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## PLANT DOMINANCE ALONG AN EXPERIMENTAL NUTRIENT GRADIENT<sup>1</sup>

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**Abstract.** Fertilization experiments in an 8-yr-old field demonstrated that N was the major limiting nutrient of N, P, K, Ca, and Mg, and suggested that Mg became limiting when N was added. After the fertilization experiments, this field was disturbed via thorough disking and divided into 36 plots for a Latin square design experiment on the effect of N:Mg fertilization ratios on vegetation patterns. By the second year, the major species had separated along the imposed N:Mg gradient, with *Agrostis scabra* dominant at the low Mg but high N end, followed by *Agropyron repens*, *Berteroa incana*, *Oenothera biennis*, and *Aristida basiramea*, which was dominant at the high Mg but low N end of the gradient. An unmanipulated resource, light availability at the soil surface, was significantly affected by the treatments. The results demonstrate that spatial heterogeneity in the relative availability of soil nutrients may be one cause of spatial heterogeneity in early successional vegetation.

**Key words:** competition; light; magnesium; nitrogen; old fields; resource ratio hypothesis; spatial variability; succession.

### INTRODUCTION

Plant communities have numerous spatial and temporal patterns in their species composition. Relatively smooth, continuous changes in vegetation have been reported along elevational and other physical gradients (e.g., Zedler and Zedler 1969, Whittaker and Niering 1975). Other patterns within apparently spatially heterogeneous vegetation can often be partially described as gradients with respect to some spatially variable factor such as water, a soil nutrient, or soil pH (e.g., Whittaker 1975, Gauch 1982). Additionally, many plant communities show relatively repeatable patterns of change in their species composition, termed "succession," following a disturbance. Drury and Nisbet (1973) argued that the same processes that explained changes in the composition of plant communities through time should explain the spatial heterogeneity of communities at any given time. Plant-community ecology may not yet be at the point of such a synthesis. However, there are some approaches to plant-community ecology that may have the potential to predict both spatial and temporal patterns. One of these is the hypothesis that plant competition for limiting resources may be an important process determining which species are dominant in a given habitat (e.g., Tilman 1982). This theory predicts that plants will be separated along a gradient of two limiting resources if plants are competing for the resources and if there are "tradeoffs" (Tilman 1982:244) in the competitive abilities of the plant species for the resources. This study was designed to test some of the assumptions and predictions of this "resource ratio hypothesis" (Tilman 1982) that are specifically related to the role that spatial heterogeneity of

nutrients might play in causing spatial patchiness in vegetation.

The approach taken was wholly experimental. Work in 1978 determined when, how, and how much of various nutrients could be added to vegetation without "burning" it, and a preliminary experiment was performed in 1979 to determine which soil nutrients might be limiting to the plants in the area to be studied. Vegetation was fertilized with macronutrients (N, P, K, Mg, Ca) supplied singly and in various combinations. These data, reported in this paper, indicated that nitrogen was the major limiting nutrient and suggested that magnesium might be limiting to some species. In 1980 and 1981, the effects of these two nutrients on the pattern of species dominance in early successional vegetation were determined by fertilizing with different ratios of N:Mg. Other potentially important resources, such as light and water, were not experimentally manipulated, although their availability was probably affected by the treatments.

### METHODS

This study was conducted at the University of Minnesota's Cedar Creek Natural History Area, located on the Anoka sandplain, 45 km north of Minneapolis, Minnesota. The field I used had not been used for agriculture since 1972 (the last crop was rye), was dominated by patches of herbaceous dicots and grasses, and had few woody plants. The most common plants, in approximate order, were *Agrostis scabra*, *Oenothera biennis*, *Agropyron repens*, *Erigeron canadensis*, *Lychnis alba*, *Crepis tectorum*, *Vicia villosa*, and *Polygonum convolvulus*. Grigal et al. (1974) found that the upper 15 cm of Sartell fine sand has  $\approx 0.3\%$  organic matter, 0.025% total nitrogen ( $18 \mu\text{mol/g}$  dry soil) and a pH of 5.3 (range 5.0–5.6). The field is located in the

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NW1/4 of the SE1/4 of Section 22, Township 34 N, Range 22W, Isanti County, Minnesota.

#### *Nutrient limitation experiments*

In 1979, a 40 × 40 m portion of the field was fertilized with various combinations of N, P, K, Ca, and Mg supplied as commercial NH<sub>3</sub>NO<sub>3</sub> (34-0-0), reagent-grade H<sub>3</sub>PO<sub>4</sub>, commercial K<sub>2</sub>O (0-0-60), USP MgSO<sub>4</sub> (Epsom salts), and reagent-grade CaCO<sub>3</sub>. These were applied twice, in early and late June, with a 0.5-m wide lawn fertilizer spreader equipped with bicycle wheels to raise the spreader above the vegetation. The fertilizers were applied singly and multiply in randomized, replicated 0.5-m wide rows and perpendicular columns; unfertilized strips 2.0 m wide were between all rows and columns and served as walkways (0.5 m wide) and controls. We applied the following total amounts: Nitrogen, 26 g/m<sup>2</sup>; Phosphorus, 4.8 g/m<sup>2</sup>; Potassium, 32 g/m<sup>2</sup>; Magnesium, 8.7 g/m<sup>2</sup>; and Calcium, 5.7 g/m<sup>2</sup>. On 25 September 1979, 0.25-m<sup>2</sup> plots were clipped to ground level, and living plant material was dried to a constant mass. An adjacent disked area was simultaneously studied (McKone 1980).

#### *N:Mg gradient experiments*

In April 1980, a 35 × 35 m area within the area studied the previous year was disturbed by disking it ≈20 times in one direction and 20 times perpendicular to that. The thorough disking was done to homogenize the soil within each of the areas to be used as experimental plots. Because of the spatial patchiness of N and Mg in this field (see Tilman 1982:Fig. 35), use of the area previously studied assured that the results of the 1979 experiment could be applied to the 1980–1981 experiment. This area was surrounded with a 1.2-m fence to exclude deer. The disked area was divided into a block of 36 plots, each 3 × 3 m; 2-m walkways were between plots. Next, each of the plots was raked manually to remove fragments of perennial vegetation from the soil surface and to smooth the soil. Two 15-cm soil cores were then collected from each plot, one from the center of the north half and one from the center of the south half. These were analyzed for total N, pH, and extractable Ca, Mg, and K. Each of the plots was assigned to one of six treatments within a 6 × 6 Latin square experimental design, by using the randomization procedure described in Cochran and Cox (1957). There were six replicates of each treatment. Each treatment occurred in each row and column in the block. The plots were then fertilized. All plots received Ca, K, and P at a rate of 4, 15, and 10 g·m<sup>-2</sup>·yr<sup>-1</sup>; the elements were supplied as above. Because McKone reported a few “patchy areas of nitrogen burn” apparently “due to excess fertilizer that fell in places where the fertilizer spreader wheels ran into a bump” (McKone 1980), I generally used lower amounts in 1980 and 1981, even though I did not observe detrimental effects in 1979. The treatments consisted of

a control and five different ratios of N to Mg. The maximum amount of NH<sub>3</sub>NO<sub>3</sub> or MgSO<sub>4</sub>·7H<sub>2</sub>O applied per plot was ≈40 g/m<sup>2</sup>. The amount of NH<sub>3</sub>NO<sub>3</sub> decreased linearly from treatments A through E, while the amount of MgSO<sub>4</sub>·7H<sub>2</sub>O increased linearly from treatments A through E. This gave a smooth gradient in N vs. Mg. Nitrogen was supplied as commercial NH<sub>3</sub>NO<sub>3</sub> fertilizer (34-0-0) and Mg as USP Epsom salts in the following amounts per year to the six treatments. Treatment A: Nitrogen, 13.6 g/m<sup>2</sup>; Magnesium, 0.0 g/m<sup>2</sup>. Treatment B: Nitrogen, 10.2 g/m<sup>2</sup>; Magnesium, 0.9 g/m<sup>2</sup>. Treatment C: Nitrogen, 6.8 g/m<sup>2</sup>; Magnesium, 1.9 g/m<sup>2</sup>. Treatment D: Nitrogen, 3.4 g/m<sup>2</sup>; Magnesium, 2.9 g/m<sup>2</sup>. Treatment E: Nitrogen, 0.0 g/m<sup>2</sup>; Magnesium, 3.8 g/m<sup>2</sup>. Treatment F: (control) no nitrogen and no magnesium. This provided a gradient from plots in which Mg should be the main limiting nutrient (treatment A) to plots in which nitrogen should be the main limiting nutrient (treatment E), plus a control (treatment F). Fertilizer was applied twice each year to each plot, in early April and late June, except for the second application in 1980, which was delayed until 8 August because of dry conditions. After mixing the fertilizer for a plot, I spread it evenly over the plot by hand from the walkways to prevent trampling damage. The flat terrain, highly porous sandy soil, and walkways 2 m wide were intended to prevent fertilizer movement between plots.

Vegetation was sampled twice the 1st yr and once the 2nd yr by clipping plants at the soil surface and sorting to species all plants within a predetermined sampling area delimited by steel rods. The sorted vegetation was dried to constant mass. The 1980 samples were collected during 28–30 July and 5–8 September by clipping 0.5 × 3.0 m and 0.5 × 1.0 m quadrats, respectively. For brevity, these were averaged for the 1980 vegetation information presented. The 1981 clipping was performed 21–22 July on 0.33 × 1.5 m quadrats. The gopher *Geomys bursarius* invaded some experimental plots in 1981 (see Tilman 1983). To avoid bias that could result from including gopher mounds in clipped areas, the area to be clipped within a plot was located slightly south of any predetermined sampling area that had a gopher mound.

Four 15-cm soil cores, each with a 5-cm<sup>2</sup> surface area, were collected from each plot on 8 September 1980, and three cores per plot were collected on 23 July 1981. These were analyzed for total N and extractable Ca, Mg, and K. Between 1100 and 1300 on 22 July 1981, light penetration was determined by taking ≈20 paired measures of light intensity above the vegetation and at the soil surface in each plot using a Lambda Instruments Model LI-185 photosynthetically active radiation cosine collector. Light penetration in each plot was expressed as the average of the ratios of paired measures of light at the soil surface to incident light.

Total nitrogen was determined by using a modifi-

TABLE 1. Fertilization of natural vegetation in an 8 yr old field. Yield is the mass of dried, aboveground vegetation. Five mineral elements were used in these experiments (N, P, K, Ca, and Mg). For part A, these were added singly to plots. For part B, they were added in various combinations. For B.2.A through B.5.B, all plots received N and two or three of P, K, Ca, Mg in all possible combinations. These treatments were grouped to allow comparison of plots receiving N and another nutrient with those receiving N and none of that nutrient. For instance, for B.2.A, the grouped treatments were two +N+K+Mg plots, two +N+K+Ca plots, two +N+Ca+Mg plots, and four +N+K+Ca+Mg plots. None of these received P. They were compared to the B.2.B group which consisted of two +N+P+K plots, two +N+P+Ca plots, three +N+P+K+Ca plots, three +N+P+K+Mg plots, and three +N+P+Mg+Ca plots using a *t* test modified for unequal sample sizes and variances. Thus, B.2.A and B.2.B are an attempt to use the available data to determine if P became limiting once N was added. Data were grouped in similar manners for the other comparisons in part B of the table.

Treatment	Yield (g/m <sup>2</sup> )	Standard error	No. plots	Significant difference?
<b>A. Single nutrient additions</b>				
1. Control (no fertilizer)	83.2	8.1	14	...
2. + Nitrogen	260.4	48.8	3	***, † ( <i>t'</i> = 8.79)
3. + Phosphorus	102.8	19.7	3	NS, †
4. + Potassium	111.2	19.0	3	NS, †
5. + Calcium	86.0	12.5	3	NS, †
6. + Mg	60.4	13.9	3	NS, †
<b>B. Multiple nutrient additions (at least 3 of the 5 nutrients)</b>				
1. +P +K +Ca +Mg (no N)	78.8	11.4	2	NS, †
2A. +N + ... (but no P)	298.	32.2	10	
2B. +N +P + ...	261.	31.4	13	NS, ‡
3A. +N + ... (but no K)	306.	45.2	7	
3B. +N +K + ...	270.	26.2	16	NS, ‡
4A. +N + ... (but no Ca)	306.	40.8	7	
4B. +N +Ca + ...	262.	26.6	16	NS, ‡
5A. +N + ... (but no Mg)	185.	12.9	9	
5B. +N +Mg + ...	342.	24.7	14	***, ‡ ( <i>t'</i> = 5.11)

† Test for significant difference between treatment and unfertilized control. NS = no significant difference,  $P > .05$ ; \*\*\* =  $P \leq .001$ .

‡ Test for significant difference between plots receiving multiple nutrients but none of a nutrient (labeled A) vs. those receiving multiple nutrients including that nutrient (labeled B).

cation of the alkaline persulfate digestion technique (D'Elia et al. 1977, Solorzano and Sharp 1980). In this modification, 1.0 g of soil was mixed with 100 mL of a reagent containing 27.0 g/L K<sub>2</sub>S<sub>2</sub>O<sub>4</sub> (low nitrogen, reagent grade) and 9 g/L NaOH; the mixture was autoclaved at 115°C for 30 min. This oxidized all organic matter and left all nitrogen as NO<sub>3</sub>. The digest was then diluted 1:100 with a buffer of pH 8.2, and NO<sub>3</sub> was determined by using the cadmium reduction method of Strickland and Parsons (1972). Calibrations of this method with inorganic and organic standards gave an *r*<sup>2</sup> of  $\geq 0.99$  for a set of six standards spanning the concentration range of the samples. Coefficients of variation for replicated samples were  $\leq 5\%$ . Extractable soil levels of Mg, Ca, and K were determined with an atomic absorption spectrophotometer (AA). For soil extracts, 5.00 g of soil were shaken for 0.5 h with 10 mL of 0.1 M of NaCl (pH adjusted to 2.5 with HCl). This was centrifuged, and the supernatant diluted, as necessary, for reading with the AA.

Statistical analyses of all data were performed by using SPSS version 7-9. In analyses of proportional data, the arcsine-square-root transformation was used to reduce heteroscedasticity. ANOVAs were performed as appropriate for a Latin square design experiment, with row, column, and treatment as factors. Interaction

terms were not analyzed. All *t* tests were performed for unpaired observations with unequal sample sizes and unequal variances. The resulting statistic, *t'*, was compared to calculated, rather than tabular, values (Steel and Torrie 1960:81).

## RESULTS

### Nutrient-limitation experiments

Of all plots receiving a single nutrient, only those receiving N had significantly more biomass than did controls (Table 1A). Of plots receiving multiple nutrients, those receiving P, K, Ca, and Mg, but no N, did not differ significantly from unfertilized controls (Table 1B). The other combinations of multiple nutrients, shown in Table 1B, were limited to plots that received N and at least two of P, K, Ca, and Mg. Plots that received a particular nutrient (such as P) in combination with N were compared with plots that received N and nutrients other than that particular nutrient. For instance, plots that received N, P, and at least one other nutrient (K, Ca, Mg) did not differ significantly from plots that received N, no P, and at least two of K, Ca, and Mg. Thus, when N was supplied, the presence of P did not lead to a significant increase in aboveground biomass. Of all plots receiving N and

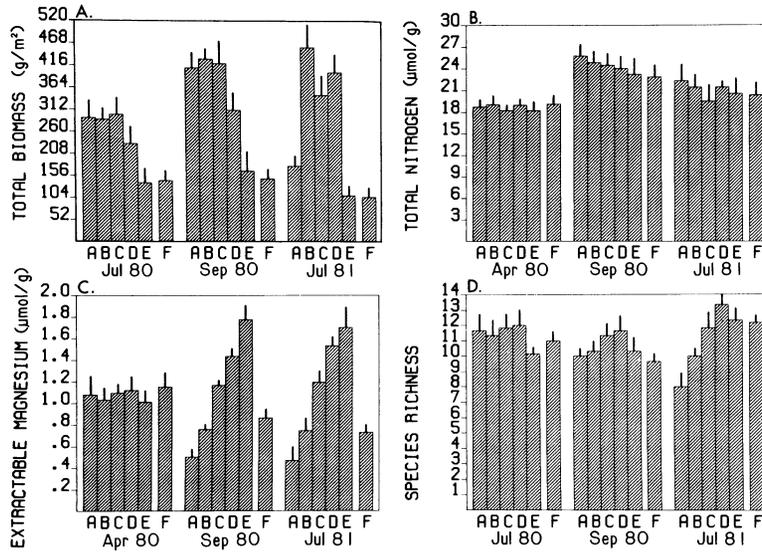


FIG. 1. Treatment effects for total biomass (above-ground vegetation, dried), total nitrogen in dry soil ( $\mu\text{mol/g}$ ), extractable magnesium in dry soil ( $\mu\text{mol/g}$ ), and plant species richness are shown along with the standard error of each treatment mean. In a graduated series, A plots had the highest availability of N and lowest of Mg; E plots had highest Mg and lowest N. F was the control (no fertilization). Treatment nutrients were first applied in April 1980, following the April 1980 sampling.

at least two other nutrients, only those receiving N and Mg had significantly more biomass than the appropriate controls (Table 1B).

*N:Mg gradient experiment*

An analysis of variance on the soil samples collected before treatment in 1980 revealed significant row and column effects existing in the field before initial fertilization, but no preexisting "treatment" effects, indicating that the Latin square was randomized without bias. The main preexisting effect was a gradient of total soil nitrogen and extractable calcium, with both higher on the north edge.

ANOVA of aboveground biomass (grams per square metre) for the July 1980 samples revealed a highly significant treatment effect ( $F = 36.4, P < .001$ ) and a highly significant column effect ( $F = 40.2, P < .001$ ). The column effect corresponded to the pretreatment column effect for nitrogen, with higher plant biomass on the north edge of the field. Using least significant differences, the higher nitrogen treatments (A, B, and C) did not differ significantly from one another, but all three had a significantly greater biomass than the higher magnesium treatments (D and E) and the control (F). Treatment D had a significantly greater biomass than treatments E and F, which did not differ significantly (Fig. 1). This same pattern was observed in September 1980, when there was a strong treatment effect ( $F = 29.2, P < .001$ ) but a less strong column effect. The July 1981 samples had a weaker column effect ( $F = 3.3, .01 \leq P < .05$ ) but a strong treatment effect ( $F = 24.8, P < .001$ ). Treatments B, C, and D had the great-

est biomass and differed significantly from A, E, and F. Treatment A had a greater biomass than treatments E and F, but not significantly, and E and F did not differ significantly (Fig. 1A).

The high nitrogen end of the N:Mg gradient (treatment A) had significantly decreased levels of extractable magnesium by September 1980. A magnesium gradient was established by the treatments (Fig. 1C). The treatments established a less striking gradient in total soil nitrogen (Fig. 1B). Total soil nitrogen was highest in treatment A and declined along the gradient

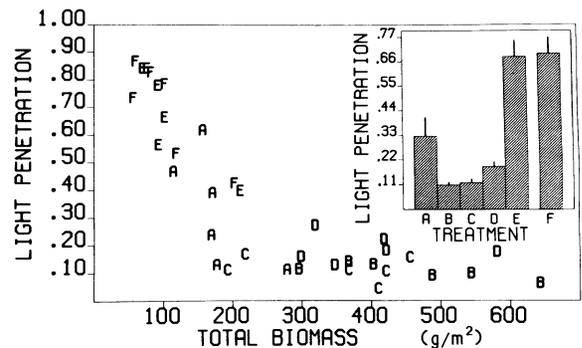


FIG. 2. The dependence of proportional light penetration to the soil surface on the total aboveground biomass of vegetation in each plot. See Fig. 1 for descriptions of treatments A-E and control F. The insert shows the treatment means and standard errors for light penetration. Where  $L$  is proportional light penetration and  $B$  is plant biomass ( $\text{g/m}^2$ ), nonlinear least-squares regression gave  $L = 58.9/B + 0.0019$ , with  $r = .92, P < .001$ .

TABLE 2. Analysis of variance and trend analysis for 1980 and 1981 plant abundance data on all plant species, which on average in at least one of these years comprised 2% or more of total community aboveground dry biomass. Average relative abundance of each species is given.  $F_{TRT}$  is the  $F$  statistic for ANOVA of treatment effects in the Latin square design experiment.  $F_{TREND}$  is the  $F$  statistic for ANOVA of linear or quadratic trends in the treatment responses. For each  $F$  statistic category, two values are given. The upper value is an  $F$  statistic based on transformed relative abundance and the lower is an  $F$  statistic based on aboveground dry biomass. Linear (L) or quadratic (Q) equations (Eq.) were chosen based on goodness of fit. For brevity,  $F$  statistics are not given for row or column effects.

Species	Life history†	1980						1981					
		Relative biomass	$F_{TRT}$		$F_{TREND}$		Relative biomass	$F_{TRT}$		$F_{TREND}$			
			$F$	$P‡$	$F$	$P‡$ Eq.		$F$	$P‡$	$F$	$P‡$ Eq.		
<b>Grasses and sedges</b>													
<i>Agropyron repens</i>	P	0.02	1.66 2.79	NS *	0.58 2.04	NS NS	L Q	0.04	2.72 1.58	* NS	1.76 2.03	NS NS	Q Q
<i>Agrostis scabra</i>	P	0.0	...§		...			0.48	2.81 6.87	* **	13.33 4.28	** **	L Q
<i>Aristida basiramea</i>	A	0.10	1.11 0.50	NS NS	0.80 0.66	NS NS	L L	0.09	6.46 4.54	** **	5.01 4.38	* *	L L
<i>Cenchrus longispinus</i>	A	0.04	1.10 2.00	NS NS	0.48 2.05	NS NS	L Q	0.01	1.35 0.87	NS NS	2.47 0.70	NS NS	L L
<i>Cyperus sp.</i>	P	0.04	7.55 1.21	** NS	2.38 1.39	NS NS	Q L	0.01	5.86 3.56	** *	7.78 4.44	** *	Q Q
<i>Setaria glauca</i>	A	0.13	0.63 2.24	NS NS	0.01 0.49	NS NS	L L	0.01	0.35 0.86	NS NS	0.05 1.86	NS NS	L Q
<i>Setaria viridis</i>	A	0.05	2.11 2.69	NS NS	4.81 3.60	* NS	Q Q	0.003	1.10 1.27	NS NS	1.82 0.24	NS NS	L L
<b>Forbs</b>													
<i>Ambrosia artemisiifolia</i>	A	0.32	2.48 8.51	NS **	6.57 16.16	* **	Q Q	0.01	0.72 1.78	NS NS	0.72 2.95	NS NS	L Q
<i>Berteroa incana</i>	P (B, A)	0.003	0.68 0.75	NS NS	2.49 2.65	NS NS	Q Q	0.11	1.36 1.58	NS NS	3.82 4.11	NS *	Q Q
<i>Chenopodium album</i>	A	0.16	2.93 6.71	* *	0.89 3.30	NS NS	L L	0.003	3.00 1.27	* NS	2.98 3.99	NS *	Q Q
<i>Erigeron canadensis</i>	A	0.0	...		...			0.03	5.11 1.33	** NS	4.38 3.34	* NS	Q L
<i>Mollugo verticillata</i>	A	0.07	5.82 5.81	** **	3.53 4.92	NS *	Q Q	0.005	1.97 1.36	NS NS	2.48 2.16	NS NS	L L
<i>Oenothera biennis</i>	B	0.004	1.93 1.10	NS NS	2.04 1.95	NS NS	L Q	0.14	1.47 2.09	NS NS	3.10 2.04	NS NS	L Q
<i>Polygonum convolvulus</i>	A	0.05	0.14 2.07	NS NS	0.36 0.78	NS NS	Q Q	0.04	0.62 1.49	NS NS	0.15 2.32	NS NS	L Q

† A = annual, B = biennial, P = perennial.

‡ NS =  $P > .05$ , \* =  $.05 \geq P > .01$ , \*\* =  $P \leq .01$ .

§ ... indicates that species was not present in any samples in the given year.

to treatment E. The high-magnesium end of the gradient (treatment E) had increased extractable Mg through time, as expected from the imposed pattern of fertilization, but no significant change in total N compared to controls.

ANOVA did not reveal any significant treatment effect on species richness  $S$  in the two initial samples (July and September 1980), but a significant effect was observed in July 1981 (Fig. 1D). An initially equal species richness in the six treatments changed to a distribution with higher species richness at lower N:Mg ratios. Comparisons of species richness between years are not valid, because different sizes and shapes of quadrats were used.

The proportion of incident light reaching the soil

surface through the vegetation varied significantly with treatment (Fig. 2:inset bar graph); the greatest attenuation was in the highest biomass plots. Fig. 2 shows a strong relationship between light penetration to the soil surface and the inverse of the total biomass in a plot. The addition of higher order terms and logarithmic terms did not explain a significantly greater proportion of the variance. The  $r^2$  indicates that 84% of the variance in the availability of light at the soil surface was explained by the total biomass of a plot, independent of the dominant plant species. In 1981, the plots with the highest biomass had an average of only 6% of incident light reaching the soil surface, whereas from 70 to 87% of the incident light reached the soil surface in unfertilized plots.

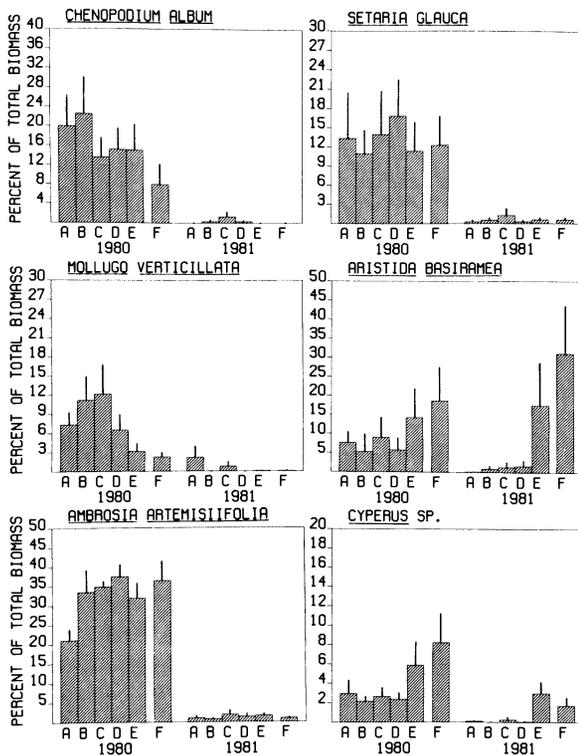


FIG. 3. The treatment effects for both 1980 and 1981 for the 6 most abundant plant species of 1980. Means and standard errors are shown. Note changing scale for y axis. Treatment codes as in Fig. 1.

#### Effects on major plant groups

In the first season following disking, annual plants as a group comprised 93% of the total biomass of all treatments combined, and annual forbs (herbaceous dicots) were twice as abundant as annual graminoids (grasses and sedges). (See data for major species in Table 2.) By the 2nd yr, annual plants had decreased to 21%, and graminoids were as abundant as forbs. Biennial forbs, mainly *Oenothera biennis*, increased from 1 to 14%, and perennial graminoids increased from 6 to 53% of the total biomass of all treatments combined. Perennial forbs were essentially absent the 1st yr, and increased to 11% of total biomass the 2nd yr, assuming that *Berteroa incana* is mainly perennial at Cedar Creek (E. Cushing, *personal communication*). ANOVA of transformed relative abundance of these plant groups revealed no significant treatment effects in either year for annual or perennial forbs as groups, and no significant effects in the 1st yr for annual or perennial graminoids as groups. Treatment effects were significant the 2nd yr for both annual and perennial graminoids as groups; annuals dominated the low-N treatments and perennials dominated the low-Mg treatments. Most of the latter effect was caused by *Agrostis scabra*.

#### Species composition of treatments

Thirty-one species of vascular plants were found in the vegetation that was clipped in 1980 and 1981. Most of these were rare enough that treatment effects, if they existed, could not be distinguished from sampling error. In 1980 there were 10 and in 1981 there were seven plant species that individually comprised  $\geq 2\%$  of total community biomass (Table 2). The average over all plots of the two 1980 samples revealed that the six most abundant species in the first year after disturbance were, in order, *Ambrosia artemisiifolia*, *Chenopodium album*, *Setaria glauca*, *Aristida basiramea*, *Mollugo verticillata*, and *Cyperus* sp. All but *Cyperus* are annuals. Of these, *Chenopodium*, *Mollugo*, and *Cyperus* showed a significant response of relative abundance to treatments (Table 2, Fig. 3). *Ambrosia*, *Chenopodium*, *Mollugo*, and *Agropyron* had significant responses of absolute abundance to treatments.

Because treatments A–E represent a gradient of N-to-Mg supply rates, trends in treatment means along the imposed gradient must also be considered. Tests for both linear and quadratic trends were performed on both relative and absolute abundance. In 1980, only the trends for *Ambrosia artemisiifolia*, *Setaria viridis*, and *Mollugo verticillata* were statistically significant (Table 2). These species had slight separation, if any, along the imposed N:Mg gradient in 1980 (Fig. 3). *Chenopodium album* seemed to reach its greatest dominance at the highest N:Mg ratios (treatments A and B) and to decline with decreasing N:Mg ratios. *Mollugo verticillata* reached its greatest dominance in treatments B and C, followed by *Ambrosia artemisiifolia* in treatments C and D, and *Aristida basiramea* and *Cyperus* sp. at the lowest N:Mg ratio (Fig. 3).

The six most abundant species in 1981 were, in order, *Agrostis scabra*, *Oenothera biennis*, *Berteroa incana*, *Aristida basiramea*, *Agropyron repens*, and *Polygonum convolvulus*. Of these, *Agrostis*, *Aristida*, and *Agropyron* had significant treatment effects based on relative abundance. *Agrostis* and *Aristida* had significant effects based on absolute abundance (Table 2, Fig. 4). Of the rarer species, *Chenopodium album*, *Crepis tectorum*, *Erigeron canadensis*, and *Cyperus* sp. had significant treatment effects based on relative abundance, and *Cyperus* had a significant effect based on absolute abundance.

Analysis of linear and quadratic trends in treatment means in 1981 showed significant trends based on relative or absolute abundance for *Aristida*, *Cyperus*, *Agrostis*, *Berteroa*, and *Erigeron* (Table 2). The patterns of distribution of the six major species along the imposed N:Mg gradient seemed much clearer by the 2nd yr of the experiment (Fig. 4). *Agrostis scabra* reached its greatest dominance at the highest N:Mg ratios, and declined consistently along the gradient. *Agropyron repens* was next, reaching its greatest dominance in treatment B. It was followed by *Berteroa incana*, which

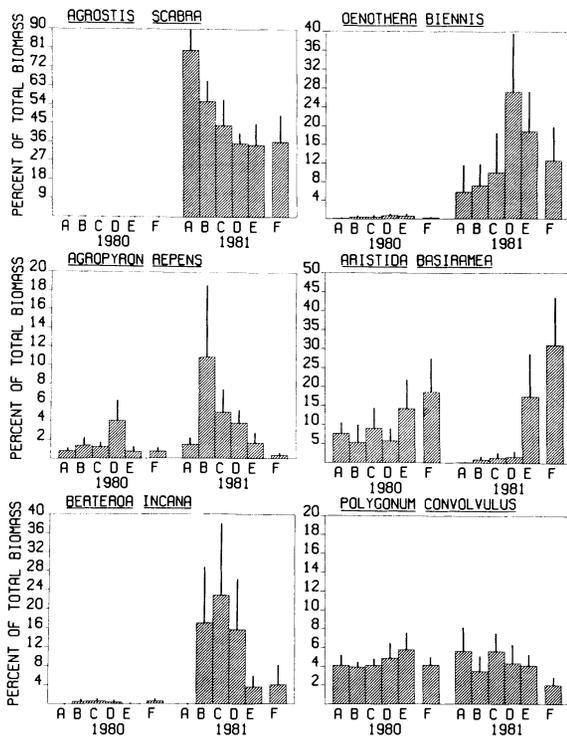


FIG. 4. Treatment effects for both 1980 and 1981 for the six most abundant species of 1981. Means and standard errors are shown. Note changing scale for y axis. Treatment codes as in Fig. 1.

reached its greatest dominance in treatment C; *Oenothera biennis*, which was most dominant in treatment D; and *Aristida basiramea*, most dominant in treatment E. The sixth most abundant species, *Polygonum convolvulus*, showed no separation along the imposed nutrient gradient in either year. Of the four rarer species that had significant treatment effects, *Crepis tectorum* did not have an apparent pattern along the gradient, *Cyperus* sp. (Fig. 3) and *Erigeron canadensis* reached their greatest dominance at low N:Mg ratios (treatment E), and *Chenopodium album* (Fig. 3) reached peak density at intermediate N:Mg ratios.

DISCUSSION

The experiments described in this paper were designed to determine if soil nutrients were limiting during early succession at Cedar Creek and to document any differences that existed in the response of individual plant species to an imposed resource-ratio gradient. A gradient was used because the resource-ratio hypothesis predicts separation of species along a gradient if the species are competing, if the manipulated resources are limiting, and if the competitors differ such that they are inversely ranked in their competitive abilities for the limiting resources (Tilman 1980, 1982).

A central assumption of this approach is that plants compete. Removal experiments have demonstrated in-

terspecific competition in terrestrial plant communities (e.g., Abul-Fatih and Bazzaz 1979, Fowler 1981, Hils and Vankat 1982). McCormick's (1968) experimental removal of annual plants from a 1-yr-old field showed that annual plants decreased the biomass per individual of perennial plants from 4 to 43 times. The removal of the annual *Ambrosia trifida* from a 1-yr-old field by Abul-Fatih and Bazzaz (1979), and the removal of various species of annuals and perennials from a 1-yr-old field by Hils and Vankat (1982) have documented strong interspecific competition during early succession.

The 1979 Cedar Creek fertilization experiments demonstrated that nitrogen was the most important limiting nutrient of those manipulated, and suggested that magnesium was the next most limiting nutrient, because magnesium became limiting when nitrogen was added (Table 1). Strong limitation by N is not surprising. Numerous studies of old fields, swards, and prairies have shown nitrogen to be a major limiting nutrient (e.g., Lawes and Gilbert 1880, Milton 1934, Huffine and Elder 1960, Gay and Dwyer 1965, Owensby et al. 1970). This has also been suggested by studies of primary succession (e.g., Cowles 1899, Cooper 1913, Crocker and Major 1955, Olson 1958, Lawrence et al. 1967).

It may be that a small proportion of the plant species in this field were Mg limited even in the absence of N fertilization, and that their response to Mg was masked because species-specific responses were not evaluated in 1979. The N:Mg gradient experiment had two treatments that can be used to test partially this possibility. Treatment E received Mg and all other nutrients except N, but treatment F did not receive any N or Mg. Comparisons of these treatments showed that *Oenothera biennis*, *Vicia villosa*, *Lychnis alba*, *Setaria viridis*, and *Chenopodium album* were more abundant in treatment E than in treatment F in 1981, which suggests Mg limitation of these species, but only two of these differences were statistically significant using ANOVA least significant differences. This is additional, though weak, support for the possible importance of Mg.

Because different species were dominant in the 8-yr-old vegetation fertilized in 1979 than in the newly disturbed soil of the 1980-1981 N:Mg gradient, there may be reason to question the importance of Mg in the N:Mg experiments. The 1979 vegetation was dominated by *Agrostis scabra*, *Oenothera biennis*, and *Agropyron repens*. Although these species were rare in 1980, they were dominant in 1981 in the N:Mg plots (Fig. 4). Additionally, in 1979 M. McKone and I performed fertilization experiments in an adjacent disked portion of this field (data in McKone [1980]). The vegetation of the disked area was similar to that of the 1980-1981 N:Mg plots. Of all nutrients added singly (N, P, K, Ca, Mg), only N had an effect on biomass that was significant compared to controls ( $t' = 5.90, P < .001$ ). The biomass of the Mg treatment was greater than that of the controls, but not significantly. For plots receiving

N and other nutrients, only those with N and Mg were significantly greater than those receiving N and nutrients other than Mg ( $t' = 2.11$ ,  $.01 < P < .05$ ). They were also significantly greater than those receiving just N ( $t' = 2.22$ ,  $.01 < P < .05$ ). Furthermore, Fig. 1 shows that the highest biomass in 1981 occurred in treatment B, which received less N but more Mg than treatment A. In both 1980 and 1981, treatment A had significantly less extractable Mg than the control. These lines of evidence strongly suggest that Mg is a limiting nutrient in the N:Mg experiments.

Whenever a limiting resource is added to a community, the increased biomass that is produced leads to an increased demand for other resources. For the N:Mg gradient, the end of the gradient most heavily fertilized with N had significantly reduced levels of Mg. The increased biomass probably also led to decreased availability of other resources. Because P, K, and Ca were added, these probably did not decline to limiting levels. However, water was not supplied. Nor was light. Soil moisture levels were not recorded, but the possibility exists for water limitation on the sandy, porous soils of Cedar Creek. The treatments had a significant effect on light availability at the soil surface. As little as 4% of the incident solar radiation reached the soil surface in fertilized plots, whereas >70% reached the surface in control plots. At 4% of incident irradiance, seedlings and plants of low stature may be light limited. The total biomass obtained in response to treatments in 1980 was such that the resultant light gradient should have paralleled the N:Mg gradient, and light intensity should have been lowest at the low Mg end of the gradient. However, in 1981, soil surface light was lowest in the middle of the gradient, and highest at the two ends, leading to a U-shaped curve along the N:Mg gradient. Because the U-shaped light gradient of 1981 was caused by the plants that grew in 1981, it probably had little impact until the plants that were seedlings and shoots in 1981 grew (or would have grown) to maturity; i.e., until at least 1982. For these reasons, it should be possible to interpret the experimental manipulations as leading to a gradient along which Mg and possibly light and water were limiting at one end (treatment A) and N was limiting at the other end (treatment E), for the 1980 and 1981 plant samples.

The lack of a clear separation of the dominant plant species along the gradient in 1980 (Fig. 3) may indicate (1) that these species, mainly annuals, do not compete, (2) that these species do not differ in their requirements and competitive abilities for N and Mg (or light or water), or (3) that one year is too brief a time for interspecific competition to lead to separation. The work of Abul-Fatih and Bazzaz (1979) and of Hils and Vankat (1982) has shown strong competition in early successional vegetation, suggesting that the first possibility is unlikely. Grime (1979) has proposed that annual plants have a "ruderal" or fugitive strategy of exploiting open habitats. The lack of clear separation

of these annuals along the imposed gradient is partially consistent with that hypothesis. However, trend analysis (Table 2) indicated that three species of annuals had significant trends along the gradient in 1980, and that two additional annual species had significant trends in 1981. This suggests that there may be differentiation of annual plants in response to the availability of N and Mg, but that a single year was not sufficient time for separation. The year after gophers invaded the experimental plots, there was a great increase in the absolute abundance of annual plants (Tilman 1983). Gopher mounds at the high N end of the gradient were dominated by *Setaria* and those at the low N end by *Polygonum*, suggesting differentiation of these two annuals.

The more distinct separation of the five dominant species of 1981 along the gradient (Fig. 4) showed that the species composition of an early successional old field could be influenced by the relative availability of soil nutrients. These results suggest that the relative availability of limiting soil nutrients may potentially explain some of the local spatial heterogeneity observed in vegetation. If this separation is caused by competition for N and Mg, but not by competition for light or water, these five species likely differ in their competitive abilities for N and Mg as follows. *Aristida* should have the lowest requirement for N (as determined by  $R^*$ , the availability of the resource needed for the species to maintain a stable equilibrium population; Tilman [1982]), but should have the highest requirement for Mg. The next best competitor for N (i.e., the next higher  $R^*$  for N) should be *Oenothera*, followed by *Berteroa*, *Agropyron*, and *Agrostis*. *Agrostis* should be the best competitor for Mg, followed by *Agropyron*, *Berteroa*, *Oenothera*, and *Aristida*. This hypothesis could be tested: (1) by performing studies of the N and Mg dependent growth physiology of these five species, (2) by performing correlational studies in unmanipulated early successional fields in which N and Mg are limiting, and (3) by performing greenhouse competition experiments for N and Mg among the five species. The hypothesis that competition for N and Mg led to the patterns of Fig. 4 could be rejected if the results of any one of these experiments were inconsistent with predictions based on the hypothesized requirements of these species for N and Mg.

Of the 10 species that averaged  $\geq 2\%$  of the total community biomass the first year after disturbance, three had significant responses of relative abundance and four had significant responses of absolute abundance to treatments (Table 2). Of the seven species that were  $\geq 2\%$  the second year, four showed significant responses of relative abundance, and three rarer species also responded significantly. Three species had significant responses of absolute abundance to treatments in 1981. Thus, nutrient fertilization had a significant impact on relative abundance of many of the dominant plants in the first year of succession and on the majority

of the dominant plants in the second year. Several other rarer plant species and the availability of another potentially limiting resource, light, were also significantly affected by the imposed treatments. The separation of the dominant plants of 1981 suggests that, either directly or indirectly, different ratios of supply rates of limiting soil nutrients are an important factor determining the plant species composition of this early successional old field.

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