PLANT STRATEGIES AND THE
Dynamics and Structure of Plant Communities

DAVID TILMAN

MONOGRAPHS IN POPULATION BIOLOGY · 26

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FOR

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Preface

The interactions between consumers and their resources, which can be a major determinant of patterns in nature, are strongly influenced by resource availabilities and by the foraging behavior of the consumers. Although it is common to think of the foraging behavior of animals, multicellular plants also have "foraging behaviors." A plant's ability to garner resources is strongly influenced by its morphology. Plant physiology and morphology interact to determine how growth depends on resource availabilities. A major advantage of plants, in addition to Harper's (1977) observation that they sit and wait to be counted, is that their above-ground morphology, and thus a major component of their foraging behavior, is visually obvious. Unfortunately, below-ground foraging effort is more difficult to observe. Plants have evolved a wondrous array of morphologies and life histories, and plant communities have many repeatable spatial and dynamic patterns. My desire to understand these was a major factor motivating this book. I started exploring these ideas more than two years ago with little idea where they would lead. I did start with the usual complement of prejudices and preconceptions, several of them highly cherished at the time, and found that some were reinforced and some rejected as I explored the logical implications of the mechanisms of competition for soil resources and light among size-structured plant populations.

Writing a book is a long, often tiring, and at times intellectually frightening journey, for there are many face-to-face encounters with the vast unknowns of our science. However, there are also exhilarating moments when disparate ideas coalesce, when patterns emerge from chaos. In looking back on the results of the past two years, I know that there is much more to be done. But the journey has produced insights into some of the fundamental processes, constraints, and tradeoffs that may have led to the broad, general patterns we see in the vegetation of the earth. I share these with you in this book. I do so in the spirit of one who knows that we have far to go before we truly understand nature. I hope that the ideas presented here may help guide you toward a better understanding of the forces shaping the evolution of plant traits and the structure and dynamics of plant communities.

This book could not have been written without the support, encouragement, and assistance of many. First and foremost, I thank my wife, Cathie, for her support during the all too frequent periods when writing led me to be distant and preoccupied. My next greatest debt is to Andrea Larsen, who prepared all the figures, corrected the text, prepared the bibliography, and assisted with almost all other aspects of manuscript preparation. Robert Buck and then Abderrahman El Haddi assisted with data analysis and with computer simulations. The ideas presented in this book have been influenced by many individuals with whom I have interacted over the years. I especially thank Nancy Huntly, Richard Inouye, John Pastor, Edward Cushing, John Tester, Eville Gorham, Hal Mooney, Margaret Davis, Peter Abrams, Lauri Oksanen, David Grigal, Deborah Goldberg, Norma Fowler, John Harper, Peter Vitousek, and David Wedin. I am deeply indebted to Hal Mooney, John Harper, Terry Chapin, John Pastor, Deborah Goldberg, Norma Fowler, Steve Pacala, Jim Grace, Scott Wilson, Nancy Johnson, Dave Wedin, Jim Grover, Jim Clark, Scott Gleeson, Steve Fifield, Barb Delaney, Bob McKane, Jenny Edgerton and a group of graduate students at The University of Michigan for their critical comments on the first draft of this book. I thank Judith May for her assistance in editing the manuscript. However, any and all errors that remain are mine. I thank the John S. Guggenheim Memorial Foundation for a fellowship that allowed me the time to start this work. I am greatly indebted to the Minnesota Supercomputer Institute for granting me time on a Cray 2. I also gratefully acknowledge support from the National Science Foundation (BSR-81143202 and BSR-8612104) for Long-Term Ecological Research at Cedar Creek Natural History Area, Minnesota. Without the support of NSF, the work presented here would not have been possible.

University of Minnesota, 1987

PLANT STRATEGIES AND THE
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CHAPTER ONE

Introduction

> There is a very extensive literature in which it is demonstrated repeatedly that the [competitive] balance between a pair of species in mixture is changed by the addition of a particular nutrient, alteration of the pH, change in the level of the water table, application of water stress or of shading. These experiments had a significant historical importance in emphasizing that the interaction between a pair of species was a function of the environment in which the interaction occurred and an anecdotal value in defining, for a specialized condition of environment and species, the effects of a particular change. It is very doubtful whether such experiments have contributed significantly either to understanding the mechanism of "competition" or to generalizing about its effects.
>
> —J. L. Harper (1977, p. 369)

The central goal of ecology is to understand the causes of the patterns we observe in the natural world. The existence of patterns—of similarities from habitat to habitat—suggests that similar forces may have been at work in different habitats. This book is concerned with some of the broader, more general patterns that have been reported for terrestrial plants and with some of the forces that may have shaped plant morphologies, life histories, and physiologies, and thus determined the structure and dynamics of plant communities. Why is it, for instance, that species with similar physiological, morphological, and life history traits are dominant in a similar order during secondary succession in quite different habitats worldwide (Billings 1938; Bazzaz 1979; Christensen and Peet 1981; MacMahon 1981;

Cooper 1981; Inouye et al. 1987a; Tilman 1987a)? What causes primary successions in Indiana (Cowles 1899), Alaska (Crocker and Major 1955), and Australia (Walker et al. 1981) to be so similar, at least for their first 200 years? Within a geographical region, much of the variation in the species composition of vegetation is associated with the local soil type, especially the parent material on which the soil formed and the eventual productivity of the vegetation on that parent material in that climatic region (e.g., Lindsey 1961; Hole 1976; Rabinovitch-Vin 1979, 1983; Jenny 1980). Why is it that, both within and among biomes, species with similar maximal heights, relative growth rates, allocation patterns, and life histories tend to be dominant at similar points along such productivity gradients? Holding productivity constant, herbivory, disturbance, or other loss rates are a major determinant of vegetation composition (e.g., Lubchenco 1978; Grime 1979; Whitney 1986). Why, in a wide variety of habitats, does vegetation change along a gradient from low to high loss rates in qualitatively similar ways? An even more striking pattern that merits further explanation is the convergence of unrelated species to a common set of physiological, morphological and life history traits in widely separated but physically similar habitats worldwide (Mooney 1977; Cody and Mooney 1978; Orians and Paine 1983; Walter 1985). Further, almost all terrestrial vascular plants are alike in their modularity and their great morphological plasticity (Harper 1977).

The cause of such similarities is a central question facing plant ecologists. Might such similarities imply that terrestrial plant evolution and community structure have been greatly influenced by a few general underlying processes? Might a relatively simple approach be able to explain all these patterns on all these scales, at least in their broad outline? Or are such patterns unrelated to each other, with each pattern requiring a unique explanation?

INTRODUCTION

CONSTRAINTS AND TRADEOFFS

Pattern in ecology is caused by the constraints of the physical and biotic environment and by the tradeoffs that organisms face in dealing with these constraints. The more general and repeatable such constraints and tradeoffs are, the more general and repeatable will be the patterns caused by them. The long-term persistence of species requires that species be differentiated, i.e., that they have tradeoffs in their abilities to respond to the constraints of their environment. This book is concerned with the causes of broad-scale patterns of differentiation among terrestrial plants and the effects of such differentiation on the dynamics and structure of plant communities.

What, then, are the major constraints terrestrial plants face? Some general constraints on plants come from their place in food webs. All species are consumers of resources, some of which may be in short supply. Vascular plants require mineral nutrients, water, carbon dioxide, and light. Their abilities to use these resources depend on temperature, pH, humidity, and the oxygenation of the soil. In addition, plants are resources for a variety of species of herbivores, parasites, pathogens, and predators, and are also subject to loss and mortality caused by various disturbances to their habitat. Thus, within a given habitat, plants are constrained by resource availability and by loss or mortality caused by disturbance and herbivory.

Another constraint comes from the physical separation of essential plant resources. Terrestrial vascular plants require light, which is obtained above the soil surface, and mineral nutrients and water, which are obtained from the soil. Because these are nutritionally essential resources for photosynthesis, each plant requires a particular ratio of nutrient to light for it to have optimal growth. For a light-limited plant to obtain more light, it must allocate more of its growth to stems and leaves, and must allocate a smaller proportion of its growth to roots. Similarly, for a nutrient-limited plant to obtain relatively more nutrient, it must allocate more of its growth to roots, and thus proportionately less to leaves or stems. Thus, if a plant adjusts its allocation so as to increase its consumption of one of these resources, it necessarily decreases the relative amount of the other resource that it can acquire. This is an inescapable tradeoff for terrestrial plants that is dictated by their morphology and the physical separation of soil resources and light. One of the major predictions of the theory developed in this book is that this tradeoff has been a dominant cause of the patterns we see in natural plant communities. This occurs because each unique habitat—each unique pattern of soil resource and light levels—favors plants with a unique morphology, physiology, and life history. Thus, the physiognomy of the vegetation within a habitat should be strongly influenced by the forces that control the vertical light gradient and the levels of limiting soil resources. If some general, repeatable processes control patterns of resource availability, these would lead to general, repeatable patterns in plant evolution and community structure.

Productivity Gradients

Two major factors determine the availabilities of a limiting soil resource and light in a habitat: the rate of supply of the soil resource and the loss or mortality rate that plants experience. As discussed in Chapter 9, loss or mortality rates and soil resource supply rates could be correlated in natural habitats, and such correlation could be a further cause of natural patterns. However, it is instructive initially to consider the effects of each of these when the other is held constant. Holding loss or mortality rates constant, the habitat in which a plant lives can be classified as falling along a gradient from areas that have a low supply rate of a limiting soil resource, low soil resource levels, low plant biomass, and high penetration of light to the soil surface, to areas with a high supply rate of the soil resource, high soil resource levels, high plant biomass, and low penetration of light to the soil surface. For convenience, I will call such gradients "productivity gradients" or "soil-resource:light gradients." Light intensity at the soil surface is important because seedlings and shoots of newly establishing plants are short, and their growth rate is influenced by the light intensity they experience. This inverse correlation between the supply rate of a limiting soil resource and light intensity at the soil surface along productivity gradients is a major constraint of the terrestrial habitat.

Throughout this book, I will distinguish between resource levels and resource supply rates for soil resources. I define a resource level as the measurable concentration of the usable form or forms of a resource in the soil. I will, at times, use resource "availability" as synonymous with resource level. I define the supply rate of a resource as the rate at which usable forms of a resource are released into the soil. I do not define a supply rate for light because the canopies of all stands of vegetation receive full sunlight. Rather, I consider how the vegetation influences the vertical light gradient, especially light intensity at the soil surface.

Productivity gradients have been found to occur on a variety of spatial scales. For instance, the sandplains of Minnesota, Wisconsin, and Michigan, or the sandplains of northern Florida, have nutrient-poor soils, low standing crop, and high penetration of light to the soil surface, whereas soils formed on glacial till in Minnesota, Wisconsin, and Michigan have higher nutrient supply rates, higher plant biomass, and lower penetration of light to the soil surface. The differing parent materials of Blackhawk Island, Wisconsin, led to the development of soils that form a natural productivity gradient (Pastor et al. 1984). Further, all habitats have small-scale spatial variability in primary productivity and standing crop. Much of this variation may be caused by local differences in the soil resource supply rates.

Such local variation in soil resource supply rates can be caused by a variety of factors, including differences in soil permeability to water, exchange sites for nitrogen or phosphorus, effects of herbivore excretion, soil erosion, topographic variability, and feedback from plants (Jenny 1980). In some cases, productivity gradients occur as distinct gradients in space, such as the soil catenas that occur along slopes. However, soil-resource:light gradients need not be obvious gradients, spatially, but can exist wherever there is point-to-point variation in supply rates of limiting soil resources. Such gradients, on both large and small spatial scales, are likely to have been a major, general, repeatable feature of the habitat in which plants have evolved and differentiated.

Loss or Disturbance Gradients

A second major habitat constraint comes from disturbance, herbivory, predation, and other non-selective sources of loss of plant parts or mortality. For convenience, I will call all of these "loss" or "disturbance." Let's consider how the availability of a limiting soil resource and light availability at the soil surface would change along a hypothetical loss rate gradient—i.e., a gradient along which the loss rate changes but soil resource supply rates are held constant. Along such a gradient, there would be relatively low levels of both the soil resource and light at the soil surface in habitats with low loss rates. Habitats with high loss rates would have relatively high levels of the soil resource and of light at the soil surface. Thus, the levels of soil resources and of light at the soil surface should be positively correlated along a loss rate gradient but negatively correlated along a productivity gradient. Although there are fewer studies of loss or disturbance gradients than of productivity gradients, the examples show that soil resource and light levels are positively correlated on such gradients. Consider, for instance, the Hubbard Brook experiments (Likens et al. 1977; Bormann and Likens 1979). The undisturbed forest had high plant biomass, low penetration of light to the soil surface, and relatively low levels of extractable soil nutrients. Clearcutting led to a great increase in light penetration to the soil surface and to a large increase in extractable soil nutrient levels, as indicated by the water leaching through the soil into the watershed. Nutrient levels increase following plant mortality because there is less plant biomass to consume nutrients as they become available (e.g., Vitousek et al. 1979, 1982). All forests and fields have natural disturbances which affect patches of various sizes within them. Averaging over disturbed and undisturbed patches within a whole forest or an entire field, the average level of extractable soil resources and of light at the soil surface should increase with the average loss rate (e.g., Swank et al. 1981; Vitousek et al. 1979, 1982; Vitousek and Matson 1985).

For simplicity, in this book I will combine all density-independent, non-selective processes causing death of plants or loss of plant biomass. I do this because, whatever the source of such loss or mortality, it should have a qualitatively similar effect on resource levels and thus a qualitatively similar effect on plant morphology and life history. Clearly, this is a major simplification which is only a first approximation for the effects of herbivores or various types of disturbances, both of which have selective, density-dependent components. I make this simplification to seek generality. However, there are many insights that would be gained from a more complex approach that included further details of the effects of specific herbivores or specific types of disturbances. These, though, are not the subject of this book. Throughout this book, I will use loss or disturbance interchangeably to refer to density-independent, non-selective losses that could be caused by herbivores, seed or seedling predators, fire, landslides, tree falls, and other processes.

TOWARD A MECHANISTIC THEORY

The tendency for soil resource and light levels to be inversely correlated when loss rates are held constant is illustrated by a variety of field and greenhouse experiments. A visually clear example is provided by an elegant field study on the optimal nutrition of spruce trees in Sweden (Fig. 1.1; Tamm, Aronsson, and Burgtorf 1974; Tamm and Aronsson 1982; Tamm 1985). In reviewing nutrient addition experiments, Harper (1977) repeatedly emphasized that such experiments were difficult to interpret because "a major effect of supplying nutrients to vegetation may simply be to speed up the time at which light becomes limiting" (p. 340). In discussing a competition experiment between a grass and a clover (Stern and Donald 1962), Harper (1977, p. 361) said:

> The grass (adequately supplied with nitrogen) overtops the clover and the advantage is progressive, leading to the almost total suppression of the clovers. At first sight such an experimental result might have been interpreted as purely a problem in nitrogen nutrition. With no applied nitrogen the nodule-bearing and nitrogen-fixing legume was at an advantage—it evaded a struggle for existence for limiting nitrogen supplies. However, given adequate nitrogen the grass became the winner. Yet it is clearly unreal to separate the partitioning of nitrogen resources from the partitioning of incident radiation. The experiment starts as a single factor experiment but quickly turns itself into a study of the interactions between factors.

Harper is, indeed, correct that this interaction between soil resources and light complicates the design, implementation and interpretation of plant competition experiments. However, these are the underlying constraints and mechanisms of plant competition, and a mechanistic theory of plant competition should include them. The theory developed here in Chapters 3, 4, 6, and 7 models the vegetative growth of a plant as a continuous process that is determined by the pattern of allocation of photosynthate to additional stem, root, or leaf biomass. The model of nutrient and light competition among continuously growing size-structured plant populations that is developed in this book was designed to be as simple as possible and still include in it the major morphological and life history traits that influence the abilities of terrestrial plants to compete for soil

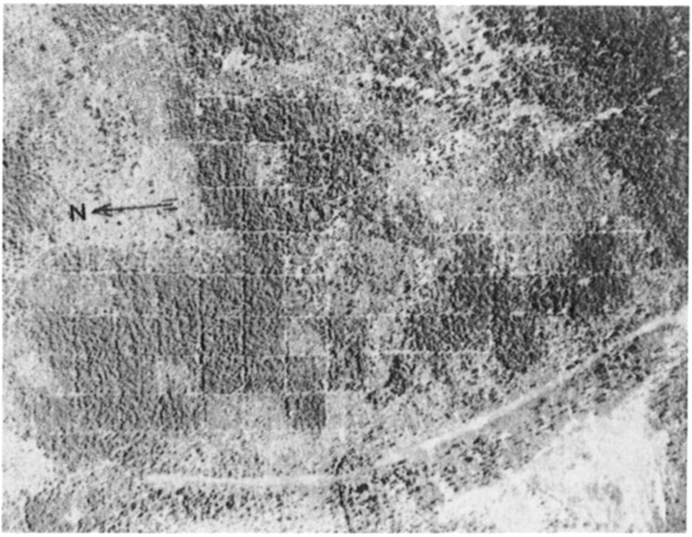


FIGURE 1.1. An aerial photograph taken in July 1975 of the Strasan, Sweden, experiments designed to determine the optimal nutrition of spruce trees. Nitrogen addition led to increased spruce biomass (the darker plots) and thus to decreased penetration of light to the soil surface. Nutrient addition began in 1967. Plots are generally 30 m × 30 m. Optimal growth occurred with the addition of N, P, K and Mg and was related to the nutrient content of the needles and the pattern of allocation to roots, needles, and stems (Tamm 1985). See Tamm et al. (1974) and Tamm (1985) for further details. The aerial photograph is reprinted from Tamm (1985) in the *Journal of the Royal Swedish Academy of Agriculture and Forestry*, Supplement 17, page 12, with the permission of the journal and the author. I thank Professor Carl Tamm for providing me with the original photograph and allowing me to reproduce it here.

resources and light. This model is used to explore a variety of questions about the evolution of plant morphologies (allocation patterns) and life histories, and about the effects of these plant traits on the dynamics and equilibrium structure of plant communities. The central goal of this book is to explore the logical implications of the mechanisms of plant competition for nutrients and light.

Most ecological theory has been phenomenological. It has described interactions such as competition or mutualism in terms of how the density of one species influences the growth rate of another species, without ever stating the actual mechanisms whereby one species influences the other. Such theory cannot explore the ramifications of these mechanisms for the evolution of species traits or for the structure and dynamics of populations, communities, and ecosystems (Tilman 1987a). This book takes a different approach—an approach that explicitly states the processes whereby individuals of one species influence individuals of that and other species. It is these mechanisms that have shaped the morphology, physiology, and life histories of species, and that have influenced the types of conditions for which each is dominant or rare. If there is to be any simplicity or generality in ecology, it will be found in environmental constraints and in the mechanisms of interaction, not in simple theories that ignore mechanisms. A major advantage of a mechanistic approach is that it can initially be narrowly focused but can be expanded, as necessary, to include other mechanisms and a larger portion of the foodweb and abiotic environment.

This book is limited in scope. It focuses on a few fundamental mechanisms of intraspecific and interspecific resource competition among terrestrial plants and the implications of these mechanisms for the evolution of plant traits and the dynamics and structure of plant communities. It does not treat plant-herbivore interactions, except the component mentioned above. This is done not to downplay the possible importance of herbivory, but to explore the logical consequences of the mechanisms of resource competition. Nor does this book explicitly consider the effects of neighbor-to-neighbor spacing in plant competition, a question addressed by Pacala and Silander (1985) and Pacala (1986). The underlying mechanisms of soil nutrient supply and the feedback effects of plants on soils are also not treated in depth. Each of these is an important area that merits further exploration and integration with the ideas presented here. However, no single study or book can encompass the full breadth of ecology. The natural, ecological world is phenomenally complex. Every insight—every hint of major underlying processes that structure it—is a hard-won advance. We now know that it is not a matter of competition versus predation versus mutualism versus disturbance as being "important" processes structuring the natural world (Quinn and Dunham 1983). All of these are important, and all must interact. However, there is still much to be gained by taking a simple perspective, and exploring the implications of a few factors, with other potentially important factors "held constant" for the sake of ease of analysis. Each advance thus gained provides the opportunity for a synthesis with advances that have been gained by making other simplifying assumptions.

The actual mechanisms of intraspecific and interspecific competition among multicellular plants are not simple. Multicellular plants have size and age dependent processes that greatly complicate any attempt to understand them. Plants are morphologically and physiologically plastic. They have a modular morphology that is composed of fairly fixed subunits (leaves, seeds, roots, stems; Harper 1977), but plants are capable of modifying, both phenotypically and genotypically, the relative allocations to these subunits. As will be discussed in Chapters 2 and 9, such morphological plasticity can influence the intraspecific and interspecific competitive ability of plants. Given such complexity, how should plant competition be viewed? One approach would be to ignore mechanisms and seek simplicity by describing the phenomenon of competition. This is just what is done by the Lotka-Volterra equations. Similarly, de Wit (1960) suggested that plant competition was so complex and so unique to each organism and habitat that there was no hope of formulating a general, mechanistic theory of plant competition. Instead, he suggested a phenomenological approach. In contrast, the approach taken in this book is to develop a simplified, but mechanistic, theory of competition that can be used to explore some of the general features of plant competition.

Mechanistic approaches impose a discipline and a limitation to vision that may be of great help in plant ecology. Some of the classical debates in plant ecology—such as the debate over whether or not a plant community exists as an entity in its own right or is an assemblage of species with individualistic responses—have occupied the efforts of far too many ecologists for far too many years. Such questions seem of trivial importance when a mechanistic approach is taken. A mechanistic approach eliminates the need to test among what may be spurious, broad-scale community generalizations that are not based on the evolutionary forces that have shaped plants, and instead focuses attention on more quantitative patterns that are predicted from underlying tradeoffs in the biology of the species and the constraints of the physical and biotic environment.

RESOURCE LIMITATION

A critical step in trying to understand plant competition is to determine what the actual mechanisms of interspecific interaction are for any given situation. The two most likely mechanisms of plant competition are resource (or exploitative) competition and allelopathic competition. Exploitative competition occurs when one plant inhibits another plant through consumption of limiting resources. Allelopathic competition occurs when one individual releases a compound that in some way inhibits growth or increases mortality of other plants. Neither of these mechanisms represents a *direct* effect of the density of one species on the growth rate of another species. In both cases, the density of each species directly influences some intermediate entity, and it is that entity that actually affects the growth rate of the other species. Thus, in order to demonstrate that species actually compete for resources in nature, it is necessary to manipulate experimentally resource levels in the field. Similarly, to demonstrate allelopathic competition in the field, it is necessary to manipulate the levels of allelopathic compounds in the field. The theory developed in this book applies only to cases of resource competition. Before any of this theory can be applied to a particular community, field experiments must be performed demonstrating that the plants are competing for resources and demonstrating which resources are limiting. Until this is done, it would be easy to gather data that seemed to support or refute this theory independent of the potential validity of the theory to that field situation.

The strength of a mechanistic approach to plant communities is that it can make explicit predictions about a wide range of patterns and processes in nature. However, a mechanistic theory can be misapplied just as easily as any other theory. A consistency between the predictions of a mechanistic theory of competition for nitrogen and light, and patterns seen in nature, for instance, is of no importance if nitrogen and light are not limiting in that community. To invoke such consistency without evidence of limitation is a potentially great danger. In this book, I will build a case on existing evidence as to the plausibility of such mechanisms as explanations for patterns we see in nature, but I wish to stress that most such cases merely demonstrate plausibility. I present them to encourage others to test the ideas developed here, not as a statement of "proof" of the underlying theory.

Finally, I should note that the approach taken in this book is conceptually quite different than that taken in Grime (1979) and leads to many conclusions that often directly contradict Grime's. Although I disagree with the ways in which he suggests various processes interact, I share with Grime (1979) the view that competition, loss rates (Grime's "disturbance"), and resource availabilities (with low availabilities being a major component of Grime's "stress") have a major influence on plant community structure. I will discuss the similarities and differences between Grime's perspective and mine as relevant throughout this book.

A PREVIEW

This book starts by using the equilibrium, resource-dependent growth isocline approach to competition developed in Tilman (1980, 1982) to demonstrate that the long-term average availability of a limiting soil nutrient and of light at the soil surface should depend on the nutrient supply rate and the loss rate of a habitat (Chapter 2). Because plants require both an above-ground resource (light) and below-ground resources (nutrients and water), plants face a tradeoff. To acquire more of one resource necessarily means that they must acquire proportionately less of another. Thus, the pattern of plant allocation to above- versus below-ground structures should influence the competitive ability of a plant in a given habitat (Chapters 4 and 5). However, all allocation to such non-photosynthetic structures as stems and roots necessarily decreases the maximal rate of vegetative growth of a plant (Chapter 3) and can thus greatly influence plant population dynamics (Chapter 6). The transient population dynamics that occur because of differences in maximal growth rates may be a major cause of the pattern of secondary succession, and may make it difficult to interpret the results of many short-term field experiments (Chapter 7). A five-year experimental study of plant distributions and successional dynamics at Cedar Creek Natural History Area, Minnesota, provides a wealth of information, much of it previously unpublished, with which to evaluate the predictions of the theory developed in this book (Chapter 8). The book ends with an exploration of some additional implications of the theory and with suggestions for further research (Chapter 9).

CHAPTER TWO

The Isocline Approach to Resource Competition

The complexities caused by the size structure of plant populations, by the linkage of nutrients and light, and by the tradeoff plants face in foraging for a limiting soil resource and light, mean that no simple theory can include all the components of plant competition. Does this necessarily mean that simple approaches are of no use? Complex models can often have much of their dynamic complexity adequately summarizable by a few equations (Schaffer 1981). In many complex processes, a few steps become rate limiting and thus become the major determinants of the patterns observed. The study of the mechanisms of plant competition is too young for us to know all the advantages and disadvantages of simple versus complex models. In this chapter I summarize a simple theory of plant competition for resources. In the remainder of this book, I develop a more complex and thus more realistic model of the mechanisms of plant competition, and compare its predictions with those based on the simpler theory developed in this chapter.

The simple theory uses the conditions that exist once each population reaches equilibrium to predict the outcome of interspecific competition for resources. This assumes that the resource requirements of various stages in the life cycle of each species can be summarized by their effect on the equilibrial resource requirements of that species. For populations that do not reach an equilibrium, I assume that long-term average resource availabilities may be a suitable approximation to equilibrial conditions. The equilibrial requirements are given by the resource-dependent growth isoclines of the species (Tilman 1980, 1982). Although much of the material in this chapter repeats earlier discussions in Tilman (1980, 1982), I also use this section to develop four basic concepts: (1) that the availabilities of all limiting resources should be positively correlated along loss rate gradients; (2) that the availability of a limiting soil resource and light should be negatively correlated along productivity gradients; (3) that plants should become separated along such gradients in a manner determined by their resource requirements; and (4) that optimal foraging of morphologically plastic plants for nutritionally essential resources should lead to a curved resource-dependent growth isocline, with morphologically plastic plants often being superior competitors compared to plants with a fixed morphology. Although I try to minimize the repetition of material that was published in Tilman (1980, 1982), some repetition is necessary. Those familiar with the earlier work may find it best to skim this chapter. I have tried to write it so that those with no familiarity with Tilman (1980) or Tilman (1982) may also understand it. The simple models developed in this chapter may be contrasted with a more complex model of allocation and growth for size-structured plants presented in Chapters 3 and 4. That model assumes that plant growth is determined by the pattern of allocation to roots, leaves, stems, and seeds. Each plant species is described by its allocation pattern, its seed size, its height at maturity, its maximal photosynthetic rate, the nutrient and light dependence of photosynthesis, the respiration rates of its different tissues, allometric and structural constraints, and other parameters.

COMPETITION FOR A SINGLE LIMITING RESOURCE

Let us first consider a case in which several different species are all limited by the same resource. What should be the outcome of interspecific competition, assuming that the interactions eventually lead to an equilibrium? In order to predict the outcome of competition for a single limiting resource, it is necessary to know the resource level at which the net rate of population change for a species is zero. This occurs when vegetative growth and reproduction balance the loss rate the species experiences in a given habitat. I call the resource level at which this occurs the R^* of that species for that limiting resource in that habitat. There are two distinct ways in which this information could be obtained. The first, and probably better, way to determine the R^* of a species in a given habitat would be to allow the species to attain its equilibrial biomass in a monospecific stand in that habitat. The level to which the species reduced the limiting resource at equilibrium would be its R^*. At equilibrium, the rate of resource consumption would equal the rate of resource supply. If a species were in a habitat in which the actual resource level was greater than R^*, the population size (by which I mean its mass per unit area once a stable age or size distribution was attained) would increase, thus reducing the resource level down toward R^*. If the resource level were less than R^*, population size would decrease, allowing the resource level to increase because of decreased consumption rates. It is only for habitats in which resource levels are at R^* that population size should remain constant. I call R^* the requirement of a species for a limiting resource.

The second way to determine R^* would be to determine the dependence of the growth rate of the species on resource levels, as illustrated by the resource-dependent growth curves of Figure 2.1. The y-axis of these figures is the long-term specific rate of growth or loss for the population ($dB/dt \cdot 1/B$, where B is biomass per unit area). If the population were a size-structured population (with population size expressed as biomass per unit area), the growth rate would be the natural logarithm of the dominant eigenvalue of the population projection matrix determined at each resource level, but in the absence of resource-independent mortality or other losses (e.g., Hubbell and Werner 1979; Vandermeer 1980). The total loss rate experienced by the population must be calculated in a comparable manner. For a size-structured population, this loss rate would be measured as the natural logarithm of the dominant eigenvalue of the population projection matrix that included all resource-independent loss terms, but no resource-dependent growth terms. The environmental availability of the resource at which the gain (from reproduction and vegetative growth) just balanced loss (from disturbance, herbivores, predation, and other mortality sources) would give R^* (Fig. 2.1).

When several species are all limited by a single resource, the one species with the lowest R^* is predicted to competitively displace all other species at equilibrium (O'Brien 1974; Tilman 1976; Hsu et al. 1977; Armstrong and McGehee 1980). The mechanism of competitive displacement is resource consumption. The population size of the species with the lowest R^* should be able to continue increasing until that species reduces the resource level (concentration) down to its R^*, at which point there would be insufficient resource for the survival of the other species. Several experimental tests of the R^* criterion of competition for a single limiting resource are summarized in Tilman (1982). One possible theoretical case is illustrated in Figure 2.1.

The theory presented here suggests that plants should compete strongly in habitats with low resource levels. This view contrasts with the assertion made by Grime (1979) that plants do not compete when they live in either "stressed" environments, such as low-nutrient environments, or in habitats with high disturbance rates. Grime's assertion, though, is inconsistent with numerous studies of intraspecific and interspecific competition. If plants did not compete on nutrient-poor soils, then, when growing in mono-

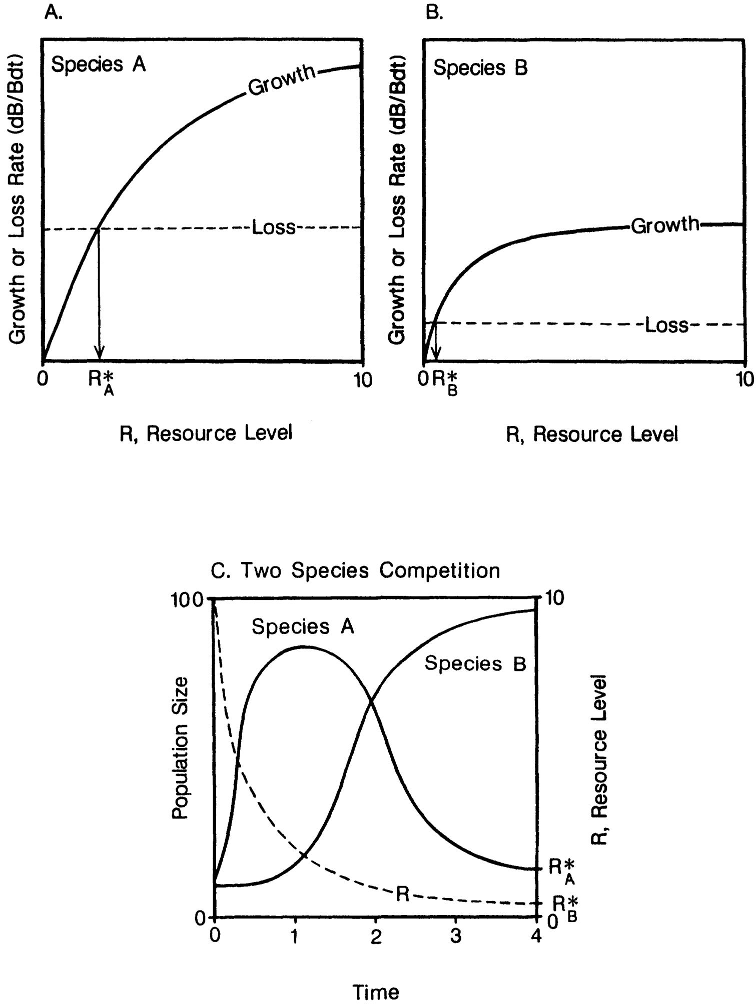
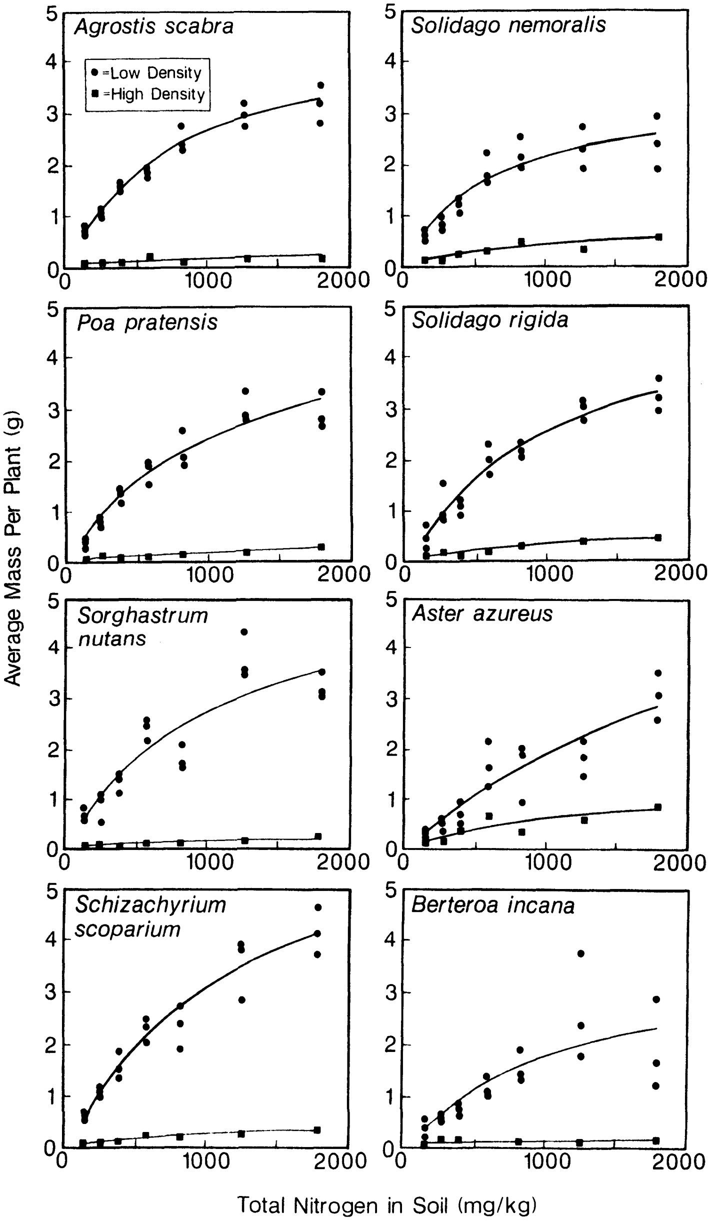


FIGURE 2.1. (A) Resource-dependent growth (solid curve) and loss (broken line) for species *A*. R_A* is the amount of the resource species *A* requires to survive in this habitat. (B) Similar curves for species *B*. (C) When two species compete for a single limiting resource (*R*), species *B*, which has the lower equilibrial resource requirement (*R**), should completely displace species *A* once equilibrium is reached.

culture, plant relative growth rates (*dB/Bdt*, where *B* is plant biomass) and average weight per plant would not decrease with increases in plant density on such soils. However, many studies have shown that relative growth rates and weight per plant decrease with increases in initial plant density on both poor and rich soils (e.g., Donald 1951; Clatworthy 1960; Harper 1961, 1977). Indeed, this decrease in the growth rate of individual plants with increases in plant density is a prerequisite for the "law" of constant final yield (Kira et al. 1953; Harper 1977). Cowan (1986) grew 8 herbs at both high and low densities along a gradient ranging from extremely nitrogen-poor subsurface sands to rich prairie soils. Along this full gradient, the final average weight per plant (Fig. 2.2) and the relative growth rate were significantly lower at high plant densities for each of the species, demonstrating strong intraspecific competition on all these soils, including the extremely nitrogen-poor soils. Inouye et al. (1980) and Inouye (1980) showed strong competition among desert annuals. Stern and Donald (1962) showed that clover displaced a grass from a nitrogen-poor soil after 133 days of competition. This competitive outcome was reversed in plots receiving high rates of nitrogen addition. Mahmoud and Grime (1976) studied competitive interactions among all pairs of three grass species (*Arrhenatherum elatius*, *Festuca ovina*, and *Agrostis tenuis*) on a rich soil and a poor soil. In comparison to the monocultures, the presence of a second species led to decreased weight per plant on their poor soil, with *Agrostis* causing a 30% decrease in the weight/shoot of *Arrhenatherum* and a 43% decrease for *Festuca*, and *Arrhenatherum* causing a 59% decrease for *Agrostis* in the low nitrogen treatment. Thus, there is experimental evidence showing both intraspecific and interspecific competition on nutrient-poor soils, as predicted by the theory summarized above.


Agrostis scabra
● =Low Density
■ =High Density
Solidago nemoralis
Poa pratensis
Solidago rigida
Sorghastrum nutans
Aster azureus
Schizachyrium scoparium
Berteroa incana
Average Mass Per Plant (g)
0
1
2
3
4
5
0
1000
2000
Total Nitrogen in Soil (mg/kg)