

EFFECTS OF DIFFERENT RESOURCE ADDITIONS ON SPECIES DIVERSITY IN AN ANNUAL PLANT COMMUNITY¹

DEBORAH E. GOLDBERG

Department of Biology, University of Michigan, Ann Arbor, Michigan 48109 USA

AND

THOMAS E. MILLER²

*W. K. Kellogg Biological Station, Michigan State University,
Hickory Corners, Michigan 49060 USA*

Abstract. A commonly observed phenomenon in plant communities is that the addition of a limiting resource leads to an increase in productivity and a decrease in species diversity. We tested the hypothesis that the mechanism underlying this pattern is a disproportionate increase in mortality of smaller or shade-intolerant species in more productive sites caused by reduction of light levels. We added water and/or one of three nutrients (nitrogen, phosphorus, and potassium) to a 1st-yr old-field community dominated by weedy annuals and measured effects on productivity, species composition, diversity, and light levels after one growing season.

Diversity was not clearly related to productivity in this experiment. Watering increased productivity, but, contrary to expectations, had no effect on density of surviving plants, species diversity, or abundance of low-growing species. Almost all the increase in biomass with watering was due to a positive response by *Ambrosia artemisiifolia*, an upright annual that was the most common species in the canopy in all treatments. The addition of nitrogen had only a small positive effect on productivity, but strongly decreased density of surviving plants, species diversity, and abundance of most low-growing species. Only *Ambrosia* increased in abundance with nitrogen addition. The phosphorus and potassium additions had little effect on the community.

We suggest that the high mortality and low diversity in the nitrogen addition plots, but not in the more productive watered plots, was due to limitation by nitrogen earlier than limitation by water during the growing season. The consequence was earlier canopy closure and greater mortality due to light limitation.

Key words: *Ambrosia artemisiifolia*; *annual plants*; *Chenopodium album*; *Lepidium campestre*; *nitrogen limitation*; *Panicum capillare*; *productivity*; *resource additions*; *species diversity*; *water limitation*.

INTRODUCTION

A widespread pattern among plant communities is a decrease in species diversity associated with increasing nutrient availability (Pratt 1984, Tilman 1984, 1987, Inouye et al. 1987, Berendse and Elberse 1988, Carson and Barrett 1988, and see Huston 1979 and Tilman 1982 for reviews of earlier literature). A number of hypotheses have been proposed to explain the decline in diversity with increasing nutrient availability, all of which suggest that competitive interactions are responsible for excluding species that could otherwise survive throughout the nutrient gradient (Grime 1973, Newman 1973, Huston 1979, Tilman 1982). In this paper, we test and expand the suggestion by Newman

(1973) that increasing competition for light as nutrients increase is the cause of this pattern.

This hypothesis suggests the following sequence of mechanisms will result in a negative correlation between diversity and nutrient availability. (1) Increasing nutrient availability results in an increase in productivity and biomass of vegetation. (2) Increasing above-ground biomass in turn leads to a decline in light availability to subcanopy plants such as seedlings or low-growing species (Tilman 1983). (3) Decreasing light availability results in greater mortality of subcanopy plants. (4) Increasing mortality leads to lower species diversity through either loss of low-growing or shade-intolerant species and/or, if mortality falls equally on all species in the community, loss of initially rare species that are more likely to go extinct with higher overall mortality.

It is well known in single-species stands that self-thinning consistently occurs at a faster rate in more fertile soils (the Sukatschew effect: Sukatschew 1928

¹ Manuscript received 8 August 1988; revised 6 March 1989; accepted 8 April 1989.

² Present address: Department of Biological Sciences, B-142, Florida State University, Tallahassee, Florida 32306 USA.

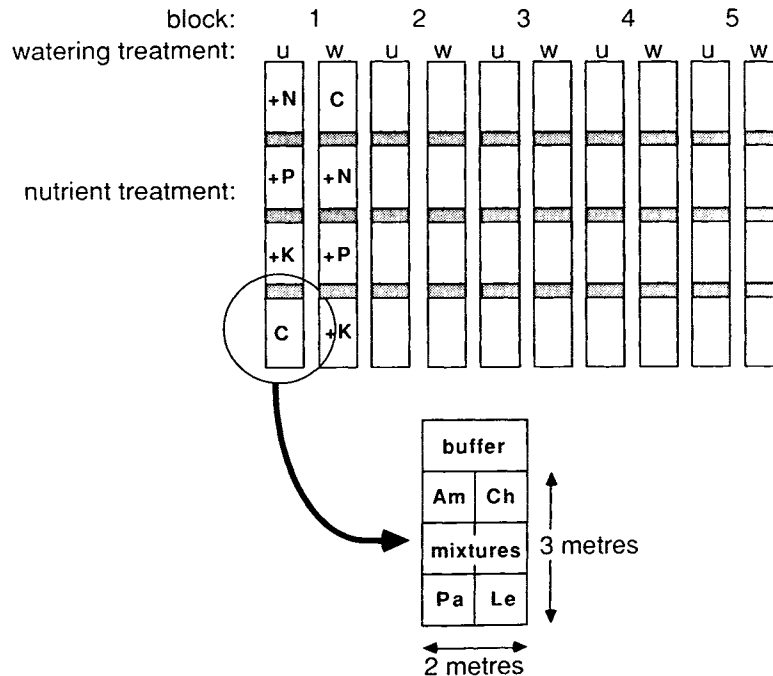


FIG. 1. Experimental design. U = unwatered, W = watered, C = nutrient control, +N = nitrogen addition, +P = phosphorus addition, +K = potassium addition, mixtures = natural community, Am = *Ambrosia artemisiifolia*, Ch = *Chenopodium album*, Pa = *Panicum capillare*, Le = *Lepidium campestre*. The four subplots within a plot designated by a species name were thinned to nine plants of that species per square metre.

in Harper 1977, Yoda et al. 1963, White and Harper 1970, Bazzaz and Harper 1976). The "light-mortality" hypothesis outlined above simply extends this phenomenon to the community level. The assumption is that individuals that emerge earlier or are larger or faster growing at the time of addition are better able to take advantage of the increase in nutrients and so grow taller and intercept more of the incoming light. Smaller plants then experience a light supply below their compensation point and die (Harper 1977, Weiner and Thomas 1986). Although few data exist even from monocultures to test whether it is indeed the smaller plants that die during thinning (see Black 1958, Schmitt et al. 1987 for exceptions), the few studies of thinning in two-species mixtures are consistent with this explanation. Using species with different growth forms, Bazzaz and Harper (1976) and White and Harper (1970) found that mortality tended to fall disproportionately on the species with a shorter growth form. No difference in rates of thinning were found in a third study that followed two species of very similar growth form (Malmberg and Smith 1982).

We added soil resources to a community of weedy annuals to test the following specific predictions of the light-mortality hypothesis. (1) Light at the soil surface is negatively correlated with aboveground biomass and with nutrient availability. (2) Probability of survival and therefore the density of surviving plants is negatively correlated with light availability. (3) Species di-

versity is negatively correlated with total density and with light availability. (4) The species that drop out of sites with resource additions are those that are slower growing, smaller, or have leaves held close to the ground or are physiologically shade intolerant (high light compensation points).

We also compared the effects of adding several different soil resources (water, N, P, K). The predictions of the light-mortality hypothesis should hold regardless of which soil resource is limiting. However, the majority of documented effects of resources on diversity are for nitrogen only or a combination of nitrogen with other nutrients. We ask if the overall relationship between diversity and productivity and the hypothesized causal relationships are the same for a given community regardless of which resource led to the increase in productivity.

Finally, we also tested two underlying assumptions of the light-mortality hypothesis, and indeed of all the hypotheses, to explain declining diversity with increasing productivity: that competition is indeed occurring and that species that decline with resource additions in the full community do not do so in the absence of competitors.

METHODS

Community

Our experimental system was a 1st-yr old-field community dominated by summer annuals at the W. K.

TABLE 1. Mean nutrient and water levels in control plots and plots with that resource added. Values with the same letter within each row and sampling date are not significantly different from each other.

	Pretreatment (3 June)		Harvest (15 September)	
	Control	Treat- ment	Control	Treat- ment
NO ₃ (mg/kg)	16.21 ^a	19.32 ^a	0.85 ^a	82.77 ^b
NH ₄ (mg/kg)	1.53 ^a	1.99 ^a	1.48 ^a	294.97 ^b
PO ₄ (mg/kg)	NA*	NA	0.0 ^a	108.01 ^b
% soil moisture (0–10 cm depth)	13.6 ^a	14.6 ^a	12.5 ^a	13.6 ^a

* NA = data not available.

Kellogg Biological Station, southwest Michigan, USA (see Miller and Werner 1987 for a description of the field). The field (Bailey Field) has been plowed in the winter or early spring (March) before germination in most years since 1977, including 1984 and 1985. This study was conducted during the growing season of 1985.

Experimental design

The experiment consisted of all combinations of two watering treatments (unwatered, watered) and four nutrient treatments (control, addition of nitrogen, phosphorus, or potassium) in a split block design, with water as the split factor (Fig. 1). We did not have combinations of the different nutrient additions. Each of the eight treatments was represented once in each of five blocks arranged across the field for a total of 40 experimental plots, established in May 1985.

To restrict the community to plants arising from seed, any perennials growing from rootstocks or rhizomes found in all plots were treated in mid-May by hand applications of a 5% solution of glyphosate (Roundup), a contact herbicide that only affects actively growing plants. Some perennials survived this treatment (mostly *Agropyron repens*) and these are included in the analyses described below.

Each treatment plot within each block contained six 1-m² subplots (Fig. 1). The center two of these subplots were left undisturbed as the natural mixture of species. The remaining four subplots were thinned to determine the response of a subset of the species to the resource additions in the absence of competition and to confirm that competition was indeed occurring in this community. One subplot was assigned to each of the four most common species in the community (*Ambrosia artemisiifolia*, *Chenopodium album*, *Lepidium campestre*, and *Panicum capillare*). These four annual species together accounted for >90% of the total aboveground biomass and >50% of the individuals in this community (see Fig. 5, below). On 25 May 1985, nine individual seedlings of the designated species were marked in each low competition subplot and all other plants were removed by handweeding. The plants were very small at this time and the weeding resulted in only

minor disturbance to the soil. The plots were reweeded as necessary over the season.

The resource additions were started on 3 June 1985, at which time germination was virtually complete (Miller 1987, from data collected in the same field in the same year). The equivalent of 10 g/m² of each nutrient in granular form was added every 2 wk for 16 wk. The total amount added (80 g·m⁻²·yr⁻¹) is somewhat higher than commercial fertilizer applications in the region (20–60 g·m⁻²·yr⁻¹) and other nutrient addition experiments in old fields (e.g., Pratt 1984, 22.4 g·m⁻²·yr⁻²; Tilman 1987, 27.2 g·m⁻²·yr⁻¹; Reed 1977, 45 g·m⁻²·yr⁻¹; Carson and Barrett 1988, 53.8 g·m⁻²·yr⁻¹). However, because nutrients were applied only once or twice in most of these enrichment experiments, the amount added at any one time in this experiment was considerably less than in these other studies. Nitrogen was added as NO₃NH₄, phosphorus as P₂O₅ (triple superphosphate), and potassium as K₂O (potash). Nutrients were scattered on the soil surface. The plots were then sprinkled lightly with water to work the granules into the soil and reduce loss by movement over the soil

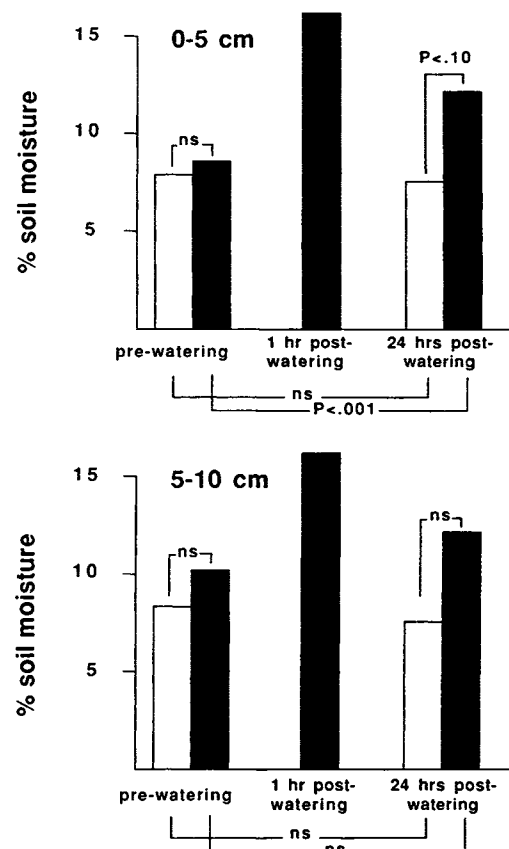


FIG. 2. Effects of watering on soil moisture. The height of the histograms represents the mean soil moisture in the five unwatered nutrient controls (open bars) or the five watered nutrient controls (solid bars).

TABLE 2. Effects of nutrient and water treatments on light, total plot biomass, density, and species diversity (ANOVAs). Error df for each ANOVA are given in the first data column except for the split factor, water, where error df = 4. Treatment means and pairwise comparisons are shown in Fig. 4 for light and in Fig. 5 for plant variables.

Variable	Error df	Source of variation							
		Block		Water (w)		Nutrient (n)		w × n	
		F	Num. df†	F	Num. df	F	Num. df	F	Num. df
% full sunlight	12	0.17	4	2.11	1	3.22†	1	0.30	3
Aboveground mass	24	0.39	4	74.73***	1	2.63†	1	0.14	3
Belowground mass	6	0.05	1	178.91*	1	0.98	1	0.34	3
Canopy height	12	0.10	2	0.39	1	0.05	1	4.36*	3
Density	24	9.34***	4	0.04	1	26.80***	1	0.85	3
Number of species	24	2.69†	4	0.16	1	42.16***	1	5.82**	3
Evenness (aboveground mass)	24	4.81**	4	2.96	1	2.91†	1	0.34	3
Evenness (density)	24	3.15*	4	1.66	1	11.35***	1	3.24*	3

† $P < .10$; * $P < .05$; ** $P < .01$; *** $P < .001$.

‡ Num. = numerator.

surface. Nutrient controls were watered at the same time.

Water addition was done every 2–3 d unless a rainfall sufficient to wet the soil to field capacity occurred. At the beginning of the season, watering was done with a flat sprinkler hose running through the center of the plots or with a standard “round-pattern” sprinkler in the middle of the plots. However, as the plants grew taller, this resulted in uneven coverage of the plots. In early July we switched to hand watering with a mist fitting on a hose, spraying each plot to be watered twice, allowing the water to soak into the soil between waterings. For all watering methods, watering was continued until the soil was soaked to field capacity.

Resource measurements

Soil samples were taken prior to resource additions from all 40 plots on 3 June and 4 d after the final fertilization and irrigation on 15 September. Each sample was a composite of six 0–10 cm deep cores from the natural mixture subplots. The surface of each soil

core (\approx top 0.25 cm) was discarded to avoid litter and any granules of fertilizer. A portion of the sample was weighed, dried, and reweighed for soil water content (expressed as a percentage of soil dry mass; soil texture is similar throughout the field so water content should be a good index of water availability). The remainder of each sample was immediately refrigerated. Within 48 h after collection, three 10-g replicates from each sample were extracted with 2 mol/L KCl (June samples) or 2 mol/L NaCl (September samples) and then analyzed for NO_3^- and NH_4^+ on a Technicon Autoanalyser II system (Technicon Instruments 1973a, 1977). For the September samples, we also analyzed PO_4^{3-} (Technicon Instruments 1973b). We used the mean of the three replicates from each sample in the statistical analyses of these data.

On 22–23 August, we measured soil water content to get an idea of the efficacy of the watering treatment. Just before watering, composites of four cores from 0–5 cm and 5–10 cm depth were collected from each of the nutrient controls in all blocks (10 plots). These samples were taken 3 d after the end of a 5-d period of daily rainfall. One hour after watering, a second set of samples was taken from the watered plots only, and 24 h after watering a third set of samples was taken from all 10 plots.

On 12 September, we measured irradiance at the soil surface and above the canopy in the natural mixtures in three of the five blocks using a LI-COR quantum sensor. We also recorded height of the canopy. The average of two measurements in each plot for irradiance and canopy height were used for statistical analyses.

Harvest

All the experimental plots were harvested between 16 and 25 September, by which time most plants had completed flowering. All individuals in the low competition subplots and in the center 50×50 cm of the

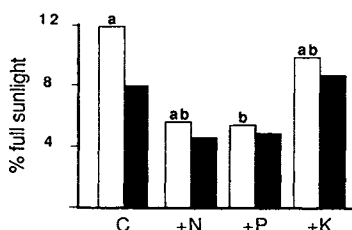


FIG. 3. Effects of the resource additions on percent of full sunlight at the soil surface, measured in September. The height of the bars represents the mean value of the five replicates of each treatment. □ unwatered plots, ■ watered plots. C indicates nutrient control (no additions). Bars within a watering treatment with different letters indicate that those nutrient treatments are significantly different by the LSD test. The ANOVA for these data is in Table 2.

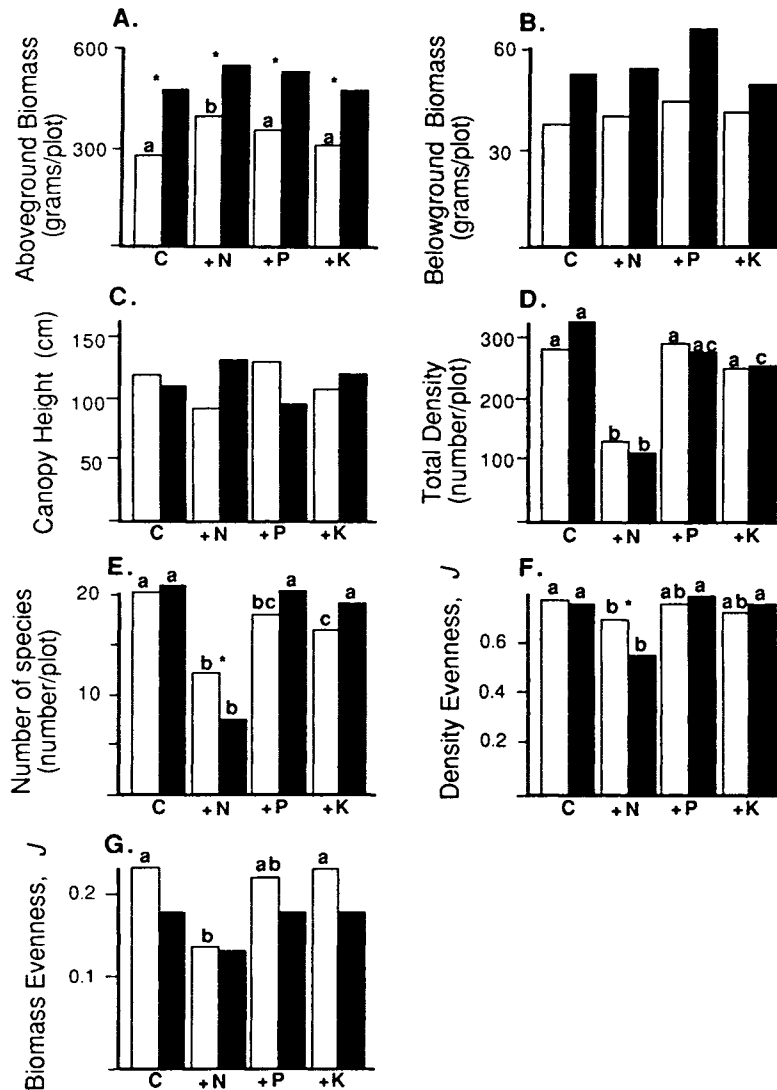


FIG. 4. Effects of the resource additions on community properties. Data presentation as in Fig. 3. * indicates that the watered and unwatered plots within a nutrient treatment are significantly different by the LSD test. The ANOVAs for these data are in Table 2.

two natural mixture subplots in each plot were harvested. Plants from the two mixture subplots were combined for all analyses reported below (area = 0.5 m²). In two of the five blocks, belowground, as well as aboveground biomass of all species were collected, using a hose to wash soil from around the roots in situ. All plants were sorted to species, counted, dried, and weighed.

Analysis

Effects of the resource additions on resource levels, community properties, and the performances of individual species were analyzed using a two-way split block ANOVA, where the error MS for the split factor, water, was the block × water interaction term (SAS 1985).

We used the least significant difference with $\alpha = .05$ (Sokal and Rohlf 1981) to test planned comparisons between treatments (between nutrient treatments within a watering treatment, between watering treatments within a nutrient treatment). Community variables were total plot aboveground biomass, belowground biomass, canopy height, density, number of species, and species evenness based on density or biomass ($J = H'/H'_{max}$, where $H' = p_i \ln p_i$ and p_i = proportion of total density or of total aboveground biomass of species i). For each of the 12 most common species (see Table 3, below), we also analyzed density, aboveground biomass per plot, and mean aboveground biomass per plant in the natural mixtures. We used paired t tests to examine the effects of competition on mean plant

TABLE 3. Effects of nutrient and water treatments on three measures of performance of the 12 most common species (ANOVAs). † Numerator df are given in parentheses below each source of variation. Error df = 4 for the split factor, water. For all other sources of variation, error df = 24 for the *F* values for density and biomass per plot and error df are given in

Species	Density (No. per plot)				Aboveground mass per plot			
	<i>F</i> _{block} (df = 4)	<i>F</i> _{water (w)} (df = 1)	<i>F</i> _{nutrient (n)} (df = 3)	<i>F</i> _{w×n} (df = 3)	<i>F</i> _{block} (df = 4)	<i>F</i> _{water (w)} (df = 1)	<i>F</i> _{nutrient (n)} (df = 3)	<i>F</i> _{w×n} (df = 3)
Erect annuals								
<i>Ambrosia artemisiifolia</i>	1.72	1.27	2.63†	2.97†	0.97	61.01**	3.51*	0.13
<i>Chenopodium album</i>	8.99***	1.41	1.79	1.89	2.49†	2.88	0.43	0.36
<i>Erigeron strigosus</i>	2.64*	0.34	11.07***	1.37	0.37	0.19	2.50†	0.68
Low annuals								
<i>Panicum capillare</i>	16.14***	21.76**	5.47**	0.41	17.46***	5.80†	4.27*	0.51
<i>Lepidium campestre</i>	3.45*	0.24	5.16**	0.10	4.51**	1.09	3.47*	0.48
<i>Barbarea vulgaris</i>	1.29	0.18	6.70**	0.65	1.14	0.32	5.90**	0.23
Erect perennials								
<i>Potentilla recta</i>	3.75*	2.79	12.25***	1.41	5.04**	0.49	7.82***	0.95
Low perennials								
<i>Silene alba</i>	2.40*	0.18	1.09	1.87	1.97	0.86	1.68	3.05*
<i>Daucus carota</i>	3.71*	1.97	4.79**	0.76	2.93*	1.57	5.58**	0.75
<i>Plantago lanceolata</i>	2.74*	0.14	6.82**	1.28	0.54	0.04	6.00**	0.80
<i>Trifolium repens</i>	2.22†	4.10	4.80**	0.40	1.88	0.01	2.61†	0.57
Rhizomatous perennials								
<i>Agropyron repens</i>	3.18*	0.40	3.92*	0.70	9.28***	0.39	3.60*	0.77

† $P < .10$; * $P < .05$; ** $P < .01$; *** $P < .001$.

‡ Treatment means and pairwise comparisons between treatments are shown in Fig. 6 for 1 or 2 representatives of each growth form. Other species in the same growth form showed similar trends.

biomass of the four species grown under reduced competition, with pairing between natural mixture and low competition subplots within each plot.

RESULTS

Resources

Before imposition of the experimental treatments in early June, soil nitrogen and moisture content did not differ between controls and the assigned addition plots (Table 1). After 3 mo of additions the nitrogen and phosphorus addition treatments had 1–2 orders of magnitude higher levels of the added nutrient than did the plots without additions (potassium was not measured; Table 1).

The watering treatment did not affect soil moisture content at the final harvest (Table 1). These soil moisture measurements were taken 4 d after the last watering, with no intervening rainfall. The measurements to check efficacy of the watering treatment in August showed marginally ($P < .10$) greater soil moisture in watered over control plots at 0–5 cm depth 24 h after watering, but no differences at 5–10 cm depth, although the trends were similar to the shallower samples (Fig. 2). Because plots were watered every 2–3 d when it didn't rain, surface soil moisture that could benefit shallow roots was likely higher in the watered plots for much of the time.

The soil resource additions also influenced light

availability in the plots (Table 2, Fig. 3). The percent of full sunlight at the soil surface at the end of the growing season was significantly lower in the phosphorus addition plots and generally lower (but nonsignificantly so) in the nitrogen and water addition plots.

Community properties

Water addition had a highly significant effect on total aboveground biomass (Table 2). Within each nutrient treatment, the watered plots had significantly more aboveground biomass than did the unwatered plots (Fig. 4A). Similar effects of water addition are evident in the data for belowground biomass, however, probably because of the smaller sample sizes, none of the treatment comparisons were significant (Table 2, Fig. 4B). The nutrient treatments had only a marginally significant ($P < .10$) effect (Table 2) on aboveground biomass and no effect on belowground biomass. Only the nitrogen addition treatment in the unwatered plots produced significantly greater aboveground biomass than the nutrient control (Fig. 4A). Plants in the nitrogen addition plots (watered or unwatered) had the typical dark green color indicating high nitrogen content. Canopy height was not significantly affected by any of the resource additions (Table 2, Fig. 4C).

Density and species diversity responded very differently to the resource additions than did aboveground biomass (Table 2, Fig. 4D–G). Water had no effects in any of the ANOVAs, but nutrient treatment had a

the first column under mass per plant. The latter are usually lower because only plots with the species present were included.

Aboveground mass per plant				
Error df	F_{block} (df = 4)	$F_{\text{water (w)}}$ (df = 1)	$F_{\text{nutrient (n)}}$ (df = 3)	$F_{\text{w} \times \text{n}}$ (df = 3)
24	1.29	13.29*	8.14***	1.93
24	1.10	1.64	0.49	0.16
17	0.63	2.03	1.16	0.80
21	1.76	0.61	0.57	0.39
21	2.39†	0.01	0.81	0.12
15	0.45	1.08	0.95	1.70
12	0.82	0.13	0.68	0.28
17	1.42	0.06	1.99	0.43
21	1.68	1.11	0.51	2.25
17	0.31	0.08	1.48	0.55
17	1.60	4.19	1.52	1.71
21	16.58***	1.11	2.04	2.21

highly significant effect on density and most diversity indices (Table 2). Nitrogen addition significantly lowered total density and, usually, diversity relative to the controls and other nutrient addition treatments. Only in the nitrogen addition plots did water have an effect, further decreasing diversity and contributing to the significant water \times nitrogen interaction (Table 2).

Patterns of variation among blocks also differed between biomass and density. Total biomass was similar among blocks, while density showed significant spatial variation (Table 2), suggesting that spatial variation in density was compensated by larger size plants in lower density plots.

Species responses

A total of 46 species were found in the natural mixture plots, but many of these were very rare (occurred in only a few plots or with proportional biomass contributions of <0.1%). We analyzed density, mass per plot, and mass per plant for the 12 most abundant species (Table 3; means and treatment comparisons for seven of these species are shown in Fig. 5). These 12 species together always accounted for at least 97% of the total plot biomass and 88% of the total number of individuals in a plot. No other species ever contributed >1% to the total biomass in any plot.

The only species observed in the canopy in any plot were *Ambrosia artemisiifolia* and *Chenopodium album*, both tall, leafy-stemmed annuals. *Ambrosia* and *Chenopodium* were also the first and second most

abundant species, respectively, in all treatments in terms of both biomass and density. As discussed below, these two species responded somewhat differently to the resource additions than did the remaining subcanopy species, which were either rosette or spreading annuals or perennials of various growth forms (except for the relatively rare *Erigeron strigosus*).

Density. Density of only 1 of the 12 species was significantly affected by watering (Table 3) and only 1 of the 48 possible pairwise comparisons was significant. In contrast, the nutrient treatments had significant effects on density for 9 of the 12 species (Table 3). Every one of the species had its lowest mean density in the nitrogen addition treatments (Fig. 5A) and 46% of the 72 possible pairwise comparisons of the +N treatments with the controls, +P, or +K treatments were significant. The decreases in density in the +N treatment for the two canopy species, *Ambrosia* and *Chenopodium*, were not significant and the magnitude of their decrease (unwatered: 20 and 19% decrease from controls; watered: 24 and 47% decrease from controls, respectively) was much less than the magnitude of decrease in the 10 subcanopy species (unwatered: mean decrease from controls = 78%, range = 50–94%; watered: mean decrease from controls = 86%, range = 52–100%). Only 11% of the possible comparisons of the phosphorus or potassium additions with the controls or with each other were significant (Fig. 5A).

Biomass per plot. Only *Ambrosia* showed a significant response to water addition in the ANOVA (Table 3) and in the pairwise comparisons; within each nutrient treatment, total plot biomass was significantly greater with watering (Fig. 5B). In contrast, the nutrient additions had significant effects on biomass per plot for 8 of the 12 species (Table 3). Again, most of the nutrient effect in the ANOVAs was due to the nitrogen treatment; all 10 subcanopy species had their lowest mass per plot in the +N treatments and, 35% of the comparisons of +N treatments with the control, +P, or +K treatments were significant (Fig. 5B). In contrast, *Ambrosia* mass per plot increased with nitrogen addition in both the watered and unwatered treatments, although the difference between nutrient controls and +N was significant only in the unwatered plots (Fig. 5B). *Chenopodium* biomass per plot was never significantly different among nutrient treatments (Fig. 5B). Again, very few of the comparisons of +P or +K with the controls or each other were significant (10% of possible comparisons; Fig. 5B).

Biomass per plant. Biomass per plant was not significantly influenced by water or nutrient additions for any of the species except *Ambrosia* (Table 3). *Ambrosia* mass per plant was significantly greater than the controls for both +N comparisons and two of the four +water comparisons (Fig. 5C). *Chenopodium* showed similar, but nonsignificant trends (Fig. 5C). For the subcanopy species, some of the planned treatment

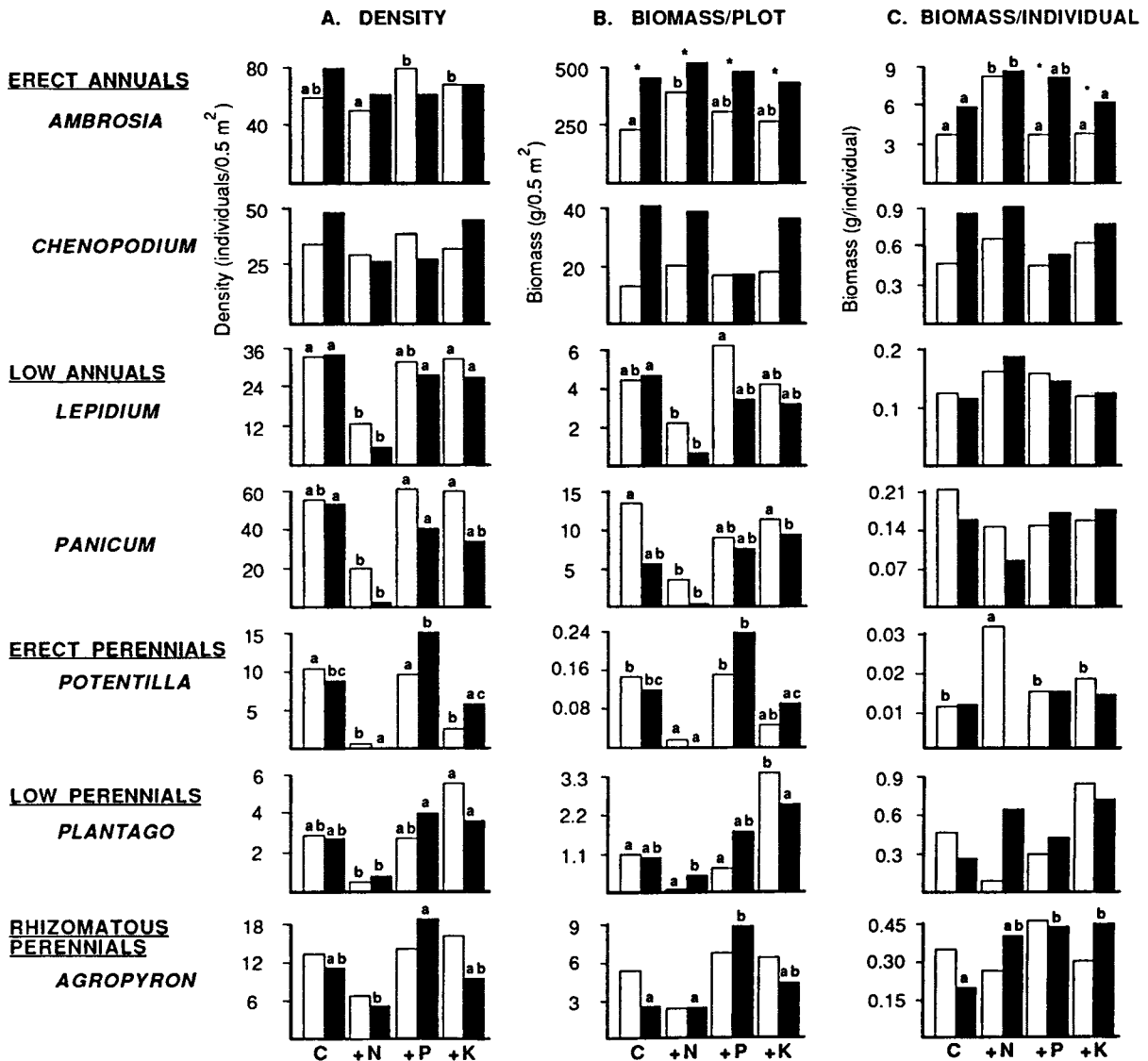


FIG. 5. Effects of the resource additions on performance of individual species. All species except *Agropyron* are entirely from seed. Data presentation as in Fig. 3. * indicates that the watered and unwatered plots within a nutrient treatment are significantly different by the LSD test. The ANOVAs for these data are in Table 3. Note the differences in scale among species.

comparisons were significant despite lack of significance of the ANOVAs; in these cases, resource additions always increased mean plant mass (Fig. 5C).

Species responses to resources in low competition

Competition strongly reduced individual growth of all four species that were grown in the low-density monocultures ($P < .001$ for all comparisons between low competition and the mixed community using paired t tests for each species; compare Figs. 5C and 6). All individuals in the low competition plots survived to the end of the growing season. None of the nutrient and water treatments significantly affected mean plant

mass under low competition (Table 4, Fig. 6). Nor was the percent reduction in mean plant mass due to competition significantly affected by the treatments (Table 4).

Productivity and diversity relationships

The light-mortality hypothesis predicts that the addition of any limiting resource will result in an increase in productivity and a decrease in diversity. However, only one of the three measures of diversity showed a significant negative correlation with productivity (Fig. 7). For all three diversity measures, it appears that at a given productivity level, the nitrogen addition plots consistently had lower diversity than did the other

TABLE 4. Effects of nutrient and water treatments on mass of plants grown with low competition. ‡ Numerator df are given in parentheses below each source of variation. Error df = 4 for the split factor, water; for other sources of variation error df are given in column 2 of the table. Only plots in which the species was present were included in the analyses.

Species	Error df	Mass per plant under low competition				Mass per plant in mixed community/ mass per plant in low competition			
		F_{block} (df = 4)	F_{water} (w) (df = 1)	F_{nutrient} (n) (df = 3)	$F_{\text{w} \times \text{n}}$ (df = 3)	F_{block} (df = 4)	F_{water} (w) (df = 1)	F_{nutrient} (n) (df = 3)	$F_{\text{w} \times \text{n}}$ (df = 3)
<i>Ambrosia artemisiifolia</i>	24	2.66†	5.45†	1.03	0.30	1.03	2.81	2.86†	1.44
<i>Chenopodium album</i>	22	1.84	3.36	0.30	0.54	0.74	1.40	0.87	0.87
<i>Panicum capillare</i>	23	2.92*	0.42	0.28	0.87	2.80†	3.54	0.62	0.13
<i>Lepidium campestre</i>	23	4.45**	2.98	0.50	2.85†	2.84†	2.15	1.94	2.46†

† $P < .10$; * $P < .05$; ** $P < .01$.

‡ Treatment means and comparisons are shown in Fig. 7.

treatments (Fig. 7). When the +N plots were excluded from the analyses, the one significant relationship became nonsignificant (Fig. 7).

To see where the prediction failed, we broke down the relationship into the three hypothesized causal relationships. As expected, light availability in the subcanopy significantly decreased with increasing aboveground biomass (Fig. 8A). At the highest biomass levels observed (all in the watered plots), irradiance at the soil surface was 3–8% of full sunlight. However, total density at the final harvest (assumed to indicate survivorship) did not decrease with decreasing light (Fig. 8B). Instead, at a given light level, density was lower (i.e., mortality was higher) in the +N plots. Finally, again as expected, number of species was strongly positively correlated with total density (Fig. 8C, other indices of diversity show similar patterns). This relationship remained significant even if the +N plots, with much lower density, were excluded.

The final prediction of the light-diversity hypothesis

was that the relative abundance of low-growing species would be lower in plots with higher aboveground biomass. Consistent with this prediction, the summed percent of total plot mass for all rosette dicots and low-growing grasses (e.g., *Panicum*) was significantly negatively related to total plot biomass (Fig. 8D). Although the relationship was still significantly negative without the +N plots, the relative abundance of low-growing species was lower in the +N plots than in the other treatments for a given aboveground biomass (Fig. 8D).

DISCUSSION

Community properties

Despite the high levels of nutrients added, water was much more limiting to community productivity than was nitrogen, and phosphorus and potassium were not limiting at all. This is unlikely to be an unusual phenomenon because of an exceptionally dry year. In fact, rainfall in 1985, the year of this study, was much higher

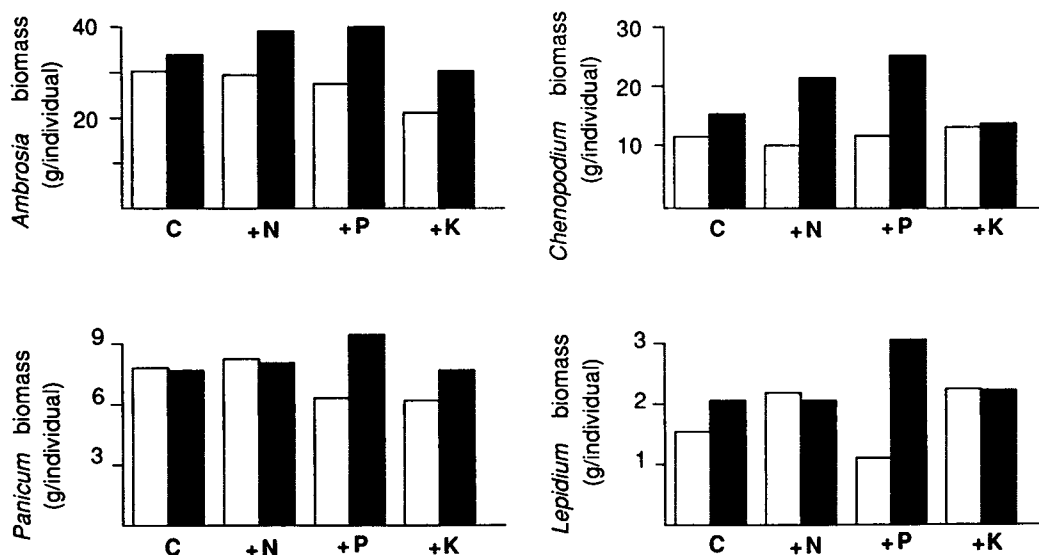


FIG. 6. Effects of resource additions on mean biomass per plant of individual species when grown at low density. The ANOVAs for these data are in Table 4.

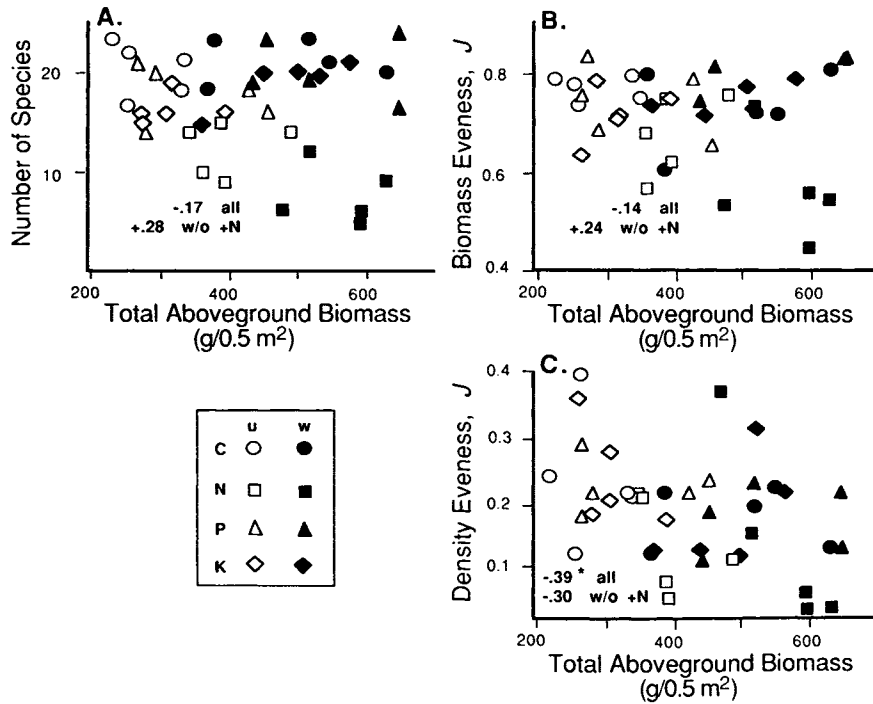


FIG. 7. Relationships between species diversity and total aboveground biomass over all experimental treatments. Correlation coefficients are for all plots ($n = 40$) and for +nitrogen plots excluded (w/o +N, $n = 30$). * $P < .05$.

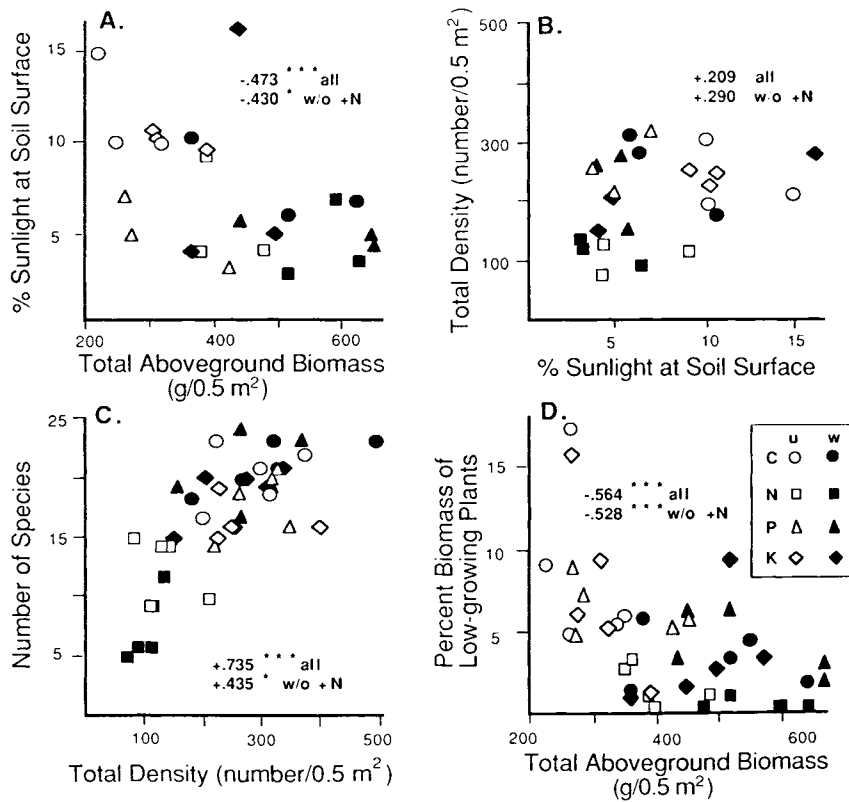


FIG. 8. Tests of the predictions of the light-mortality hypothesis for relationships among total biomass, light availability, total density, and species diversity. Correlation coefficients are for all plots ($n = 40$) and for +nitrogen plots excluded (w/o +N, $n = 30$). * $P < .05$; *** $P < .001$.

(541 mm, May through August) than average (386 mm, 1981–1985).

Whether or not addition of a limiting resource led to a decrease in diversity in this experiment depended on the identity of the limiting resource. Even though addition of water led to a greater increase in productivity than did addition of nitrogen, diversity decreased only with nitrogen addition. This is not consistent with the light-mortality hypothesis or, indeed, any of the hypotheses in the literature to explain diversity–productivity relationships. These all predict that diversity should decrease with increasing productivity, regardless of the cause of the increase. Our result is not due to different effects of water and nitrogen on light levels, at least as measured at the end of the growing season, because light levels were similar between the nitrogen and water addition plots. The result does appear to be related to differences in effect of nitrogen and water on mortality. Mortality in the nitrogen addition plots was consistently higher than in any of the other treatments, regardless of light availability measured at the end of the growing season.

One possible explanation of the higher mortality and consequent loss of species with nitrogen addition than with water addition is toxic effects of the added nitrogen. We cannot exclude this possibility but several points argue against it. First, surviving individuals in the +N plots were not smaller than in the other treatments for any species; in fact, several of the species that decreased in density with nitrogen addition significantly increased in size of surviving plants. It is, however, possible that seedlings experienced a toxic effect but plants that survived some sort of initial nutrient shock were able to benefit from the excess nitrogen, as Specht (1963) found for some species in an Australian heath with phosphorus additions. However, the amounts of N added during the seedling stage of these plants were similar to or lower than all other N addition experiments in old fields or in commercial agricultural fields (see Methods). Second, the four species grown in the low competition plots also showed no negative effects of nitrogen addition or growth or, in contrast with the mixed community plots, on survival. Third, many of the species in the plots are common weeds in fertilized agricultural fields. Although the total amount of nitrogen added in our plots over the season is somewhat higher than typical commercial fertilizer applications in the region, the amount added at any one time is very much less. We would not expect strong negative responses to such a common environment for these plants. Finally, if the higher mortality with N addition was due to toxicity, addition of water as well as N would be expected to lessen the effect because of dilution. Instead, the trend was for overall mortality, and mortality for each species to be even lower when both N and water were added.

An alternative hypothesis to explain the contrasting effects of the nitrogen and water additions on mortality

and diversity is an extension of the light-mortality hypothesis that includes the effects of timing of limitation by each resource. Specifically, we suggest that addition of a resource that is limiting earlier in the growing season will be more likely to increase mortality and reduce diversity relative to controls than will addition of a resource that is limiting later in the growing season. The reasoning is that addition of a resource that is limiting earlier in the season will lead to earlier canopy closure and thus induction of light limitation to sub-canopy plants at a time when they are smaller and more likely to respond to light limitation by death rather than by reduced growth only. This assumes that, in our experiments, nitrogen was limiting to growth early in the season and water relatively later, which cannot be tested with our experimental design.

This phenology extension of the light-mortality hypothesis assumes that smaller individuals are more likely to die than larger individuals at the same low levels of light because they are less able to withstand a negative carbon balance. Several studies with monocultures and two-species mixtures have shown that smaller plants are more likely to experience density-dependent mortality (Black 1958, White and Harper 1970, Bazzaz and Harper 1978, Schmitt et al. 1987). However, these studies do not distinguish between higher mortality of smaller plants because they receive less light and because they are less able to survive at low light.

It is important to note that the phenology hypothesis predicts eventual reductions in diversity, even with an increase only in a later limiting resource, because species with reduced growth, but not survival, will also likely have reduced fecundity. Over several generations, this will lead to declining population sizes and, eventually, local extinction. Thus, we would expect that if our experiment had been carried out for a longer period of time, diversity would eventually have declined even in the water addition treatment. This suggests that, for communities at equilibrium, resource phenology will have a relatively small effect on patterns of diversity along productivity gradients. However, for communities subject to periodic disturbance, resource phenology could play an important role in determining spatial gradients of diversity because of its effect on the rate of competitive exclusion (cf. Huston 1979).

Although we know of no experiments that have compared the effects of adding resources to natural communities at different times of the season, an experiment by Reed (1977) does support the idea that the timing of resource addition influences the community-level consequences of resource additions. In a 1st-yr old field dominated by *Ambrosia artemisiifolia* and with many other of the species found in our plots, Reed added the same total quantity of NPK fertilizer in a single pulse at the beginning of the season or in 5 or 10 pulses spread throughout the season. He found that the addition of a single pulse early in the season led to a much

greater reduction in diversity than did application of the same total quantity in a sequence of smaller pulses. This result is consistent with our hypothesis that earlier addition has greater effects on diversity although the mechanisms that produced this result cannot be demonstrated without detailed demographic and resource data. Reed's result is, however, also consistent with a toxicity effect of added nutrients on seedlings, but not on older plants. It is possible that similar phenology considerations may explain some of the other examples in the literature of where nutrient or water addition did not result in decreased diversity despite increases in productivity or biomass (e.g., Mellinger and McNaughton 1975, Wakefield and Barrett 1979, Chapin and Shaver 1985, Walker and Peet 1985).

Species composition

The increase in total community aboveground biomass with water and nitrogen addition was almost entirely because of the positive response of *Ambrosia artemisiifolia* to both of these resources. All other species either decreased or showed no significant change in aboveground biomass with addition of either resource. An important question then is what traits of *Ambrosia* allowed it to respond positively to both resources to a much greater extent than any other species.

We suggest that *Ambrosia* has an initial size advantage, through possession of such traits as slightly earlier germination than the other annuals (Miller 1987) and larger seeds and cotyledons. Numerous experimental studies have shown that any of these traits may produce a competitive advantage in early growth stages and that this advantage persists throughout the life cycle (Black and Wilkinson 1963, Ross and Harper 1972, Watkinson et al. 1983, Gross 1984, Stanton 1984, 1985). The upright growth form of mature *Ambrosia* plants also confers an advantage in light acquisition over low-growing plants such as *Lepidium*, *Daucus*, *Plantago*, and *Trifolium*.

Because of its initially larger size and upright growth form, *Ambrosia* should be able to gain disproportionately from the resource additions and be less likely to suffer the increased mortality resulting from earlier canopy closure and light limitation. Any *Ambrosia* individuals that are below the canopy (e.g., that emerged later, cf. Miller 1987) should suffer the same fate as subcanopy individuals of other species. Mortality of *Ambrosia* in the +N plots would then be less than that for other species only because a smaller part of the *Ambrosia* population is beneath the canopy.

This general explanation is supported by the comparison with *Chenopodium album*, the second most abundant species in all plots and the only other species found in the canopy. *Chenopodium* is also an upright annual and so has an advantage in access to light later in the season, but germinates slightly later in the season (Miller 1987) and has much smaller seeds (0.47 mg) than *Ambrosia* (3.61 mg). *Chenopodium* showed no

significant responses to the additions of nitrogen or water; it does not increase as does *Ambrosia* nor does it decrease as do all the remaining species, which are all either low-growing annuals or slower growing perennials.

The differences in species composition among treatments are therefore consistent with the hypothesis that competition for light plays a role in diversity reduction with increasing productivity. The species that increase in relative abundance with resource addition are those that have the tallest growth forms. Similar to the results reported here, Willis (1963) found that fertilization of dune communities led to a reduction in diversity due to a loss of the "small" plants, primarily rosette forms and bryophytes (see also Tilman 1987). The changes in species composition we observed would only be consistent with the toxicity hypothesis if, for some unknown reason, susceptibility to very high nitrogen levels was correlated with growth form.

Conclusions

The relationship between resource availability, productivity, and diversity is clearly not simple. Although decreasing diversity with increasing productivity (above some minimum value) is still the more common result, the contrasting effects of water and nitrogen on productivity and diversity in this study point out the need for a more comprehensive theory. Previous ideas about the relationship between productivity and diversity suggest that a similar relationship should hold no matter what the cause of variation in productivity. We have speculated that phenology of resource limitation may explain some of the variability in results of resource addition experiments, but much more detailed demographic data are needed to test these ideas and other possible mechanisms.

ACKNOWLEDGMENTS

We thank Lisa Bradshaw, Lisa Huberty, Rob Creed, Beth Kohler, Laura Riley, and Craig Osenberg for assistance in the field or laboratory and Earl Werner, Alice Winn, and two anonymous reviewers for comments on the manuscript. This research was supported by a USDA grant (84-CR-CR-1-1396) to T. E. Miller and P. A. Werner. Kellogg Biological Station Contribution Number 664.

LITERATURE CITED

- Bazzaz, F. A., and J. L. Harper. 1976. Relationship between plant weight and numbers in mixed populations of *Sinapsis arvensis* (L.) Rabenh. and *Lepidium sativum* L. *Journal of Applied Ecology* 13:211-216.
- Berendse, F., and W. T. Elberse. 1990. Competition, succession, and nutrient availability. In J. Grace and D. Tilman, editors. *Perspectives in plant competition*. Academic Press, New York, New York, USA, in press.
- Black, J. N. 1958. Competition between plants of different initial seed sizes in swards of subterranean clover (*Trifolium subterraneum* L.) in relation to size of seed. *Australian Journal of Agricultural Research* 8:1-14.
- Black, J. N., and G. N. Wilkinson. 1963. The role of time of emergence in determining the growth of individual plants in swards of subterranean clover (*Trifolium subterraneum*

- L.). *Australian Journal of Agricultural Research* **14**:628–638.
- Carson, W. P., and G. W. Barrett. 1988. Succession in old-field plant communities: effects of contrasting types of nutrient enrichment. *Ecology* **69**:984–994.
- Chapin, F. S., III, and G. R. Shaver. 1985. Individualistic growth response of tundra plant species to environmental manipulations in the field. *Ecology* **66**:564–576.
- Grime, J. P. 1973. Control of species density in herbaceous vegetation. *Journal of Environmental Management* **1**:151–167.
- Gross, K. L. 1984. Effects of seed size and growth form on seedling establishment of six monocarpic perennial plants. *Journal of Ecology* **72**:369–387.
- Harper, J. L. 1977. *Population biology of plants*. Academic Press, New York, New York, USA.
- Huston, M. 1979. A general hypothesis of species diversity. *American Naturalist* **113**:81–101.
- Inouye, R. S., N. J. Huntley, D. Tilman, and J. R. Tester. 1987. Pocket gophers (*Geomys bursarius*), vegetation, and soil nitrogen along a successional sere in east central Minnesota. *Oecologia (Berlin)* **72**:178–184.
- Malmberg, C., and H. Smith. 1982. Relationship between plant weight and density in mixed populations of *Medicago sativa* and *Trifolium pratense*. *Oikos* **38**:365–368.
- Mellinger, M. V., and S. J. McNaughton. 1975. Structure and function of successional vascular plant communities in central New York. *Ecological Monographs* **45**:161–182.
- Miller, T. E. 1987. Effects of emergence time on survival and growth in an early old-field plant community. *Oecologia (Berlin)* **72**:272–278.
- Miller, T. E., and P. A. Werner. 1987. Competitive effects and responses between plant species in a first-year old-field community. *Ecology* **68**:1201–1210.
- Newman, E. I. 1973. Competition and diversity in herbaceous vegetation. *Nature* **244**:310–311.
- Pratt, C. R. 1984. Response of *Solidago graminifolia* and *S. juncea* to nitrogen fertilization applications: changes in biomass allocation and implications for community structure. *Bulletin of the Torrey Botanical Club* **111**:469–478.
- Reed, F. C. 1977. Plant species number, biomass accumulation and productivity of a differentially fertilized Michigan old-field. *Oecologia (Berlin)* **30**:43–53.
- Ross, M. A., and J. L. Harper. 1972. Occupation of biological space during seedling establishment. *Journal of Ecology* **60**:77–88.
- SAS. 1985. *SAS user's guide: statistics*. Version 5 edition. SAS Institute, Cary, North Carolina, USA.
- Schmitt, J., J. Eccleston, and D. W. Ehrhardt. 1987. Dominance and suppression, size-dependent growth, and self thinning in a natural *Impatiens capensis* population. *Journal of Ecology* **75**:651–665.
- Sokal, R. R., and F. J. Rohlf. 1981. *Biometry*. Second edition. W. H. Freeman, New York, New York, USA.
- Specht, R. L. 1963. Dark Island Heath (Ninety-mile Plain, South Australia). VII. The effect of fertilizers on composition and growth, 1950–60. *Australian Journal of Botany* **11**:67–94.
- Stanton, M. L. 1984. Seed variation in wild radish: effect of seed size on components of seedling and adult fitness. *Ecology* **65**:1105–1112.
- . 1985. Seed size and emergence time within a stand of wild radish (*Raphanus raphanistrum* L.): the establishment of a fitness hierarchy. *Oecologia (Berlin)* **67**:524–531.
- Technicon Instruments Corporation. 1973a. Nitrate and nitrate in water and wastewater. Industrial Method Number 100-70W. Tarrytown, New York, USA.
- . 1973b. Orthophosphate in water and wastewater. Industrial Method Number 94-70W. Tarrytown, New York, USA.
- . 1977. Individual/simultaneous determinations of nitrogen and/or phosphorus in BD acid digests. Industrial Method Number 329-74W. Tarrytown, New York, USA.
- Tilman, D. 1982. Resource competition and community structure. *Monographs in Population Biology*. Princeton University Press, Princeton, New Jersey, USA.
- . 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.
- . 1987. Secondary succession and the pattern of plant dominance along experimental nitrogen gradients. *Ecological Monographs* **57**:189–214.
- Wakefield, N. G., and G. W. Barrett. 1979. Effects of positive and negative nitrogen perturbations on an old-field ecosystem. *American Midland Naturalist* **101**:159–169.
- Walker, J., and R. K. Peet. 1985. Composition and species diversity of pine-wiregrass savannas of the Green Swamp, North Carolina. *Vegetatio* **55**:163–179.
- Watkinson, A. R., W. M. Lonsdale, and C. G. Firbank. 1983. A neighborhood approach to self-thinning. *Oecologia (Berlin)* **56**:381–384.
- White, J., and J. L. Harper. 1970. Correlated changes in plant size and number in plant populations. *Journal of Ecology* **58**:467–485.
- Weiner, J., and S. C. Thomas. 1986. Size variability and competition in plant monocultures. *Oikos* **47**:211–222.
- Willis, A. J. 1963. Braunton Burrows: the effects on the vegetation of the addition of mineral nutrients to the dune soils. *Journal of Ecology* **51**:353–374.
- Yoda, K., T. Kira, H. Ogawa, and K. Hozumi. 1963. Self-thinning in overcrowded pure stands under cultivated and natural conditions. *Journal of Biology, Osaka City University* **14**:107–129.