OLD-FIELD SUCCESSION ON A MINNESOTA SAND PLAIN[1]

RICHARD S. INOUYE,[2] NANCY J. HUNTLY,[2] DAVID TILMAN, JOHN R. TESTER,
MARK STILLWELL, AND KATHLEAN C. ZINNEL
*Department of Ecology and Behavioral Biology, University of Minnesota,
Minneapolis, Minnesota 55455 USA*

Abstract. Vegetation and soils were sampled in 22 old fields ranging in age from 1 to 56 yr since abandonment. Soil nitrogen concentration increased significantly with field age. Vegetation cover, total aboveground plant biomass, and litter cover increased significantly with soil nitrogen. Light penetration to the soil surface was negatively correlated with total plant biomass. Field age and soil nitrogen concentration were used as independent variables in simple regression and partial correlation analyses to determine the relative importance of such time-dependent processes as dispersal vs. the availability of a limiting resource (nitrogen) as predictors of patterns in species richness or the abundance of various plant groups. Species richness per field and within-field heterogeneity in species composition increased with field age. Local species richness decreased with increasing soil nitrogen. Cover of annuals and introduced species decreased with field age and nitrogen; however, annuals contributed an important part of total vegetative cover even in 25-yr-old fields. Cover of perennials and woody species increased with soil nitrogen and field age. Although the fields were bordered by woods, woody species contributed <15% cover even in the oldest fields. For several plant groups the relationship between cover and soil nitrogen within individual fields was the opposite of that among all fields. These patterns suggest that while soil nitrogen is an important determinant of local species composition and abundance, dispersal and colonization, which are dependent on field age, determine which species are present in a field.

Key words: Cedar Creek Natural History Area; Minnesota; nitrogen; old field, resources; succession; time.

INTRODUCTION

Time is intrinsic to the concept of succession, which has often been defined as the repeatable change in community composition through time following a disturbance (e.g., Drury and Nisbet 1973). One class of models for succession assumes a simple direct effect of time on changes in species occurrence and abundance. Differences in dispersal rates and growth rates of species are thus hypothesized to be responsible for many of the successional patterns observed in old fields and in the intertidal (e.g., Egler 1954, Connell and Slatyer 1977). Other models suggest that time-dependent changes in resource availability control succession. The role of time is thus hypothesized to be indirect, with species responding directly to resources. Christensen and Peet (1984), for example, suggested that species became more restricted in their distribution with time, due to competitive displacement from areas where they were less efficient at using resources, and Tilman (1982, 1985) has suggested that changes in the relative availability of limiting resources, in particular nitrogen and

light, drive changes in species composition during succession.

In this paper we report results of a study of limiting soil resources and vegetation in a chronosequence of 22 old fields, ranging in age from 1 to 56 yr since abandonment. Our objectives were both to document successional patterns in vegetation and soils, and to compare field age and soil nitrogen as predictors of successional changes in vegetation. We examined how plant species richness changes with field age; how plant species composition changes as fields age, and how predictable those changes are; and whether species richness, species composition, and soil nitrogen are correlated, both between and within fields.

METHODS

Study site

Cedar Creek Natural History Area (Cedar Creek) is located on the Anoka County Sand Plain ≈50 km north of Minneapolis, Minnesota. The 2200-km² sand plain was formed 12 000–13 000 yr ago by glacial outwash at the end of the Wisconsin glaciation. Cedar Creek lies between prairie to the west and deciduous forest to the east. Prairie species increased in importance ≈8000 yr ago (Cushing 1963). The resulting vegetation was a mixture of fire-maintained oak savannah and

TABLE 1. Field, soil nitrogen, and diversity data for 22 old fields surveyed in 1983. Quadrat diversity measures are average values for all quadrats in a field. Average Jaccard similarity index is the average of all pairwise comparisons of quadrats within a field. Sample size is 100 quadrats in each field, except for fields 22 and 29, for which it is 150 quadrats.

Field	Year last culti- vated	Last crop	Field age (yr)	Field area (ha)	Soil N (mg/kg) Ave.	Min.	Max.	Field species richness	Quadrat Species richness	H'	Average Jac- card index
72	1927	potato	56	3.0	870	429	1873	51	9.61	1.62	31.7
69*	1934	corn	49	4.1	684	366	1383	68	11.99	1.70	31.9
32	1941	corn	42	3.0	759	487	1428	61	8.65	1.47	29.0
35	1941	oats	42	1.9	706	397	1691	59	7.22	1.44	26.9
45	1943	corn	40	11.1	456	191	1508	45	10.43	1.59	32.2
5	1947	oats	36	12.4	631	292	1399	42	5.43	1.04	39.2
27	1947	unknown	36	8.4	447	291	901	49	11.47	1.61	35.2
76	1952	soybeans	31	2.4	560	303	914	49	7.69	1.15	34.0
77	1952	soybeans	31	5.9	530	253	932	64	11.29	1.56	30.2
70	1955	soybeans	28	8.8	513	238	967	53	10.93	1.67	35.5
21	1957	soybeans	26	3.7	656	443	918	31	7.20	1.35	45.2
22*	1957	soybeans	26	8.8	520	148	1054	61	10.27	1.30	28.0
26	1957	soybeans	26	4.3	402	190	647	47	9.54	1.32	39.0
47	1959	soybeans	24	14.6	790	410	1507	48	7.88	1.18	33.1
44	1961	soybeans	22	6.4	551	287	1183	43	7.59	1.44	37.9
53	1961	soybeans	22	5.9	556	304	933	29	7.03	1.31	52.3
24	1968	soybeans	15	11.3	393	196	653	47	10.06	1.51	34.9
29*	1968	soybeans	15	4.8	442	225	1328	52	11.49	2.09	41.7
4	1971	rye	12	3.7	387	239	526	22	5.11	0.93	48.6
40	1972	rye	11	6.4	574	360	945	45	8.56	1.23	38.3
39	1975	rye	8	6.2	357	246	571	41	11.44	1.87	51.7
41	1982	rye	1	4.0	435	308	750	34	8.99	1.31	51.3

* Fields in which quadrats were located along the edge of unmanipulated control plots rather than on permanent transects.

prairie, upland deciduous forest, and lowland marshes and swamps (Cushing 1963). Soils at Cedar Creek are primarily outwash sediments of well-sorted fine (Sartell and Zimmerman series) and medium (Nymore series) sands (Grigal et al. 1974), which are poor in nitrogen (Tilman 1983, 1984). Agricultural practices further depleted nitrogen from these soils, with the result that secondary succession in abandoned fields begins under conditions of significant nitrogen limitation. Experiments in four old fields at Cedar Creek indicate that nitrogen limits primary productivity in fields ranging in age from 10 to 49 yr since abandonment (Tilman 1984): none of the other nutrients added to experimental plots (Mg, Ca, P, K, trace minerals, H_2O) in three fields produced consistent increases in total plant biomass; nitrogen is the primary limiting resource in these soils.

The Cedar Creek area was first settled by Europeans in 1856. Some selective and clearcut logging was done shortly after settlement. The earliest record of clearing land for cultivation was 1885, and most of the land was first cultivated between 1900 and 1910 (Pierce 1954).

Sampling

In 1983 we sampled vegetation and soils in 22 old fields at Cedar Creek. Fields ranged in age since abandonment from 1 to 56 yr; last crop was known for all but one field (Table 1). The 22 fields we sampled were all located on well-drained upland sands in the Zimmerman, Sartell, or Nymore series (Grigal et al. 1974). Slopes ranged from 0 to 15%. Each field was bordered on at least one side by upland forest vegetation (primarily red oak, pin oak, and their hybrids) or by other fields that were themselves bordered by forest. There were differences in the last crop planted in these fields, and hence the timing of the last cutting or plowing also varied. We believe, however, that the similarity in soils and climate make these 22 fields a valid chronosequence in which to look for successional patterns. In each of 19 of the fields we established four parallel transects 40 m long spaced 25 m apart. On each transect we sampled 25 quadrats, 1 × ½ m, spaced at 1½-m intervals, for a total of 100 quadrats in each field. In one of those fields, field 21, one transect was not parallel to the others because of the size and shape of the field. In the remaining 3 fields transects were located on the sides of unmanipulated control plots that were part of a separate experimental study. While the spacing between these transects was different, quadrat size and spacing between quadrats on each transect was the same.

Within each quadrat we estimated percent cover of bare ground, litter, and vegetation by species. Vegetation within a quadrat was viewed as if projected onto a two-dimensional plane, and cover of each species,

bare ground, and litter were estimated visually. Percent cover for all plant species, bare ground, and litter were calculated to sum to 100%. Litter estimates were affected most by our sampling method. Cover was not allocated to litter where the litter was covered by live vegetation; thus, as vegetation increased, cover allocated to litter necessarily decreased.

We took a 10-cm soil core at the center of each quadrat. Total nitrogen was analyzed colorimetrically following persulfate digestion (Tilman 1984). Organic matter content was measured in every fifth quadrat on each transect by ashing ≈10 g of soil. We measured pH using a 1:1 dilution of soil with deionized water that was allowed to equilibrate for 30 min.

In 1984 we sampled plant biomass and measured light penetration in the 19 fields with permanent transects. These measurements, three on each transect, were taken at points different from those where we estimated percent cover. At each location we clipped, at ground level, a strip of vegetation 10 cm wide and 200 cm long. Samples were sorted into three categories (grasses, forbs, and litter), dried, and weighed. Before clipping, light readings were taken above the vegetation and at ground level using a 1.0 m long, integrating, cosine-corrected LI-COR quantum sensor. Light readings were taken within ±2 h of solar noon on clear days. Light penetration was calculated as the proportion of the light above vegetation that reached ground level.

We attempted to minimize two sources of sampling error. First, to minimize the effect of differences in sampling among groups, each of four teams sampled one transect in each field. Second, because the percent cover of species changes during the season, we sampled all fields during 2-wk period (21 July 1983 to 4 August 1983). Order of sampling was arbitrary, but we avoided correlation of sampling order with field age. At the time we sampled, warm-season species had completed most of their aboveground growth and cool-season species were still present.

Analyses

For most analyses we grouped plant species based on their life history, growth form, and historical origin. Although this ignores patterns at the species level, it serves several useful purposes. The first of these is simplification. We encountered >150 species in our study; it is much easier to find general patterns when a limited number of plant groups are considered. Second, life history categories may be useful in testing particular models of succession. Third, we can look at particular groups of species (e.g., introduced species, true prairie species) to see if there are consistent changes in the abundance of these groups with field age. Plants were categorized using data from Gleason and Cronquist (1963), Curtis (1959), and E. Cushing, B. Delaney, and T. Morley (personal communication in each case).

Species richness was calculated for individual quadrats and for each field as a whole. Jaccard index values

(Goodall 1978) were calculated for all pairs of quadrats within each field and for all pairs of fields. This index provides a measure of similarity, ranging from 0 to 100, for two sample units based on overlap in species composition (larger values of this index indicate greater similarity). The form of the index we used employs only presence/absence data, and thus reflects differences in species composition. Index values for pairs of quadrats within a field provide a measure of similarity of quadrats within a field; values for pairs of fields compare similarity in species composition between fields.

Statistical analyses were done using SPSS version 7.9 (Nie et al. 1975). Percent cover and proportional cover values were transformed by taking the arctangent of the square root of $X/(1 - X)$, for regression analyses. Except where stated otherwise, statistical analyses were performed using average percent cover and average soil nitrogen for each field, rather than individual quadrat data. Analyses reported here were performed using percent cover. Results of analyses using proportional cover (percent cover divided by total vegetative cover) were very similar to those reported here. Correlations of percent cover for various plant groups vs. soil nitrogen concentration within individual fields included quadrats on which cover of those groups was zero. Analyses without those quadrats gave similar results. Correlations typically decreased in significance when zeros were omitted (i.e., fewer fields had significant correlations), but the nature of the relationships was not changed by deleting zero points.

We did both simple and partial correlations using field age and average field soil nitrogen as predictors of species richness and cover of the various plant groups. Partial correlations were used to test the relative importance of age and soil nitrogen as predictors of successional changes.

Results

Soil resources

Average total soil nitrogen (TN; expressed in milligrams per kilogram of soil) in the top 10 cm increased significantly with field age in years ($TN = 6.84 \cdot Age + 369.19$; $r = 0.67$, $N = 22$, $P < .001$). Field means ranged from 357 to 870 mg/kg (Table 1); range and standard deviation were positively correlated with field mean. Average percent organic matter content was not significantly correlated with field age ($r = 0.33$, $P = .133$) or with average field nitrogen ($r = 0.15$, $P = .516$). For all fields together, organic matter (OM) was highly correlated with total nitrogen on individual quadrats ($OM = 0.003 \cdot TN + 0.41$; $r = 0.89$, $N = 408$, $P < .001$).

Field age and average pH were not significantly correlated (pH $= -0.004 \cdot Age + 5.64$; $r = -0.32$, $N = 22$, $P = .14$). For all fields together, pH was weakly correlated with nitrogen concentration on individual quadrats (pH $= -0.0002 \cdot TN + 5.67$, $r = -0.20$, $N =$

TABLE 2. Soil type (Grigal et al. 1974) and within-field correlations between soil nitrogen concentration and pH, species richness, and percent cover of three plant groups. These correlations were calculated using individual quadrat data.

Field	Field age (yr)	Soil type†	pH	Species richness	Annual forbs	Introduced species	True prairie species
			— Correlation coefficient between soil nitrogen concentration and:				
72	56	ZmB/ZmC	NS	−0.17*	NS	NS	−0.20*
69	49	ZmB	−0.52***	−0.48***	−0.44***	−0.35***	NS
32	42	ZmB	NS	−0.24**	NS	NS	0.38***
35	42	ZmB/LnA	NS	−0.36***	NS	0.57***	−0.47***
45	40	ZmB/ZmC	−0.29**	−0.65***	−0.49***	0.45***	−0.63***
5	36	ZmB	−0.27**	−0.55***	−0.31**	0.46***	−0.35***
27	36	ZmB	NS	−0.30***	NS	NS	NS
76	31	ZmB/ZmC	−0.24*	−0.35***	−0.26**	NS	0.30**
77	31	ZmB/ZmC	−0.32**	−0.50***	−0.39***	−0.25*	0.36***
70	28	ZmB	NS	NS	−0.21*	NS	NS
21	26	ZmC	NS	0.18*	0.33***	NS	NS
22	26	ZmB/ZmC	−0.17*	NS	0.16*	0.45***	NS
26	26	ZmB	NS	0.26**	0.32***	0.32***	0.26**
47	24	NyB	−0.44***	−0.45***	−0.50***	NS	NS
44	22	ZmB	−0.27**	−0.54***	−0.47***	0.41***	−0.38***
53	22	ZmB/ZmC	0.22*	NS	NS	NS	NS
24	15	ZmB	0.41***	NS	NS	NS	−0.34***
29	15	SaB	NS	−0.28***	−0.25**	0.50***	−0.32***
4	12	ZmB	−0.37***	NS	0.31**	0.47***	NS
40	11	SaB	−0.28**	NS	NS	NS	−0.25**
39	8	SaB	0.39***	−0.36***	NS	0.66***	−0.60***
41	1	SaB	−0.43***	NS	0.44***	0.36***	NS

† ZmB: Zimmerman fine sands, 0–6% slopes; ZmC: Zimmerman fine sands, 6–15% slopes; SaB: Sartell fine sands, 0–6% slopes; NyB: Nymore sand, 6–15% Slopes; LnA: Lino fine sands, 0–4% slopes.
* $P < .05$; ** $P < .01$; *** $P < .001$; NS $P > .05$.

2144, $P < .001$). Within individual fields, however, there were significant positive and negative correlations between pH and nitrogen concentration (Table 2). The nature of the relationship between nitrogen and pH (i.e., whether it was positive or negative) did not vary systematically with field age or soil type.

Vegetation, bare ground, and litter

Cover of all vascular plants increased with both field age and soil nitrogen concentration (Table 3a, Fig. 1). Percent cover of vascular plants was more strongly correlated with nitrogen than with age. Cover of non-vascular plants was not linearly correlated with age (Table 3b, Fig. 1) but did decrease linearly with soil nitrogen alone and in a partial correlation in which age was controlled (Table 3b).

Percent bare ground decreased with field age and with soil nitrogen (Table 3c, Fig. 2), but neither age nor nitrogen concentration was significant when the other was controlled for in a partial correlation analysis (Table 3c). Cover by litter was positively correlated with soil nitrogen but not age (Table 3d, Fig. 2). The positive correlation between litter cover and soil nitrogen remained significant in a partial correlation when age was controlled for (Table 3d). On individual quadrats, litter was negatively correlated with total vegetative cover ($r = -0.45$, $N = 2300$, $P < .001$).

Biomass samples, taken in 19 fields in 1984, showed that litter, total vegetational standing crop (grasses + forbs), and grass biomass were all positively correlated with average field nitrogen concentration (Table 4). Only litter mass was significantly correlated with field age. Light penetration (L), the proportion of light above vegetation that reached ground level, was negatively correlated with standing crop (SC) ($L = -0.002 \cdot SC + 0.90$; $r = -0.76$, $N = 19$, $P < .001$).

Species richness

We tested for patterns in plant species richness at three levels. First, we examined mean quadrat species richness (SR) for each field. Second, we examined individual quadrat SR for all fields combined and for each field separately. Third, we examined total SR for each field.

Average quadrat SR per field was not significantly correlated with field age ($r = 0.32$, $P = .076$) or average field nitrogen concentration ($r = 0.29$, $P = .096$).

When the data for all quadrats in all fields were analyzed as a group, SR was negatively correlated with nitrogen ($SR = -0.004 \cdot TN + 11.5$; $r = -0.27$, $N = 2262$, $P < .001$). When these data were considered on a field-by-field basis, 15 fields had significant correlations between SR and nitrogen concentration (Table 2). Of these 15 correlations, 13 were negative and 2 were positive. There was no obvious relationship be-

TABLE 3. Correlation coefficients of field means for vegetation variables with field age and mean total soil nitrogen concentration in the 22 fields. Within-field Jaccard similarity indices are means of values calculated by comparing all pairs of quadrats within a field. $N = 22$.

	Simple correlation coefficients		Partial correlation coefficients	
	With age	With soil nitrogen	With age	With soil nitrogen
a) % cover, vascular plants	0.55** (0.008)	0.69*** (0.001)	0.18 (0.438)	0.51* (0.018)
b) % cover, nonvascular plants	−0.12 (0.587)	−0.49* (0.019)	0.32 (0.159)	−0.56** (0.009)
c) % cover, bare ground	−0.60** (0.003)	−0.65*** (0.001)	−0.30 (0.184)	−0.42 (0.060)
d) % cover, litter	0.38 (0.079)	0.64*** (0.001)	−0.07 (0.751)	0.56** (0.009)
e) Species richness (per field)	0.54** (0.005)	0.35 (0.110)	0.47* (0.032)	−0.04 (0.862)
f) Jaccard index (within fields)	−0.70*** (0.001)	−0.48** (0.011)	−0.58** (0.006)	−0.04 (0.880)

$*P < .05$; $**P < .01$; $***P < .001$; the specific P values are given in parentheses.

tween field age and the significance of the relationship between SR and nitrogen.

Field SR (the total number of species found in all quadrats in a field) was positively correlated with field age (Table 3e, Fig. 3). (This analysis included fields 22 and 29, for which $N = 150$. Similar results were obtained when those two fields were omitted.) There was no correlation between field SR and field size. With age controlled for, there was no correlation between field SR and average field nitrogen (Table 3e). With average nitrogen concentration controlled for, field SR was positively correlated with field age. Field SR was marginally correlated with range in nitrogen concentration in a field when average nitrogen was held constant ($r = 0.38$, $N = 22$, $P = .09$). Field SR was not significantly correlated with range in nitrogen concen-
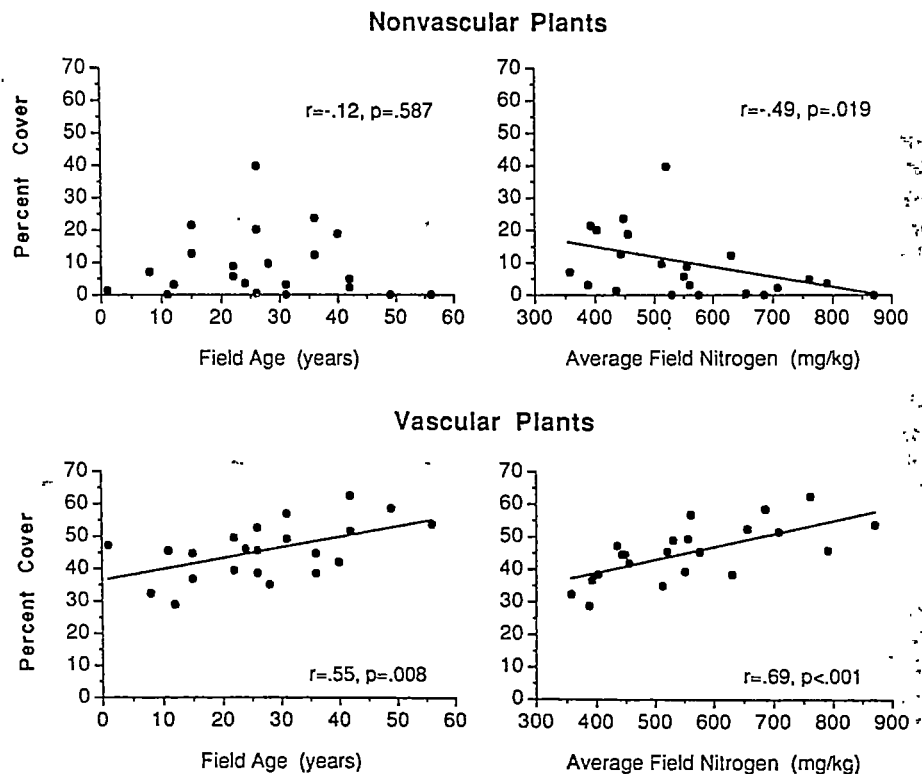

FIG. 1. Percent cover of vascular and nonvascular plants, plotted against field age and average field nitrogen. Each point represents the average cover for all quadrats in a single field. Average field nitrogen is the average nitrogen concentration of all quadrats in a single field. Lines drawn in this and similar figures represent linear regressions calculated using untransformed data for percent cover. Correlation coefficients and P values are for data transformed as described in Methods: Analyses.

441

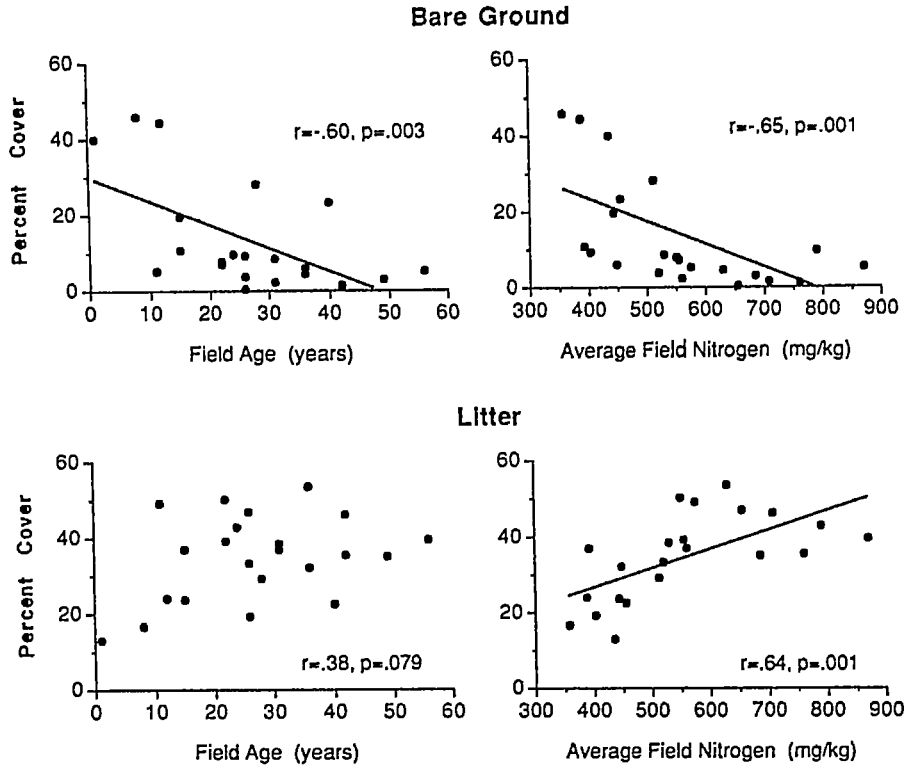## Bare Ground

Litter

Fig. 2. Percent cover of bare ground and litter, plotted against field age and average field nitrogen concentration.

tration when field age and average nitrogen were held constant ($r = 0.20$, $N = 22$, $P = .40$).

Average Jaccard index value per field was negatively correlated with field age and with average nitrogen concentration (Table 3f, Fig. 4), indicating that there was less plot-to-plot variation in species composition in younger fields than in older fields. With age controlled for, there was no correlation between average Jaccard index value and average nitrogen concentration; with average nitrogen controlled for, the average Jaccard index value was negatively correlated with age (Table 3f) and with range in field nitrogen concentration ($r = -0.46$, $P = .03$).

Jaccard indices calculated by comparing species lists for all possible pairs of fields were negatively correlated with the difference in age of the two fields (Fig. 4). This indicates that there was a significant change in species composition as fields aged. These Jaccard indices were also negatively correlated with the difference in average nitrogen concentration for the two fields ($r = -0.27$, $P < .001$).

Plant species composition between fields

Cover of annual plants decreased and cover of perennial plants increased with field age and with average field nitrogen concentration (Table 5, Fig. 5). Annual cover was negatively correlated with age when soil nitrogen was controlled. Partial correlations of perennial cover with field age and with soil nitrogen were sig-

nificantly positive. Biennial plants were much less common than annuals or perennials; cover of this group was not significantly correlated with either field age ($r = 0.16$, $P = .49$) or soil nitrogen ($r = -0.08$, $P = .73$).

Cover of grasses was positively correlated with field age and average soil nitrogen concentration, while cover of forbs was negatively correlated with field age (Table 5, Fig. 6). Within these two groups, however, life history was correlated with field age and soil nitrogen. Both annual grasses and annual forbs were negatively

TABLE 4. Correlation coefficients of average biomass with field age and average soil nitrogen concentration in 19 fields. Average soil nitrogen data are from 1983. Biomass samples were taken in 1984. $N = 19$.

Biomass	Simple correlation coefficients	
	With age	With soil nitrogen
Standing crop (grasses + forbs)	0.35 (0.069)	0.49* (0.017)
Grasses	0.35 (0.074)	0.47* (0.021)
Forbs	0.10 (0.338)	0.15 (0.266)
Litter	0.36* (0.050)	0.64*** (0.001)

* $P < .05$; ** $P < .01$; *** $P < .001$; the specific P values are given in parentheses.
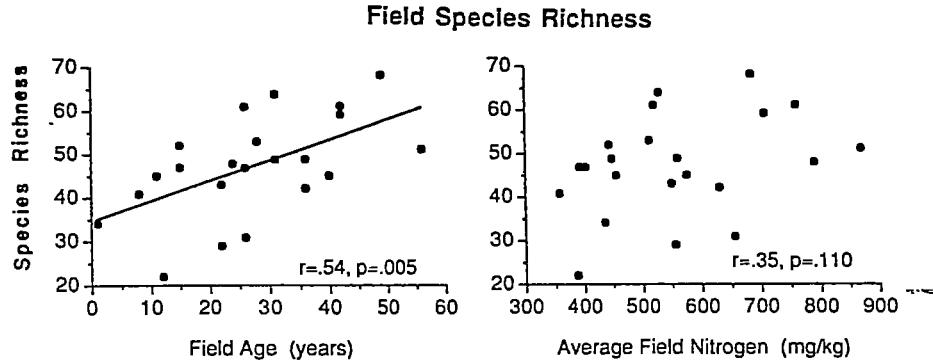
Field Species Richness

FIG. 3. Number of species found in each field, plotted against field age and average field nitrogen concentration.

correlated with field age, and annual forbs were negatively correlated with soil nitrogen. Both perennial grasses and perennial forbs were postively correlated with field age and soil nitrogen (Table 5). Partial correlations of grasses and forbs with field age. and soil nitrogen were not significant.

Sedges and woody plants were less common than grasses and forbs. Both groups increased in abundance with field age and soil nitrogen (Table 5). However, even in the oldest fields woody species contributed <15% cover (Fig. 7). Cover of woody species was positively correlated with field age when soil nitrogen concentration was controlled for.

Because soil nitrogen is a limiting nutrient in these old fields, we suspected that plant species able to fix atmospheric nitrogen might be at an advantage over species lacking that ability. Cover of legumes did not exceed 6% in any field, and cover of legumes was not significantly correlated with field age ($r = 0.21$, $P = .35$) or with soil nitrogen ($r = 0.03$, $P = .90$).

Simple correlations showed that cover of introduced species decreased with field age and with soil nitrogen, cover of native species increased with nitrogen but was not dependent on age, and cover of true prairie species increased with age and nitrogen (Table 6, Fig. 8). Partial correlation coefficients of cover of each of these three

groups with age and with nitrogen showed some distinct differences. For introduced and for true prairie species, cover was significantly correlated with field age when nitrogen was controlled for; however, for none of the three groups was cover significantly correlated with nitrogen when age was controlled for (Table 6). When these three groups were further broken down into annual and perennial grasses and forbs, the only significant correlations for subsets of introduced species were negative, and age was generally a better predictor of cover than was soil nitrogen (Table 6).

Of native species, only for annual forbs was cover significantly negatively correlated with soil nitrogen and with field age. For perennial forbs and for annual grasses, cover was significantly positively correlated with nitrogen and with age. Annual forbs was the only subset of this group that showed a significant partial correlation; cover of annual forbs was negatively correlated with age when nitrogen was controlled for.

Of true prairie species, simple correlations showed that cover of annuals (both grasses and forbs) was negatively correlated with soil nitrogen, while cover of perennials was positively correlated with nitrogen and with field age. Partial correlations gave similar results. Annual species in this group were negatively correlated with nitrogen when age was controlled for, and peren-
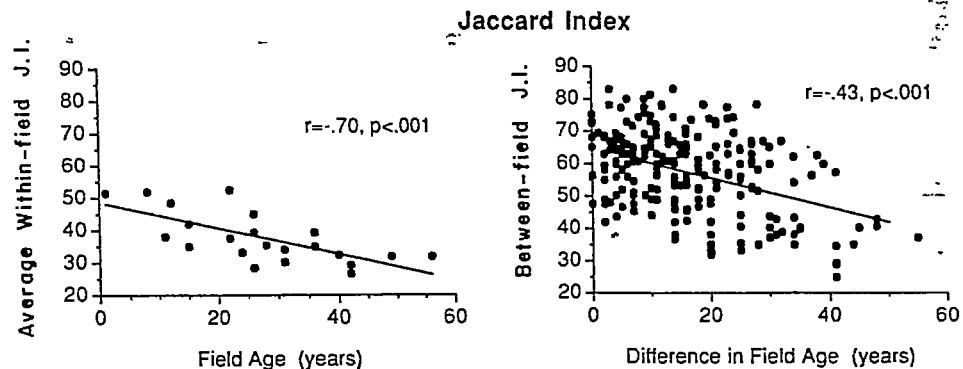
Jaccard Index

FIG. 4. (a) Average Jaccard index. plotted against field age. Average Jaccard index is the average of the indices calculated by comparing all pairs of quadrats within a given field. (b) Jaccard index, plotted against difference in field age. Here points represent indices calculated by comparing all pairs of fields; these are plotted against the difference in age of the two fields.

TABLE 5. Correlation coefficients of transformed average percent cover of various plant groups with field age and average soil nitrogen concentration in 22 fields. These groups include all vascular plants, regardless of growth form or historical origin. $N = 22$.

	Simple correlation coefficients		Partial correlation coefficients	
Mean % cover	With age	With nitrogen	With age	With nitrogen
Annuals	−0.74*** (0.001)	−0.63** (0.002)	−0.55** (0.011)	−0.28 (0.218)
Perennials	0.77*** (0.001)	0.76*** (0.001)	0.55** (0.009)	0.52* (0.015)
Grasses	0.46* (0.031)	0.47* (0.028)	0.23 (0.323)	0.24 (0.289)
Forbs	−0.37 (0.087)	−0.22 (0.317)	−0.31 (0.174)	0.04 (0.877)
Sedges	0.58** (0.005)	0.44* (0.039)	0.42 (0.058)	0.10 (0.678)
Woody plants	0.77*** (0.001)	0.57** (0.006)	0.64** (0.002)	0.12 (0.630)
Annual grasses	−0.52** (0.013)	−0.29 (0.196)	−0.46* (0.037)	0.09 (0.690)
Perennial grasses	0.53** (0.012)	0.48* (0.024)	0.31 (0.166)	0.21 (0.372)
Annual forbs	−0.74*** (0.001)	−0.68*** (0.001)	−0.52* (0.016)	−0.37 (0.099)
Perennial forbs	0.49* (0.021)	0.56** (0.007)	0.19 (0.406)	0.36 (0.115)

*$P < .05$; **$P < .01$; ***$P < .001$; the specific P values are given in parentheses.

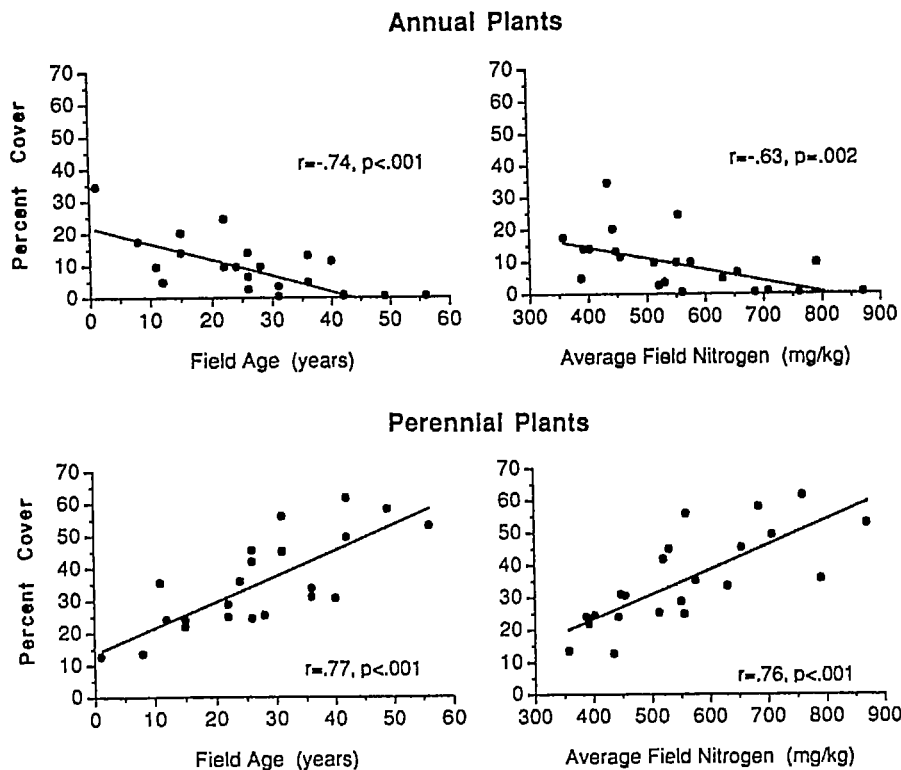
FIG. 5. Percent cover of annual plants and perennial vascular plants, plotted against field age and average field nitrogen concentration.
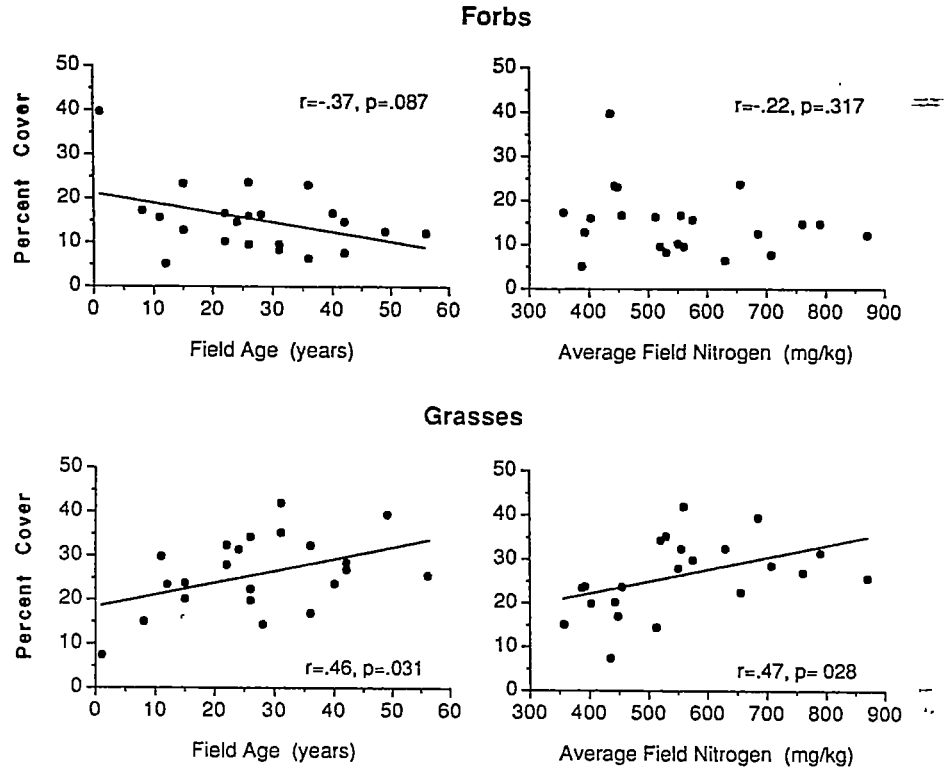
Forbs

FIG. 6. Percent cover of grasses and forbs, plotted against field age and average field nitrogen concentration.
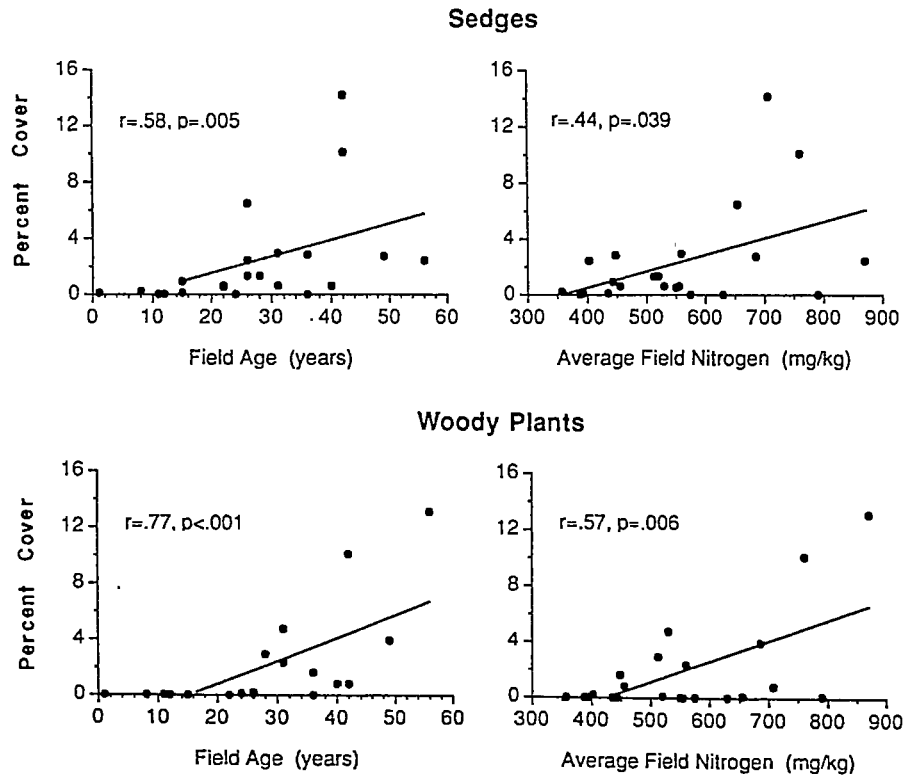

FIG. 7. Percent cover of sedges and woody plants, plotted against field age and average field nitrogen concentration.

TABLE 6. Correlation coefficients of transformed average percent cover with field age and soil nitrogen concentration for groups of different historical origin. $N = 22$.

Mean % cover	Simple correlation coefficients		Partial correlation coefficients	
	With age	With nitrogen	With age	With nitrogen
Introduced species	−0.72***	−0.56**	−0.56**	−0.16
	(0.001)	(0.006)	(0.008)	(0.490)
Annual forbs	−0.72***	−0.65***	−0.51*	−0.33
	(0.001)	(0.001)	(0.019)	(0.141)
Perennial forbs	−0.39	−0.18	−0.38	0.12
	(0.071)	(0.431)	(0.094)	(0.593)
Annual grasses	−0.44*	0.14	−0.48*	0.23
	(0.039)	(0.537)	(0.029)	(0.307)
Perennial grasses	−0.48*	0.38	−0.33	−0.09
	(0.025)	(0.082)	(0.149)	(0.690)
Native species				
Not true prairie	0.12	0.35	−0.16	0.37
	(0.599)	(0.111)	(0.478)	(0.103)
Annual forbs	−0.67***	−0.51*	−0.52*	−0.11
	(0.001)	(0.016)	(0.017)	(0.636)
Perennial forbs	0.44*	0.47*	0.19	0.26
	(0.041)	(0.028)	(0.398)	(0.255)
Annual grasses	0.45*	0.50**	0.18	0.30
	(0.024)	(0.013)	(0.375)	(0.169)
Perennial grasses	−0.06	0.24	−0.14	0.27
	(0.802)	(0.280)	(0.535)	(0.231)
True prairie	0.64**	0.39	0.55**	−0.06
	(0.002)	(0.072)	(0.011)	(0.809)
Annual forbs	−0.19	−0.55**	0.29	−0.58**
	(0.407)	(0.008)	(0.206)	(0.006)
Perennial forbs	0.66***	0.63**	0.42	0.34
	(0.001)	(0.002)	(0.060)	(0.127)
Annual grasses	−0.34	−0.64***	0.14	−0.58**
	(0.112)	(0.001)	(0.568)	(0.006)
Perennial grasses	0.50*	0.15	0.54**	−0.28
	(0.017)	(0.498)	(0.011)	(0.214)

* $P < .05$; ** $P < .01$; *** $P < .001$; the specific P values are given in parentheses.

nial species were positively correlated with age when nitrogen was controlled for.

Plant composition and nitrogen within fields

We also examined correlations between plant groups and soil nitrogen within each field. For all groups there were significant correlations in some fields and not in others. In many instances this was because particular plant groups were rare or absent in some fields. Cover of perennial vascular plants, for example, was highly positively correlated with soil nitrogen within 13 of 14 fields >25 yr old. but there were significant correlations in only 4 of 9 fields <25 yr old.

Particularly interesting are the variables for which the relationship between cover and soil nitrogen within fields was qualitatively different from that observed between fields. Annual forb cover, which was negatively correlated with nitrogen over all fields (Table 5), was significantly correlated with nitrogen in 8 of 12 fields <27 yr old. In 5 of these fields, annual forb cover was positively correlated with nitrogen. Annual forb cover was negatively correlated with nitrogen in all

fields >30 yr old for which cover and nitrogen were significantly correlated (Table 2).

In a simple regression using all fields together, percent cover of introduced species was negatively correlated with nitrogen (Table 6). In 10 of 12 fields in which there were significant correlations, however, cover of introduced species was positively correlated with soil nitrogen (Table 2). Intercepts of these regressions were increasingly negative in older fields, reflecting the decrease in absolute cover of these species with increasing field age.

True prairie species showed the reverse pattern of that for introduced species. In a simple regression using all fields together, cover of true prairie species was marginally positively correlated with nitrogen (Table 6). However, in 9 of 13 fields in which there were significant correlations, these species were negatively correlated with nitrogen (Table 2). True prairie perennial grasses were largely responsible for this pattern. This group was negatively correlated with soil nitrogen in 12 of 15 fields that had significant correlations between cover and soil nitrogen.

DISCUSSION

Soils

While soil nitrogen levels in newly abandoned fields are typically low (Rice et al. 1960), succession at Cedar Creek may be more nitrogen limited than is usual. Average nitrogen concentration values in Cedar Creek fields ranged from ≈350 to 870 mg/kg dry soil. values that are up to an order of magnitude lower than those reported for other abandoned agricultural systems (e.g., Aarssen and Turkington 1985). The rate of increase that we observed in average soil nitrogen, ≈7 $mg \cdot kg^{-1} \cdot yr^{-1}$, is quite close to measured rates of atmospheric nitrogen input, assuming atmospheric nitrogen remains in the upper 10 cm of soil.

We suspect that the low levels of nitrogen, and the resulting low productivity, are at least partly responsible for the relatively slow rate of succession at Cedar Creek. One measure of the slow rate of succession at Cedar Creek is the high abundance of annual plants in moderately old fields, such as the 10–25% cover by annuals in 22-yr-old fields. Although abandoned fields in many parts of the eastern and central United States develop a woody canopy of shrubs or trees relatively quickly (e.g., Beckwith 1954, Thompson 1954, Quarterman 1957, Levin 1966, Peet and Christensen 1980), woody plants were rare even in our oldest fields. The increased importance of true prairie species in older fields suggests that, in the absence of a woody canopy, vegetation in these fields is becoming similar to that found in tall grass prairie.

In contrast to several other studies of succession (e.g., Crocker and Major 1955, Christensen and Peet 1984), we did not find a strong correlation between soil pH and field age. Correlations between pH and soil nitrogen within individual fields were also variable, and in general pH was not as good a predictor of cover of the various plant groups as was soil nitrogen. Nitrogen, however, did change significantly with field age. and was significantly correlated with abundance of many plant groups. Total aboveground plant biomass increased significantly with total soil nitrogen in these fields, and the proportion of incident light penetrating to the soil surface decreased significantly with increased plant biomass. Thus, this chronosequence represents a gradient in resource availability as well as a gradient in time. Young fields have low soil nitrogen, low plant biomass, and high light availability, whereas older fields have high soil nitrogen, high plant biomass, and low penetration of light to the soil surface. If nitrogen and light are limiting resources in these fields, the resource ratio hypothesis of succession predicts that species should be separated along this nitrogen : light gradient in an order determined by their requirements for nitrogen and light (Tilman 1985). Tilman (1986) reported that, for nine Cedar Creek species, there was a significant rank order correlation between the order of occurrence of the species during succession and its abil-

ity to grow at low soil nitrogen levels. Early successional species grew significantly more rapidly at low nitrogen levels.

Species richness

Species composition changed significantly with field age (Fig. 4). In a comparison of all pairs of fields, the similarity between fields decreased as the difference in field age increased. This suggests that there is a continuous process of species replacement and change during secondary succession at Cedar Creek. Although average species richness per quadrat in a field was essentially independent of field age, SR was negatively correlated with soil nitrogen concentration when quadrats in all fields were analyzed as a group. This tendency for quadrats to be less species rich in areas with richer soils is consistent with conclusions of many other reports (e.g., Beadle 1966, Dix and Smeins 1967, Whittaker and Niering 1975, Huston 1979, Tilman 1982). A similar pattern was observed within individual fields. Of 15 fields with significant correlations between soil nitrogen and quadrat species richness, 13 correlations were negative. We did find weak but significant positive relationships between SR and nitrogen in two fields of intermediate age; however, no apparent characteristics of these two fields suggested why they should have a different pattern. Nitrogen fertilization in four Cedar Creek fields has shown significant ($P < .01$) decreases in species richness with increasing nitrogen availability (Tilman 1987). After 4 yr of nitrogen fertilization, >50% of the species initially present were displaced from the highest nitrogen plots, on average. Such decreases in species richness with increasing resource availability are consistent with predictions of resource competition theory (Tilman 1982).

Species richness per field increased significantly with field age. Two factors contribute to SR at the field level: SR within quadrats, which did not change with field age, and variability in species composition among quadrats. The average within-field Jaccard index value, the result of making all pairwise comparisons of quadrats within each field, decreased significantly with field age (Fig. 4), indicating that variability among quadrats was greater in older fields. The increase in field SR with field age, then, was largely due to an increase in the between-quadrat heterogeneity in older fields.

Resource-based models of community structure predict that species richness should be higher in fields with a greater range in resource availability (e.g., Tilman 1982). Our older fields, where between-quadrat similarity was lowest and total field species richness was highest, also had the highest average soil nitrogen concentration and the greatest range in soil nitrogen. There was not, however, a significant correlation between field SR and range in nitrogen when age and average nitrogen were held constant through partial correlation analysis. While simple linear regression showed total field SR to increase with nitrogen, apparently contradicting

Introduced Species

Native (NTP) Species
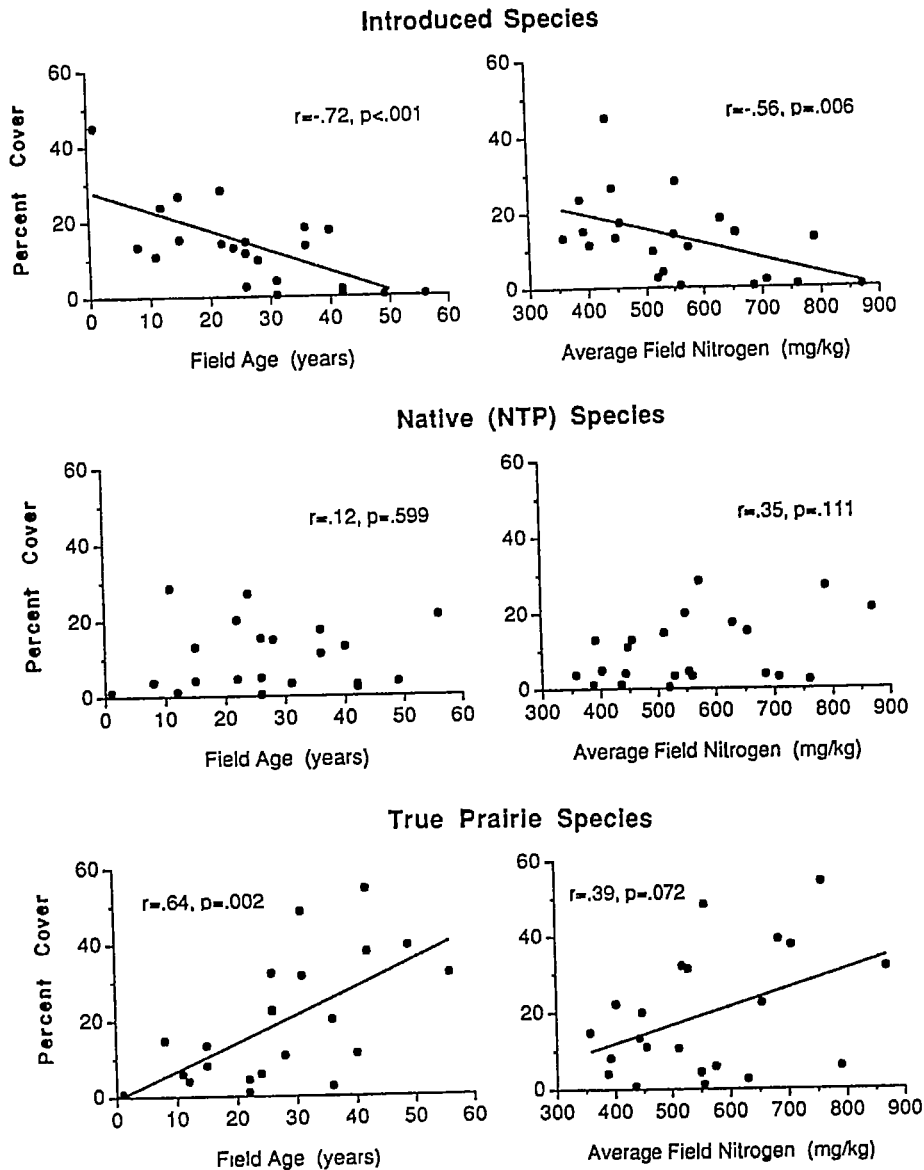

True Prairie Species

Fig. 8. Percent cover of introduced species, native species (but not true prairie species), and true prairie species, plotted against field age and average field nitrogen concentration.

the data for quadrat species richness, the correlation between total field SR and nitrogen disappeared when field age was held constant (Table 2). The monotonic increase in field species richness with succession suggests that early successional species are not often displaced from older fields, perhaps because of gopher disturbances and localized patches of nitrogen-poor, high-light soils. Even in the most nitrogen-rich field (field 72) there were patches that were almost as nitrogen poor as the average for the most nitrogen-poor field (Table 1). Interestingly, Aarssen and Turkington (1985) also reported that the same species present in their youngest field were still present in their oldest field.

We do not think that the increase in field SR with

field age can be explained by different rates of disturbance in fields of different ages (see Armesto and Pickett 1985, Loucks et al. 1985). Gophers are the most common source of disturbance in these fields, and gopher mound density decreased with field age (mounds were counted at the same time we sampled vegetation; Inouye et al. 1987). It is important to note, however, that even though the density of mounds decreased with field age, the impact of individual mounds is likely to be greater in older fields, where vegetative cover is greater and light penetration is lower.

Increases in SR have been reported during early succession in a number of studies (e.g., Lakela 1939, Nicholson and Monk 1974, Bazzaz 1975; but see Tra-

mer 1975). The range in species richess in our fields (22–68, for fields 1–49 yr old) is similar to that reported by Bazzaz (1975; 31–77, for fields 1–40 yr old). While Bazzaz attributed the high diversity in his oldest field to the addition of shrub and tree layers, our fields lack any significant shrub or tree layer. The increase in species richness in our older fields is largely due to the addition of species native to tallgrass prairie, a diverse ecosystem that lacked significant shrub or tree canopies.

It has been argued theoretically (Horn 1974) and demonstrated empirically (e.g., Shafi and Yarranton 1973 and references therein) that diversity is highest at some intermediate stage of succession. Our data do not show any trend towards decreasing species richness in the oldest fields. Indeed, species richness in fire-maintained oak savannah, the vegetation on these soils before agriculture, is even greater than that in our most species-rich old field (White 1983). Species richness does decline where oak savannah is not burned. In such areas a pronounced shrub layer develops, and a large component of the herbaceous vegetation present in burned areas is lost (White 1983). It may be, then, that given enough time, and in the of absence of fire, we would see a decline in species richness in Cedar Creek fields.

Perhaps the difference between our species richness patterns and those reported in several other studies of secondary succession are related to differences in the dynamics of plant invasion, growth, and extinction. Our study suggests that the level of soil nitrogen has a major impact on the successional sequence at Cedar Creek. Because our newly abandoned fields are, on average, very nitrogen poor, and because nitrogen levels change slowly, it is likely that many early successional species have been competitively displaced by mid-successional species before the late successional species can successfully invade the community. If that is so, the species richness we observe may more closely reflect the limits set, at equilibrium, by competition and herbivory. In contrast, secondary succession on nitrogen-rich soils is much more rapid. Late successional species often grow rapidly in such habitats following disturbance, and eventually displace both early and mid-successional species (Tilman 1985). Where nutrients are not limiting in the first stages of succession, and hence all species are able to grow initially, species richness may reflect colonization differences initially, and competitive displacement after colonization is complete.

Patterns among and within fields

For some plant groups, the relationship between cover and nitrogen changed with field age. Such changes suggest that different factors may be important in limiting these groups at different successional stages. Annual forb cover, for example, was positively correlated with soil nitrogen in younger fields and negatively correlated with soil nitrogen in older fields. Greenhouse trials (Tilman 1986) and field fertilization experiments indicate that these species are nitrogen limited at levels of soil nitrogen typical of young fields. In young fields, then, annual forbs are likely to be most abundant where soil nitrogen is greatest. However, as fields age and total vegetative cover increases, these species are more likely to be limited by light, due to shade cast by taller perennial species. Under these conditions annual forbs are most likely to be found on the higher-light, more nitrogen-poor soils and in association with other high-light areas, such as gopher mounds (Tilman 1983).

Nonvascular plants, too, may have been limited by different factors in young and old fields. Cover of this group was highest in intermediate-aged fields. In young fields, slow rates of establishment and growth may limit nonvascular plants, while in older fields, where cover of vascular plants is much higher, competition for light may be most limiting. The observations that soil nitrogen was negatively correlated with cover of nonvascular plants and positively correlated with cover of vascular plants are consistent with the suggestion that the shorter nonvascular species are restricted to poor soils by the taller vascular species (Tilman 1985).

Several groups showed quite different patterns of abundance when data for individual fields were contrasted with data for all fields combined. The most striking of these were introduced species, true prairie species, and true prairie perennial grasses.

These differences in within-field and between-field patterns are less surprising when the partial correlations between cover and soil nitrogen are compared with simple linear correlations. Cover of introduced species decreased with soil nitrogen among all fields, yet within 10 of the 12 fields for which there were significant within-field correlations, cover of this group increased with nitrogen (Table 2). Introduced species, then, showed an overall decrease in abundance with increasing field age, while they remained most common within each field on those quadrats where soil nitrogen was highest. The reverse was true for true prairie species. These species were more abundant in older fields and in fields with higher average soil nitrogen. Within 9 of the 13 fields for which there were significant within-field correlations, however, cover of these species was negatively correlated with nitrogen (Table 2).

There are two likely, non-exclusive causes of these patterns. First, most introduced species are agricultural weeds, are often annual, and tend to have greater maximal relative growth rates as seedlings than native, perennial species (see Grime and Hunt 1975, Tilman 1986). In young fields, which have not yet reached a competitive equilibrium determined by their resource availabilities, differences in maximal growth rates may be the main determinant of plant abundances (Tilman 1985). Because growth rate differences would be great-

est on the richest soils, in young fields species with greater maximal growth rates would initially dominate the richest sites. However, as these species were competitively displaced by species that were superior competitors for low-light but nitrogen-rich habitats, the introduced species would become negatively correlated with nitrogen within a field.

A second possible cause is disturbance caused by gophers. Gopher disturbance tends to decrease with the successional age of fields at Cedar Creek. Because gopher activity, within a field, is greater in more productive areas (Tilman 1983, Reichman and Smith 1985), fast-growing short-lived plants, which dominate gopher mounds, may be more common on richer soils in young fields, which have high gopher activity.

It is less clear why cover of introduced species decreased with increasing field age and soil nitrogen. Rice et al. (1960) found that an early successional species had the greatest growth rate on rich soils, a middle successional species was next, and a late successional species had the lowest growth rate on rich soils. Tilman (1986) found a similar pattern using nine Cedar Creek species. Growth rates of early species, including an introduced species, were generally higher than those of late species across the entire range of soil nitrogen concentration values tested (roughly 50–900 mg/kg). There was no indication that growth rates of these nine species leveled off at the highest nitrogen values, nor were maximum growth rates of late successional, native species higher than those of early species. Nitrogen-dependent growth rates alone, then, do not predict the replacement of early successional species by late successional species (Tilman 1986).

It is clear from our data, however, that true prairie species did increase in abundance with soil nitrogen and field age, and that introduced species showed a corresponding decline. In all likelihood a second resource axis plays an important role in determining the abundance of these species. Competition for light is likely to increase as total cover and biomass increase (Harper 1977, Tilman 1982, 1985, 1986). Light competition may be particularly important at the establishment stage. Under such conditions, perennial plants, particularly perennials that form a dense sward (e.g., many perennial grasses), can be at a distinct advantage relative to annual species that must establish from seed every year. Perennials, which can use energy stored in previous years, can rapidly overtop annual plants in the spring (Harper 1977).

Herbivory is another factor that may influence the replacement of species that are common in the younger fields (e.g., Lubchenko 1983, McBrien et al. 1983). If herbivores feed selectively on introduced weedy plants they could reduce growth rates of these species and allow less preferred species to establish and grow. Alternatively, selective feeding by herbivores in patches with richer soils may slow the rate of plant species replacement by maintaining conditions favorable for

early successional species. Gophers in particular may have this effect. We have observed increased gopher mound production on plots experimentally enriched with nitrogen in several fields (Tilman 1983). Gopher mounds provide bare ground and a high-light environment that is typically exploited by weedy introduced species.

Differences between among-field and within-field correlations of species richness or abundance of several plant groups with soil nitrogen can be interpreted as representing differences in long-term vs. short-term vegetational dynamics. Between-field patterns may represent relatively long-term successional dynamics that are more closely representative of equilibrium processes, particularly at Cedar Creek, where successional changes take place relatively slowly. Within-field patterns, especially in young fields, may be more representative of short-term dynamics of plant-plant interactions, such as differences in short-term growth rates.

Nitrogen vs. time as predictors

Neither nitrogen nor time proved to be a consistently better predictor of the variables we examined. There were, however, some general patterns that are suggestive of the ways that these two factors influence successional changes at Cedar Creek. For vascular plants, for nonvascular plants, and for litter, cover was better correlated with nitrogen than with time. This is consistent with results of fertilization experiments that showed nitrogen to be the primary limiting soil nutrient at Cedar Creek, and suggests that productivity is nitrogen limited under more natural conditions as well. Local species richness (number of species per 0.5-m^2 quadrat) was better correlated with soil nitrogen than with field age. This suggests that resource availability plays an important role in determining local species composition as well as abundance (Tilman 1982). Field species richness, however, was better correlated with field age. Time, acting through differences in dispersal and colonization rates, may thus play an important role in determining which species are present in particular fields, while resource-based interactions determine which species are found in particular places within fields. Thus, our work suggests that the pattern of secondary succession on a Minnesota sand plain results both from dispersal and other time-dependent processes and from changes in the availability of a major limiting soil resource, nitrogen.

LITERATURE CITED

Aarssen, L. W., and R. Turkington. 1985. Vegetation dynamics and neighbour associations in pasture-community evolution. Journal of Ecology 73.585–603.
Armesto, J. J., and S. T. A. Pickett. 1985. Experiments on

disturbance in old-field plant communities: impact on species richness and abundance. Ecology 66:230–240.

Bazzaz, F. A. 1975. Plant species diversity in old-field successional ecosystems in southern Illinois. Ecology 56: 485–488.

Beadle, N. C. W. 1966. Soil phosphate and its role in molding segments of the Australian flora and vegetation, with species reference to xeromorphy and sclerophylly. Ecology 47:992–1007.

Beckwith, S. L. 1954. Ecological succession on abandoned farm lands and its relationship to wildlife management. Ecological Monographs 24:349–376.

Christensen, N. L., and R. K. Peet. 1984. Convergence during secondary forest succession. Journal of Ecology 72:25–36.

Connell, J. H., and R. O. Slatyer. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. American Naturalist 111: 1119–1144.

Crocker, R. L., and J. Major. 1955. Soil development in relation to vegetation and surface age at Glacier Bay, Alaska. Journal of Ecology 43:427–448.

Curtis, J. T. 1959. The vegetation of Wisconsin. The University of Wisconsin Press, Madison, Wisconsin, USA.

Cushing, E. J. 1963. Late-Wisconsin pollen stratigraphy in east-central Minnesota. Dissertation. University of Minnesota, Minneapolis, Minnesota, USA.

Dix, R., and F. Smeins. 1967. The prairie, meadow and marsh vegetation of Nelson County, North Dakota. Canadian Journal of Botany 45:21–58.

Drury, W. H., and I. C. T. Nisbet. 1973. Succession. Journal of the Arnold Arboretum, Harvard University 54:331–368.

Egler, F. E. 1954. Vegetation science concepts 1. Initial floristic composition, a factor in old-field vegetation development. Vegetatio 4:412–417.

Gleason, H. A., and A. Cronquist. 1963. Manual of vascular plants of northeastern United States and adjacent Canada. D. Van Nostrand, Princeton, New Jersey, USA.

Goodall, D. W. 1978. Sample similarity and species correlation. Pages 99–149 in R. H. Whittaker, editor. Ordination of plant communities. Dr. W. Junk, The Hague, The Netherlands.

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. 1974. The ecology of secondary succession. Annual Review of Ecology and Systematics 5:25–37.

Huston, M. A. 1979. A general hypothesis of species diversity. American Naturalist 113:81–101.

Inouye, R. S., N. J. Huntly, D. Tilman, and J. R. Tester. 1987. Pocket gophers (Geomys bursarius), vegetation, and soil nitrogen along a successional sere in east central Minnesota. Oecologia (Berlin), in press.

Lakela, O. 1939. A floristic study of a developing plant community on Minnesota Point, Minnesota. Ecology 20: 544–552.

Levin, M. H. 1966. Early stages of secondary succession on the Coastal Plain, New Jersey. American Midland Naturalist 75:101–131.

Loucks, O. L., M. L. Plumb-Mentjes, and D. Rogers. 1985. Gap processes and large-scale disturbances in sand prairies. Pages 71–83 in S. T. A. Pickett and P. S. White, editors. The ecology of natural disturbance and patch dynamics. Academic Press, New York, New York, USA.

Lubchenko, J. 1983. Littorina and Fucus: effects of herbivores, substratum heterogeneity, and plant escapes during succession. Ecology 64:1116–1123.

McBrien, H., R. Harmsen, and A. Crowder. 1983. A case of insect grazing affecting plant succession. Ecology 64:1035–1039.

Nicholson, S. A., and C. D. Monk. 1974. Plant species diversity in old-field succession on the Georgia Piedmont. Ecology 55:1075–1085.

Nie, N. H., C. H. Hull, J. G. Jenkins, K. Steinbrenner, and D. H. Bent. 1975. SPSS: statistical package for the social sciences. McGraw-Hill, New York, New York, USA.

Peet, R. K., and N. L. Christensen. 1980. Succession: a population process. Vegetatio 43:131–140.

Pierce, R. L. 1954. Vegetation cover types and land use history of the Cedar Creek Natural History Reservation, Anoka and Isanti counties, Minnesota. Thesis. University of Minnesota, Minneapolis, Minnesota, USA.

Quarterman, E. 1957. Early plant succession on abandoned cropland in the Central Basin of Tennessee. Ecology 38: 300–309.

Reichman, O. J., and S. C. Smith. 1985. Impact of pocket gopher burrows on overlying vegetation. Journal of Mammalogy 66:720–725.

Rice, E. L., W. T. Penfound, and L. M. Rohrbaugh. 1960. Seed dispersal and mineral nutrition in succession in abandoned fields in central Oklahoma. Ecology 41:224–228.

Shafi, M. I., and G. A. Yarranton. 1973. Diversity, floristic richness, and species evenness during a secondary (postfire) succession. Ecology 54:897–902.

Thompson, J. W. 1954. Plant succession on abandoned fields in the central Wisconsin sand plain area. Bulletin of the Torrey Botanical Club 70:34–41.

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 plant succession. American Naturalist 125:827–852.

———. 1986. Nitrogen-limited growth in plants from different successional stages. Ecology 67:555–563.

———. 1987. Secondary succession and the pattern of plant dominance along experimental nitrogen gradients. Ecology, in press.

Tramer, E. J. 1975. The regulation of plant species diversity on an early successional old-field. Ecology 56:905–914.

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., and W. A. Niering. 1975. Vegetation of the Santa Catalina Mountains, Arizona. V. Biomass, production and diversity along the elevation gradient. Ecology 56:771–790.