

Root competition can cause a decline in diversity with increased productivity

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Summary

1 Plant community theory often invokes competition to explain why species diversity declines as productivity increases. Competition for *all* resources might become more intense and lead to greater competitive exclusion or, alternatively, competition for light only could become more intense and exclude poor light competitors.

2 To test these hypotheses, we constructed communities of seven old-field species using combined monocultures. Constructs experienced no interspecific competition, only shoot competition or only root competition, with and without fertilizer. Diversity in these limited interaction communities was compared to diversity in unfertilized and fertilized mixtures of the seven species.

3 Diversity decreased with fertilization in mixtures and in communities with only root competition. Shoot competition had small effects on the community and did not contribute to changes in diversity with fertilization.

4 Root competition may strongly impact plant community structure in unproductive communities where light never becomes limiting, or under non-equilibrium conditions following human disturbances.

Key-words: community structure, fertilization, old field, null community, combined monocultures design

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Introduction

Habitat productivity is an important determinant of plant community structure. The relationship between productivity and species diversity depends on the spatial scale surveyed, and appears to be highly variable even at a given scale (reviewed by Mittelbach *et al.* 2001; Waide *et al.* 1999), but some general patterns have emerged. At an intermediate spatial scale (within biomes but across communities), the productivity-diversity relationship is most often unimodal, with diversity peaking at intermediate productivity (Mittelbach *et al.* 2001; Waide *et al.* 1999). When productivity is manipulated experimentally via fertilization, species diversity almost always decreases (DiTommaso & Aarssen 1989; Gough *et al.* 2000). These patterns are apparent whether diversity (*sensu lato*) is

measured as species richness or as a diversity index that incorporates relative abundances of species.

Many hypotheses attempt to explain why diversity decreases from intermediate to high productivity (reviewed in Rajaniemi 2003a; Rosenzweig & Abramsky 1993). For plant communities, two alternative hypotheses have received the most attention. The total competition hypothesis proposes that competition for all resources has increasing effects on diversity as productivity increases (Grime 1977; Huston 1979). The light competition hypothesis, on the other hand, predicts a shift from competition for soil resources at low productivity to competition for light at high productivity. This hypothesis predicts that competition for light reduces diversity more than competition for soil resources (Goldberg & Miller 1990; Newman 1973) or that complete light limitation (at high resources) allows less coexistence than is possible at intermediate resource levels, given the spatial heterogeneity in the limiting resource (Tilman & Pacala 1993). In either case, increasing effects of light competition reduce diversity.

Very little direct experimental evidence is available for evaluating these hypotheses. Competition does reduce diversity in many, but not all communities, as

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demonstrated by two experimental methods. Firstly, species richness and diversity may increase following removal of a dominant species (Abul-Fatih & Bazzaz 1979; Armesto & Pickett 1986; Bobbink *et al.* 1987; Gurevitch & Unnasch 1989; Keddy 1989; Leps 1999; Smith *et al.* 1999; Wardle *et al.* 1999; Zamfir & Goldberg 2000; but see Allen & Forman 1976; Belsky 1992; Hils & Vankat 1982; Pinder 1975; Spackova *et al.* 1998). Secondly, the effect of competition on diversity can also be observed by comparing actual diversity to diversity in a null community based on low-density plots (Goldberg & Estabrook 1998) or combined monocultures (Zamfir & Goldberg 2000). Few studies have tested whether the effect of competition on diversity increases with increasing productivity. In one study, removing the dominant prevented a drop in diversity following fertilization in an old field, suggesting that competition was responsible for decreased diversity (Gurevitch & Unnasch 1989), but the effect of competition from a dominant species did not increase with increasing resources in two other studies (Belsky 1992; Leps 1999), and the total effect of competition on diversity did not increase with increasing water availability in a community of desert annuals (Goldberg *et al.* unpublished data).

Increasing total effects of competition on diversity are predicted by both the total competition and light competition hypotheses, which can only be distinguished if the effects of root and shoot competition are separated. No study has yet directly manipulated root and shoot competition separately to measure their effects on the community, but several authors have indirectly manipulated root and shoot competition by manipulating resources. In an old field (Carson & Pickett 1990) and a dune grassland (Gibson 1988), tying back shoots to increase light increased species richness, while fertilization had no effect, suggesting that competition for light had greater effects on diversity than competition for soil resources. In another old field experiment, on the other hand, fertilization reduced richness and diversity while artificial shading did not, suggesting that increased light competition did not explain the drop in diversity with fertilization (Rajaniemi 2002).

To test the total competition and light competition hypotheses directly, we used a combined-monocultures design to separate the effects of root and shoot competition on diversity in an unproductive old field. In the combined-monocultures design (Goldberg 1994), each species in the community is grown in a monoculture, without interspecific competition (see also Austin 1982; Austin & Austin 1980). The abundance of each species in monoculture is equal to its abundance in a null community, the community that would exist in the absence of species interactions. The relative densities or biomasses of the summed monocultures determine the relative abundance of each species in the null community and these values can be used to calculate diversity in the null community. This null community can then

be compared to a mixture of all the species grown together. We expanded this design by also growing species so that they experienced only shoot competition or only root competition with the rest of the community, enabling us to characterize the communities that would exist if only shoot competition or only root competition were present. Mixtures and each type of limited interaction community (no competition, only root competition, or only shoot competition) were constructed with and without fertilizer.

The two hypotheses predict different patterns for diversity in the communities with limited interactions. The total competition hypothesis predicts that fertilization will not affect diversity in the community with no competition, but will reduce diversity in the communities with either shoot or root competition alone, as well as in mixtures, because increased competition for any or all resources is expected to contribute to reduced diversity. The light competition hypothesis, on the other hand, predicts that fertilization will reduce diversity only in communities with shoot competition.

Methods

STUDY SYSTEM AND SPECIES

This experiment was conducted in an old field at the University of Michigan's Matthaei Botanical Gardens in Ann Arbor, MI (83°40' W, 42°17' N). The field was removed from agricultural use about 40 years ago, and is mowed annually to prevent encroachment of shrubs. Mowing was suspended during the experiment. The field is dominated by perennial clonal grasses and herbs.

Seven of the 10 dominant species in the field were chosen for this experiment: two grasses (*Poa compressa* and *Bromus inermis*) and five forbs (*Hieracium caespitosum*, *Achillea millefolium*, *Daucus carota*, *Potentilla recta*, and *Plantago lanceolata* – nomenclature follows Voss 1972, 1985, 1996). Together, these species comprised between 44% and 99% (mean = 83%) of the biomass in 0.25 m² plots of unmanipulated vegetation (T.K. Rajaniemi, unpublished data), with their combined dominance varying inversely with the abundance of two patchily distributed species, *Rhus typhina* L. and *Solidago altissima* L. (personal observation). When plots of natural vegetation are fertilized, *Poa* and *Bromus* become more dominant, *Hieracium* is frequently eliminated, and the other forbs are reduced in density (Rajaniemi 2001). Therefore, these seven species comprise a community which is expected to show a strong diversity response to fertilization.

EXPERIMENTAL DESIGN

Experimental treatments were designed to create communities of the seven species that experienced no interspecific competition, only shoot competition, only root competition, or both root and shoot competition.

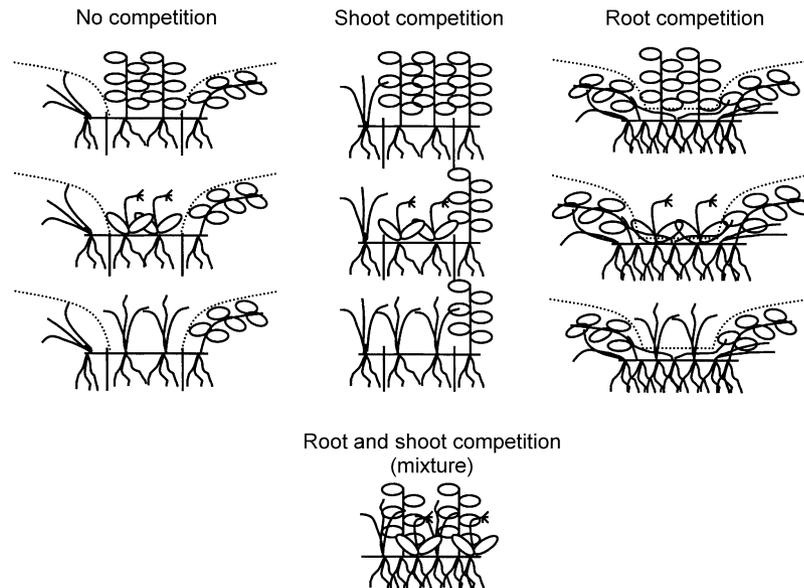


Fig. 1 The expanded combined-monocultures design. The design is illustrated for a community of three species for clarity, but the experiment used a community of seven species. Plots with no competition have one species with trenching and a net. Shoot-competition plots have one species with trenching but no net. Root-competition plots are planted with all species, and only one species grows up through a net. Mixtures, experiencing both root and shoot competition, have all species planted together, without nets or trenching.

(Note that these treatments manipulate all interspecific interactions, so that facilitative as well as competitive effects are possible, and that plants in all treatments experience intraspecific interactions. However, the hypotheses we test and our experiment focus on the effects of interspecific competition on the community.) The community with both root and shoot competition was simply a mixture of the seven species in a single plot (Fig. 1, bottom). The communities with limited interactions were created using the combined-monocultures approach, with each 'community' comprising seven separate plots, one for each species. To characterize the community with no competition, each species was grown in monoculture, in a plot in which roots from outside the plot were excluded by trenching and shoots from outside the plot were held back with nets (Fig. 1, left). In the community with only shoot competition, each species was planted in monoculture, with roots from outside excluded by trenching but shoots of neighbouring plants allowed to shade the plot (Fig. 1, centre). In the community with only root competition all seven species were planted in each of seven plots. A different species in each plot was designated as the target species, and nets were used to hold down the shoots of the remaining six species, while the target species grew up through the net (Fig. 1, right). Thus, the target species experienced root competition with the remaining species both inside and outside the plot, but the other species were unable to shade the target species. The summed abundances of the seven target species in their separate plots described the community with only root competition.

Each of these communities was replicated with and without fertilizer in each of four blocks. Each block

contained two unfertilized and two fertilized mixtures (four plots), plus one unfertilized and one fertilized plot for each species in each of the three limited-interaction communities (seven species \times three interaction treatments \times two fertilizer treatments = 42 plots), for a total of 184 plots. These plots were randomly arranged within each block.

Plots were constructed by removing the existing vegetation and the top layer of soil from well spaced areas, replacing the soil, and transplanting the desired species. Each plot measured 20 cm \times 150 cm, with the long edge orientated east to west; the narrow plot shape allowed the intact vegetation that surrounded each plot to shade the entire width of the plot in the shoot-competition treatments. In May 1998, the plot locations were delimited, the edges of each plot were cut with a shovel, and the sod, containing most of the roots inside the plot and the top 5–10 cm of soil, was lifted out. The plot was then filled with tilled soil from another section of the field, to bring the soil back to its original level. The pre-existing vegetation surrounding plots was left intact (although certainly disturbed) to shade plots or provide competing roots where appropriate.

All plants in the plots were transplanted from other areas of the field in June 1998. No-competition and shoot-competition plots of *Achillea*, *Daucus*, *Plantago*, and *Potentilla* were created by planting two ramets of the selected species into each of four random locations in the plot, for a total of eight ramets per plot. For the remaining species, individual ramets were tightly clumped and difficult to identify, so no-competition and shoot-competition plots of *Poa*, *Bromus*, and *Hieracium* received four 10 cm \times 10 cm turf blocks of the selected species. These plantings resulted in approximately

equal initial cover (~12%) of each species. Mixtures and root-competition plots received all seven species in an additive design, with eight ramets each of *Achillea*, *Daucus*, *Plantago*, and *Potentilla* and four 10 cm × 10 cm blocks each of *Poa*, *Bromus*, and *Hieracium*, with each species again planted into four random locations.

To prevent roots of surrounding vegetation from growing into the plots, no-competition plots and shoot-competition plots were trenched (Fig. 1). A machete was used to cut at least 10 cm into the soil (up to 25 cm if no rocks were hit) around the perimeter of each plot. Trenching was begun 25 June 1998 and was repeated every 2 weeks during the growing season, then every 4 weeks starting in July 1999, after it became apparent that few roots were entering the plots within 2 weeks.

To prevent shading of the target species, nets were installed 9–11 July 1998 in no-competition and root-competition plots (Fig. 1). Nets were 2-cm mesh black nylon (Bird-X, Dalen Products, Knoxville, Tennessee), and were large enough to extend at least 20 cm beyond each edge of the plot. In no-competition plots, the centre portion of the net that covered the inside of the plot was removed. The net was fastened to the ground with turf staples along the edge of the plot, and the vegetation surrounding the plot was held back under the net. In root-competition plots, the net was similarly fastened to the ground with turf staples around the edges of the plot, but the centre portion of the net was not removed. Shoots of all but one species inside the plot were guided under the net and toward the edge of the plot. Shoots of the target species were pulled through the net and allowed to grow upright.

Fertilizer was added to half the plots to supply 5.0 g N, 2.2 g P, and 4.2 g K/m² on 24 July 1998 and 3.0 g N, 1.3 g P, and 2.5 g K/m² on 26 April 1999, 23 June 1999, and 28 April 2000. A slow-release 13-13-13 NPK fertilizer, Scotts Osmocote (Scotts Company, Marysville, Ohio) was sprinkled on the soil surface inside the plots and over a 20-cm-wide buffer zone around each plot. This level of fertilization is less than used in many fertilization experiments (Carson & Pickett 1990; Gibson 1988; Gough *et al.* 2000) and was intended to be closer to levels that might result from atmospheric nitrogen deposition (Jefferies & Maron 1997).

All plots were hand-weeded every 2 weeks to remove any species other than those planted. Once each year, RoundUp herbicide (Monsanto, San Ramon, California) was applied to leaves of *Rumex acetosella* that invaded the plots, because hand weeding did not successfully eliminate this species. In the second year, a border of transplanted *Bromus inermis* was added to the south (long) edge of shoot interaction plots to provide more shade to the interiors of these plots.

MONITORING AND HARVEST

Cover of each species in each plot was recorded at the end of the first growing season (October 1998) and

approximately every 6 weeks throughout the following two growing seasons (May, June, July, and October 1999 and April, June, and July 2000). One hundred regularly spaced pins were dropped in each plot, and the species identity of each leaf hit by a pin recorded.

To document the effects of fertilizer, levels of available nitrogen and inorganic phosphorus were measured in single soil cores (2.5 cm diameter × 10 cm deep) collected from all plots on 2 October 1998 and in three pooled cores collected from all plots on 14 July 2000. Nutrients were extracted in KCl and analysed in a flow-injection analyser.

Before harvest, light penetration into plots was measured using a sunfleck ceptometer (Decagon, Pullman, Washington) on 11 July 2000. Photosynthetically active radiation (PAR) was measured across 40 cm of the length of each plot at 5, 15, 25, 35, and 45 cm above the soil surface and above all vegetation. PAR measurements were converted into percent of full sunlight.

Fine root samples were collected from soil cores in all plots on 22–25 July 2000 to provide relative measures of total root biomass in plots. Seven soil cores (2.5 cm diameter × 10 cm deep) were collected per plot and combined, and roots were washed from the cores in a 2-mm-mesh sieve. Root samples were dried at 65 °C for 48 hours and weighed.

Plant shoots were harvested 29 July–17 August 2000. All shoots were clipped at 2 cm above the soil surface. In mixture plots, shoots were separated by species; in root-competition plots, shoots were separated into target (unshaded) species and all other species. All shoots were dried at 65 °C for 48 hours and weighed.

ANALYSIS

Responses of root and shoot biomass in plots to block (a random effect), fertilizer, root competition, and shoot competition (all fixed effects) were examined with a four-way General Linear Model (GLM; Systat 9.0, SPSS Inc., 1998). Per-plot biomass included only the target species (the only species present) in no-competition and shoot-competition plots, and all seven species in root-competition plots and mixtures. Effects of treatments on available nitrogen and phosphorus in 1998 and 2000 were also analysed with the four-way GLM.

Light availability was analysed with a repeated measures design, with block, fertilizer, root competition, and shoot competition as factors, and percent full sunlight at the different heights above the soil surface as the repeated measure. Values of percent full sunlight were arcsine-square-root transformed for normality.

To investigate the effects of fertilizer and competition on community structure, measures of species diversity and relative abundance of each species were calculated for mixtures and for each limited interaction community, following Goldberg (1994), with each set of cover estimates and harvest biomass as measures of species abundance. In the combined-monocultures design, the abundance of each species in the null

community is equal to its abundance in monoculture (without interspecific competition), and relative abundance of each species in the null community can be calculated based on the total abundance of all species in the summed monocultures. For example, the relative abundance of species i in the null community with no interspecific competition and no fertilizer is $RY_{in} = Y_{in}/\Sigma Y_{in}$, where Y_{in} is the biomass or cover of species i in unfertilized no-competition plots, and ΣY_{in} is the summed biomass or cover of all seven species in unfertilized no-competition plots. These relative abundances can be used to calculate Simpson's diversity index, $1/D = 1/\Sigma(RY_{in})^2$, for the community with no interspecific competition and no fertilizer. Similar calculations give relative abundance and diversity in communities with no competition, only shoot competition, or only root competition, each with and without fertilizer.

The four-way GLM was used to test for response of diversity (at the time of each cover estimate and at harvest) and relative abundance (at harvest only) of each species to block, fertilizer, root competition and shoot competition. Relative abundance data were arcsine-square-root transformed for normality.

Results

Fertilizer increased phosphorus in the soil in 1998 ($F_{1,168} = 26.442$, $P < 0.001$) but did not affect available nitrogen in the first growing season ($F_{1,168} = 1.312$, $P = 0.254$). Competition treatments had no effects on soil resource availability in this year. By 2000, fertilizer had increased P in all competition treatments ($F_{1,173} = 30.848$, $P < 0.001$; no separate effects of root or shoot competition) and increased N in all competition treatments, although most dramatically in root-competition plots ($F_{1,173} = 4.247$, $P = 0.041$ for the fertilizer \times root \times shoot interaction). In both years, phosphorus levels were higher in blocks 1 and 2 ($F_{3,168} = 15.495$, $P < 0.001$ in 1998; $F_{3,173} = 5.782$, $P = 0.001$ in 2000).

Fertilizer increased root and shoot biomass in individual plots (fertilizer effect on shoot biomass: $F_{1,173} = 39.012$, $P < 0.001$, on root biomass: $F_{1,173} = 50.887$, $P < 0.001$; Fig. 2) and reduced light at the soil surface (fertilizer effect: $F_{1,173} = 24.081$, $P < 0.001$, fertilizer \times height interaction: $F_{4,692} = 4.787$, $P = 0.001$; Fig. 3), as expected. Light levels also tended to be lowest in block 1 (block effect: $F_{3,173} = 7.751$, $P < 0.001$).

Plots with only root competition and with both root and shoot competition (i.e. mixtures) had similar fine root biomass (Fig. 2, root \times shoot interaction non-significant: $F_{1,173} = 2.662$, $P = 0.105$), indicating that the potential for root competition was similar in the two treatments, as intended. While mixtures had significantly more total shoot biomass than root-competition plots (root \times shoot interaction: $F_{1,173} = 4.812$, $P = 0.030$; Fig. 2), the actual difference in shoot biomass was small, suggesting that neighbours held under nets were able to grow nearly as well as the unimpeded plants in mixtures.

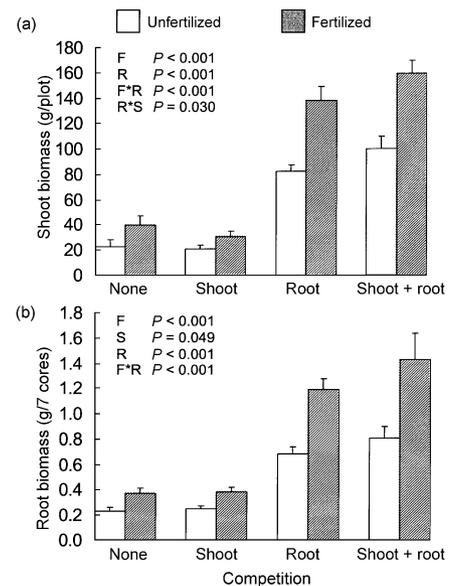


Fig. 2 Effects of experimental treatments on (a) total shoot biomass in each plot (including target and non-target species) and (b) total fine root biomass in seven cores from each plot ($n = 184$). Error bars are 1 SE. P -values are shown for significant effects (F, fertilizer; S, shoot interactions; R, root interactions).

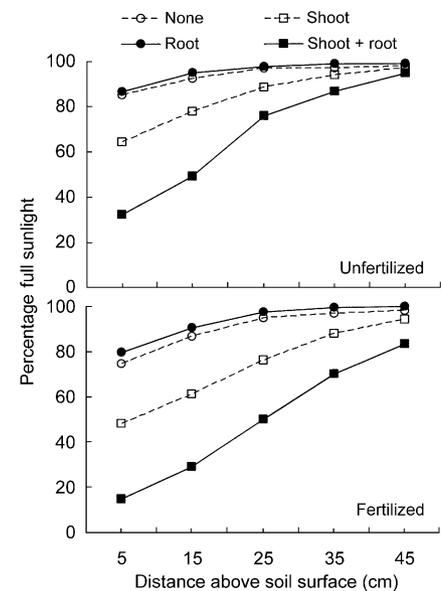


Fig. 3 Effects of experimental treatments on light profiles ($n = 184$ at each height) in July 2000. Error bars are 1 SE.

In contrast, plots with only shoot competition probably had less intense shoot competition than those with both root and shoot competition. The presence of shoot competition decreased light availability as planned (shoot effect: $F_{1,173} = 233.194$, $P < 0.001$, shoot \times height interaction: $F_{4,692} = 58.972$, $P < 0.001$; Fig. 3), but the shading effect was larger in mixtures than in shoot-competition plots (root \times shoot interaction: $F_{1,173} = 34.364$, $P < 0.001$, root \times shoot \times height interaction: $F_{4,692} = 7.918$, $P < 0.001$; Fig. 3). Target plants in mixtures were shaded by a number of different

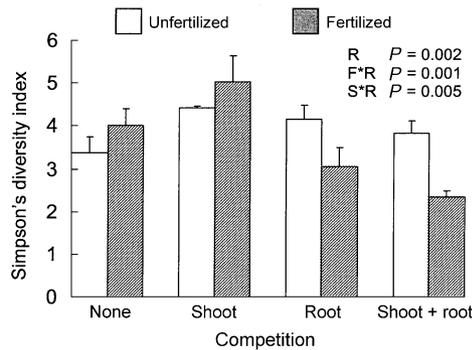


Fig. 4 Effects of fertilizer and species interactions on species diversity (Simpson's diversity index, $1/D$) in the limited-interaction communities and mixtures ($n = 40$). Diversity based on harvest biomass for all communities is shown, without the effects of light as a covariate. See text for calculation of diversity in limited-interaction communities. Error bars are 1 SE. P -values are shown for significant effects (F, fertilizer; S, shoot interactions; R, root interactions).

species both inside and outside the plots, whereas in shoot-competition plots they were similarly shaded by the surrounding vegetation, but there were only a few individuals of the same species inside the plot.

The root and shoot biomass data suggest that no-competition and shoot-competition plots did not reach equilibrium. These plots had less root and shoot biomass than root-competition plots and mixtures, and experienced a smaller biomass response to fertilizer (root effect: $F_{1,173} = 255.135$, $P < 0.001$ and $F_{1,173} = 212.743$, $P < 0.001$; fertilizer \times root interaction: $F_{1,173} = 14.834$, $P < 0.001$ and $F_{1,173} = 18.911$, $P < 0.001$ for shoot and root biomass, respectively; Fig. 2). Root-competition plots (where both the target species and non-target root competitors were included in per-plot biomass) and mixtures (with all seven species included) started with more biomass per plot, but we expected no-competition and shoot-competition plots to fill in and reach similarly high biomasses by the end of the experiment. The lower final biomass of these plots affects the interpretation of diversity patterns (see Discussion).

At harvest, fertilizer reduced species diversity as expected, but only when root competition was present (fertilizer \times root interaction: $F_{1,29} = 14.577$, $P = 0.001$; Fig. 4). Contrary to the predictions of both the total competition and light competition hypotheses, the effect of shoot competition on diversity did not change consistently with fertilizer. Shoot competition decreased diversity in mixtures compared with root competition only, but increased diversity in the community with only shoot competition compared with no competition (shoot \times root interaction: $F_{1,29} = 9.474$, $P = 0.005$; Fig. 4). This pattern was explained by the lower light levels in mixtures than in shoot-competition plots; the effect became non-significant when light at 5 cm was used as a covariate in the analyses ($F_{1,28} = 0.403$, $P = 0.531$), even though the covariate itself was not significant ($F_{1,28} = 1.220$, $P = 0.279$). The

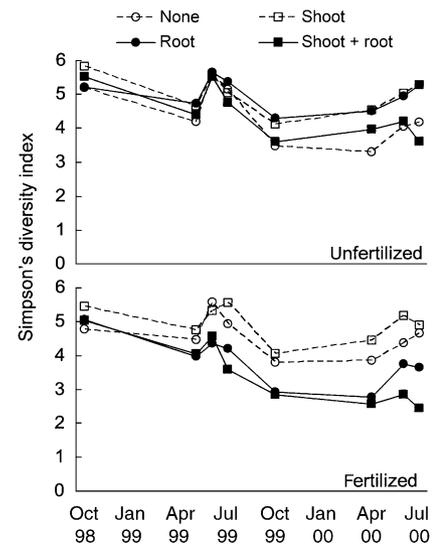


Fig. 5 Effects of fertilizer and species interactions on species diversity (Simpson's diversity index, $1/D$) in the limited-interaction communities and mixtures, for diversity based on cover measurements taken throughout the experiment.

root \times fertilizer interaction remained significant when the covariate was included ($F_{1,28} = 15.041$, $P = 0.001$). Furthermore, shoot competition did not contribute to decreased diversity in fertilized monocultures: fertilizer had similar effects on diversity in communities with only root competition and with both root and shoot competition (fertilizer \times root \times shoot interaction non-significant: $F_{1,29} = 9.474$, $P = 0.713$). A similar pattern of fertilizer reducing diversity in the presence of root competition was first observed in plant cover data for June 1999, and remained significant in all subsequent cover measurements (Fig. 5).

The diversity pattern was driven mainly by changes in the relative abundance of two species. *Poa* increased in relative abundance with fertilizer, but only in communities with root competition (fertilizer \times root interaction: $F_{1,29} = 6.974$, $P = 0.013$; Fig. 6). *Daucus* followed the reverse pattern, with fertilizer decreasing its relative abundance only when root competition was present (fertilizer \times root interaction: $F_{1,29} = 5.724$, $P = 0.023$; Fig. 6).

Discussion

The results of this experiment tend to support the total competition hypothesis over the light competition hypothesis to explain reduced diversity following fertilization. Fertilization decreased diversity when root competition was present, as predicted by the total competition hypothesis. However, the effect of root competition was sufficient to explain the entire drop in diversity following fertilization, a result predicted by neither hypothesis. The role of shoot competition in the fertilization-diversity relationship in this study remains unclear.

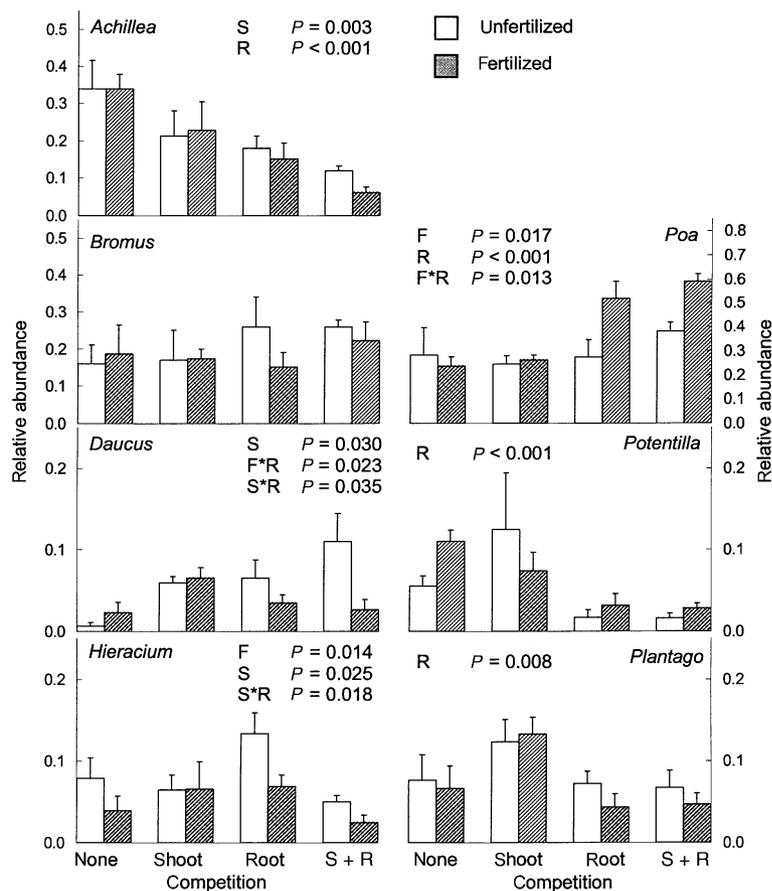


Fig. 6 Effects of fertilizer and species interactions on relative abundance of each species in the limited interaction communities and mixtures ($n = 40$). Relative abundance is based on harvest biomass for all communities. Error bars are 1 SE. P -values are shown for significant effects (F, fertilizer; S, shoot interactions; R, root interactions). Block effects, also included in the model, were significant only for *Plantago* ($P = 0.010$).

EVALUATION OF ASSUMPTIONS

Interpretation of our results requires a number of assumptions; some of these were met in the experiment, while others were not. First, fertilizer produced the expected relationship between productivity and diversity in this experiment by increasing shoot and root biomass in all plot types and decreasing diversity in mixtures. Also, root-competition plots accurately represented the community with only root competition. They had the same potential for root competition as the fully competing mixtures, with similar root biomass, but little or no potential for shoot competition, with light levels similar to those in no-competition plots. On the other hand, shoot-competition plots eliminated root competition, as indicated by their low root biomass relative to mixtures, but had more light and presumably less intense shoot competition than mixtures. Therefore, the shoot competition treatment was not a strong test of the effects of shoot competition on the community.

A key unmet assumption was that all plots would reach an equilibrium biomass. At equilibrium, the abundance of each species in monoculture equals its potential abundance in a hypothetical null community.

Many no-competition and shoot-competition plots had low, clearly non-equilibrium biomasses; the null communities based on these plots therefore had non-equilibrium species composition and diversity. Mixtures and root-competition plots were more likely to have achieved equilibrium biomass and composition: these plots were initially planted with higher total biomass, allowing greater opportunity for interactions to affect relative abundances. Therefore, communities with different competition treatments in this experiment were likely approaching equilibrium at different rates. In an attempt to correct for this problem, we repeated the GLM for species diversity using data expected to reflect the four community types at more equal distances from equilibrium. This analysis compared diversity in July 1999 for mixtures and root competition communities (assumed to approach equilibrium quickly) to diversity in July 2000 for shoot competition and no competition treatments (assumed to approach equilibrium slowly). All diversity values were based on species cover. This analysis confirmed the results found for harvest data. The fertilizer by root interaction and the root by shoot interaction remained significant ($F_{1,29} = 5.205$, $P = 0.030$ and $F_{1,29} = 5.892$, $P = 0.022$, respectively), although the patterns were

less strong than in the initial analysis. Using light as a covariate eliminated the root by shoot interaction ($F_{1,28} = 2.702$, $P = 0.111$), as in the original analysis. This result suggests that differences among communities in their distance from equilibrium did not affect our basic conclusions.

Measuring root as well as shoot biomass of each species would give a more complete picture of the effects of competition on abundance (Zobel & Zobel 2002), especially in the short term, before effects on plant lifetime fitness and recruitment are expressed (Cahill 2002). However, measuring root biomass in an accurate and unbiased way presents difficulties (Cahill 2002), particularly when roots of multiples species must be separated. Given these difficulties, shoot biomass alone may give the most accurate measure of abundance available in this experiment (Cahill 2002).

EFFECTS OF COMPETITION ON COMMUNITY STRUCTURE

In the unfertilized community of seven species, neither root nor shoot competition had strong effects on diversity. The lack of any dramatic effects is not surprising, given that the species selected for the experiment were naturally abundant in this field. Competition for resources may be preventing other species from persisting in the old-field community, but such species were not incorporated into the experiment and were prevented from establishing in plots. While diversity was not affected, both shoot and, especially, root competition did affect species composition of the community even without fertilizer.

In both fertilized and unfertilized communities, shoot competition affected the relative abundance of only three species, *Achillea*, *Hieracium* and *Daucus* (Fig. 5). Furthermore, *Daucus* abundance was increased, rather than decreased, by shoot interactions. Shading appeared to enhance germination of *Daucus* seedlings (personal observation), while other species produced few if any seedlings. More generally, shoot competition is expected to be unimportant to community structure in unproductive environments (Grime 1977; Tilman 1988), and shoot competition generally has small effects on individual fitness at low productivity (e.g. Twolan-Strutt & Keddy 1996; Wilson & Tilman 1991, 1993). Theory predicts, though, that the effects of shoot competition on community structure should increase with fertilization (Grime 1977; Tilman 1988), a pattern that was not observed in this experiment.

As noted above, the shoot competition treatment was not a strong test of the effects of shoot competition on the community. Shoot competition did not have strong additive effects on diversity above and beyond root competition effects (diversity was similar in communities with only root and with both root and shoot competition), but we cannot conclude whether shoot effects alone might influence diversity in this community. Other observations, however, suggest that shoot

competition may have been relatively unimportant in this community. Standing crop biomass in fertilized mixtures was similar to that in experiments finding that effects of shoot competition on individuals were small and did not increase with increasing productivity (Belcher *et al.* 1995; Cahill 1999; Peltzer *et al.* 1998), and lower than biomass in studies finding increasing effects of shoot competition with increasing productivity (Twolan-Strutt & Keddy 1996; Wilson & Tilman 1991, 1993). Also, the vegetation in this community is short (most of the biomass is below 50 cm; T. K. Rajaniemi, unpublished data) and does not form a canopy and subcanopy, so that few species are likely to be restricted to the lowest light levels near the soil surface.

Root competition had much stronger effects on community structure than did shoot competition. In the unfertilized community, root competition did not affect diversity, but did influence relative abundance of five of the seven species. This impact of root competition supports the hypothesis that competition for soil resources is an important determinant of community structure in unproductive environments (Tilman 1988; Tilman & Pacala 1993). Root competition also tends to have strong effects on individual fitness at low productivity (Cahill 1999; Peltzer *et al.* 1998; Wilson 1993; Wilson & Tilman 1991, 1993).

Most importantly, the effect of root competition on diversity increased with fertilization; this increase in root effects explained the entire drop in diversity in fertilized mixtures. The diversity pattern was driven largely by the abundance of *Poa*; fertilizer appeared to give this species a strong advantage in root competition. While the total competition hypothesis predicted that root competition would at least contribute to the productivity-diversity pattern, the mechanism by which root competition might produce this pattern is not clear.

Fertilization might increase the intensity of root competition, but even intense root competition is not expected to lead to competitive exclusion because uptake of soil resources is expected to be size symmetric, with uptake directly proportional to plant size (Newman 1973; Schwinning & Fox 1995; Zobel 1992). Therefore, fertilization might increase root competition intensity by leading to increased total root biomass or by inducing root growth in a narrow zone near the surface, reducing differences in rooting depths. But even under intense competition, a small plant should still be able to acquire some soil resources and survive; larger, better competitors cannot pre-empt soil resources as they can light.

One possible explanation for the effects of root competition on diversity in this experiment is below-ground size asymmetry. Root competition may become size asymmetric if soil resources are patchily distributed and large plants are able to reach and exploit patches faster, thereby pre-empting the resources from smaller plants (Schwinning & Weiner 1998). Greenhouse competition experiments indicate that at least

one species used in this experiment, *Bromus inermis*, may have size asymmetric effects in root competition (Rajaniemi 2003b). If pellets of fertilizer create resource patches that can be pre-empted by species such as the grasses, which have extensive root systems, size asymmetric root competition may reduce diversity. More work is needed to determine whether this mechanism is plausible or general.

Another possible explanation for the root competition effect is that fertilization might change the relationships between plant species and soil microbes such as mycorrhizal fungi, and only indirectly influence plant diversity. In this system, soil fungi do not seem to affect plant diversity or the diversity-fertilization relationship, although they do influence plant community composition (Allison 2001).

Conclusions

In this unproductive old field, changes in root competition can explain the reduction in diversity that results from fertilization. The results of this experiment confirm the results of an indirect manipulation of competition intensity at the same site: artificial shading alone had little effect on diversity, suggesting that it is the below-ground interactions that caused diversity to drop when plots were fertilized (Rajaniemi 2002). The importance of root competition in this system may be attributed to the short, unlayered canopy and the lack of light limitation. Competition for light plays an important role in the productivity-diversity relationship in more productive grasslands (Carson & Pickett 1990; Gibson 1988).

Below-ground interactions may also be particularly important under the non-equilibrium conditions created by our experiment. In the transient dynamics following a disturbance, the ability to dominate space and resources below-ground may allow species to establish dominance before light becomes limiting. The ability to dominate below-ground should be strongest in adult clonal plants, which were used in our experiment and which dominate most grasslands. In dense cohorts of seedlings, on the other hand, competition for light may lead to assemblage-level thinning and random species loss (Goldberg & Miller 1990; Stevens & Carson 1999a, 1999b). If resource pulses from pollution are accompanied by other forms of vegetation disturbance, root competition may have strong effects on human-impacted plant communities.

Our results also may apply only to dominant species experiencing artificial increases in nutrient availability. Light competition may be more important for rarer species, which were not included in our experiment, especially if they rely on reproduction from seed. Shading, even at the low levels present in our system, might suppress germination of seedlings of some species. In contrast, shading may also enhance seedling survival, as it did for *Daucus*. Finally, responses of communities to natural productivity gradients, along which species

composition is likely to change, may differ from the responses of a fixed set of species to fertilization (Allison & Goldberg 2002). A more complete understanding of the effects of root and shoot competition along productivity gradients will require longer-term experiments with a wider range of species.

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References

- Abul-Fatih, H.A. & Bazzaz, F.A. (1979) The biology of *Ambrosia trifida* L. I. Influence of species removal on the organization of the plant community. *New Phytologist*, **83**, 813–816.
- Allen, E.B. & Forman, R.T.T. (1976) Plant species removals and old-field community structure and stability. *Ecology*, **57**, 1233–1243.
- Allison, V.J. (2001) *Direct and indirect effects of arbuscular mycorrhizal fungi on plant community composition*. PhD Dissertation, University of Michigan, Ann Arbor.
- Allison, V.J. & Goldberg, D.E. (2002) Species-level versus community-level patterns of mycorrhizal dependence on phosphorus: an example of Simpson's paradox. *Functional Ecology*, **16**, 346–352.
- Armesto, J.J. & Pickett, S.T.A. (1986) Removal experiments to test mechanisms of plant succession in oldfields. *Vegetatio*, **66**, 85–93.
- Austin, M.P. (1982) Use of a relative physiological performance value in the prediction of performance in multispecies mixtures from monoculture performance. *Journal of Ecology*, **70**, 559–570.
- Austin, M.P. & Austin, B.O. (1980) Behaviour of experimental plant communities along a nutrient gradient. *Journal of Ecology*, **68**, 891–918.
- Belcher, J.W., Keddy, P.A. & Twolan-Strutt, L. (1995) Root and shoot competition intensity along a soil depth gradient. *Journal of Ecology*, **83**, 673–682.
- Belsky, A.J. (1992) Effects of grazing, competition, disturbance and fire on species composition and diversity in grassland communities. *Journal of Vegetation Science*, **3**, 187–200.
- Bobbink, R., During, H.J., Schreurs, J., Willems, J. & Zielman, R. (1987) Effects of selective clipping and mowing time on species diversity in chalk grassland. *Folia Geobotanica and Phytotaxonomica*, **22**, 363–376.
- Cahill, J.F. (1999) Fertilization effects on interactions between above- and belowground competition in an old field. *Ecology*, **80**, 466–480.
- Cahill, J.F. (2002) What evidence is necessary in studies which separate root and shoot competition along productivity gradients? *Journal of Ecology*, **90**, 201–205.
- Carson, W.P. & Pickett, S.T.A. (1990) Role of resources and disturbance in the organization of an old-field plant community. *Ecology*, **71**, 226–238.
- DiTommaso, A. & Aarssen, L.W. (1989) Resource manipulations in natural vegetation: a review. *Vegetatio*, **84**, 9–29.

- Gibson, D.J. (1988) The maintenance of plant and soil heterogeneity in dune grassland. *Journal of Ecology*, **76**, 497–508.
- Goldberg, D.E. (1994) Influence of competition at the community level: an experimental version of the null models approach. *Ecology*, **75**, 1503–1506.
- Goldberg, D.E. & Estabrook, G. (1998) Separating the effects of number of individuals sampled and competition on species diversity: an experimental and analytical approach. *Journal of Ecology*, **86**, 983–988.
- Goldberg, D.E. & Miller, T.E. (1990) Effects of different resource additions on species diversity in an annual plant community. *Ecology*, **71**, 213–225.
- Gough, L., Osenberg, C.W., Gross, K.L. & Collins, S.L. (2000) Fertilization effects on species density and primary productivity in several herbaceous plant communities. *Oikos*, **89**, 428–439.
- Grime, J.P. (1977) Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *American Naturalist*, **111**, 1169–1194.
- Gurevitch, J. & Unnasch, R.S. (1989) Experimental removal of a dominant species at two levels of soil fertility. *Canadian Journal of Botany*, **67**, 3470–3477.
- Hils, M.H. & Vankat, J.L. (1982) Species removals from a first-year old-field plant community. *Ecology*, **63**, 705–711.
- Huston, M. (1979) A general hypothesis of species diversity. *American Naturalist*, **113**, 81–101.
- Jefferies, R.L. & Maron, J.L. (1997) The embarrassment of riches: atmospheric deposition of nitrogen and community and ecosystem processes. *Trends in Ecology and Evolution*, **12**, 74–78.
- Keddy, P.A. (1989) Effects of competition from shrubs on herbaceous wetland plants: a 4-year field experiment. *Canadian Journal of Botany*, **67**, 708–716.
- Leps, J. (1999) Nutrient status, disturbance and competition: an experimental test of relationships in a wet meadow. *Journal of Vegetation Science*, **10**, 219–230.
- Mittelbach, G.G., Steiner, C.F., Scheiner, S.M., Gross, K.L., Reynolds, H.L., Waide, R.B., Willig, M.R., Dodson, S.I. & Gough, L. (2001) What is the observed relationship between species richness and productivity? *Ecology*, **82**, 2381–2396.
- Newman, E.I. (1973) Competition and diversity in herbaceous vegetation. *Nature*, **244**, 310–311.
- Peltzer, D.A., Wilson, S.D. & Gerry, A.K. (1998) Competition intensity along a productivity gradient in a low-diversity grassland. *American Naturalist*, **151**, 465–476.
- Pinder, J.E. (1975) Effects of species removal on an old-field plant community. *Ecology*, **56**, 747–751.
- Rajaniemi, T.K. (2001) *Explaining the productivity-diversity relationship in plants: changing effects of competition on the community*. PhD Dissertation, University of Michigan, Ann Arbor.
- Rajaniemi, T.K. (2002) Why does fertilization reduce plant species diversity? Testing three competition-based hypotheses. *Journal of Ecology*, **90**, 316–324.
- Rajaniemi, T.K. (2003a) Explaining productivity-diversity relationships in plants in press. *Oikos*, **101**, 449–457.
- Rajaniemi, T.K. (2003b) Evidence for size asymmetry of belowground competition in press. *Basic and Applied Ecology*, **4**, 239–247.
- Rosenzweig, M.L. & Abramsky, Z. (1993) How are diversity and productivity related? *Species Diversity in Ecological Communities: Historical and Geographical Perspectives* (eds R.E. Ricklefs & D. Schluter), pp. 52–65. University of Chicago Press, Chicago.
- Schwinning, S. & Fox, G.A. (1995) Population dynamic consequences of competitive symmetry in annual plants. *Oikos*, **72**, 422–432.
- Schwinning, S. & Weiner, J. (1998) Mechanisms determining the degree of size asymmetry in competition among plants. *Oecologia*, **113**, 447–455.
- Smith, M.D., Hartnett, D.C. & Wilson, G.W.T. (1999) Interacting influence of mycorrhizal symbiosis and competition on plant diversity in tallgrass prairie. *Oecologia*, **121**, 574–582.
- Spackova, I., Kotorova, I. & Leps, J. (1998) Sensitivity of seedling recruitment to moss, litter and dominant removal in an oligotrophic wet meadow. *Folia Geobotanica*, **33**, 17–30.
- Stevens, M.H.H. & Carson, W.P. (1999a) Plant density determines species richness along an experimental fertility gradient. *Ecology*, **80**, 455–465.
- Stevens, M.H.H. & Carson, W.P. (1999b) The significance of assemblage-level thinning for species richness. *Journal of Ecology*, **87**, 490–502.
- Tilman, D. (1988) *Plant Strategies and the Dynamics and Structure of Plant Communities*. Princeton University Press, Princeton, New Jersey.
- Tilman, D. & Pacala, S. (1993) The maintenance of species richness in plant communities. *Species Diversity in Ecological Communities: Historical and Geographical Perspectives* (eds R.E. Ricklefs & D. Schluter), pp. 13–25. University of Chicago Press, Chicago.
- Twolan-Strutt, L. & Keddy, P.A. (1996) Above- and below-ground competition intensity in two contrasting wetland plant communities. *Ecology*, **77**, 259–270.
- Voss, E.G. (1972) *Michigan Flora: A Guide to the Identification and Occurrence of the Native and Naturalized Seed-Plants of the State. Part I. Monocots*. Cranbrook Institute of Science, Bloomfield Hills, MI.
- Voss, E.G. (1985) *Michigan Flora: A Guide to the Identification and Occurrence of the Native and Naturalized Seed-Plants of the State. Part II. Dicots (Sauraceae – Cornaceae)*. Cranbrook Institute of Science, Bloomfield Hills, MI.
- Voss, E.G. (1996) *Michigan Flora: A Guide to the Identification and Occurrence of the Native and Naturalized Seed-Plants of the State. Part III. Dicots (Pyrolaceae – Compositae)*. Cranbrook Institute of Science, Bloomfield Hill, MI.
- Waide, R.B., Willig, M.R., Steiner, C.F., Mittelbach, G., Gough, L., Dodson, S.I., Juday, G.P. & Parmenter, R. (1999) The relationship between productivity and species richness. *Annual Review of Ecology and Systematics*, **30**, 257–300.
- Wardle, D.A., Bonner, K.I., Barker, G.M., Yeates, G.W., Nicholson, K.S., Bardgett, R.D., Watson, R.N. & Ghani, A. (1999) Plant removals in perennial grassland: vegetation dynamics, decomposers, soil biodiversity, and ecosystem properties. *Ecological Monographs*, **69**, 535–568.
- Wilson, S.D. (1993) Belowground competition in forest and prairie. *Oikos*, **68**, 146–150.
- Wilson, S.D. & Tilman, D. (1991) Components of plant competition along an experimental gradient of nitrogen availability. *Ecology*, **72**, 1050–1065.
- Wilson, S.D. & Tilman, D. (1993) Plant competition and resource availability in response to disturbance and fertilization. *Ecology*, **74**, 599–611.
- Zamfir, M. & Goldberg, D.E. (2000) The effect of initial density on interactions between bryophytes at individual and community levels. *Journal of Ecology*, **88**, 243–255.
- Zobel, M. (1992) Plant species coexistence – the role of historical, evolutionary and ecological factors. *Oikos*, **65**, 314–320.
- Zobel, M. & Zobel, K. (2002) Studying plant competition: from root biomass to general aims. *Journal of Ecology*, **90**, 578–580.

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