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Resource Use Patterns Predict Long-Term Outcomes of Plant Competition for Nutrients and Light

Ray Dybzinski* and David Tilman[†]

Department of Ecology, Evolution, and Behavior, University of Minnesota, St. Paul, Minnesota 55108

abstract: An 11-year competition experiment among combinations of six prairie perennial plant species showed that resource competition theory generally predicted the long-term outcome of competition. We grew each species in replicated monocultures to determine its requirements for soil nitrate (R^*) and light (I^*). In six pairwise combinations, the species with the lower R^* and I^* excluded its competitor, as predicted by theory. In the remaining two pairwise combinations, one species had a lower R^*, and the second had a lower I^*; these species pairs coexisted, although it is unclear whether resource competition alone was responsible for their coexistence. Smaller differences in R^* or I^* between competing species led to slower rates of competitive exclusion, and the influence of R^* differences on the rate of competitive exclusion was more pronounced on low-nitrogen soils, while the influence of I^* differences was more pronounced on high-nitrogen (low-light) soils. These results were not explained by differences in initial species abundances or neutrality. However, only a few of our paired species coexisted under our experimentally imposed conditions (homogeneous soils, high seeding densities, minimal disturbance, regular water, and low herbivory levels), suggesting that other coexistence mechanisms help generate the diversity observed in natural communities.

Keywords: competition, light, nitrogen, resource.

Although competition for resources is frequently cited as an important determinant of terrestrial plant community structure (e.g., Fowler 1986; Casper and Jackson 1997; Raynaud and Leadley 2004), few experiments have tested

* Corresponding author; e-mail: dybz0001@umn.edu.

† E-mail: tilman@umn.edu.

whether species' resource requirements influence the outcome of their interactions (Grover 1997; Miller et al. 2005). In a recent review, Miller et al. (2005) found that there were many tests of resource competition theory for rapidly growing organisms, especially algae and zooplankton, but only four articles in the past 20 years tested it with terrestrial plants in field experiments (Tilman 1983; Tilman and Wedin 1991; Kirkham et al. 1996) or field studies (Inouye et al. 1987). Miller et al. (2005, p. 439) suggested that "more experimental work in a variety of natural systems is seriously needed."

Skeptics of resource competition theory have questioned its applicability. They have variously argued that the complications of uptake dynamics in terrestrial plants preclude simple predictions (e.g., Craine et al. 2005); that coexistence comes from mutualisms or synergism, not interspecific trade-offs in competition (e.g., Thompson 1987); and that interspecific differences of any sort are ultimately unimportant (e.g., Hubbell 2001). Because the discipline has not reached consensus on resource competition theory's role in shaping terrestrial plant communities, its dearth of tests likely reflects the inherent difficulties in conducting experiments under field conditions with long-lived organisms (Grover 1997; Miller et al. 2005), for which competitive displacement may require a decade or longer.

Resource competition theory. Resource competition theory predicts the dynamics of species interactions based on resource dynamics and each species' resource use traits (Tilman 1982). Building on the work of MacArthur (1972), Maguire (1973), Taylor and Williams (1975), and others, Tilman (1982) showed that, in theory, a plant population in a monoculture with a single limiting resource would grow and reduce the concentration of that resource to an equilibrial level termed R^*, at which point growth would be balanced by losses. Given different physiologies, morphologies, and biotic interactions, different species are expected to have different R^*s (Tilman 1990), and indeed, the same species might have different R^*s for the same resource in different ecological situations.

When species compete for a single resource, the species with the lower R^* is predicted to win, as demonstrated for

rapidly growing organisms (Tilman 1976, 1977; Hansen and Hubbell 1980; Sommer 1989; Grover 1991; Smith 1993). Because the winner (with a lower R^*) reduces resource concentrations below the break-even point for the loser (with a higher R^*), the loser's losses exceed its gains, and its population declines exponentially. Tilman and Wedin (1991) and Wedin and Tilman (1993) tested this prediction by growing five perennial grass species in monocultures and in pairs. As expected, high nitrate concentrations under seedlings decreased with time to a lower species-specific concentration, R^*, in mature monocultures. In all four of their competition pairings, the species with the lower R^* won, independent of its initial abundance or initial life-history stage (seed or adult; Wedin and Tilman 1993).

With only one limiting resource and no other limiting factors or constraints, species are not predicted to stably coexist at equilibrium (Tilman 1982), though several species can stably persist if resource levels undergo sustained oscillations (Armstrong and McGehee 1980; Grover 1997; Huisman and Weissing 1999). However, if a second resource or physical factor, such as soil pH or temperature, potentially limits growth, then stable equilibrial coexistence is possible (Tilman 1982), as demonstrated for rapidly growing organisms (Tilman 1977, 1981; Kilham 1986; Sommer 1986; Rothhaupt 1988, 1996).

Competition for light. In contrast to competition for soil resources, competition for light has the complicating characteristic of being directional and asymmetric (Tilman 1988; Weiner 1990; Rees and Bergelson 1997; Perry et al. 2003). While the very same roots that reduce soil resource concentrations via uptake must subsequently extract resources at the low concentrations that they created, light interception is fundamentally different. Leaves reduce light below them, but the leaves that cause the reduction do not suffer the lower light levels that they create, though other leaves on that same plant may.

Tilman (1988) modeled the effects of plant traits that could influence the outcome of light competition. First, seed mass influences the ability of seedlings to grow under a canopy such that species with heavier seeds may be better light competitors (Black 1958). Second, height affects light preemption such that taller species may be better light competitors (Black 1960). Finally, canopy density also affects light preemption such that species with denser canopies may be better light competitors. A species-specific value termed I^*, measured as the fraction of light that remains at the soil surface in a monoculture, is a potentially useful metric that integrates the effects of height and density.

It has been shown theoretically (Huisman and Weissing 1994, 1995) and confirmed empirically (Huisman et al. 1999; Passarge et al. 2006) that when planktonic species compete for light, the species that reduces light to a lower level in a well-mixed monoculture wins, analogous to the R^* outcome for nutrients. Similarly, in a simulation model, Tilman (1988) showed that when seed mass and maximum adult height were held constant across terrestrial plant species, species with lower I^*s were better light competitors. Moreover, he showed that in some cases, species were able to coexist when light and soil nutrients were limiting. However, interspecific differences in seed mass or maximum adult height could greatly change the outcome of competition from that predicted by the I^* approximation (Tilman 1988).

Experiment description. Here, we report the results of an experiment that differs in three ways from that of Tilman and Wedin (1991). First, we used six native late-successional grasses that coexist across much of the North American prairie but that tend to reach peak dominance in different regions. Second, we used a much wider total soil nitrogen (N) gradient, comparable to the range found across the North American plains (Parton et al. 1989). Third, we investigated competition for light in addition to competition for N.

We established monocultures and pairwise competition subplots across a total soil N gradient in a common garden. Plant biomass and canopy height (both of which depended on total soil N) determined light availability, which was not otherwise experimentally manipulated. For each species pair at each N level, two competition subplots were established, one with relative seed abundances sown in a 70 : 30 ratio and the second in a 30 : 70 ratio, allowing us to test the influence of initial abundances and thus neutrality (Hubbell 2001).

We tested whether resource competition theory predicted the long-term outcome of competition based on monoculture R^*, I^*, height, and seed mass. Specifically, we tested the theoretical predictions that species with lower R^*s would exclude their competitors on low-N soils; that species with lower I^*s, greater vegetative height, and greater seed mass would exclude their competitors on high-N (low-light) soils; and that interspecific trade-offs between R^* and I^*, height, and seed mass would lead to coexistence. In addition, we tested whether the magnitude of interspecific differences in R^*, I^*, and height would predict the rate at which the biomass of competing species diverged and, if so, whether the influence of those differences shifted along the N gradient.

Methods

Establishment

In 1988, we removed the top 75 cm of soil from a section of old field at Cedar Creek Natural History Area

(CCNHA), Bethel, Minnesota, leaving subsurface sandy soil. We designed our experiment as a classic split plot: total soil N was specified at the plot level (14 plots, 2.4 m × 16 m each), and species monocultures and competition pairings were specified at the subplot level (23 subplots per plot, 1.2 m² each, 23 × 14 = 322 subplots in total). Subplots were surrounded by galvanized steel barriers driven between 20 and 25 cm into the soil. A belowground gopher fence (1 m deep, 30 cm wide) and an aboveground rodent/deer fence (2 m tall) enclosed the area.

To create an N gradient, between 0 and 20 cm of the subsurface sandy soil was removed from each of the 14 plots, and a corresponding depth of black soil was added and mixed, via repeated rototilling, to a depth of about 20 cm. Different ratios of black soil to sandy soil created different total soil N levels. On average, our gradient extended from 225 to 3,600 mg N kg^{-1} soil (the gradient in Tilman and Wedin 1991 ranged from 90 to 1,200 mg N kg^{-1} soil). Our method had the side effect of creating a correlated soil texture gradient, which likely affected water-holding capacity (Wedin and Tilman 1993). However, we were careful to amend rainfall such that soils were unlikely to reach wilting point (Wedin and Tilman 1993). If decreased water availability slowed nitrate diffusion rates, the texture gradient would have amplified our N gradient; relatively less nitrate would have diffused on soils that both were low in total soil N and had less water-holding capacity.

We used six native perennial prairie grasses: *Schizachyrium scoparium* (little bluestem), *Andropogon gerardii* (big bluestem), *Bouteloua gracilis* (blue grama), *Panicum virgatum* (switchgrass), *Agropyron smithii* (western wheatgrass), and *Buchloe dactyloides* (buffalo grass). Species names follow those of Gleason and Cronquist (1963). Note that *A. smithii*, which is native to the North American prairie, should not be confused with *Agropyron repens*, which is a common invasive species at CCNHA and the subject of previous work (Wedin and Tilman 1993). Prairie Restorations (Princeton, MN) provided the seeds, which we planted in late May 1989 at densities expected to generate equal numbers of live seedlings based on germination trials (*Schizachyrium*: 7.1 g m^{-2}; *Andropogon*: 8.8 g m^{-2}; *Bouteloua*: 4.0 g m^{-2}; *Panicum*: 5.6 g m^{-2}; *Agropyron*: 8.6 g m^{-2}; *Buchloe*: 31.3 g m^{-2}).

Each of the 14 N levels contained a monoculture of each species and competition subplots (*Bouteloua* vs. *Andropogon*, *Bouteloua* vs. *Agropyron*, *Panicum* vs. *Agropyron*, *Schizachyrium* vs. *Agropyron*, *Panicum* vs. *Buchloe*, *Bouteloua* vs. *Schizachyrium*, *Bouteloua* vs. *Panicum*, and *Panicum* vs. *Schizachyrium*). Logistical constraints prevented us from using all possible species pairs. We established two subplots of each pairwise combination at each N level,

with each species in a pair having a disproportionately larger share of the initial seed density in one subplot (70%) and a smaller share in the second subplot (30%). Total seed density in competition plots equaled the seeding density of monocultures. We also planted one four-species subplot at each N level with *Agropyron*, *Bouteloua*, *Panicum*, and *Schizachyrium*, each seeded at 25% of its monoculture density. All plots and subplots were spatially randomized.

We made two mistakes in the initial seeding. One subplot that was supposed to be *Andropogon* 70%, *Bouteloua* 30% was seeded as *Agropyron* 70%, *Bouteloua* 30%. One subplot that was supposed to be *Panicum* 70%, *Schizachyrium* 30% was seeded as *Panicum* 70%, *Bouteloua* 30%. These two subplots are included in analyses as they were actually seeded.

Maintenance

To ensure that only N and light were limiting, all subplots received 18 g of P_2O_5, K_2O, $CaCO_3$, and $MgSO_4$ plus trace metals every year in early May and late June, and they received rainfall amendments to ensure that the experiment received 3 cm water per week from mid-May to early September. We weeded the experiment two or three times per field season until 2000 to remove any species not prescribed to a subplot and burned it in early spring each year, before the grasses began growing, to prevent aboveground litter accumulation.

Data Collection

Before seeds were sown, we collected soil from each monoculture to determine total soil N content. Four cores (5 cm diameter, 20 cm deep) were collected from each monoculture, homogenized, dried, ground, and analyzed in duplicate via the persulfate digestion method (see Tilman 1984).

We sampled aboveground biomass, sorted to species, by clipping a 10 × 50- or 10 × 100-cm strip in each subplot in 1989–1993, 1996, and 1999 at the peak of the growing season (usually late July to early August). Except in 1990, root biomass was also collected from monocultures using three evenly spaced root cores (5 cm diameter, 20 cm deep). We report dry weights.

From 1989 to 2002, we sampled 0.1 M KCl-extractable nitrate in each monoculture 23 times. Either two or four soil cores were collected from each monoculture (2.5 cm diameter, 20 cm deep) during the growing season. Techniques follow those of Wedin and Tilman (1993), except soil samples were chilled in the field and extracted immediately after collection at the laboratory.

We sampled light penetration 2.5 cm above the soil

surface in each monoculture four times (once in August 1999 and three times in July and August of 2002) using a LI-COR photosynthetically active radiation cosine collector and integrating meter within an hour of solar noon on cloudless days. At each monoculture, one sample was taken above the vegetation, and five were taken below. We measured the canopy height of each species in early October 2002 by holding a ruler next to each monoculture and recording the visually estimated mean height of the highest vegetative structures (bolts and seed heads excluded). Seed mass was determined by hulling 10 seeds of each of the six species.

Analysis

We report the R^* of each monoculture as the average of the 13 measured nitrate concentrations that were collected between 1991 and 2002, excluding the 10 measurements that were taken between 1989 and 1990. In general, nitrate concentrations went down in these first 2 years and then either remained constant or increased over the remaining 11, suggesting that they had equilibrated as of 1991. Light penetration was calculated as the photon flux at the soil surface divided by the photon flux above the canopy (limited to photosynthetically active radiation). We report the I^* of each monoculture as the average of the four light-penetration measurements.

To predict the outcome of competition, we calculated resource-dependent nullclines in plots of I^* versus R^*. Because there was no a priori fit between these two values and because neither could be assumed to be known without error, we first calculated, via regressions, the dependence of I^* on ln [total soil N] and of R^* on total soil N (all 12 regressions, $P < .006$; lowest $R^2 = 0.483$; median $R^2 = 0.809$) along with their 95% confidence intervals. We then reduced the resulting equations to give equations for the interdependence of I^* and R^* and their 95% confidence intervals. We also determined the slope (but not the magnitude) of the resource consumption vectors (Tilman 1982) as light consumed per year divided by milligrams nitrate consumed per kilogram soil per year. When we extrapolated our light measurements across the season, the light consumption was simply $1 - I^*$. Because the N in aboveground tissues at the end of the season represents, to a first approximation, the N that was taken up during that season, nitrate consumption was $4.43 \times N_S \times B$, where 4.43 converts N to nitrate, N_S is the mean species fraction N in aboveground tissues at the end of the season (see fig. C5 in the online edition of the *American Naturalist*), and B is the mean eighth- and eleventh-year aboveground biomass, expressed in milligrams biomass grown per kilogram soil (assuming a rooting depth of 1 m and soil bulk density of 1.62 g cm^{-3}). Although consumption

vector slopes tended to flatten with increasing total soil N, for simplicity we present the average of each species' 14 consumption vector slopes.

An analysis was performed to quantify the effect of interspecific differences in monoculture R^* and I^* on the rate at which winners' biomass diverged from losers' biomass in competition subplots, that is, the rate of divergence (Grover 1991; Passarge et al. 2006). The rate of divergence was calculated from linear regressions of ln [aboveground biomass + 0.01] versus year for each species in competition subplots at each of the 14 N levels. The slope of the fitted curve for the eventual loser was subtracted from that for the eventual winner (in the cases of coexistence, the slope of the species with the lower equilibrial biomass was subtracted from the slope of the species with higher equilibrial biomass) to give the rate of divergence. Because these slopes were estimated values rather than known values, we used their estimated standard errors to reflect their uncertainty (Fuller 1987). Specifically, we weighted the difference in slopes for each competition subplot as the reciprocal of the sum of the squared standard errors from their two slopes (Fuller 1987). The predictors in the model were total soil N, plot-level interspecific differences (loser's minus winner's: R^* [ΔR], I^* [ΔI], and height [Δh]), and the N $\times$ ΔR and N $\times$ ΔI interactions. The N $\times$ Δh interaction was also included in an earlier model, but it was highly nonsignificant.

All analyses were performed with JMP, version 6.0.3 (SAS Institute, Cary, NC). Unless otherwise stated, Type III multiple regressions were used, and significant main effects remained significant when interactions were removed from models. In all analyses, the total soil N for each monoculture subplot was used as a covariate when the response was measured in monocultures as well. For responses measured in pairwise competition subplots, the average total soil N for all six monocultures at a given N level (plot) was used as the covariate. For clarity, several of the figures use averages from the seven lowest N levels and from the seven highest N levels instead of showing all 14 levels separately.

Results

In the eleventh year of the experiment, all of the monocultures of all six species had appreciable aboveground biomass (figs. 1*A*, C1 in the online edition of the *American Naturalist*), which increased along the total soil N gradient and depended on species identity (ln [N]: $F = 91.10$, df $= 1, 72$, $P < .0001$; species: $F = 12.71$, df $= 5, 72$, $P < .0001$; ln [N] $\times$ species: $F = 1.00$, df $= 5, 72$, $P = .42$; $R^2 = 0.69$). Vegetative height increased with total soil N and depended on the species and the species $\times$ N interaction (ln [N]: $F = 68.31$, df $= 1, 72$, $P < .0001$; spe-

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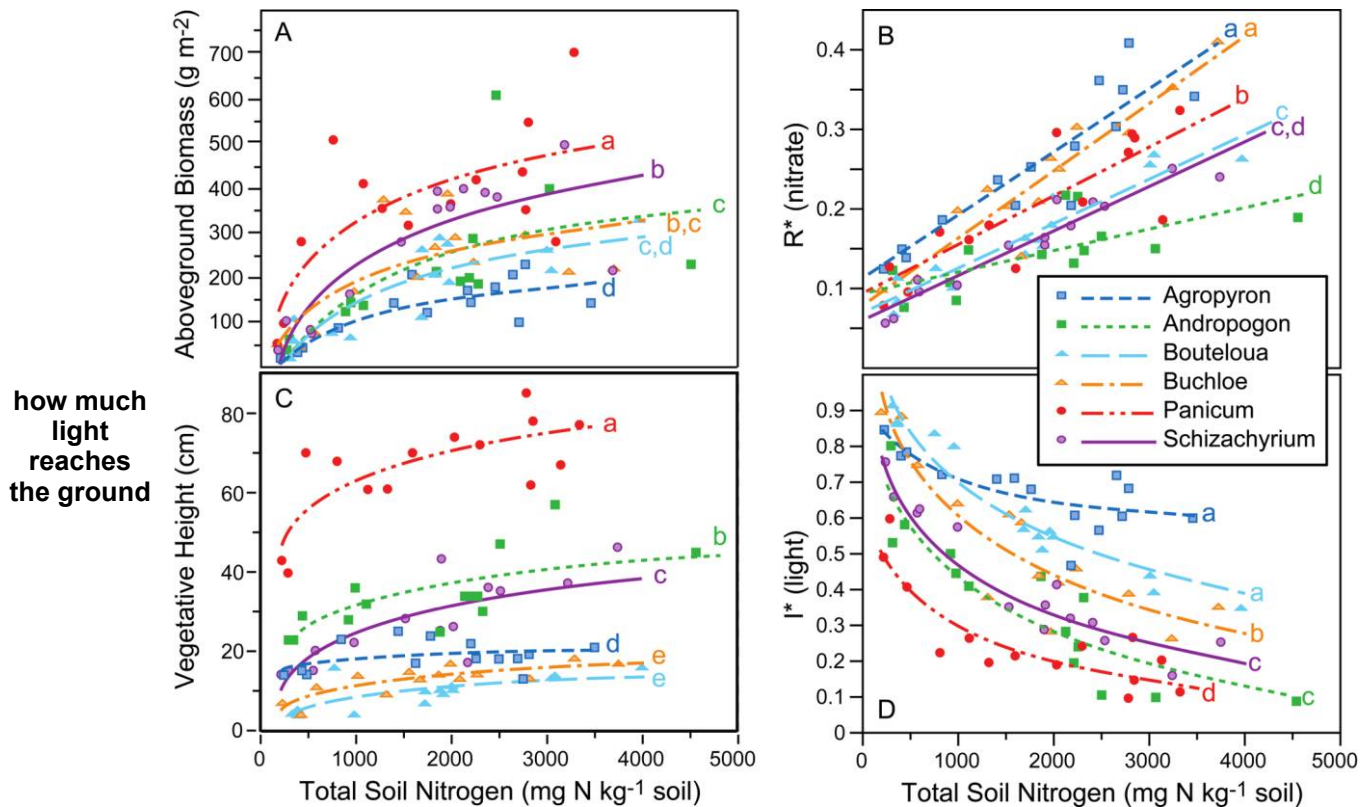
Figure 1: Monoculture (*A*) eleventh-year aboveground biomass, (*B*) extractable nitrate concentration (mg NO_3^- kg^{-1} soil; R^*), (*C*) thirteenth-year height (excluding bolts and seed heads), and (*D*) fraction light penetration to soil surface (I^*) as influenced by the nitrogen (N) gradient. *A*, *C*, and *D* were fit to ln [total soil N]. Least squares means of species with the same letter are not significantly different ($P > .05$; calculated after multiple regression using ln [total soil N] or total soil N, species, and their interaction).

cies: $F = 187.11$, df $= 5, 72$, $P < .0001$; ln [N] × species: $F = 3.94$, df $= 5, 72$, $P = .0033$; $R^2 = 0.93$; fig. 1*C*). Seed mass differed among species (table 1).

Mean extractable nitrate in monoculture (R^*) increased along the N gradient and depended on species identity and the N × species interaction (N: $F = 188.87$, df $= 1, 72$, $P < .0001$; species: $F = 21.68$, df $= 5, 72$, $P < .0001$; N × species: $F = 4.67$, df $= 5, 72$, $P = .0009$; $R^2 = 0.81$; fig. 1*B*). The significance of the interaction was largely due to *Andropogon*. When it was removed from the analysis, the N × species interaction became marginally nonsignificant (N: $F = 171.44$, df $= 1, 60$, $P < .0001$; species: $F = 16.17$, df $= 4, 60$, $P < .0001$; N × species: $F = 2.43$, df $= 4, 60$, $P = .0567$; $R^2 = 0.81$; fig. 1*B*).

Light penetration in monoculture (I^*) decreased along the N gradient and depended on species identity and the N × species interaction (ln [N]: $F = 379.28$, df $= 1, 72$, $P < .0001$; species: $F = 72.43$, df $= 5, 72$, $P < .0001$; ln [N] × species: $F = 5.87$, df $= 5, 72$, $P = .0001$; $R^2 = 0.91$; fig. 1*D*). The significance of the interaction was largely due to *Agropyron*. When we removed it from the

analysis, the N × species interaction became less significant (ln [N]: $F = 372.92$, df $= 1, 60$, $P < .0001$; species: $F = 55.57$, df $= 4, 60$, $P < .0001$; ln [N] × species: $F = 2.72$, df $= 4, 60$, $P = .038$; $R^2 = 0.91$; fig. 1*D*).

Competition

Despite their ability to persist in monocultures (fig. 1*A*), not all species persisted in competition. In six of the eight competition pairings, the species whose nullcline fell outside that of its competitor lost biomass exponentially over time (i.e., was "competitively displaced"; fig. 2, *A* and *D*, *B* and *E*, *C* and *F*; fig. 3, *A* and *D*, *B* and *E*, *C* and *F*). In all six of these cases, the species that was competitively displaced had higher mean R^* and I^* than its competitor or an equivalent mean R^* and a higher mean I^* than its competitor (fig. 1*B*, 1*D*).

Schizachyrium coexisted with *Panicum* (fig. 4*E*), and *Bouteloua* coexisted with *Panicum* (fig. 4*D*). In both of these cases, the nullclines of the two species either crossed and were statistically similar (fig. 4*B*) or crossed if ex-

Table 1: Hulled seed mass with standard errors

Species	Mass (mg)
Agropyron	$3.27 \pm .43^{A}$
Andropogon	$1.70 \pm .14^{B}$
Buchloe	$1.57 \pm .20^{B}$
Panicum	$1.45 \pm .07^{B}$
Schizachyrium	$.40 \pm .08^{C}$
Bouteloua	$.21 \pm .05^{C}$

Note: Values with the same letter are not significantly different ($P > .05$).

trapolated (fig. 4*A*). The sole four-species combination resulted in the coexistence of *Schizachyrium* and *Panicum* (consistent with their two-species pairing) and the exclusion of *Bouteloua* and *Agropyron* (consistent with their responses to competition with *Schizachyrium*; fig. 4*C*, 4*F*).

The rate of divergence of populations in the two-species subplots was dependent on the differences in R^* and I^* of the competing species measured in monoculture (fig. 5). Greater differences led to faster exclusion. There was a significant interaction between total soil N and interspecific differences in R^*. Differences in R^* led to a relatively greater rate of divergence under low-N conditions (steeper slope) than under high-N conditions (shallower slope; fig. 5*B*). The interaction between total soil N and interspecific differences in I^* was also significant but opposite in sign. Differences in I^* led to a relatively greater rate of divergence under high-N (low-light) conditions (steeper slope) than under low-N (high-light) conditions (shallower slope; fig. 5*C*). Finally, interspecific difference in maximum vegetative height (Δh) significantly predicted the rate of divergence, but its sign was opposite of what was expected: smaller differences in height led to a greater rate of divergence. The results of a Type III regression on the rate of divergence were as follows: total soil N: $F = 0.94$, df $= 1, 105$, $P = .33$; ΔR: $F = 67.62$, df $= 1, 105$, $P < .0001$; ΔI: $F = 20.61$, df $= 1, 105$, $P < .0001$; N $\times \Delta R$: $F = 10.13$, df $= 1, 105$, $P = .001$; N $\times \Delta I$: $F = 8.79$, df $= 1, 105$, $P = .0019$; Δh: $F = 7.33$, df $= 1, 105$, $P = .0079$; $R^2 = 0.563$. The significance of the above predictors did not change when entered in a Type II regression in the order listed.

Initial Abundance

The ratio at which paired species were seeded (70% of species *a* and 30% of species *b* or vice versa) had almost no effect on the long-term outcome of competition (figs. 6, B1 in the online edition of the *American Naturalist*), although the identity of the species involved did (figs. 2–4). Species tended to have greater biomass in competition subplots where they were heavily seeded than in those

where they were lightly seeded in the early years of the experiment, as indicated by the positive difference between aboveground biomass in these two types of subplots (*t*-test of 0 mean for first-year data: $t = 11.72$, df $= 109$, $P < .0001$; fig. 6). As time went on, this difference diminished and was indistinguishable from 0 by the eighth year and later (eighth year: $t = 0.32$, df $= 109$, $P = .75$; eleventh year: $t = 0.40$, df $= 109$, $P = .69$; fig. 6). When analyzed separately, only *Bouteloua-Schizachyrium* pairwise plots showed evidence of differential composition based on seeding rates in the eleventh year ($t = 2.14$, df $= 13$, $P_{\text{one-tailed}} = .0258$; fig. B1*F*), though not in the eighth year ($t = 0.71$, df $= 13$, $P_{\text{one-tailed}} = .24$; fig. B1*F*). For all other species pairs in the eleventh year, $P_{\text{one-tailed}} > .11$ (fig. B1).

Discussion

Our experimental results generally support the predictions of resource competition theory. For 11 years, we grew six dominant prairie grasses in monocultures, in eight pairwise combinations, and in a single four-species combination across an experimental N gradient with 14 levels. Using R^* values (equilibrial soil nitrate concentration) and I^* values (equilibrial light penetration to soil surface) measured in monocultures across the N gradient (fig. 1*B*, 1*D*), we constructed nullclines (fits of I^* vs. R^*) for each species. We compared the nullclines of species grown in pairwise combinations. In six cases, one species' nullcline fell outside its competitor's nullcline (figs. 2*A*–2*C*, 3*A*–3*C*), and that species was competitively excluded (figs. 2*D*–2*F*, 3*D*–3*F*). In two cases, the nullclines of paired species either crossed (fig. 4*B*) or crossed if extrapolated (fig. 4*A*), and the species pair coexisted (fig. 4*D*, 4*E*). Trade-offs in their abilities to compete for N and light may have caused their coexistence, though the evidence supporting this hypothesis was equivocal. In the case of our four-species combination, two species coexisted, and two species were excluded (fig. 4*F*), consistent with its constituent pairwise outcomes. In only one of our pairwise combinations did initial abundance have any effect on eleventh-year subplot composition, and that effect was minor and diminished with time (fig. B1*F*). Overall, species interactions were stable, largely predictable, and not neutral (fig. 6).

In addition to largely predicting the eventual outcome of competition, interspecific differences in R^* and I^* also predicted the quantitative rate at which that outcome was achieved (i.e., the rate of divergence). In our experiment, the rate of divergence ranged from rapid competitive displacement (e.g., fig. 3*D*) to sustained coexistence (e.g., fig. 4*E*). Resource competition theory suggests that the reason that a species with high R^* and I^* values eventually loses to a species with low R^* and I^* values is that the competitor holds resource concentrations at a point where the losing
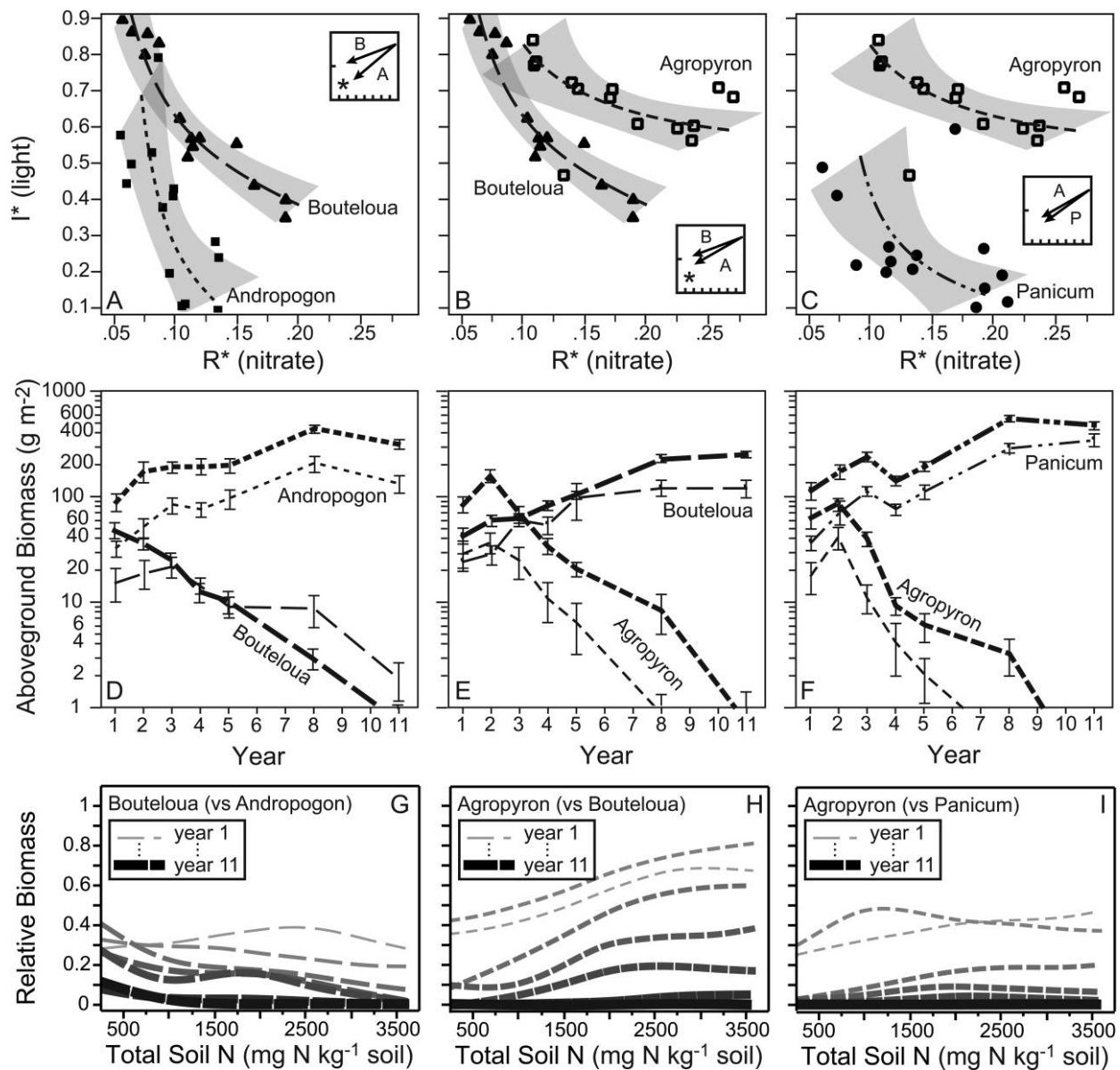
Figure 2: *A–C,* Empirical nullclines derived by relating I^* and R^* via their mutual dependence on total soil nitrogen (N; see fig. 1*B*, 1*D*). Species symbol and line styles follow figure 1. Gray areas show 95% confidence intervals. Insets show mean consumption vector slopes for the species pair scaled to 1 I^* unit for every 4 R^* units (if plotted outside the inset, all consumption vectors appear essentially flat because of the larger plot's scaling). Asterisks indicate significant differences ($P < .05$) in mean consumption vector slope. *D–F,* Aboveground biomass for competing species over time. Thin and thick lines represent the average biomass of the seven lowest and the seven highest experimental N levels, respectively. Bars represent standard errors. *G–I,* Relative biomass across the experimental N gradient of the species in the competition pairing that had lower biomass in the eleventh year of the experiment (moving average with data points omitted for clarity). The thinnest gray line shows the first year's response. Progressively thicker and darker lines show the responses of years 2–5, 8, and 11.

species' losses exceed its gains (Tilman 1982). When the interspecific difference between R^* and I^* values is small, the loser's losses should only slightly exceed its gains, and the rate of divergence between them should be slow. When that difference is great, the loser's losses should vastly ex- ceed its gains, and the rate of divergence between them should be fast. Consistent with these predictions, our re- sults showed that greater interspecific differences in R^* and I^* led to faster rates of divergence (fig. 5). Moreover, the results supported the prediction that N competition
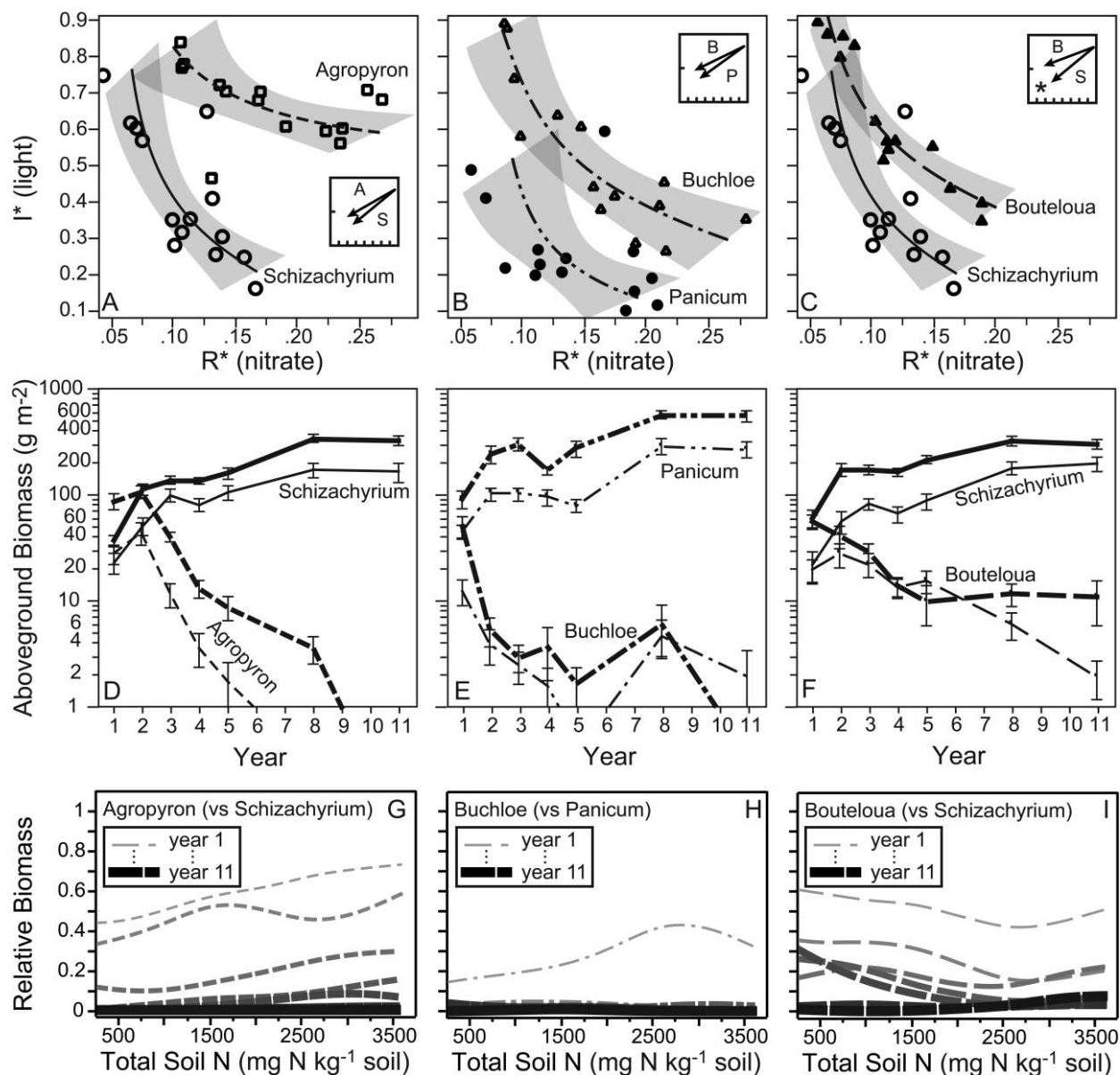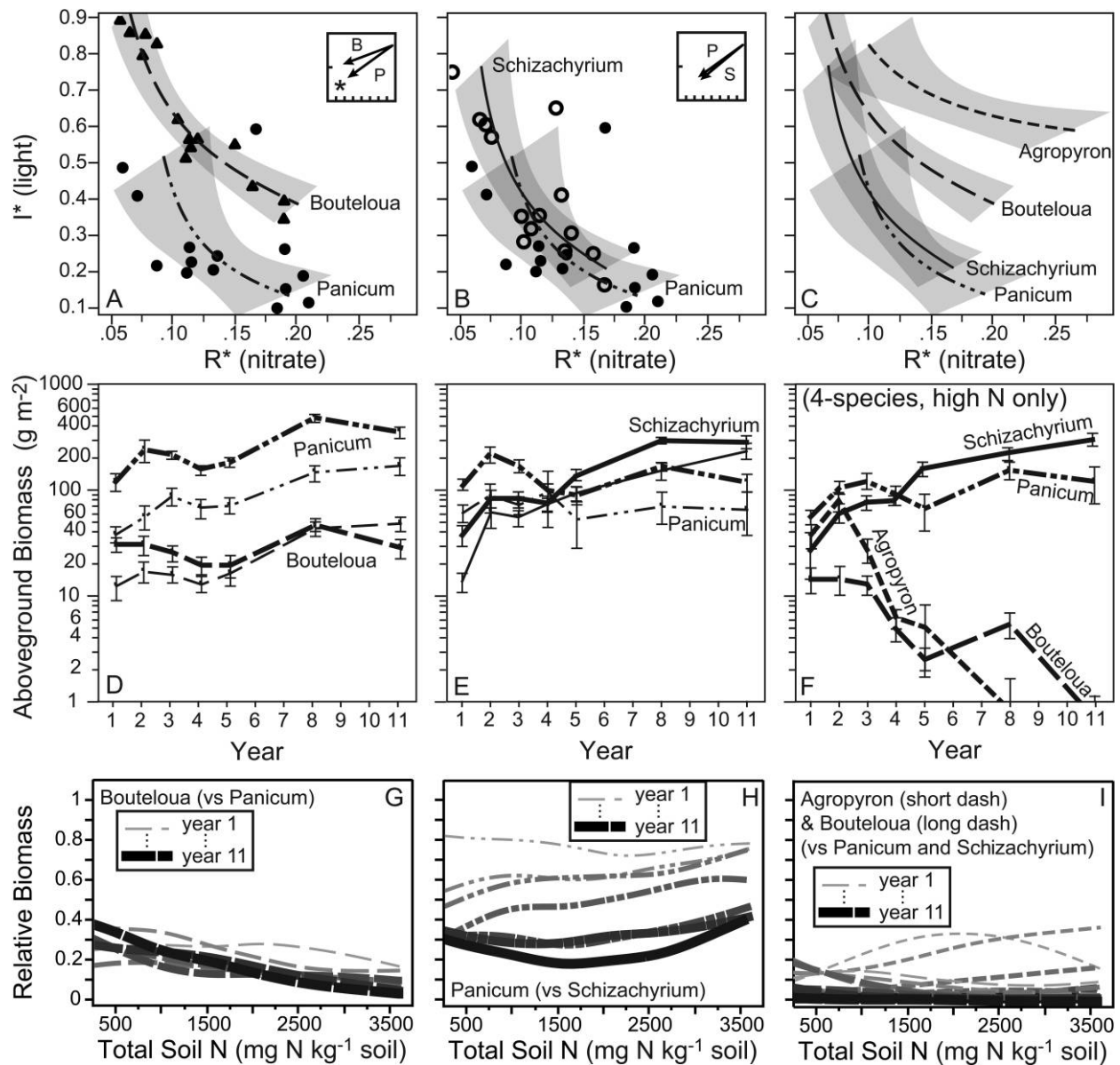
Figure 3: Empirical nullclines and consumption vector slopes (*A–C*), aboveground biomass over time (*D–F*), and relative biomass across the N gradient (*G–I*) for competing species. See figure 2 for details.

should be more pronounced on lower-N soils (steeper slope on lower-N soils; fig. 5*B*) while light competition should be more pronounced on higher-N soils (steeper slope on higher-N soils; fig. 5*C*).

Competition for Soil Resources

There are several possible reasons why R^* values largely predicted the outcomes of competition (figs. 1*B*, 2–4, 5*B*), despite the seeming complexity of soils, plants, N move-ment, diffusion limitation, and species-specific minerali-zation rates (e.g., Wedin and Tilman 1990; Huston and DeAngelis 1994; Grover 1997; Raynaud and Leadley 2004; Craine et al. 2005). First, the spatial nature of soil nutrient uptake (Huston and DeAngelis 1994) may slow the rate of competitive exclusion, but our results show that it did not prevent competitive exclusion. In those areas where two species both forage for soil nutrients, a low-R^* species should increase its biomass at the expense of a high-R^* species. After all, the resource concentrations under the

Figure 4: Empirical nullclines and consumption vector slopes (*A–C*), aboveground biomass over time (*D–F*), and relative biomass across the N gradient (*G–I*) for competing species. See figure 2 for details.

high-R^* species are, by definition, high; the low-R^* species' gains should exceed its losses. The low-R^* species should grow into the area occupied by the high-R^* species and then reduce soil nitrate to a level below that required for the survival of the high-R^* species. Indeed, Wedin and Tilman (1993) reported that species that won in vegetation-vegetation competition (achieved by removing a partition separating the roots of adjacent well-established monocultures) did so without ever producing appreciable aboveground biomass in the losing species' subplot.

Rather, invasion by the winners' roots into the adjacent 0.37 × 0.37-m subplot and subsequent lowered levels of soil nitrate were sufficient to drive losers (the higher-R^* species) extinct (Wedin and Tilman 1993).

The second reason why resource competition theory was predictive even in the face of complexity was that we measured the long-term average R^* for each species by taking the average of 13 measurements collected over a span of 12 years. Thus, while N supply likely varies over time, our measurements represent the long-term average effect of
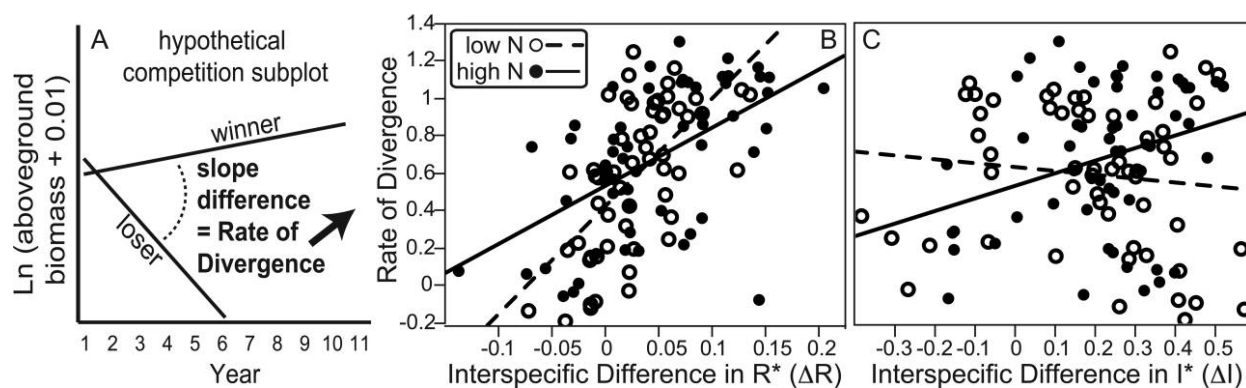
Figure 5: *A*, Rate of divergence for populations in two-species competition subplots (winner's slope − loser's slope at a given nitrogen [N] level, ln [g m^{-2}] year^{-1}) as predicted by interspecific differences in R^* (*B*) and I^* (*C*; loser's R^* or I^* − winner's R^* or I^* at that same N level). Open circles and dashed lines represent relationships on the seven lowest N levels, and closed circles and solid lines represent relationships on the seven highest N levels.

each species on soil nitrate levels and hence on its competitors. The predictive ability of R^* values based on long-term averages does not negate the possibility that nutrient fluctuations can affect species abundances but does demonstrate that, in the long term for our species, such fluctuations neither prevented competitive displacement nor qualitatively changed the outcome of competition from that predicted by an equilibrial theory of resource competition.

Light Competition, Vegetative Height, and Seed Mass

Light appeared to be colimiting in our experiment for three reasons. The nullclines were curved (figs. 2, 3, 4*A*–4*C*) and thus fit the profile of interactive-essential resources (Tilman 1988). The root-to-shoot ratio of four of our six species decreased as total soil N increased (fig. C4 in the online edition of the *American Naturalist*), suggesting that they invested more in light foraging as N became more available. The interspecific I^* differences between competing species predicted their rate of divergence (fig. 5*C*) even after we controlled for the effects of R^*, and those differences were more influential on high-N (low-light) soils.

Because light was colimiting, theory suggests that seed mass and maximum vegetative height should, in combination with R^* and I^*, predict the outcome of competition (Tilman 1988). However, seed mass was not predictive. In only one of our pairwise combinations did the species with significantly heavier seeds win (table 1; fig. 2*D*). Seed mass is expected to influence mainly competition among seedlings, giving an advantage to a seedling that is taller than its neighbors (Black 1958). However, as in native prairies, seedling densities and recruitment from seedlings were low

in these subplots after the first year, and competitive interactions were mainly among established individuals.

Height was more predictive; in five of the six cases of exclusion, the taller species won, consistent with theory (fig. 1*C*; fig. 2*D*, 2*F*; fig. 3*D*–3*F*). However, the rate of divergence between species of similar height was faster than that between species of disparate height, contrary to expectation, because a relatively tall (but sparse, high I^*) species (*Agropyron*) was excluded rapidly in three of the pairings (fig. 1*C*; fig. 2*E*, 2*F*; fig. 3*D*) and because two species of disparate height coexisted (*Panicum* and *Bouteloua*; figs. 1*C*, 4*D*). Thus, in our case of grasses, which generally have photosynthetic tissues from the soil surface to the canopy, I^*, which integrates the effects of height and density, appeared to be a better predictor of the outcome of competition than height alone.

Alternative Explanations

Other traits that were correlated with R^* and I^* corresponded with the outcome of competition. Species that had a lower tissue percentage N tended to win (fig. C5). Species that produced more aboveground (figs. 1*A*, C1) and belowground (fig. C3 in the online edition of the *American Naturalist*) biomass tended to win. Species that invested proportionately more in roots tended to win (fig. C4). However, apart from their expected influence on R^*, seed mass, height, and I^* (Tilman 1990), there is little theoretical reason to expect that these traits should influence the outcome of competition. Indeed, many of the species that had biomass that was equal to or greater than their competitor's biomass early in the experiment ultimately lost (e.g., *Agropyron*; fig. 2*E*). Thus, while the biomass of monocultures in equilibrium may have predicted
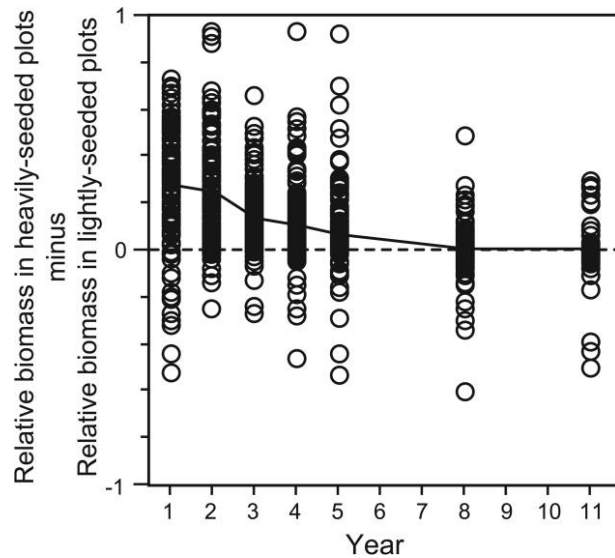
Figure 6: At all 14 nitrogen (N) levels, each two-species pairing was planted twice: once with 70% seed of the first species and 30% seed of the second and once with this ratio reversed. Each point represents the relative aboveground biomass difference between 70% seeding and 30% seeding of a particular species pairing at a particular N level. Lines connect the means. By year 8, each two-species pairing at each N level had approximately the same composition, regardless of initial planting density. Figure B1 in the online edition of the *American Naturalist* contains separate plots for each species pair.

the outcome of competition, biomass by itself was not driving the interaction.

Hubbell (2001) proposed an alternative mechanism for the maintenance of plant species diversity, neutral theory, which assumes that all species are identical such that none enjoys a competitive advantage over any other. In his model, species abundances undergo "random walks" such that, on average, regionally abundant species tend to dominate sites after disturbance. By planting the species in our pairwise combinations at reciprocal densities (70% of species *a* with 30% of species *b* and vice versa), we experimentally made each species in a pair "regionally abundant" in separate subplots. However, the species planted at a higher density in a given subplot had no long-term advantage over the species planted at a lower density (figs. 6, B1). For example, *Bouteloua* always excluded *Agropyron*, even when *Agropyron* was planted at a higher initial density and had greater biomass during the first few years of the experiment (figs. 2E, B1B). With one minor exception (fig. B1F; see "Results"), the other five pairwise interactions that led to exclusion behaved similarly (fig. B1A, B1C–B1E). The two pairs of species that coexisted ultimately equilibrated at the same relative biomass at each N level, irrespective of initial density (fig. B1H, B1I). Thus, the

long-term outcome of competition between our six native prairie grasses was not neutral; if it had been, the data in figures 6 and B1 would have generally tended toward 1 and −1 instead of converging on 0.

Coexistence

Two of our eight pairs of species coexisted: *Bouteloua* coexisted with *Panicum* (fig. 4D), and *Schizachyrium* coexisted with *Panicum* (fig. 4E). In both cases, their coexistence was stable and did not appear to be founder controlled because subplots seeded with different ratios of the competing species converged on common compositions over time. Subplots seeded with a higher density of a given species initially had a higher relative biomass of that species (t-test of 0 mean for the first year of data; *Bouteloua-Panicum*: $t = 6.14$, df $= 13$, $P < .0001$; *Schizachyrium-Panicum*: $t = 2.90$, df $= 12$, $P = .0134$; fig. B1H, B1I), but that difference had disappeared by the eleventh year (*Bouteloua-Panicum*: $t = 0.39$, df $= 13$, $P = .70$; *Schizachyrium-Panicum*: $t = 0.66$, df $= 12$, $P = .52$; fig. B1H, B1I).

By what mechanism or mechanisms did *Bouteloua* or *Schizachyrium* coexist with *Panicum*? Because all three species use the C4 photosynthetic pathway, it is unlikely that differences in phenology explained their coexistence. Differential depth of N uptake may have contributed to the coexistence of *Panicum* and *Bouteloua* (McKane et al. 1990); in a ^{15}N tracer post hoc experiment, *Bouteloua* took up significantly less of its N from 12 cm (39%) than *Panicum* did (49%), as compared to uptake at 2 cm (fig. A1 in the online edition of the *American Naturalist*). This suggests an as yet untested possibility that *Bouteloua* may have had a lower R^* in shallow soil and *Panicum* a lower R^* in deep soil, effectively splitting nitrate into two resources: shallow nitrate and deep nitrate. However, there was no significant difference in the depth of N uptake between *Schizachyrium* and *Panicum* (fig. A1).

These two pairs of species may have coexisted via an N-light trade-off, but the evidence in support of this is equivocal. Stable coexistence via such a trade-off requires that three conditions hold (Tilman 1982). First, each species must be a better competitor for a different limiting resource. This condition appears to have been met; *Bouteloua* and *Schizachyrium* had lower mean R^*s than *Panicum* (fig. 1B), and their nullclines fell below that of *Panicum* along the R^* axis (fig. 4A, 4B). Similarly, *Panicum* had a lower mean I^* than either *Bouteloua* or *Schizachyrium* (fig. 1D), and its nullcline fell below those of *Bouteloua* and *Schizachyrium* along the I^* axis (fig. 4A, 4B). However, the nullclines of *Bouteloua* and *Panicum* crossed only if extrapolated (fig. 4A), suggesting that there was no actual two-species equilibrium point if each species had con-

sumed resources in biculture as they did in monoculture. Moreover, the nullclines of *Schizachyrium* and *Panicum*, while clearly offset from each other, overlapped considerably (fig. 4*B*), raising uncertainty about whether they actually crossed.

The second and third conditions for stable coexistence via an N-light trade-off are that a different resource limits each species at equilibrium and that each species consumes relatively more of the resource that most limits it, thus causing each species to be relatively more limited by changes in conspecific density than by changes in heterospecific density (Tilman 1982). It is unclear whether these conditions were met. On one hand, the ratios of belowground to aboveground biomass of *Bouteloua* and *Schizachyrium* decreased both as total soil N increased (fig. C4*D*, C4*F*) and in response to post hoc experimental shading (fig. A2 in the online edition of the *American Naturalist*), suggesting that light was limiting for them (Poorter and Nagel 2000). *Panicum* exhibited neither response (figs. A2, C4*E*). Thus, *Bouteloua* and *Schizachyrium* (lower R^*) may have been consuming relatively more light, the resource that most limited their growth, while *Panicum* (lower I^* species) may have been consuming relatively more N, the resource that most limited its growth. These observations of belowground and aboveground biomass allocation suggest that the second and third conditions for stable coexistence were met.

However, the slopes of these species' consumption vectors suggest that these conditions may not have been met. First, the shallower slope of the *Bouteloua* (lower R^*) consumption vector indicated that it was consuming relatively more N (fig. 4*A*), the resource that least limited its growth, while the steeper slope of the *Panicum* (lower I^*) consumption vector indicated that it was consuming relatively more light (fig. 4*A*), the resource that least limited its growth. These conditions are expected to lead to founder control, which we did not observe (fig. B1*H*). Second, the slopes of the *Schizachyrium* and *Panicum* consumption vectors were statistically indistinguishable, indicating that each species consumed the same relative amount of N and light. This condition is expected to lead to the competitive exclusion of one or the other species, depending on the ratio of N to light in a given plot, which we did not observe (fig. 4*E*).

Why did their allocations to belowground and aboveground biomass suggest that these pairs of species should stably coexist via an N-light trade-off while their consumption vector slopes suggested the opposite? One possibility is that the consumption vector slopes are correct, that the way these species allocated was coincidental, and that these two pairs of species stably coexisted via other mechanisms. Another possibility is that these two pairs of species did in fact stably coexist via an N-light trade-off,

that the way these species allocated to belowground and aboveground biomass explained their stable coexistence, and that the consumption vectors are misleading.

We do not know which of these is correct, but note that, to date, theoreticians have made the simplifying assumption that plant species have fixed ratios of belowground to aboveground biomass that they are unable to dynamically shift in response to resource limitations (Tilman 1988; Reynolds and Pacala 1993; Rees and Bergelson 1997). Because this assumption is clearly false (Poorter and Nagel 2000), it would be interesting to relax it and determine its effect on coexistence. We suggest that nullclines and consumption vectors derived from monocultures (where individuals allocate in response to conspecifics only) may not completely characterize the resource consumption traits of species in competition (where individuals allocate in response to both conspecifics and heterospecifics). In particular, if a better soil resource competitor allocates more to aboveground structures in response to shading by its competitor (as suggested by our post hoc shading experiment; fig. A2) and if a better light competitor allocates more to belowground structures in response to nutrient depletion by its competitor, then the slopes of their consumption vectors might shift so as to stabilize the two-species equilibrium point.

As a final consideration on the subject of coexistence, we note that a compositional change between *Bouteloua* and *Panicum* across the N gradient was also consistent with coexistence via an N-light trade-off. The relative biomass of *Bouteloua* in *Bouteloua-Panicum* subplots decreased from 0.375 to 0.125 across the N : light gradient (for data of the eleventh year: $R^2 = 0.17$, $F = 2.39$, df $= 1, 27$, $P = .024$; also, see fig. 4*G*). This accords with theory (Tilman 1988), which predicts that the better N competitor (*Bouteloua*) should decrease in relative biomass at the expense of the better light competitor (*Panicum*) as soil N becomes more abundant. However, the relative biomass of *Schizachyrium* in *Schizachyrium-Panicum* subplots was uncorrelated with the N gradient in the eleventh year of the experiment ($R^2 = 0.01$, $F = 0.48$, df $= 1, 25$, $P = .63$; see fig. 4*H*), which is not consistent with coexistence via an N-light trade-off.

Implications for Species Diversity

If species with low R^*s and low I^*s so clearly dominated in our experiment and there were so few trade-offs between low R^*s and low I^*s, then why do nearby natural communities contain between 15 and 30 species m^{-2} and between 100 and 200 species ha^{-1}? Two important differences exist between our experiment and natural communities. First, subplots were seeded at a very high rate, watered, protected from mammalian herbivory and dis-

turbance, and fertilized with nutrients other than N. Natural recruitment is unlikely to be so high nor the conditions for successful germination and seedling survival so ideal. Thus, inferior competitors in our experiment faced higher densities of competitors than they would face in natural communities, perhaps preventing coexistence as "fugitive" species (Horn and MacArthur 1972). Three biodiversity experiments were created at CCNHA using methods and seeding rates that were comparable to those used in this experiment (see Tilman et al. 1996, 2001; Reich et al. 2004), and little competitive exclusion has occurred in them after more than 12 years. However, actual germination success in these biodiversity experiments was much lower than germination success in our experiment (D. Tilman, personal observation), consistent with the idea that high establishment rates favor competitive exclusion while low establishment rates favor coexistence (Hurtt and Pacala 1995).

Second, although all six species used in our experiment survived well in monocultures and occur in our region, only *Andropogon* and *Schizachyrium* are regionally common. Interestingly, they had the two lowest R^*s (fig. 1*B*) and the second and third lowest I^*s (fig. 1*D*) measured in our experiment. As a result, they were competitively dominant, and of the four regionally rare species, only *Panicum* coexisted with them. All others were displaced.

There is reason to believe that many of our key findings may generalize to other systems. In a study that also predicted competitive outcomes using monoculture nutrient and light concentrations, Passarge et al. (2006) found that phytoplankton species exhibited no trade-offs in their ability to compete for phosphorus and light. In other words, none of their species' nullclines crossed, a result that was mirrored by at least six of our eight species pairs (figs. 2*A*–2*C*, 3*A*–3*C*). As a result, none of their species pairs coexisted, and Passarge et al. (2006) suggest that other mechanisms must be operating to maintain phytoplankton diversity.

Summary

Plant species resource use traits in monoculture (R^* and I^*) predicted the rate of divergence between pairs of species (fig. 5) and the identity of the winner in our six cases of competitive exclusion (figs. 2, 3). The predictive power of I^* in this experiment relative to seed size and height was likely a special case for light competition between species of similar life history, seed size, and maximum height that competed mainly as adults. Initial abundance had no effect on the outcome of competition, and there was only one detectable shift in dominance along our experimental N gradient (fig. 4*G*). In total, these results suggest that, consistent with the predictions of resource competition theory, the resource requirements of individual species determine the long-term outcomes of interspecific interactions. However, only two of our eight competition pairings resulted in coexistence, and it was unclear whether their coexistence was because of an N-light trade-off. Thus, while competition for multiple resources might maintain some diversity in natural communities, other mechanisms are almost certainly operating to maintain the remainder.

Literature Cited

Armstrong, R. A., and R. McGehee. 1980. Competitive exclusion. American Naturalist 115:151–169.

Black, J. N. 1958. Competition between plants of different initial seed sizes in swards of subterranean clover (*Trifolium subterraneum* L.) with particular reference to leaf area and the light microclimate. Australian Journal of Agricultural Research 9:299–318.

———. 1960. An assessment of the role of planting density in comparison between red clover (*Trifolium pratense* L.) and lucerne (*Medicago sativa* L.) in the early vegetative stage. Oikos 11:26–42.

Casper, B. B., and R. B. Jackson. 1997. Plant competition underground. Annual Review of Ecology and Systematics 28:545–570.

Craine, J. M., J. Fargione, and S. Sugita. 2005. Supply pre-emption, not concentration reduction, is the mechanism of competition for nutrients. New Phytologist 166:933–940.

Fowler, N. 1986. The role of competition in plant communities in arid and semiarid environments. Annual Review of Ecology and Systematics 17:89–110.

Fuller, W. 1987. Measurement error models. Wiley, New York.

Gleason, H. A., and A. Cronquist. 1963. Manual of vascular plants of northeastern United States and adjacent Canada. Van Nostrand, New York.

Grover, J. P. 1991. Resource competition among microalgae in variable environments: experimental tests of alternative models. Oikos 62:231–243.

———. 1997. Resource competition: population and community biology series. Chapman & Hall, London.

Hansen, S. R., and S. P. Hubbell. 1980. Single-nutrient microbial competition: qualitative agreement between experimental and theoretically forecast outcomes. Science 207:1491–1493.

Horn, H. S., and R. H. MacArthur. 1972. Competition among fugitive species in a harlequin environment. Ecology 53:749–752.

Hubbell, S. P. 2001. The unified neutral theory of biodiversity and biogeography. Princeton University Press, Princeton, NJ.

Huisman, J., and F. J. Weissing. 1994. Light-limited growth and competition for light in well-mixed aquatic environments: an elementary model. Ecology 75:507–520.

———. 1995. Competition for nutrients and light in a mixed water column: a theoretical analysis. American Naturalist 146:536–564.

———. 1999. Biodiversity of plankton by species oscillation and chaos. Nature 402:407–410.

Huisman, J., R. R. Jonker, C. Zonneveld, and F. J. Weissing. 1999. Competition for light between phytoplankton species: experimental tests of mechanistic theory. Ecology 80:211–222.

Hurtt, G. C., and S. W. Pacala. 1995. The consequences of recruitment limitation: reconciling chance, history and competitive differences between plants. Journal of Theoretical Biology 176:1–12.

Huston, M. A., and D. L. DeAngelis. 1994. Competition and coexistence: the effects of resource transport and supply rates. American Naturalist 144:954–977.

Inouye, R. S., N. J. Huntley, D. Tilman, J. Tester, M. Stillwell, and K. Zinnel. 1987. Old-field succession on a Minnesota sand plain. Ecology 68:12–26.

Kilham, S. S. 1986. Dynamics of Lake Michigan natural phytoplankton communities in continuous cultures along a Si : P loading gradient. Canadian Journal of Fisheries and Aquatic Sciences 43: 351–360.

Kirkham, F. W., J. O. Mountford, and R. J. Wilkins. 1996. The effects of nitrogen, potassium and phosphorus addition on the vegetation of a Somerset peat moor under cutting management. Journal of Applied Ecology 33:1013–1029.

MacArthur, R. H. 1972. Geographical ecology. Harper & Row, New York.

Maguire, B. 1973. Niche response structure and the analytical potentials of its relationship to the habitat. American Naturalist 107: 213–246.

McKane, R. B., D. F. Grigal, and M. P. Russelle. 1990. Spatiotemporal differences in ^{15}N uptake and the organization of an old-field plant community. Ecology 71:1126–1132.

Miller, T. E., J. H. Burns, P. Munguia, E. L. Walters, M. M. Kneitel, P. M. Richards, N. Mouquet, and H. L. Buckley. 2005. A critical review of twenty years' use of the resource-ratio theory. American Naturalist 165:439–448.

Parton, W. J., C. V. Cole, J. W. B. Stewart, D. S. Ojima, and D. S. Schimel. 1989. Simulating regional patterns of soil C, N, and P dynamics in the U.S. central grasslands region. Pages 99–108 *in* M. Clarholm and L. Bergstrom, eds. Ecology of arable land. Kluwer, Dordrecht.

Passarge, J., S. Hol, M. Escher, and J. Huisman. 2006. Competition for nutrients and light: stable coexistence, alternative stable states, or competitive exclusion? Ecological Monographs 76:57–72.

Perry, L. G., C. Neuhauser, and S. M. Galatowitsch. 2003. Founder control and coexistence in a simple model of asymmetric competition for light. Journal of Theoretical Biology 222:425–436.

Poorter, H., and O. Nagel. 2000. The role of biomass allocation in the growth response of plants to different levels of light, CO_2, nutrients and water: a quantitative review. Australian Journal of Plant Physiology 27:595–607.

Raynaud, X., and P. W. Leadley. 2004. Soil characteristics play a key role in modeling nutrient competition in plant communities. Ecology 85:2200–2214.

Rees, M., and J. Bergelson. 1997. Asymmetric light competition and founder control in plant communities. Journal of Theoretical Biology 184:353–358.

Reich, P. B., D. Tilman, S. Naeem, D. S. Ellsworth, J. Knops, J. Craine, D. Wedin, and J. Trost. 2004. Species and functional group diversity independently influence biomass accumulation and its response

to CO_2 and N. Proceedings of the National Academy of Sciences of the USA 101:10101–10106.

Reynolds, H. L., and S. W. Pacala. 1993. An analytical treatment of root-shoot ratio and plant competition for soil nutrient and light. American Naturalist 141:51–70.

Rothhaupt, K. O. 1988. Mechanistic resource competition theory applied to laboratory experiments with zooplankton. Nature 333: 660–662.

———. 1996. Laboratory experiments with a mixotrophic chrysophyte and obligately phagotrophic and phototrophic competitors. Ecology 77:716–724.

Smith, H. V. 1993. Applicability of resource-ratio theory to microbial ecology. Limnology and Oceanography 38:239–249.

Sommer, U. 1986. Nitrate and silicate competition among Antarctic phytoplankton. Marine Biology 91:345–351.

———. 1989. Nutrient status and nutrient competition of phytoplankton in a shallow, hypertrophic lake. Limnology and Oceanography 34:1162–1173.

Taylor, P., and P. Williams. 1975. Theoretical studies on the coexistence of competing species under continuous flow conditions. Canadian Journal of Microbiology 21:90–98.

Thompson, K. 1987. The resource ratio hypothesis and the meaning of competition. Functional Ecology 1:297–303.

Tilman, D. 1976. Ecological competition between algae: experimental confirmation of a resource-based competition theory. Science 192: 463–466.

———. 1977. Resource competition between planktonic algae: an experimental and theoretical approach. Ecology 58:338–348.

———. 1981. Tests of resource competition theory using four species of Lake Michigan algae. Ecology 62:802–825.

———. 1982. Resource competition and community structure. Princeton University Press, Princeton, NJ.

———. 1983. Plant succession and gopher disturbance along an experimental gradient. Oecologia (Berlin) 60:285–292.

———. 1984. Plant dominance along an experimental nutrient gradient. Ecology 65:1445–1453.

———. 1988. Plant strategies and the dynamics and structure of plant communities. Princeton University Press, Princeton, NJ.

———. 1990. Mechanisms of plant competition for nutrients: the elements of a predictive theory of competition. Pages 117–141 *in* J. B. Grace and D. Tilman, eds. Perspectives on plant competition. Academic Press, San Diego, CA.

Tilman, D., and D. Wedin. 1991. Dynamics of nitrogen competition between successional grasses. Ecology 72:1038–1049.

Tilman, D., D. Wedin, and J. Knops. 1996. Productivity and sustainability influenced by biodiversity in grassland ecosystems. Nature 379:718–720.

Tilman, D., P. B. Reich, J. Knops, D. Wedin, T. Mielke, and C. Lehman. 2001. Diversity and productivity in a long-term grassland experiment. Science 294:843–845.

Wedin, D., and D. Tilman. 1993. Competition among grasses along a nitrogen gradient: initial conditions and mechanisms of competition. Ecological Monographs 63:199–229.

Wedin, D. A., and D. Tilman. 1990. Species effects on nitrogen cycling: a test with perennial grasses. Oecologia (Berlin) 84:433–441.

Weiner, J. 1990. Asymmetric competition in plant populations. Trends in Ecology & Evolution 5:360–364.