

# Why does fertilization reduce plant species diversity? Testing three competition-based hypotheses

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## Summary

**1** Plant species diversity drops when fertilizer is added or productivity increases. To explain this, the total competition hypothesis predicts that competition above ground and below ground both become more important, leading to more competitive exclusion, whereas the light competition hypothesis predicts that a shift from below-ground to above-ground competition has a similar effect. The density hypothesis predicts that more above-ground competition leads to mortality of small individuals of all species, and thus a random loss of species from plots.

**2** Fertilizer was added to old field plots to manipulate both below-ground and above-ground resources, while shade cloth was used to manipulate above-ground resources alone in tests of these hypotheses.

**3** Fertilizer decreased both ramet density and species diversity, and the effect remained significant when density was added as a covariate. Density effects explained only a small part of the drop in diversity with fertilizer.

**4** Shade cloth and fertilizer reduced light by the same amount, but only fertilizer reduced diversity. Light alone did not control diversity, as the light competition hypothesis would have predicted, but the combination of above-ground and below-ground competition caused competitive exclusion, consistent with the total competition hypothesis.

*Key-words:* density–diversity curves, productivity–diversity relationships, root and shoot competition intensity

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## Introduction

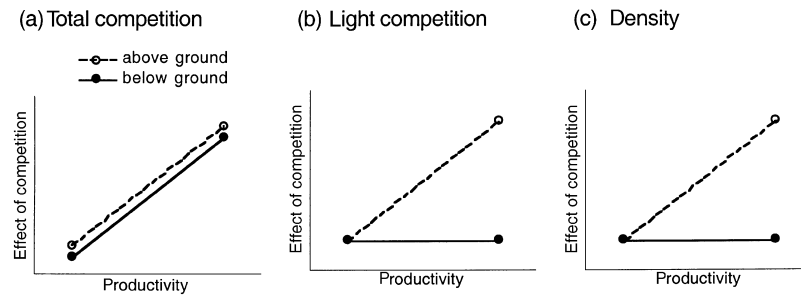
Plant community ecologists have shown much interest in the relationship between productivity and diversity. Diversity usually drops when fertilizer is added to a plant community (DiTommaso & Aarssen 1989; Gough *et al.* 2000), and along natural gradients of increasing productivity, diversity decreases or shows a unimodal pattern, increasing then falling (Waide *et al.* 1999; Gross *et al.* 2000). These patterns emerge whether diversity is expressed as species richness or as a diversity index. Although many processes can potentially explain these patterns (Rosenzweig *et al.* 1993), most research in plants has focused on competition (Abrams 1995; Rajaniemi 2001).

Competition seems likely to contribute to the productivity–diversity relationship because productivity interacts with resource levels. Increased soil resources

lead to increased productivity, but as plants grow larger, shading reduces light availability. Competition for both resources therefore changes with productivity.

There are three mechanisms by which competition may cause diversity to drop as soil resource availability increases (Fig. 1). Under each mechanism, it is changing availability of resources, not productivity itself, that drives the diversity patterns seen along productivity gradients. Competition may become more important both above ground and below ground, leading to mortality that reduces evenness and diversity as well as competitive exclusion that reduces species richness (total competition, Fig. 1a; Grime 1973). Alternatively, competition may shift from mainly below ground when soil resources are scarce to mainly above ground when soil resources are abundant but shading is intense (light competition, Fig. 1b; Newman 1973). This hypothesis predicts that shoot competition causes more mortality and competitive exclusion than does root competition, perhaps because the tallest species can pre-empt light. Finally, increased competition for light may cause community-level thinning: small,

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**Fig. 1** Three hypotheses for the effects of above-ground and below-ground competition on diversity: (a) total competition, (b) light competition, (c) density.

**Table 1** Expected effects of experimental treatments. Fertilizer was added at the rate of 15 g N m<sup>-2</sup> year<sup>-1</sup>; shadecloth blocked 50% of sunlight

	Control	Fertilizer	Shadecloth
Resource availability			
Mineral resources	Low	High	Low
Light at soil surface	High	Low	Low
Competition effects			
Below-ground (total competition)	Low	High	Low
Below-ground (light competition)	High	Low	High
Above-ground	Low	High	High
Expected diversity			
Total competition hypothesis	High	Low	High
Light competition hypothesis	High	Low	Low

shaded individuals of all species die, density drops and species are lost from plots randomly (density hypothesis, Fig. 1c; Goldberg & Miller 1990; Oksanen 1996; Stevens & Carson 1999). The density and competition hypotheses are not mutually exclusive: competitive exclusion and random species loss may occur simultaneously.

The total competition and light competition hypotheses have been evaluated by measuring the effects of root and shoot competition on individual plants along fertilization gradients (reviewed in Twolan-Strutt & Keddy 1996). Experiments on individual plants, however, cannot predict patterns of diversity. Competition intensity may increase with fertilization, but if competition reduces the fitness of all species by the same proportion, neither richness nor evenness of the community will change (except through random species loss under the density hypothesis). That is, all the species will still be present at the same relative abundance, but with reduced absolute abundance. Increased competition intensity will only reduce diversity if some species are affected more strongly than others.

Few studies manipulate competition directly to determine its effects on species richness or diversity (but see Goldberg & Estabrook 1998; Rajaniemi & Goldberg 2000; Zamfir & Goldberg 2000; studies reviewed in Gurevitch & Unnasch 1989) and none of these have manipulated root and shoot competition separately. Competition may be manipulated indirectly, however, by manipulating resources, and two studies have used this approach to measure the

community-level effects of root and shoot competition. In both dune grasslands (Gibson 1988) and an old field (Carson & Pickett 1990), adding nutrients had no effect on species richness, but increasing light by tying back surrounding vegetation increased richness, supporting the light competition hypothesis.

The density hypothesis has been tested in only three studies, and their results conflict. Rapson *et al.* (1997) reasoned that if density effects cause species to be lost from plots at random, larger plots should lose fewer species, but they found that increasing plot size did not eliminate species richness patterns along a natural productivity gradient. In a first-year old field, density did partially predict species richness, but density was unrelated to light availability, calling into question the mechanism proposed for the density hypothesis (Goldberg & Miller 1990). In the most direct test, on the other hand, changes in stem density completely accounted for the changes in species richness along a fertilization gradient in a first-year old field (Stevens & Carson 1999).

I performed a community-level experiment in an old field to test contrasting predictions of the total competition, light competition and density hypotheses (Table 1). Fertilizer should increase soil resource availability and reduce light availability due to increased plant biomass and shading, whereas shadecloth increases light limitation without changing below-ground resources. The total competition hypothesis predicts that fertilizer should reduce species richness

and diversity more than shade cloth, because competition for both above-ground and below-ground resources reduces diversity, while the light competition hypothesis predicts that fertilizer and shade cloth should have the same effect on species richness and diversity, as long as light levels are similar in the two treatments (Table 1). The density hypothesis predicts that any changes in species richness with either fertilizer or shade should be explained by changes in plant density.

## Methods

### EXPERIMENTAL TREATMENTS

This experiment was conducted in an old field at the University of Michigan Matthaei Botanical Gardens in Ann Arbor, Michigan, USA (83°40' W, 42°17' N). The field was removed from agricultural use about 40 years ago and has been mowed annually to reduce encroachment of shrubs. Mowing was suspended during the experiment. The field is dominated by perennial clonal grasses and herbs, including *Poa compressa*, *Hieracium caespitosum* and *Bromus inermis* (nomenclature follows Voss 1972, 1985, 1996).

Ten 1.5 × 2.5 m plots were established in each of five blocks on 12 June 1997. Treatments were applied to the entire plot and vegetation was monitored in two evenly spaced 0.5 × 0.5 m quadrats within each plot for two growing seasons.

One of four soil resource treatments was applied to each plot: control (no resource manipulation), fertilized or watered (two levels). In the fertilized treatment 13-13-13 N-P-K pelletized fertilizer was hand-broadcast onto plots three times each year (19 June, 17 July and 20 August 1997 and 11 June, 19 July and 5 August 1998) for a total of 15 g N, 6.6 g P and 12.45 g K m<sup>-2</sup> year<sup>-1</sup>. Fertilizer was applied during heavy rain to avoid the need for watering. Watering treatments were included because productivity may have been water-limited rather than nutrient-limited. Plots were watered to field capacity after every 3 days without rain or after 6 days without rain. A third watering treatment, watered after 9 days without rain, was planned, but these plots never required watering in the first year. They were treated as controls in the second year and were included as a second set of control plots in analyses. Watering and fertilizer treatments were not crossed.

A shade treatment was crossed with the soil resource treatments. A sheet of black polypropylene shade cloth was attached to bamboo stakes at the corners of the plot and suspended about 1 m above the ground. Shade cloth blocked 50% of incident light and extended 0.5 m beyond the south side of each plot to reduce sunlight entering the plot at an angle.

### VEGETATION AND RESOURCE MONITORING

Soil samples were collected from all plots on 26 August 1997, 6 days after fertilizer was applied. In each plot,

three soil cores (2.5 cm diameter × 10 cm deep) were collected and pooled to test for available nitrogen. An additional three cores per plot were removed, bagged in sterile polyethylene sample bags (Fisher Scientific, Pittsburgh, Pennsylvania, USA) and replaced in the ground until 1 October 1997 before pooling to measure nitrogen mineralization. Available nitrogen was extracted with 2 M KCl and the resulting solution was analysed for nitrate-N and ammonia-N content. Nitrogen mineralization rate was calculated as  $(N_{\text{bagged}} - N_{\text{initial}})/\text{days}$ .

Light profiles were measured on 19 September 1997 with a Decagon Sunfleck Ceptometer (Decagon, Pullman, Washington, USA). The ceptometer integrates photosynthetically active radiation (PAR) at 1-cm intervals along a 40-cm wand. The wand was placed north-south across each plot and PAR was recorded at 10, 20, 30, 40 and 50 cm above the soil surface, and above all vegetation and shade cloth (to measure full sunlight). Percentage of total available PAR was calculated for each height.

Relative soil moisture was measured in all plots in the second year of the experiment, on 15 August and 17 August 1998. All water-treatment plots had been watered on 14 August, following a rainfall on 8 August. Soil moisture was measured with a Time Domain Reflectometer (1502B Metallic TDR, Tektronix, Beaverton, Oregon, USA). Because values were only used to compare treatment effects, they were not calibrated and converted to percentage soil moisture.

At the end of each growing season, one of the 0.25 m<sup>2</sup> quadrats was harvested from each plot. Quadrats were harvested during 19 September to 12 October 1997 and 24 August to 4 September 1998. At each harvest, live plants were sorted by species, number of ramets per species was recorded, and plants and litter were dried at 65 °C for 48 h and weighed. The three most abundant species (*Poa compressa*, *Bromus inermis* and *Hieracium caespitosum*) were so numerous that counting all of their ramets was impractical. For those species, I counted ramets in two 0.16 × 0.20 m subplots within the quadrat, and estimated total quadrat density from density in the subplots. When shrubs grew in the harvested quadrats, their entire biomass was measured in 1997; in 1998, however, only their leaves and new branches were weighed, so that the measured biomass reflected the current year's production, as it did for the herbaceous plants.

From the harvest data, I calculated total quadrat ramet density, standing crop biomass, litter biomass, species richness and Simpson's diversity index ( $1/D = 1/\sum p_i^2$ , where  $p_i$  is the proportion of ramets represented by species  $i$ ). Diversity was based on proportional numbers of ramets to allow comparison with simulated values in tests of the density hypothesis (see below). Diversity based on proportional biomass gave qualitatively similar results in 1997 and qualitatively and quantitatively similar results in 1998 (data not shown).

**Table 2** *P*-values from GLM of effects of treatments on plant resources: soil available nitrogen and nitrogen mineralization rate in 1997 ( $n = 40$ ; sample size is smaller than for other data because soil was sampled from only one of two untreated plots in each block), and soil moisture 1 and 3 days after all water-treatment plots were watered in 1998 ( $n = 50$ ). Factors include block, fertilization (0 or 15 g N m<sup>-2</sup> year<sup>-1</sup>), shade (none or 50% shade cloth) and water (none, added every 3 days without rain, or added every 6 days without rain). No fertilizer  $\times$  water interactions are possible because these treatments were not crossed

Source	d.f.	<i>P</i>		d.f.	<i>P</i>	
		Available nitrogen	Nitrogen mineralization		Soil moisture (day 1)	Soil moisture (day 3)
Block	4	0.509	0.872	4	0.693	0.126
Fertilizer	1	< 0.001	0.097	1	0.075	0.094
Water	2	0.794	0.965	2	< 0.001	0.559
Shade	1	0.017	0.144	1	0.094	0.732
Fertilizer $\times$ shade	1	0.053	0.169	1	0.506	0.653
Water $\times$ shade	2	0.781	0.776	2	0.843	0.549
Error	28			38		

#### ANALYSES

All analyses were conducted with the General Linear Modelling (GLM) function in SYSTAT 7.0 (Wilkinson 1997). Most analyses included block, fertilizer treatment (0 or 15 g N), water treatment (every 3 days, every 6 days, or not added), and shade (0 or 50%) as categorical factors. The interaction terms fertilizer  $\times$  shade and water  $\times$  shade were also tested; no other interactions could be tested because the design was not a complete factorial. Data from harvests in different years were analysed separately.

The response variables tested with this GLM model included measures of soil resources (available nitrogen and nitrogen mineralization rate in 1997; soil moisture in 1998) and vegetation characteristics (ramet density, standing crop biomass, litter biomass, species richness and Simpson's diversity index, all measured and analysed for both years). Standing crop biomass in 1998 was natural-log transformed for homogeneity of variance (untransformed data gave similar *P*-values); all other variables met the assumptions for parametric tests without transformation. Light profiles were examined with a repeated-measures GLM, with all four factors and two interaction terms, and light levels at the different heights above the soil surface as the repeated measure.

To test the density hypothesis, the GLMs for species richness and diversity were repeated with ramet density as a covariate. If reduced diversity in treated plots results entirely from random thinning, treatment effects should become non-significant when density is included in the analysis. Comparing the adjusted least squares means from this analysis gives the effect of treatments on richness or diversity that cannot be explained by random thinning, that is, the effect above and beyond the effect of reduced diversity. Density effects were also explored using computer programs to simulate random thinning from high-density plots (using methods described by Goldberg & Estabrook 1998; Stevens & Carson 1999). These methods gave

qualitatively and quantitatively similar results to the covariate analysis and will not be discussed here.

#### Results

Water did not appear to be limiting during the experiment. Although watering increased soil moisture on the day after watering (Table 2), water and the water by shade interaction had no effects on soil moisture after 3 days (Table 2), or on any other measured resource or vegetation parameter (Tables 2–4). In addition, soil moisture was not significantly affected by any of the other treatments (Table 2). Block effects were also unimportant, with significant effects in only one of the many analyses conducted (Tables 2–4). I therefore focused on nutrient and shading effects on resources and on vegetation and diversity.

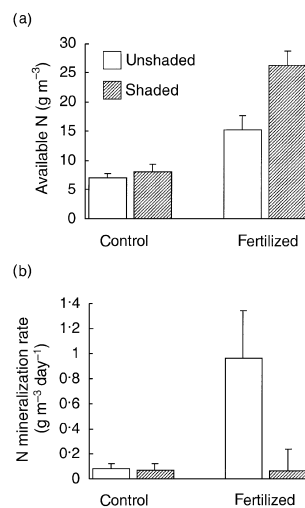
As expected, fertilizer increased available nitrogen; this increase appeared to be more dramatic under shade (Fig. 2a; nearly significant fertilizer by shade

**Table 3** *P*-values from GLM repeated-measures analysis of percentage of full sunlight penetrating the vegetation in 1997 ( $n = 50$ ). Factors as in Table 2; height above the soil surface (10, 20, 30, 40 or 50 cm) is the repeated factor

Source	d.f.	<i>P</i>
Block	4	0.194
Fertilizer	1	< 0.001
Water	2	0.544
Shade	1	< 0.001
Fertilizer $\times$ shade	1	0.013
Water $\times$ shade	2	0.892
Error (between heights)	37	
Height	7	< 0.001
Height $\times$ block	16	0.572
Height $\times$ fertilizer	4	0.314
Height $\times$ water	8	0.147
Height $\times$ shade	4	< 0.001
Height $\times$ fertilizer $\times$ shade	4	0.017
Height $\times$ water $\times$ shade	8	0.583
Error (within heights)	148	

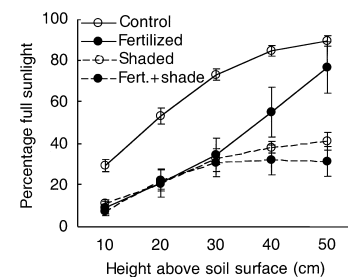
**Table 4** *P*-values from GLM of effects of treatments on vegetation characteristics (*n* = 50). Standing crop biomass was ln-transformed in 1998, untransformed in 1997

Source	d.f.	<i>P</i>				
		Standing crop	Litter mass	Density	Species richness	Species diversity
1997 harvest						
Block	4	0.021	0.803	0.845	0.156	0.350
Fertilizer	1	0.011	0.879	0.075	0.001	< 0.001
Water	2	0.489	0.342	0.565	0.324	0.137
Shade	1	0.064	0.022	0.494	0.702	0.562
Fertilizer × shade	1	0.058	0.729	0.853	0.196	0.516
Water × shade	2	0.790	0.426	0.975	0.207	0.178
Error	38					
1998 harvest						
Block	4	0.135	0.569	0.752	0.683	0.100
Fertilizer	1	0.033	0.031	< 0.001	< 0.001	< 0.001
Water	2	0.962	0.584	0.560	0.344	0.840
Shade	1	0.173	0.003	0.515	0.429	0.598
Fertilizer × shade	1	0.161	0.247	0.159	0.476	0.767
Water × shade	2	0.250	0.999	0.156	0.749	0.319
Error	38					



**Fig. 2** Effects of fertilizer and shade on (a) available nitrogen ( $\text{NO}_3\text{-N}$  and  $\text{NH}_4\text{-N}$ ) and (b) nitrogen mineralization rate over 2 weeks in September 1997. Error bars are one standard error. GLM results are shown in Table 2.

interaction, Table 2). Although nitrogen mineralization tended to be highest in unfertilized, shaded plots (Fig. 2b), neither fertilizer, shade, nor their interaction had a significant effect (Table 2). Also as planned, fertilizer and shade reduced light near the soil surface (at 10 cm) to similar levels (Fig. 3). Shade produced a light profile that was consistently lower than the control (Fig. 3; significant height by shade interaction, Table 3). The effect of fertilizer on light depended on the presence of shade: fertilized plots had similar light levels to shaded plots up to 30 cm above the soil surface, but above this height were more similar to control plots (Fig. 3; significant height by fertilizer by shade interaction, Table 3). Because the vegetation was



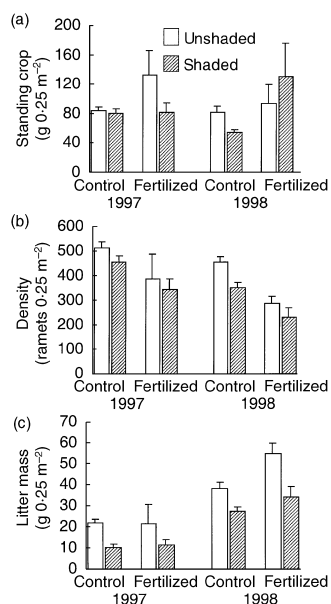
**Fig. 3** Light profiles in 1997, showing variation in percentage of photosynthetically active radiation above the vegetation that penetrates the vegetation to the indicated height. Error bars are one standard error. GLM results are shown in Table 3.

fairly short, most light measurements above 30 cm were also above the bulk of the vegetation.

Effects of the treatments on vegetation were mostly similar in the two years, although the trends were generally stronger and more significant in 1998. The fertilizer by shade interaction was not significant for any vegetation response (Table 4) and will not be mentioned further.

As expected, standing crop increased with fertilizer (Fig. 4a, Table 4), as did litter mass in 1998 (Fig. 4b, Table 4). Shade had no effect on standing crop (Fig. 4a, Table 4), as expected if nitrogen is the limiting resource, but shade significantly reduced litter mass in both years (Fig. 4b, Table 4). As predicted by the density hypothesis, ramet density decreased with fertilizer (significant only in 1998); shade had no significant effect on density, although density was consistently lower in shaded plots (Fig. 4c, Table 4). In both years, species richness and diversity decreased with fertilizer but shade had no effect (Fig. 5, Table 4).

Although fertilizer reduced density in 1998 by about a third (Fig. 4b) and species richness and density were



**Fig. 4** Response vegetation variables to treatments. GLM results are shown in Table 4.

linearly related (slope = 0.011,  $R^2 = 0.269$ ,  $P < 0.001$ ), total plot density did not fully account for diversity patterns. When density was included as a covariate in GLMs (Table 5), its effect was never significant, while fertilizer continued to cause reduced richness and diversity, and shade to have no effect. Changes in density accounted for only a small part of the observed changes in richness and diversity. In 1998, species richness (adjusted for density) decreased by 3.74 species following fertilization (Fig. 5), compared with 4.40 species when unadjusted, suggesting that random thinning alone may have decreased richness in fertilized plots by an average of 0.66 species. Adjustment reduced the effect of fertilizer on Simpson's diversity index from 0.74 to 0.54. Results were similar for plots harvested in 1997 (data not shown).

**Table 5**  $P$ -values from GLMs of treatment effects on species richness and Simpson's diversity index ( $n = 50$ ), when ramet density of the plot is included as a covariate

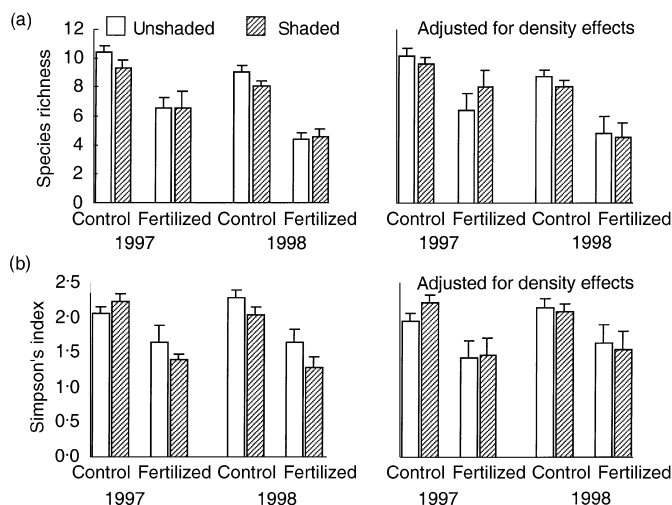
Source	d.f.	$P$	
		Species richness	Species diversity
1997 harvest			
Block	4	0.207	0.429
Fertilizer	1	0.004	0.001
Water	2	0.365	0.092
Shade	1	0.594	0.453
Fertilizer $\times$ shade	1	0.183	0.143
Density	1	0.205	0.482
Water $\times$ shade	2	0.217	0.181
Error	37		
1998 harvest			
Block	4	0.786	0.111
Fertilizer	1	< 0.001	< 0.017
Water	2	0.245	0.773
Shade	1	0.522	0.726
Density	1	0.133	0.080
Fertilizer $\times$ shade	1	0.718	0.913
Water $\times$ shade	2	0.558	0.599
Error	34		

## Discussion

Of the three hypotheses to explain why species richness and diversity usually drop when a plant community is fertilized (Fig. 1), the total competition hypothesis receives the most support from these results.

### DENSITY DOES NOT FULLY EXPLAIN DIVERSITY

The density hypothesis proposes that increased light competition kills small individuals of all species and that species are lost from plots at random. Although



**Fig. 5** Response of (a) species richness and (b) Simpson's diversity index to fertilizer and shade, before (left) and after (right) adjusting for the effects of density. Error bars are one standard error. GLM results are shown in Tables 4 and 5.

density dropped in fertilized plots, more species were lost than would be expected if only species-random mortality were operating (4–5 observed vs. < 1 predicted). Species-random mortality may have contributed to the loss of species richness with fertilization, but some other factor, such as species differences in competitive ability, had a much greater influence.

Light competition can easily cause species-random mortality among non-clonal plants if all species have some small individuals. In clonal species, however, the smallest ramets could be rescued by carbon transfer from larger ramets. These species would be less likely to die than those that are non-clonal or have only weak connections among ramets. The density hypothesis therefore might not be expected to hold in this predominantly clonal community. Because degrees of integration are unknown, I was not able to test for any pattern in mortality. Clonality does appear to affect density-diversity relationships in fens: density and diversity are linearly related for bryophytes, which are expected to have little physiological integration, but there is no relationship for highly clonal vascular plants (Bergamini *et al.* in press). Such differences would also explain why density explained very little of the species richness pattern in this experiment or in the Rapson *et al.* (1997) study, but explained all or part of the richness patterns in two first-year old fields (Goldberg & Miller 1990; Stevens & Carson 1999). Establishment of seedlings would predominate in the first year even for clonal species, and species-random mortality would be more likely.

#### LIGHT COMPETITION ALONE DOES NOT CAUSE COMPETITIVE EXCLUSION

The light competition hypothesis predicts that shoot competition contributes much more to mortality and competitive exclusion than root competition does. Shadecloth was used to increase light limitation without changing below-ground resources (both relative to control plots) and diversity was compared with fertilized plots, where the increased biomass reduced light at the soil surface to similar levels. Above-ground competition was similar in the two treatments, but only the fertilizer treatment decreased richness and diversity, suggesting that factors other than light competition control this community. It is possible that experimental shading of canopy plants might have made them light limited, reducing their ability to suppress other species, but the dominants, *Poa* and *Bromus*, have been shown not to be affected by shading. Biomass and growth rate remained unchanged when the plants were grown in pots without competition under 50% or 75% shadecloth (50% or 25% of full sunlight, the range of values measured between 30 cm and 50 cm above the soil surface; Rajaniemi 2001).

This result contrasts with previous studies in which light competition reduced species richness (Gibson 1988; Carson & Pickett 1990). Although the overall

level of light limitation was similar to this study (similar light levels in unfertilized and fertilized plots in Carson & Pickett 1990), the vegetation in both previous studies was taller and had a distinct canopy and subcanopy. Here, individuals of most species reached heights of only 20–30 cm and, as they had at least some leaves in relatively high-light regions, may have been able to avoid light limitation.

Light enhancement, achieved in both of the previous studies by tying back canopy plants, was not practical for the short vegetation studied here. However, the light competition hypothesis predicts that richness and diversity will be high whenever light levels are high (unproductive/unfertilized vegetation or productive vegetation with canopy tied back) and low whenever light levels are low (productive/fertilized vegetation or unproductive vegetation with artificial shade). Shading of unfertilized plots would provide an equally strong test of the hypothesis as light enhancement in fertilized plots.

#### BELOW-GROUND COMPETITION CONTRIBUTES TO COMPETITIVE EXCLUSION

The total competition hypothesis predicts that both root and shoot competition contribute to greater mortality and competitive exclusion with fertilizer, and thus that shaded plots, in which only light limitation is manipulated, should show a reduced effect. Fertilized plots did indeed have lower diversity than shaded plots.

Again, this result contrasts with previous findings. The effects of root competition on individual fitness generally *decrease* with fertilization (Wilson & Tilman 1991, 1993; Putz & Canham 1992; Peltzer *et al.* 1998; Cahill 1999). Competition intensity would only be expected to increase if plant biomass increased faster than nutrient availability, giving more grams of root competing for each gram of nutrient. While root biomass was not measured in this experiment, patterns in above-ground biomass suggest that below-ground biomass may not have greatly increased with fertilizer.

Above-ground biomass did not show strong responses to fertilization. In 1997 fertilized plots had on average 50% more above-ground biomass than control plots, but in 1998 the biomass increase was only 15% (Fig. 4). Furthermore, these biomass increases may have largely reflected the presence of more shrubs (mainly *Rhus typhina*) in fertilized plots. When plots with large shrubs were excluded from the analyses, fertilizer increased biomass by only 12% in 1997 and had no significant effect in 1998, although fertilizer effects on richness and diversity did not change (Rajaniemi 2001). These shrubs re-sprouted from stems that had been mowed for many years before the experiment began; their size seemed to be correlated with the size of the existing stem and unrelated to fertilizer addition (personal observation). Below-ground biomass is likely to have increased even less than above-ground biomass following fertilization as root

allocation of individual plants typically decreases with increasing nitrogen availability (Reynolds & D'Antonio 1996).

While total root competition intensity may not have increased with fertilizer, different species in this community appear to respond differently to fertilizer and this may have changed their relative competitive abilities. When individual plants were grown in pots, fertilization increased allocation to roots in *Poa compressa* and decreased it in *Hieracium caespitosum* and *Plantago lanceolata* (Rajaniemi 2001). These allocation shifts may have increased the below-ground competitive ability of *P. compressa*, one of the dominant species in fertilized plots, while decreasing that of *H. caespitosum* and *P. lanceolata*, contributing to their decreased relative abundance or total loss from these plots.

Competitive exclusion in fertilized plots probably resulted from the additive or interactive effects of root and shoot competition, rather than from root competition alone. Mortality of rosettes, which explained most of the drop in diversity (*Hieracium caespitosum* was eliminated from fertilized plots by the second year, and other rosette species had lower density, Rajaniemi 2001), cannot be accounted for by root competition, but shoot competition alone did not eliminate any species. An experimental treatment crossing fertilizer with light enhancement would be useful in testing for interactions between root and shoot competition but is probably not practical in this system.

Alternatively, the increased biomass in the first year may have been converted into higher litter biomass in the second year, and litter effects may have eliminated rosette species. This explanation, however, seems unlikely because the amount of litter present was small and increased little with fertilizer (from 160 g m<sup>-2</sup> to 200–240 g m<sup>-2</sup>). Previous experiments showing litter effects on species richness or diversity in old fields usually reported higher litter masses (650–850 g m<sup>-2</sup>, Carson & Peterson 1990; 500 g m<sup>-2</sup>, Facelli & Facelli 1993; 300 g m<sup>-2</sup> unfertilized, 600 g m<sup>-2</sup> fertilized, Foster & Gross 1998) and reported increased diversity after removal of the entire litter mass. Litter also does not explain plots with fertilizer and shade, where diversity dropped without a change in litter mass.

A separate experiment with plants from the same community in which competition was directly manipulated also supports the total competition hypothesis. Seven dominant species were grown in mixtures and in monocultures that experience no competition, only root competition, or only shoot competition from the surrounding vegetation, both with and without fertilizer (Rajaniemi 2001). Each set of monocultures reveals the composition of a particular null community, the community that would exist in the absence of some type of species interactions (Goldberg 1994). For example, the biomass of each species in a set of seven monocultures with no competition from the surrounding vegetation and no fertilizer indicates which species would persist, and what their relative

abundances would be, in a null community with no competition. Diversity indices can be calculated for the null communities from each set of monocultures and compared with diversity in mixtures to show the effects of total, root and shoot competition on diversity, and how those effects change with fertilizer. Diversity dropped with fertilization when species competed below-ground, but not when they only competed above-ground (Rajaniemi 2001).

These two experiments address only short-term changes in community structure following fertilization. Tilman (1988) emphasizes that transient dynamics following a perturbation may result in very different patterns than will be seen when the community reaches an equilibrium. The general pattern of reduced diversity following fertilization seems to be consistent in both short-term and long-term experiments (Gough *et al.* 2000) but long-term experiments show shifts in species composition occurring after 10 or more years of fertilization (Inouye & Tilman 1995; Turkington *et al.* 2002). Therefore, the patterns observed here may reflect equilibrium diversity for fertilized plots but not equilibrium species composition, and help to explain short-term changes in diversity following fertilization. The mechanisms involved, however, may be only transient and may be very different from those that maintain a lower equilibrium diversity in fertilized plots.

## Conclusions

Random thinning, shoot competition and root competition may all have contributed to decreased species richness and diversity following fertilization in this unproductive old field. Decreased density could account for the loss of less than one species on average from a plot, with the majority excluded by increasing effects of competition for soil resources, perhaps in combination with increasing competition for light.

The relative importance of the three mechanisms may depend on characteristics of the community. Compared with this study, random thinning was more important in first-year old fields (Goldberg & Miller 1990; Stevens & Carson 1999), where most species are non-clonal, and competition for light was more important in old fields (Carson & Pickett 1990) and grasslands (Gibson 1988) with canopy and subcanopy vegetation layers.

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