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Experimental Nitrogen Gradients**



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SECONDARY SUCCESSION AND THE PATTERN OF PLANT DOMINANCE ALONG EXPERIMENTAL NITROGEN GRADIENTS¹

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Abstract. In 1982, experimental nitrogen gradients were established on both existing and disturbed (disked) vegetation in three fields (abandoned 14, 25, and 48 yr) and on existing vegetation in native oak savannah. Each of these seven gradients contained five or six replicates of each of nine treatments that differed in the annual rate of nitrogen addition. In none of the fields did plant biomass, height, species richness, or light penetration respond to addition of P, K, Ca, Mg, S, and trace metals. In contrast, plant biomass and height increased significantly, and light penetration and species richness decreased significantly, with added nitrogen along all seven gradients. On average, >60% of the species had been displaced from high-nitrogen treatments by 1985.

Nitrogen addition led to a period of transient dominance by certain species. Species that reached peak relative abundance in high-nitrogen treatments in 1982 tended to be rare in all but the low-nitrogen treatments by 1985. In contrast, the relative abundances of most species that dominated the high-nitrogen treatments in 1985 did not increase along the nitrogen gradients in 1982.

The relative or absolute abundances of most common species changed significantly along the experimental gradients in at least 1 yr. By 1985, many common species were differentiated in their distributions along the seven gradients. In general, early successional annuals and short-lived perennials and plants of short stature at maturity reached their peak abundance in low-nitrogen plots, whereas plots receiving high rates of nitrogen addition were dominated by long-lived herbaceous and woody species that are taller at maturity.

A survey of 22 old fields at Cedar Creek, Minnesota, showed that total and available soil nitrogen increased during succession and that major species had individualistic, fairly Gaussian distributions along this temporal nitrogen gradient. The distributions along the experimental gradients of most of the common species were consistent with the pattern observed in the old-field survey, demonstrating that nitrogen influences the pattern of secondary succession at Cedar Creek. The major exception was *Agropyron repens*, an early successional grass that dominated high-nitrogen treatments on six of the seven gradients.

Comparisons of species responses on the disturbed plots with those on plots of existing (undisturbed) vegetation showed that, by 1985, most species responded similarly to the nitrogen gradients despite great differences in their initial abundances. For instance, *Agropyron repens*, an initial dominant of Field A but rare in Fields B and C, was a dominant in the high-nitrogen treatments in both the disturbed and undisturbed plots of these three fields. It invaded into and rapidly increased in abundance in numerous high-nitrogen plots from which it was initially absent. *Schizachyrium scoparium* declined along the nitrogen gradients both in undisked plots in which it was initially dominant and in disked plots in which it was initially rare. Such similarities suggest that the outcome of interspecific interactions among old-field plants is highly dependent on nitrogen supply rates, but fairly independent of initial plant abundances.

Key words: convergence; diversity; experimental gradients; light; nitrogen; old fields; prairie plants; sandy soils; succession; transient dynamics.

INTRODUCTION

Many factors, including the availabilities of limiting resources, the past history of a habitat, the physical characteristics of a habitat, herbivory, mutualism, and disturbance, can influence the structure and dynamics

of plant communities. In this paper, I present experimental studies designed to determine the effects on successional vegetation of two of these factors: the rate of supply of a limiting soil resource and the past history of the vegetation. Both observational and theoretical studies have suggested that nutrient supply rates can control the course of succession and the abundances of species in communities (e.g., Olson 1958, Snaydon

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1962, Pigott and Taylor 1964, Tilman 1982, 1985). However, only experimental studies can determine how the species composition, diversity, and dynamics of successional vegetation depend on the supply rate of a limiting soil nutrient. If resource supply rates do structure natural communities, then the responses of species to experimental nutrient gradients should be similar to the correlational patterns observed in natural vegetation. However, it has also been argued that plant communities have considerable inertia. Thus, it is thought that once an individual plant has become established at a site, it may be able to prevent the establishment of other individuals of the same or different species because the new individuals would have to invade the area as seedlings or shoots, and could be shaded out or outcompeted for soil resources by the established plants. This could lead communities to have multiple stable equilibria (Lewontin 1969, Strobeck 1973, May 1977, 1979), i.e., to have the state of a community at equilibrium depend on both interspecific interactions and on past history, with the particular equilibrium attained determined by the initial densities and the order of colonization of the species.

In this paper, I report the results of field experiments performed at Cedar Creek Natural History Area, Minnesota. Nitrogen is the major limiting nutrient at Cedar Creek (Tilman 1983, 1984). In 1982, I established replicated experimental nitrogen gradients on the existing vegetation in four fields of different successional ages and on newly disturbed (disked) soil in three of these fields. These seven experiments document the effects of nitrogen supply rates on species diversity, species dominance, and population dynamics during secondary succession at Cedar Creek. Because disking killed most of the existing perennial plants and favored plants that started from seed or small rhizome fragments, there were great differences in the initial sizes and life history stages of individuals and in the initial densities of species between the disked and undisked experiments. Initial species abundances also differed greatly among the four fields. These experiments can thus help determine the extent to which the responses of plant species to different rates of supply of nitrogen depend on the initial abundances and life history stages of the species. I also report the dependence of plant abundances on soil nitrogen that was observed in a survey of vegetation and soils in a chronosequence of 22 old fields at Cedar Creek, and compare these patterns with the response of these species to the experimental nitrogen gradients.

The 369 plots that make up the seven experimental nitrogen gradients document the effects of different rates of supply of a major limiting soil resource, nitrogen, on the diversity, composition, and dynamics of disturbed and undisturbed old-field and native oak savannah vegetation. In combination with the old-field survey data, they provide a detailed observational and

experimental data set against which alternative hypotheses of community structure may be tested.

METHODS

Study site

This work was performed on level, upland, well-drained fields in the University of Minnesota's Cedar Creek Natural History Area, situated 45 km north of Minneapolis, Minnesota, USA (45°24' N, 93°12' W). Cedar Creek is located on a large, thick (20–40 m) sandplain that was deposited by glacial streams about 14 000 yr ago. The Eurasian annuals that invaded the area with agriculture (between 1890 and 1910: Pierce 1954) were the initial dominants of fields upon abandonment from agriculture. They were replaced by perennials, especially native prairie species (Inouye et al. 1987). Few trees had re-established, even in unburned fields >50 yr old.

Old-field survey

In 1983, we performed a survey of the soils and vegetation of 22 Cedar Creek old fields that had been abandoned from agriculture for from 1 to 56 yr. All fields were level, well-drained, and located on similar (Zimmerman, Sartell, or Nymore) sandy soils. The old-field survey, but not responses on a species-by-species basis, is discussed in Inouye et al. (1987). Twenty-five soil samples, each with a matched vegetation sample, were collected at 1.5-m intervals along each of four parallel transects per field, with the transects being 25 m apart. Fields A and B, described below, each had six transects. This gave a total of 2300 sampling points, but 38 soil samples were lost. Total N was measured on all samples, but percent organic matter on about every fifth sample. To sample vegetation, a 0.5 × 1.0 m quadrat was centered around the site at which each soil sample was to be taken, and percent cover of each species present was estimated. To standardize these estimates, we spent 2 d training before we began. We used cardboard cutouts of known cover but various shapes to help estimate cover within quadrats and we divided ourselves into four teams, with each team doing one transect per field. To determine the dependence of the abundance of a species on soil nitrogen, based on this old-field survey, the observed total soil nitrogen levels for all samples in all 22 fields were divided into 40 classes of equal size on a natural log scale (classes 0.05 ln units wide). The average percent cover of a species was then computed for each interval. These were then smoothed once using running averages over a range of three nitrogen classes.

In 1986, we collected two soil samples per transect (eight per field) in 16 of these old fields. Immediately upon collection, 2 mol/L KCl was used to extract ammonium and nitrate. Samples were shaken for 30 min, then allowed to settle overnight at 5°C before extract-

able ammonium and nitrate levels were determined using a two-channel Technicon Autoanalyzer.

Experimental fields

In each of four fields, a level area with fairly uniform vegetation was chosen for the experimental plots. The youngest field, Field A, was last cultivated and planted, to soybeans, in 1968. It had been abandoned 14 yr when this work began. It had a Sartell fine sand soil, an excessively well-drained soil formed in sandy outwash and aeolian sediments (Grigal et al. 1974). Before experimentation, the dominant species (those with the greatest biomass) in Field A were *Agropyron repens*, *Berteroa incana*, *Agrostis scabra*, *Achillea millefolium*, *Erigeron canadensis*, *Aristida basiramea*, *Ambrosia artemisiifolia*, *Poa pratensis*, and *Potentilla recta*.

Field B was last farmed in 1957 (last crop, soybeans). It was 25 yr old in 1982. It had a Zimmerman fine sand soil, similar to the Sartell sand except for a thicker B₂₁ (Grigal et al. 1974). The dominant plant species in this field in 1982 were *Schizachyrium scoparium*, *Poa pratensis*, *Panicum oligosanthos*, *Lespedeza capitata*, *Cyperus filiculmis*, *Rosa arkansana*, *Solidago rigida*, and *S. nemoralis*.

The oldest of the abandoned fields, Field C, was last farmed, to corn, in 1934. It was 48 yr old in 1982. It had a Zimmerman fine sand soil. The dominant plants in this field were *Schizachyrium scoparium*, *Artemisia ludoviciana*, *Poa pratensis*, *Stipa spartea*, *Sorghastrum nutans*, *Solidago nemoralis*, *Aster azureus*, *Ambrosia coronopifolia*, and *Carex* sp. Field C contained many seedlings and a few scattered saplings of *Quercus macrocarpa*, *Q. ellipsoidalis*, and *Q. borealis*, especially at the field edges, but no mature trees.

The field of native oak savannah, Field D, had never been clear-cut or plowed. Although possibly grazed by cattle prior to 1940, it had not been grazed since then. Its soil was a Sartell fine sand. It was one of several compartments in a prescribed burn experiment (White 1983). Since 1966 it had been burned, generally in late April or early May, for 2 yr in succession followed by 1 yr without burning. The entire field, including the experimental plots, was burned on 27 April 1982, 17 April 1984, and 11 April 1985, but not in 1983. (Fields A, B, and C had never been burned.) To avoid the shade cast by scattered oaks, the area chosen was an opening, $\approx 20 \times 60$ m, that had no mature trees but was dominated by native prairie species. The dominant species were *Carex muhlenbergii*, *Andropogon gerardi*, *Sorghastrum nutans*, *Artemisia ludoviciana*, *Carex pensylvanica*, *Solidago graminifolia*, *Poa pratensis*, *Schizachyrium scoparium*, *Stipa spartea*, *Panicum perlongum*, *Rubus* sp., *Helianthemum bicknellii*, and *Liatris aspera*.

Experimental plots were fenced to exclude above-ground and below-ground mammalian herbivores such as deer, pocket gophers, and rabbits. Galvanized weld-

ed-wire hardware cloth (6×6 mm opening) was buried to a depth of 84 cm. Additional hardware cloth extended 60 cm above the ground, and wire fence with an opening size of 10×10 cm extended to 1.8 m above the ground. Gophers initially present in the fenced areas were trapped and removed, as were any that subsequently invaded. Invasions were common only in Field A, which had high gopher density.

Experimental design

Identical experimental nitrogen gradients were established both on the existing vegetation of Fields A, B, and C and on adjacent newly disturbed (disked) areas within each of these three fields. The three disturbed gradients were established by thoroughly disking, in April 1982, a level 35×55 m area ≈ 20 times in one direction, 20 times perpendicular to that, and 5 times diagonally, using a tractor-pulled 45 cm diameter agricultural disk harrow. Disking pulverized the existing vegetation and left bare soil. The disturbed plots were then hand-raked to smooth the soil surface and remove any remaining clumps of vegetation. Each of these six experimental nitrogen gradients (three disturbed, three undisturbed) consisted of six replicates of each of nine different treatments, giving 54 plots for each gradient in Fields A, B, and C. Because of the smaller area available in Field D, I established a gradient only on undisturbed vegetation, with just five replicates of each of the nine treatments. The plots were 4×4 m in Fields A, B, and C, but were 2×4 m in Field D. All plots were separated by 1-m buffers. A completely randomized experimental design was used for each of the seven nitrogen gradients. The plots were laid out in 6×9 grids in Fields A, B, and C. Field D had a 3×17 grid. Six plots in Field D that contained large mounds of the thatching ant *Formica obscuripes* or clumps of the shrub *Corylus* were not used.

Treatments consisted of no nutrient addition (labeled treatment I) and eight different types of nutrient addition. These eight treatments, labeled A through H, all received the same mixture of P, K, Ca, Mg, S, and citrate-chelated trace metals each year but differed in the amount of nitrogen added each year (Table 1). Nitrogen was added as commercial pelletized ("slow release") 34-0-0 NH₄NO₃ fertilizer. Nutrients were applied by manual broadcasting from plot margins twice each year (1982–1985), with half of the nutrients applied in mid-May and half in late June. Before nutrient addition in 1982, four 15 cm long soil cores were collected in each plot.

Sampling methods

Vegetation within each of the 369 plots was sampled each year by clipping at the soil surface all plants within a strip 10 cm wide by 3 m long. Prior to clipping, a 3 m long steel rod was slid along the soil surface to mark the edge of the area to be sampled. This rod acted as

TABLE 1. Nutrient addition rates for the nine treatments of the nitrogen gradient experiments. Nitrogen was added as NH_4NO_3 (commercial 34-0-0 fertilizer).

Treatment	Nitrogen (N) added ($\text{g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$)	Other nutrients†
A	0.0	All
B	1.0	All
C	2.0	All
D	3.4	All
E	5.4	All
F	9.5	All
G	17.0	All
H	27.2	All
I	0.0	None

† Other nutrients consisted of a mixture of P, K, Ca, Mg, S, and citrate-chelated trace metals. These were applied at the following rates: P_2O_5 , $20.0 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ (as commercial 0-46-0 fertilizer); K_2O , $20.0 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ (commercial 0-0-61); CaCO_3 , $40.0 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ (as fine-ground commercial lime); MgSO_4 , $30.0 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ (U.S. Pure Epsom salts); CuSO_4 , $18.0 \mu\text{g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$; ZnSO_4 , $37.7 \mu\text{g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$; CoCO_2 , $15.3 \mu\text{g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$; MnCl_2 , $322.0 \mu\text{g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$; and NaMoO_4 , $15.1 \mu\text{g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$.

a guide for rechargeable electric lawn-edging shears used to clip the vegetation. These shears were mounted in a metal frame with guides to separate the vegetation into a 10 cm wide strip and a basket to catch the vegetation. The first vegetation sample was clipped parallel to, but 25 cm in from, the left edge of each plot. The ends of the 3-m strip were 50 cm from the front and back edges of each plot. The second through fifth samples were similarly located: parallel to and 25 cm from the right edge, 50 cm from the left edge, 50 cm from the right edge, and 75 cm from the left edge of each plot, respectively. There were a few instances in Field A in which the sampling areas were moved to the next location to avoid a fresh gopher mound.

Two samples were collected in the undisturbed plots of Fields A, B, and C in 1982. Otherwise, each plot was sampled once per year. For the undisturbed vegetation in Field A, samples were clipped on 11–14 July 1982, 10–13 August 1982, 11–13 July 1983, 9–12 July 1984, and 8–10 July 1985. The vegetation of the disked gradient in Field A was sampled on 4 August 1982, on 13–14 July 1983, on 12–16 July 1984, and on 10–12 July 1985. For the undisturbed gradient in Field B, samples were collected on 14–19 July 1982, 13–18 August 1982, 5–10 August 1983, 6–10 August 1984, and 5–7 August 1985. The disked gradient in Field B was sampled on 5 August 1982, 10–12 August 1983, 6–8 August 1984, and 8–12 August 1985. The undisturbed gradient in Field C was clipped on 20–26 July 1982, 18–25 August 1982, 18–24 August 1983, 13–16 August 1984, and 13–16 August 1985. The disturbed gradient in Field C was sampled on 9–10 August 1982, 24–29 August 1983, 16–20 August 1984, and 15–21 August 1985. For consistency with later years, the 1982 data collected on 10–13 August in Field A, on 14–19 July in Field B, and on 20–26 July in Field C are not re-

ported here. The undisturbed gradient in Field D was sampled on 26–31 August 1982, 30 August to 2 September 1983, 23–29 August 1984, and 26–28 August 1985. Younger fields were sampled earlier in the year because they reached peak standing crop sooner than older fields and native savannah.

After clipping, litter was sorted from living plants and plants were sorted to species, with Gleason and Cronquist (1963) as the primary taxonomic reference. Some samples were identified at the University of Minnesota Herbarium. Reference specimens and a working herbarium are maintained at Cedar Creek. For species with taxonomic names revised since Gleason and Cronquist (1963), the current name is used, but that of Gleason and Cronquist is mentioned. Only species in the Cyperaceae (sedges) gave repeated problems. Sedges were rare in Fields A, B, and C but were dominant in Field D. Because samples were collected when few sedges were in flower or fruit and because only aboveground parts were collected, they were difficult to identify to species. Cyperaceae were separated into two genera, *Cyperus* sp. and *Carex* sp. Field collections made in 1984 indicated that *Cyperus* spp. were mainly (>90%) *Cyperus filiculmis*. *Carex* spp. included *C. pennsylvanica*, *C. muhlenbergii*, and *C. foenea*. In the summer of 1984, Dr. Gerald Wheeler checked the identification of the samples of *Carex* sp. and *Cyperus* sp. collected in 1982, 1983, and 1984. Because identification of sedges to species remained problematic, I report these at the level of genus.

After sorting to species, all stems of a given species from a given plot were arranged in order of increasing height or length and the median heights or lengths were determined. For upright species, such as grasses and most forbs, these measurements approximated heights in the field. For vines, they did not. For this reason, vines were not included in any analyses involving height in this paper. The average height of the vegetation in a plot was determined by multiplying the median height of each common species by its biomass, summing these, and dividing the sum by the total biomass of these species. A species was considered common if it made up at least 2% of the total plant biomass for a gradient (averaged over all treatments) in at least 2 of the 4 yr and if it was present in at least 20 of the plots in at least 2 yr.

Next, each species was dried to constant mass at 40°C and then weighed. Although all species were weighed and used to determine species richness, biomass and height responses are reported here only for the common species of each experimental gradient.

Data were entered, verified, and analyzed using KnowledgeMan and Statgraphics software on an IBM PC-XT. All absolute abundances are reported as grams per square metre of aboveground, dry, living biomass. Relative abundances were calculated by dividing the absolute abundance of a species in a plot by the total aboveground dry plant biomass (excluding litter) in

that plot. The response of a variable to a particular experimental nitrogen gradient was determined by (1) linear regression of its values in all replicates of treatments A through H against the annual rate of nitrogen addition or (2) quadratic multiple regression, with the independent variables being the annual rate of nitrogen addition and this rate squared. The quadratic method approximated a Gaussian (bell-shaped) curve. A linear regression was called significant only if $P < .05$, based on a two-tailed test. I present only those quadratic regressions with a significant peak, i.e., with a positive linear term and a negative second-order term, and with $P < .05$ both for the overall regression and for the inclusion of the second-order term. Highly significant will imply that $P < .01$.

For each of the common species, its "center of mass" along an experimental nitrogen gradient was calculated for 1984 and 1985. This was determined by multiplying its average relative abundance in a treatment by the rate of nitrogen addition to that treatment, and summing this over all treatments (except treatment I). This sum was then divided by the sum of the relative abundances of this species over these treatments. This gave the rate of nitrogen addition at which a species reached its mean relative abundance along the experimental gradient. It was used to determine the order of occurrence of the major species along the experimental gradients.

Chemistry and light measurement

Total soil nitrogen was determined by alkaline persulfate digestion followed by colorimetric measurement of nitrate using cadmium reduction and sulfanilamide reagents (D'Elia et al. 1977; modified as in Tilman 1984). Soil organic matter content was determined by combustion. P, K, Ca, and Mg were extracted with 0.5 mol/L HCl and measured using an inductively coupled plasmasspectrometer. Each year, at about the date a field was clipped, light penetration through the vegetation was determined. This was done on cloudless days within 2 h of solar noon. Light penetration was determined as the ratio of light intensity at 3 cm above the soil surface to that incident on the vegetation. The light probes were 3 cm thick. For simplicity, this will be called the light penetration to the soil surface. In 1982, a Lambda Instruments cosine collector for photosynthetically active radiation (PAR) was used to make 10 measurements of penetration in each plot. From 1983 on, a 1 m long integrating PAR collector was used to make four estimates of light penetration in each plot. Average light penetration is reported here.

RESULTS

Old-field survey

The 1983 survey of the vegetation and soils of 22 old fields showed that total soil nitrogen increased significantly with field age along this chronosequence (Fig.

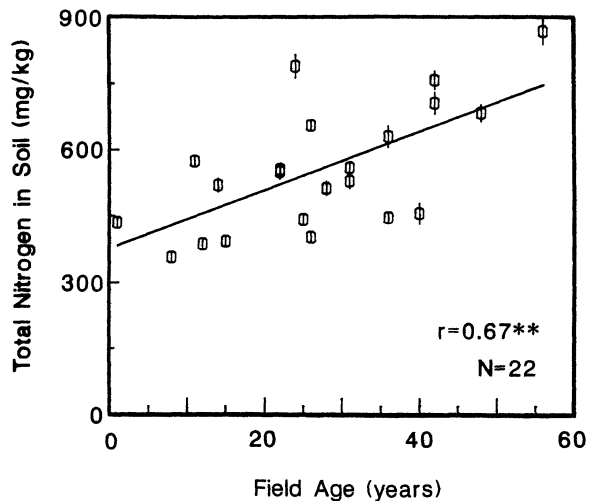


FIG. 1. Total soil nitrogen (as N) of successional fields increased significantly with field age, based on a chronosequence. Each point shows the mean (\square) and standard error (vertical bar) of total soil nitrogen in 22 Cedar Creek Natural History Area old fields. Data are from Inouye et al. (1987).

1; Inouye et al. 1987). Where TN is total soil nitrogen (in milligrams of N per kilogram of soil), and AGE is years since abandonment, the regression gave $TN = 369 + 6.8 \text{ AGE}$. The survey in 1986 of 16 of these fields showed that available soil nitrogen (the sum of N in KCl-extractable NH_4 and NO_3 ; mg/kg soil) increased with field age ($y = 0.41 + 0.012 \text{ AGE}$; $r = 0.60$, $n = 16$, $P \leq .05$; where y is available N). Available N also increased with total soil N for these 16 fields ($y = -0.05 + 0.0015 \text{ TN}$; $r = 0.73$, $n = 16$, $P \leq .01$). Further, a study of in-situ nitrogen mineralization rates in Fields A, B, C, and D showed that nitrogen mineralization rates increased significantly with total soil nitrogen ($r = 0.92$, $P \leq .05$; Pastor et al. 1987).

Of the 20 plant species with the greatest average percent covers over all samples in the 1983 old-field survey, 15 were also common species in at least one of the seven nitrogen gradient experiments. For each of these 15 species, I determined the dependence of its percent cover on total soil nitrogen by dividing the soil samples into 40 classes and calculating average percent cover for each. After smoothing, these gave the curves of Fig. 2. I also calculated linear regressions of percent cover on total soil nitrogen and multiple (quadratic) regressions of percent cover on TN and TN^2 . Data from a given field were used only if the species being considered was present in at least one quadrat in that field. Of these 15 common species, 12 had significant linear or quadratic regressions of their percent cover on total soil nitrogen (Fig. 2).

Experimental nitrogen gradients

Soil chemistry.—Table 2 gives the pretreatment means and standard errors of total soil N, pH, and

Old Field Plant Abundances

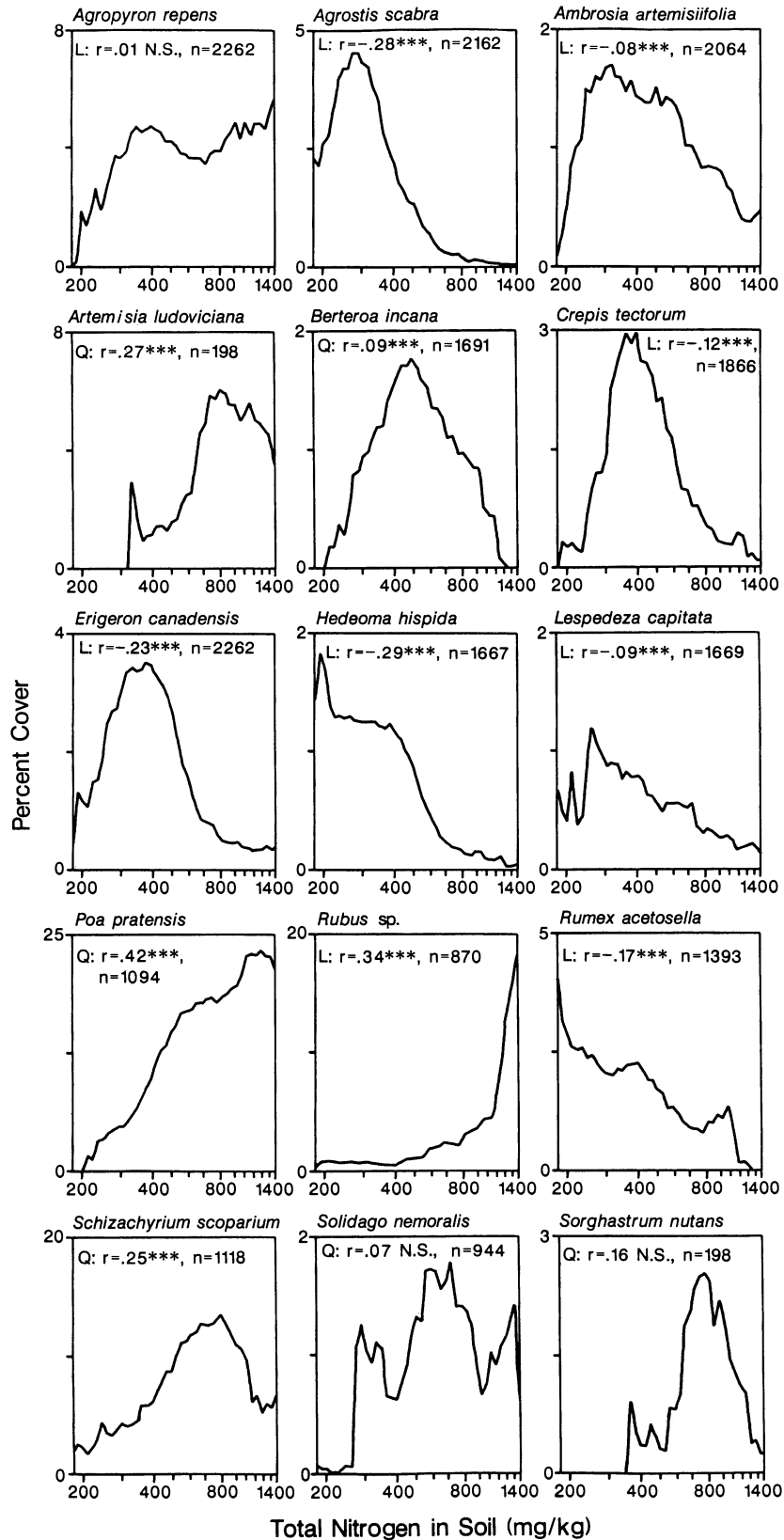


TABLE 2. Soil chemistry of the four fields before treatment. For each field, the mean levels, standard error (SE), and number of data points (*n*) are given for total soil nitrogen (milligrams of N per kilogram of soil), pH, and extractable Mg, Ca, K, and P. Units for all minerals are mg/kg soil.

Nutrient		Undisturbed fields				Disturbed fields		
		A	B	C	D	A	B	C
N	Mean	584	378	638	593	601	452	701
	SE	5.13	5.22	5.71	15.1	6.61	6.43	6.64
	<i>n</i>	216	216	216	45	216	216	216
pH	Mean	5.67	5.23	5.85	5.57	5.59	5.06	5.48
	SE	0.01	0.01	0.01	0.03	0.01	0.01	0.13
	<i>n</i>	216	216	216	45	216	216	216
Mg	Mean	270	214	249	365	129	112	187
	SE	10.7	5.28	18.8	6.57	3.23	7.14	14.2
	<i>n</i>	54	54	54	45	54	54	54
Ca	Mean	494	267	728	806	662	271	752
	SE	9.35	3.94	9.48	18.4	18.5	4.25	11.8
	<i>n</i>	54	54	54	45	54	54	54
K	Mean	95	83	127	134	95	89	118
	SE	1.83	1.30	2.66	2.90	1.68	1.48	3.18
	<i>n</i>	54	54	54	45	54	54	54
P	Mean	80	133	131	118	69	101	126
	SE	0.63	2.51	1.99	0.22	1.32	4.72	3.81
	<i>n</i>	54	54	54	45	54	54	54

extractable P, K, Ca, and Mg for each experimental gradient, all from 0–15 cm depth soil cores. Within each gradient and among all gradients there were significant positive correlations among N, K, Ca, and Mg. These were negatively correlated with P and with light penetration to the soil surface in unfertilized plots. Because total soil nitrogen (TN, milligrams of N per kilogram soil) and soil organic matter (OM, percent) were highly correlated ($OM = 0.003 TN + 0.4$; $r = 0.89$, $n = 408$, $P < .001$; Inouye et al. 1987) within Cedar Creek old fields, I only report total soil nitrogen here.

Limitation by nutrients other than nitrogen.—ANCOVA with contrasts revealed that treatment A, which received additions of all nutrients except N, and treatment I, which received no nutrients, did not differ significantly in their total aboveground plant biomass in any of the years for any of the seven experimental gradients. Similar analyses were performed on a species-by-species basis using the absolute abundances of the common species of each gradient for each year. Of the 232 contrasts performed, only seven were significant ($P < .05$), each being for a different species.

Biomass, light, height, and litter.—Linear regression showed that total aboveground biomass in both the undisturbed gradients (Fig. 3A–D) and the disturbed

gradients (Fig. 4A–C) increased highly significantly ($P < .01$) with the rate of nitrogen addition to the plots in each of the 4 yr. Light penetration to the soil surface decreased highly significantly with the rate of nitrogen addition for all gradients and all years, except for the undisturbed gradient in Field C in 1984 (Fig. 3E–H, Fig. 4D–F). Average height of the vegetation increased significantly with the rate of nitrogen addition along each gradient each year, except for the disked gradient in Field B in 1984 (Fig. 3I–L, Fig. 4G–I). In 1985, several of the treatment-H plots deviated substantially from these patterns, especially in Fields B and C. These plots had a thick, dense litter layer in the spring of 1985 that prevented the growth of most plants and led to low aboveground production in 1985. The litter was produced by the luxuriant growth of *Poa pratensis* the preceding year. For all gradients, litter was unaffected by treatment in 1982, increased significantly with the rate of N addition along a few gradients in 1983, and increased significantly along all gradients in 1984 and 1985 (Fig. 3Q–T, Fig. 4M–O). Litter was essentially absent from the disturbed gradients in 1982 because disking and raking had removed it from the soil surface that spring.

Species richness.—In 1982, there was a significant

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FIG. 2. Abundances (percent cover) of major plant species vs. total soil nitrogen (as N) observed in a survey of 22 old fields located at Cedar Creek. These 15 species were common species in at least one of the seven nitrogen gradient experiments and in the old-field survey. The curves shown were obtained by computing the average percent cover for a species in each of 40 soil nitrogen classes, followed by a single smoothing using a three-point running average. Also shown are the results of linear (L) and quadratic (Q) regressions of percent cover on total soil N, using data from all old fields in which the given species occurred. The correlation coefficient, r , for the linear regression (L) is shown for each species unless the quadratic (Q) regression explained significantly more of the variance. NS means $P > .05$; *** means $P < .001$.

Undisturbed Gradients

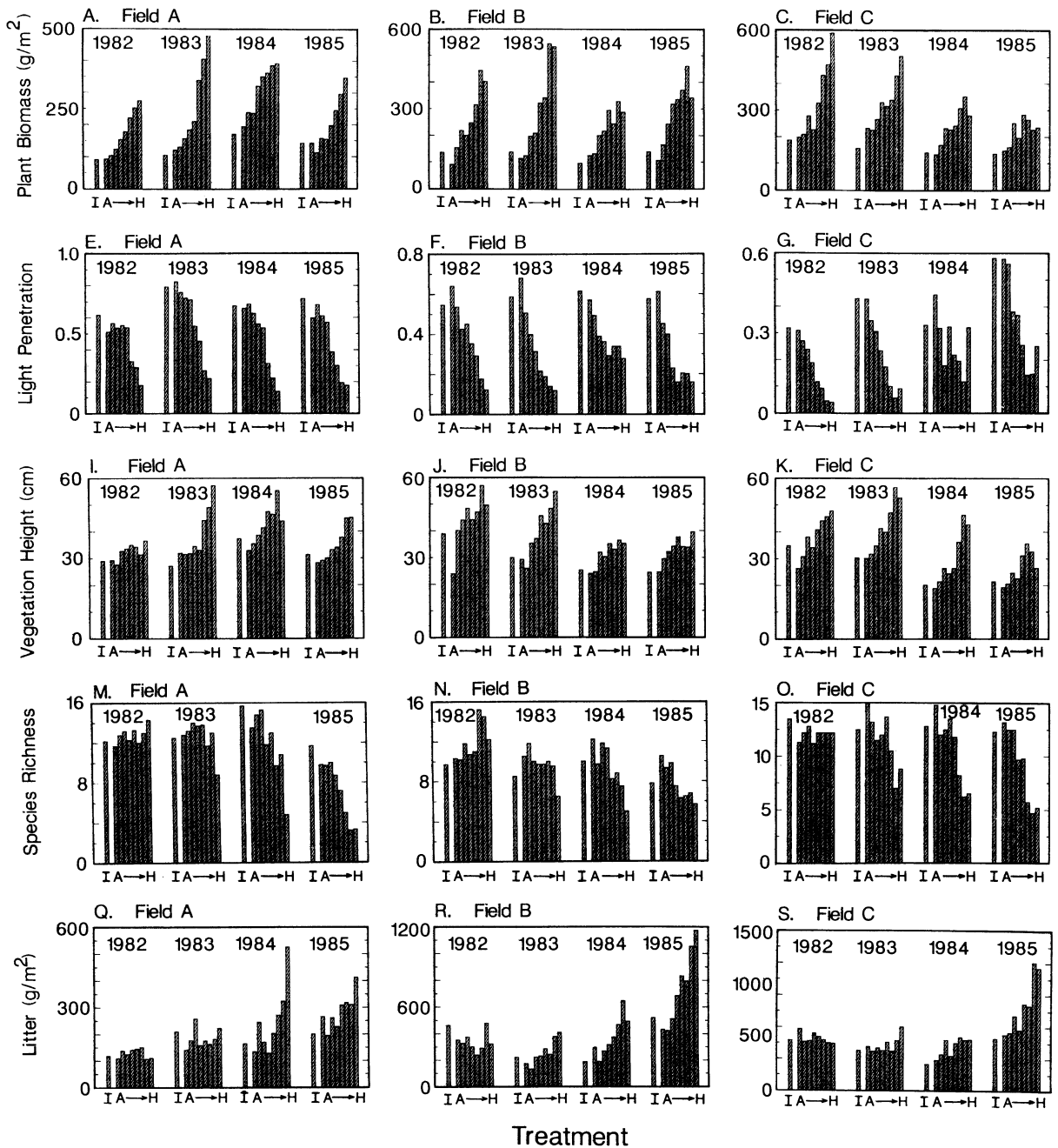


FIG. 3. Each bar in each part of this figure shows the average value of the ordinate variable over all five or six replicates of a treatment for a particular field and year, for the undisturbed gradients in Fields A, B, C, and D. Treatment I, the control, received no nutrients. It is shown separate from, and to the left of, treatments A through H. Treatments A through H form the nitrogen gradient, with the rate of nitrogen addition increasing progressively from treatment A (no nitrogen) to treatment H (highest rate of nitrogen addition each year). See Table 1. Treatments A–H all received the same mixture of P, K, Ca, Mg, S, and trace metals. Parts A–D of this figure show total aboveground dry biomass of living plants in all treatments in 1982, 1983, 1984, and 1985 in the undisturbed gradients of Fields A, B, C, and D, respectively. The proportion of light penetrating to the soil surface is similarly shown in parts E–H. Average vegetation height, shown in parts I–L, was calculated as a weighted (by biomass) average of heights of the common species (as defined by Tables 3, 5, 7, and 9). Species richness, shown in parts M–P, is the average number of species found in the 0.3-m² samples collected in the replicates of each treatment. Parts Q–T show treatment average litter masses.

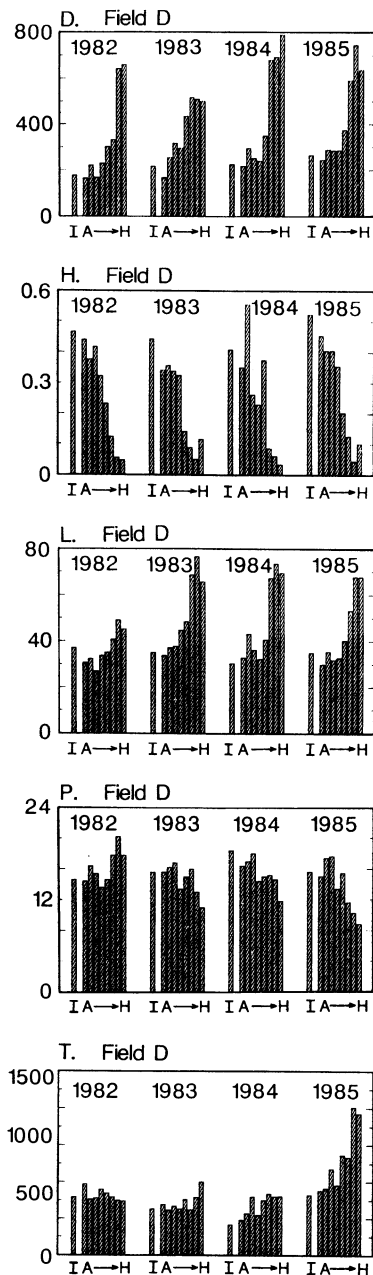


FIG. 3. Continued.

tendency for species richness to increase with added nitrogen along the undisturbed gradients in Fields B and D, based on linear regression (Fig. 3M–P). In 1983, 1984, and 1985, species richness declined significantly ($P < .05$) along each of the seven experimental nitrogen gradients (Fig. 3M–P, Fig. 4J–L). On average over all gradients, >60% of the species originally present in treatment H were absent by 1985.

Species responses to experimental gradients

Field A, undisturbed gradient.—Of the 69 plant species identified in the samples clipped from the undisturbed gradient in Field A, I will discuss only the 10 common species (Table 3). The responses of these 10 species are shown in Table 3 and Fig. 5. These 10 species accounted for 92% of the total biomass of 1982 through 1985. The absolute abundance of *Agropyron repens* increased highly significantly along the nitrogen gradient all 4 yr (Table 3). Its relative abundance decreased along the gradient in 1982, and then increased in 1983–1985 (Fig. 5A, Table 3). By 1985, *A. repens* accounted for 90% of the total biomass summed over all treatments in Field A. *Berteroa incana*, *Ambrosia artemisiifolia*, and *Erigeron canadensis* increased along the nitrogen gradient in 1982, but tended to decline along the gradient in 1984 and 1985, though only *B. incana* declined significantly in 1985 (Table 3, Fig. 5). Quadratic regression showed that the absolute abundances of all three species and the relative abundances of *B. incana* and *E. canadensis* increased significantly at low nitrogen levels and decreased significantly at high nitrogen levels in 1983, but not in other years. Both *Agrostis scabra* and *Hedeoma hispida* had significant quadratic regressions for their absolute abundances in 1982, indicating that they reached their peak abundances at intermediate rates of nitrogen addition. Both decreased along the nitrogen gradient in 1983 and 1984 (Fig. 5, Table 3). The remaining five species showed few or no significant responses to the nitrogen gradient. The median heights of the common species tended to increase with nitrogen addition. Of the 15 significant correlations between median height and nitrogen added, only that for *Agrostis scabra* in 1983 was negative.

In 1982, the relative abundance of all annuals, combined, increased highly significantly ($r = 0.49$, $n = 48$) along the undisturbed nitrogen gradient in Field A, whereas the relative abundance of perennials decreased highly significantly ($r = -0.48$, $n = 48$). None of these groups responded significantly to the nitrogen gradient in 1983. In 1984, however, annual grasses ($r = -0.28$, $n = 48$), annual forbs ($r = -0.31$, $n = 48$), and perennial forbs ($r = -0.46$, $n = 48$) decreased significantly in relative abundance along the gradient and perennial grasses increased significantly ($r = 0.59$, $n = 48$). For 1985, only the regressions for annual grasses ($r = -0.34$, $n = 48$) and perennial grasses ($r = 0.31$, $n = 48$) were significant.

Disturbed Gradients

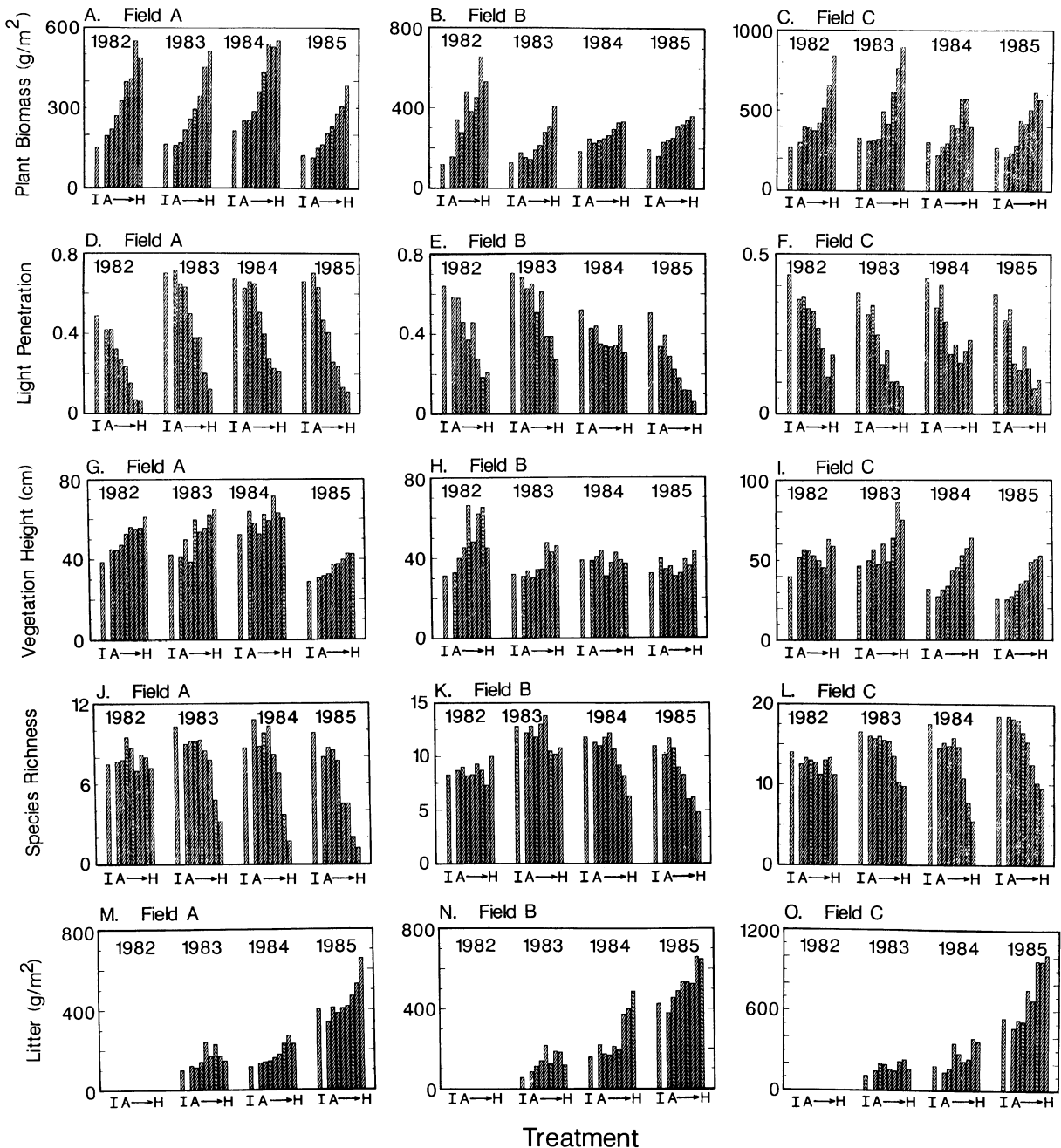


FIG. 4. Each bar in each part of this figure shows the average value of the ordinate variable over all six replicates of a treatment for the disturbed (disked) gradients in Fields A, B, and C. Data are displayed as in Fig. 3.

Field A, disturbed gradient.—Of the 37 species identified in the samples from the disturbed gradient in Field A, I will discuss only the six common species (Table 4). Their response to the gradient are given in Table 4 and Fig. 6. The absolute abundance of *Agropyron repens* increased highly significantly along the nitrogen gradient in each year (Table 4). Its relative

abundance increased highly significantly along the gradient all years except the first (Fig. 6). By 1985, it constituted 96% of all the biomass harvested from all treatments of this gradient. The annuals *Setaria glauca*, *Ambrosia artemisiifolia*, and *Polygonum convolvulus* were abundant in 1982, but rare the following years. *Ambrosia artemisiifolia* increased along the gradient in

TABLE 3. Linear (L) and quadratic (Q) regressions of plant relative and absolute abundance vs. the rate of nitrogen addition for the common species in the undisturbed plots in Field A. $N = 48$ for all regressions.

Species	Life history†	Relative abundance				Absolute abundance			
		1982	1983	1984	1985	1982	1983	1984	1985
Correlation coefficients‡									
<i>Agropyron repens</i>	P, G	-0.33 L *	0.29 L *	0.57 L **	0.31 L *	0.49 L **	0.67 L **	0.70 L **	0.87 L **
<i>Berteroa incana</i>	A/P, F	0.49 L **	0.36 Q *	-0.34 L *	-0.29 L *	0.69 L **	0.45 Q **	-0.19 L NS	-0.28 L *
<i>Potentilla recta</i>	P, F	-0.00 L NS	0.12 L NS	-0.25 L NS	-0.02 L NS	0.15 L NS	0.13 L NS	-0.16 L NS	-0.01 L NS
<i>Poa pratensis</i>	P, G	-0.08 L NS	-0.06 L NS	-0.03 L NS	-0.12 L NS	0.11 L NS	0.09 L NS	0.04 L NS	0.03 L NS
<i>Agrostis scabra</i>	P, G	-0.26 L NS	-0.41 L **	-0.34 L *	-0.15 L NS	0.40 Q *	-0.38 L **	-0.32 L *	-0.16 L NS
<i>Achillea millefolium</i>	P, F	-0.01 L NS	-0.18 L NS	-0.30 L *	-0.24 L NS	0.16 L NS	0.40 Q **	-0.16 L NS	-0.21 L NS
<i>Crepis tectorum</i>	A, F	-0.21 L NS	0.34 Q *	0.15 L NS	a§	-0.01 L NS	0.52 Q **	0.15 L NS	a
<i>Erigeron canadensis</i>	A, F	-0.06 L NS	0.38 Q **	-0.12 L NS	-0.17 L NS	0.28 L *	0.37 Q *	-0.04 L NS	-0.16 L NS
<i>Hedeoma hispida</i>	A, F	-0.13 L NS	-0.39 L **	-0.47 L **	-0.27 L NS	0.45 Q **	-0.20 L NS	-0.40 L **	-0.24 L NS
<i>Ambrosia artemisiifolia</i>	A, F	0.31 L *	0.15 L NS	-0.24 L NS	-0.27 L NS	0.43 L **	0.32 Q *	-0.13 L NS	-0.17 L NS

† P = perennial, A = annual, G = grass, F = forb.

‡ The correlation coefficients, r , for linear (L) regressions are shown, except when the quadratic (Q) regression was significant. In that case, its multiple correlation coefficient is given, as is the significance for the inclusion of the quadratic term. NS means $P > .05$; * means $.05 > P > .01$; ** means $P < .01$, using a two-tailed test.

§ a = absent that year.

1982, but tended to decline along the gradient after that (Table 4, Fig. 6). *Polygonum convolvulus* responded similarly (Table 4, Fig. 6). The median heights of most species increased significantly along the gradient, based on linear regression. For no species did median height decline significantly along the gradient.

Averaged over all treatments, annuals, as a group, were most abundant in 1982, and then declined sharply as perennials increased in abundance. Neither annuals nor perennials, as groups, had their relative abundances significantly dependent on the rate of nitrogen addition in 1982, based on linear regression. In 1983, both annual grasses ($r = -0.37$, $n = 48$) and annual forbs ($r = -0.55$, $n = 48$) decreased along the disturbed gradient in Field A, and perennial grasses increased ($r = 0.55$, $n = 48$). Their responses were similar and significant ($P < .05$) in both 1984 and 1985.

Field B, undisturbed gradient.—There were 51 species identified in the samples clipped from undisturbed nitrogen gradient plots of Field B. The six common species (Table 5) accounted for 88% of the total plant biomass harvested in these plots. Their responses to the gradient are shown in Table 5 and Fig. 7. In 1982, *Agropyron repens* was found in samples from only 10 of the 54 plots and it represented <0.5% of the biomass in any of the treatments. By 1985, it was present in 24 plots and it accounted for an average of 28% of the biomass in the highest nitrogen treatment (Fig. 7). It

rapidly dominated those high-nitrogen treatments in which it originally occurred. In 1982, it was present in only 5 of the 18 plots assigned to the three highest nitrogen treatments (treatments F, G, and H), but it was present in 14 of these plots by 1985. In 1985, it had an average abundance of 253 g/m² in the plots it had invaded since 1982. Though present in 5 of the 18 plots for treatments C, D, and E in 1982, it had invaded only 2 additional plots by 1985, with an average abundance of 4.2 g/m² in the newly invaded plots. Thus, *Agropyron repens* invaded into and rapidly increased in abundance in many high-nitrogen plots. Based on linear regression, its absolute abundance increased significantly along the nitrogen gradient in 1983. In 1984 and 1985, both its relative and absolute abundances increased significantly along the gradient (Table 5, Fig. 7), just as in Field A.

The absolute abundance of *Schizachyrium scoparium* had a significant quadratic regression in all 4 yr, indicating that it reached its peak absolute abundance at intermediate rates of nitrogen addition (Table 5). Its relative abundance was not affected by the gradient in 1982, 1983, or 1984, but it decreased highly significantly along the gradient in 1985 (Table 5, Fig. 7). *Rumex acetosella* increased along the gradient in 1982, but tended to decrease along the gradient in later years. *Lespedeza capitata*, a legume, decreased in its relative abundance along the nitrogen gradient all 4 yr (Table

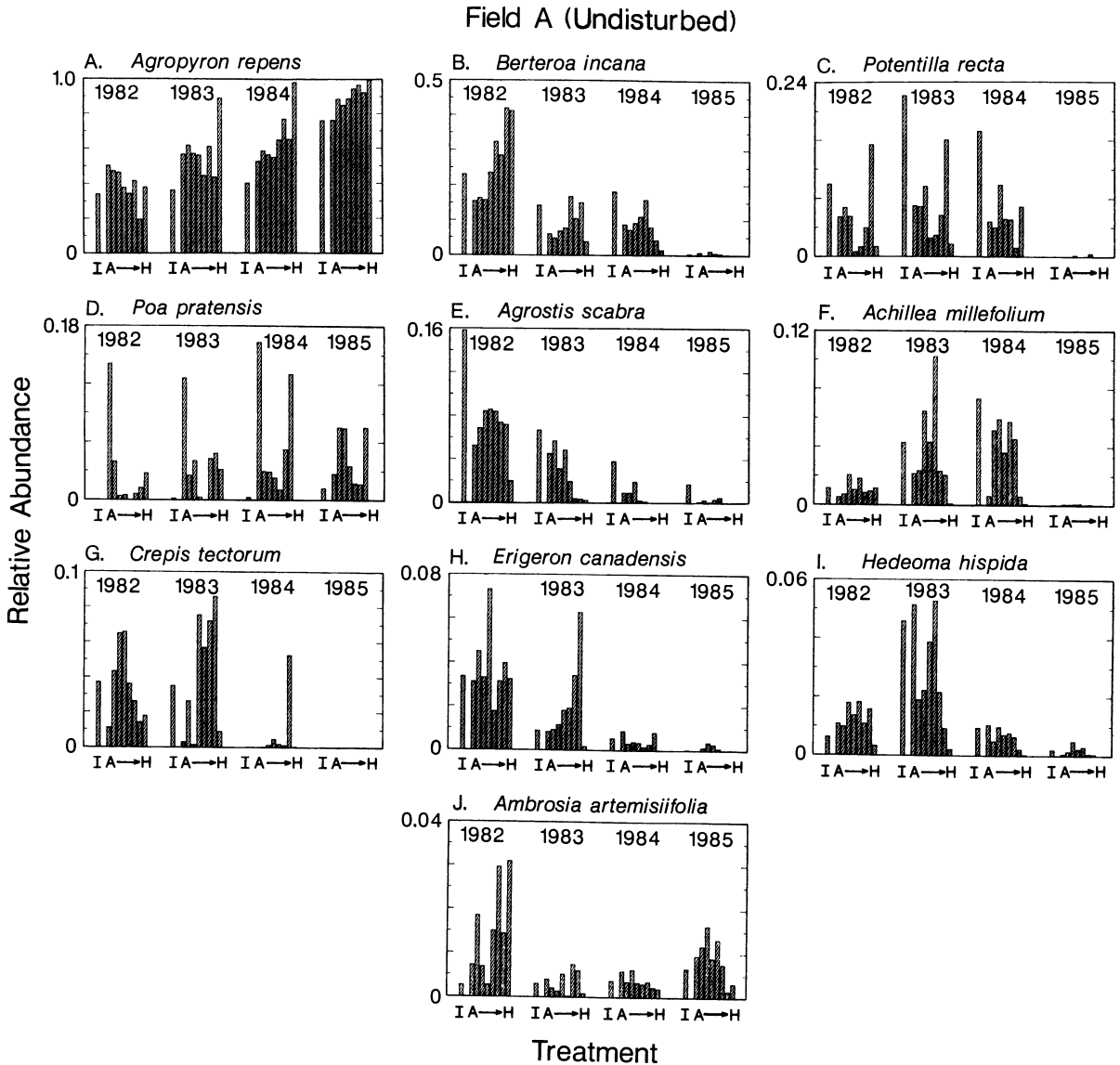


FIG. 5. Relative (proportional) abundances of the 10 common species of the undisturbed gradient of Field A (the 14-yr-old field) in 1982, 1983, 1984, and 1985 are shown on a treatment-by-treatment basis. Each bar is the average relative abundance of a species in the six replicates of each treatment. Treatment I is the unmanipulated control and treatments A-H form the nitrogen gradient (from low to high rates of annual N addition). Species are presented in the same order (from most to least abundant, on average) in this figure as in Table 3.

5, Fig. 7). In all years, the only significant trends in the median heights of plant species along the gradient were for height to increase with the rate of nitrogen addition.

In 1982, the relative abundance of annual grasses and of annual forbs increased significantly along the undisturbed nitrogen gradient in Field B. Linear regressions gave $r = 0.29$ and $r = 0.35$, respectively, with $n = 48$. Perennial grasses and perennial forbs decreased along the gradient, but not significantly. All perennials combined decreased significantly along the gradient in 1982 ($r = -0.38$, $n = 48$). Perennial forbs were the only plant group responding significantly to the nitro-

gen gradient in 1983 ($r = -0.32$, $n = 48$). In 1984, annuals as a group decreased significantly ($r = -0.31$, $n = 48$) along the gradient but perennials increased significantly ($r = 0.38$, $n = 48$). Woody perennials, which had been unaffected by the gradient in 1982 and 1983, increased significantly in their relative abundance along the gradient in 1984 ($r = 0.32$, $n = 48$). Legumes decreased significantly in their abundance along the gradient ($r_{1982} = -0.29$, $r_{1983} = -0.31$, $r_{1984} = -0.28$; $n = 48$). No regressions were significant for 1985.

Field B, disturbed gradient.—Of the 45 species pres-

TABLE 4. Linear (L) and quadratic (Q) regressions of plant relative and absolute abundance vs. the rate of nitrogen addition for the common species in the disturbed (disked) plots in Field A. *N* = 48 for all regressions.

Species	Life history†	Relative abundance				Absolute abundance			
		1982	1983	1984	1985	1982	1983	1984	1985
Correlation coefficients‡									
<i>Agropyron repens</i>	P, G	-0.03 L NS	0.55 L **	0.40 L **	0.38 L **	0.60 L **	0.87 L **	0.76 L **	0.91 Q **
<i>Ambrosia artemisiifolia</i>	A, F	0.39 L **	-0.23 L NS	-0.26 L NS	-0.46 L **	0.62 L **	-0.20 L NS	-0.26 L NS	-0.35 L *
<i>Setaria glauca</i>	A, G	-0.14 L NS	-0.27 L NS	a§	-0.22 L NS	0.12 L NS	-0.23 L NS	a	-0.20 L NS
<i>Berteroa incana</i>	A/P, F	-0.36 L *	-0.38 L **	-0.25 L NS	-0.28 L *	-0.20 L NS	-0.27 L NS	0.38 Q *	-0.27 L NS
<i>Polygonum convolvulus</i>	A, F	0.46 L **	-0.11 L NS	-0.18 L NS	-0.11 L NS	0.76 L **	0.01 L NS	-0.15 L NS	-0.01 L NS
<i>Erigeron canadensis</i>	A, F	-0.17 L NS	-0.47 L **	0.10 L NS	-0.26 L NS	-0.15 L NS	-0.41 L **	-0.08 L NS	-0.26 L NS

† P = perennial, A = annual, G = grass, F = forb.

‡ The correlation coefficients, *r*, for linear (L) regressions are shown, except when the quadratic (Q) regression was significant. In that case, its multiple correlation coefficient is given, as is the significance for the inclusion of the quadratic term. NS means $P > .05$; * means $.05 > P > .01$; ** means $P < .01$, using a two-tailed test.

§ a = absent that year.

ent in the disturbed plots of Field B, eight were common (Table 6, Fig. 8). In 1982, *Agropyron repens* occurred in 26 of the 54 plots and was <1% of total biomass. By 1985, it was present in 51 plots and constituted 42% of the total biomass. Most of this increase was caused by invasion into and rapid growth in the high-nitrogen plots (Fig. 8). In 1983, 1984, and 1985, both its absolute and relative abundances increased significantly along the nitrogen gradient (Table 6). *Schizachyrium scoparium*, which had been a dominant in the field before disking, greatly increased in abundance

in the low-nitrogen treatments from 1982 to 1985, but did not increase in the high-nitrogen treatments (Table 6, Fig. 8). *Agrostis scabra* became more abundant in all treatments from 1982 to 1984, and then declined. Its absolute and relative abundances tended to decline along the gradient in 1983, 1984, and 1985 (Table 6, Fig. 8).

Polygonum convolvulus and *Panicum oligosanthes* tended to have quadratic responses to the gradient, but *Rumex acetosella* tended to decline along the gradient (Table 6, Fig. 8). By 1985, *Poa pratensis* had a signif-

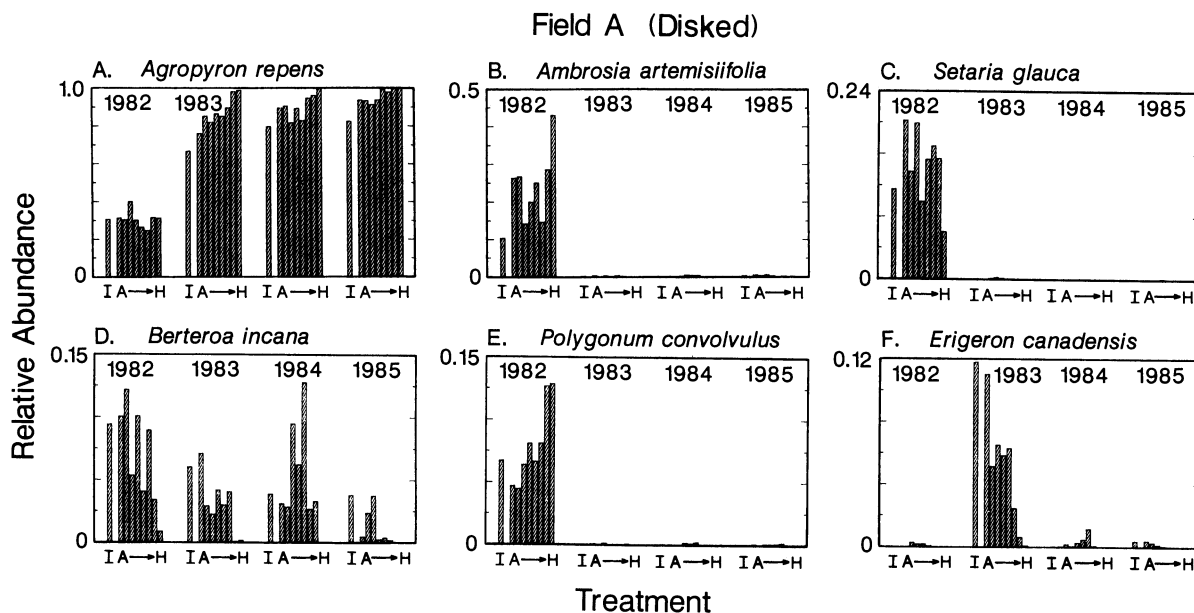


FIG. 6. Relative abundances of the six common species of disked plots in Field A (14-yr-old field). Data presentation as in Fig. 5. Species are shown in order of their average abundance, as for Table 4.

TABLE 5. Linear (L) and quadratic (Q) regressions of plant relative and absolute abundance vs. the rate of nitrogen addition for the common species in the undisturbed plots of Field B. $N = 48$ for all regressions.

Species	Life history†	Relative abundance				Absolute abundance			
		1982	1983	1984	1985	1982	1983	1984	1985
Correlation coefficients‡									
<i>Schizachyrium scoparium</i>	P, G	-0.07 L NS	-0.12 L NS	-0.16 L NS	-0.45 L **	0.65 Q **	0.74 Q *	0.47 Q **	0.38 Q *
<i>Poa pratensis</i>	P, G	-0.14 L NS	-0.01 L NS	0.03 L NS	0.04 L NS	0.07 L NS	0.26 L NS	0.19 L NS	0.21 L NS
<i>Agropyron repens</i>	P, G	0.11 L NS	0.20 L NS	0.34 L *	0.54 L **	0.20 L NS	0.33 L *	0.37 L **	0.54 L **
<i>Panicum oligosanthos</i>	P, G	0.20 L NS	0.48 L **	0.37 L **	0.33 Q **	0.47 L **	0.61 Q *	0.41 L **	0.36 Q *
<i>Rumex acetosella</i>	A/P, F	0.36 L *	-0.30 L *	-0.27 L NS	-0.26 L NS	0.68 L **	0.02 L NS	-0.23 L NS	-0.17 L NS
<i>Lespedeza capitata</i>	P, Lg	-0.28 L *	-0.28 L *	-0.27 L NS	-0.21 L NS	-0.20 L NS	0.33 L *	-0.23 L NS	-0.16 L NS

† P = perennial, A = annual, G = grass, F = forb, Lg = legume.

‡ The correlation coefficients, r , for linear (L) regressions are shown, except when the quadratic (Q) regression was significant. In that case, its multiple correlation coefficient is given, as is the significance for the inclusion of the quadratic term. NS means $P > .05$; * means $.05 > P > .01$; ** means $P < .01$, using a two-tailed test.

icantly quadratic (Gaussian) distribution of both absolute and relative abundances along the gradient (Table 6, Fig. 8). In 1982, it was present in only 16 plots, but occurred in 42 plots in 1985. In total, for all of the common species, there were 15 significant regressions of median height against the rate of nitrogen addition, of which 11 were positive. The exceptions were all species that declined in absolute abundance along the gradient.

Averaged over all treatments, annuals were most

abundant in 1982 and declined in abundance each year thereafter. As a group, the absolute abundance, but not the relative abundance, of perennials increased significantly ($P < .05$) along the gradient all 4 yr. Both the absolute and relative abundance of annual grasses increased significantly along the gradient in 1983 ($r = 0.63$, $n = 48$), but not in any other year. The absolute abundance of annual forbs increased significantly along the gradient in 1982 ($r = 0.49$, $n = 48$), but not in any other year.

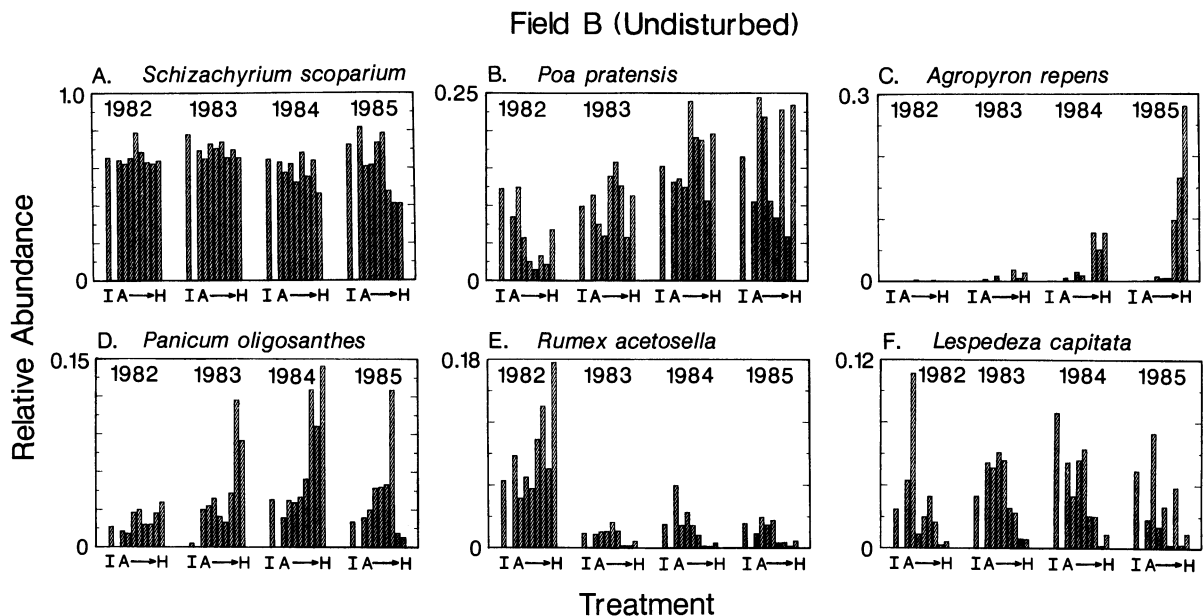


FIG. 7. Relative abundances of the six common species of the undisturbed plots of Field B (25-yr-old field) are shown as averages for each treatment in 1982, 1983, 1984, and 1985. Treatment I is the unmanipulated control and treatments A-H form the nitrogen gradient (from low to high rates of annual N addition). See also Table 5.

TABLE 6. Linear (L) and quadratic (Q) regressions of plant relative and absolute abundance vs. the rate of nitrogen addition for the common species in the disturbed (disked) plots in Field B. $N = 48$ for all regressions.

Species	Life history†	Relative abundance				Absolute abundance			
		1982	1983	1984	1985	1982	1983	1984	1985
Correlation coefficients‡									
<i>Setaria glauca</i>	A, G	0.31 Q*	0.48 L**	-0.08 L NS	0.10 L NS	0.45 Q**	0.64 L**	-0.02 L NS	0.31 Q*
<i>Schizachyrium scoparium</i>	P, G	0.41 Q**	-0.32 L*	-0.54 L**	-0.62 L**	0.53 Q*	-0.13 L NS	-0.39 L**	-0.58 L**
<i>Agropyron repens</i>	P, G	0.19 L NS	0.28 L*	0.53 L**	0.75 L**	0.24 L NS	0.44 L**	0.58 L**	0.83 L**
<i>Polygonum convolvulus</i>	A, F	0.24 L NS	0.35 Q*	-0.10 L NS	-0.03 L NS	0.59 Q*	0.41 Q*	-0.07 L NS	0.01 L NS
<i>Poa pratensis</i>	P, G	-0.04 L NS	0.11 L NS	0.15 L NS	0.36 Q*	0.08 L NS	0.26 L NS	0.22 L NS	0.39 Q**
<i>Panicum oligosanthes</i>	P, G	-0.12 L NS	0.14 L NS	0.41 Q*	-0.16 L NS	-0.05 L NS	0.14 L NS	0.44 Q**	0.29 Q*
<i>Agrostis scabra</i>	P, G	0.04 L NS	-0.22 L NS	-0.39 L**	-0.22 L NS	0.14 L NS	-0.04 L NS	-0.32 L*	-0.24 L NS
<i>Rumex acetosella</i>	A/P, F	-0.23 L NS	-0.50 L**	-0.09 L NS	0.13 L NS	0.35 Q*	-0.40 L**	-0.07 L NS	0.12 L NS

† P = perennial, A = annual, G = grass, F = forb.

‡ The correlation coefficients, r , for linear (L) regressions are shown, except when the quadratic (Q) regression was significant. In that case, its multiple correlation coefficient is given, as is the significance for the inclusion of the quadratic term. NS means $P > .05$; * means $.05 > P > .01$; ** means $P < .01$, using a two-tailed test.

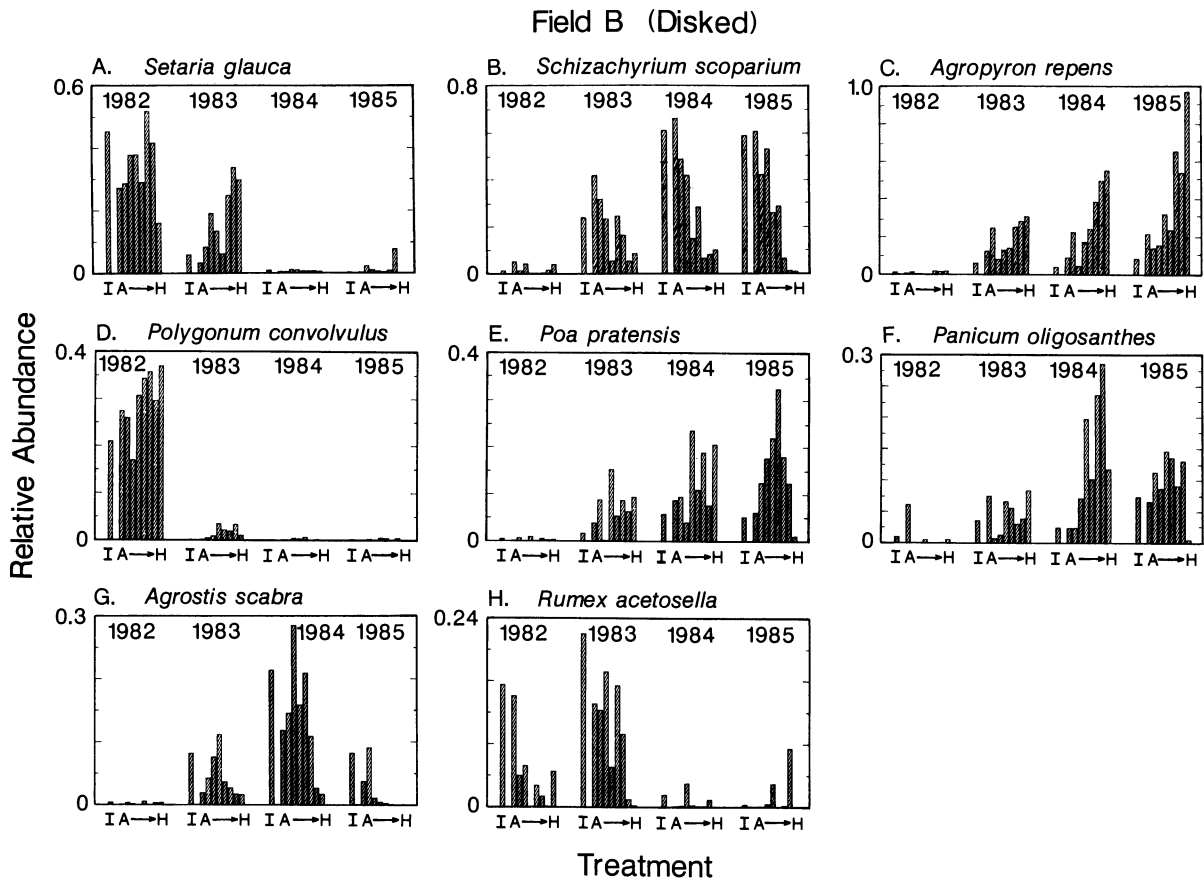


FIG. 8. Relative abundances of the eight common species of the disked plots of Field B (25-yr-old field). Each bar is the treatment mean for a given year. Treatment I is the unfertilized control and treatments A-H form the nitrogen gradient (from low to high rates of annual N addition). See also Table 6.

TABLE 7. Linear (L) and quadratic (Q) regressions of plant relative and absolute abundance vs. the rate of nitrogen addition for the common species in the undisturbed plots in Field C. $N = 48$ for all regressions.

Species	Life history†	Relative abundance				Absolute abundance			
		1982	1983	1984	1985	1982	1983	1984	1985
Correlation coefficients‡									
<i>Poa pratensis</i>	P, G	-0.08 L NS	0.74 Q **	0.78 Q **	0.61 Q **	0.53 Q **	0.77 Q **	0.83 Q **	0.65 Q **
<i>Schizachyrium scoparium</i>	P, G	-0.10 L NS	-0.62 L **	-0.62 L **	-0.56 L **	0.49 L **	-0.36 L *	-0.51 L **	-0.57 L **
<i>Artemisia ludoviciana</i>	P, F	0.36 L *	0.26 L NS	-0.41 L **	0.44 Q *	0.66 L **	0.43 L **	-0.32 L *	-0.40 L **
<i>Agropyron repens</i>	P, G	0.10 L NS	0.35 L *	0.21 L NS	0.54 L **	0.02 L NS	0.40 L **	0.26 L NS	0.52 L **
<i>Solidago nemoralis</i>	P, F	-0.15 L NS	-0.31 L *	-0.46 L **	-0.34 L *	0.12 L NS	-0.28 L *	-0.45 L **	-0.39 L **
<i>Ambrosia coronopifolia</i>	P, F	0.25 L NS	-0.25 L NS	0.36 Q *	-0.22 L NS	0.58 L **	-0.08 L NS	0.19 L NS	-0.04 L NS
<i>Sorghastrum nutans</i>	P, G	0.04 L NS	-0.24 L NS	-0.31 L *	-0.28 L *	0.13 L NS	-0.17 L NS	-0.29 L *	-0.26 L NS
<i>Panicum oligosanthes</i>	P, G	0.43 L **	0.31 Q *	0.14 L NS	-0.08 L NS	0.56 L **	0.38 Q *	0.20 L NS	0.01 L NS

† P = perennial, G = grass, F = forb.

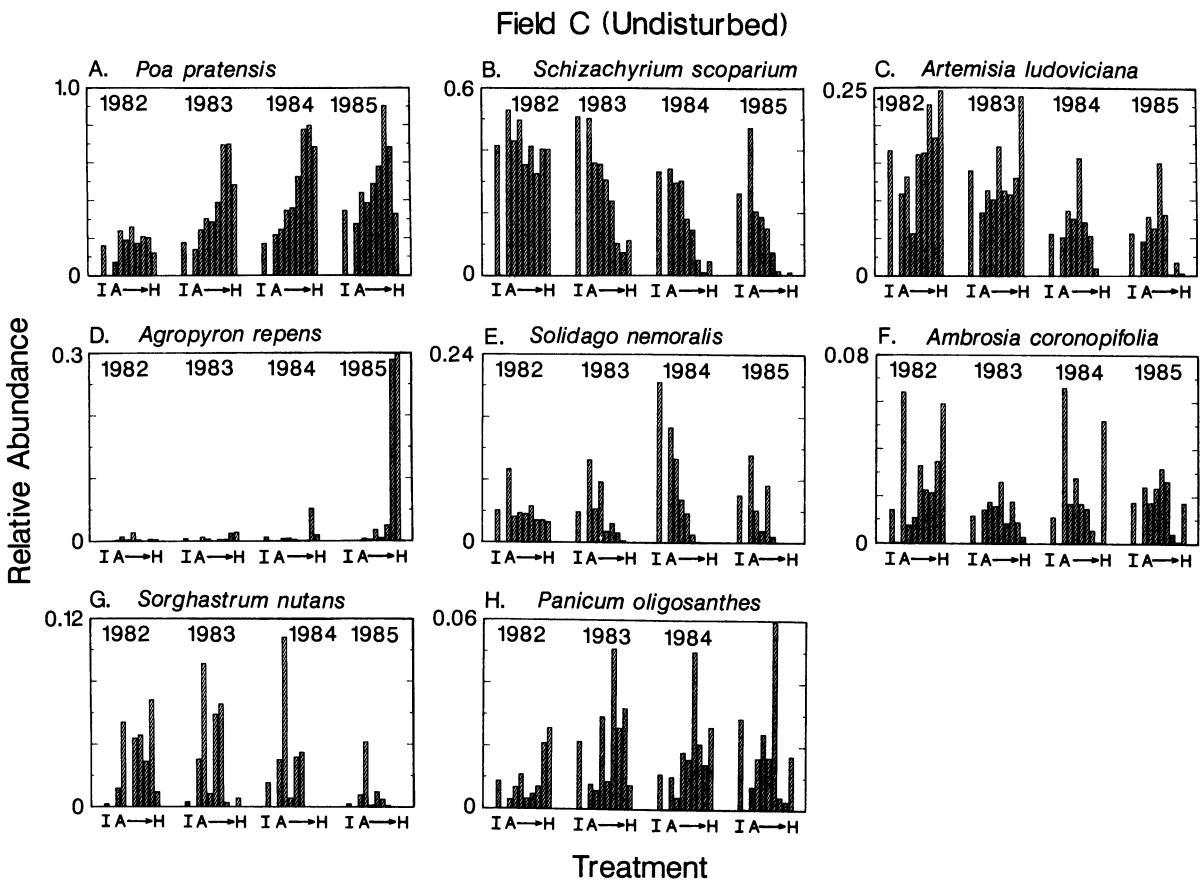
‡ The correlation coefficients, r , for linear (L) regressions are shown, except when the quadratic (Q) regression was significant. In that case, its multiple correlation coefficient is given, as is the significance for the inclusion of the quadratic term. NS means $P > .05$; * means $.05 > P > .01$; ** means $P < .01$, using a two-tailed test.

FIG. 9. Relative abundances of the eight common species of the undisturbed plots in Field C (48-yr-old field) are shown as treatment means for each year. Treatment I is the unfertilized control and treatments A-H form the nitrogen gradient (from low to high rates of annual N addition). See also Table 7.

TABLE 8. Linear (L) and quadratic (Q) regressions of plant relative and absolute abundance vs. the rate of nitrogen addition for the common species in the disturbed (disked) plots in Field C. $N = 48$ for all regressions.

Species	Life history†	Relative abundance				Absolute abundance			
		1982	1983	1984	1985	1982	1983	1984	1985
Correlation coefficients‡									
<i>Artemisia ludoviciana</i>	P, F	-0.20 L NS	0.09 L NS	0.31 L *	0.04 L NS	-0.02 L NS	0.48 L **	0.47 Q **	0.42 Q *
<i>Setaria glauca</i>	A, G	0.28 L *	0.33 L *	-0.24 L NS	0.38 Q *	0.53 L **	0.48 L **	-0.26 L NS	0.41 Q *
<i>Polygonum convolvulus</i>	A, F	-0.09 L NS	0.51 L **	0.47 L **	0.48 L **	0.50 L **	0.59 L **	0.55 L **	0.51 L **
<i>Panicum oligosanthes</i>	P, G	-0.11 L NS	0.37 Q *	-0.41 L **	-0.42 L **	0.33 Q *	0.43 Q **	0.47 Q **	-0.25 L NS
<i>Agropyron repens</i>	P, G	0.01 L NS	0.22 L NS	0.41 L **	0.29 L *	0.13 L NS	0.36 L *	0.35 L *	0.36 L *
<i>Erigeron canadensis</i>	A, F	a§	-0.13 L NS	0.30 L *	0.30 L *	a	0.18 L NS	0.32 L *	0.34 L *
<i>Schizachyrium scoparium</i>	P, G	-0.23 L NS	-0.41 L **	-0.39 L **	-0.39 L **	-0.19 L NS	-0.32 L *	-0.44 L **	-0.45 L **
<i>Poa pratensis</i>	P, G	-0.08 L NS	-0.22 L NS	-0.21 L NS	-0.47 L **	-0.05 L NS	-0.14 L NS	-0.05 L NS	-0.39 L **

† P = perennial, A = annual, G = grass, F = forb.
 ‡ The correlation coefficients, r , for linear (L) regressions are shown, except when the quadratic (Q) regression was significant. In that case, its multiple correlation coefficient is given, as is the significance for the inclusion of the quadratic term. NS means $P > .05$; * means $.05 > P > .01$; ** means $P < .01$, using a two-tailed test.
 § a = absent that year.

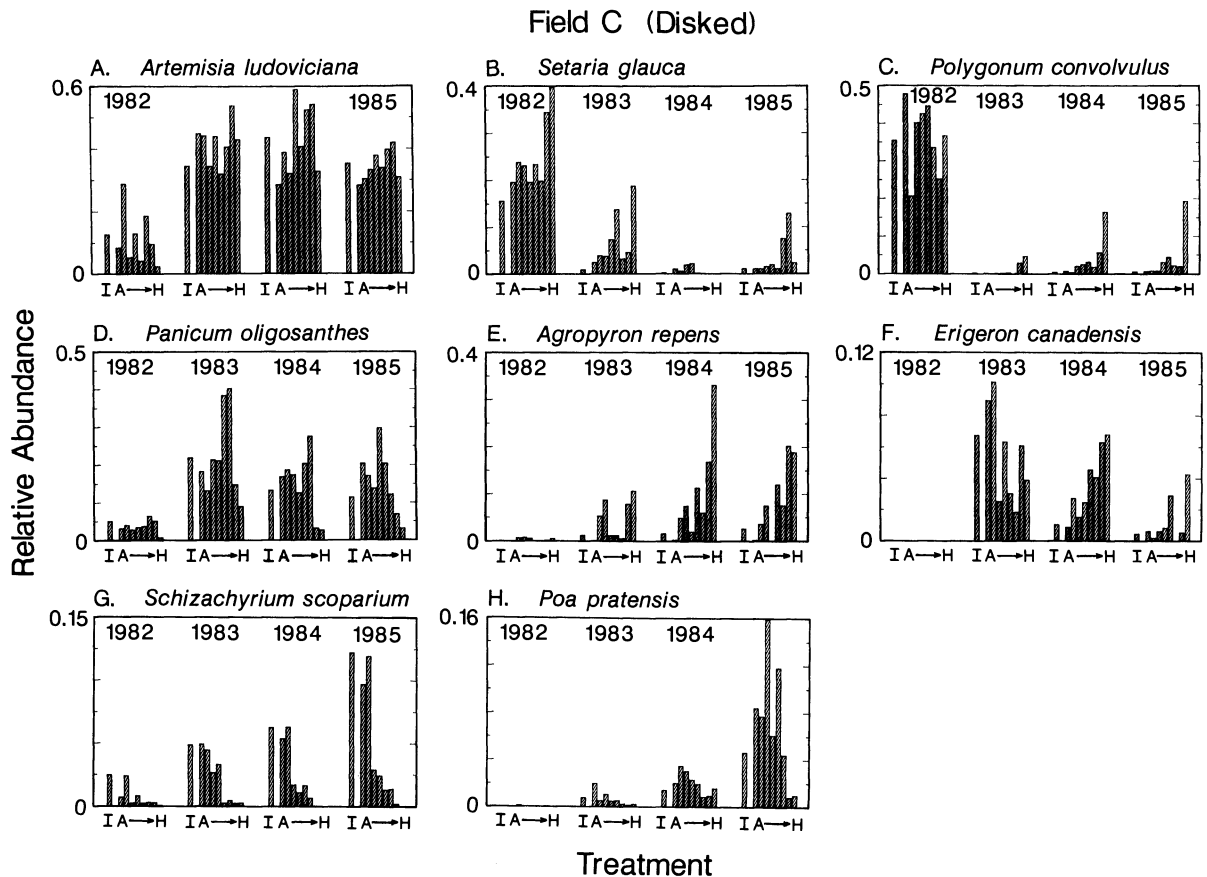


FIG. 10. Relative abundances of the eight common species of the disked plots of Field C (48-yr-old field). Each bar is the treatment mean for a given year. Treatment I is the unfertilized control and treatments A-H form the nitrogen gradient (from low to high rates of annual N addition). See also Table 8.

TABLE 9. Linear (L) and quadratic (Q) regressions of plant relative and absolute abundance vs. the rate of nitrogen addition for the common species in the undisturbed plots in Field D. $N = 40$ for all regressions.

Species	Life history†	Relative abundance				Absolute abundance			
		1982	1983	1984	1985	1982	1983	1984	1985
		Correlation coefficients‡							
<i>Carex</i> sp.	P, S	-0.32 L *	-0.10 L NS	-0.13 L NS	0.16 L NS	0.53 L **	0.31 L *	0.55 Q **	0.54 L **
<i>Artemisia ludoviciana</i>	P, F	0.07 L NS	0.48 Q *	0.25 L NS	0.40 Q *	0.36 L *	0.64 Q **	0.38 L **	0.50 Q **
<i>Sorghastrum nutans</i>	P, G	-0.07 L NS	-0.16 L NS	-0.38 L *	-0.37 L *	0.24 L NS	0.03 L NS	-0.29 L NS	-0.30 L NS
<i>Poa pratensis</i>	P, G	-0.11 L NS	0.01 L NS	0.42 Q *	0.44 Q *	0.48 Q *	0.45 Q *	0.55 Q **	0.53 Q **
<i>Solidago graminifolia</i>	P, F	0.41 Q *	0.51 Q *	0.48 L **	0.44 L **	0.44 L **	0.45 L **	0.52 L **	0.42 L **
<i>Ambrosia coronopifolia</i>	P, F	0.24 L NS	-0.35 L *	-0.16 L NS	0.14 L NS	0.62 L **	-0.17 L NS	0.09 L NS	0.22 L NS
<i>Rubus</i> sp.	P, W	-0.19 L NS	0.39 L **	0.51 L **	0.70 L **	0.02 L NS	0.46 L **	0.66 L **	0.60 L **
<i>Helianthemum bicknellii</i>	P, F	-0.14 L NS	-0.25 L NS	-0.23 L NS	-0.30 L NS	0.28 L NS	-0.21 L NS	-0.20 L NS	-0.25 L NS
<i>Panicum perlongum</i>	P, G	-0.04 L NS	-0.43 L **	-0.38 L *	-0.43 L **	0.29 L NS	-0.34 L *	-0.32 L *	-0.48 L **
<i>Lathyrus venosus</i>	P, Lg	-0.11 L NS	-0.24 L NS	-0.30 L NS	-0.38 L *	-0.03 L NS	0.32 Q *	-0.25 L NS	-0.33 L *
<i>Cyperus</i> sp.	P, S	-0.03 L NS	0.30 L NS	-0.20 L NS	-0.25 L NS	0.28 L NS	0.30 L NS	-0.11 L NS	-0.25 L NS
<i>Panicum oligosanthes</i>	P, G	-0.12 L NS	0.11 L NS	0.13 L NS	-0.21 L NS	0.21 L NS	0.20 L NS	0.32 L *	-0.07 L NS

† P = perennial, S = sedge, G = grass, F = forb, W = woody plant, Lg = legume.

‡ The correlation coefficients, r , for linear (L) regressions are shown, except when the quadratic (Q) regression was significant. In that case, its multiple correlation coefficient is given, as is the significance for the inclusion of the quadratic term. NS means $P > .05$; * means $.05 > P > .01$; ** means $P < .01$, using a two-tailed test.

Field C, undisturbed gradient.—Of the 63 plant species observed in the undisturbed plots of Field C, the eight common species, whose responses are given in Table 7 and Fig. 9, accounted for 90% of the total plant biomass of all treatments from 1982 through 1985. *Agropyron repens* was initially rare, occurring in only 16 plots and constituting <1% of the biomass of any treatment in 1982. In 1985, it occurred in 21 plots, making up 60% of the total biomass of the three treatment-H plots in which it occurred. As in Field B, *Agropyron repens* invaded into and increased in abundance in many high-nitrogen treatment plots. The high-nitrogen plots from which it was absent were dominated by *Poa pratensis*. Based on linear regressions, both the absolute and relative abundances of *Agropyron repens* increased significantly along the nitrogen gradient by 1985.

The absolute abundance of *Schizachyrium scoparium* increased significantly along the gradient in 1982. Both its absolute and relative abundances decreased along the gradient in 1983, 1984, and 1985 (Table 7, Fig. 9). *Poa pratensis* had quadratic responses to the nitrogen gradient, reaching its peak abundance at intermediate nitrogen levels. *Artemisia ludoviciana* increased along the gradient in 1982, decreased along the gradient in 1984, and had a quadratic response in 1985.

Solidago nemoralis decreased along the gradient in 1983, 1984, and 1985. *Sorghastrum nutans* declined along the gradient by 1984 and 1985 (Fig. 9, Table 7). *Panicum oligosanthes* increased along the gradient in 1982, had a quadratic response in 1983, but had no significant response in 1984 or 1985. The only significant effects of nitrogen on the height of any common species in any of the years were for plant height to increase along the gradient.

In 1983, 1984, and 1985, annual forbs increased significantly in relative abundance along the gradient ($r = 0.42$, $r = 0.41$, and $r = 0.45$, respectively; $n = 48$). In 1984, the relative abundance of perennial grasses increased significantly ($r = 0.32$, $n = 48$). That of perennial forbs decreased significantly along the gradient in 1984 and 1985 ($r = -0.53$, $r = -0.57$; $n = 48$).

Field C, disturbed gradient.—Of the 68 species observed in these plots, eight were common (Table 8, Fig. 10). *Agropyron repens* was initially rare, occurring in only 11 of the 54 plots in 1982. By 1985, it was present in 23 plots, and had increased greatly in its abundance in the high-nitrogen plots in which it was present. Based on linear regression, its absolute abundance increased significantly along the gradient in 1983, as did its absolute and relative abundances in 1984 and 1985 (Table 8, Fig. 10). *Schizachyrium scoparium*, dominant in

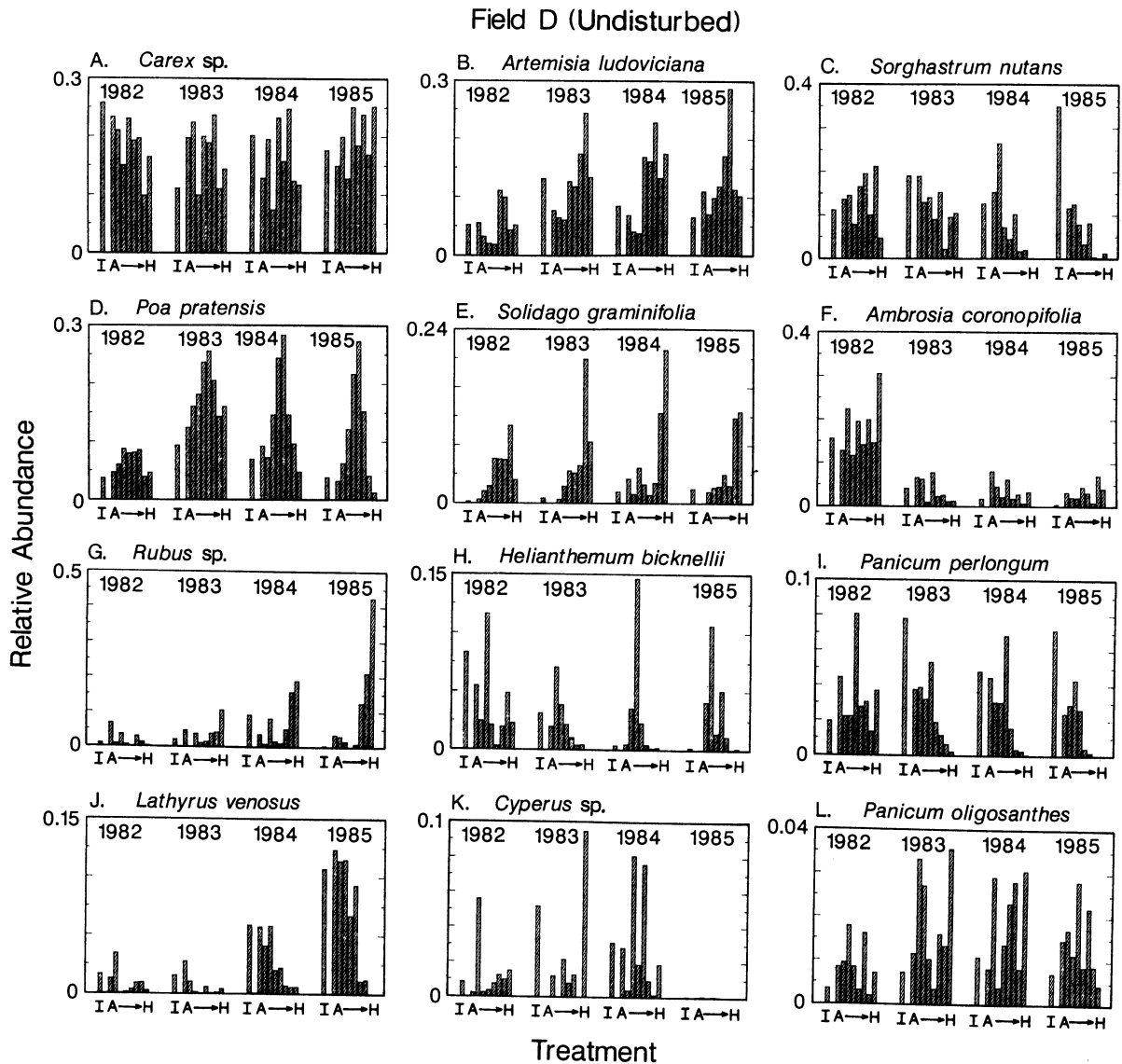


FIG. 11. Relative abundances of the 12 common species of Field D, the field of native oak savannah. Each bar is the mean of five replicates of each treatment for a given year. Treatment I is the unfertilized control and treatments A-H form the nitrogen gradient (from low to high rates of annual N addition). See also Table 9.

the field before disking, increased greatly in abundance in the low-nitrogen treatments (Table 8, Fig. 10). In 1983, 1984, and 1985, both its absolute and relative abundances decreased significantly along the nitrogen gradient. *Poa pratensis* declined along the gradient by 1985 (Fig. 10, Table 8). It was present in only 10 plots in 1982, but occurred in 50 plots in 1985. For the plots it invaded, it reached its peak absolute abundance at intermediate rates of nitrogen addition. *Panicum oligosanthos* had a quadratic response to nitrogen. *Artemisia ludoviciana* increased in absolute abundance along the gradient in 1983 and had a quadratic response in 1984 and 1985 (Table 8, Fig. 10). *Polygonum convolvulus* increased along the gradient all 4 yr (Table 8, Fig.

10). In 1982, 1983, and 1984, the only significant ($P < .05$) effect of the rate of nitrogen addition on the median heights of the common species was for height to increase along the gradient. In 1985, the heights of two species declined significantly along the gradient.

Annuals were most abundant in 1982 and declined in abundance each year thereafter. In 1982, the absolute abundances of annual grasses ($r = 0.51, n = 48$) and annual forbs ($r = 0.54, n = 48$) increased significantly along the nitrogen gradient, but the absolute abundance of perennials did not, based on linear regression. In 1983, both the relative and absolute abundances of annual grasses increased significantly ($P < .05$) along the gradient, but perennial grasses were not signifi-

cantly dependent on the rate of nitrogen addition. In 1984, the absolute and relative abundances of annual grasses ($r = -0.31$ and $r = -0.29$, respectively; $n = 48$) decreased significantly along the gradient, but those of annual forbs increased ($r = 0.42$ and $r = 0.34$, respectively; $n = 48$). Perennials were not significantly affected in 1984. In 1985, the relative abundance of annuals increased ($r = 0.54$, $n = 48$) and that of perennials decreased ($r = -0.38$, $n = 48$) along the gradient.

Field D, undisturbed gradient.—Of the 104 species observed in the samples clipped in Field D, the 12 common species accounted for 77% of the total biomass harvested. Their responses are given in Table 9 and Fig. 11. The identification of *Carex* to species indicated that $\approx 40\%$ of the *Carex* sp. were *C. muhlenbergii*, $\approx 9\%$ were *C. pensylvanica*, and $\approx 3\%$ were *C. foenea*. The remaining 48% could not be identified to species. *C. foenea* tended to reach its peak relative abundance in low-nitrogen treatments, *C. pensylvanica* in intermediate, and *C. muhlenbergii* in the high-nitrogen treatments.

Artemisia ludoviciana (Table 9) increased in biomass along the gradient in 1982, but tended to have quadratic responses thereafter. *Poa pratensis* had a consistent quadratic response. *Sorghastrum nutans* declined along the gradient in 1984 and 1985 (Table 9, Fig. 11). *Solidago graminifolia* increased significantly in its absolute abundance along the gradient in all years. Its relative abundance was quadratic in 1983 and linearly increasing in 1984 and 1985 (Table 9, Fig. 11). *Rubus* sp. was not significantly affected by the experimental gradient in 1982, but its absolute and relative abundances increased highly significantly along the gradient in 1983, 1984, and 1985. *Panicum perlongum*, in contrast, was not affected in 1982, but its absolute and relative abundances decreased significantly in 1983, 1984, and 1985 (Table 9, Fig. 11). The absolute and relative abundance of a legume, *Lathyrus venosus*, declined significantly along the gradient in 1985 (Fig. 11, Table 9). The other species were never significantly affected by the nitrogen gradient. The only significant effect of the nitrogen gradient on plant height was for height to increase along the gradient.

In 1983, 1984, and 1985, the relative abundance of perennial grasses decreased significantly along the gradient ($r = -0.46$, $r = -0.56$, $r = -0.69$, respectively; $n = 40$), and that of woody plants increased significantly ($r = 0.33$, $r = 0.40$, $r = 0.67$, respectively; $n = 40$). In 1985, legumes decreased significantly along the gradient ($r = -0.40$, $n = 40$).

DISCUSSION

These experiments were motivated by three main interests: (1) to establish through replicated field experiments the effects of different supply rates of a limiting soil resource on the diversity, species composi-

tion, and dynamics of change of successional vegetation; (2) to determine if the dependence of plant species abundances on soil nitrogen that was observed in the old-field survey was consistent with that observed on the experimental nitrogen gradients; and (3) to determine the extent to which initial differences in vegetational composition influenced the patterns observed after 4 yr of growth on experimental nitrogen gradients.

Patterns of resource limitation

The addition of P, K, Ca, Mg, S, and trace metals (treatment A) did not lead to any significant increase in total aboveground plant biomass compared with the unfertilized controls (treatment I) in any of the fields in any of the years. On a species-by-species basis, there were 7 instances out of 232 possible for which the addition of all nutrients except N led to a significant increase in biomass. These could be Type I errors. These results suggest that the growth of the common plants was not limited by P, K, Ca, Mg, S, Cu, Mn, Mo, Co, or Zn. Nitrogen was also the main limiting nutrient in another old field at Cedar Creek (Tilman 1984). Thus, nitrogen is probably the most important limiting nutrient throughout succession at Cedar Creek, although water and other soil resources may limit some species in some habitats.

Although only nitrogen was varied experimentally along the gradients, the supply rate of nitrogen and light penetration to the soil surface became negatively correlated because nitrogen addition led to increased plant biomass (Figs. 3 and 4). On average, $\approx 60\%$ of the incident light reached the soil surface in treatment A, but only $\approx 10\%$ reached the soil surface in treatment H. Litter accumulation in high-nitrogen plots (Figs. 3 and 4) further decreased the penetration of light to the surface of the mineral soil. Inverse correlations between nitrogen and light have been reported in many studies (e.g., Donald 1958, Aspinall 1960, Stern and Donald 1962, Harper 1977, Elberse et al. 1983). These correlations make it difficult to separate the effects of nutrients and light in any experiment. However, as Harper (1977:340–362) suggests, it would be naive to interpret nutrient addition experiments without also considering the negative correlation between nutrients and light. Although I discuss the possible role of light along these gradients, I must stress that light was not experimentally manipulated.

Species richness

The survey of 22 Cedar Creek old fields found a highly significant tendency for the species richness (SR) of individual quadrats to decrease with increasing total soil nitrogen ($SR = -0.004 \text{ TN} + 11.5$; $r = -0.27$, $n = 2262$, $P < .001$; Inouye et al. 1987). The nitrogen addition experiments gave a similar response. From 1983 on, nitrogen addition significantly decreased species richness along all seven experimental nitrogen gradients. This suggests that soil nitrogen may exert

significant control over local species richness within successional fields at Cedar Creek. The decreased species richness observed along these experimental gradients was consistent with the view that nutrient addition makes plots more homogeneous spatially, forcing more species to compete for the same limiting resource (Tilman 1982). The experimental results observed at Cedar Creek were similar to many previous observational and experimental studies (e.g., Milton and Davies 1947, Al-Mufti et al. 1977, Huston 1980, see review in Tilman 1982).

Dominance patterns

Because the initial vegetation contained many long-lived perennial plants, it seems unlikely that the vegetation would reach new equilibria (determined by the experimentally imposed rates of nitrogen supply) within 4 yr. However, through time, the species did become increasingly distinct in their distributions along the gradients (Figs. 5–11). Thus, the 1984 and 1985 distributions may be at least partially indicative of the long-term effects of the nitrogen gradients on abundances of the common species. Because the seven experimental gradients differed in the initial abundances and life history stages of the common species, comparisons of the responses of these species to the different gradients should indicate the relative importance of initial composition vs. soil nutrient supply rates on the structure of these successional communities. If the responses of individual species to these gradients were determined mainly by their initial abundances, this would support the view that history was an important determinant of the successional pattern. On the other hand, if the responses were determined more by the supply rate of the limiting soil resource than by initial composition, this would suggest that community composition tends to converge toward a point determined by the availability of the limiting soil resource. I explore these possibilities by comparing the response of each species that was common on at least two of the seven experimental nitrogen gradients.

By 1985, both the absolute and relative abundances of *Agropyron repens*, the most abundant grass, increased significantly along both the disturbed and undisturbed experimental gradients in the fields in which it occurred: Fields A, B, and C (Figs. 5–10). Despite its initial rarity in Fields B and C, it invaded into and dramatically increased in abundance in many high-nitrogen plots. Independent of its initial abundance, *Agropyron* seemed to be approaching the same absolute abundance in the high-nitrogen treatments (treatment H) for both the disked and the undisturbed gradients of Fields A, B, and C (Fig. 12). The greatest variance in its 1985 absolute abundance occurred in the 19 plots from which it was absent in 1982. For the 17 plots in which it was present in 1982, *Agropyron* seemed to be approaching an absolute abundance of ≈ 390 g/m² by 1985. Such convergence toward a biomass that was

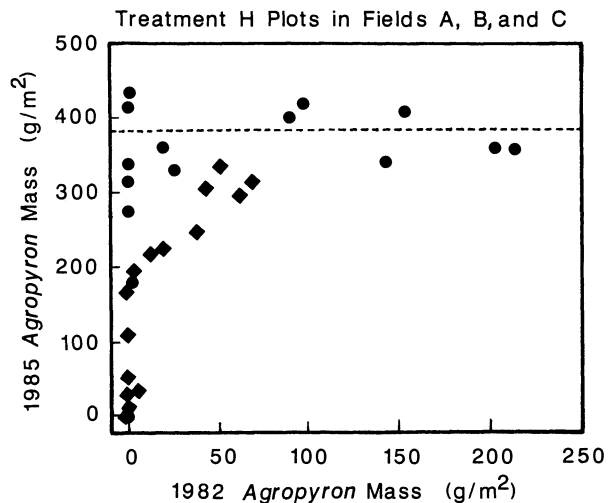


FIG. 12. The aboveground biomass of *Agropyron repens* in the treatment H plots of disked (●) and undisturbed (◆) gradients in Fields A, B, and C in 1982 and 1985. There were four undisturbed plots and three disked plots from which *Agropyron* was absent in both 1982 and 1985. Note that the abundance of *Agropyron* in 1985 was independent of its abundance in 1982, except for plots from which it was absent in 1982.

independent of its initial abundance shows that *Agropyron* did not have multiple stable equilibria in the high-nitrogen plots.

Of the other common grasses, *Poa pratensis* tended to have a Gaussian distribution along the nitrogen gradients in the disked plots of Fields B and C and the undisturbed plots of Fields C and D (Figs. 8–11), reaching its peak abundance at intermediate rates of nitrogen supply. It did not have any significant response to nitrogen for the undisked plots in Fields A and B. The relative abundance of *Schizachyrium scoparium* decreased highly significantly along the nitrogen gradients in all fields in which it was common (Figs. 7–10). *Panicum oligosanthos* had mainly quadratic responses to the nitrogen gradients (Figs. 7–11). *Agrostis scabra* decreased significantly along both gradients on which it was common (Figs. 5 and 8). *Sorghastrum nutans* decreased in relative abundance in both Fields C and D (Figs. 9 and 11). The annual *Setaria glauca*, only common on disked gradients, was quite rare by 1984 and 1985, but seemed to increase along the gradients (Figs. 6, 8, and 10).

Forbs were generally less abundant than grasses. *Ambrosia artemisiifolia*, an annual forb, was a common species in both disked and undisked plots in Field A. In both experiments, its absolute and relative abundances tended to decrease along the gradient by 1984 and 1985. *Rumex acetosella* decreased significantly along the nitrogen gradient in the disked plots in Field B in 1983, after which it was rare. It decreased significantly along the gradient in 1983 and 1984 in the undisked plots in Field B. The relative abundance of

Berteroa incana decreased significantly along the nitrogen gradient in the disked and undisturbed plots of Field A. In 1985, four of the five significant responses of *Artemisia ludoviciana* were quadratic (Figs. 9–11, Tables 7–9). However, none of its 1984 responses were significantly quadratic, with two of these being positive and two negative correlations (Tables 7–9). *Ambrosia coronopifolia*, *Erigeron canadensis*, and *Polygonum convolvulus* showed no consistent responses to the gradients. Although each had some cases that seemed contradictory, these were never significantly so in 1984 or 1985 (Tables 3–9).

Thus, of the species in common among two or more gradients, nine species had qualitatively similar distributions along the experimental nitrogen gradients by the 3rd or 4th yr of the experiment, but three had ambiguous responses. This demonstrates that the rate of supply of a limiting soil resource, nitrogen, exerts a major and often repeatable influence on plant species abundances in these old-field communities. Despite great initial differences in the abundances of species for these seven gradients, their composition converged. Such convergence suggests that the initial composition of the vegetation, i.e., its history, may not be as important a determinant of the long-term patterns observed in these old-field communities as the supply rate of a limiting soil resource.

Further, these results suggest that the point-to-point spatial heterogeneity in vegetational composition observed within these old fields may be caused by point-to-point differences in nitrogen supply rates within the soils of these fields. The observed separation of species along these seven experimental gradients, and the similarities among these seven gradients, support a Gleasonian, individualistic perspective, as have other nutrient-addition experiments (e.g., Shaver and Chapin 1980, review in Tilman 1982). The tendency for each species to reach its peak abundance at a particular rate of nitrogen supply suggests that these species may be differentiated in their abilities to grow and compete along these gradients (Tilman 1982, 1983, 1985).

The initial abundances of species did influence the dynamics of individual plots. The absence in 1982 of *Agropyron repens* from most plots in Fields B and C caused an initial divergence in the dominance patterns of the high-nitrogen treatments in these fields. This divergence was magnified by the response of *Poa pratensis* and *Schizachyrium scoparium*. *Poa pratensis* dominated treatment-H plots from which *Agropyron repens* was absent. *Schizachyrium scoparium* dominated high-nitrogen plots that lacked both *Agropyron* and *Poa*. Despite this initial divergence, *Agropyron repens* was able to invade and dominate high-nitrogen plots that had been dominated by *Schizachyrium scoparium* or *Poa pratensis*. In addition, *Poa pratensis* displaced high-density stands of *Schizachyrium scoparium* from which it and *Agropyron repens* were initially absent. This suggests that there was a competitive

hierarchy in the high-nitrogen plots, with *Agropyron repens* being the superior competitor, followed by *Poa pratensis* and then *Schizachyrium scoparium*. This ranking is identical to the order of peak abundance of these three species along the nitrogen gradients (Figs. 7–10), with *Schizachyrium* most abundant in low-nitrogen plots, *Poa* in intermediate plots, and *Agropyron* in high-nitrogen plots. These results, as well as the convergences discussed above, suggest that multiple stable equilibria, as defined by Connell and Sousa (1983), cannot be demonstrated in these old-field communities.

Physiognomy

The vegetation along all seven experimental nitrogen gradients shared certain physiognomic and life history features. Along all seven gradients, there was a tendency for vegetation to be short and spreading at low rates of nitrogen supply and tall and erect at high rates of supply (Figs. 3 and 4). Species with a rosette or short, spreading growth form, such as *Agrostis scabra* and *Berteroa incana* in Field A, *Agrostis scabra* and *Rumex acetosella* in Field B, *Solidago nemoralis* in Field C, and *Lathyrus venosus* in Field D were more common at low rates of nitrogen addition than at high rates. Woody plants, though rare, were more abundant at the higher rates of nitrogen addition. Of the three most abundant grasses, *Agropyron repens* was the tallest and dominated the most nitrogen-rich plots. *Poa pratensis* was next tallest, and dominated plots receiving intermediate rates of N addition, whereas *Schizachyrium scoparium* was the shortest species and dominated low-nitrogen plots. Such patterns suggest that plant height and life form may have been an important element influencing the position along an experimental gradient at which each species reached its peak abundance. The responses of the common species to the seven gradients can be used to further evaluate this idea.

Because plant height is a phenotypically plastic trait, I determined the maximal height of each common species as an estimate of its potential stature at maturity. For this, I used the greatest treatment average height at the time of clipping for each species in a given field and year. I then determined if there was a significantly positive rank order correlation between these maximal observed heights and the order of occurrence of the major species along an experimental nitrogen gradient. Orders of occurrence were based on the calculated "centers of mass" of the relative abundance distributions along each experimental gradient. I included in these analyses only those species that were at least 1% of the total biomass harvested across all treatments in a given field and year (Table 10). Sample sizes for each gradient were small, but 13 of the 14 rank order correlations were positive, with 4 of these significant at $P < .05$. These results suggest that plants with greater maximal heights tend to be dominant in

more nutrient-rich habitats. Because competition for light is the most likely factor selecting for greater vegetative height in plants (e.g., Givnish 1982, Westoby 1984, Tilman 1985, 1986a), these results support the view that competition for light, as well as competition for nutrients, may have influenced the responses of species to these experimental nutrient gradients. These results are reminiscent of many observations of plant physiognomy along natural productivity gradients (e.g., Beard 1944, 1955, 1983, Whittaker 1975:161–167, Cody and Mooney 1978), which have shown that species dominant in more productive habitats are taller at maturity than those dominant in less productive habitats.

Transient population dynamics

Before the nitrogen gradient experiments were begun in the undisturbed areas of Fields A, B, C, and D, annual plants are common in Fields A and B but rare in Fields C and D. For the undisturbed gradients in Fields A and B, the relative abundance of annual plants, as a group, increased significantly with nitrogen addition in 1982 but decreased significantly by 1984. The relative abundance of all perennial plants, as a group, decreased significantly along these gradients in 1982 but increased significantly along these gradients by 1984. Thus, when annuals were common in the areas to be used for the undisturbed nitrogen gradient experiments, nitrogen addition led to a period of transient dominance by annuals, which then decreased in abundance as various perennials increased. The perennials initially decreased in relative abundance along the experimental gradients, and then increased along them. Similar patterns of transient dynamics occur for individual species (Figs. 5–11). Thus, the immediate response to addition of nitrogen was often quite different from the response observed several years later. Because annuals as seedlings have greater relative growth rates than herbaceous perennials (Grime and Hunt 1975, Tilman 1986b), the initial dominance by annuals may have been caused by them rapidly overtopping perennials immediately after fertilization. By the 2nd or 3rd yr, nitrogen addition may have allowed perennials to increase the stores of energy and nutrients in their rhizomes, and thus to grow taller early in the season than annuals and displace the annuals from high-nitrogen treatments.

Many ecological experiments, including deWit competition experiments, nutrient addition experiments, and herbivore manipulations, last only one or two field seasons. In such experiments, it is common to interpret the observed changes in species abundances at the end of the experiment as indicative of the long-term effect of the factor manipulated. If, as reported here, such experiments actually lead to transient population dynamics, the experiments, whenever possible, should be allowed to proceed for many field seasons to determine the actual long-term effects.

TABLE 10. Spearman rank order correlation coefficients between height at maturity of common plants and the position (rate of nitrogen addition) along each experimental gradient at which each species was dominant (as determined by its abundance "center of mass" on the gradient).*

Gradient	1984			1985		
	r_s	n	P	r_s	n	P
Field A, undisturbed	0.50	5	.16	1.00	2	.50
Field A, disturbed	1.00	2	.50	1.00	2	.50
Field B, undisturbed	0.54	7	.11	0.43	7	.16
Field B, disturbed	-0.40	4	.20	0.07	7	.40
Field C, undisturbed	0.71	8	.03	0.72	7	.04
Field C, disturbed	0.77	6	.04	0.75	7	.03
Field D, undisturbed	0.37	12	.10	0.43	11	.08

* r_s is the rank correlation coefficient, n is the number of species > 1% of total biomass that year, and P is probability of such a correlation coefficient, using a one-tailed test.

Comparisons with distributional patterns

The chronosequence of 22 Cedar Creek old fields showed that total soil nitrogen increased during secondary succession (Fig. 1) and that the abundances of most species common during secondary succession at Cedar Creek were significantly dependent on total soil nitrogen (Fig. 2). Such correlations suggest that nitrogen may be an important factor determining the species compositions of these old fields and the dynamics of successional change within them. The experimental nitrogen gradients provided a test of this possibility. The distribution of each species with respect to soil nitrogen that was observed in the old-field survey (Fig. 2) can be compared with its response to nitrogen addition. If the two responses are similar, this would be experimental support for the role of nitrogen in structuring these successional communities. Fifteen of the 20 most abundant species in the old-field survey (based on the average percent cover of each species in the 2300 sample quadrats) were also common species in some of the nitrogen gradient experiments. The old-field survey revealed that all but 3 of these 15 species had a highly significant dependence of their percent cover on total soil nitrogen, based on linear or quadratic regressions using all quadrats from all old fields in which a species occurred (Fig. 2). The exceptions were *Agropyron repens*, *Sorghastrum nutans*, and *Solidago nemoralis*. Only the curve for *Solidago nemoralis* is suggestive of a distribution with more than one peak. The other curves can be considered to be parts of a Gaussian curve.

If the abundance of a species is determined by soil nitrogen, and if this species has an approximately Gaussian distribution with respect to soil nitrogen, then its response to nitrogen addition should depend on the nitrogen level in the experimental field. If the nitrogen level in a field is at or beyond the peak of the Gaussian curve for that species, it should decline in abundance with nitrogen addition. If a field has a nitrogen level that is less than the level at which its Gaussian curve reaches its peak, then low rates of nitrogen addition

should lead to increased abundance of that species and high rates should lead to decreased abundance, i.e., the response to an experimental nitrogen gradient should be a Gaussian curve.

Based on the old-field quadrat data, there were seven species that had significantly negative linear regressions of their percent cover on total soil nitrogen: *Agrostis scabra*, *Ambrosia artemisiifolia*, *Crepis tectorum*, *Hedeoma hispida*, *Erigeron canadensis*, *Lespedeza capitata*, and *Rumex acetosella*. Based on the regressions for 1983, 1984, and 1985 of Tables 3–8, five of these seven species consistently decreased in relative abundance along the gradients, as expected. The exceptions were the annual forbs *Crepis tectorum* and *Erigeron canadensis*, neither of which had consistent responses to the gradients.

Artemisia ludoviciana, *Berteroa incana*, *Poa pratensis*, and *Schizachyrium scoparium* all had significantly quadratic (Gaussian) distributions in the old-field survey (Fig. 2). *Berteroa incana* reached its peak cover in the old fields at a total soil nitrogen (N) of ≈ 500 mg/kg of soil and was common only in Field A. Because total soil nitrogen (as N) levels in Field A were > 500 mg/kg soil (Table 2), to be consistent with its old-field pattern, it should have declined with nitrogen addition, which it did in 1984 and 1985 (Table 3). *Artemisia ludoviciana*, *Poa pratensis*, and *Schizachyrium scoparium* had peak abundances in their old-field distributions that occurred at total soil nitrogen levels higher than the mean (Table 2) of any of the experimental gradients. Thus, these three species should have Gaussian (quadratic) distributions along the experimental gradients. Of the significant responses of the relative abundance of *Artemisia ludoviciana* in 1984 and 1985 (Tables 7–9), two were quadratic, one was linearly decreasing and one was linearly increasing along the experimental nitrogen gradients. Of the significant responses of *Poa pratensis* for these years, five were quadratic and one was linearly decreasing. However, the relative abundance of *Schizachyrium scoparium* decreased along all the gradients on which it was common in 1983, 1984, and 1985. Its only significantly quadratic responses were for its absolute abundance in the undisturbed plots of Field B, which were the most nitrogen-poor of the plots.

Rubus sp., a woody plant, was the only common species to have its percent cover increase significantly linearly with total soil nitrogen, based on the old-field survey (Fig. 2). It was common only on the experimental gradient in Field D. It increased highly significantly in both its relative and absolute abundance along this gradient in 1984 and 1985. Thus, of the 12 species for which percent cover in the old fields was significantly dependent on total soil nitrogen, 8 species consistently responded to the experimental nitrogen gradients in a manner supporting the hypothesis that soil nitrogen levels were a major determinant of their observed abundance patterns along the successional

chronosequence. *Crepis tectorum*, *Artemisia ludoviciana*, and *Erigeron canadensis* had some responses that agreed and some that disagreed with those expected based on their distributions in the old-field survey (Fig. 2).

Thus, these experiments have shown that nitrogen addition often caused species that are common on nitrogen poor soils, which are generally early successional species, to decrease in abundance and caused species that are common on richer soils, which are usually late successional species, to increase in abundance. There are, though, two major exceptions. *Schizachyrium scoparium* is a late successional species at Cedar Creek, being absent from fields < 12 yr old and reaching its peak abundance in 35–45 yr old fields (Tilman 1986b). It consistently declined in abundance following nitrogen addition. Although *Agropyron repens* is an early successional species that is present in newly abandoned fields and reaches its peak abundance in 5–15-yr-old fields (Tilman 1986b), it increased dramatically and consistently in abundance following nitrogen addition (Figs. 5–10). Although the cover of *Agropyron repens* was not significantly dependent on total soil nitrogen using all 2262 old-field samples combined (Fig. 2), its cover was significantly linearly or quadratically dependent on soil nitrogen within 9 of the 22 individual fields. Seven of these regressions were positive, one was quadratic and one was negative. The negative regression occurred in the field with the highest average total soil nitrogen of these nine fields. Although these data show a strong tendency for *Agropyron* to be more abundant in nitrogen-rich areas within individual fields, its field-average cover decreased with field age for fields > 10 yr old, despite the tendency for these older fields to be more nitrogen-rich. This suggests that *Agropyron repens* may be an early successional species of nutrient-rich soils, whereas other species, such as *Ambrosia artemisiifolia* and *Agrostis scabra*, may be early successional species of poor soils. If this were so, *Agropyron repens* would be maintained only in a habitat that was frequently disturbed and had rich soils. *Schizachyrium scoparium*, on the other hand, tends to be restricted to the lower nitrogen soils of individual fields, but is rare in or absent from early successional fields, perhaps because of its slow growth rate (Tilman 1986b) or low probability of colonization.

There are other possible explanations for the inconsistent response of *Agropyron* and *Schizachyrium*. For instance, *Agropyron*, a cool-season grass, may be favored over *Schizachyrium*, a warm-season grass, in the fertilization experiments because fertilizer is applied during early and late spring, *Agropyron*'s growing season. A second possibility is that the dominance of *Agropyron* is transient, and that it is favored initially after fertilization or disturbance because of a great maximal growth rate. A nitrogen-limited growth experiment showed that *Agropyron* seedlings attained 3.3 times the biomass of *Schizachyrium* seedlings after 12 wk of

growth on a rich soil (Tilman 1986b). If its dominance is transient, *Agropyron* may be displaced later on in these nitrogen addition experiments as other species, such as slow growing, late successional woody species, grow in the high nitrogen treatment plots. Such transient dominance by *Agropyron* would be consistent with it being an early successional species of rich sites.

Compared with other secondary successions, old-field succession at Cedar Creek is slow. Fields that had been forested before agriculture have had little re-growth of trees in them even 60 yr after abandonment from farming. In contrast, there is a closed canopy of tree saplings after 10 or 15 yr during many other secondary successions (e.g., Horn 1971, Peet and Christensen 1980). The slowness of re-establishment of woody vegetation at Cedar Creek is not caused by a lack of propagules, for the old fields are surrounded by oak forest, and seedlings of woody plants occur throughout the fields. Nor is woody plant growth inhibited by fire. None of the 22 fields in the old-field survey had been burned, and yet woody plants made up at most 13% of the cover of any of the fields (Inouye et al. 1987). The old-field survey did show that woody plant cover increased with field age and with total soil nitrogen at Cedar Creek (Tilman 1986a, Inouye et al. 1987). Further, woody plant biomass increased with the rate of nitrogen addition for the experimental gradients. Comparisons of total soil nitrogen levels in several old fields and their adjacent woodlots (which had never been clear-cut or farmed) showed that the woodlots had 1.5 to 3 times more nitrogen than the fields (D. Tilman, *personal observation*). These observations suggest that the slow rate of re-establishment of woody plants at Cedar Creek may be caused, in part, by the low levels of nitrogen and the slow rate of accumulation of nitrogen in these porous, excessively well-drained, nitrogen-impooverished soils. If this is so, woody plant dominance on the nitrogen-poor soils of Cedar Creek may have more in common with many cases of primary succession than with cases of secondary succession on rich soils.

Many processes other than the accumulation of nitrogen, and its effect on plant interactions, can influence succession. For instances, these experiments have suggested that some species, because of rapid rates of vegetative growth, may attain a period of transient dominance on nutrient-rich soils before being displaced by more slowly growing species that are superior competitors for those soils. The 4 yr that these experiments have proceeded to date is too short a period to determine how many of the patterns reported here are transient effects. It seems likely, though, that many of the current dominants of the high-nitrogen plots will be displaced by woody plants. Many woody plants, even under optimal conditions, have lower rates of vegetative growth than herbaceous plants (Grime and Hunt 1975). This suggests that there may be qualitative differences between secondary succession on a poor soil

and that on a rich soil. After an initial period of transient dynamics, successional dynamics on a poor soil may depend mainly on the slow displacement of one species by another as nutrients accumulate, much as has been reported for several primary successions. In contrast, for secondary successions on rich soils, it is likely that colonization rates and maximal growth rates could be major determinants of the successional sequence, because rapid colonization and rapid growth could allow species to attain periods of transient dominance during the time required for more slowly growing species to arrive in a habitat and attain the biomass needed to displace them.

Conclusions

These experiments have demonstrated that the rate of supply of nitrogen, the major limiting nutrient, had consistent, significant effects on species richness and species abundances along seven different experimental nitrogen gradients. Species richness declined highly significantly along these experimental gradients, with >60% of the species initially present being lost from the high-nitrogen treatments by 1985. Through time, the common species became increasingly differentiated in their distributions along the gradients. The majority of the species that were common on two or more gradients responded similarly to the gradients. There was a tendency for species of short stature to dominate low-nitrogen treatments and for taller species to dominate high-nitrogen treatments. Although light was not experimentally manipulated, the results of these experiments were generally consistent with the view (Tilman 1985, 1986a) that plants compete for both nitrogen and light along these gradients, and that each species is a superior competitor at a different point along these gradients. The decrease in diversity with nutrient addition, the transient dominance of early successional species, the separation of species along the gradients according to their life histories and morphologies, and the consistencies between the pattern of species responses to the experimental nitrogen gradients and their distribution with respect to nitrogen in the old fields were all qualitatively consistent with predictions of a theory of plant competition for limiting resources that I have developed elsewhere (Tilman 1982, 1985, 1986a).

These experiments suggest that soil nitrogen has a major role in determining the composition, species richness, and successional dynamics of the nitrogen-poor fields of Cedar Creek. The slow rate at which woody plants come to dominate these formerly forested fields may be caused by the nitrogen impoverishment of the fields and the slow rate of accumulation of nitrogen at Cedar Creek. However, succession is a sufficiently complex process that it is extremely unlikely that a single factor, such as soil nitrogen, will ever explain it. This is especially so for secondary successions in habitats with nutrient-rich soils, for which

colonization rates and transient dynamics caused by differences in maximal growth rates should have a greater impact and soil nutrients a lesser impact than at Cedar Creek.

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LITERATURE CITED

- Al-Mufti, M., C. Sydes, S. Furness, J. Grime, and S. Band. 1977. A quantitative analysis of shoot phenology and dominance in herbaceous vegetation. *Journal of Ecology* **65**:759-792.
- Aspinall, D. 1960. An analysis of competition between barley and white persicaria. II. Factors determining the course of competition. *Annals of Applied Biology* **48**:637-654.
- Beard, J. S. 1944. Climax vegetation in tropical America. *Ecology* **25**:127-158.
- . 1955. The classification of tropical American vegetation-types. *Ecology* **36**:89-100.
- . 1983. Ecological control of the vegetation of southwestern Australia: moisture versus nutrients. Pages 66-73 in F. J. Kruger, D. T. Mitchell, and J. U. M. Jarvis, editors. *Mediterranean-type ecosystems*. Springer-Verlag, Berlin, Germany.
- Cody, M. L., and H. A. Mooney. 1978. Convergence versus nonconvergence in Mediterranean-climate ecosystems. *Annual Review of Ecology and Systematics* **9**:265-321.
- Connell, J. H., and R. O. Sousa. 1983. On the evidence needed to judge ecological stability or persistence. *American Naturalist* **121**:789-824.
- D'Elia, C. F., P. A. Steudler, and N. Corwin. 1977. Determination of total nitrogen in aqueous samples using persulfate digestion. *Limnology and Oceanography* **22**:760-764.
- Donald, C. M. 1958. The interaction of competition for light and for nutrients. *Australian Journal of Agricultural Research* **9**:421-435.
- Elberse, W. Th., J. P. van den Bergh, and J. G. P. Dirven. 1983. Effects of use and mineral supply on the botanical composition and yield of old grassland on heavy-clay soil. *Netherlands Journal of Agricultural Sciences* **31**:63-88.
- Givnish, T. J. 1982. On the adaptive significance of leaf height in forest herbs. *American Naturalist* **120**:353-381.
- Gleason, H. A., and A. Cronquist. 1963. *Manual of vascular plants of Northeastern United States and adjacent Canada*. Van Nostrand Reinhold, New York, New York, USA.
- Grigal, D. F., L. M. Chamberlain, H. R. Finney, D. V. Wroblewski, and E. R. Gross. 1974. Soils of the Cedar Creek Natural History Area. Miscellaneous report 123. University of Minnesota Agricultural Experiment Station, Saint Paul, Minnesota, USA.
- Grime, J. P., and R. Hunt. 1975. Relative growth rate: its range and adaptive significance in a local flora. *Journal of Ecology* **63**:393-422.
- Harper, J. L. 1977. *Population biology of plants*. Academic Press, New York, New York, USA.
- Horn, H. S. 1971. *The adaptive geometry of trees*. Princeton University Press, Princeton, New Jersey, USA.
- Huston, M. 1980. Soil nutrients and tree species richness in Costa Rican forests. *Journal of Biogeography* **7**:147-157.
- Inouye, R. S., N. J. Huntly, D. Tilman, J. R. Tester, M. Stillwell, and K. C. Zinnel. 1987. Old-field succession on a Minnesota sand plain. *Ecology* **68**:12-26.
- Lewontin, R. C. 1969. The meaning of stability. Pages 13-24 in *Diversity and stability in ecological systems*. Brookhaven Symposia in Biology, Number 22.
- May, R. M. 1977. Thresholds and breakpoints in ecosystems with a multiplicity of stable states. *Nature* **269**:471-477.
- . 1979. The structure and dynamics of ecological communities. Pages 385-407 in R. M. Anderson, B. D. Turner, and L. R. Taylor, editors. *Population dynamics*. Blackwell Scientific, Oxford, England.
- Milton, W., and R. Davies. 1947. The yield, botanical and chemical composition of natural hill herbage under manuring, controlled grazing and hay conditions. *Journal of Ecology* **35**:65-89.
- Olson, J. S. 1958. Rates of succession and soil changes on southern Lake Michigan sand dunes. *Botanical Gazette* **119**:125-129.
- Pastor, J., M. Stillwell, and D. Tilman. 1987. Nitrogen mineralization and nitrification in four Minnesota old fields. *Oecologia (Berlin)* **71**:481-485.
- Peet, R. K., and N. L. Christensen. 1980. Succession: a population process. *Vegetatio* **43**:131-140.
- Pierce, R. L. 1954. *Vegetation cover types and the land use history of Cedar Creek Natural History Reservation, Anoka and Isanti Counties, Minnesota*. Thesis. University of Minnesota, Duluth, Minnesota, USA.
- Pigott, C. D., and K. Taylor. 1964. The distribution of some woodland herbs in relation to the supply of nitrogen and phosphorus in the soil. *Journal of Ecology* **52** (supplement): 175-185.
- Shaver, G. R., and F. S. Chapin III. 1980. Response to fertilization by various plant growth forms in an Alaskan tundra: nutrient accumulation and growth. *Ecology* **61**:662-675.
- Snaydon, R. W. 1962. Micro-distribution of *Trifolium repens* L. and its relation to soil factors. *Journal of Ecology* **50**:133-143.
- Stern, W. R., and C. M. Donald. 1962. Light relationships in grass-clover swards. *Australian Journal of Agricultural Research* **13**:599-614.
- Strobeck, C. 1973. *N* species competition. *Ecology* **54**:650-654.
- Tilman, D. 1982. *Resource competition and community structure*. 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.
- . 1985. The resource ratio hypothesis of succession. *American Naturalist* **125**:827-852.
- . 1986a. Evolution and differentiation in terrestrial plant communities: the importance of the soil resource: light gradient. Pages 359-380 in T. Case and J. Diamond, editors. *Community ecology*. Harper and Row, New York, New York, USA.
- . 1986b. Nitrogen-limited growth in plants from different successional stages. *Ecology* **67**:555-563.
- Westoby, M. 1984. The self-thinning rule. *Advances in Ecological Research* **14**:167-225.
- White, A. S. 1983. The effects of thirteen years of annual prescribed burning on a *Quercus ellipsoidalis* community in Minnesota. *Ecology* **64**:1081-1085.
- Whittaker, R. H. 1975. *Communities and ecosystems*. Macmillan, New York, New York, USA.