

# Effects of nitrogen addition on successional dynamics and species diversity in Michigan old-fields

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## Summary

**1** We examined the impact of nitrogen addition on early successional dynamics and plant species diversity in replicate plots of an old-field succession treatment in south-western Michigan, USA, for 7 years following abandonment from agriculture.

**2** Nitrogen addition significantly increased above-ground plant biomass, but had no effect on the displacement or persistence of different life-history groups. Annual species made up a similar proportion of community biomass and decreased at equivalent rates in control and nitrogen-addition microplots. Perennial species biomass increased at similar rates in the control and nitrogen-addition microplots.

**3** Annual species dominated initially, but declined in abundance over the first 4 years and were replaced by biennials and then herbaceous perennials. The resulting high numbers of species losses and gains were not affected by nitrogen addition.

**4** Nitrogen addition did not affect mean species density or the Shannon index of diversity. There was also no temporal change in the similarity of species composition between control and nitrogen-addition microplots, indicating that nitrogen addition did not cause divergence over time in community composition. In year 7, similar species dominated the nitrogen-addition and control microplots, but there were differences in species composition and abundance of the subordinate species in each community.

**5** Only in year 6 of this study was there a significant negative relationship between community biomass and the Shannon diversity index. There was no significant relationship between community biomass and species density in any of the first 7 years following abandonment. Thus, the community response to increased biomass due to nitrogen addition was expressed primarily through changes in community structure, not richness.

**6** The effects of nitrogen addition on the early successional dynamics, species composition and consequently diversity of a plant community may depend on initial site conditions. The response to nitrogen enrichment may be slower in sites such as ours with fertile soils that become dominated by herbaceous perennial dicots.

*Keywords:* community structure, fertilization, long-term studies, nitrogen, old-field, plant succession, species composition, species diversity, species turnover

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## Introduction

Secondary succession is a pervasive phenomenon in terrestrial landscapes, and although the empirical patterns of succession have been described in a variety of regions, understanding the factors underlying these patterns remains a challenge to ecologists (Tilman

1988; Glenn-Lewin *et al.* 1992; Huston 1994). Although species composition changes (often predictably) over time in a successional system, how these changes are related to levels of productivity and site fertility is not well understood (Tilman 1988; Glenn-Lewin *et al.* 1992; Huston 1994). There is increased interest in understanding the factors that determine temporal patterns of diversity in natural and experimentally manipulated plant communities (Marrs 1993; Tilman 1993, 1996; Huston 1994). This knowl-

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edge may help us direct succession to dominance by native or more desirable plant communities (cf. Luken 1990; Huenneke *et al.* 1990; Hobbs & Huenneke 1992; Marrs 1993).

The rate of succession, particularly changes in the dominant species, life history or life form, is predicted to be faster and diversity lower in higher fertility sites (Huston & Smith 1987; Tilman 1988; Huston 1994). Although a number of studies have examined the impact of nutrient additions on species diversity in old-fields of different ages, few studies have followed successional dynamics in response to fertilization, and most of these are short-term (1–3 years; DiTommaso & Aarssen 1989; Luken 1990). Furthermore, the results of these experiments are varied. Some studies suggest that nutrient addition decreases or has no effect on the rate of succession. Carson & Barrett (1988) found that nutrient additions allowed annuals to persist in newly abandoned fields, and to re-establish in a 3-year old-field, and so reduced the rate of succession. Similarly, nitrogen addition allowed annuals to persist as dominants through the fifth year of succession on a semi-arid sagebrush site (McLendon & Redente 1991). Harcombe (1977) also found that fertilization reduced the rate of succession to woody species in a humid tropical forest by increasing the abundance of an herbaceous perennial. On the other hand, Bakelaar & Odum (1978) found that nutrient additions in an 8-year old-field reduced evenness of species biomass, but did not affect the species or life-history composition of the community. Melinger & McNaughton (1975) found that the response to fertilization differed among sites abandoned for different lengths of time. In a 6-year old-field, nutrient enrichment shifted dominance from an early succession species, *Phleum pratense*, to a later succession species, *Solidago altissima*. In a 17-year old-field, the nutrient addition doubled the biomass of the dominant species, *S. altissima*.

Short-term studies that examine the effect of nitrogen addition on successional old-fields of different ages cannot address the dynamic processes of changes in community composition, structure and diversity that typify successional communities (cf. Pickett 1987). Long-term, replicated experimental studies that document turnover in species and life-history composition are needed to determine how nitrogen enrichment influences successional dynamics, species composition and diversity, and to identify the factors that may control these processes. Understanding the factors that influence these dynamics is critical for identifying the mechanisms that drive succession at a particular site and for extrapolating results between sites.

The objective of our study was to examine the effects of nitrogen addition on the early successional dynamics and patterns of diversity at a site with moderately high soil fertility. The experiments were conducted as part of the Long-Term Ecological Research

(LTER) project in agricultural ecology at the W. K. Kellogg Biological Station (KBS) in south-western Michigan, USA. The replicate plots used for these studies had the same site history prior to abandonment and were dispersed over a large spatial scale (48 ha). Here we report the results of the first 7 years of an experiment examining the effects of annual nitrogen additions on successional dynamics and plant community diversity, structure and composition in undisturbed successional plots at this site. This time period includes a complete turnover in species composition and life-history types, from initial dominance by annual species to biennials and then herbaceous perennials that can persist in this area for 40–50 years (Gross & Werner 1982; Burbank *et al.* 1992).

In this paper we address the following questions. (i) Does nitrogen addition affect the persistence and rate of replacement of different life-history groups in this successional community? (ii) Does nitrogen addition influence the number of individual species lost or gained during early succession? (iii) What effects does nitrogen addition have on the patterns of diversity (species density) and community structure (Shannon diversity) during early succession in this old-field community?

## Methods

### STUDY SITE

We conducted the experiment in south-western Michigan, USA, at the LTER site in agricultural ecology at the W. K. Kellogg Biological Station (KBS, 85°22' W longitude, 42°24' N latitude) of Michigan State University. The site had been primarily under continuous corn production for more than 20 years prior to the establishment of this LTER site in 1989, except for strip-cropping of wheat and corn for 2 years in the 1970s and production of alfalfa on the western side of the site for 4 years in the 1980s. The soil, primarily Kalamazoo silt loam (Typic Hapludalf, sandy to silty clay loam), is well-drained and of moderate fertility (potential nitrogen mineralization rate =  $0.431 \mu\text{g N g soil}^{-1} \text{ day}^{-1}$ , inorganic phosphorus =  $71.1 \mu\text{g P g soil}^{-1}$ , based on extraction of 10 g soil in 100 ml 2 M KCl; Robertson *et al.* 1997). The physical and chemical soil characteristics at the KBS-LTER site are described in greater detail by Robertson *et al.* (1997). The mean annual temperature is 9 °C (30 year mean) and annual precipitation is 860 mm year<sup>-1</sup>, with about half falling as snow in the winter months. More information on the KBS-LTER is available on the home page: <http://lter.kbs.msu.edu/>.

### EXPERIMENTAL DESIGN

Our studies were conducted on the old-field succession treatment of the KBS-LTER (Treatment 7)

that was abandoned from agricultural cultivation in spring 1989 to provide a reference for the six agronomic treatments established at the site. We report the effects of nitrogen addition on successional dynamics, community biomass and plant diversity for the first 7 years following abandonment. The experimental design included all six replicates of the LTER succession treatment with two levels of nitrogen addition (zero and  $12 \text{ g N m}^{-2}$ ) established in  $5 \text{ m} \times 5 \text{ m}$  permanent microplots located at the north-west section of each 0.9-ha replicate plot. The fertilized microplot received a single pulse of  $12 \text{ g m}^{-2}$  of nitrogen as ammonium nitrate pellets ( $120 \text{ kg N ha}^{-2}$ , typical of fertilizer levels for corn production in this region) in early July of each year. The timing and level of nitrogen addition was set to correspond to that used for corn in the annual row crop treatments of the LTER. The second permanent microplot was not fertilized as a control.

The annual addition of ammonium nitrate increased potential N mineralization rates relative to the control ( $0.744 \pm 0.10$  vs.  $0.492 \pm 0.04 \mu\text{g N g soil}^{-1} \text{ day}^{-1}$ ; mean  $\pm$  SE of April, May, June, September and November 1996 measurements). Nitrate pools in the early spring (prior to that year's fertilization, April 1996) were also higher in the nitrogen-addition microplots ( $3.26 \pm 0.80$  vs.  $1.88 \pm 0.83 \mu\text{g NO}_3\text{-N g soil}^{-1}$ ) but these differences disappeared by May. Ammonium pools remained constant over the growing season and did not differ between treatments ( $3.35 \pm 0.16$  in control vs.  $3.28 \pm 0.27 \mu\text{g NH}_4\text{-N g soil}^{-1}$  in nitrogen-addition microplots; mean  $\pm$  SE of April, May, June and September 1996 measurements) except following fertilization. The addition of ammonium nitrate fertilizer had no detectable effect on soil pH ( $6.45 \pm 0.02$  in control vs.  $6.41 \pm 0.04$  in nitrogen-addition microplots in May 1996).

Plant biomass and species composition were sampled each year (1989–95) in early August from one  $1\text{-m}^2$  quadrat ( $0.5 \text{ m} \times 2.0 \text{ m}$ ) located in the central  $9\text{-m}^2$  of each microplot. The location of the harvested strip was varied each year to avoid re-clipping areas adjacent to the previous harvest. All plants rooted in the quadrat were clipped at the soil surface, separated by species, dried at  $60^\circ\text{C}$  to a constant weight, and weighed to the nearest  $0.01 \text{ g}$ . Gleason & Cronquist (1991) was used as the taxonomic authority throughout the study.

#### INDICES OF DIVERSITY AND SIMILARITY

Throughout this paper, we use the microplot as our unit of measure for comparing diversity among treatments. We refer to the mean number of species per  $1\text{-m}^2$  quadrat as species density and distinguish this from species richness, which is the cumulative number of species encountered across replicates (Magurran 1988, p. 9). We estimated species diversity using the Shannon diversity index:  $H' = -\sum p_i (\log p_i)$ , where  $p_i$

is the proportion of biomass per  $1\text{-m}^2$  quadrat accounted for by species  $i$ .

Similarity of species composition between the control and nitrogen-addition microplots was compared using both the Sorensen index, which accounts only for species presence (Magurran 1988), and the Schoener index, which accounts for both species presence and abundance (Schoener 1970). The Sorensen coefficient of similarity was calculated as  $SO = 2a / (2a + b + c)$ , where  $a$  is the number of species in common between the control and nitrogen-addition microplots,  $b$  is the number of species unique to the control microplot, and  $c$  is the number of species unique to the nitrogen-addition microplot. The Schoener similarity index is:  $SC = 100[1 - 1/2 \sum |p_{vi} - p_{vi'}|]$ , where  $p_{vi}$  is the proportion of the  $i$ th species in the control microplot and  $p_{vi'}$  is the proportion of the  $i$ th species in the nitrogen-addition microplot. We calculated these similarity indices for each pair of control and nitrogen-addition microplots within a replicate, and then calculated means for the six replicates.

#### SPECIES TURNOVER

To examine species turnover, we counted the number of species lost and gained per  $1\text{-m}^2$  sample quadrat between each year of the study. If a species was present in year  $x$  but not year  $x + 1$ , it was counted as a loss. If a species was present in year  $x + 1$  but not year  $x$ , it was counted as a gain. We expressed the number of species lost and gained as the mean over the six replicate plots. Because we sampled different areas of the treatment plot each year, some of the apparent species losses and gains could be the result of small-scale spatial variability in species composition in these plots. However, for this analysis, we assume that the scale of spatial variability (within  $9 \text{ m}^2$ ) is equivalent in control and nitrogen-addition microplots.

#### STATISTICAL ANALYSIS

We used repeated-measures analysis of variance to test for the between-subject main effect of nitrogen addition, and the within-subject main effect of year and the nitrogen  $\times$  year interaction (von Ende 1993). We analysed community biomass, species density, Shannon diversity and species gains and losses. We also examined the treatment effects on the abundance (total and proportional) of different life-history groups to test the effect of nitrogen addition on early successional dynamics in this community. A significant nitrogen  $\times$  year interaction in the repeated-measures analysis of the biomass of life-history groups indicated that the patterns of loss of annual biomass or gain of perennial biomass were non-parallel in the control and nitrogen-addition microplots (von Ende 1993), and that nitrogen addition influenced the replacement of annual biomass by perennial

biomass over time. Biomass values were log transformed prior to analysis. To evaluate how community biomass related to species density and Shannon diversity at this site, and to determine whether this relationship varied over time, we used regression analysis to examine the relationship between community biomass and the two diversity measures, species density and Shannon diversity, for each year of the study. The SAS procedure GLM (version 6) was used for all statistical analyses (SAS 1989).

## Results

### BIOMASS AND SUCCESSIONAL DYNAMICS

#### Total above-ground biomass

Across all years, addition of nitrogen increased mean above-ground plant biomass in this successional community by 59% ( $399 \pm 81 \text{ g m}^{-2}$  vs.  $633 \pm 121 \text{ g m}^{-2}$ ). The repeated-measures ANOVA showed a significant positive effect of nitrogen addition on plant community biomass (Table 1 and Fig. 1a). Community biomass also varied significantly across years (Table 1). However, the nitrogen  $\times$  year interaction was not significant, indicating a parallel response of community biomass to nitrogen addition over time.

#### Successional patterns

Annual plant species dominated the community during the first year following abandonment from agriculture (Fig. 1b,c). Both the control and nitrogen-addition microplots were dominated by annual dicots, including *Chenopodium album*, *Amaranthus retroflexus*, *Abutilon theophrasti* and *Ambrosia artemisiifolia*. The most common annual grass species

were *Setaria faberi*, *Setaria lutescens*, *Digitaria sanguinalis* and *Panicum dichotomiflorum*. *Agropyron repens*, a rhizomatous perennial grass, was abundant in one of the six replicates (Rep. 6) which had a slightly different management (4 years of alfalfa in the 1980s) prior to abandonment.

Annuals declined in biomass after the first year and were replaced by winter annuals, biennials and perennial dicots and grasses (Fig. 1d,e). The dominant species in the second year was a biennial, *Conyza canadensis*, which accounted for 65% of the above-ground biomass in the control microplots. By the third year both the control and nitrogen-addition microplots were dominated by herbaceous perennials, and dicots continued to be more abundant than grasses (Fig. 1d,e). By the fourth year the dominant perennials were *Solidago canadensis* and *Aster pilosus*, and these species persisted as dominants over the next 3 years in both the control and nitrogen-addition microplots. *Agropyron repens* was initially a dominant species in one replicate (Rep. 6), which accounted for the variability in perennial grass biomass (Fig. 1e).

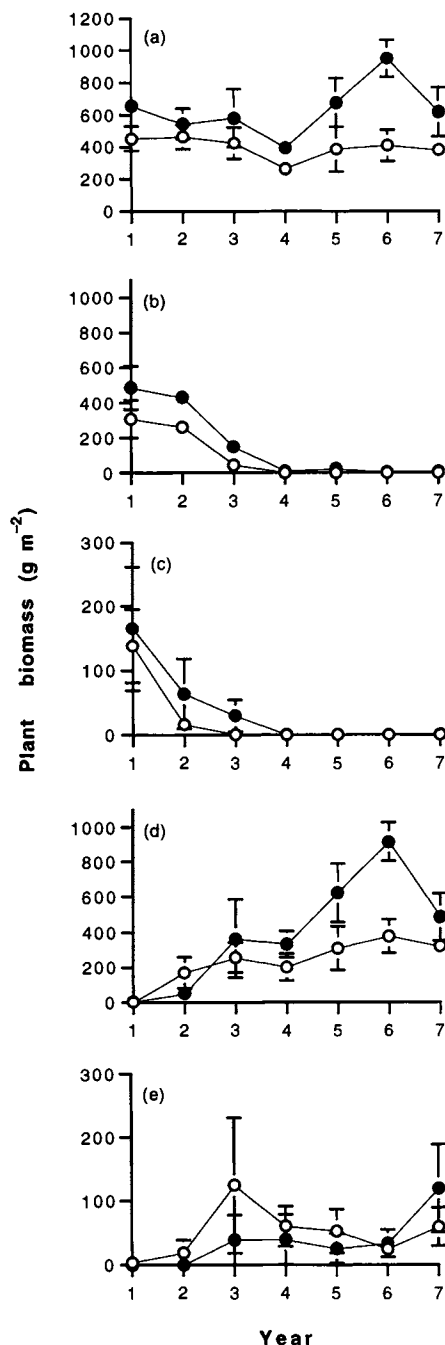
#### Response of functional groups to nitrogen addition

There was a significant positive effect of nitrogen addition on annual dicot biomass (Table 1 and Fig. 1b), but no significant effect on annual grass biomass (Table 1 and Fig. 1c). The significant year effect for both annual dicots and grasses reflects the significant decline in their biomass over the first 3 years following abandonment in both control and nitrogen-addition microplots (Table 1 and Fig. 1b,c). However, there was no significant nitrogen  $\times$  year interaction, indicating that the rates of decline in annual dicot and annual grass biomass were equi-

**Table 1** Repeated-measures analysis of variance for effect of nitrogen addition on the community biomass, biomass of life-history groups, species gains and losses, species density and the Shannon diversity index. The Type III sums of squares and significance levels of effects are shown for each variable. The analysis of biomass variables was carried out on log-transformed data. Greenhouse-Geisser adjusted probabilities were used to evaluate significance of within-subject effects (year and nitrogen  $\times$  year). Treatment means and standard errors are shown in Figs 1–3

	Between-subjects source		Within-subjects source		
	Nitrogen	Error	Year	Nitrogen $\times$ year	Error
d.f.	1	10	6	6	60
Community biomass	4.56*	7.14	3.33*	1.08	11.23
Annual dicot biomass	32.76**	17.61	375.57***	5.77	98.29
Annual grass biomass	0.65	25.85	163.45***	8.91	63.03
Perennial dicot biomass	1.01	35.09	259.76***	17.76	80.51
Perennial grass biomass	13.74	177.00	73.06**	2.56	93.86
d.f.	1	10	5	5	50
Species gains	6.13	86.69	137.24*	2.13	454.14
Species losses	5.01	43.36	96.29	23.07	342.14
d.f.	1	10	6	6	60
Species density	8.05	122.38	605.95***	33.95	552.95
Shannon diversity	0.18	3.02	6.46***	0.59	7.49

\*  $P < 0.05$ ; \*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$ .



**Fig. 1** Temporal patterns of (a) community, (b) annual dicot, (c) annual grass, (d) perennial dicot and (e) perennial grass biomass (mean  $\pm$  SE) in control (open circles) and nitrogen-addition (solid circles) microplots in the successional treatment of the KBS-LTER for years 1–7 (1989–95). Note the different scales for the dicots and grasses.

valent in control and nitrogen-addition microplots. Nitrogen addition did not cause annual dicots and grasses to persist longer or to be displaced earlier in this successional community. In addition, we found no significant nitrogen main effects or nitrogen  $\times$  year interactions in the analysis of the proportional biomass of annual dicots and grasses (data not shown).

Nitrogen addition had no statistically significant

effect on the biomass of perennial dicots or grasses (Table 1 and Fig. 1d,e). The significant year effect for perennial dicot biomass reflects the increase in abundance of perennial dicots in these microplots over the first 7 years following abandonment (Fig. 1d). There was no significant nitrogen  $\times$  year interaction, indicating that perennial dicots increased in abundance at similar rates in the control and nitrogen-addition microplots. In contrast, the biomass of perennial grasses did not vary among years, and this group typically comprised less than 20% of the total community biomass in any one year (Fig. 1e). There was no significant nitrogen  $\times$  year interaction for perennial grass biomass. Nitrogen addition neither delayed nor accelerated the appearance of perennial dicot and grass biomass in this community. In addition, we found no significant nitrogen main effects or nitrogen  $\times$  year interactions in the analysis of proportional biomass of perennial dicots and grasses.

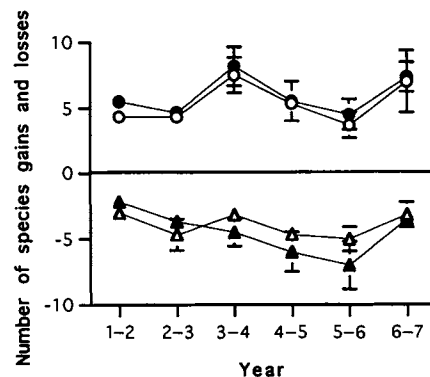
#### *Species gains and losses in response to nitrogen addition*

There was no significant effect of nitrogen addition on the number of species gained or lost annually during the first 7 years of succession (Table 1 and Fig. 2). There was, however, a significant effect of year on species gains (Table 1 and Fig. 2), with a large gain of species between years 3 and 4 (1991–92). Over the first 4 years following abandonment, species gains exceeded species losses and consequently species density increased (Fig. 3a). This corresponds to the time of transition to dominance by perennial species (and exclusion of annuals) at this site (Fig. 1b–e).

#### SPECIES DIVERSITY AND COMPOSITION

##### *Species density and Shannon diversity*

The total number of species encountered across all replicates increased from 15 species in year 1 to 39



**Fig. 2** Mean number of species gains (circles) and losses (triangles) in control (open symbols) and nitrogen-addition (solid symbols) microplots in the successional treatment of the KBS-LTER for years 1–7 (1989–95).

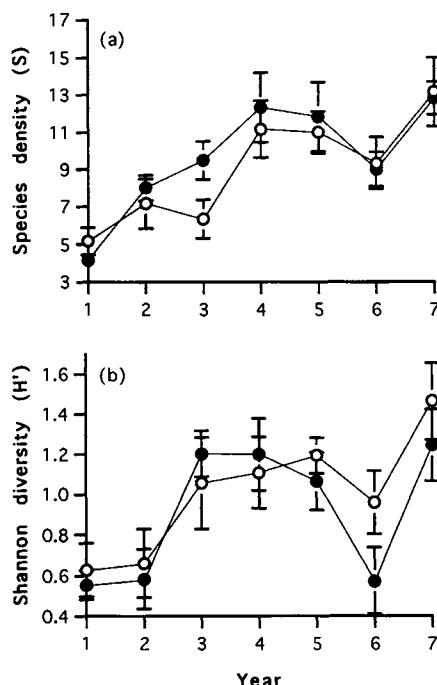


Fig. 3 Mean species density (a) and Shannon diversity (b) in control (open circles) and nitrogen-addition (solid circles) microplots in the succession treatment of the KBS-LTER for years 1–7 (1989–95).

species in year 7 in the control microplots, and from 11 species in year 1 to 36 species in year 7 in the nitrogen-addition microplots. The mean species density is lower than total species richness across the site due to spatial variation in species composition.

There was no significant effect of nitrogen addition on mean species density (number of species  $m^{-2}$ ) or the Shannon diversity index, but there was a significant effect of year on both measures (Table 1 and Fig. 3a,b). Mean species density increased from 5 in year 1 to 13 in year 7 in the control microplots, and from 4 in year 1 to 13 in year 7 in the nitrogen-addition microplots. The increase in species density over the first 4 years following abandonment coincided with the turnover in dominance by annuals and biennials to herbaceous perennial species in these microplots (Fig. 1b–e) and with the large number of species gains between years 3 and 4 (Fig. 2). There was no significant nitrogen  $\times$  year interaction that would suggest a divergence in mean species density and Shannon diversity in control and nitrogen-addition microplots over time.

#### Species composition and community similarity

We compared the similarity in species composition between control and nitrogen-addition microplots using both the Sorensen and Schoener indices to determine if nitrogen addition caused a divergence in

species composition over time (Fig. 4). Neither the Sorensen index nor the Schoener index changed significantly over time in this successional community ( $P = 0.90$  and  $P = 0.23$ , respectively), indicating no divergence in species composition between the control and nitrogen-addition microplots over the 7 years of the study.

Examination of the proportional biomass responses of individual species to nitrogen addition in year 7 (1995) indicated that there was little change in the composition of the dominant species in response to nitrogen addition (Table 2). In 1995, *Aster pilosus*, *Daucus carota*, *Solidago canadensis* and *Agropyron repens* were four of the five most abundant

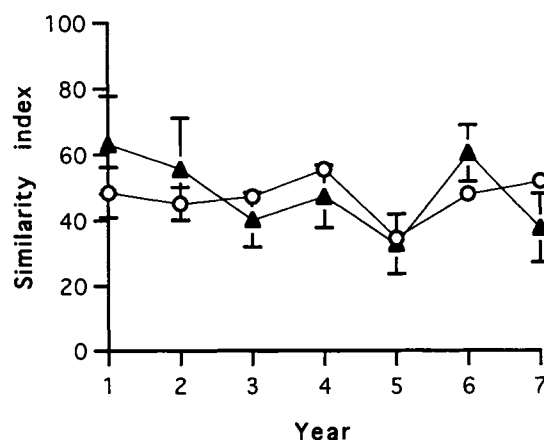


Fig. 4 Similarity in species composition between control and nitrogen-addition microplots in the succession treatment estimated by the Sorensen index (circles) and Schoener index (triangles) for years 1–7 (1989–95).

Table 2 Mean proportional abundance of species in the control and nitrogen-addition microplots in year 7 (1995). The species are ranked and grouped by their proportional abundance in the control microplots (species accounting for less than 1% of community biomass are not included). A blank indicates that the species was not present in the samples

Species	Control	Nitrogen addition
> 10%		
<i>Aster pilosus</i>	0.278	0.182
<i>Daucus carota</i>	0.166	0.063
<i>Solidago canadensis</i>	0.144	0.215
<i>Agropyron repens</i>	0.109	0.102
1–10%		
<i>Solidago graminifolia</i>	0.051	
<i>Trifolium pratense</i>	0.040	0.002
<i>Hieracium floribundum</i>	0.035	
<i>Phleum pratense</i>	0.028	
<i>Arctium minus</i>	0.023	
<i>Hypericum perforatum</i>	0.022	0.008
<i>Erigeron annuus</i>	0.018	0.005
<i>Poa pratensis</i>	0.015	0.082
<i>Trifolium repens</i>	0.012	0.001
<i>Taraxacum officinale</i>	0.011	0.003

species in both control and nitrogen-addition microplots. However, among the subordinate species (those accounting for less than 10% of community biomass) there was a number of shifts in abundance between the control and nitrogen-addition microplots (Table 2). These results suggest that the differences in species composition in the control and nitrogen-addition microplots (Fig. 4) were not due to shifts in dominant species, but rather to changes in the composition and abundance of subordinate species.

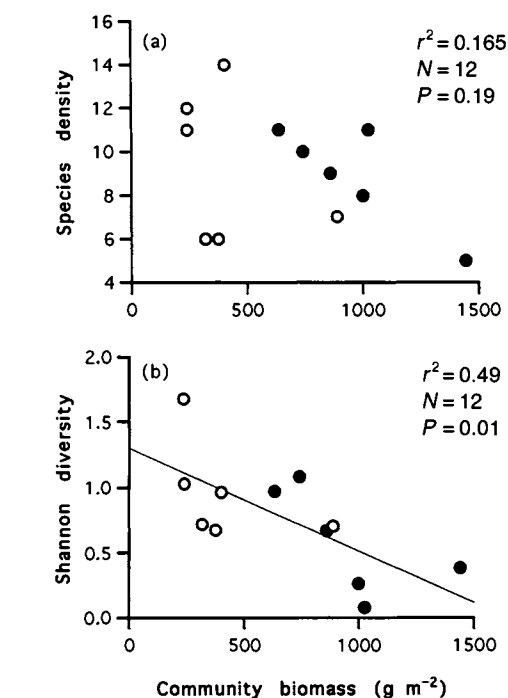
#### Community biomass and diversity

The nitrogen addition created a community biomass gradient across which we could examine the response of species density and Shannon diversity over the 7 years since abandonment. We examined the relationship between community biomass and the two measures of diversity year-by-year (to account for changes in species composition over time), and found no significant relationship between community biomass and species density in any year (Table 3; 1994 data shown in Fig. 5a). However, there was a significant negative relationship between community biomass and the Shannon diversity index in just one of the years (year 6, 1994; Table 3 and Fig. 5b).

## Discussion

### SUCCESSIONAL DYNAMICS

The successional patterns observed on the experimental plots at the KBS-LTER site over the first 7 years following abandonment from agriculture are typical of those we have observed across old-fields of



**Fig. 5** Relationship between community biomass per 1-m<sup>2</sup> quadrat and species density (a) and Shannon diversity (b) for year 6 (1994) in the succession treatment of the KBS-LTER (control = open circles; nitrogen addition = solid circles).

different ages (a chronosequence) in this area (Gross & Werner 1982; Burbank *et al.* 1992). Annuals and biennials are rapidly replaced in these communities by herbaceous perennial species that can persist for 40–50 years (Gross & Werner 1982; Huberty 1994; Foster & Gross 1997). Trees and shrubs are typically

**Table 3** Regression statistics for the relationship between total community biomass and (a) species density, (b) the Shannon diversity index across control and nitrogen-addition microplots in each year of the study ( $n = 12$  for each year)

Dependent variable	Year	Slope	$r^2$	$P$
(a) Species density				
	1	−0.00035	0.002	0.90
	2	0.0047	0.15	0.21
	3	−0.0022	0.07	0.40
	4	0.0086	0.13	0.26
	5	−0.0011	0.01	0.73
	6	−0.0030	0.16	0.19
	7	0.0015	0.02	0.69
(b) Shannon diversity				
	1	0.0005	0.14	0.24
	2	0.0005	0.09	0.34
	3	−0.0004	0.13	0.25
	4	0.0005	0.05	0.50
	5	−0.0003	0.14	0.24
	6	−0.0008	0.49	0.01
	7	−0.0009	0.32	0.06

slow to establish in successional fields at KBS, in part because of competition with established herbaceous perennials (Harrison & Werner 1984; Gross 1987).

Similar patterns of succession and rapid change in dominance by different life-history groups occur in old-fields on fertile soils in central Illinois (Bazzaz 1975) and New Jersey (Myster & Pickett 1988, 1992). In contrast, rates of succession and the transition to perennial-dominated fields, and eventually woodlands, is much slower on low-fertility soils on sand plains in Minnesota (Inouye *et al.* 1987, 1994; Tilman 1988). At that site, plant cover is low and annuals persist for up to 30 years (Inouye *et al.* 1987; Tilman 1988; Gleeson & Tilman 1990). These patterns of succession across sites are consistent with the hypothesis that the rate of succession varies with soil fertility and will be faster on higher fertility soils (Tilman 1988; Huston 1994).

If nitrogen addition within a given site influences rates of succession, then we expected to see this reflected in the rate of loss of annual species biomass and/or the rate of increase in perennial species biomass. We found no effect of nitrogen addition on the persistence of annuals (Fig. 1b,c) or the increase in biomass of perennials (Fig. 1d,e). Both nitrogen addition and control plots became dominated by perennial dicots within 4 years following abandonment. These results contrast with those of McLendon & Redente (1991; a semi-arid sagebrush site) and Carson & Barrett (1988; a mesic old-field site), who found that fertilization delayed succession from annual to herbaceous perennial communities.

In addition, if nitrogen addition had changed the rate of succession, we expected to see this reflected in the number of species lost and gained in these treatments. Although there were rapid changes in community composition over the first 4 years following abandonment at this site, nitrogen addition did not affect the average number of species lost or gained per year over the first seven years following abandonment (Fig. 2). In contrast, Tilman (1993) found that in older successional communities on a Minnesota sand plain, nitrogen addition increased loss rates of perennial species and thus led to changes in species composition and diversity over time. There was very little turnover in species composition in the control plots in his study, which may be a consequence of the experiments being conducted in older successional fields.

#### NITROGEN ENRICHMENT AND DIVERSITY

While fluctuation in diversity is expected during secondary succession, species richness and evenness are expected to decline eventually as competitive exclusion occurs. Nutrient enrichment is expected to lead to both a rapid domination by later successional species, and a rapid reduction of species diversity (Huston 1994). A large number of studies in North America

and Europe have found that the increase in production with nutrient additions is accompanied by a decrease in species richness or Shannon diversity (DiTommaso & Aarssen 1989; Tilman & Pacala 1993; Marrs 1993). Despite a significant increase in plant biomass in response to nitrogen addition, we did not see any reduction in mean species density or the Shannon diversity index over the 7 years of this study. The result may be due, in part, to the high initial fertility of these sites at the time of abandonment. Several studies in the literature have shown that nutrient additions to relatively fertile fields have little or no effect on species diversity (Mellinger & McNaughton 1975; Carson & Barrett 1988). Although low productivity old-field sites on a Minnesota sand plain typically show a reduction in diversity with nitrogen addition, there has been no long-term effect of nitrogen addition on species richness at a more productive prairie savannah site (Tilman 1993).

One explanation for the lack of a diversity response to nutrient additions in high productivity sites is that the species that colonize such sites are equivalent competitors, and so may be less responsive to a nutrient addition (Chapin *et al.* 1986; Goldberg 1987; Carson & Barrett 1988; DiTommaso & Aarssen 1989; Huston 1994). The shift from early successional annual species with high maximum growth rates and short life-spans to mid-successional perennial species with lower maximum growth rates and longer life spans may allow prolonged co-existence of competitors (Huston 1979, 1994) and a delayed response to nitrogen addition. Under such conditions it may take more time for species differences in competitive ability to be expressed following nitrogen additions to nutrient-rich sites. Instead, the differential effects of nutrient addition on species performance in higher productivity sites may be expressed initially through changes in relative abundance (and therefore biomass evenness).

The results of our study are consistent with this hypothesis. The nitrogen-addition treatments expanded the biomass gradient in this community (Fig. 5) but there was no relationship between community biomass and species density in any year of the study (Table 3). However, in year 6, we found a significant relationship between community biomass and Shannon diversity in these microplots (Table 3 and Fig. 5). This result suggests that nitrogen addition may be changing the dominance structure of these communities. If biomass evenness becomes significantly lower over time in the fertilized plots than the control plots, then species density may also be reduced as the subordinate species are excluded from the community (Huston 1994). Therefore, it will take longer at this higher fertility site to see the decrease in species richness that has been observed in lower fertility communities, such as those in Minnesota (Tilman 1993) and Rothamsted (Silvertown 1980; Johnston 1994).



OTHER FACTORS INFLUENCING THE  
RESPONSE TO NITROGEN ADDITION

There are other factors that might account for the lack of a diversity response to nitrogen addition observed in our study. First, the timing or level of nitrogen addition may have influenced the magnitude of the effect of fertilization on both biomass and diversity (Chapin *et al.* 1986; McKane *et al.* 1990; Huberty 1994) and the species composition of the communities (DiTommaso & Aarssen 1989). The annual nitrogen addition in early July may have been too late in the growing season to influence community composition or above-ground biomass in the succession plots, particularly after they became dominated by herbaceous perennials.

Secondly, the initial species composition and diversity of a community may influence the response to fertilization, and the response to fertility may differ among life forms (Silvertown 1980; DiTommaso & Aarssen 1989, Marrs 1993). In particular, perennial grasses often dominate the plant communities in old-fields and pastures where nitrogen addition reduces species richness (Inouye & Tilman 1995; Foster & Gross 1997). Old-fields that are dominated by perennial grasses – especially those that produce recalcitrant litter – may show a stronger response to nutrient enrichments than those, such as the KBS-LTER site, dominated by perennial dicots.

Thirdly, past and current management regimes, especially the annual removal of vegetation to control colonization or species performance (Vestergaard 1985; Marrs 1987; Marrs 1993), may interact with the effects of nitrogen addition on species diversity. Some plant communities in which species richness responds to experimental nutrient additions (Oomes & Mooi 1981; Bobbink 1991) are subjected to annual mowing regimes that change the dominance structure of the community.

## Conclusions

Successional plant communities provide a model system for testing a variety of ecological hypotheses regarding the controls on biodiversity that could be applied to the management and restoration of plant communities (e.g. Luken 1990; Tilman 1996). Inouye & Tilman (1995) have stressed the value of long-term studies to detect responses to resource manipulations in successional communities, as these patterns may be slow to emerge in communities dominated by perennial plant species. The results reported in this study suggest that the factors influencing diversity and successional dynamics may be operating on longer time scales than have been observed in other studies. Understanding the various mechanisms that influence the rate and pattern of succession on a given site is increasingly important as we attempt to develop better abilities to manage and maintain biologically

diverse communities in the face of anthropogenic changes in resource levels (Marrs 1993).

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