

## SPECIES RICHNESS OF EXPERIMENTAL PRODUCTIVITY GRADIENTS: HOW IMPORTANT IS COLONIZATION LIMITATION?<sup>1</sup>

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**Abstract.** The biodiversity of a site should depend on the interplay of local colonization (gain) and extinction (loss) rates, but few theoretical explanations of diversity patterns on productivity gradients have included effects of productivity on colonization. In an 11-yr study, experimental increases in productivity via nitrogen addition generally led to decreased species richness in four grassland fields. Decreased diversity in productive plots was caused as much by lower rates of species gain as by greater rates of loss of existing species. Annual grasses and forbs had high gain and loss rates, but these were independent of productivity. In contrast, the rates of gain of perennial grass and forb species declined with productivity, and their rates of loss increased.

Species richness was dependent on litter mass and on light penetration, but not on aboveground living plant mass, suggesting that there was no direct effect of productivity on diversity. Diversity in periodically burned prairie, which had low litter mass, was independent of productivity by the 10th and 11th yr of the study. Results suggest that diversity is lower in productive grasslands because accumulated litter, and possibly lower light penetration, inhibit germination and/or survival of seedlings, and thus decrease rates of establishment by new species. Higher productivity also leads to higher rates of loss, presumably via competitive displacement, of existing species. Results do not support the hypothesis that soil N heterogeneity controls diversity on the temporal and spatial scales of this study.

*Key words:* Canonical Correspondence Analysis; Detrended Correspondence Analysis; Gradient Analysis; ordination; simulation.

### INTRODUCTION

The interdependence of species richness and productivity is one of the more general biodiversity patterns on earth (e.g., Grime 1979, Kruger and Taylor 1979, Wheeler and Giller 1982, Bond 1983, Abramsky and Rosenzweig 1984, Owen 1988, Moore and Keddy 1989, Puerto et al. 1990, Itow 1991, Palmer 1991, and reviews in Huston 1979, Tilman 1982, Tilman and Pacala 1993). Numerous alternative explanations for the effects of productivity on diversity have been proposed. Grime (1973, 1979), for instance, suggested that productive habitats have lower diversity because of more intense competition. Newman (1973) countered that competition is equally strong in both fertile and infertile habitats, but that strong competition for light in productive habitats inherently favors the tallest species, whereas many alternative traits confer competitive ability for nutrients and thus allow numerous species to coexist in infertile habitats. Huston (1979) proposed that species richness is maintained by periodic disturbances that slow competitive displacement, and that displacement rates are greater in more productive habitats. Goldberg and Miller (1990) suggested that the decrease in light penetration caused by in-

creased productivity should increase mortality rates for slow-growing or shade-intolerant species and for seedlings, and thus increase local extinction rates. Tilman (1982) hypothesized that spatial heterogeneity in resource availability was a major factor allowing species to coexist, and that such heterogeneity, and thus diversity, should be maximal in moderately productive habitats. Abrams (1988) countered that there need be no relationship between spatial heterogeneity and productivity, but this has been disputed (Tilman and Pacala 1993).

Almost all of these hypotheses have made the tacit assumption that increased productivity should lead to an increased probability of local extinction of species already present in a habitat. However, island biogeographic theory (MacArthur and Wilson 1967) and models of metapopulation dynamics (e.g., Gilpin and Hanski 1991) suggest that the species richness of a habitat is maintained by a dynamic equilibrium between both local extinction and local colonization. Changes in productivity could, in theory, influence diversity through effects on both colonization and extinction rates. Thus, increased productivity could lead to decreased diversity if it led (1) to a decreased probability of successful colonization, or (2) to an increased probability of local extinction, or (3) to both. If there is empirical evidence that productivity influences col-

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onization rates, diversity theories will need to be modified to account for this.

In this paper the results of an 11-yr experimental study of the effects of resource enrichment on the species richness of three successional grasslands and a stand of native prairie are reported. Because plant species abundances were sampled in all 207 plots each year, these experiments provide information on the effects of productivity and other correlated variables, such as living plant mass, light penetration, and litter, on species richness and on local colonization and extinction rates. The response of control plots to a severe drought that occurred in 1988 are reported in Tilman and El Haddi (1992). Changes in species abundances that resulted from nitrogen treatments are reported in Tilman (1987, 1988).

#### METHODS

Methods are described in detail in Tilman (1987), which reports results for the first 4 yr of this study. Experiments were performed in four level, sandy, upland, well-drained grassland fields within Cedar Creek Natural History Area, Minnesota. Three of the fields, called Fields A, B, and C, had been abandoned from farming 14, 25, and 48 yr, respectively, when this work began in 1982, and have never been burned. The fourth field, Field D, is a prairie opening within a stand of native oak savannah that has been maintained as oak savannah via prescribed burns in 2 out of every 3 yr, starting in 1966. Field D was burned in early spring (usually early May) of 1982, 1984, 1985, 1987, 1988, 1990, and 1991. All four sites had grassland vegetation, with few trees or shrubs. Before experiments began, Field A was dominated by *Agropyron repens*, *Berteroa incana*, *Poa pratensis*, and *Agrostis scabra*; Field B by *Schizachyrium scoparium*, *Poa pratensis*, and *Rumex acetosella*; Field C by *Schizachyrium scoparium*, *Artemesia ludoviciana*, and *Poa pratensis*; and Field D by *Carex muhlenbergii*, *Andropogon gerardi*, *Sorghastrum nutans*, *Ambrosia coronopifolia*, *Helianthemum bicknellii*, and *Artemesia ludoviciana*.

**Nitrogen gradients.**—Experimental nitrogen (N) gradients were established on existing vegetation in each field. A set of plots, each 4 × 4 m and separated by 1-m walkways, were established in Fields A, B, and C. The 54 plots per field were randomly assigned to receive 1 of 9 different treatments, with six replicates per treatment per field. The treatments consisted of (1) a control, called treatment I, that received no nutrient additions, (2) treatment A, which received P, K, Ca, Mg, S, and trace metals, but no N (amounts in Table 1 of Tilman 1987), and (3) a set of seven different N addition treatments, all of which received the same nutrients as treatment A, plus inorganic N. The latter were called treatments B through H, and received, respectively, either 1, 2, 3.4, 5.4, 9.5, 17, or 27.2 g · m<sup>-2</sup> · yr<sup>-1</sup> of N, supplied as commercial pelletized ammonium nitrate fertilizer (NPK content 34–0–0). Nutrients were added to plots

in two equal doses each year, in early to mid-May and in late June, by manually broadcasting from the walkways. An identical experimental design was used in Field D, except that there were five replicates per treatment, and plots were 2 × 4 m. Soil pH was monitored and kept at the pH of controls (treatment I) by annual addition of commercial fine ground lime. Plots that received more NH<sub>4</sub>NO<sub>3</sub> also had to receive more lime to prevent acidification.

**Vegetation sampling.**—Each year, a 10 cm wide by 3 m long strip of vegetation was clipped at the soil surface in each plot, sorted to litter and living (which was sorted to species), dried, and weighed. A different portion of each plot was clipped each year (Tilman 1987). Each year, Field A was clipped during early to mid-July, Field B during early August, Field C during mid-August, and Field D during late August to early September. The total number of vascular plant species identified in the sorted sample of a given plot in a given year is its species richness.

**Light.**—Proportional light penetration through the vegetation was measured at the time of clipping each year except 1991 and 1992. A Lambda Instruments photosynthetically active radiation meter with a 1 m long integrating strip collector was used to measure light flux above and below the vegetation. The latter readings were taken 2.5 cm (the height of the collector) above the litter layer. The ratio of light flux below the vegetation to light flux above it is called the proportional penetration of light through the vegetation.

**Species turnover.**—Changes in species richness result from the loss of species formerly present, and the gain of new species. Because different subsections of each plot were sampled each year, part of any apparent losses and gains are sampling error (Nilsson and Nilsson 1985). To minimize this, I combined data from either 2- or 3-yr intervals to obtain a better estimate of the species actually present in a given plot during that time interval. A species was considered to have been lost from a plot if it was present at some time during one interval but absent at all times during the later interval. A species was considered to have been gained by a plot if it was absent at all times in the earlier interval but present at some time during the later interval. The number of species gained or lost in a plot was divided by the species richness of that plot to give the proportion of species formerly present that were gained or lost. Additionally, species were classified as being either annual forbs, annual grasses, perennial forbs, perennial grasses, woody plants, or other (an amalgam of legumes, biennials, and sedges). For each of these life history groups, species gains and losses were calculated by comparing the initial composition of each plot (1982 + 1983 + 1984 data combined) with its final composition (1990 + 1991 + 1992 data combined).

**Data analysis.**—Data were analyzed on a Sun Sparc workstation using SAS statistical software. ANOVAs used the SAS GLM routine, and contrasts among treat-

ment means used the Student–Newman–Keuls test. Results were termed significant only if  $P \leq .05$ .

### RESULTS

**Species richness per field.**—In total, across all 11 yr of sampling, 87 different species of vascular plants were observed in the experimental plots in Field A, 78 species in Field B, 81 species in Field C, and 132 species in Field D. The total number of species observed in a combined sample of all plots in a given field in a given year is called species richness per field. The increased spatial heterogeneity in soil N created within each field by the different rates of N addition did not increase species richness per field in any of the fields (Fig. 1). Species richness per field declined in all four fields from 1982 to 1986. Species richness per field reached its lowest level during the 1988 drought (Fig. 1; see Tilman and El Haddi 1992). It increased from 1988 to 1992 in all four fields, but 1992 species richness per field did not exceed that of 1982 or 1986 (Fig. 1).

**Treatment effects on species richness.**—The number of species observed in a given plot in a given year is its species richness. For each year of the experiment, an analysis of variance was performed to determine the dependence of species richness on treatment, field, and the field  $\times$  treatment interaction. For the 1st yr, 1982, analysis of variance revealed significant field ( $F_{3,171} = 22.8, P < .01$ ) and treatment ( $F_{8,171} = 2.39, P = .02$ ) effects on species richness but no field  $\times$  treatment interaction ( $F_{24,171} = 1.39, P = .12$ ). In each of the 10 subsequent years, ANOVA revealed highly significant field (minimum  $F$  value, over all 10 yr:  $F_{3,171} = 24.7, P < .001$ ) and treatment (minimum  $F$  value:  $F_{8,171} = 5.93, P < .001$ ) effects. The field  $\times$  treatment interaction was significant in 1986 ( $F_{24,171} = 2.82, P < .001$ ), 1988 ( $F_{24,171} = 1.59, P < .05$ ), 1991 ( $F_{24,171} = 1.85, P < .05$ ), and 1992 ( $F_{24,272} = 2.56, P < .05$ ) but nonsignificant ( $P > .05$ ) in the other 7 yr.

In years in which there were no significant field  $\times$  treatment interactions, such as 1990, species richness can be averaged across fields to show the general effect of treatments (Fig. 2A), which was for higher rates of N addition to lead to lower species richness. On average, the highest N treatment had less than half the species richness of controls. Most life history groups decreased in species richness along the gradient, with perennial forbs showing the greatest decline (Fig. 2A). When averaged across treatments, these 1990 data show that species richness was highest in Field D, next highest in Field C, then B, and then A (Fig. 2B); each field was significantly different from each of the others (Student–Newman–Keuls test,  $P < .05$ ). This corresponds with older fields being more species rich, just as was observed in controls (treatment I) in 1982. When there were significant field  $\times$  treatment interactions, as in 1991 and 1992, results must be compared on a field-by-field basis (Fig. 3). In 1991 and 1992, there were significant treatment effects on species richness for Field

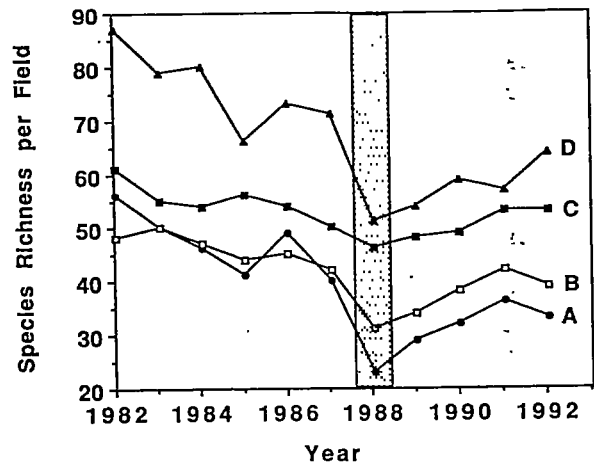


FIG. 1 Total species richness per field is the total number of species observed, in a given year and field, in all replicates of all treatments of the nitrogen gradient experiment. Letters A, B, C, and D refer to Fields A, B, C, and D. The shaded area indicates the time of occurrence of the 1988 drought, which was the most severe drought of the past 50 yr (Tilman and El Haddi 1992).

A (1991:  $F_{8,45} = 12.3, P < .0001$ ; 1992:  $F_{8,45} = 3.08, P < .01$ ), Field B (1991:  $F_{8,45} = 6.14, P < .0001$ ; 1992:  $F_{8,45} = 7.8, P < .0001$ ), and Field C (1991:  $F_{8,45} = 8.13, P < .0001$ ; 1992:  $F_{8,45} = 13.9, P < .0001$ ), but not for Field D (1991:  $F_{8,36} = 1.62, P = .15$ ; 1992:  $F_{8,36} = 1.05, P = .42$ ).

In 1982, but never in subsequent years, high N treatments had greater species richness than controls (Fig. 3A). In 1982 there were significant positive correlations between the rate of nitrogen addition and species richness in Fields B (Pearson  $r = 0.34, n = 54, P = .01$ ) and D ( $r = 0.35, n = 45, P = .02$ ), and no significant correlations in Fields A ( $r = -0.18, n = 54, P = .19$ ) and C ( $r = -0.03, n = 54, P = .85$ ). For each subsequent year (1982 through 1992), for each field, there were significant ( $P \leq .05$ ) negative correlations between the rate of N addition and species richness (e.g., 1986 results in Fig. 3B), except for Field D in 1992 ( $r = -0.25, n = 45, P = .10$ ; Fig. 3C).

Analysis of variance of the total data set with treatment, field, and year as factors showed that there were highly significant treatment, field, and year effects on species richness, and that all two-way interactions were highly significant (Table 1). The significant year effect and the significant year  $\times$  treatment and year  $\times$  field interactions result from three processes. First, species richness was highest at the start of the experiment and declined from the 1st to the 6th yr in the nitrogen treatments, but to a different extent depending on treatment and field (Fig. 4). The greatest declines in species richness occurred in the highest nitrogen treatments in Field A. Initially, Field D had a similar decline, but by 1991 species richness did not differ among its treatments (Fig. 4). Species richness also declined from 1982–

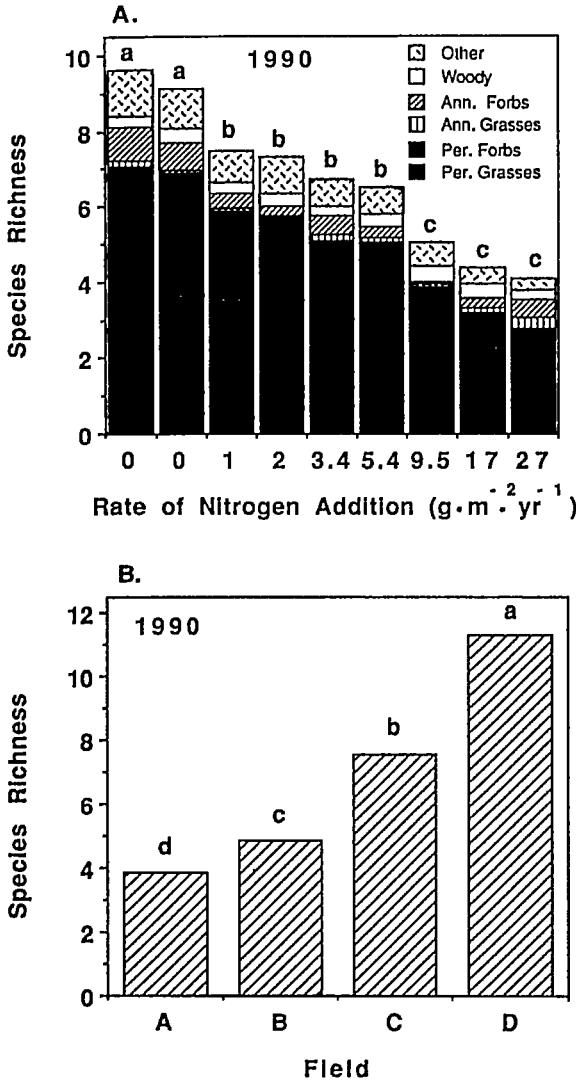


FIG. 2. (A) Dependence of species richness per plot (averaged across all fields) on the rate of nitrogen addition. Note that the first (left side) bar labeled "0" is treatment I, which received no nutrients, and the other "0" is treatment A, which received all nutrients except N. Means that share the same lowercase letter do not differ significantly in total species richness per plot, based on a Student-Newman-Keuls test,  $P \leq .05$ . Data are for 1990, in which year the ANOVA treatment  $\times$  field interaction was not significant. Each bar is subdivided to show the average (across all fields) species richness of six different plant life history classes in each treatment. (B) Dependence of species richness on the identity of the field. Student-Newman-Keuls test (lowercase letters as above) showed that all fields differ significantly from each other ( $P < .05$  for all comparisons).

1986 in the intermediate N treatments in Fields A, B, and C, but not in Field D (Fig. 4). Second, there was a major drought in 1987 and 1988 that led to the loss of  $\approx 37\%$  of the species richness in the controls (Tilman and El Haddi 1992) but to lesser losses in the intermediate and high N treatments (Fig. 4). The drought

had a greater effect on species richness in Fields A and D than in Field B (Fig. 4; Tilman and El Haddi 1992). Third, after the drought, species richness increased more rapidly in the controls in Fields A and C and in all treatments in Field D than in other treatments and fields (Fig. 4).

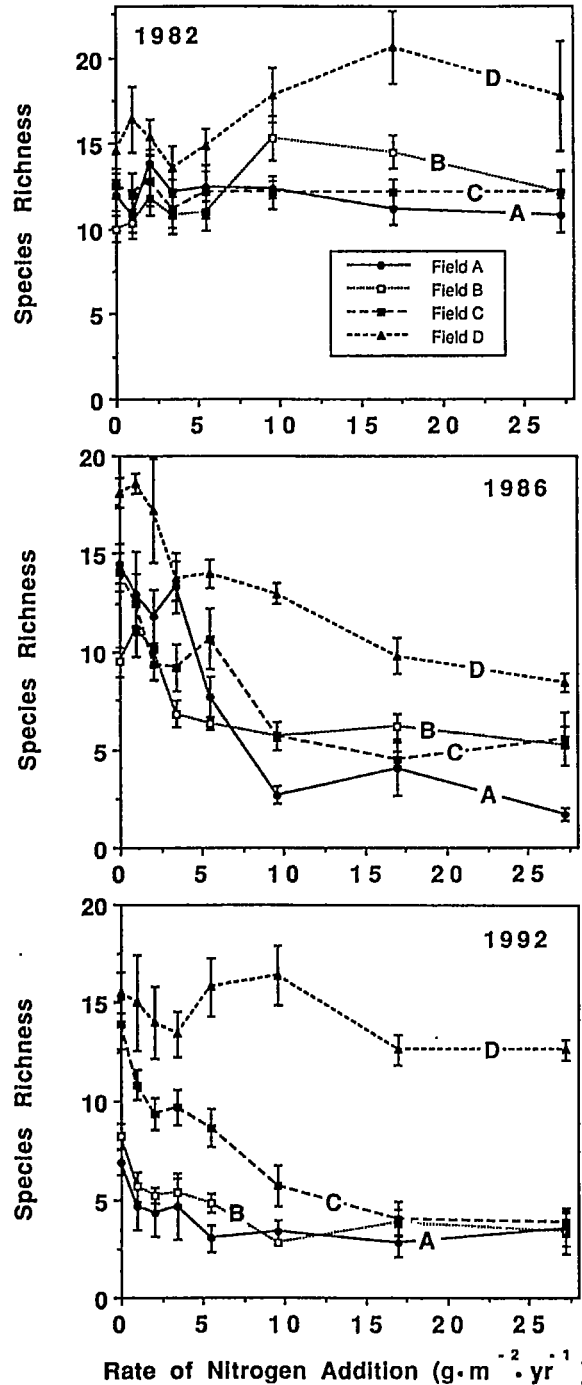


Fig. 3. Species richness per plot (mean  $\pm 1$  SE) in 1982, 1986, and 1992 in Fields A, B, C, and D, graphed against the rate of addition of N.

TABLE 1. Analysis of variance of species richness with Field (A, B, C, or D), Treatment (nine levels), and Year (1982 through 1992) as factors. All interaction terms were calculated. There are 1539 degrees of freedom for error. *F* values shown are based on Type III sum of squares.

	df	<i>F</i>	<i>P</i>
Overall model	395	15.02	.0001
Field	3	643.11	.0001
Treatment	8	133.56	.0001
Year	10	174.34	.0001
Field × Treatment	24	7.88	.0001
Field × Year	30	10.42	.0001
Treatment × Year	80	4.92	.0001
Field × Treatment × Year	240	0.99	.5300

The field × treatment interaction was significant both in the overall ANOVA and in a separate ANOVA of species richness during the 10th and 11th yr of the study. A major cause of this was the markedly different effect of resource enrichment on species richness in Field D than in the other fields. In the successional

fields, increased rates of N supply led to fairly consistent declines in diversity for each year from 1983 on. This same pattern generally held in Field D for the first half of the study, but declines were less dramatic and often not significant. In 1991 and 1992, however, species richness in plots receiving the highest rates of N addition in Field D did not differ significantly from controls ( $P \leq .05$ , Student–Newman–Keuls Test; Fig. 4), whereas in all other fields high N treatments had significantly fewer species than controls.

*Treatment effects on litter, light, and living biomass.*—For each year of the study, there was a significant ( $P \leq .05$ ,  $n = 54$ ) positive Pearson correlation between the rate of N addition and aboveground living biomass in Field A. Such correlations were also significant for all years except 1988, the year of the drought, in Fields B and D, and except 1988 and 1989 in Field C. Litter mass was significantly ( $P \leq .05$ ) positively correlated with the rate of N addition in all years in Field D, in all years except 1983, 1984, and 1992 for

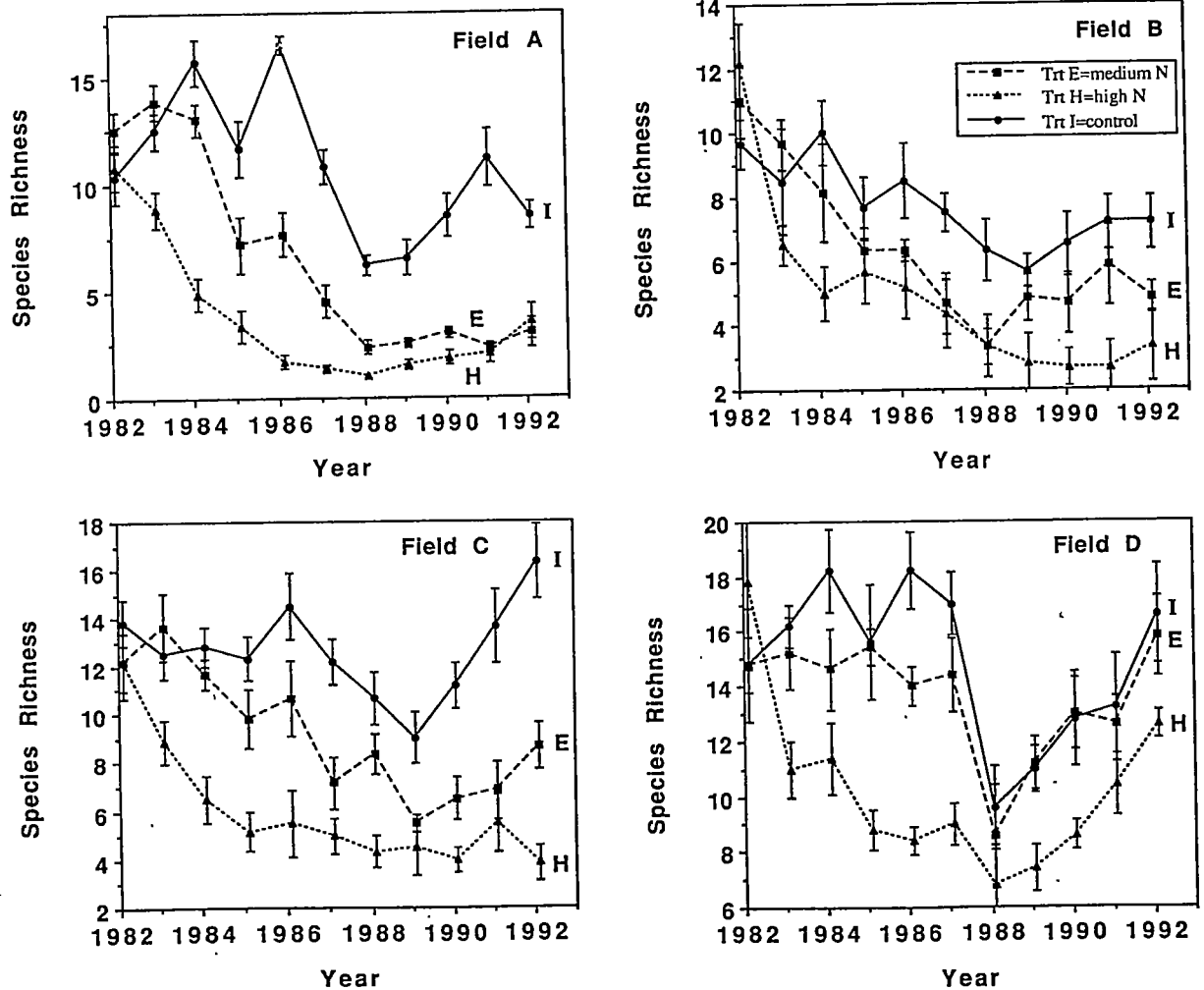


Fig. 4. Mean  $\pm 1$  SE of species richness per plot for treatment I (no nutrients added, —), treatment E ( $5.4 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$  of N, ---), and treatment H ( $27 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ , ····), graphed against year for Fields A, B, C, and D.

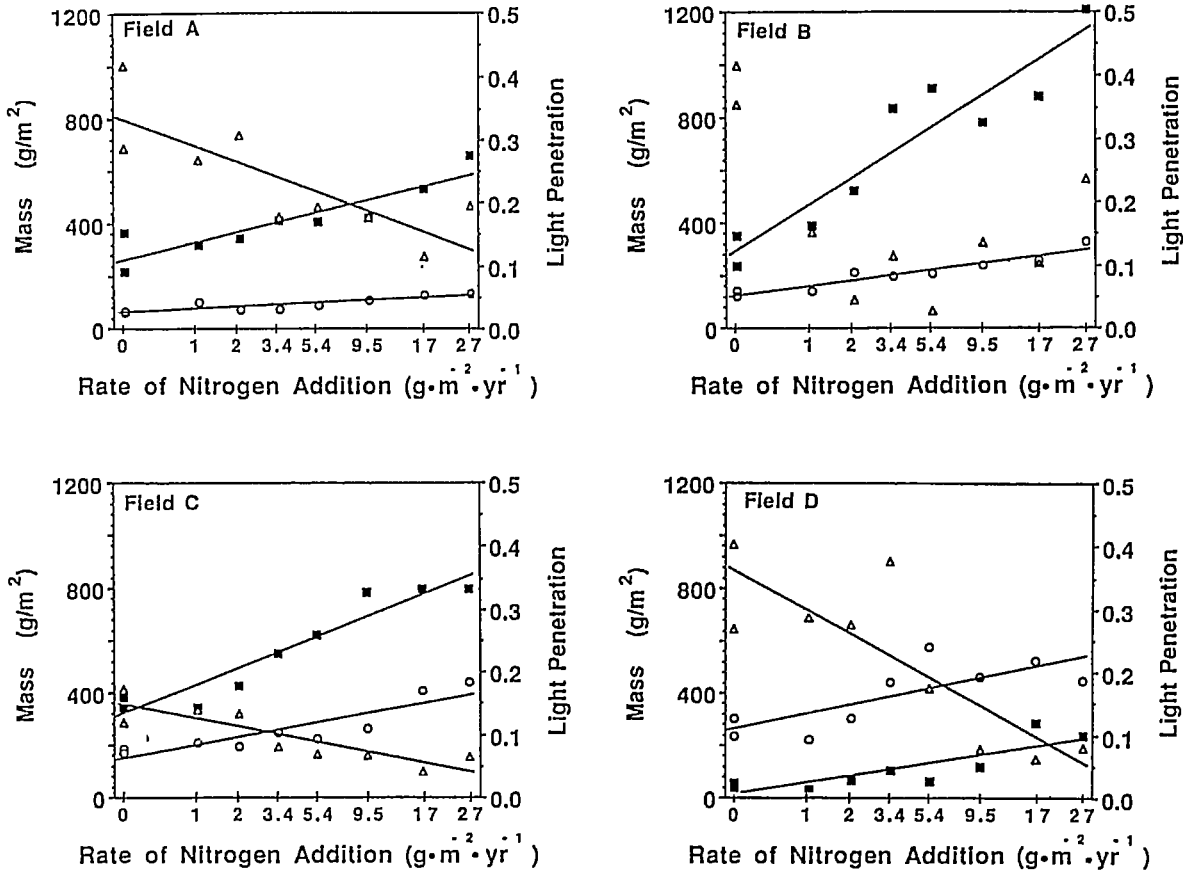


Fig. 5. Dependence of aboveground living plant mass (○), litter (■), and light penetration through the vegetation (Δ) on the rate of nitrogen addition (log of 1 + rate of N addition) in each field in 1990. Fitted lines are from linear regressions, which were significant ( $P < .05$ ,  $n = 9$ ) for all cases except for light penetration in Field B.

Field A, and except 1982 for Fields B and C. Light penetration was significantly ( $P \leq .05$ ) negatively correlated with the rate of N addition in all years in Field A, in all years except 1990 in Field B, except 1984 in Field C, and except 1989 in Field D. Results for 1990 (Fig. 5) are typical of most years except the drought year. After the first few years, the three unburned fields (Fields A, B, and C) generally had 2–5 times more litter than living biomass, whereas the burned field (Field D) had 2–5 times more living biomass than litter.

*Species turnover: two-year intervals.*—Species gains and losses were calculated using adjacent 2-yr intervals. When combined data for 1982 and 1983 were compared to combined data for 1984 and 1985, the number of species gained per plot (Fig. 6) and the proportion gained per plot were significantly negatively correlated with the rate of N addition for each field ( $P < .01$  for all eight correlations). The number of species lost per plot (Fig. 6) and the proportion lost per plot were significantly positively correlated with N addition in each field ( $P < .01$  for all eight correlations).

Each 2-yr interval was also compared with its immediately preceding interval (i.e., 1982 + 1982 vs.

1984 + 1985, 1984 + 1985 vs. 1986 + 1987, 1986 + 1987 vs. 1988 + 1989, 1988 + 1989 vs. 1990 + 1991) to calculate proportion gained and lost per plot throughout the experiment. These are summarized in Fig. 7, which shows results, averaged across all fields, for 6 of the 9 treatments. In control plots and in plots that received all nutrients except N (treatments I and A), gains balanced losses for the first two time intervals (Fig. 7A, B). However, during the drought (1986 + 1987 compared to 1988 + 1989), proportion lost increased, and proportion gained decreased. The recovery of species richness after the drought (1988 + 1989 compared to 1990 + 1991) occurred with losses back at predrought levels, but with gains higher than ever previously observed (Fig. 7A, B). Plots receiving high rates of N addition (e.g., treatments F and H, Fig. 7E, F) initially had higher proportion lost and lower proportion gained than the controls, but these were similar to controls by the final time interval. Plots receiving moderate rates of N addition had intermediate responses (Fig. 7C, D). All plots had an increase in proportion gained after the drought.

*Life histories and species gains or losses.*—A 3-yr

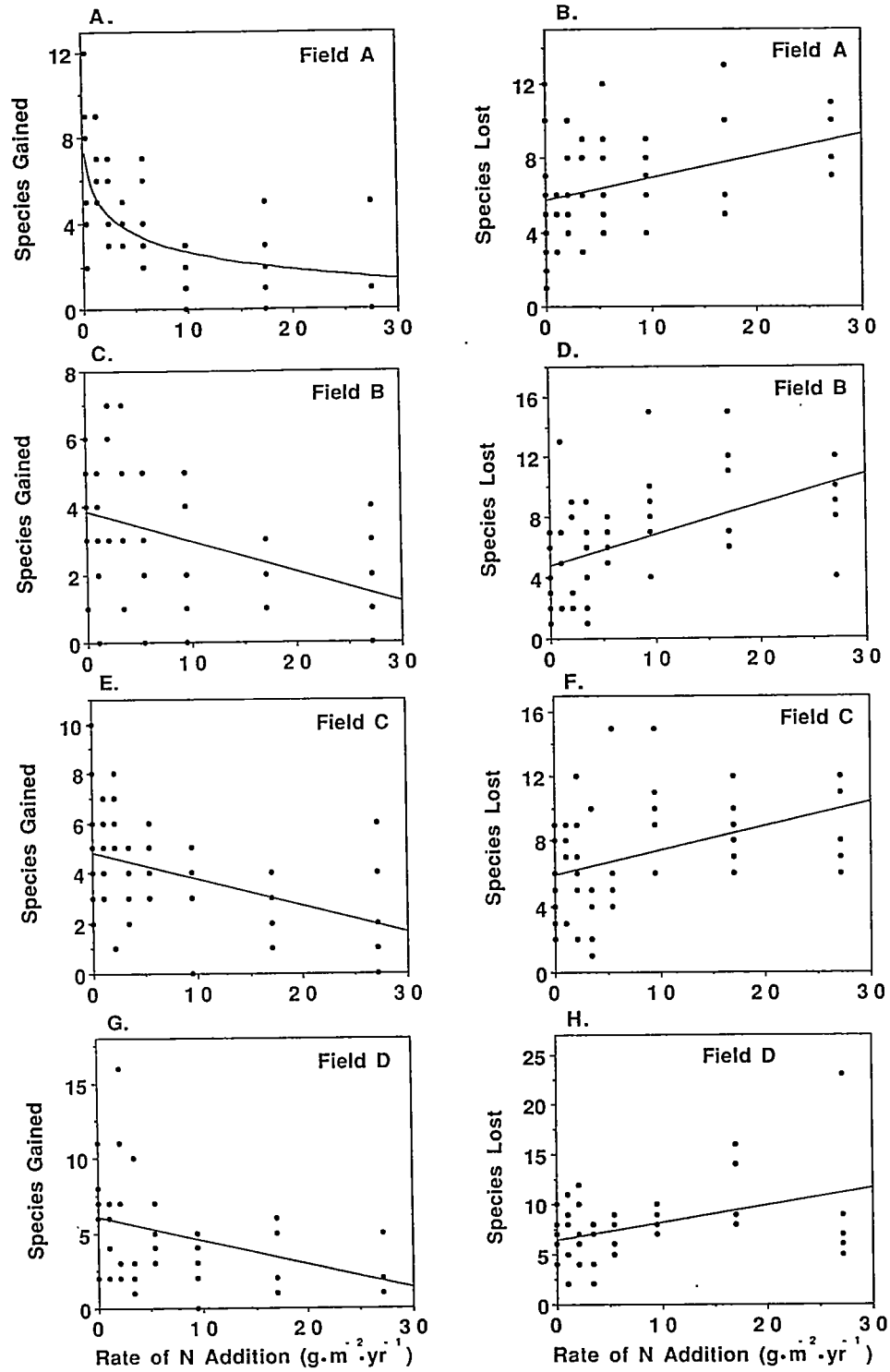


Fig. 6. Dependence of initial species gains and losses on the rate of nitrogen addition, based on a comparison of 1982 + 1983 data with 1984 + 1985 data for each plot in each field. Each fitted straight line has both an intercept and slope that are significantly different from zero ( $P < .05$  in all cases). A curve is shown for the species gained data for Field A because it provided a significantly better fit than a straight line.

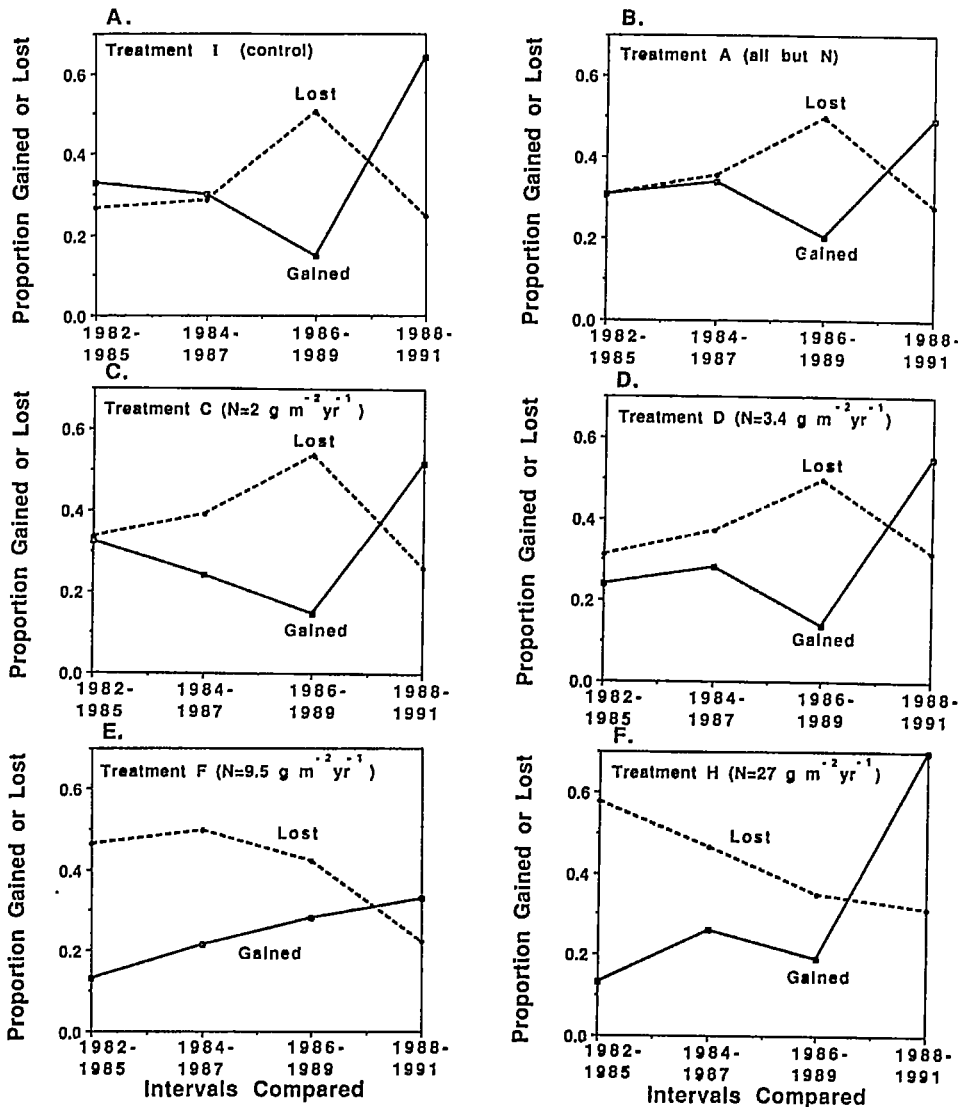


Fig. 7. Dependence of average (across all fields) proportion of species gained (—) or lost (---) is graphed against the time interval. Note that 1982–1985 refers to a comparison of 1982 + 1983 data with 1984 + 1985 data, that 1984–1987 refers to a comparison of 1984 + 1985 data with 1986 + 1987 data, etc. Results are shown for 6 of the 9 different nutrient treatments in the experiment. The 1986–1989 period compares predrought conditions (1986 + 1987) with drought conditions (1988 + 1989), and the 1988–1991 period compares drought conditions with postdrought conditions.

interval was used to compare the initial (1982 + 1983 + 1984) and final (1990 + 1991 + 1992) composition of each plot. Species gains and losses from the initial to the final 3-yr interval were calculated for each of five different life history classes for control plots (treatment I) and for the high N plots (treatment H), and averaged across all fields (Table 2). The average species richness of control plots declined by  $\approx 11\%$  during the study, mainly because of a loss of annual forbs (Table 2). Annual forbs were also lost from the high N plots, but the 47% decline in species richness in these plots was caused mainly by the lower gains in perennial grasses and perennial forbs, and by the higher losses of these same groups (Table 2).

The average number of species of a given life history that were gained or lost for a given treatment in each field was divided by its average initial species richness to calculate proportion gained or lost for that treatment. In general, neither the proportion of annual forbs gained nor the proportion lost was significantly correlated with the rate of N addition in any field ( $P > .05$ ,  $n = 9$ ) or for all fields combined ( $P > .05$ ,  $n = 36$ ). The only exception was a significant positive correlation between the proportion of annual forbs lost and N addition for Field B ( $P > .05$ ,  $n = 9$ ). Similarly, the proportion of annual grasses gained or lost was independent of N addition for each field separately ( $P < .05$ ,  $n = 9$ ) and for all fields combined ( $P < .05$ ,  $n$



TABLE 2. Average number of species of various life histories gained into, lost from, or occupying control plots (treatment I) or high N plots (treatment H).\*

Life history	Control plots				High N plots			
	SR initial	SR final	Species gained	Species lost	SR initial	SR final	Species gained	Species lost
Annual grasses	1.0	0.4	0.1	0.5	0.9	0.5	0.3	0.5
Annual forbs	3.9	2.3	0.5	2.1	2.6	1.4	0.7	1.9
Perennial grasses	4.7	5.1	1.4	1.0	4.5	3.3	0.5	2.3
Perennial forbs	7.8	7.3	2.9	3.3	6.1	2.1	0.5	4.8
Woody	0.6	0.6	0.1	0.2	0.5	0.5	0.2	0.2
Other	1.8	1.8	0.8	0.7	1.5	0.8	0.3	1.1
Total	19.8	17.5	5.8	7.8	16.1	8.6	2.5	10.8

\* SR initial is species richness for the initial 3 yr of the study; SR final is for the final 3 yr. Species gained or Species lost are based on comparisons of species composition of plots during the initial and final 3 yr of the study. All results shown are averages per plot calculated for the four fields combined.

= 36), except for a significantly positive correlation for proportion gained in Field D ( $P > .05$ ,  $n = 9$ ). Neither proportion of woody plants gained nor lost was significantly dependent on N addition for any comparison.

In contrast, for all fields combined, and for each field except Field D, the proportion of perennial forbs gained was significantly negatively correlated, and the proportion lost was significantly positively correlated, with N addition. Similarly, for all fields combined, the proportion of perennial grasses gained was significantly negatively correlated, and the proportion lost was significantly positively correlated with N addition. However, for individual fields, proportion perennial grasses gained was significantly correlated with N addition only in Field A, and proportion lost only in Fields B, C, and D. On average, annual grasses and annual forbs had greater proportional gains and losses than perennial grasses, perennial forbs, or woody plants.

*Litter mass, living plant mass, and light penetration.*—Data from each field were used to determine if there were significant Spearman rank order correlations between species richness (1989 through 1992 data) and living plant mass, litter mass, or proportional light penetration through the vegetation. Light data were not collected in 1991 or 1992. During the 8th through the 11th yr of this study, species richness had significantly negative rank order correlations with living plant mass in 11 of the 16 possible comparisons (Table 3), and with litter mass in 14 of the 16 possible comparisons. Species richness and light penetration had significant positive rank order correlations in 5 of 8 possible comparisons (Table 3).

Because plant mass, litter mass, and light penetration were co-dependent, multiple regression was used to determine their statistically independent effects, but was not performed for 1991 and 1992 because light data were not collected. Multiple regressions of 1989 or 1990 species richness on aboveground living plant mass, litter mass, and proportional light penetration, performed for each field (Table 4), revealed that species richness was a significantly decreasing function of litter

mass for 7 of the 8 cases. In the other case (Field B, 1989) the relationship was only marginally significant ( $P = .057$ ). In none of the fields or years did multiple regression reveal that species richness was significantly dependent on aboveground living plant mass (Table 4). However, in 3 of the 8 cases, multiple regression showed that species richness was significantly higher in plots with higher light penetration through the vegetation (Table 4).

#### DISCUSSION

This experiment determined the long-term effects of productivity on the species richness of successional and native grasslands. After the 1st yr, higher rates of N

TABLE 3. Spearman rank order correlation coefficients ( $r_s$ ) between species richness and the listed variable for 1989, 1990, 1991, or 1992 using data on a field-by-field basis. For Field A, B, or C,  $n = 54$ , but for D,  $n = 45$ . Light penetration was not measured in 1991 or 1992:

	Plant mass	Litter mass	Light penetration
1989			
Field A	-0.54**	-0.67**	0.54**
Field B	-0.41*	-0.45**	0.49*
Field C	-0.10 <sup>NS</sup>	-0.66**	0.64**
Field D	-0.07 <sup>NS</sup>	-0.37*	0.27 <sup>NS</sup>
1990			
Field A	-0.54**	-0.57**	0.52**
Field B	-0.31*	-0.58**	0.24 <sup>NS</sup>
Field C	-0.41**	-0.49**	0.55**
Field D	0.14 <sup>NS</sup>	-0.30*	0.13 <sup>NS</sup>
1991			
Field A	-0.72**	-0.65**	
Field B	-0.55**	-0.46**	
Field C	-0.46**	-0.51**	
Field D	0.24 <sup>NS</sup>	0.06 <sup>NS</sup>	
1992			
Field A	-0.28*	-0.46**	
Field B	-0.62**	-0.59**	
Field C	-0.69**	-0.56**	
Field D	-0.19 <sup>NS</sup>	-0.03 <sup>NS</sup>	

\*  $.01 < P \leq .05$ , \*\*  $P \leq .01$ , and <sup>NS</sup> means  $P > .05$ .

TABLE 4. Multiple regressions of species richness on litter mass, aboveground living plant biomass, and light penetration through vegetation for 1989 and 1990. *F* values, based on Type II sum of squares, indicate if estimated slopes or intercepts differ from 0. \*  $.05 \geq P > .01$ ; \*\*  $P \leq .01$ , and <sup>NS</sup> means  $P > .05$ . *df* = 1, 52 for Fields A, B, and C, and *df* = 1, 41 for Field D.

	Regression slopes			Regression intercept
	Litter	Biomass	Light	
1989				
Field A	-0.007 <i>F</i> = 14.28**	-0.007 <i>F</i> = 3.72 <sup>NS</sup>	2.07 <i>F</i> = 0.31 <sup>NS</sup>	8.27 <i>F</i> = 33.86**
Field B	-0.002 <i>F</i> = 3.79 <sup>NS</sup>	-0.004 <i>F</i> = 2.61 <sup>NS</sup>	0.42 <i>F</i> = 0.02 <sup>NS</sup>	6.82 <i>F</i> = 47.48**
Field C	-0.002 <i>F</i> = 7.13**	0.003 <i>F</i> = 1.99 <sup>NS</sup>	19.9 <i>F</i> = 15.82**	6.27 <i>F</i> = 30.83**
Field D	-0.007 <i>F</i> = 5.19*	0.001 <i>F</i> = 0.31 <sup>NS</sup>	0.10 <i>F</i> = 0.05 <sup>NS</sup>	11.62 <i>F</i> = 169.67**
1990				
Field A	-0.004 <i>F</i> = 6.26*	-0.009 <i>F</i> = 1.36 <sup>NS</sup>	8.31 <i>F</i> = 10.52**	4.31 <i>F</i> = 12.08**
Field B	-0.003 <i>F</i> = 9.82**	0.0004 <i>F</i> = 0.01 <sup>NS</sup>	0.040 <i>F</i> = 0.00 <sup>NS</sup>	6.87 <i>F</i> = 47.40**
Field C	-0.005 <i>F</i> = 7.53**	-0.0003 <i>F</i> = 0.01 <sup>NS</sup>	18.96 <i>F</i> = 13.17**	8.62 <i>F</i> = 46.87**
Field D	-0.011 <i>F</i> = 4.79*	0.003 <i>F</i> = 0.85 <sup>NS</sup>	-1.55 <i>F</i> = 0.26 <sup>NS</sup>	11.89 <i>F</i> = 52.07**

addition consistently led to lower species richness in all fields except the burned native prairie, Field D. By the 10th and 11th yr of the experiment, nitrogen treatments in the burned prairie did not differ in species richness. Experimental increases in productivity often lead to decreased plant diversity (e.g., Tilman 1982, 1987, Carson and Barrett 1988, Pysek and Leps 1991). However, in some studies, especially short-term ones, increased productivity either had no consistent effect on diversity (Carson and Pickett 1990, Goldberg and Miller 1990), led to increased diversity (Pringle 1990), or to an increase followed by a decrease (Carson and Barrett 1988). The increase in species richness at high rates of N addition during the 1st yr of my study was transient. It seemed to result from nitrogen-dependent germination of seed-banking species, most of which were absent by 1983. Such transients may explain why short-term studies often provide ambiguous results for the effects of nutrient enrichment on species richness (e.g., Carson and Barrett 1988, Carson and Pickett 1990, Goldberg and Miller 1990).

The drought of 1988 led to a sharp decrease in species richness (Figs. 1 and 4). As discussed by Tilman and El Haddi (1992), and as illustrated in Fig. 7, this decrease in species richness was caused both by decreased species gains and by increased species losses. The unfertilized control plots (treatment I) in Fields C and D seem to have recovered from the drought by 1992 (Fig. 4), but control plots in Fields A and B had not regained their predrought species richness by then (Fig. 4).

MacArthur and Wilson (1967) suggested that the species richness of a habitat should depend on the interplay of colonization and extinction rates. Thus,

changes in species richness along productivity gradients should depend on the effects of productivity on both the colonization and extinction probabilities of species. By decomposing the dynamics of species richness into these two components, it may be possible to gain greater insight into the forces controlling species richness along productivity gradients or in response to other biotic or abiotic variables.

The number of species gained and lost per treatment during this study provide estimates of these components, but include sampling noise (Nilsson and Nilsson 1985). Some of the species "gained" may have been present previously but not sampled. Some of the species "lost" may still be present but rare. Proportion gained and lost were also calculated to try to compensate for these potential biases. However, when plots have similar species richness, such as when initial changes are compared, neither index should be biased.

This study showed that both colonization and extinction rates were affected by productivity, and that these were equally important determinants of species richness. The initial responses (1982 + 1983 compared to 1984 + 1985; Fig. 6) clearly showed that fewer new species were gained and that a greater number of existing species were lost in more productive plots than in controls. Proportional gains and losses responded similarly.

The treatments that received no nitrogen had proportional gains that balanced proportional losses for the first two time interval comparisons (Fig. 7), but were impacted by the 1988 drought, which led to greater losses and lower gains. Recovery from the drought involved greater proportional gains than in previous years, but proportional losses were not lower. Thus,

the recovery of species richness after the drought was caused more by increased rates of colonization than by decreased rates of extinction in the more species-poor plots.

The initial decrease in species diversity in the high N treatments was caused both by decreased gains of new species and by increased losses of existing species (Fig. 7). The difference between proportion lost and gained was initially great, but it declined in successive time intervals as plots became more species poor. In theory, if a treatment leads to a new equilibrium species richness, losses and/or gains should initially diverge from controls, but should eventually become equal to each other as the new dynamic equilibrium is established. The approximate equality of loss and gain rates in control plots before the drought, and the higher gain rate after species richness declined because of the drought, suggest that species richness is regulated around some quasi-equilibrium in these fields. However, a rigorous test of this would require the experimental addition and removal of species from replicated plots.

As might be expected, annual grasses and annual forbs had higher turnover (proportional gains and losses) than perennials or woody species, but their gains and losses did not depend on productivity. Thus, most of the change in species richness along the productivity gradient was caused not by annuals but by perennial forbs and perennial grasses because these life history groups had both higher loss and lower gain rates at higher rates of N addition.

Species lost from control plots were, on average, replaced by new species (Fig. 6), but many species lost from enriched plots were not replaced by colonists, especially in the unburned fields in which litter accumulated (Table 4). Because all treatments within a given field likely experienced similar rates of arrival of seed of potential colonists, the lower rate at which species were gained in enriched plots suggests that fewer propagules were able to germinate, become established, and/or survive until harvest in enriched plots than in less productive plots. This may be caused by competitive exclusion, or by other biotic or abiotic differences among treatments. Thus inhibition of seedling establishment or survival was a major cause of the decrease in species richness observed in many high N treatments.

The greater loss of species from high N plots shows that there was also a disproportionate local extinction of existing species in the high N treatments. This might have resulted from competitive displacement of shorter species by taller species that were better able to obtain light in more productive plots. The greater loss of species also might have resulted from recruitment failure after the death of an existing individual.

Goldberg and Miller (1990) suggested that low availability of light for subcanopy plants would increase mortality and decrease diversity by driving rare species to extinction or by excluding low-growing or shade-

intolerant species. They found that N addition led to decreased light penetration, increased mortality of subcanopy plants, and decreased diversity in a 1st-yr-old field. However, water addition led to a similar decrease in light penetration, but did not increase mortality nor decrease species richness, perhaps because N led to more rapid canopy closure.

Goldberg and Miller studied the effects of productivity on diversity on a much shorter time scale than I did. They showed that diversity declined when seedlings and other plants of short stature were overtopped and died during a growing season. In contrast, my measure of species gains recorded the number of new species that survived to the time of harvest, which was in mid-to-late growing season. Thus, the lower species gains per treatment in my high N treatments may be caused by the same forces that Goldberg and Miller (1990) said caused higher mortality. Newly germinated plants are short, live in a low light environment in high N treatments, and may have higher mortality, and thus lower effective colonization (species gains) in productive plots. The significant correlations between species richness and light penetration in 5 of 8 cases (Table 3) support this hypothesis. However, in multiple regressions that included light, litter, and living biomass (Table 4), light was significant in only 3 of 8 cases.

An alternative explanation for the lower species gain per plot in high N treatments is that accumulated litter may have inhibited germination or increased mortality for seedlings and other small plants. Litter can inhibit germination, growth, and survivorship (e.g., Sydes and Grime 1981, Gross and Werner 1982, Monk and Gabrielson 1985, Bergelson 1990, Carson and Peterson 1990, Tilman and Wedin 1991). Carson and Peterson (1990) found that removal of litter significantly increased seedling densities, and addition of litter decreased seedling densities and species richness in an old field. Bergelson (1990) observed that litter of *Poa annua* inhibited emergence and survival of annual forbs the next year. Litter inhibition caused monocultures of a perennial grass, *Agrostis scabra*, to oscillate, with oscillations becoming seemingly chaotic on plots with the greatest litter mass (Tilman and Wedin 1991).

Thus, the thick litter layers that accumulated in high N plots (Fig. 5), especially those not burned, may have led to lower species richness. The native prairie lacked a litter layer in 2 out of 3 yr because of spring burning and always had much less litter than the other fields (Fig. 5). In all other fields, which were never burned, there were significantly negative Spearman rank order correlations between litter mass and species richness for each of the final 4 yr (Table 3). However, there was only one significant rank order correlation between litter mass and species richness in the native prairie (Table 3), and this occurred in 1989 when the field was unburned. Multiple regressions showed that species richness was a significantly declining function of litter mass in 7 of 8 comparisons (Table 4). This suggests

that litter mass, and possibly light penetration, are important factors preventing the establishment of new species and leading to the loss of existing species in productive grasslands.

Although there were significant rank order correlations between species richness and living plant mass (Table 3), multiple regressions failed to show a single instance in which species richness was significantly dependent on aboveground living plant mass (Table 4). Thus, these experiments suggest that it was not productivity or aboveground living biomass, per se, but the increased litter and possibly the decreased light associated with higher productivity, that led to lower species richness.

These results suggest that few of the species in these fields are capable of establishing in areas with a dense litter layer, and that this limits the diversity of productive, but unburned, grasslands. Because these grasslands are normally unproductive, and because fire was prevalent before European settlement of Minnesota, there would have been little selection favoring plant traits that allowed establishment in dense litter. As such, the decline in diversity following nutrient enrichment might also be attributed to there being a smaller pool of species capable of colonizing productive sites because few grassland or prairie species are adapted to dense litter, which had historically been a rare occurrence. This explanation may also apply to diversity patterns in the grasslands of England and northern Europe (e.g., Grime 1979, Bakker 1989), which mainly are of anthropogenic origin (Ellenberg 1988).

A survey of British grasslands by Al-Mufti et al. (1977) and Grime (1979) demonstrated that species richness was related to total aboveground standing crop including litter. Peak plant species richness occurred for sites with between 500 and 600 g/m<sup>2</sup> of litter plus living plant mass. Surveys of Dutch salt marshes and grasslands, reviewed by Bakker (1989), also found that plant species richness was dependent on the sum of living plus litter mass. The experimental results presented here may explain why the sum of living plus litter mass was correlated with species richness in their studies. This sum is a simple way to measure the magnitude of inhibition by litter and by light interception.

*Heterogeneity and diversity.*—My results are inconsistent with the spatial heterogeneity hypothesis of diversity, which predicts that greater spatial heterogeneity in soil nutrient supply rates should lead to greater diversity (e.g., Tilman 1982). The seven different nitrogen treatments should have greatly increased the total spatial heterogeneity in N supply rates within each field, but they led to lower total species richness per field (Fig. 1), even before the drought. However, an increase in species richness would require the invasion and establishment of species that had been absent from these fields prior to manipulations. Few new species have invaded these fields, perhaps because species that can do well in fertile plots are rare on the infertile soils

of this region. Thus, these experiments show that, in the absence of colonization by new species, increased nutrient heterogeneity leads to decreased local diversity. However, if colonization limitation were overcome by the addition of propagules of novel species, or by allowing the study to continue for many more years, different results might occur.

The results presented here reinforce the frequently observed dependence of species richness on productivity, but suggest that this may result from two forces: lower rates of establishment of seedlings, and higher rates of displacement of existing species in more productive habitats. These changes in colonization and extinction may be at least partially caused by the dense litter that accumulated in productive plots. The generality of such a litter effect can be determined only by other studies, but litter inhibition has been observed in both grasslands (Al-Mufti et al. 1977, Grime 1979, Monk and Gabrielson 1985, Bergelson 1990, Carson and Peterson 1990, Tilman and Wedin 1991), and forests (Sydes and Grime 1981).

The greater generality of this study is that ecological factors, such as productivity or disturbance, may influence both colonization dynamics and local extinctions. Many theories of diversity along productivity gradients have considered possible effects of productivity on extinction but failed to include the effects of productivity on colonization. Future theories need to incorporate such effects, and their mechanistic bases, into an island biogeographic, metapopulation (see Gilpin and Hanski 1991), or neighborhood (Pacala 1986) perspective.

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