Constraints and tradeoffs: toward a predictive theory of competition and succession

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The development of mechanistic, predictive ecological theory will entail the explicit inclusion of organismal tradeoffs, of environmental constraints, and of the basic mechanisms of interspecific interaction. This approach was used to address the causes of species dominance and successional dynamics in sandplain vegetation in Minnesota. A series of field experiments performed over the last eight years have shown that the major constraints on plants were soil nitrogen and disturbance, with nitrogen competition being a major force. Nutrients other than nitrogen (P, K, Ca, Mg, S and trace metals), herbivory, and light were of minor importance. As predicted by theory, the superior nitrogen competitors were the species that, when growing in long-term monocultures in the field, lowered soil extractable N the most. These species had high root biomass and low tissue N levels.

Seven alternative hypotheses of succession, each named after its underlying tradeoff, were proposed and tested. The colonization – nutrient competition hypothesis provided the best explanation for the initial dominance (years 0 to 40) of herbs, whereas the nutrient versus light competition hypothesis best explained the long-term dominance by woody plants. Hypotheses involving transient dynamics caused by differences in maximal growth rates were rejected. In total, the results demonstrate that the inclusion of simple mechanisms of interspecific interactions, and of allocation-based tradeoffs, can allow models to predict the composition and successional dynamics of vegetation.

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Introduction

Prediction is a major goal of science and an increasing necessity in ecology as the environmental problems of the earth escalate. However, predictive ecological theory, which is also called mechanistic theory (Schoener 1986), is in its infancy. Traditional theory has provided broad and important insights into the forces controlling species' dynamics and diversity (e.g., MacArthur and Wilson 1967, Schaeffer 1981, May 1986). However, theory that does not explicitly include environmental variables (e.g. nutrient loading rates or climate) cannot predict how changes in these will affect an ecosystem. Models that do not include the mechanisms of interactions among organisms can describe the phenomenol-

ogy of population interactions, but cannot make a priori predictions of the dynamics or outcome of these interactions (e.g., Tilman 1977, 1987, Schoener 1986). The mere inclusion of environmental variables and mechanisms of interactions, however, does not assure the development of useful theory, for such theory can be as complex and difficult to understand as a natural ecosystem. As discussed below, this dilemma – that realism begets complexity – can be mitigated by developing theory that explicitly incorporates environmental constraints and the evolutionary tradeoffs that organisms face in dealing with them, and by including simple mechanisms with parameters that abstract the details of underlying processes.

Toward predictive ecology theory

What information is needed to predict the dynamics and structure of populations in nature? Predictive theory should explicitly include the manner, method or mode whereby one organism interacts with another, and whereby an organism interacts with its physical environment. Thus, if two species compete because they both consume the same resource, this resource should be explicitly included in the model with resource consumption being the actual mechanism of competition. Or, if species compete through the production of allelopathic compounds, the dynamics of these should be included. Thus mechanistic models explicitly include the ways in which individual organisms deal with their biotic and abiotic environmental constraints, i.e., with those factors that influence an individual's probability of survival, growth, and reproduction (Schoener 1986).

There are numerous potential mechanisms of interactions among organisms, each of which can be studied at various levels of detail. Each level of detail can provide insights. However, once the basic mechanisms of interaction are included in a model, additional complexity may lead to little, if any, increase in the ability of the model to predict community dynamics and composition. This is because the parameters describing the basic mechanisms of interspecific interaction can summarize or abstract (sensu Schaffer 1981) most of the complexity associated with more detailed explanations. Such abstraction, though, requires that parameters be measured under appropriate conditions (Tilman 1990). The ability of simple mechanisms to summarize the effects of the more detailed underlying mechanisms means that mechanistic models need not be complex. Just such an effect was found in models of algal nutrient competition, with the simpler, less physiologically realistic model actually being the better predictor of competition (Tilman 1977).

Similarly, the inclusion of environmental constraints need not lead to complex models. Although there are numerous potential environmental constraints, the problem is simplified because it is unlikely that all constraints are equally important. In any given habitat, ecosystem, or geographic region, most of the observed pattern may be caused by one or a few environmental constraints, but different constraints are likely to be important in different habitats. The importance of a particular constraint can be readily determined experimentally. A major constraint on the survival, growth and reproduction of individual organisms comes from all organisms being, of thermodynamic necessity, consumers, and most being subject to predation, herbivory or disease (e.g., Hutchinson 1959). Thus consumer-resource interactions are a central element of all mechanistic theory of population dynamics and community structure (e.g., Gilpin and Ayala 1973, Tilman 1977, 1982, May and Anderson 1983, Schoener 1986).

Mechanistic theory is further simplified once the tradeoffs that organisms face in dealing with their constraints are explicitly included. Most ecology and evolutionary patterns result from the interplay of environmental constraints and unavoidable organismal tradeoffs. For instance, most theory that can explain the coexistence of numerous species has assumed, either implicitly or explicitly, that organisms have tradeoffs in their abilities to respond to one or more constraints (e.g., Grubb 1977, Connell 1978, Huston 1979, Tilman 1982, Cody 1986, Chesson 1986) as have theories of succession (e.g., Werner and Platt 1976, Tilman 1985, Huston and Smith 1987), or of the maintenance of genetic diversity within a population (e.g., Slatkin 1978, Gillespie 1984). The only alternative to constraints and tradeoffs is neutrality, with organisms or genes assumed to be functionally identical or neutral (e.g., Kimura 1983), and with diversity maintenained by an equilibrium between specification and extinction (e.g., Rosenzweig 1975, Hubbell and Foster 1986) or between mutation and selection (e.g., Lande 1976). The latter hypotheses, although they surely explain some of the diversity of nature, cannot explain the broader scale patterns of differentiation and diversity seen in different habitats and along geographic gradients.

Organismal traits are ultimately based on allocation (e.g., Cody 1966, Mooney 1972). A plant that allocates more carbon to the production of stem has less to allocate to roots, leaves or seeds. An animal that allocates more protein to flight muscle has less to allocate to a digestive system or to some other physiological or morphological function. An animal that allocates a greater proportion of its time to one activity has less for another behavior. Thus, a change in the morphology, physiology or behavior of an organism that increases its fitness in response to one suite of environmental constraints should have a cost that decreases its fitness under other conditions. Although this need not be universally true, beneficial traits that do not have costs should become fixed and thus have little influence on observed intraspecific and interspecific differences.

Tradeoffs simplify theory because they limit species traits to a small subset of all potential combinations. For two traits, such as the size and number of seeds produced by an individual plant, the tradeoff between these traits limits the relevant parameters to a single curve, whereas the entire seed size versus seed number plane would be needed for a model that ignored tradeoffs. For a tradeoff among three traits (e.g., allocation to root, stem, or leaf), the universe of all trait combinations is the full three-dimensional space, whereas each individual plant is necessarily constrained to falling at some point on a plane within this volume.

Although this seems obvious, or even trivial, classical phenomenological models do not include tradeoffs. It is difficult to modify them to have tradeoffs because they do not explicitly include either the environmental constraints to which the tradeoffs respond or the organismal traits that are involved in the tradeoffs. Within
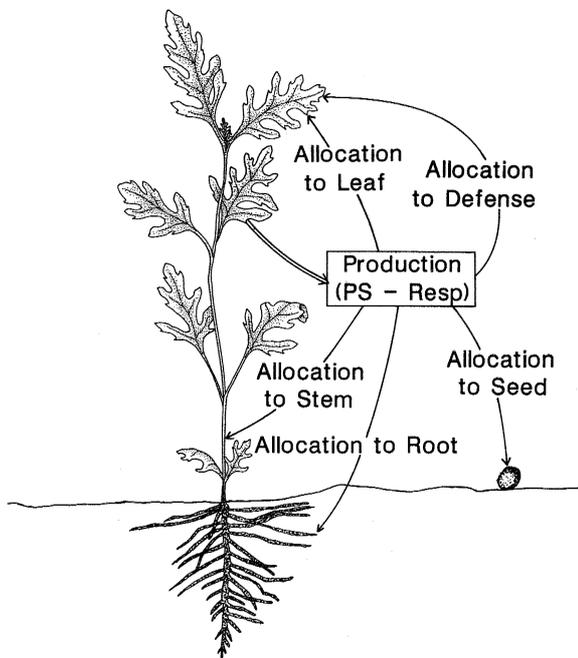
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Fig. 1. Plant morphology and physiology is controlled by the pattern of allocation to alternative morphological structures and physiological systems (Mooney 1972). This is illustrated symbolically as the allocation of plant production (photosynthesis minus respiration) to the production of additional leaf, stem, or root tissue, or to seed or defensive compounds.

the Lotka-Volterra competition model, for instance, there are no explicit tradeoffs among parameters. All combinations of r, k and $a_{i,j}$ are equally likely, even though most such combinations are morphologically, physiologically and behaviorally impossible. Tradeoffs limit parameters to some point on a biologically possible multidimensional surface, thus eliminating all other points in the full hypervolume as ecologically impossible.

Thus, the development of predictive ecological theory requires (1) the determination of the major environmental constraints, (2) the determination of the tradeoffs that organisms face in dealing with these constraints, and (3) the explicit inclusion of these constraints and tradeoffs as the mechanisms of intraspecific and interspecific interaction.

This approach has already been quite successful. Evolutionary models that include constraints and tradeoffs have predicted traits as diverse as foraging patterns in response to spatially and temporally variable predation risk (Werner 1984) and sex allocation patterns (Charnov 1982). Mechanistic models of consumer-resource interactions have made a priori predictions of the dynamics of algal competition for two limiting nutrients (e.g., Tilman 1976, 1977, Sommer 1985), of bacterial competition for sugars in combination with inhibitors (Hansen and Hubbell 1980), of algal nutrient competition along a temperature gradient (Tilman et al. 1981), of interac-
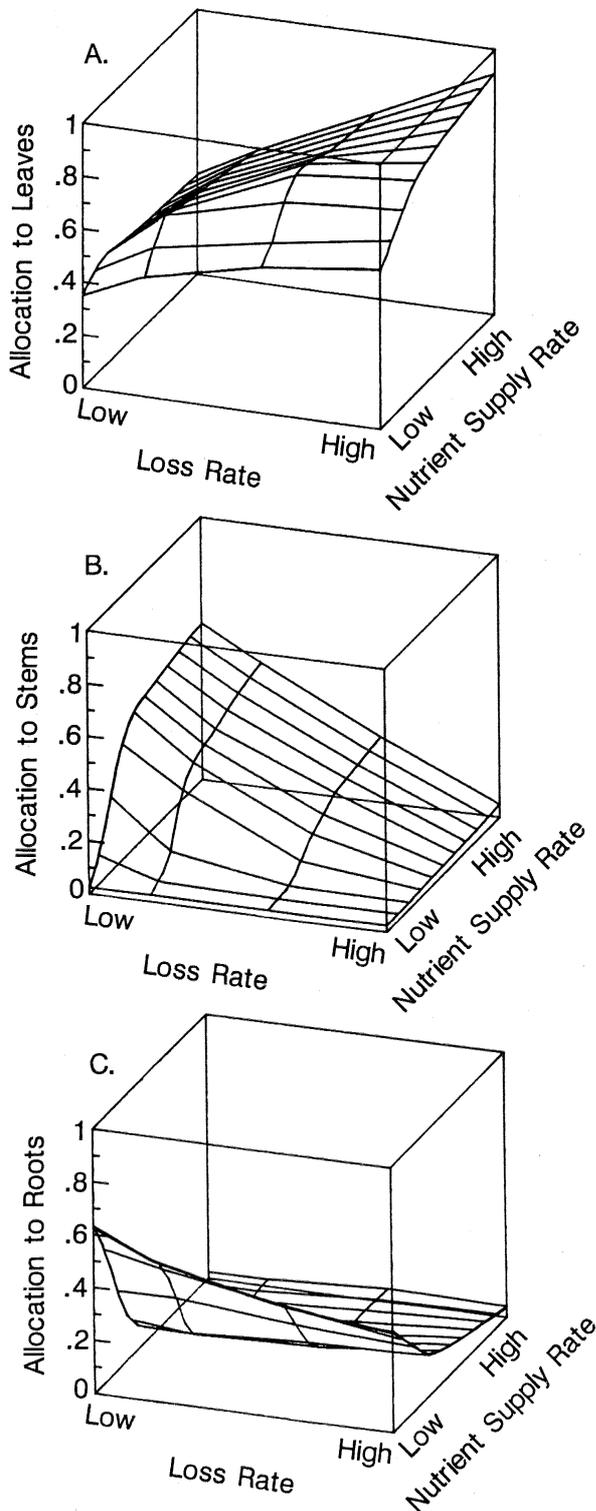
Fig. 2. When a model of plant growth (called "ALLOCATE"), in which each plant has a fixed pattern of allocation to leaf, root, and stem, was solved numerically, with a hundred or more different allocation patterns simultaneously competing, the competitively dominant pattern of allocation depended on environmental conditions (Tilman 1988). High allocation to stem was favored in fertile, undisturbed habitats; high allocation to leaves was favored in fertile, highly disturbed habitats, and the highest allocation to roots was favored in undisturbed, infertile habitats. Figure from Tilman (1988).

A. Single Nutrient Additions

Treatment: F=15.1***
Year: F=89.0***
Field: F=20.8***

B. Experimental Nitrogen Gradient

Treatment: F=106***
Year: F=149***
Field: F=154***

C. Herbivore Exclosures

Herbivores: F=1.57 NS
Nitrogen: F=158.***
Field: F=49.4***

■ Control
▨ No Herbivore

D. Shading Experiments
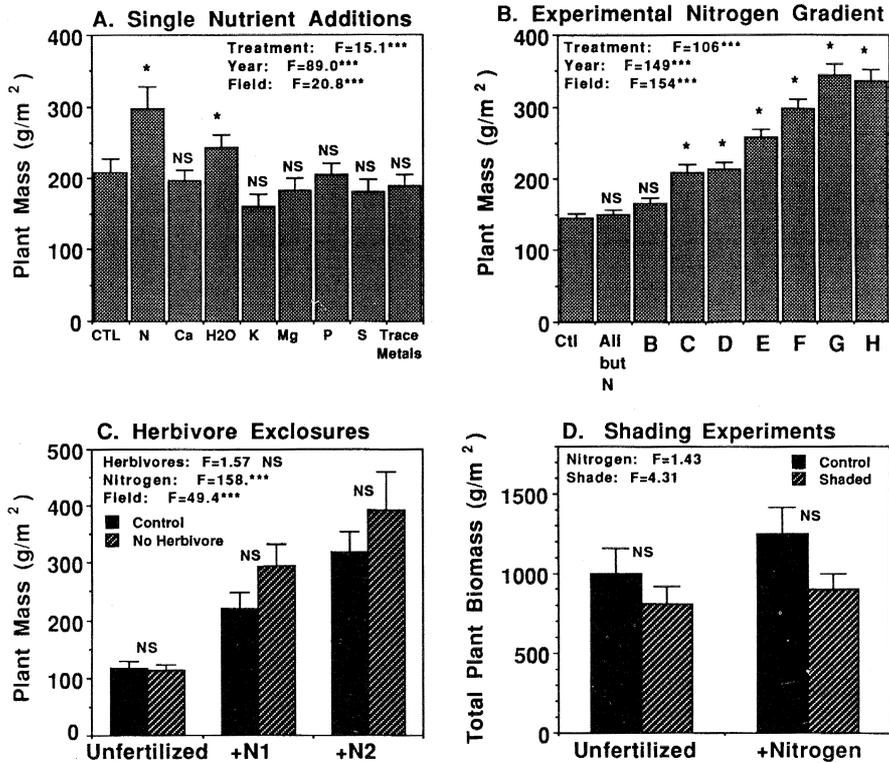
Nitrogen: F=1.43
Shade: F=4.31

■ Control
▨ Shaded

Fig. 3. The results of four different field experiments performed at CCNHA, Minnesota.
(A) An experiment in which various nutrients were added one at a time to replicate plots in four different fields for eight years in a row (1982–1989). ANOVA of the effects of treatments, years, and fields on aboveground biomass in these 144 plots showed that all were highly significant. The addition of N led to significantly greater biomass than in the unmanipulated control.
(B) In another experiment, N and all other nutrients were added at various rates to replicated plots in four different fields over an eight year period. ANOVA revealed that treatment, year and field were all highly significant factors. There was no significant effect (NS) of adding all nutrients but N, compared to controls, but biomass increased with the rate of N addition (treatments B to H have increasingly greater annual rates of N addition; Tilman 1987).
(C) A different experiment involved the exclusion of various functional groups of herbivores from replicated plots in three different fields (Huntly and Inouye, in preparation). The experiment was performed on unfertilized vegetation, as well as on plots receiving either 5.4 or 17.0 g m^{-2} yr^{-1} of N. ANOVA showed no significant effect of any of the herbivore treatments on total aboveground plant mass, but a highly significant effect of N and of field. Contrasts of controls with sham fences with plots from which all herbivores were removed (shown above) were not significant, but suggest that herbivores may be suppressing biomass on the more fertile plots.
(D) Unfertilized and fertilized plots in a field were divided into areas that were either shaded or unshaded (control). ANOVA and contrasts reveal no significant effects of shade or nitrogen in this experiment on total plant biomass (aboveground plus belowground).

tions among two zooplankton species competing for two algal species (Rothhaupt 1988), and of nitrogen competition among various combinations of five grass species (Wedin and Tilman, in review; Tilman and Wedin, in review). Simple models of the mechanisms of disease transmission have predicted disease dynamics and explained effectiveness of vaccination programs (e.g., May 1982a, b). Thus, there is good reason to believe the approach outlined above can be successful in predicting patterns in more complex communities and ecosystems.

The constraints and tradeoffs of terrestrial plants

For most terrestrial plants, the availability of soil resources, of light, of germination sites (often disturbed areas), and the intensity of herbivory are major envi-

ronmental constraints. The tradeoffs that plants face in dealing with these constraints are directly attributable to differences in biomass and nutrient (often nitrogen) allocation patterns (Fig. 1). For a version of the model implied by Fig. 1, in which plants differed in allocation to leaf, stem and root, but had identical physiologies and identical susceptibilities to sources of loss and mortality, numerical solution of a series of differential equations (called "ALLOCATE"; Tilman 1988) showed that many allocation patterns were viable in the absence of competition, but only one or a few closely related patterns could persist when competing with all other allocation patterns in a habitat with particular environmental conditions. The superior allocation pattern, though, depended on the relative intensities of the environmental constraints (Fig. 2), which, in this case, were the rate of

loss of biomass (a surrogate for the disturbance or herbivory rate) and the rate of supply of the limiting nutrient (productivity). This model could be made more realistic by the inclusion of differential allocation to seed production, differential seed dispersal ability, and herbivory. This added realism would give the model new features and allow it to make predictions about different aspects of ecosystems. However, one major qualitative feature would still hold: there would be a simple mapping of environmental conditions to the organismal traits favored by those conditions. This mapping is the central prediction of such models, and it is only possible to make such predictions when mechanistic models are used.

Competition and succession on a sandplain

I would now like to illustrate the approach outlined above by providing an overview of work that we have been doing for the past eight years on the plants, soils, and herbivores of Cedar Creek Natural History Area (CCNHA), Minnesota. I shall also briefly mention some preliminary findings of more recent work. The site, and many of our general methods, are described in Tilman (1987, 1988).

We began by performing nutrient addition, shading, and herbivore exclusion experiments to determine what environmental factors constrained the plants. Of all soil resources added singly to replicated plots in four different fields (see Tilman 1988: 247–249), the only consistently significant response came from nitrogen (ammonium nitrate; Fig. 3A). There was a significant water response in only one of the eight years, 1988, which was a major drought year. Interestingly, there was little or no nitrogen response that year. There were strong year and field effects (Fig. 3A). There has never been any consistently significant response to P, K, Ca, Mg, S, Mn, Mo, Cu, Fe, Co, Cu, or B, whether added singly (Fig. 3A) or in combination (Fig. 3B, treatment "All but N"). Biomass increased with the rate of nitrogen addition (Fig. 3B). Thus, nitrogen is the most important limiting soil resource.

In a separate nitrogen addition and shading experiment, there was a significant effect of nitrogen addition on shoot biomass ($F_{1,43}=10.6$, $P<0.01$), but no significant shade effect ($F_{1,43}=2,34$, $P>0.10$), and no significant nitrogen $\times$ shade interaction ($F_{1,43}=0.33$, $P>0.1$). When total plant biomass (aboveground plus belowground biomass) was analyzed, there were no significant treatment effects, but, as before, shaded plots had less biomass than unshaded plots (Fig. 3D).

In a recent full factorial experiment in which the experimental variables are disturbance intensity (mechanical disturbance to soil surface and plants) and nitrogen addition rate, Scott Wilson and I are finding that both disturbance and nitrogen have strong and significant effects on productivity, species composition and species diversity.

Nancy Huntly and Richard Inouye (in preparation) performed a herbivore exclusion experiment in three fields, with various herbivore guilds excluded from unfertilized vegetation, from vegetation receiving moderate rates of N addition, and from plots receiving a high rate of N addition. Analysis of the effects of the treatments on total aboveground plant biomass revealed a strong and significant nitrogen effect and a slight but non-significant herbivore effect (Fig. 3C), with the effect of herbivory seeming to be greater on fertilized plots. When they analyzed data on a species-by-species basis, there were few significant changes in the absolute or relative abundances of the common plant species caused by herbivores, but some rare plants, especially legumes, increased in the absence of herbivores, and the data suggested that there might be interactions among the herbivore guilds.

Thus, our field manipulations have demonstrated that the availability of soil nitrogen is the major environmental constraint at CCNHA and that disturbance frequency/intensity is next most important. Water replaces nitrogen as a dominant variable during drought years. Light intensity and herbivory may be having an impact, but their impact is less than that of N, disturbance or water in these old fields. Other factors, such as P, K, Ca, Mg, S and trace metals are having no direct impact on plants, although sodium, through its effect on herbivores, does indirectly affect plants (Inouye et al. 1987a).

Competition for soil nitrogen

Although nitrogen addition leads to increased plant biomass and to changes in the relative abundance of plant species at CCNHA (Tilman 1987) this need not imply that plants are competing for nitrogen (e.g., Grime 1979). Do plants living on the nitrogen impoverished soils of CCNHA compete? To address this question, we planted seedlings of three common grasses (*Agropyron repens, Poa pratensis,* and *Schizachyrium scoparium*) in established vegetation, in areas from which all plants had been removed, and in areas that contained the roots of neighboring plants, but from which the shoots were held to the side so as not to shade a transplant (Wilson and Tilman, in review). After a field season of growth on unfertilized plots, we found an equal and highly significant reduction in transplant final mass and growth rate either in the presence of all neighbors or in the presence of just their roots (Wilson and Tilman, in review). Seedlings without neighbors grew from three to six times more rapidly than those with either neighbors or just the roots of neighbors. This demonstrated the existence of competition and showed that it was competition for a soil resource. The same experiment was also performed on plots that had received nitrogen for the previous five years. There was also strong competition in these plots, but the competition was for light, not for soil nutrients (Wilson and Tilman, in review).
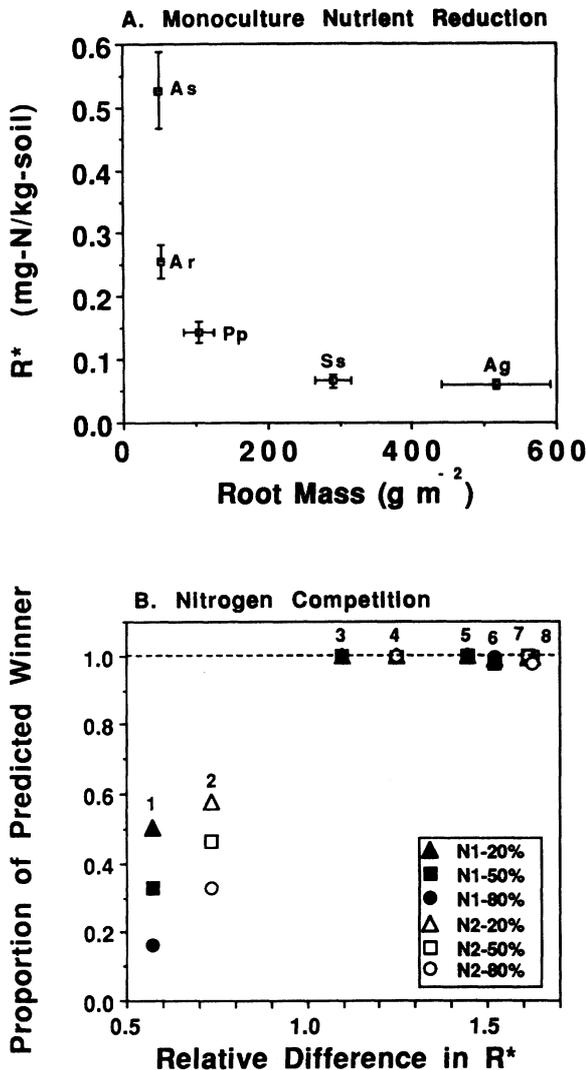
A. Monoculture Nutrient Reduction

B. Nitrogen Competition

Fig. 4. (A) The dependence of R* for nitrogen on the root biomass of five species of grasses. R* measured in 3 yr old monocultures of the species grown on low N soils. As = *Agrostis scabra*, Ar = *Agropyron repens*, Pp = *Poa pratensis*, Ss = *Schizachyrium scoparium*, Ag = *Andropogon gerardi*. Data from Tilman and Wedin (in review).
(B) Outcome of competition among various pairs of grass species, on extremely low N ("N1") and on low N soils ("N2"). The predicted winner is the species with the lower R* (see Fig. 4A). Its treatment-average portion of total biomass in plots after three years of competition is shown. Relative difference in R* is the difference in the R*'s of the two competitors divided by their average R*. Note that the predicted winner did win, independent of its initial abundance (20%, 50%, or 80%) when two species had large differences in their R*'s, but that displacement had not yet occurred after 3 yr for pairs with similar R*'s. Numbers refer to particular species pairs on a given soil N level. Data from Wedin and Tilman (in review) and Tilman and Wedin (in review).

Thus, there is strong competition for nitrogen on the infertile, sandy soils of CCNHA and this grades into competition for light on rich soils. What, though, are

the mechanisms of competition, and how might the outcome of competition be predicted?

Mechanisms of nitrogen competition

In theory, reduction in the soil solution concentration of a resource is the most basic mechanism of competition for a soil resource. As one plant consumes a soil resource, the soil solution concentration that another plant experiences is reduced. A wide variety of models of competition for a single limiting resource predict that the outcome of competition is determined by differences in the levels to which equilibrial monocultures of species can lower the concentration of the limiting resource (e.g., O'Brien 1974, Tilman 1977, 1982, 1990, Hsu et al. 1977). The level to which the soil solution concentration of a limiting resource is reduced by an equilibrial monoculture of a species is called R*. R* is the resource concentration a species requires for it to be able to persist in a habitat. A comparable concept, that of threshold density, exists for host-microparasite interactions (May 1982a, b). The species with the lowest R* for a limiting soil resource is predicted to be the superior competitor for that resource (Tilman 1980, 1990). It should displace all other species, independent of initial densities, from all habitats in which that resource is limiting. Two species should persist when limited by a single nutrient only if they have identical R*'s. This means that it should be possible to predict the outcome of nutrient competition by growing species in equilibrial monoculture gardens and directly observing their R*'s.

R* is predicted to depend on numerous plant traits, including root mass, uptake dynamics per unit root mass, tissue loss rate via herbivory and senescence, nutrient conservation abilities, photosynthetic rates, respiration rates and maximal growth rates (Tilman 1990). The R* measured in equilibrial monocultures is thus a summary variable – an abstracted variable (sensu Schaffer 1981) – that includes the effects of all the underlying physiological and morphological traits of that species. Models that include such traits show each of these influences on R* (Tilman 1990). These traits, though, are interdependent because of allocation-based tradeoffs. When such tradeoffs are included in these models, the optimal pattern of allocation includes high root biomass (but with a balance between root and shoot), low tissue nutrient concentrations, efficient nutrient conservation, and perhaps high allocation to herbivore defense (Tilman 1990). The major costs plants pay for these beneficial traits are low maximal rates of nutrient uptake and of photosynthesis (from low tissue N; Field and Mooney 1986) and low relative growth rates (from low photosynthetic rates and low allocation to leaves). The traits predicted to cause high competitive ability for a limiting soil nutrient are similar to the traits that Chapin (1980) found for plants that dominate naturally nutrient poor areas. This suggests that nutrient competition, not just tolerance, may have
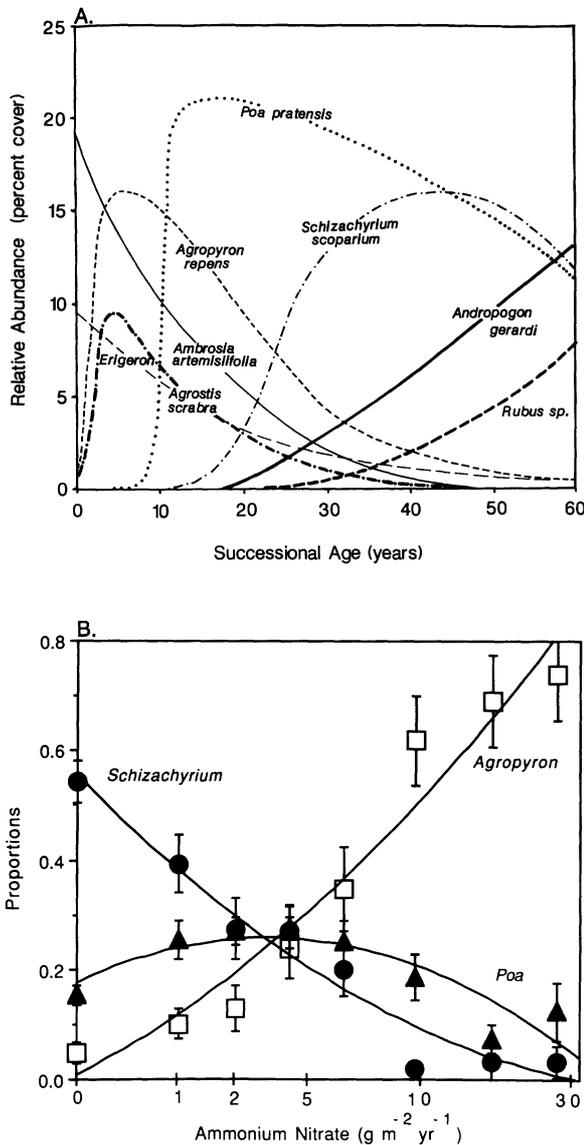
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Fig. 5. (A) The dependence of the relative abundance of the successional dominants of CCHNA on successional age, based on a chronosequence of old fields (Inouye et al. 1987c, Tilman 1988).
(B) The dependence of the proportional abundance of three dominant successional grasses on the rate of N addition to sucessional vegetation. These data are from the same experiment illustrated in Fig. 3B. Data are means and standard errors over three successional fields, using observed relative abundances of these species in 1989, the eight year of the experiment. *Schizachyrium scoparium* (solid circles) declines with N addition; *Poa pratensis* (solid triangles) reaches its peak abundance at intermediate rates of N addition; *Agropyron repens* (open squares) is increasingly abundant in plots receiving high rates of N addition. The x-axis is on a log scale, based on log $(1 + N$ addition rate.)

been a strong force favoring the evolution of these traits in plants of infertile habitats.

Tests of the R* hypothesis

To test these ideas, we established an experimental garden in which we grew five different grass species both in monoculture and in various competitive combinations along an experimental nitrogen gradient (Wedin and Tilman, in review; Tilman and Wedin, in review). After three years of growth in monoculture on infertile soils, the five grass species (*Agrostis scabra, Agropyron repens, Poa pratensis, Schizachyrium scoparium,* and *Andropogon gerardi*) differed in the levels to which each reduced the concentration of extractable soil ammonium and nitrate. The species that decreased soil ammonium and nitrate concentration the most in low nitrogen soils had greater root biomass (Fig. 4A), lower tissue N concentrations, and lower maximal growth rates than the other species (Tilman and Wedin, in review). This is consistent with predictions of theory (Tilman 1990) and provides an underlying mechanism for the patterns reported by Chapin (1980).

Our competition experiments supported the predictions of resource competition theory. For species pairs with large differences in their R* for nitrogen (the sum of extractable soil ammonium and nitrate), the species with the lower R* had, after three years, displaced the other species from the low N plots independent of initial seed planting ratios (Wedin and Tilman, in review, Tilman and Wedin, in review). For instance, *Schizachyrium scoparium* displaced *Agrostis scabra* and it displaced *Agropyron repens*. *Andropogon gerardi* displaced *Agropyron repens* and it displaced *Agrostis scabra* (Fig. 4B). The two species that persisted for the three years of the experiment were quite similar in their R*'s for N (*Agrostis scabra* and *Agropyron repens*; Fig. 4). One other species, *Poa pratensis,* was part of these experiments but is not included in Fig. 4B because of poor germination and early growth. In total, Dave Wedin and I have found that species with high allocation to root, low tissue N, low allocation to seed or rhizome, low maximal growth rates, and perhaps greater root longevity have lower R*'s for nitrogen and are superior competitors for nitrogen. These results are the first demonstration that terrestrial plants differ in their R*'s, that these R*'s are determined by allocation patterns and physiologies, and that these R*'s can predict the outcome of interspecific competition.

Successional dynamics

Theory

We studied the five grasses discussed above because they are dominants during old field succession at CCNHA (Fig. 5A). What might cause this successional sequence? In theory, a successional pattern, like any ecological pattern, is caused by constraints and tradeoffs. Although there are many potential environmental constraints and many potential tradeoffs, the major

constraints on plants in successional habitats are (1) access to the disturbed site, i.e., colonization (e.g., Drury and Nisbet 1973, Pickett 1976, Noble and Slatyer 1980, Huston and Smith 1987); (2) availability of limiting soil resources (e.g., Clements 1916, Crocker and Major 1955, Odum 1960, Golley 1965, Robertson and Vitousek 1981); (3) the availability of light (e.g., Cooper 1923, Horn 1971, Shugart 1984, Tilman 1985); and (4) herbivores, pathogens, and other sources of loss and mortality (Connell and Slatyer 1977, Walker 1981, Brown 1984, van der Maarel 1984, van der Maarel et al. 1985). Each of these constraints can be overcome by allocation to particular structures or physiological functions, but all such allocation patterns necessarily reduce proportional allocation to other structures or functions, causing tradeoffs (Fig. 1).

Given these four constraints, there are six different combinations of two-way tradeoffs among these traits, four three-way tradeoffs, and one four-way tradeoff. Each of these combinations represents a unique successional hypothesis. Most of these, in some form, have been discussed in one or more of the papers cited in the preceding paragraph. Although a few of these hypotheses may explain most successional sequences, there is no a priori reason for rejecting any as impossible. I will discuss the six different two-way tradeoffs, but only briefly mention three-way and four-way tradeoffs. For clarity, each hypothesis is explicitly named after its underlying tradeoff.

Hypotheses of succession

1. The colonization – nutrient competition hypothesis
A tradeoff between allocation to seed versus allocation to root would cause species to be differentiated in their ability to colonize a disturbed site versus their ability to compete for a limiting soil resource. This tradeoff is likely to be important during the early stages of succession on nutrient poor substrates. The successional sequence would proceed, on average, from species that were good colonists but poor nutrient competitors, to species that were poor colonists but good nutrient competitors.

2. The colonization – light competition hypothesis
Here the tradeoff is between allocation to seed and dispersal structures versus allocation to stem, leaves, and photosynthetic machinery. The initial dominants of succession, the superior colonists, would be replaced by species that were progressively poorer colonists but better light competitors.

3. The colonization – herbivory hypothesis
If plants are differentiated in allocation to seed versus herbivore defense, the superior colonists would be dominant initially, but be replaced by species that were poorer colonists but more resistant to herbivory. This requires that herbivory be a significant force throughout

succession, or that the intensity of herbivory increase during succession. It could not explain succession if herbivory intensity decreased during succession.

4. The nutrient: light ratio hypothesis
This has been called the resource ratio hypothesis of succession, since it states that each species is specialized on a particular ratio of the limiting resources, and that succession should occur whenever this ratio changes. If plants are differentiated in their pattern of allocation of nitrogen and/or carbon to roots versus to stem and leaves, succession should occur if the relative availability of nutrients and light changes through time, assuming that these resources are limiting.

5. The herbivory – nutrient competition hypothesis and
6. The herbivory – light competition hypothesis
These two hypotheses are closely related, and thus discussed together. Both assume that there is a tradeoff between susceptibility to herbivory versus competitive ability (e.g., Lubchenco 1978). Given this tradeoff, succession should occur whenever there is a long-term change in the intensity of herbivory. If herbivory is of low intensity during early succession and increases as plant and herbivore biomass accumulates, succession should proceed from species that are superior competitors (for either nutrient or light) to species that are inferior competitors in the absence of herbivory but superior competitors in its presence. The opposite successional sequence (in terms of plant traits) would occur if the intensity of herbivory decreased during succession. Clearly different plant traits, and thus different plant species, would be favored during such successions on nutrient poor soils than on nutrient rich soils.

7. Maximal growth rate tradeoffs
There are several other successional hypotheses that result from differences in allocation. Because high allocation to anything other than leaves and photosynthetic systems should decrease a plant's maximal growth rate (Monsi 1968, Tilman 1988), a cost of high allocation to roots, stems, or defensive compounds is a lower maximal growth rate. Thus, there can be tradeoffs between maximal growth rate and nutrient competition, between maximal growth rate and light competition, and between maximal growth rate and herbivore defense. Differences in maximal rates of vegetative growth can cause successional transient dynamics (Tilman 1988). For the *maximal growth rate – nutrient competition hypothesis*, which would apply to succession on nutrient poor soils, the initial successional dominants would be fast growing, leafy plants with high tissue nutrient concentrations and low allocation to roots. They would be replaced by a sequence of plants that had progressively slower rates of vegetative growth but progressively greater allocation to roots. The *maximal growth rate – light competition hypothesis* would apply to successions on rich soils, with the early successional species being

A. Woody Plants
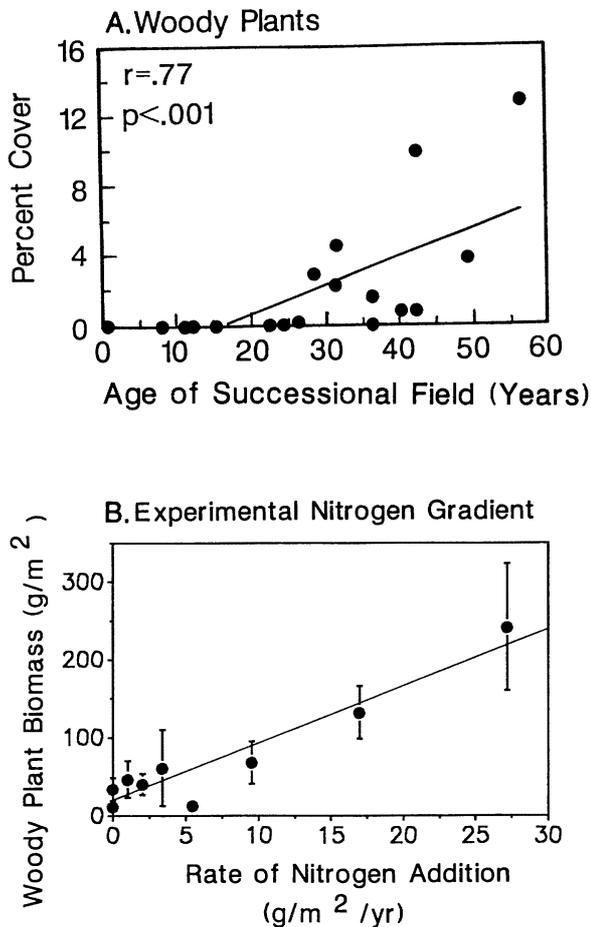

B. Experimental Nitrogen Gradient

Fig. 6. (A) Woody plant abundance (percent cover) increases during succession at Cedar Creek, with woody plants more abundant in older, more N rich fields (data from Inoye et al. 1987c).
(B) In the N addition plots (those illustrated in Figs 3B and 6B), woody plant biomass increases highly significantly with the rate of N addition in 1989. Mean and standard errors are shown for the two oldest fields, where woody plants were relatively common (see Fig. 7A).

short and leafy, and latter successional species having progressively greater allocation to stem (light competitive ability), and thus lower rates of vegetative growth. The *maximal growth rate – herbivory hypotheses* would predict a successional sequence from fast-growing, undefended plants to slow-growing well-defended plants.

These two-way tradeoffs assume that a change in allocation to one plant trait will only affect one other plant trait. If a change in allocation to one trait influenced the pattern of allocation to several other plant traits, as seems likely, there could be three-way and four-way tradeoffs. One possible three-way tradeoff, for instance, could be among colonization, competitive ability for nutrient and competitive ability for light. During succession on a nutrient impoverished substrate, the major tradeoff, initially, would be between colo-

nization and nutrient competition, as discussed above. If colonization were more rapid than nutrient accumulation in this habitat, this successional sequence would grade into a tradeoff between nutrient versus light competition. If colonization were slower than nutrient accumulation, the successional sequence would grade from a colonization – nutrient competition tradeoff into a colonization – light competition tradeoff. Another three-way tradeoff that could be important in successions on nutrient rich substrates is a tradeoff among colonization ability, light competitive ability and herbivore resistance. This would define a plane of possible plants, with colonization ability being a major determinant of early successional dominants, but with the identity of the later dominants being determined by the intensity of herbivory and tradeoffs between competitive ability versus herbivore resistance.

This large number of alternative hypotheses of succession may seem counterproductive because science, after all, is the search for simplicity. The simplicity we will find in ecology, however, is unlikely to be the simplicity associated with having only a few alternative hypotheses. Rather, our simplicity will come from an overlying mechanistic framework that allows us to determine the cause of a given pattern. For almost all ecological patterns, this framework is provided by the concept of environmental constraints and organismal tradeoffs. Field experiments can readily determine what the major constraints are in a given environment. Experimental studies of the relationships between plant traits and these environmental variables can be used to quantify tradeoffs and eliminate alternative hypotheses. Further simplicity will come as we learn which environmental constrains and tradeoffs are of greatest importance in broad classes of habitats, and how their relative importance changes along major geographic gradients (e.g., Vitousek 1982, Vitousek and Sanford 1986).

Successional dynamics at CCNHA

Before farming began in the 1880's, the upland habitats at CCNHA were a mosaic of oak savanna (open oak woodlands), prairie openings, and scattered stands of oak forest, pine forest, and maple forest. Farming led to major losses of soil N and C. A newly abandoned field has less than ⅓ of the total soil N found in adjacent uncultivated areas. A chronosequence of 22 old fields suggests thatt N slowly accumulates in these soils (Inouye et al. 1987c), but more than 100 yr may be required for a field to return to its pre-agricultural soil N content (Tilman 1988).

The initial dominants of succession are annuals and short-lived perennials, many of which are agricultural weeds (Fig. 5A). These are replaced by a sequence of perennial grasses, with the dominant grasses after about 50 yr being the native prairie species *Schizachyrium scoparium* (little bluestem) and *Andropogon gerardi*
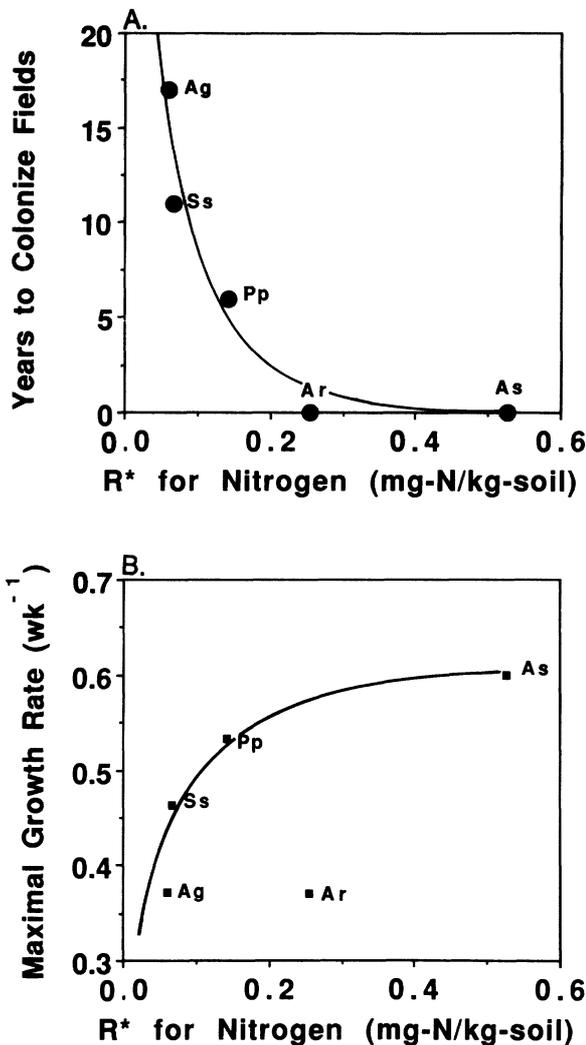
Fig. 7. (A) There is a strong inverse correlation between the average number of years a species requires to colonize a field and its R* for nitrogen, i.e., its ability to compete for N. Early successional species have a high R* (poor N competitors) but are rapid colonists, but late successional species, which are poor colonists, have a low R* and thus are superior N competitors. R*'s are from Tilman and Wedin (in review).
(B) For four of the five species there is a tradeoff between maximal growth rate and R* for nitrogen, with the species with the lower R* having a lower maximal growth rate (RGR). R*'s and RGR's from Tilman and Wedin (in review).

(big bluestem). Woody plants, mainly shrubs, vines, and seedlings or saplings of oaks and white pine, slowly increase in abundance, and comprise about 12% of cover after 60 yr.

Our nitrogen addition experiments allow us to determine the extent to which this pattern can be explained by the nutrient: light ratio hypothesis. If this successional sequence is caused by the slow accumulation of nitrogen and the associated increase in plant biomass and decrease in light penetration, then N addition should favor later successional species, and species

should become separated along an experimental N gradient in the same order that they occur during succession. After eight years of growth along experimental N addition gradients on both the existing vegetation and on initially disturbed (disked) soils in four different fields, there was a significant and consistent pattern of species separation (e.g., Tilman 1987). For instance, Agropyron repens, Poa pratensis, and Schizachyrium scoparium were significantly separated (Fig. 5B). However, their order of occurrence along these experimental N gradients clearly refutes the nutrient:light ratio hypothesis of succession (compare Fig. 5A and 5B). If Agropyron is an early successional species because of superior competitive ability in low N but high light habitats, it should decrease in abundance as N is added. It increased, displacing most other species from high N plots. Similarly, if Schizachyrium is dominant during later succession because it is a superior competitor in higher N but lower light habitats, it should increase in abundance when N is added. It consistently declined. Moreover, our garden experiments showed that Schizachyrium is a much better competitor for N than Agropyron (Wedin and Tilman, in review). Thus, there is no evidence that the successional sequence of the dominant herbs was caused by a nutrient:light tradeoff. In contrast, woody plants are increasingly abundant in the older, more N rich fields of late succession (Fig. 6A), and woody plant biomass increases highly significantly in response to N addition (Fig. 6B). Indeed, woody plants may be displacing Agropyron from high N plots. Thus, the nutrient:light ratio hypothesis can not explain the early, herbaceous phase of succession, but may explain the transition from herbaceous to woody plants.

A survey of plant allocation patterns in fields of different successional ages has shown that early successional plants have significantly higher leaf, seed, and stem allocation, and significantly lower root allocation, than later successional species (Gleeson and Tilman 1990). During the first 60 yr of succession, roots increase from 35% of total biomass to about 80%, but seed and reproductive structures decline from about 8% of total biomass in young fields to less than 0.5% in the oldest fields. If plants with higher allocation to roots, such as Schizachyrium scoparium, are superior nutrient competitors, which we demonstrated in our competition gardens (Wedin and Tilman, in review), then these data demonstrate that nitrogen competition, not light competition, is a major force during the first 40 yr of succession. This is supported by the observations that percent allocation to stem declined for the first 15 yr and then remained constant for the next 45 yr of succession (Gleeson and Tilman 1990), and that average plant height only increased 5 cm during this 60 yr. Thus, the colonization – light competition hypothesis and the light competition – herbivory hypothesis are unable to explain the first 40 to 60 yr of succession at CCNHA.

If high allocation to seed allows a plant to be a superior colonist (e.g., Werner and Platt 1976), then these

allocation patterns suggest that the herbaceous phase of our succession may be explained by the colonization – nutrient competition hypothesis. If this hypothesis is correct, there should be a tradeoff between nutrient competitive ability (measured as the R^* for N of the five species grown in the garden experiment) and colonization rate. We estimated colonization rates using the average number of years each of the five grasses required to colonize abandoned fields. The early dominants, *Agrostis* and *Agropyron*, are rapid colonists but have high R^*'s and are poor N competitors (Fig. 7A). The late successional species, *Schizachyrium* and *Andropogon*, are poor colonists, requiring 11 to 17 yr to colonize a field, but have the lowest R^* for N (Fig. 7A) and are superior N competitors.

Agropyron, an agricultural weed whose Swedish common name means "quick root", allocates 30% or more to rhizome (Håkansson 1967, Tilman and Wedin, in review), and thus can spread rapidly (Håkansson 1967, Werner and Rioux 1977). *Agrostis* allocates 7%–10% to seed, producing 9400–16000 viable seed m^{-2} that are born on a tumbleweed-like culm, and thus widely dispersed. *Poa* is somewhat rhizomatous and allocates 2%–7% to seed on low N soils. Neither *Schizachyrium* nor *Andropogon* are rhizomatous, and neither allocates more than 2% to seed. Thus, the colonization rates of these species are consistent with their pattern of allocation to seed and rhizome on low N soils.

The results of pairwise competition in the gardens provide further support for the colonization–nutrient competition hypothesis. Although *Schizachyrium* requires more than 30 yr to displace *Agropyron* during succession, this displacement occurred in three years when the colonization limitation on *Schizachyrium* was eliminated by planting both species in garden plots (Wedin and Tilman, in review).

Lower relative growth rates are predicted to be caused by decreased allocation to leaf and decreased maximal photosynthetic rates, which should result from lower leaf N (Field and Mooney 1986). The late successional herbs, which are superior N competitors, often had lower relative rates of vegetative growth than the superior colonists (Fig. 7B). This is correlational support for the maximal growth rate–colonization hypothesis. However, the competition plots in our experimental gardens refute this hypothesis (Wedin and Tilman, in review). The greatest difference in maximal rates of vegetative growth was between *Agrostis* and *Andropogon*. When these two species were planted simultaneously in a competition plot, there was no obvious period of dominance by the faster growing species, *Agrostis*, before the more slowly growing species, *Andropogon*, attained dominance. Although the difference in growth rates should give *Agrostis* an initial advantage, this advantage is too small to account for more than a year advantage, much less the 40 or more years required for *Andropogon* to become abundant during old field succession at CCNHA.

We have less data with which to evaluate hypotheses that involve herbivory. In almost every case that herbivores have been studied, we have found some effect on plants, but the effects have often been small (e.g. Fig. 3C). Richard Inouye and Taber Allison are finding that deer browsing has a significant effect on growth rates of trees, but it may not be sufficient to account for the slow rate of woody plant reestablishment at CCNHA. Herbivory and disturbance by the plains pocket gopher (*Geomys bursarius*) influences plant species diversity and slows the rate of succession (Tilman 1983, Inoye et al. 1987b), but does not seem to drive the pattern of succession. As already mentioned, the exclosure of small mammal and insect herbivores did not cause major changes in species composition. Although more work is needed, at the present time it seems that herbivory is not frequently a major factor controlling our successional pattern.

Thus, of all the alternative hypotheses presented above, the major explanation for the herbaceous period of succession seems to be the colonization – nutrient competition hypothesis. The best explanation for the transition from a prairie grassland to an oak woodland seems to be the nutrient:light ratio hypothesis. This suggests that a three-way tradeoff among colonization, nutrient competition, and light competition may determine most of the successional pattern at CCHNA.

Conclusions

All organisms face environmental factors that constrain their survival, growth and reproduction. Each organism also faces unavoidable, allocation-based tradeoffs in its ability to respond to these constraints (e.g., Cody 1966, Mooney 1972). These constraints and tradeoffs represent the mechanisms that can lead to pattern on all levels of ecological organization. Models that explicitly include these constraints and tradeoffs are, in theory, capable of making a priori predictions of the dynamics and outcome of ecological interactions. In many cases, especially cases involving the interactions among numerous species, mechanistic models that explicitly include constraints and tradeoffs are simpler and more easily tested than more phenomenological models.

A variety of such models of competition for a limiting nutrient predict that the species that can reduce the concentration of the limiting resource to the lowest level should competitively displace all other species (O'Brien 1974, Tilman 1977, 1980, 1990). Our studies of competition among five grass species competing for N support this prediction, and demonstrate that the differences among these species are based on allocation. Other studies of the mechanisms of nutrient competition between algae (e.g., Tilman 1976, Sommer 1985), of competition for sugars by bacteria (Hansen and Hubbell 1980), and of zooplankton competition for algae (Rothhaupt 1988), have all shown that the inclusion of mecha-

nisms allows a priori prediction of the dynamics and outcome of these interspecific interactions.

Successional patterns are also caused by constraints and tradeoffs, which provide a concise way to formulate alternative successional hypotheses. Numerous such hypotheses were tested via field experiments and observations at CCNHA, Minnesota. Our tests suggest, for successions on nutrient-depleted soils, that the tradeoff between colonization ability and competitive ability for nitrogen is the major determinant of the 40 to 60 yr period of herbaceous succession. The low abundance of woody plants during this period seems to be less related to colonization abilities than to their poor ability to compete on low N soils. This suggests that, as nitrogen slowly accumulates in this habitat, the tradeoff between nitrogen and light competitive abilities will be an increasingly important explanation of the successional pattern.

Other plant communities will have other constraints, and other sucessions will be explained by other processes. However, the underlying mechanisms are the same, and are based on the actual constraints of each environment and the tradeoffs organisms face in dealing with these. Studies of these mechanismns in a variety of habitats will allow us to determine how the importance of various potential constraints changes along major geographic, climatic or disturbance gradients. This, then, would allow us to develop a more holistic theory of the dynamics and structure of ecosystems, but a theory capable of making testable a priori predictions of the impact of changes in environmental variables on the dynamics, diversity, composition, and stability of these ecosystems. The pursuit of mechanistic, predictive models should become a high priority for ecology if we are to wisely manage the ever dwindling natural resources of this planet, and preserve its biotic diversity.

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