Chapter 2 Resources, Competition and the Dynamics of Plant Communities

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2.1 Introduction

As discussed in Chapter 1, there are many factors that influence the structure of plant communities. A central goal of plant ecology is to understand the processes and mechanisms that cause the patterns we see. This is no easy task, however. There are more than 300,000 species of terrestrial vascular plants world-wide, and more than 1,000,000 species of animal. Any given habitat may contain from a few plant species to hundreds of different species, all of which are potentially interacting with each other, with their abiotic environment, with soil micro-organisms, and with herbivores, pathogens, predators, pollinators and dispersal agents. Thus, plant community structure is likely to be influenced by interspecific competition, by herbivory, by predation, and by mutualism. Additionally, the habitat in which plants live is not constant. Rainfall, temperature, and the population densities of various herbivores, predators and mutualists change through time, on both short and long time scales. The natural, ecological world may be one of the most complex systems that scientists have tried to understand. One way to approach such a complex system is to start with a few important processes, and see what features of the system can and cannot be explained using those processes.

Numerous observational and experimental studies, reviewed later in this chapter, have shown strong effects of the availabilities of nutrient resources and light on the species diversity, species composition, and species dominance of both aquatic and terrestrial plant communities. In this chapter, I shall explore the possible effects of interspecific competition for resources on plant community structure. I shall first present a simple model of plant competition for resources, and then compare its theoretical predictions with the patterns observed in a variety of plant communities worldwide. This is not meant to imply that other processes, such as herbivory, are unimportant. Rather, it is done in the hope of finding a simple theory that can predict the broad, general patterns we observe in plant communities. Such a simple theory could then be expanded, as needed, to describe nature more realistically.
2.2 Theory

Ecologists define interspecific competition (i.e. competition between different species) as an interaction in which increases in the population density of one species lead to decreases in the per capita growth rate and population density of another species (see Box 1.4). This definition, however, does not specify the mechanisms whereby each species inhibits the other. At least for most plants, it seems unlikely that inhibition is a direct result of changes in density as such (but see Section 1.6.3). Rather, changes in the population density of one plant species are likely to affect the availabilities of various resources, such as nitrogen, water, phosphorus and light, and thus influence the growth of other species indirectly.

2.2.1 Competition for a single resource

The basic information needed to predict the outcome of competition for resources is the dependence of the rates of population growth of

Fig. 2.1. Each part of this figure shows the dependence of the per capita rate of reproduction (solid curve) and the per capita rate of mortality (broken line) of a species on resource availability. For each species and each resource, the resource availability at which reproductive rate equals mortality rate is indicated by the arrow pointing at \( R \). Note that Species A has a lower \( R^* \) for resource 1 but a higher \( R^* \) for resource 2 than Species B. The \( R^* \) of a species is the amount of a resource the species requires to survive in a habitat. The four \( R^* \) values from this figure are used to construct Fig. 2.2.
each species on resource availability. In the following discussion, \( N \) refers to the population density of a species, i.e. to the number of individuals per unit area. Consider, for instance, the dependence of the per capita rate of reproduction, expressed as \( dN/dt \cdot 1/N \), of species \( A \) on the availability of a limiting resource, \( R_1 \) (Fig. 2.1a). For a species to exist in a habitat, its reproductive rate must be greater than or equal to its mortality rate. If species \( A \) lived in a habitat in which it experienced the mortality rate indicated by the broken line, its mortality rate (\( m_A \)) would equal its reproductive rate only in habitats with \( R_{A,1}^* = 1.0 \) of the resource (Fig. 2.1a). If a habitat had less \( R_1 \) than this, the population density of species \( A \) would decline. As the population density declined, the rate of consumption of the resource would decline, and resource availability would increase. If a habitat had more \( R_1 \) than \( R_{A,1}^* \), the population density of species \( A \) would increase, leading to an increased rate of consumption of the resource, and thus to a lower availability of the resource. In the absence of interspecific competition, the population density of species \( A \) would equilibrate at the point at which its rate of resource consumption equaled the rate of resource supply, and its reproductive rate equaled its death rate. At equilibrium, species \( A \) would thus maintain \( R_1 \) at a level of \( R_{A,1}^* \) (called the 'requirement' of species \( A \) for \( R_1 \)). Similarly, based on the curves in Fig. 2.1c, species \( B \) has a requirement of \( R_{B,1}^* = 4.0 \). If species \( A \) and \( B \) competed for this resource, and if this interaction went to equilibrium, theory predicts that the single species with the lower requirement for the resource would displace all other species (Tilman, 1976; Hsu, Hubbell & Waltman, 1977). Thus, species \( A \) should displace species \( B \) when both are limited by \( R_1 \) because species \( A \) can reduce \( R_1 \) below the level required for the existence of species \( B \).

There have been several experimental studies of plant competition for a single limiting resource. The first attempt to test this theory was an experimental study of nutrient competition between two species of freshwater algae (Tilman, 1976, 1977). This work showed that the species with the lower \( R^* \) for the limiting resource (either phosphorus or silicate) competitively displaced the other species. Many additional studies have been performed since then, with most of them showing that \( R^* \) differences corresponded with differences in competitive ability as predicted by theory (Tilman, 1981; Holm & Armstrong, 1981; Hansen & Hubbell, 1980; Tilman et al., 1982).

### 2.2.2 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. A resource is limiting if increases in its availability bring about an increase in plant growth rate. Information on the dependence of plant growth on resources which are not limiting under natural conditions is of no ecological importance. Plants require many different resources, including \( \text{H}_2\text{O} \), light, and various forms of N, P, K, Ca, Mg, S, Co, Cu, Mo, Mn and Zn. Each of these are essential to plant survival. Thus the growth rate of a nitrogen-limited plant is not increased by addition of P or K or any resource other than nitrogen. For essential resources, the growth rate of a plant is determined by the availability of the one resource in lowest supply relative to need (Chapter 12). However different forms of an essential resource, such as the ammonia and nitrate forms of nitrogen, can be substituted for each other. This chapter will only consider competition for limiting, essential resources. A more complete development of theory can be found in Tilman (1982).

2.2.3 Resource isoclines

Although resource competition theory is best expressed using differential equation models (Tilman, 1977, 1982, 1985), its major features can be understood graphically (Tilman, 1980). Consider species A of Fig. 2.1. It requires \( R_{A,1}^* = 1.0 \) of resource 1 and \( R_{A,2}^* = 3.0 \) of resource 2 in order to maintain a stable population. These requirements define the resource-dependent growth isocline of Fig. 2.2a. For all environments that have availabilities of \( R_1 \) and \( R_2 \) that fall on this isocline, the reproductive rate of species A will equal its mortality rate; there will be no change in its population density (it is in equilibrium and \( \frac{dN}{dt} = 0 \)). If resource availabilities fall outside this isocline (further from the origin), population density will increase (\( \frac{dN}{dt} > 0 \)). Population density will decrease (\( \frac{dN}{dt} < 0 \)) if resource availabilities fall inside the isocline. The right angle corner in the isocline means that species A is limited by either \( R_1 \) or \( R_2 \), whichever is in lower supply relative to its need. It is equally limited by \( R_1 \) and \( R_2 \) at the corner of the isocline. Above this point, changes in \( R_2 \) have no effect on its growth rate, and it is limited by \( R_1 \). On the horizontal portion of the isocline, it is limited by \( R_2 \), and changes in \( R_1 \) do not affect its growth. To see this, choose several different points on the growth isocline, and see, for each point, how addition of \( R_1 \) or \( R_2 \) would affect the growth of species A.

2.2.4 Resource consumption vectors

Equilibrium will occur when resource consumption equals resource supply, and reproduction equals mortality. Reproduction equals mortality for any point on the growth isocline. The actual point on the
isocline that will be the equilibrium point in a given habitat depends on the rates of resource consumption and supply. Optimal foraging theory (Rapport, 1971; Tilman, 1982) predicts that a plant should consume essential resources in the proportion in which it is equally limited by them. This is illustrated with the consumption vector, $C_A$, which is parallel to the broken line from the origin through the corner of the isocline (Fig. 2.2a). The broken line shows the optimal ratio of $R_1 : R_2$ for species A (i.e. the $R_1 : R_2$ ratio it requires for growth).

2.2.5 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. The 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

$$dR_j/dt = a(S_j - R_j),$$

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. 2.2a,
leads to the equilibrium point shown with a dot. At the equilibrium point, the population density of species A is such that its total rate of resource consumption equals the total rate or resource supply, and its reproductive rate equals its mortality rate.

2.2.6 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. The \( R^* \) of species A and B of Fig. 2.1 give the isoclines shown in Fig. 2.2b. The point at which these isoclines cross is a two-species equilibrium point; that is, 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. 2.2b). 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. 2.2b). Comparably, species B is a superior competitor 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 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. 2.2b), 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 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.

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). 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).

2.2.7 Multispecies competition

Finally, let us consider a case in which five different species compete for two essential resources. Again, let us assume that these species

Fig. 2.3. (a) The isolines for 5 different plant species (A–E), and their consumption characteristics define regions in which various species or pairs of species may exist. For instance, Species A and B could coexist stably in any habitats that had supply points (S_1, S_2) that fell within the region labelled ‘A+B’. (b) Competition between the 5 species would lead them to be separated along a resource supply ratio gradient as illustrated. This could be considered to be a gradient from low to high S_1:S_2 ratios, such as from point x to point y in Fig. 2.3(a). (c) Seven species (A to G) are shown competing for two resources. Spatial heterogeneity in the supply rates of the resources is illustrated by the circular resource supply regions. This could allow many species to coexist in resource-poor habitats (circle 2), but would not allow more than two species to coexist in resource-rich habitats (circle 4). (d) Simulations of cases in which 40 species competed for two resources in a spatially heterogeneous habitat led to these diversity curves. Note that diversity falls more rapidly with resource enrichment when all resources but one are added (case 2) than when the supply rates of all resources are increased (case 1). Modified from Tilman (1980; 1982).
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. 2.3a), and predicts that the species should, at equilibrium, be separated along a $S_1 : S_2$ resource ratio gradient (Fig. 2.3b). 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 competitor for $R_2$. At all points along the gradient, $R_1$ and $R_2$ are important limiting resources for some of the species.

Let us now apply this theory to a variety of patterns observed in plant communities, including species diversity patterns, species dominance patterns and succession. The graphical version of resource competition theory presented here is an equilibrium theory. It predicts what the ultimate, long-term outcome of competition would be in a habitat once change had ceased. If its predictions are consistent with patterns observed in natural communities, resource competition may be an important process in these communities. Of course such consistency does not mean that other processes are unimportant.

2.3 Species diversity

In the form in which it has been discussed so far, this theory makes an almost trivial prediction about the number of species that can coexist in a habitat. It predicts that the number of species that can coexist, at equilibrium, can be no greater than the number of limiting resources. Thus, for a habitat in which there is a single limiting resource, the one species with the lowest requirement for that resource should displace all other species at equilibrium (see Box 1.1). Two species could coexist on two resources, 10 species could coexist on 10 resources, and so on. This raises a problem, however. Experimentation has shown that there are, at most, four or five resources limiting plants in most habitats, and yet there may be hundreds of species coexisting in these habitats. What might be the explanation of this?

2.3.1 Spatial heterogeneity

One explanation could be that natural habitats are not uniform. So far the model has assumed that all plants in a habitat experience the same rate of resource supply. However, 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). This means that a habitat has both an average supply point and variance within it.
Different plants, depending on where they are located, experience different rates of resource supply. Such variance could be illustrated graphically by showing all of the different supply points experienced by the individual plants in a heterogeneous habitat. Let the circles in Fig. 2.3c include 99% of the point-to-point spatial heterogeneity in the (S1, S2) 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 (S1, S2), i.e. that the circle overlap its region of existence. For instance, all seven species could stably coexist in a habitat with the heterogeneity represented by the circle number 2 (Fig. 2.3c), because there are microsites in which each species can survive.

2.3.2 Resource availability

How should species richness depend on resource availability? Consider two different ways in which resource levels might change. First, it could be that richer habitats are richer in all resources. If that were so, this theory would predict that there would be maximal species richness in habitats that were moderately resource poor, providing that spatial heterogeneity of the resources—the diameter of the circles—did not increase more than linearly with the resource level (Tilman, 1982). As shown in Fig. 2.3c no species could exist in habitat 1, seven species could coexist in the slightly more resource rich habitat 2, four species could coexist in the even richer habitat 3, and two species could coexist in the even richer habitat 4. Simulations of similar cases in which 40 species were assumed to be competing for two essential resources gave the diversity curve in Fig. 2.3d (case 1). This theory thus predicts that maximal species richness should occur in moderately resource poor habitats, habitats that have just enough resources for species survival in the absence of interspecific competition.

Consider, also, a second case in which S2 increases but S1 remains constant, such as for habitats 2, 5 and 6 of Fig. 2.3c. Again, there is maximal plant diversity in resource poor habitats. In this case, all resources but R1 are being added, and diversity falls more rapidly with resource richness because R1 becomes the only limiting resource (Fig. 2.3d, case 2).

2.3.3 Observational studies

This prediction agrees well with many observational and experimental studies of both planktonic algal communities and terrestrial plant communities. For instance, Beadle (1966) observed that the maximal diversity of Australian xeromorphic and rainforest genera
Fig. 2.4. The dependence of plant community diversity on resource richness (or some measure of resource richness) for a variety of habitats. Figures redrawn from: 
(a) Beadle (1966); (b) Bond (1983); (c) Tilman (1982) based on data in Ashton (1977); 
(d) Dix & Smeins (1967); (e) Tilman (1982) based on data in Holdridge et al. (1971); 
and (f) Al-Mufti et al. (1977). Note that Bond estimated above-ground plant biomass 
in arbitrary units by using the area under a plant foliage-height profile. Tilman 
normalized the data of Ashton & Holdridge et al., on soil phosphorus (P) and 
potassium (K) levels, and then used the summation of these normalized variables as a 
measure of soil resource richness. Dix & Smeins divided their study areas into drainage 
types which they ranked from those with the best drainage to those with the poorest. 
Al-Mufti et al., estimated productivity by summing the total above ground plant 
biomass and the soil litter of each area. For all the figures it is assumed that the x axis is 
a measure of the availability of various limiting soil resources, with habitats with the 
greatest availability being at the right hand side of each graph.

occurred in very phosphorus-poor soils, and that areas with richer 
soils were more species poor (Fig. 2.4a). Shmida et al. (1984) found 
that the regions with the highest plant diversity within Israel had 
fairly low rainfall; a graph of species richness versus regional rainfall 
gave a humped curve.
Two of the world's most diverse plant communities, the fynbos vegetation of South Africa and the heath scrublands of Australia, occur on very nutrient-poor soils. In both of these areas, nearby areas with more resource-rich soils have much lower diversity (Goldblatt, 1978; Kruger & Taylor, 1979; Specht & Rayson, 1957; Specht, 1963). This is illustrated by a comparative study performed in South African vegetation by Bond (1983; Fig. 2.4b).

The number of species of Malaysian tropical rainforest woody species had a similar dependence on the availability of two important soil resources, phosphorus and potassium (Ashton, 1977; Fig. 2.4c). The work of Holdridge et al. (1971) in the New World tropical forests of Costa Rica (Fig. 2.4e) showed that the most diverse forests occurred on moderately resource-poor soils, and that rich soils supported many fewer species. For North American prairie, Dix & Smeins (1967), reported that the greatest plant diversity occurred in areas with low water availability (Fig. 2.4d). A humped diversity curve was also reported by Al-Mufti et al. (1977) for British vegetation; maximal diversity occurred in habitats with low productivity, as measured by the total of plant standing crop and litter (Fig. 2.4f). Other studies in other habitats have also shown that maximal species richness occurs in moderately resource-poor terrestrial habitats, as predicted by theory (e.g. Young, 1934; Huston, 1980; Mellinger & McNaughton, 1975; Whittaker & Niering, 1975). Additionally, similar patterns have been reported for the planktonic algae of a variety of lakes and the oceans (e.g. Steeman-Nielsen, 1954; Fischer, 1960; Dugdale, 1972; Smaida, 1975; Blasco, 1971; Nelson & Goering, 1978; Williams, 1964; Patrick, 1963, 1967; Patten, 1962; Schelske & Stoemer, 1971). Consistent with theoretical predictions, for both terrestrial and aquatic plant communities, maximal species diversity occurs in moderately resource-poor habitats. Very resource-rich habitats and extremely resource-poor habitats can support the long-term persistence of many fewer species.

2.3.4 Experimental studies

Because few habitats are sufficiently resource-poor to be below the diversity peak (Fig. 2.4), and because most additions of nutrient resources represent major increases in resource supply, most experimental additions of limiting resources should lead to decreased diversity. Such fertilization experiments have been performed in a variety of habitats world-wide, and have shown just this pattern. For instance, fertilization of British pastures led to dramatic decreases in species richness during a 17 year experiment (Milton, 1940, 1947). In experiments performed on turf transplanted from British coastal sand dunes, Willis & Yemm (1961) and Willis (1963) found that the
number of coexisting species fell from 22 to 5 following the addition of a complete mineral fertilizer, whereas the species richness of controls did not decrease. They observed similar, but less dramatic decreases in species richness in undisturbed natural vegetation. Bakelaar & Odum (1978) found that the species diversity of an eight-year-old field (abandoned from agriculture eight years previously) fell significantly following application of a fertilizer containing N, P and K. Kirchner (1977) found that the diversity of North American short-grass prairie decreased significantly after three years of watering and fertilization.

![Graphs showing changes in Shannon index of diversity over time for different treatments](image)

Fig. 2.5. Effects of fertilization on the species diversity of the Park Grass Experiments at Rothamsted, England. The Shannon Index of species diversity, $H'$, measures both the total number of species in the community and the evenness of their relative abundance distributions. The more equally dominant species are, and the more species there are, the greater the value of $H'$. (a) and (b) show that there were no significant changes in diversity during a 100-year period in the unfertilized control plots. (c) and (d) show that the diversity of plots fertilized with a complete mineral fertilizer containing N, P, K, Ca and Mg fell dramatically through time. Many of the grasses and forbs living in this regularly mowed pasture are long-lived perennial plants which have a large proportion of their biomass in below-ground storage organs. This may account for the slow rate of species displacement. Modified from Tilman (1982).

The most long-term fertilization study that has been performed (and, indeed, the most long-term research in ecology) is the Park Grass Experiment. In 1856 in Rothamsted, England, a mowed
pasture was divided into 20 plots, each receiving a different combination of mineral fertilizers (Lawes & Gilbert, 1880). Although this research was started to determine which mineral elements could improve the yield of hay, Lawes & Gilbert became fascinated with the effects of the treatments on the diversity and species composition of the plots. From 1862 onwards, there have been several censuses of the abundances of the species in these plots (Thurston, 1969). Throughout the experiments, there were no significant changes in the species diversity (Fig. 2.5a and b) or the species composition (Fig. 2.6a) of the unfertilized control plots. In contrast, the species diversity of the plots receiving all mineral fertilizers, with a high rate of nitrogen application (as ammonium) fell dramatically (Fig. 2.5c,d). These plots became dominated by a single species that comprised 90–99% of the total plant biomass (Fig. 2.6c,d). The grass Holcus lanatus dominated the plot which was unlimed and had a pH less than about 4.0. Another grass, Alopecurus pratensis, dominated the next higher pH plot, and two grasses, Alopecurus and Arrhenatherum elatius, coexisted in the plot with the highest pH (Fig. 2.6b,c,d).

The effect of fertilization on diversity was not limited to the plots receiving unusually high rates of nitrogen addition. For every year in which the Park Grass Experiments have been sampled, there has been a negative correlation between the species richness of the plots and their total above-ground biomass (Silvertown, 1980; Tilman, 1982). To the extent to which the addition of particular nutrients led to increased plant biomass, those nutrients also led to a lower number of coexisting species. Soil pH, which changed in response to fertilization, also had a great effect on diversity (Silvertown, 1980; Tilman, 1982).

In summary, a simple theory of plant competition for limiting resources predicts that plant communities should have maximal diversity in moderately resource poor habitats. Both observational and experimental studies performed in a wide variety of terrestrial and aquatic habitats are consistent with this prediction.

2.4 Patterns in species dominance

2.4.1 Observational studies

Anyone who has walked through a pasture, a prairie, or an abandoned field will have noticed patterns in the vegetation. Often a field will seem to be a mosaic made up of clumps of various species. Alternatively, there may be fairly distinct zones in which each species is dominant, as is frequently the case along even minor elevational gradients. Some species seem to reach their greatest abundance on hill tops, some on the slopes, and others at the bottom of the hills.
(Chapter 1). There have been numerous attempts to explain such patterns in vegetation. Most of these have shown a strong correlation between some soil characteristic, such as moisture content (water holding capacity), nitrogen concentration or pH, and the observed

Fig. 2.6. The dynamics of change in four of the Park Grass Experiment plots at Rothamsted, England. (a) Plot 12 was unfertilized. Plots 14, 11–1 limed and 11–1 unlimed received complete mineral fertilizer. (b) Because Plot 14 received its nitrogen as nitrate, its soil became more alkaline, having a pH of 6.0 by the 1960s. Plot 11–1 received its nitrogen as ammonia, and its soils became very acidic (see Chapter 12). (c) The portion of Plot 11–1 that was limed to raise its pH was dominated by a different grass species (Alopecurus pratensis) than (d) the unlimed portion (Holcus lanatus). Modified from Tilman (1982).
pattern (e.g. Box, 1961; Beals & Cope, 1964; Zedler & Zedler, 1969). For instance, for understory woodland herbs, Pigott & Taylor (1964) found that Deschampsia caespitosa was most abundant on the bottom of dales, that the nettle Urtica dioica was most abundant just up from the base of the slopes, and that the sides of the slopes were dominated by Murcurialis perennis. This pattern seemed to be caused by differences in the nitrogen and phosphorus contents of these soils and in the requirements of these species for N and P. Snaydon (1962) looked at the distribution of white clover, Trifolium repens, in relation to several soil characteristics in both a 10×10 m area and a 130 km² area. In both areas, he observed that white clover was most common in soils with high calcium and high phosphorus levels. Within the 10×10 m area, he found that calcium and phosphorus levels varied by a factor of 3 between spots as close together as one metre, and this local variation in soil chemistry corresponded with the distributional pattern of white clover. On broader scales, white clover was only present in local areas that were rich in calcium and phosphorus and had soils of higher pH.

In the vegetation of the upper Galilee of Israel, there is considerable variation in the composition of mature, stable plant communities, even though they experience similar climatic conditions. Rabinovitch-Vin (1983) found that this variation corresponded closely with the original parent material on which these soils had formed. Similar correspondence between original parent material and the ultimate composition of the vegetation on a site have been reported in a variety of areas (e.g. Olson, 1958; Lindsey, 1961; Hole, 1976). Such patterns strongly suggest that the availabilities of various soil resources are an important determinant of the composition of terrestrial plant communities. Similar patterns have been reported for a variety of algal communities by Smith (1983), who found that the nitrogen to phosphorus (N:P) ratio of lake water was a major determinant of the abundance of various nitrogen-fixing blue-green algae. These blue-green algae reached their greatest abundance at low N:P ratios, as might be expected because of their ability to use atmospheric N₂ as a nitrogen source and their high requirements for P (Fig. 2.7).

2.4.2 Experimental studies

There are other possible explanations for at least some of the patterns summarized above. Just as soils influence plants, so plants influence soils. Although the N:P ratios of lakes may correlate well with the relative abundances of blue-green algae, they may also correlate well with some other factor which is the true cause of the pattern. Cause and effect are difficult to separate in any purely observational study. This can be at least partially overcome through experimentation.
Fig. 2.7. (a) A hypothetical case of competition between a nitrogen-fixing plant (Species A) and a plant incapable of nitrogen fixation (Species B). Note that the N-fixer should be the superior competitor in very N-poor habitats (where the N:P supply ratio is low). In N-rich habitats (with high N:P ratios), both species should be P-limited, and Species B, the non-fixer, should displace Species A. If P were added to a habitat where both species were coexisting, it would favour the N-fixer, as illustrated by the vertical arrow. The addition of N to such a habitat would favour the non-fixer, as shown by the horizontal arrow. (b) In both Lake Washington (northwest USA) and Lake Trummen (Sweden) the greatest abundance of blue-green algal species capable of nitrogen fixation occurred during years in which the ratio of total nitrogen to total phosphorus was low, as predicted above. Modified from Tilman (1982) and Smith (1985).

Schindler (1977) reported the results of some intriguing research in the Experimental Lakes Area of Canada in which whole lakes were fertilized with different ratios of nitrogen to phosphorus. For instance, when Lake 227 was fertilized with an N:P ratio of 31:1, the lake was dominated by the green alga *Scenedesmus*, which is not capable of nitrogen fixation. When the N:P fertilizer was changed to give a ratio of 11:1, a nitrogen-fixing blue-green alga, *Aphanizomenon*, became dominant. After fertilization of another lake, Lake 226NE, with an N:P ratio of 12:1, there was a dramatic increase in the abundance of another blue-green alga, *Anabaena* (see
also Kilham & Kilham, 1982). Similar results have been obtained when natural algal communities were allowed to compete for nutrients in laboratory experiments (Tilman & Kiesling, 1983). When the N:P ratio was low, various species of blue-green algae capable of nitrogen-fixation became dominant. When N:P ratios were high, and there was ample silicon, various species of diatoms (shell-bearing algae), became dominant. Thus, there is direct experimental evidence that the correlations reported by Smith (1983) for a wide variety of lakes world-wide are indicative of differences in the competitive abilities of blue-green algal species and other algal species for nitrogen and phosphorus.

Just as nitrogen-fixing blue-green algae reach their greatest abundance in nitrogen-limited lakes, so legumes and other terrestrial vascular plants capable of symbiotic nitrogen fixation, reach their greatest abundance in habitats with nitrogen-poor soils (e.g. Campbell, 1927; Young, 1934; Foote & Jackobs, 1966). If legumes are superior competitors for nitrogen, but inferior competitors for other resources such as phosphorus, calcium or light, legumes should decrease in abundance when nitrogen is added (see Fig. 2.7a), but become more abundant when all resources except nitrogen are added.

The Park Grass Experiment at Rothamsted provides several opportunities to test this hypothesis (Tilman, 1982). Averaging over all samples collected in a plot during the 130 years of these experiments, those plots receiving no fertilizer contained 7.9% legumes by biomass. The plot receiving all nutrients except N contained 21.4% legumes. Thus, adding all nutrients except nitrogen led to an approximately threefold increase in the abundance of legumes. In contrast those plots receiving nitrogen averaged less than 0.5% legumes. In addition, several plots were fertilized with nitrogen for a period, and then fertilized with all nutrients but nitrogen thereafter. During the period that it was fertilized with N, plot 15 averaged 0.07% legumes but averaged 20% of the total biomass during the subsequent period when all nutrients except nitrogen were added. Thus, both the whole lake fertilization experiments and the Park Grass Experiments have shown dramatic changes in the relative abundances of nitrogen-fixing plants. These changes are consistent with predictions based on the assumption that nitrogen-fixing plants are superior competitors for nitrogen but are inferior competitors for other resources, such as phosphorus and light (Fig. 2.7a).

In addition to their effects on legumes, each pattern of fertilization in the Park Grass Experiment has tended to favour a different plant species. For instance, several of the plots received different amounts of two limiting soil nutrients, nitrogen and phosphorus. Looking only at those plots with similar pH (from 4.2–6.0), different plant species were dominant at different relative avail-
abilities of N and P (Fig. 2.8a). Thus, changes in the relative rates of supply of two limiting resources led to separation of the major species along a gradient, just as theory predicts should happen when plants compete for essential resources (Fig. 2.3).

Tilman (1984) established an experimental N:Mg gradient by fertilizing a newly disturbed field with different ratios of nitrogen and magnesium. By the second year of the experiment, five of the six most abundant species were distinctly separated along the gradient (Fig. 2.8b). Similar experiments, performed in a variety of plant communities around the world (e.g. Milton, 1934; Willis & Yemm, 1961; Specht, 1963; Ginzo, et al., 1982; Tilman, 1982), have shown major changes in plant dominance following fertilization. Such
results are consistent with the hypothesis that competition for
resources is an important process influencing the local abundance of
species. They demonstrate experimentally that different supply rates
of soil resources lead to dominance by different species. More
research is needed, however, before we will be able to predict which
species will become dominant in a particular habitat in response to a
particular set of environmental conditions or manipulations.

2.5 Primary succession

When bare ground is newly exposed following such events as glacial
recession, sand dune formation, landslide or volcanic eruption, the
ground is colonized by a series of species in a process that is called
primary succession (Chapter 1). The species replacements observed
during primary succession often seem to correspond with changes in
the availabilities of soil nutrients and light at the soil surface. For
instance, recession of glaciers in Glacier Bay, Alaska, has exposed
105 km of bare gravel and sand substrate during the 225 year warming
period since the Little Ice Age (Lawrence, 1979). When initially
exposed, the substrate had very low levels of nitrogen, and the initial
colonists to the habitat showed signs of extreme nitrogen deficiency
(Lawrence et al., 1967). Nitrogen is the main limiting soil resource in
all primary successions, because the mineral substrates in which soils
form contain little nitrogen, but do contain sufficient amounts of P,
K, Ca, Mg, and other minerals required by plants (Jenny, 1980). At
Glacier Bay, nitrogen levels increased 5 to 10 fold within 100 years
(Crocker & Major, 1955; Fig. 2.9a). As soil nitrogen levels increased,
total plant biomass increased, and the proportion of light penetrating
to the soil surface decreased. As these changes occurred, the
dominant species changed from short, nitrogen-fixing species such as
black crust-forming soil algae, lichens Stereocaulon and Lepho-
lemma and a rose Dryas drummondii, to such taller species such as
nitrogen-fixing alders, to the even taller cottonwood trees, and finally
the even taller spruce and fir trees (Cooper, 1923, 1939; Lawrence,
1958; Lawrence et al., 1967; Reiners et al., 1971; Worley, 1973). A
qualitatively similar pattern has been reported for primary succession
following sand dune formation along the southern coast of Lake
Michigan (Covles, 1899; Olson, 1958; Robertson & Vitousek, 1981).

What could cause such patterns? Although numerous factors are
involved, plant competition for limiting resources may play a central
role in these and other primary successions and in secondary succes-
sions on poor soils (Tilman, 1982, 1985). Just as species that differ in
their competitive abilities for two essential resources should become
separated along a spatial gradient in the relative availabilities of the
resources (Fig. 2.3b), so should species be separated through time
along a temporal gradient of the relative availabilities of resources.
(a) Soil change in Glacier Bay, Alaska

(b) Glacier Bay succession

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Light (at the soil surface)
No matter what the limiting resources might be, theory predicts that there can be a directional and predictable change in the species composition of a plant community only to the extent that there are regular and predictable changes in the relative availabilities of the limiting resources. Because the relative availability of two resources can be approximated by their ratio, this has been called the resource ratio hypothesis of succession (Tilman, 1982, 1985). A major temporal gradient in primary successions is from habitats that have high light at the soil surface but low soil nitrogen, to habitats that have low light at the soil surface but high availability of nitrogen. If some of the major species involved in succession at Glacier Bay, Alaska, differ in their requirements for light and nitrogen as illustrated in Figure 2.9b, then the observed changes in soil nitrogen and light could explain at least the broad pattern of succession observed there.

2.5.1 The soil-resource:light gradient

During primary succession in Glacier Bay, there is a major and obvious change in the structure of the vegetation. The initial dominants are short, and as succession proceeds, these species are replaced by others which are increasingly tall.

Why are taller species dominant later in primary succession? As plant biomass increases, less light reaches the soil surface. Light is a directional resource, supplied from above, so that taller plants can obtain a greater proportion of the light. The simplest indicator of the ability of plants to compete for light is their height at maturity (Givnish, 1982). During at least the first few hundred years, primary succession tends to be a directional process in which the richness of the soil and plant height both increase. The increased height of the mature dominant plants is consistent with the hypothesis that competition for light is an important process on richer soils.

Similar patterns have been reported in mature, non-successional vegetation around the world. If soils within an area are ranked from

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Fig. 2.9. By sampling sites in a primary succession at Glacier Bay, Alaska, USA, which had been deglaciated at different times during the past 200 years, a time sequence of total nitrogen levels can be obtained. Both the nitrogen in the mineral portion of the soil and the total nitrogen in the mineral portion plus the forest floor layer increased during succession. After Crocker & Major (1955). (b) The pattern of species replacement in succession may depend on the ability to compete for nitrogen and for light. This figure shows light at the soil surface decreasing through succession while total soil nitrogen levels increase. The hypothesis is that species which are superior competitors for nitrogen (such as lichens and Dryas) are poor competitors for light, and vice versa. The major species (or species groups) are assumed to be separated in their requirements for nitrogen, with lichens the best competitors, followed by Dryas, alder, cottonwood, spruce and then fir, the worst nitrogen competitor. The species are assumed to be ranked in reverse order in their competitive abilities for light. Modified from Tilman (1982, 1985).
those that have the lowest availability of a limiting soil resource to
those that have the highest availability, the dominant plant species
are found to change from plants that are short at maturity to plants
that are tall at maturity (Tilman, 1986). Such gradients can be
considered to be gradients in the relative availability, or ratio, of soil
resources versus light. I call them soil-resource:light gradients
(Tilman, 1986). For instance, on sandy soils of Michigan, Wisconsin
and Minnesota, the most nitrogen-poor soils are dominated by
lichens, forbs and grasses, with only scattered individuals of cherry
bushes and oak trees. Richer soils have an oak savannah vegetation.
Still richer soils have closed canopy oak forests, and the richest soils
are dominated by closed-canopy maple forests (Hole, 1976). The
species dominant on poor soils are short at maturity, while the species
dominant on richer soils are increasingly taller at maturity along this
soil resource:light gradient.

Similarly, in the areas of California, Chile, Italy, South Africa,
and Australia that have a Mediterranean-type climate, the vegeta-
tion ranges from open, low scrublands with plants about 0.3 m tall
in areas with poor soils to dense scrub dominated by different species
reaching 10 m at maturity on the most moist soils (Cody & Mooney,
1978; Beard, 1983). In the case of the British flora, Grime (1979)
reports that taller species tend to be found in areas with richer soils,
whereas shorter plants tend to be found in habitats with poor soils.
For the new world tropics, Beard (1944, 1955) observed that the
height of the dominant species depended on the number of months
per year that an area received rainfall. The most productive regions,
which received 12 months of rainfall a year, were dominated by
species that ranged from 40–50 m in height. Increasingly less
productive regions of the new world tropics were dominated by
species that were progressively less tall. The driest area that he
recognized was a scrubland-cactus assemblage which averaged 2–4 m
in height.

Thus, along a gradient from resource-poor (dry) to resource-rich
(wet) sites, there is a replacement of species, with the species
dominant in the most resource-rich sites being much taller than those
dominant in the resource-poor areas. Marks (1983) reported a similar
pattern for the areas in which native North American plants were
dominant before European disturbance. The shorter species,
common in secondary succession today, were dominant in such
resource poor habitats as sand plains, gravel bars, limestone out-
crops, talus slopes, rock crevices, eroded ridgetops, and eroded
stream banks, whereas the taller species, such as maple, were
dominant on rich soils.

This strong tendency for species dominant on rich soils to be taller
at maturity than those dominant on poor soils is consistent with the
hypothesis that taller species are superior competitors for light.
However, why are species that are shorter at maturity favoured on resource-poor soils? To answer this question, it is necessary to consider the forces that control the evolution of plant life histories. Put simply, the theory of evolution by natural selection states that a trait that leads to a greater net reproductive rate will be favoured over other traits. In a habitat in which individuals of a species are not light-limited, there is no selective advantage for increases in height (except, perhaps, for seed dispersal), or for delayed reproduction. Thus, shorter individuals, capable of earlier reproduction would be favoured. In a habitat in which individuals are light-limited, those which delayed reproduction, and allocated more of their potential growth to increases in height, could be favoured, since they would acquire a greater proportion of the limiting resource, light.

There is another potential cost, in addition to reduced or delayed reproduction, that plants face in order to be superior competitors for light. Taller plants require a stronger stem for the support of their photosynthetic tissues (Chapter 9). However, these plants must still transport essential soil resources from their roots to their leaves. Thus, they must allocate a greater proportion of their potential growth to the production of structural and transport tissues, and they must bear the energetic cost of the respiration of these tissues. Such costs cause woody perennial plants to have much lower maximal rates of weight gain, as seedlings, than herbaceous (non-woody) perennial plants, and cause herbaceous perennial plants to have lower seedling growth rates than annual plants (Grime & Hunt, 1975).

Thus, several major life history traits of plants may be strongly influenced by the position along a soil resource:light gradient at which a species is a superior competitor. In general, plants that are good competitors for nutrients, but poor competitors for light, should be shorter at maturity, reproduce sooner, and have a greater maximal rate of weight gain than species that are superior competitors for light (Tilman, 1985, 1986). There should be a smooth gradation in these traits along a soil-resource:light gradient, and although there are many other factors which influence the evolution of plant life histories, a major axis for differentiation of plant life histories and speciation has been the gradient from nutrient-poor to nutrient-rich habitats (i.e. the soil resource:light gradient; Tilman, 1985, 1986).

2.6 The dynamics of plant communities

So far in this chapter, I have discussed broad relationships between the species composition and diversity of plant communities and the availabilities of various resources. I have focused on patterns in mature vegetation and on the rather slow dynamics of primary succession. I did this because these are some of the more obvious and
clear patterns, and because a simple, equilibrium theory of plant competition for resources, like that illustrated in Figs 2.1–2.3, has the potential to predict such patterns. However, many of the dynamic changes in plant communities with which we are familiar occur on much shorter time scales. Many of us have seen dramatic changes within a one or two year period following abandonment of a garden plot or a farmer's field. To predict such dynamics, it is necessary to use explicit, differential equation models of plant competition for resources (Tilman, 1985). Although I will not present such models here, I do want to point out that the short-term dynamics observed following the perturbation or manipulation of a plant community can be quite different from the long-term, equilibrium effect of that same manipulation.

This makes it extremely difficult to interpret the results of short-term, manipulative experiments. Consider, for instance, the primary succession at Glacier Bay, Alaska. What might happen to the composition of an early successional plant community if it were fertilized with nitrogen? Figure 2.9b predicts that the long-term effects would be a more rapid succession, with spruce and fir becoming dominant sooner. However, the immediate effects could be quite different. If the early successional, shorter species do have greater maximal growth rates (as discussed above), the immediate response to the addition of nitrogen could be an increase in their abundance. Just after nutrients are added, the habitat will have unusually high availabilities of nutrients for the ambient light level. The species capable of growing most rapidly under those situations would dominate initially. Those species should be the ones with the greater maximal growth rates. Eventually, as these species grew, they would reduce light to a lower level, and conditions would then begin to favour later successional species. Computer simulations of such cases have shown that the initial effect of fertilizers is to increase the abundance of early successional species, whereas the long-term effect is to favour late successional species (Tilman, 1985). Thus, because there are differences in the maximal growth rates of species, it is very difficult to interpret the immediate effects of any manipulation unambiguously. Long-term experimentation is required.

Probably because richer land is more commonly used for agriculture, the vast majority of documented secondary successions have occurred on rich soils, where much of the initial dynamics may reflect nothing more than differences in the maximal growth rates of the species (Egler, 1954, 1976). However, it has often been observed that the species sequence of secondary succession is similar to, but much faster than, the species sequence in nearby primary successions. If the life histories of species have evolved to correspond with the point along a soil-resource:light gradient where they are the superior competitors, a dynamic model of plant competition for these
resources would predict such similarity. The initial dominance by species that are shorter, and better nutrient competitors, however, would not result from competition for nutrients on these nutrient rich soils, but come from the greater maximal growth rates that such species have evolved (Tilman, 1985). As I believe is illustrated by much of the work on secondary successions on rich soils, too detailed a view of the short-term dynamics of plant communities may obscure the simple, general underlying causes.

2.7 Conclusions

Many different processes control the structure of plant communities. This chapter has taken a broad look at one of these processes, namely plant competition for limiting resources. A variety of observational and experimental studies, performed in an assortment of aquatic and terrestrial habitats world-wide, have shown that the species richness, species composition and species dominance of plant communities are greatly affected by the availabilities of limiting resources. At least in broad outline, many of these patterns are consistent with the predictions of a simple theory of plant competition for essential resources. As predicted by theory, the plant communities with the greatest diversity within a region occur in resource-poor habitats. Increases in the supply rates of limiting resources lead to decreased diversity. Much of the local spatial heterogeneity of plant abundances may be caused by local spatial heterogeneity in the availability of soil resources.

The broad patterns of primary succession and of secondary succession on poor soils correspond with changes in the relative availabilities of limiting resources. Theory predicts that succession should be a predictable and directional process only to the extent that the processes controlling the supply rates of limiting resources are predictable and directional. In many of these successions, soil resources increase and the availability of light at the soil surface decreases, leading to a gradient through time in the soil resources:light ratio. The separation of successional species along these temporal gradients is very similar to their separation along comparable spatial gradients in mature communities. Both of these patterns are potentially explained by a simple model of resource competition.

Thus, many of the broad, long-term patterns observed in plant communities may be the result of interspecific competition for various limiting resources. Such correspondence does not mean that other processes are unimportant in structuring these plant communities, but the simple theory that predicts them may provide a framework for more detailed studies.