two or more species for two limiting resources, it is only necessary to superimpose their isoclines and consumption vectors. Consider the two isoclines shown in Fig. 8.5b. These isoclines cross because species A is a better competitor for $R_1$ and species B is a better competitor for $R_2$. The point at which these isoclines cross is a two-species equilibrium point, i.e. a point of potential coexistence of these two species. At this point, the reproductive rates of both species A and B equal their mortality rates. However, these species will only be able to coexist in habitats with certain resource supply points (Fig. 8.5b). If habitats have low supply rates of $R_1$ and
high supply rates of $R_2$, such as at supply point $x$, both species will be limited by $R_1$. Species A, which is the superior competitor for $R_1$, will reduce the level of $R_1$ down to a point on its isocline at which there is insufficient $R_1$ for the survival of species B. Thus, species A will competitively displace species B from habitats with low $S_1 : S_2$ ratios (Fig. 8.5b). Comparably, species B is a superior competitor for $R_2$ (has a lower $R^*$ for $R_2$) and it will displace species A from habitats in which both species are limited by $R_2$. Such habitats have high $S_1 : S_2$ ratios.

The two species can coexist in intermediate habitats in which each species is relatively more limited by a different resource, species A by $R_2$ and species B by $R_1$. For habitats with supply points within the region defined by the consumption rates of these species at the two-species equilibrium point (Fig. 8.5b), the consumption of the two species will eventually reduce resource levels down to the equilibrium point. Thus, the resource requirements of these two species define habitats in which one species is dominant, both stably coexist or the other is dominant. Along a resource ratio gradient, such as from supply point $x$ to supply point $y$ to supply point $z$, there is a smooth transition from dominance by species A, to coexistence of A and B, to dominance by species B. This resource ratio gradient is a gradient from low $S_1 : S_2$ ratios to high $S_1 : S_2$ ratios. Such separation along the $S_1 : S_2$ gradient only occurs if the species are differentiated in their requirements for $R_1$ and $R_2$, with the superior competitor for one resource being the inferior competitor for the other resource.

### 8.4.5 Experimental tests

Several experimental studies of algal competition for limiting phosphate and silicate have shown that this simple theory can predict the outcome of interspecific competition, including stable coexistence (Tilman 1976, 1977, 1982; Tilman et al. 1982; Carney et al. 1988). Additionally, the distributional patterns of algal species along natural resource ratio gradients in Lake Michigan are consistent with their requirements for the limiting resources and the outcome of laboratory competition experiments among the species (Tilman 1982). There have not yet been studies of the applicability of this theory to competition for two or more resources by terrestrial plants.

### 8.5 Multispecies communities

As developed so far, resource competition theory seems to predict the outcome of resource competition experiments, but the predicted outcomes seem discordant with nature. If a single resource is limiting to all plants, as seems to be the case for nitrogen in the old fields and prairie of Cedar Creek Natural History Area, Minnesota, this theory predicts that a single species should eventually dominate these habitats. Two species
could coexist if there were two limiting resources, and so on, but there
could never be more species than there were limiting resources in the
habitat. However, despite the strong experimental evidence that nitro-
gen is the only limiting resource, except in a drought year when water
becomes limiting, Cedar Creek fields contain from 70 to more than 200
different species of vascular plants. Observations over the past decade
show that these species are persisting in these fields, and that species that
were driven to low density because of the drought are reinvading and
becoming re-established. All of this suggests that 70–200 species are
stably coexisting in a habitat in which there is only one demonstrably
limiting resource. How could this occur?

Clearly, any explanation for the existence of such biodiversity must
be more complex than the simple resource competition theory pre-
sented above. Of the many processes that can, in theory, explain the
stable coexistence of multispecies communities (reviewed in Tilman &
Pacala 1993), there are four distinct explanations that incorporate
resource competition among plants. Each of these explanations starts
with the simplifying assumptions of the basic model of resource
competition: (i) that organisms live in a spatially homogeneous habitat,
(ii) that all interactions go to equilibrium, (iii) that the entire food web
can be approximated by just the link between consumer species and
their resources, and (iv) that all organisms within a habitat experience
exactly the same resource concentrations at the same time. Each of these
theories accepts three of the four simplifying assumptions above, but
modifies one of these to make it more realistic. Thus, each of these
explanations is one logical step more realistic than the simple model of
resource competition discussed previously.

8.5.1 Spatially discrete individuals

The models of resource competition presented above assumed that all
individuals of all species experienced exactly the same resource concen-
trations at any given instant. This mathematically convenient assump-
tion is not biologically realistic. Terrestrial plants occur as discrete
individuals. Each individual consumes resources in its immediate neigh-
bourhood. Thus, an individual mainly competes with its immediate
neighbours (Pacala 1986a,b; Goldberg 1987; Pacala & Silander 1990).
An individual plant with a low $R^*$ for a limiting resource would reduce
the concentration of that resource in its immediate vicinity down to its
$R^*$, but this would not affect the growth of a plant species with a higher
$R^*$ that did not live in its neighbourhood.

Models can be formulated to deal with plants as spatially discrete
individuals that only influence resource concentrations in their immedi-
ate vicinity, but such models are not yet analytically tractable. The
essential, though highly abstracted, features of resource competition
among spatially discrete individual plants can be captured in ‘metapop-
ulation’ models, such as those of Levins and Culver (1971), Horn and MacArthur (1972), Hastings (1980) or Shmida and Ellner (1984). Their models have shown that spatial subdivision can allow the stable coexistence of two competitors even though one is a superior competitor in any given habitat. The inferior competitor could coexist, but only if it were a superior disperser or had a lower loss rate than the superior competitor.

These models do not explicitly include resources, but rather rank species from being the best competitor (i.e. species with the lowest $R^*$ for a limiting resource) to the worst competitor (species with the highest $R^*$). A habitat is considered as being divided into a series of patches, each the size of an individual plant. The abundance of a species is represented as $p$, the proportion of patches that are occupied by that species. Species disperse randomly among all patches. If a superior competitor invades a patch occupied by an inferior competitor, the superior competitor displaces the inferior competitor from that patch. These ecological assumptions, as applied to a single species, are expressed in the following equation, which was first proposed by Levins (1979):

$$\frac{dp}{dt} = cp(1-p) - mp$$  

(8.5)

where $m$ is the mortality (local extinction) rate and $c$ is the colonization rate. Propagules disperse at random among all sites. The propagule production rate by the occupied sites, $cp$, is multiplied by the proportion of unoccupied sites, $1-p$, to give the rate of production of newly occupied sites. A site becomes vacant when the individual occupying that site dies. The local mortality rate, $m$, is multiplied by $p$, the proportion of occupied sites, to give the rate at which occupied sites become empty.

Building on Hastings (1980), Tilman (1993) extended this work to show that it could explain, in theory, the stable coexistence of a potentially unlimited number of species competing for a single limiting resource. For this work, the equation describing the dynamics of site occupancy by the $i$th species, for a series of $n$ species ranked from the best competitor (species 1) to the worst competitor (species $n$), is:

$$\frac{dp_i}{dt} = c_i p_i \left(1 - \sum_{j=1}^{i} p_j \right) - m_i p_i - \left( \sum_{j=1}^{i-1} c_j p_j p_i \right)$$  

(8.6)

There is one such equation for each species. The dynamics of each species depend on colonization (the first term), on mortality (the term $-m_i p_i$), and on competitive displacement (the last term). A species is only affected by species that are superior competitors, i.e. have a lower rank (lower $R^*$).

It is possible for any number of competing species to stably coexist, at equilibrium, with this model if there are the appropriate interspecific
trade-offs among them (Tilman 1993). Specifically, coexistence requires that an inferior competitor be a superior colonist and/or have greater longevity than its superior competitor. Moreover, there is an analytical limit to similarity of competitively adjacent species. This limit to similarity means that it is not sufficient for an inferior competitor to be a better colonist, for example, than its superior competitor, but rather that it must be better by a specified amount that is greater the greater the abundance of its superior competitor (Tilman 1993).

Coexistence occurs because the superior competitor is unable to occupy all sites within a given habitat. Even in the absence of competitors, there is a portion of the habitat that is always unoccupied by the best competitor. These open sites can allow the long-term persistence of another species if it has sufficiently great dispersal and/or longevity to survive in the open sites, despite the competitive displacement that comes when its superior competitors invade and despite the lost reproduction that comes from its propagules landing in sites occupied by its superiors. However, this second species also has a finite dispersal ability and experiences some mortality. It thus cannot occupy the full remainder of the habitat. The sites it leaves open can allow the persistence of an inferior competitor, if it has sufficiently greater colonization and/or longevity. This process may continue without limit. No matter how many species there are, they cannot occupy all potential sites within an infinite environment as long as each species has finite dispersal ability and all experience some mortality (Tilman 1993; see also Chapters 14 & 15).

Although there have been no direct tests of the applicability of this hypothesis to Cedar Creek grasslands, it is supported by much circumstantial evidence. Monocultures of Schizachyrium, which were planted at high densities, were rarely invaded by other plant species, whereas monocultures of species with higher $R^*$ values for nitrogen were frequently invaded and had to be constantly weeded. There was also a marked interspecific trade-off between the nitrogen competitive abilities of the five grass species we studied and their colonization abilities. Schizachyrium and Andropogon allocate less than 1% of their biomass to seed, have seed with a low viability and require 11–17 years to invade most abandoned fields. In contrast, Agrostis and Agropyron, which have much higher $R^*$ values, have much greater allocation to seed, also reproduce via rhizomes and invade most abandoned fields within 1 or 2 years. A comparable trade-off occurs during succession (Gleeson & Tilman 1990). Because plant species that allocated more to root were better nitrogen competitors in our garden experiments (Tilman & Wedin 1991b), this allocation pattern suggests that there is a strong trade-off between competitive ability and colonization ability. If this is so, the theory discussed above may explain the stable coexistence of numerous species in these grassland fields.
8.5.2 Spatial heterogeneity

It has long been suggested that spatial heterogeneity within a habitat might account for the coexistence of numerous competitors. This hypothesis modifies the assumption of spatial homogeneity, but retains the other three simplifying assumptions made by the original theory. The essential idea is that each species is a superior competitor for a particular suite or intensity of environmental factors, and that point-to-point variability in these factors could allow numerous species to coexist.

This hypothesis cannot explain the coexistence of numerous species living in a habitat in which there is a single limiting resource and no other limiting factors. In such a case, point-to-point heterogeneity in the supply rate of the single limiting resource could not allow more than one species to persist, at equilibrium. This occurs because the species with the lowest $R^*$ for this resource would reduce resource concentration to its $R^*$ at all points in the habitat. That species would be more abundant in areas with higher rates of resource supply and less abundant in areas with lower rates of supply, but it would be the only species at equilibrium.

There are, however, other ways that spatial heterogeneity could influence species diversity. For instance, the growth (and thus $R^*$) of species could be influenced by a physical factor such as temperature or pH, and this physical factor may vary spatially in intensity. If species were differentiated in their abilities to compete for a single limiting resource at different intensities of this physical factor, such heterogeneity could allow a potentially unlimited number of species to coexist. A situation with five competitors is illustrated in Fig. 8.6. Species A is the superior resource competitor at 10 °C, species B at 11 °C, species C at 12 °C, species D at 13 °C and species E at 14 °C. In any homogeneous habitat, in which plants living in all localities experience exactly the

![Fig. 8.6 Nitrogen competition along a temperature gradient. The five species are differentiated in the temperature at which they have their greatest competitive ability (i.e. lowest $R^*$). A single species would win in nitrogen competition in a homogeneous habitat, but all five species could coexist in the range of temperatures of Habitat 1.](image-url)
same temperature, only a single species will win. However, if there were spatial heterogeneity in temperature, such as might occur along an elevational gradient or with respect to aspect and microtopography, it is possible for several or all of these species to coexist stably as long as propagules arrive in the proper locations. Thus, the interspecific differentiation and trade-off illustrated in Fig. 8.6 could allow a large, potentially unlimited, number of species to coexist in a habitat with spatial heterogeneity in a physical factor such as temperature or pH.

Alternatively, if there are two limiting essential resources, such as nitrogen and phosphate or nitrogen and light, spatial heterogeneity could allow numerous species to coexist. Let us consider a case in which five different species compete for two essential resources. Again, let us assume that these species are differentiated such that each species is a superior competitor for a particular ratio of the limiting resources, and that each species consumes the resources in the ratio in which it is equally limited by them. This gives regions in which various pairs of species can coexist (Fig. 8.7a) and predicts that the species should, at equilibrium, be separated along an $S_1:S_2$ resource ratio gradient (Fig. 8.7b). The point at which each species reaches its greatest abundance along the resource ratio gradient is determined by its requirements for the limiting resources. Thus, species A is dominant at low $S_1:S_2$ ratios because it is the best competitor for $R_1$ but the worst

![Figure 8.7](image-url) (a) Zero net growth isoclines for five species and their consumption vectors (not shown) create regions in which various pairs of species can stably coexist or a single species is dominant. The five species have an interspecific trade-off in their competitive abilities for $R_1$ versus $R_2$. If habitats have spatial heterogeneity in resource supply rates, such as indicated by the circle, more species could potentially coexist than there were limiting resources. (b) The interspecific trade-off above leads to separation of these five species along a gradient in the relative rates of supply of these two resources.
competitor for \( R_2 \). At all points along the gradient, \( R_1 \) and \( R_2 \) are important limiting resources for some of the species.

Spatial heterogeneity in \( S_1 \) and \( S_2 \) might occur along elevational gradients or in response to heterogeneity in substrates and parent material from which soils form or from excretion of wastes by herbivores (e.g. Lehman 1982). Such heterogeneity is represented not by a single resource supply point, but by a cloud of such supply points, with each point representing the average resource supply rates experienced by an individual plant. There is much spatial heterogeneity in the levels of nutrients in both soils and lakes (e.g. Burgess & Webster 1980; Lehman 1982; Yost et al. 1982). Such variance can be illustrated graphically by showing all of the different supply points experienced by the individual plants in a heterogeneous habitat. Let the circle in Fig. 8.7a include 99% of the point-to-point spatial heterogeneity in the \((S_1, S_2)\) as experienced by individual plants in a habitat. Such spatial heterogeneity can allow many more species to coexist than there are limiting resources. All that is required for a species to exist in a habitat is that there be some site with a suitable \((S_1, S_2)\), i.e. that the circle overlaps its region of existence, and that its propagules arrive in that site. For instance, five species could stably coexist in a habitat with the heterogeneity represented by the circle in Fig. 8.7a because there are sites in which each species can survive.

### 8.5.3 Resource fluctuations and non-equilibrium conditions

It is also possible that resource concentrations and populations do not go to equilibrium but fluctuate. Armstrong and McGehee (1976a,b, 1980) showed that such resource fluctuations could allow an unlimited number of species to stably persist in a spatially homogeneous habitat in which all individuals of all species experienced the same resource concentrations at any given time. Fluctuations allow species to persist because of non-linearities in the resource-dependent growth curves of the consumer species.

Levins (1979) provided a clear example of this. Consider two species, both of which are limited by the same resource. Species A has a linear resource-dependent growth curve, whereas species B has a non-linear curve (Fig. 8.8a). Both species experience the same mortality rate, \( m \), giving an \( R_A^* \) that is less than \( R_B^* \). Thus, in a non-fluctuating environment, species A should competitively displace species B. How would resource fluctuations around a mean of \( \bar{R} = R_A^* \) affect the long-term average growth rates of species A and B?

Because species A has a linear resource-dependent growth curve, fluctuations below \( \bar{R} \) lead to decreases in growth rate that are exactly balanced by the increases in growth caused by fluctuations above the mean. Thus, the long-term average growth rate of species A is independent of the variance in resource availability (Fig. 8.8b). In contrast, the
sigmoid shape of the resource-dependent growth curve of species B means that fluctuations below the mean of $\bar{R}$ lead to small decreases in growth, whereas comparable fluctuations above the mean lead to greater increases in growth. Thus, the long-term average growth rate of species B increases as the magnitude of the fluctuations, as measured by the variance around $\bar{R}$, increases (Fig. 8.8b). This means that the variance in $\bar{R}$ is functioning as if it were a resource for species B.

The responses of these two species can be used to create zero net growth isoclines for the case in which a single fluctuating resource is decomposed into two components, its mean and its variance (Fig. 8.8c). The isocline for species A is a straight line because it is unaffected by variance. The curved isocline of species B shows that species B has a higher $R^*$ for the resource in an unvarying habitat at equilibrium (variance = 0), but that its requirements are lower as the magnitude of resource fluctuations increases (Fig. 8.8c). The point at which the two curves cross represents coexistence. This point can be stable if species B
‘consumes’ the variance more than does species A. This is likely because species B is a specialized consumer of resource pulses and thus could quickly decrease resource concentration when it is above the mean. Thus, a species with opportunistic foraging can coexist with a resource competitor that has a lower $R^*$, if resource concentration fluctuates. The relative abundances of the superior competitor and the opportunist should depend on the magnitude of the resource fluctuations. With small fluctuations, the superior competitor would displace the opportunist. They would coexist with intermediate fluctuations, and the opportunist would displace the superior competitor in a highly fluctuating environment.

Sommer (1984, 1985) showed that pulses of phosphate and/or silicate could allow the long-term persistence of many more algal species than there were limiting resources, whereas the number persisting in habitats at equilibrium did not exceed the number of limiting resources. Grover (1988, 1989, 1990, 1991) obtained similar results, and demonstrated the underlying physiological bases for such coexistence. It seems highly likely that desert annual plants are exploiters of pulses of rainfall, and that this allows numerous species of annuals, each specialized on a different pattern or timing or magnitude of rainfall, to persist with long-lived, deep-rooted perennials that are better water competitors in general. Many perennial plants differ in the season of their growth and may differ in the timing of their exploitation of soil resources (McKane et al. 1990), which may be an important factor allowing them to persist in their natural habitats.

8.5.4 Multiple trophic levels

Hutchinson (1959) suggested that trophic complexity might allow numerous competitors to coexist. This was supported by Paine’s (1966, 1969) work on intertidal invertebrates, which showed that removal of starfish, the top predator, caused the loss of many rocky intertidal species. Levin et al. (1977) explicitly modelled multitrophic-level food webs and tested their model in laboratory food webs containing phage viruses, their bacterial prey, and the sugar that limited the growth of the bacteria. Their model predicted that the number of distinct viral strains could not exceed the number of distinct bacterial strains, but that the number of bacterial strains could be greater than the number of limiting sugars if some bacterial strains were more limited by viral attack and others more by the sugar. Their experimental food webs confirmed this prediction. They found that two bacterial strains could coexist on a single limiting substrate, but only if, as predicted, the bacterial strain that was more susceptible to viral attack was also the better competitor for the substrate.

This theory has been generalized to any food web (Tilman 1982). At equilibrium in a spatially homogeneous habitat in which all organisms
simultaneously experience the same resource concentrations, the number of predator species cannot exceed the number of their prey species, and the number of prey species cannot exceed the sum of the number of their limiting resources plus the number of predator species. Thus, a single limiting resource can support a single prey (consumer) species, which can support a single predator. However, if there is a prey species that is either a better resource competitor but more susceptible to predation, or a poorer competitor but more resistant to predation, it may be able to invade into and persist in this food web. If this happens, there are now two prey species, which could allow the invasion of another predator species. However, the addition of another predator species could allow a further prey species to invade. This process could continue indefinitely if all species have the appropriate trade-offs. Thus, it is conceptually possible for a potentially unlimited number of consumer (prey) species to coexist in a homogeneous non-spatial habitat at equilibrium in which there is a single limiting resource if the habitat also has the right suite of predators (Tilman 1982).

Thus, a grassland field, such as an old field or stand of prairie at Cedar Creek Natural History Area, could conceivably contain over 100 plant species, all competing for a single limiting resource (nitrogen), if the plant species were appropriately differentiated with respect to competitive ability versus susceptibility to herbivory. At the present time, there are few data with which to evaluate this idea (see Chapter 13).

8.6 Conclusions

There is strong evidence that both terrestrial and aquatic plants compete for limiting resources in natural, managed and agricultural habitats. Competition both within and among species is thus one of the major forces determining the distribution and abundance of plant species and the biodiversity of plant communities. The simple theory of resource competition presented in this chapter captures the essence of this interaction.

If two plants compete for a limiting resource, each influences the other through its effect on the environmental concentration of the limiting resource. For spatially homogeneous habitats that have reached equilibrium, the effect of each species on the other is measured by the R* of each species. A single variable, R*, which is directly measurable by growing a plant in monoculture, integrates the effects of the morphology, physiology and life history of a plant species on its resource competitive ability. The available experimental evidence suggests that R* can correctly predict the long-term outcome of nutrient competition among terrestrial plants and among various aquatic organisms. It is a useful first step in understanding the mechanisms of competition.

However, natural habitats are unlikely to be spatially homogeneous, individual plants are spatially discrete, resource levels often oscillate
because of external environmental forces and plants live in complex food webs in which they are influenced not only by resource competition but also by various herbivores, pathogens, parasites and mutualists. All such factors directly influence plant dynamics and thus can modify the effects of plant competition. The four hybrid models discussed above all emphasize the need to consider the joint effects of interspecific resource competition and other constraints on plant fitness. Each of these is presented as a distinct model for mathematical convenience. Clearly, plants living in any natural habitat may experience all these constraints simultaneously. One of the major challenges facing plant ecology is the synthesis of such constraints into a more general theory that can help us better understand the forces that control the dynamics and diversity of plant communities.