This is to certify that the

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DOMINANCE, DIVERSITY, AND RESOURCE COMPETITION
IN OLD-FIELD PLANT COMMUNITIES

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Lisa Ellen Huberty

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DOMINANCE, DIVERSITY, AND RESOURCE COMPETITION IN OLD-FIELD PLANT COMMUNITIES

By

Lisa Ellen Huberty

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ABSTRACT

DOMINANCE, DIVERSITY, AND RESOURCE COMPETITION IN OLD-FIELD PLANT COMMUNITIES

By

Lisa Ellen Huberty

I conducted species removal and resource addition experiments in a first- and second-year old-field in southwestern Michigan to test two mechanistic hypotheses about the relationship between diversity and productivity: 1) plant diversity declines with increasing fertility due to increasing competition intensity from the dominant species, and 2) the time of resource addition within a season influences the magnitude of competition intensity, and consequently the effect of a dominant species on community structure.

In the first-year annual old-field the effect of the dominant species, Chenopodium album, on subordinate community biomass, evenness, diversity, and nitrogen acquisition depended on the time of nitrogen addition. When nitrogen was added early in the growing season (early July) both the dominant species and the subordinate community increased in biomass and total nitrogen content relative to the unfertilized control. However, when nitrogen was added mid- or late-season, the dominant species pre-empted the added nitrogen and exhibited a disproportionate increase in biomass relative to the subordinate community. The subordinate plant community had increased tissue nitrogen concentrations but did not increase in biomass. The degree of canopy development appears to determine the ability of dominant and subordinate species to acquire added nutrients and allocate them to increased growth rather than storage, and thus, influences the magnitude of the effect of the dominant species on diversity and community structure.

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In the second-year old-field community the composition and abundance of species in the subordinate community varied seasonally, while Conyza canadensis was the clear biomass dominant. Biomass evenness and diversity but not richness declined with increasing C. canadensis biomass. Nitrogen addition reduced evenness and diversity but not richness, but the magnitude of this effect did not vary with the time of nitrogen addition. Rather the biomass of life-history/growth form groups and individual species varied with time of nitrogen addition. Light penetration was lower and nitrogen availability was higher in nitrogen addition plots early and mid-season, but by mid-August, resources declined to the same low level in control and nitrogen addition plots.

Finally, I present a general graphical and statistical approach to evaluate the absolute and relative response of a species biomass hierarchy to experimental treatments or environmental perturbations.

I did this for me.

ACKNOWLEDGMENTS

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INTRODUCTION

INTRODUCTION

A commonly observed pattern in nature is that at some spatial scales species diversity increases and then declines with increasing productivity (reviews by Tilman 1982, Tilman and Pacala 1993, Rosenzweig and Abramsky 1993). This pattern has been well-documented in a variety of terrestrial plant communities (reviews by Tilman 1982, Tilman and Pacala 1993, DiTommaso and Aarssen 1989), but the mechanism(s) underlying this pattern is often debated (Tilman 1993).

Numerous mechanisms have been proposed to explain the decline in plant diversity at high levels of fertility. Some authors have proposed that competition intensity increases with increasing productivity, leading to the loss of species (Grime 1973, 1979). Specifically, competition intensity for resources from one or a few dominant species may underlie the pattern of decreasing diversity with increasing fertility (Grime 1987). Newman (1973) Goldberg and Miller (1990) suggested that as productivity increases light penetration declines and shade-intolerant or slow-growing species, and seedlings experience higher mortality rates. Tilman (1982) argued that spatial heterogeneity in resources is higher in moderately productive habitats. Each of these hypotheses invokes plant competition for resources as an important mechanism leading to the decline in plant diversity with increasing productivity. This dissertation focuses on the mechanism of reduction of species diversity through increased competition intensity for resources from one or a few dominant species as fertility increases (Grime 1987).

There is a good deal of controversy in the literature about the mechanisms of plant competition for resources in productive habitats. One view, associated most frequently with Tilman (1982, 1988) but supported by others (Newman 1973, 1983, Grubb 1985, Taylor et al. 1990), argues that as soil fertility increases and above-ground plant biomass increases, light becomes relatively more limiting than soil nutrients. This leads to a trade-off in above- and below-ground resource competition and no change in the magnitude of competition intensity with increasing fertility. The opposing view, most commonly associated with Grime (1973, 1979, 1987) but also articulated by others (Huston 1979, Southwood 1988, Keddy 1989a, Bertness 1991, Campbell et al. 1991b) argues that both above- and below-ground competition intensity increase with increasing soil fertility.

Thesis organization

This thesis addresses several questions regarding the consequences of variation in the seasonal timing of nitrogen pulses for diversity, community structure, and resource competition in old-field plant communities. It is divided into five chapters. The first chapter provides an orientation to the ecological questions that motivated this work, and describes the plant communities and study sites where the research was conducted. Chapter 2 describes the effects of removing a dominant species and varying the seasonal timing of nitrogen addition on diversity, community structure, indices of competition intensity, and nitrogen uptake by the dominant species and the subordinate community in a one-year old-field. In Chapter 3, the effects of varying the seasonal timing of nitrogen addition on community structure and resource availability in a second-year old-field community are examined. The seasonal patterns of diversity and community structure in the second-year old-field community are described. The results demonstrate a link between the time of nitrogen addition and seasonal patterns of mineral nitrogen availability, nitrogen mineralization, and light depletion. Chapter 4 describes a graphical and statistical method for examining shifts in species biomass hierarchies in response to an experimental treatment. The analysis demonstrates the differences between absolute and relative responses to nitrogen additions. Chapter 5 summarizes the conclusions of the preceding chapters and discusses the implications of this research for further study of the relationship between plant diversity and productivity and mechanisms of plant competition.

Description of field sites

The first experiment was conducted in south-western Michigan at the Long Term Ecological Research (LTER) site in agricultural ecology (labeled A in Figure 1) at the W. K. Kellogg Biological Station (KBS, 85° 22' W longitude, 42° 24' N latitude). For more than 20 years prior to the establishment of this LTER site in 1989, the land had been under continuous corn (Zea mays) production, except for strip-cropping of wheat and corn for two years in the 1970's, and production of alfalfa on the western side of the site for 4 years in the 1980's. The soil is primarily Kalamazoo silt loam (Typic Hapludalf, sandy to silty clay loam), and is well-drained and of moderate fertility (Whiteside et al. 1959). One of the eight treatments in this LTER is an old-field succession treatment abandoned from agricultural cultivation in spring 1989. At the north end of each of the six replicate 0.9 hectare plots in the succession treatment is a 20 x 30 m area plowed and disced each year in late April or early May to maintain an annual plant community.

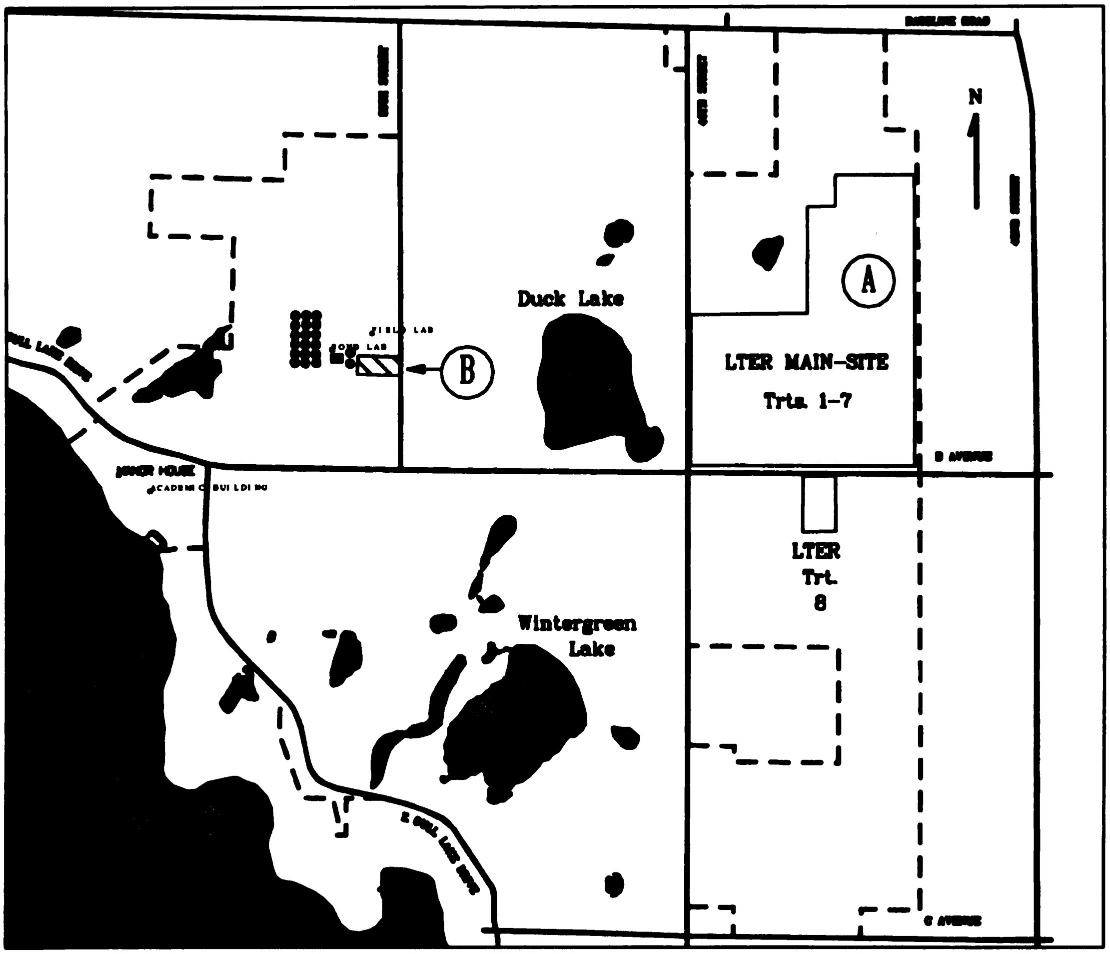


Figure 1. Locations of the annual old-field site (A) and the second-year old-field site (B) at W. K. Kellogg Biological Station, Kalamazoo County, Michigan.

The second experiment was conducted in a second-year abandoned old-field (labeled B in Figure 1) at Michigan State University's W. K. Kellogg Biological Station in southwestern Michigan (85° 23' W longitude, 42° 24' N latitude). The old-field is one in a chronosequence of 1-hectare fields planted to soybeans and abandoned in sequential years since 1989. The field in this study was planted to soybean (Glycine max (L.) Merr.) in May 1991 with no fertilizer application, and was abandoned in the fall after the soybean harvest. The soil is of the Kalamazoo series.

Description of plant communities

Plant succession following abandonment from agriculture in southwestern Michigan is characterized by an initial dominance by annual grasses and dicots in the first year and a rapid succession to mixture of biennials, perennials, winter annuals, and summer annuals in the second year (Gross and Werner 1982). Perennial species, such as Solidago species, Aster species, and Daucus carota often dominate by the third year after abandonment. Wind dispersed woody species can colonize in the first few years post-abandonment.

To address the effects of a dominant species on community structure, biomass, and nitrogen acquisition, the first experiment (described in Chapter 2) was conducted in an annual old-field plant community located in the successional treatment of the Long Term Ecological Research (LTER) site in agricultural ecology at W.K. Kellogg Biological Station (KBS). This annual plant community is maintained by annual plowing in late April or early May. The species composition is typical of agricultural fields in southwestern Michigan in the first year of abandonment. The dominant dicots included Chenopodium album, Amaranthus retroflexus, Ambrosia artemisiifolia, and

Abutilon theophrasti. The dominant monocots included *Setaria faberi*, *S. lutescens*, *S. viridis*, *Panicum dichotomiflorum*, and *P. capillare*. Winter annuals and perennials were less abundant than the summer annuals. The winter annuals included *Barbarea vulgaris*, *Oxalis stricta*, and *Stellaria media*. Perennial species, such as *Apocynum cannibinum*, *Asclepias syriaca*, *Lactuca* spp., and *Rumex* spp., are patchily distributed on the 50 hectare scale, but locally abundant on the one-hectare scale.

To address the effects of the time of nitrogen addition on community structure and resource availability, the second experiment (described in Chapter 3) was conducted in an second-year old-field. The experiment covered an area of 11 x 8 m. The vegetation was dominated by summer annuals (*Abutilon theophrasti*, *Amaranthus retroflexus*, and *Chenopodium album*) in 1992 and by *Conyza canadensis* (a winter annual or biennial) with a diverse mixture of winter annuals, biennials, perennials, and summer annuals during the summer of 1993 when the study was conducted.

CHAPTER 2

DOMINANCE, DIVERSITY, AND RESOURCE COMPETITION IN AN ANNUAL OLD-FIELD PLANT COMMUNITY

INTRODUCTION

A common pattern in herbaceous plant communities is that species diversity declines with naturally or experimentally increased fertility (Reed 1977, Bakelaar and Odum 1978, Silvertown 1980, Inouye et al. 1987, Tilman 1987, Carson and Barrett 1988, Gurevitch and Unnasch 1989, Goldberg and Miller 1990; reviews by Tilman 1982, 1988, DiTommaso and Aarssen 1989). Numerous mechanisms involving variation in local extinction and colonization probabilities have been proposed to explain these patterns (see references in Tilman 1993). The decrease in plant species diversity when soil nutrients are abundant is often correlated with the dominance of one or a few species, and the mortality or low recruitment of rare (= smaller stature) species (Willis 1963, Tilman 1987, Goldberg and Miller 1990). Plant community biomass often increases in response to increasing fertility, but individuals or species may have differential abilities to capture, store, assimilate, and allocate added nutrients to growth (Pate 1983, Campbell et al. 1991a, Grime 1994) resulting in a biomass or size-based hierarchy of competitive ability and consequent decreases in species diversity. This chapter focuses on an experimental test of the mechanism(s) of reduction of species diversity through increased competition intensity for resources from one or a few dominant species as fertility increases (Grime 1987).

There are two alternative views about the nature of plant competition in productive habitats. One view, associated most frequently with Tilman (1982, 1988) but supported by others (Newman 1973, 1983, Grubb 1985, Taylor et al. 1990), argues that as soil fertility increases and above-ground plant biomass increases, light becomes relatively more limiting than soil nutrients. This leads to a trade-off in above- and below-ground resource competition, but no change in the magnitude of competition intensity, with increasing fertility.

The opposing view, most commonly associated with Grime (1973, 1979, 1987) but also articulated by others (Huston 1979, Southwood 1988, Keddy 1989a, Bertness 1991, Campbell et al. 1991b) argues that both above- and below-ground competition intensity increase with increasing soil fertility. Recently, Grime (1994) has argued that there is a covariance between the resource demands of plant roots and shoots. In order to acquire biomass for exploring the above-ground environment for light, the shoot requires water and nutrients provided by the roots. In order for the roots to explore the soil for water and nutrients they require carbon fixed by the leaves. This interdependence of photosynthesis and nutrient capture underlies Grime's hypothesis that competition intensity for both light and nutrients increases with soil fertility.

Increasing competition intensity from the dominant plant species in fertile environments may alter two community attributes that determine species diversity as measured by the Shannon diversity index (H'): species richness and evenness. First, by having disproportionate access to resources above and/or below ground, the dominant species may acquire more added resources and allocate them to growth. The positive feedbacks between asymmetry in size, resource capture, and growth, called resource preemption (Grace 1990) or asymmetric competition (Weiner 1986, 1990, Wilson 1988), lead to low evenness of biomass distribution across species within a growing season, and thus, lower diversity as measured by H'. Second, the dominant species may reduce species richness by reducing the germination, survival, growth, and reproduction of less common species. This is one set of mechanisms thought to generate the descending portion of the hump-shaped response of species diversity to resource richness (Grime 1979, Huston 1979, Tilman 1982).

A common experimental method to determine the effect of a dominant competitor or predator on species diversity and community structure in plant and animal communities is to remove the dominant species (Connell 1961, Paine 1966, Dayton 1975, Lubchenco 1980, Armesto and Pickett 1986). Several studies in terrestrial plant communities have demonstrated that removing the dominant species can increase the diversity of the subordinate plant community (Abul-Fatih and Bazzaz 1979, Armesto and Pickett 1985, Gurevitch and Unnasch 1989, Keddy 1989b). However, such results are not universal; other studies have shown that the removal of the dominant species leads to a decrease or no change in the species diversity of the subordinate community (Pinder 1975, Allen and Forman 1976, Hils and Vankat 1982). To test the hypothesis that increasing competition intensity from the dominant species results in decreasing diversity with increasing soil fertility, the dominant species must be removed over a range of soil fertility. If the hypothesis is correct, then the removal of the dominant species should increase species richness, evenness, and/or diversity, and the magnitude of this effect should increase at higher fertility levels. I am aware of only one study where the response of the plant community to removal of a dominant plant species has been examined at two levels of soil fertility (Gurevitch and Unnasch 1989). They found that removal of the dominant perennial grass species, Dactylis glomerata, from a 24-year-old field increased richness and diversity, and the effect on richness was greater in fertilized plots than in control plots.

Plant species vary in phenology (Swieringa and Wilson 1972, Mellinger and McNaughton 1975, Reed 1977), and these differences in growth phenology can affect resource demands and resource depletion patterns. Consequently, a species' response to a resource pulse may depend on the time of resource addition relative to their development status (Mengel and Kirkby 1978, Watson

1984, Benner and Bazzaz 1985, 1988) and/or the degree to which a biomass/height hierarchy has developed among individuals or species (Benner and Bazzaz 1987). Reed (1977) showed that in an annual old-field a single large pulse of nitrogen early in the season reduced diversity more than the same total amount of nitrogen applied in smaller amounts over the growing season. However, I am aware of no studies in natural plant communities that have varied the time of a single large pulse of nitrogen during the growing season to address whether the stage of development of the biomass/height hierarchy influences the response of dominant and subordinate species to increased soil fertility.

I conducted a species-removal experiment and varied the time of nitrogen addition to address the following questions about competition intensity, community structure, and resource competition in an annual old-field plant community: (1) What is the effect of the dominant plant species on the biomass and the species richness, evenness, and diversity of the subordinate plant community? (2) How does the impact of the dominant species change when the time of a nutrient pulse is varied within a growing season? (3) What is the effect of the dominant species and the time of nitrogen addition on light penetration to the soil surface and nitrogen acquisition by the subordinate plant community?

METHODS

Study site

The experiment was conducted in south-western Michigan at the Long Term Ecological Research (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. For more than 20 years prior to the establishment of this LTER site in 1989, the land had been under continuous corn (Zea mays) production, except for strip-cropping of wheat and corn for two years in the 1970's, and production of alfalfa on the western side of the site for 4 years in the 1980's. The soil, primarily Kalamazoo silt loam (Typic Hapludalf, sandy to silty clay loam), is well-drained and of moderate fertility (Whiteside et al. 1959). The mean annual temperature is 9°C (30 year mean) and annual precipitation is 860 mm/y, with about half falling as snow in the winter months. One of the eight treatments in this LTER is an old-field succession treatment abandoned from agricultural cultivation in spring 1989. At the north end of each of the six replicate 0.9 hectare plots in the succession treatment is a 20 m x 30 m area plowed and disced each year in late April or early May to maintain an annual plant community. The most common and abundant species in this community include Chenopodium album (common lambsquarters), Amaranthus retroflexus (redroot pigweed), Abutilon theophrasti (velvet leaf), Ambrosia artemisiifolia (common ragweed), Setaria faberi (giant foxtail), S. lutescens (yellow foxtail), S. viridis (green foxtail), Panicum dichotomiflorum (fall panicum), and P. capillare (witchgrass). The field experiment described in this chapter was conducted in this annually disturbed area.

Experimental design

The experimental design included 4 blocks of the LTER succession treatment X 2 species removal levels (no removal and removal of the dominant species, Chenopodium album) X 4 times of nitrogen addition (none and 0, 2, and 4 weeks after removing C. album). Four blocks where C. album had been abundant during the previous three years were chosen for the experiment. The treatments were arranged in a complete randomized block design using 1

m^2 plots (2.0 X 0.5 m). A 1 m border with the plant community left intact separated the plots on each side. Chenopodium album was removed between July 6 and 8, 1992 (about 5 weeks after the soil had been plowed and disced) by pulling or clipping seedlings. By this time most of the germination of C. album had occurred, and the plants were a maximum of 10 cm tall. The biomass of C. album seedlings removed in July accounted for about 22 percent of the final biomass of the unfertilized plant community. The removal treatment was not repeated during the growing season. Thus, a small amount of C. album (1 to 3 percent of the total community biomass) was present in the removal treatments at the final harvest. Nitrogen was applied in a single pulse at 32 g N/m^2 as ammonium nitrate (320 kg N/ha, typical of fertilizer levels for corn production in this region) 0, 2 and 4 weeks after removing C. album. The time of nitrogen addition treatments are henceforth referred to as early- (July 9), mid- (July 24) and late-season (August 7). No nitrogen was applied to the control plots.

Measures of biomass, light penetration and nitrogen acquisition

The ability of the plants to respond to this nutrient pulse was measured as the biomass and nitrogen acquired above-ground at harvest on August 21, two weeks after the final nutrient addition. The plants were harvested by clipping the stems at the soil surface, separated by species, dried at 60°C, and weighed to ± 0.01 g.

To determine plant tissue nitrogen content, the dried plant material (including all above-ground tissue) was ground by species on a rough gauge screen using a Wiley mill and a fine gauge screen using a Cyclotec grinding mill (Tecator Model 1093). The finely ground samples were dried at 48°C for 12-24 hours before weighing duplicate samples of about 1 mg for nitrogen analysis. The duplicate samples were analyzed for total nitrogen content using a Carlo-Erba nitrogen/carbon analyzer (Model 1500 Series 2). Tissue nitrogen concentration is defined as the percent nitrogen content of the above-ground tissue. Total nitrogen content per species was calculated by multiplying the tissue nitrogen concentration of each species by its above-ground biomass. The total nitrogen content of the subordinate community is the sum per plot of the total nitrogen content of each species. Subordinate community nitrogen concentration was calculated by dividing the total nitrogen content of the subordinate community by the biomass of the subordinate community in each plot.

Light measurements were taken on August 1 between 11:00 and 13:00 using a 40-cm long integrating light probe (Sunfleck PAR ceptometer, Decagon Devices Model SF-80, Pullman, WA) to determine the effect of the dominant species and the time of nitrogen addition on light penetration to the soil surface. Photosynthetically active radiation (PAR) was measured above the plant canopy and 1 cm above the soil surface with the light probe oriented west to east along the center of the 2-m length of the plot. Light penetration is expressed as the percent of PAR above the plant canopy penetrating to 1 cm above the soil surface. One light reading per plot was taken and light penetration is expressed as the mean percent light penetration in four replicate plots. Because the light measurements were taken before the August 7 nitrogen addition, only the control, early- and mid-season nitrogen treatments are included in this analysis.

Indices of diversity and competition intensity

Species richness was calculated as the number of species per plot. The Shannon diversity index was calculated as $H' = -\sum p_i (\log p_i)$, where p_i is the proportion of biomass per plot accounted for by species i. The Pielou index of biomass evenness was calculated as $J = H' / H_{max}$, where H_{max} = log of species richness. Species richness, evenness and diversity were calculated per plot, and are expressed as the mean of four replicates. Evenness and diversity were calculated based on biomass rather than numbers of individuals because biomass has been shown to be an important predictor of competitive ability in plants (Gaudet and Keddy 1988 and references therein; review by Goldberg and Barton 1992).

Two measures of competition intensity were calculated for the control and each time of nitrogen addition. Absolute competition intensity, a measure of the reduction of subordinate community biomass by the dominant species, was calculated as $ACI = (B_r - B_c)$, where B_r = the biomass of the entire subordinate community when C. album was removed and B_c = the biomass of this assemblage of species when C. album was present in a plot. The index of absolute competition intensity may increase in response to nitrogen addition because the performance of the subordinate community increases with increasing fertility in the absence of the dominant species (increase B_r) apart from the decline in subordinate community performance in the presence of the dominant species (decreasing B_c) (Reader et al. 1994). Thus, an index of relative competition intensity was calculated as $RCI = (B_r - B_c) / B_r$. This gave a measure of the reduction of the subordinate community biomass by the dominant species relative to its biomass unimpeded by the dominant species at a given level of nutrient addition. These indices are modifications of the more typical form of the equations in which the impact of competitors (the entire surrounding community) is measured on a single target individual (Wilson and Keddy 1986, Reader and Best 1989, Wilson and Shay 1990, Wilson and Keddy 1991, Wilson and Tilman 1991a, 1993, Reader et al. 1994). However, because the objective was to test the hypothesis that competition intensity from the dominant species increases with increasing fertility, the formula for quantifying competition intensity was modified to assess the response by the subordinate community.

Statistical analysis

Analysis of variance was used to test for the main effects of removal of C. album and time of nitrogen addition on the plant biomass variables, species richness, evenness, diversity, plant tissue nitrogen concentration, and total nitrogen content. The three way interaction of block x removal x nitrogen time was used as the error term to test for the significance of the main effects and their interactions. The values of the residuals were independent of the means for the biomass and diversity variables. Thus, the analyses of variance for these variables were performed on the untransformed data. Tissue nitrogen concentrations and percent light penetration values were arcsin square root transformed prior to the analysis of variance. The ANOVA for total nitrogen content was performed on the untransformed data. A significant main effect of time of nitrogen addition in the ANOVA was further decomposed using the Dunnett's t-test to make pairwise comparisons between control and nitrogen addition at the three times of nitrogen addition. The Dunnett's t-test allowed a determination of which times of nitrogen addition had significant effects on community biomass, richness, evenness, diversity, and plant nitrogen content. Analysis of variance was used to test the effect of the time of nitrogen addition on absolute and relative competition intensity. Linear regression was used to test the relationship between total community biomass and C. album biomass and the indices of competition intensity. The SAS procedure GLM (version 6) was used for all statistical analyses (SAS 1989).

RESULTS

Biomass responses

Removal of the dominant species, C. album, significantly reduced the biomass of the whole community (Figure 2a, Table 1); the subordinate community did not increase in biomass enough to compensate for the removal of C. album within this single growing season(Figure 2a, b). Community biomass increased significantly in response to nitrogen addition both in treatments where C. album was present and removed. However, the effect of nitrogen addition on community biomass declined when the addition came later in the growing season; the positive effect of nitrogen addition on community biomass was significant by Dunnett's t-test only for the early- and mid-season nitrogen addition treatments (Table 2).

The biomass of the subordinate plant community increased significantly with nitrogen addition and the magnitude of the response depended on the time of the nitrogen addition and whether or not C. album was removed (Figure 2b, Table 1). When C. album was present, the subordinate community biomass increased in response to the early-season addition of nitrogen, but not to the mid- or late-season addition of nitrogen. When C. album was removed, the subordinate community biomass increased with both the early- and mid-season addition of nitrogen. However, the magnitude of the biomass increase in the subordinate community declined when the nitrogen addition came later in the season (Figure 2b). These results suggest that a strong dominance hierarchy develops over the season in this annual plant community and affects the ability of subordinate members of the community to respond to a nutrient pulse.

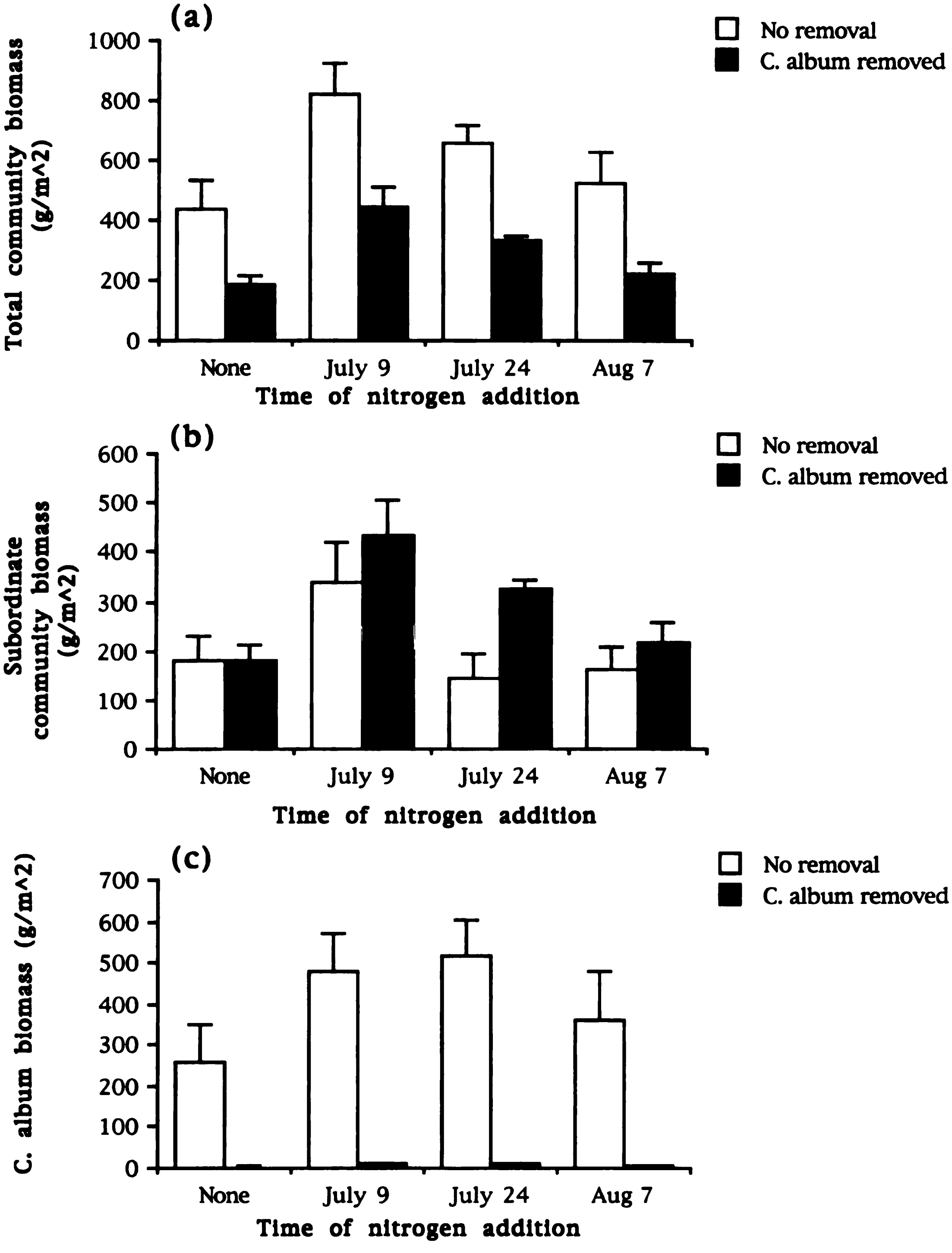


Figure 2. Effects of the removal of *Chenopodium album* and the time of nitrogen addition on a) total community biomass, b) subordinate community biomass, and c) *Chenopodium album* biomass (error bar = 1 standard error).

Table 1. Effects of species removal and time of nitrogen addition on total community biomass, subordinate community biomass, Chenopodium album biomass, species richness, biomass evenness (J), and species diversity (H') (ANOVAs). Error df for each ANOVA = 9. Treatment means are shown in Figure 2 and 5.

			Source of variation					
			Block num df ‡ = 3	Removal num df = 1	Time of N addition num df = 3	Removal x time num df = 3	Block x removal num df = 3	Block x time num df = 9
Variable	Model F	Model r^2	F	F	F	F	F	F
Total community biomass	23.64 ***	98.3	25.93 ***	234.57***	47.00 ***	1.56	17.28 ***	1.13
Subordinate community biomass	4.31 *	91.3	9.17 **	10.12 *	13.38 **	2.00	0.17	1.17
C. album biomass	11.42 ***	88.4	15.86 ***		6.97 *			
Species richness	3.44 *	89.4	15.77 ***	3.46 †	1.33	0.63	2.52	1.29
Biomass evenness	4.70 *	92.0	9.98 **	20.32 **	3.35 †	0.72	11.04 **	0.87
Biomass species diversity	6.44 **	94.0	6.50 *	36.75 ***	3.97 *	1.07	20.14 ***	1.09

† $P < 0.10$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

‡ num = numerator

Table 2. Pairwise comparisons of the effect of time of nitrogen addition on total community biomass, subordinate community biomass, *Chenopodium album* biomass, species richness, biomass evenness (J), and species diversity (H') using Dunnett's t-test (alpha = 0.05, df = 9, critical value of Dunnett's t = 2.812).

Variable	MSD †	MSE ‡	Pairwise comparison of time of nitrogen addition		
			none v. early-season	none v. mid-season	none v. late-season
Total community biomass	82.08	3408.6	320.19 ***	185.28 ***	62.72
Subordinate community biomass	103.49	5419.2	205.52 ***	53.42	9.27
C. album biomass	176.18	7852.5	222.35 ***	256.40 ***	104.54
Species richness	2.00	2.03	-0.63	0.75	-0.25
Biomass evenness	0.11	0.006	-0.07	-0.12 ***	-0.03
Species diversity	0.22	0.03	-0.19	-0.25 ***	-0.08

† MSD = minimum significant difference

‡ MSE = mean standard error

The dominant species, C. album, increased significantly in biomass in response to the early and mid-season nitrogen addition (Figure 2c, Table 2). Chenopodium album also increased in biomass in response to the late-season nitrogen addition, but this effect was not significant. In the mid- and late season nitrogen addition treatments the increase in total community biomass was accounted for entirely by the increase in C. album biomass; the subordinate community did not increase in biomass at either of these times when C. album was present (Figure 2b).

The responses of individual species in the subordinate community to the time of nitrogen addition depended on whether C. album was present in the community (Figure 3a-c) or removed (Figure 4a-c) from the community. When C. album was present, the biomass of several of the subordinate species increased in response to the early-season nitrogen addition (Figure 3a). The final biomass of Ambrosia artemisiifolia, Setaria faberi, Abutilon theophrasti, S. lutescens, and Digitaria sanguinalis doubled relative to the unfertilized control when nitrogen was added early in the season (July 9). However, when nitrogen was added mid-season (July 24), few of the subordinate species increased in biomass. In fact, several of the species that increased in biomass in the early season nitrogen addition treatment declined in biomass when nitrogen was added mid-season (Figure 3b). Likewise, few species responded strongly to the late-season nitrogen addition when C. album was present (Figure 3c).

In contrast, when C. album was removed from the community, the biomass of several species in the subordinate community increased in response to both mid- and late-season nitrogen addition (Figure 4b, c). However, no single subordinate species acquired the biomass dominance of C. album. There was some variation in which subordinate species responded most

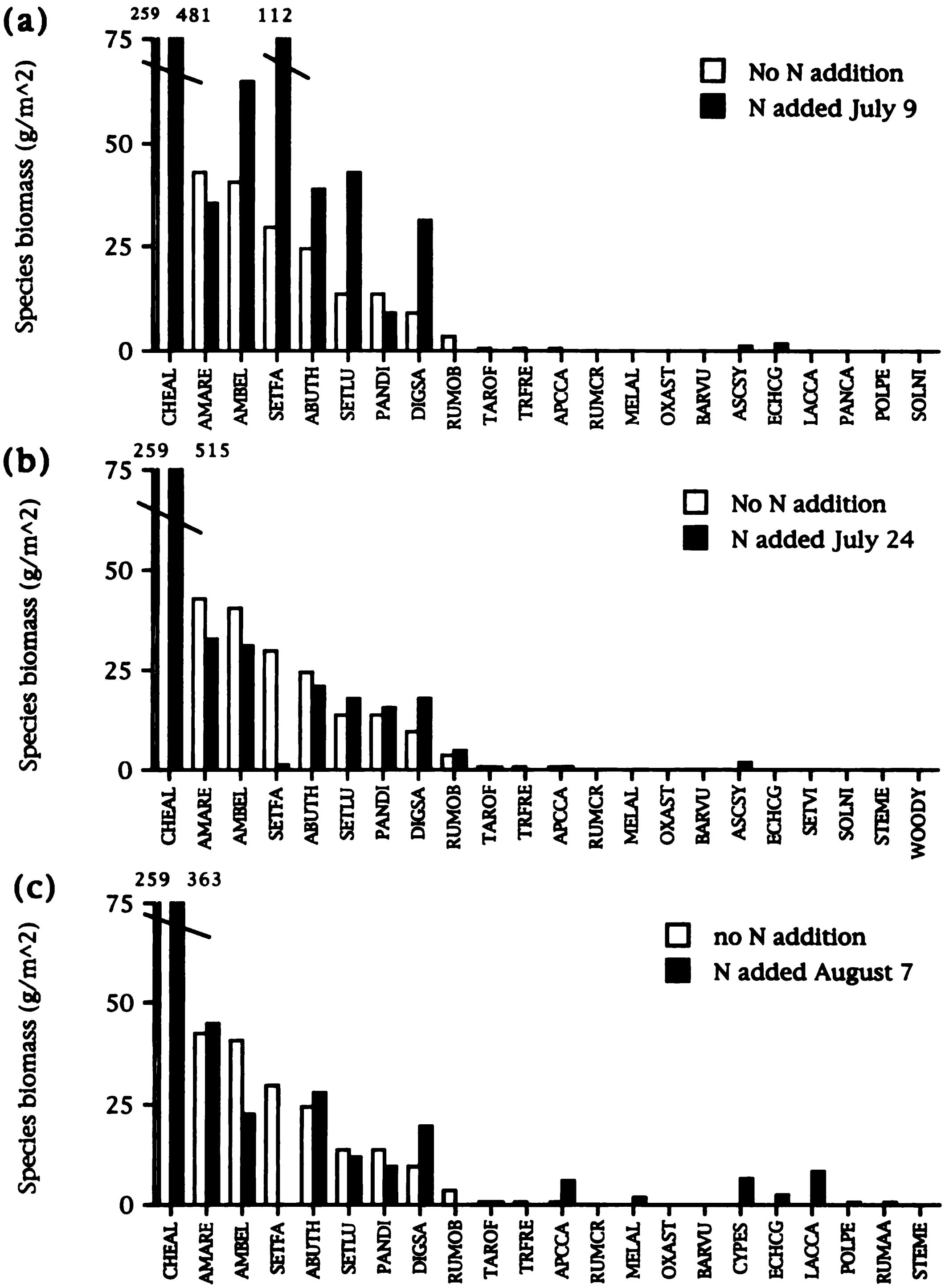


Figure 3. Species biomass responses to nitrogen addition: a) early nitrogen addition (July 9), b) mid-season nitrogen addition (July 24), and c) late season nitrogen addition (August 7) when the dominant species, Chenopodium album, was present. The corresponding species names for the five-letter Bayer codes on the x-axis are listed in Table 3.

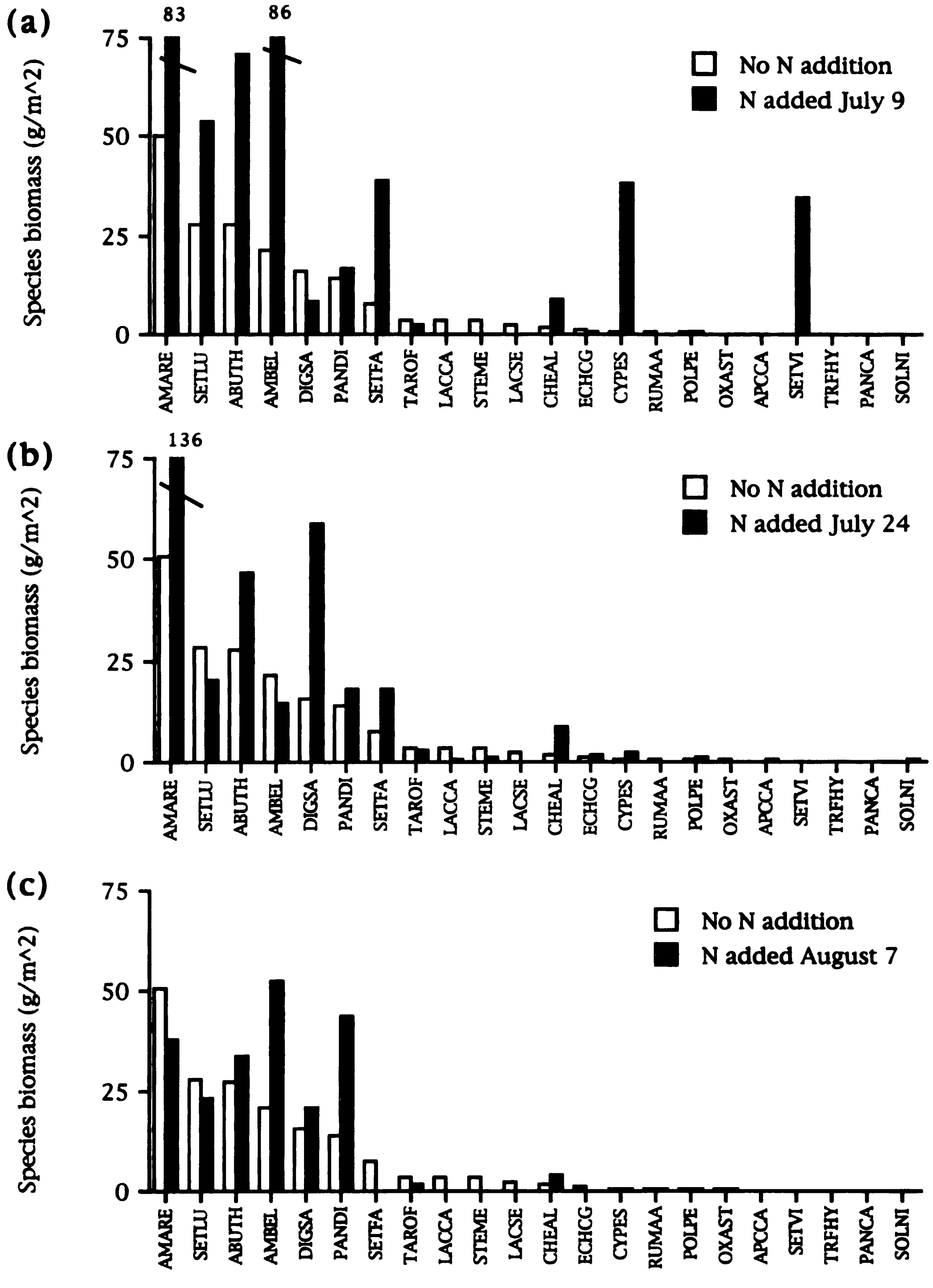


Figure 4. Species biomass responses to nitrogen addition: a) early nitrogen addition (July 9), b) mid-season nitrogen addition (July 24), and c) late season nitrogen addition (August 7) when the dominant species, Chenopodium album, was removed. The corresponding species names for the five-letter Bayer codes on the x-axis are listed in Table 3.

Table 3. Five-letter Bayer codes (WSSA 1984) for weed species and their corresponding scientific and common names.

Bayer code	**Scientific name**	**Common name**
Annual dicots		
ABUTH	Abutilon theophrasti	velvet leaf
AMARE	Amaranthus retroflexus	redroot pigweed
AMBEL	Ambrosia artemisiifolia	common ragweed
CHEAL	Chenopodium album	common lambsquarters
POLPE	Polygonum persicaria	ladysthumb
SOLNI	Solanum nigrum	common nightshade
Annual monocots		
DIGSA	Digitaria sanguinalis	large crabgrass
ECHCG	Echinocloa crus-galli	barnyard grass
PANCA	Panicum capillare	witchgrass
PANDI	Panicum dichotomiflorum	fall panicum
SETFA	Setaria faberi	giant foxtail
SETLU	Setaria lutescens	yellow foxtail
SETVI	Setaria viridis	green foxtail
Winter annuals and biennials		
BARVU	Barbarea vulgaris	yellow rocket
OXAST	Oxalis stricta	yellow woodsorrel
STEME	Stellaria media	common chickweed
Perennial dicots		
APCCA	Apocynum cannibinum	hemp dogbane
ASCSY	Asclepias syriaca	common milkweed
LACCA	Lactuca canadensis	tall lettuce
LACSE	Lactuca serriola	prickly lettuce
MELAL	Silene alba	campion
RUMAA	Rumex acetosella	red sorrel
RUMCR	Rumex crispus	curly dock
RUMOB	Rumex obtusifolius	broadleaf dock
TAROF	Taraxacum officinale	dandelion
Perennial monocots		
CYPES	Cyperus esculentus	yellow nutsedge
Perennial nitrogen-fixers		
TRFRE	Trifolium repens	white clover
TRFHY	Trifolium hybridum	hybrid clover
WOODY		unidentified woody biomass

strongly at each time of nitrogen addition (Figure 4a-c). For example, Amaranthus retroflexus, Setaria lutescens, Abutilon theophrasti, Ambrosia artemisiifolia, and S. faberi responded strongly to the early-season nitrogen addition and less to the mid- and late-season nitrogen addition treatments. Digitaria sanguinalis and Panicum dichotomiflorum responded little to the early-season nitrogen addition, but doubled in biomass when nitrogen was added mid- or late-season. In an absolute sense, the strongest responses to nitrogen addition occurred among subordinate species with the highest biomass in control plots. None of the species of low biomass in the control plots responded to nitrogen addition as strongly as did the abundant subordinate species (Figure 4a-c).

Effects on species richness, evenness, and diversity

The removal of the dominant species, C. album, resulted in a marginally significant increase in species richness (Figure 5a, Table 1). There was no significant effect of time of nitrogen addition on species richness (Table 1).

The removal of C. album in control and nitrogen addition plots resulted in a significant increase in biomass evenness across species as measured by the Pielou evenness index (Figure 5b, Table 1). The time of nitrogen addition also significantly affected evenness and this was most pronounced when C. album was present in the community (Figure 5b). Biomass evenness in treatments where C. album was present decreased most relative to the control when nitrogen was added mid-season and less when nitrogen was added early or late in the season (Table 2). Even when C. album was removed, biomass evenness declined slightly when nitrogen was added early and mid-season, suggesting that a new dominance hierarchy was being established among the

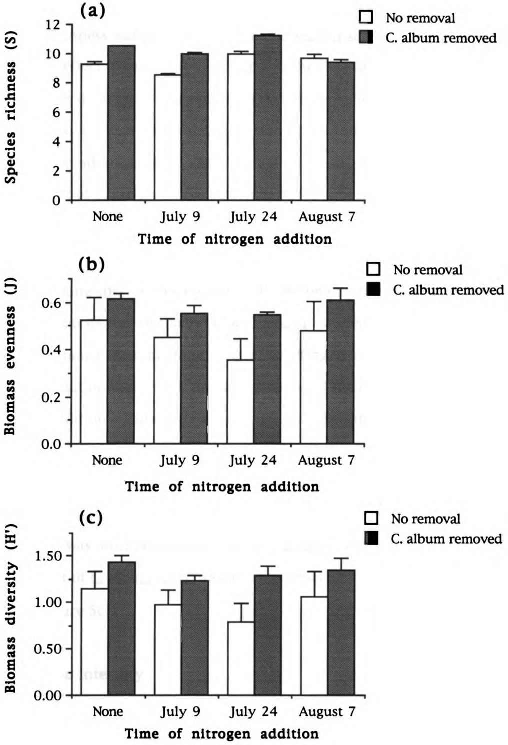


Figure 5. Diversity and community structure responses to the removal of Chenopodium album and the time of nitrogen addition: a) species richness, b) biomass evenness, and c) biomass diversity (error bar = 1 standard error).

remaining species. The magnitude of the effect of the dominant species on biomass evenness was greatest with the mid-season addition of nitrogen.

The effect of removing C. album and the time of nitrogen addition on the Shannon diversity index paralleled the effects on evenness (Figure 5c, Tables 1 and 2). Removal of C. album significantly increased H' in the control and nitrogen addition plots. This result is interesting because, it shows the strong effect of C. album on the structure of the subordinate community. When C. album was removed and no nitrogen was added, the biomass of the subordinate community did not change (Figure 2b), but the distribution of biomass among species (evenness and H') became more equitable (Figure 5b, c). This suggests that the removal of C. album resulted in a redistribution of resources among the remaining species, resulting in a change in the biomass hierarchy, but no increase in the total biomass of the community. The time of nitrogen addition significantly affected the diversity index (Table 1). Early, mid-, and late season nitrogen addition reduced H' relative to the unfertilized controls (Figure 2c); however this effect was significant only in the mid-season nitrogen addition treatment (Table 2). The decline in H' with addition of nitrogen was most pronounced when C. album was present. The magnitude of the effect of C. album on H' was greatest when nitrogen was added mid-season (Figure 5c).

Competition intensity

Absolute and relative competition intensity from the dominant species, C. album, increased when nitrogen was added (Table 4). However, there was considerable variation among replicates in both indices of competition intensity and thus the standard errors were large. Consequently, the effect of the time of nitrogen addition on absolute competition intensity (the absolute

Table 4. Effect of time of nitrogen addition on the absolute and relative competition intensity indices (± standard error, see Methods for calculation of absolute and relative competition intensity).

Time of nitrogen addition	Absolute competition intensity	Relative competition intensity
None	2.6 ± 36	0.01 ± 0.19
July 9	94.4 ± 70	0.21 ± 0.18
July 24	177.8 ± 39	0.57 ± 0.14
August 7	56.4 ± 28	0.27 ± 0.16

reduction of subordinate community biomass by C. album) was only marginally significant ($F_{3,12}$ = 2.53, p = 0.11, r^2 = 0.39). The effect of time of nitrogen addition on relative competition intensity was not statistically significant ($F_{3,12}$ = 1.80, p = 0.20, r^2 = 0.31). Both indices of competition intensity were greatest when nitrogen was added mid-season, consistent with the result that biomass evenness and diversity in the presence of the dominant species declined most when nitrogen was added mid-season.

Both the absolute and relative indices of competition intensity increased significantly as the biomass of the dominant species, C. album, increased (Figure 6a, b, absolute index, $F_{1,14}$ = 4.25, p = 0.06, r^2 = 0.23; relative index, $F_{1,14}$ = 7.11, p = 0.02, r^2 = 0.34). However, there was not a significant relationship between the total biomass of the plant community and either the absolute or relative index of competition intensity (Figure 7a, b, absolute index, $F_{1,14}$ = 0.48, p = 0.50, r^2 = 0.03; relative index, $F_{1,14}$ = 0.40, p = 0.54, r^2 = 0.03). This may be due to the single anomalous point in the lower right corner of the plots.

Light availability

Light penetration to the soil surface on August 1 was significantly higher in plots where the dominant species, C. album, was removed than in plots where it was not removed (Figure 8, Table 5). Nitrogen addition reduced light penetration in both the removal and no removal treatments (Figure 8, Table 6). Light penetration on August 1 was lower in the early season nitrogen addition treatment than in the mid-season nitrogen addition treatment, suggesting that delaying nitrogen addition within a season affected light depletion by the plant community. The relative magnitude of the effect of the dominant species on light availability increased with nitrogen addition (Figure 8). Chenopodium album reduced light penetration by 38 percent in

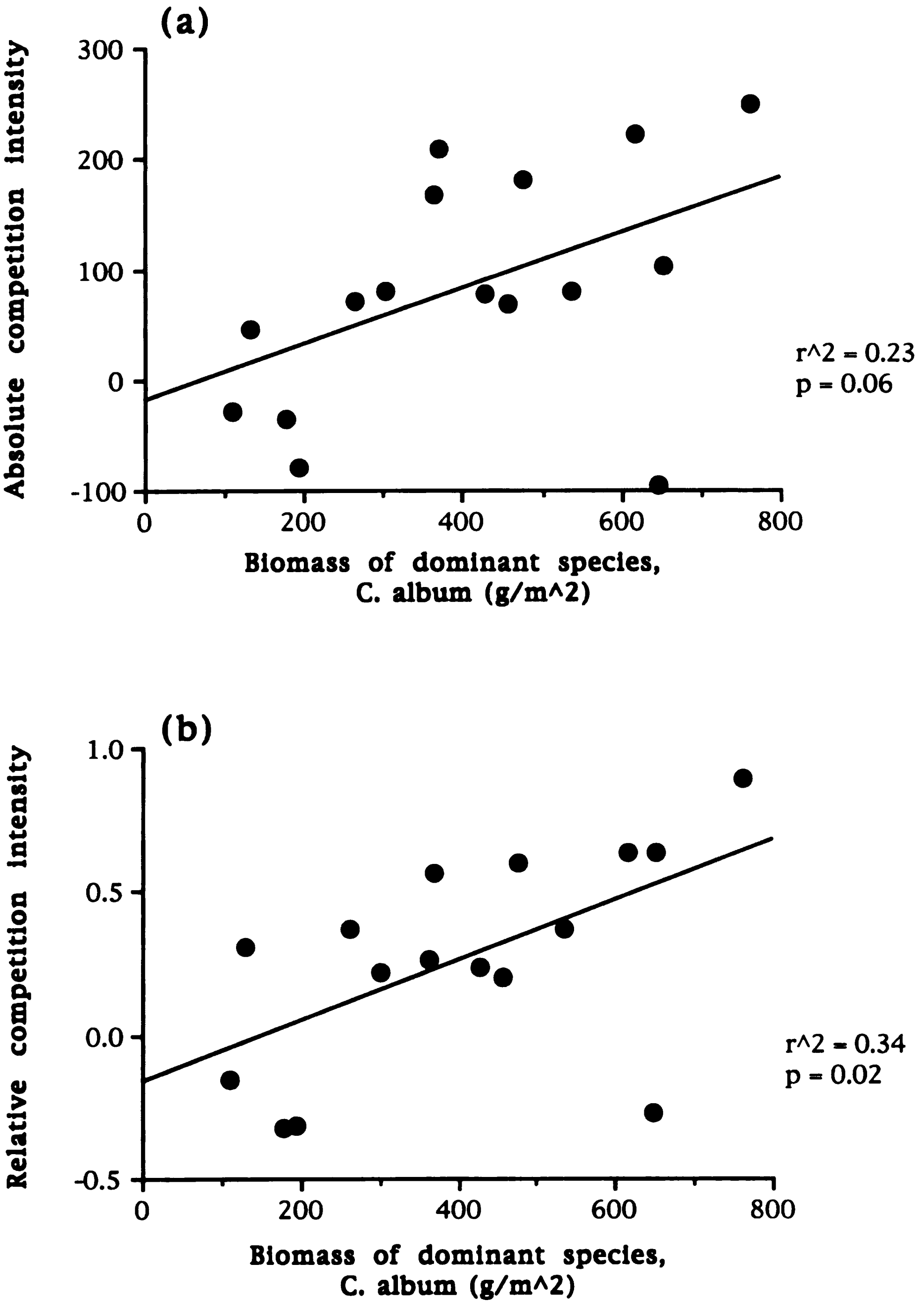


Figure 6. Relationship between the biomass of the dominant species, Chenopodium album, and a) absolute competition intensity and b) relative competition intensity.

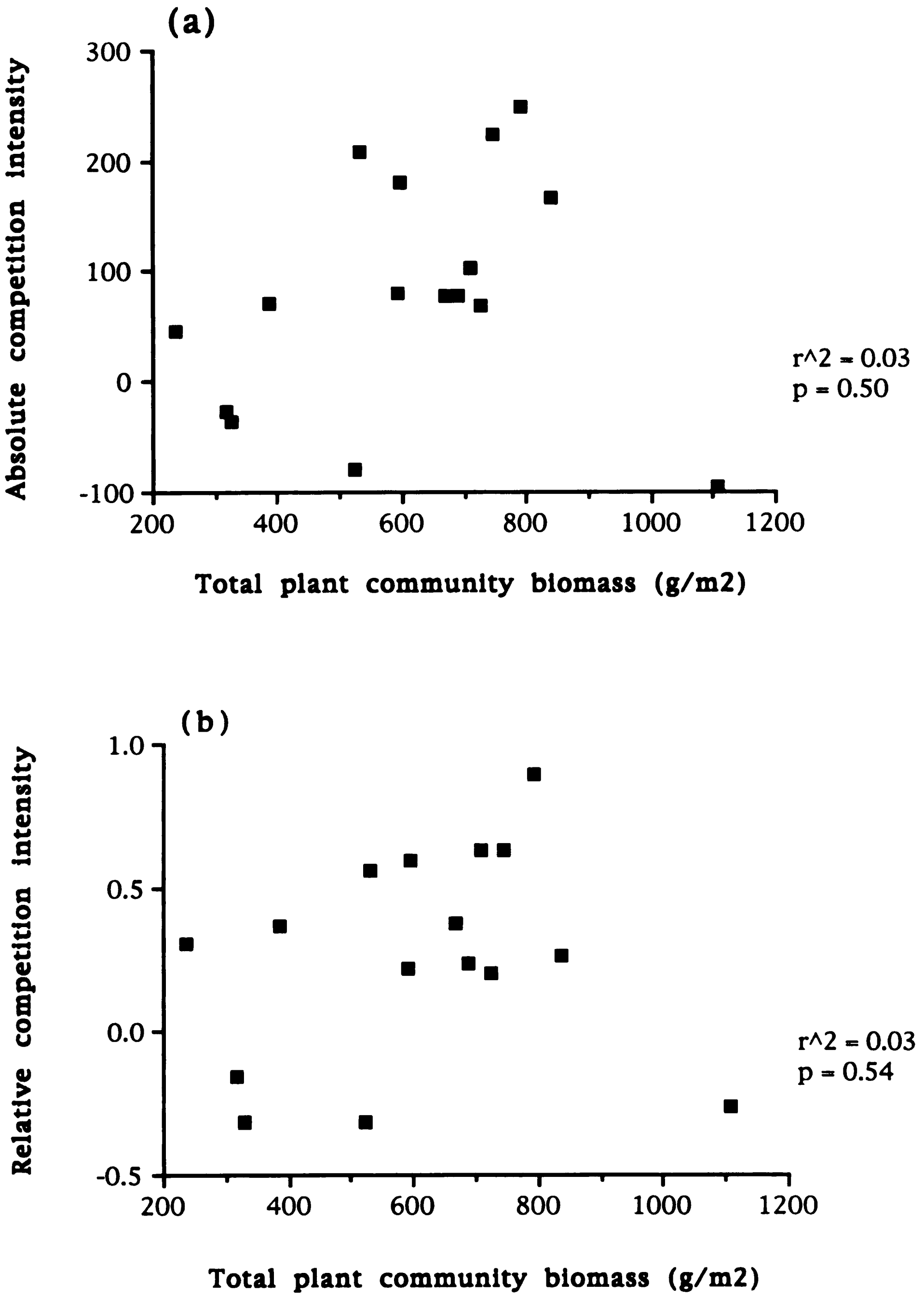


Figure 7. Relationship between total plant community biomass and a) absolute competition intensity and b) relative competition intensity.

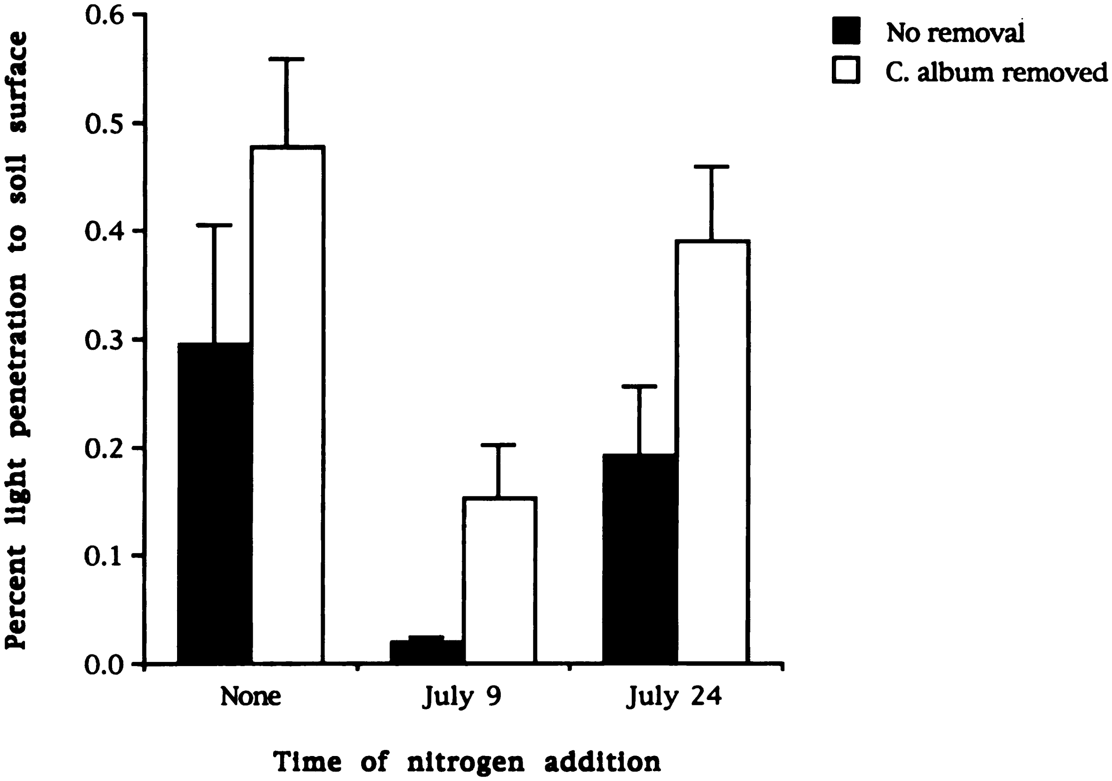


Figure 8. Effect of the removal of the dominant species and time of nitrogen addition on percent light penetration to the soil surface measured August 1.

Table 5. Results of analysis of variance for effects of species removal and time of nitrogen addition on light penetration, tissue nitrogen concentration and total nitrogen content of the dominant species, *Chenopodium album*, and the subordinate community. Error df for each ANOVA = 9. Treatment means are shown in Figures 8, 9, and 10.

			Source of variation					
			Block num df ‡ = 3	Removal num df = 1	Time of N addition num df = 3	Removal x time num df = 3	Block x removal num df = 3	Block x time num df = 9
Variable	model F	model r^2	F	F	F	F	F	F
Light penetration (num df for time = 2)	29.61 ***	0.99	35.56 ***	110.70 ***	112.17 ***	0.25	6.62 *	6.88 *
Tissue nitrogen concentration								
Dominant species, *Chenopodium album*	10.34 **	0.96	2.68	41.31 ***	47.45 ***	0.82	0.29	2.98 †
Subordinate community	13.80 ***	0.97	5.13 *	34.49 ***	71.71 ***	1.86	7.18 **	1.27
Total nitrogen content								
Dominant species, *Chenopodium album*	16.57 ***	0.98	8.67 **	211.16 ***	7.86 **	7.41 *	7.71 **	1.01
Subordinate community	6.15 **	0.94	11.29 **	39.41 ***	11.99 **	4.50 *	1.25	0.97

† $P < 0.10$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

‡ num = numerator

Table 6. Pairwise comparisons of the effect of time of nitrogen addition on light penetration, tissue nitrogen concentration and total nitrogen content using Dunnett's t-test (alpha = 0.05, df = 9, critical value of Dunnett's t = 2.853).

			Pairwise comparison of time of nitrogen addition		
Variable	MSD †	MSE ‡	none v. early-season	none v. mid-season	none v. late-season
Light penetration	.078	.00298	***	***	
Tissue N concentration					
Dominant species, *Chenopodium album*		8.489E-6	***	***	***
Subordinate community	.002	2.84E-6		***	***
Total N content					
Dominant species, *Chenopodium album*		1.92	***	***	***
Subordinate community		1.45	***	***	***

† MSD = minimum significant difference

‡ MSE = mean standard error

the plots with no nitrogen addition, 87 percent in the early season nitrogen addition treatment, and 51 percent in the mid-season nitrogen addition treatment.

Nitrogen acquisition by the dominant species

There were significant effects of species removal and time of nitrogen addition on the tissue nitrogen concentration of the dominant species, C. album, at harvest (Table 5). Because the C. album removal was done only once (in early July), any individuals that germinated later in the season remained in the removal treatments, but were shorter than the rest of the subordinate plant community. This provided an opportunity to examine how the ability to acquire nitrogen differs when a species is a subordinate in the ground-layer (and light-limited) or a dominant in the canopy. The tissue nitrogen concentration of C. album was significantly higher in the removal plots, where it was a ground layer subordinate, than in the control plots, where it was the dominant species in the canopy (Figure 9a). Furthermore, the tissue nitrogen concentration of C. album increased as the nitrogen addition came later in the growing season when it was both the dominant and a subordinate member of the community (Table 6, Figure 9a).

The effects of species removal and time of nitrogen addition on the total nitrogen content of C. album were significant (Table 5). The total nitrogen content of C. album was much higher in the control plots where it was the canopy dominant than in removal plots where it was the ground layer subordinate (Figure 9b). This result indicates that as a subordinate, C. album acquired some of the added nitrogen (i.e., had higher nitrogen concentration than the unfertilized control), but did not allocate it to growth, and suggests that C. album may have been light-limited when it was a subordinate member of the community. When C. album was the canopy dominant, its total nitrogen

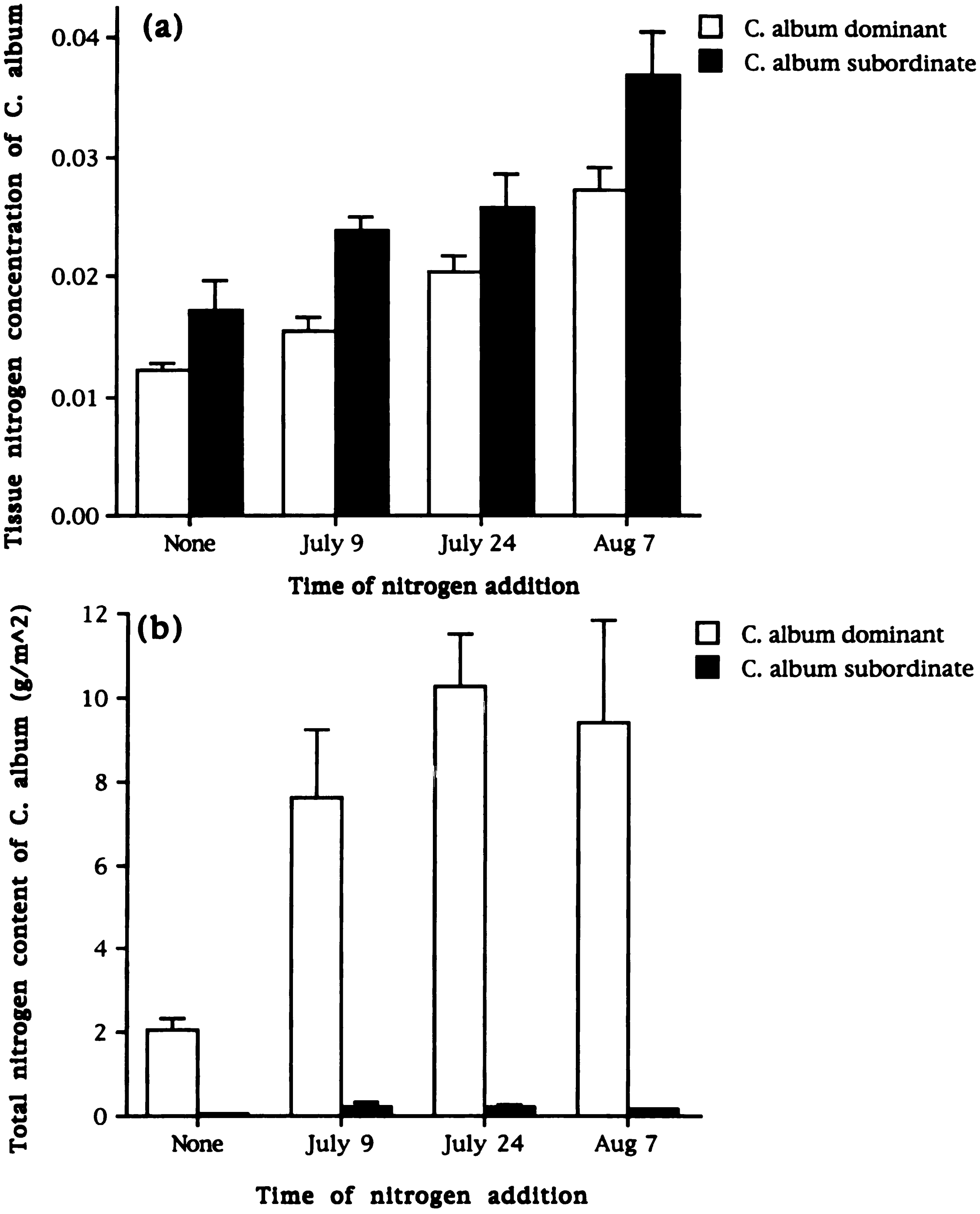


Figure 9. Tissue nitrogen concentration of C. album (a) and total nitrogen content of C. album (b) in response to removal of C. album and time of nitrogen addition. Note that C. album in removal treatment were seedlings that emerged after the removal treatment in early July.

content was 4 to 5 times higher and its biomass was 2 times higher in plots where nitrogen was added than in control plots, indicating that it had allocated nitrogen uptake to growth and was not light limited. When it was the canopy dominant, the increase in total nitrogen content of C. album relative to the unfertilized control was maintained at each time of nitrogen addition (Table 6).

Nitrogen acquisition by the subordinate plant community

There was a significant effect of removing C. album on the tissue nitrogen concentration of the subordinate community in control plots and nitrogen addition treatments (Table 5, Figure 10a). The subordinate community had higher tissue nitrogen concentrations when C. album was removed than when it was present (Figure 10a). The total nitrogen content of the subordinate community was also significantly higher when C. album was removed (Table 5, Figure 10b).

The effect of the time of nitrogen addition on the tissue nitrogen concentration of the subordinate community was significant (Table 5). The tissue nitrogen concentration of the subordinate community was higher in the mid- and late season nitrogen addition treatments than in the control plots (Table 6, Figure 10a). The subordinate community acquired some of the mid- and late season nitrogen addition (i.e. increased its tissue nitrogen concentration relative to the unfertilized control). But in the mid- and late season nitrogen treatments, it did not allocate the additional nitrogen to growth when C. album was present (Figure 2b). However, the subordinate community increased tissue nitrogen concentration, total nitrogen content, and growth in the mid- and late season nitrogen addition treatments when C. album was removed. As had been observed in C. album, the tissue nitrogen

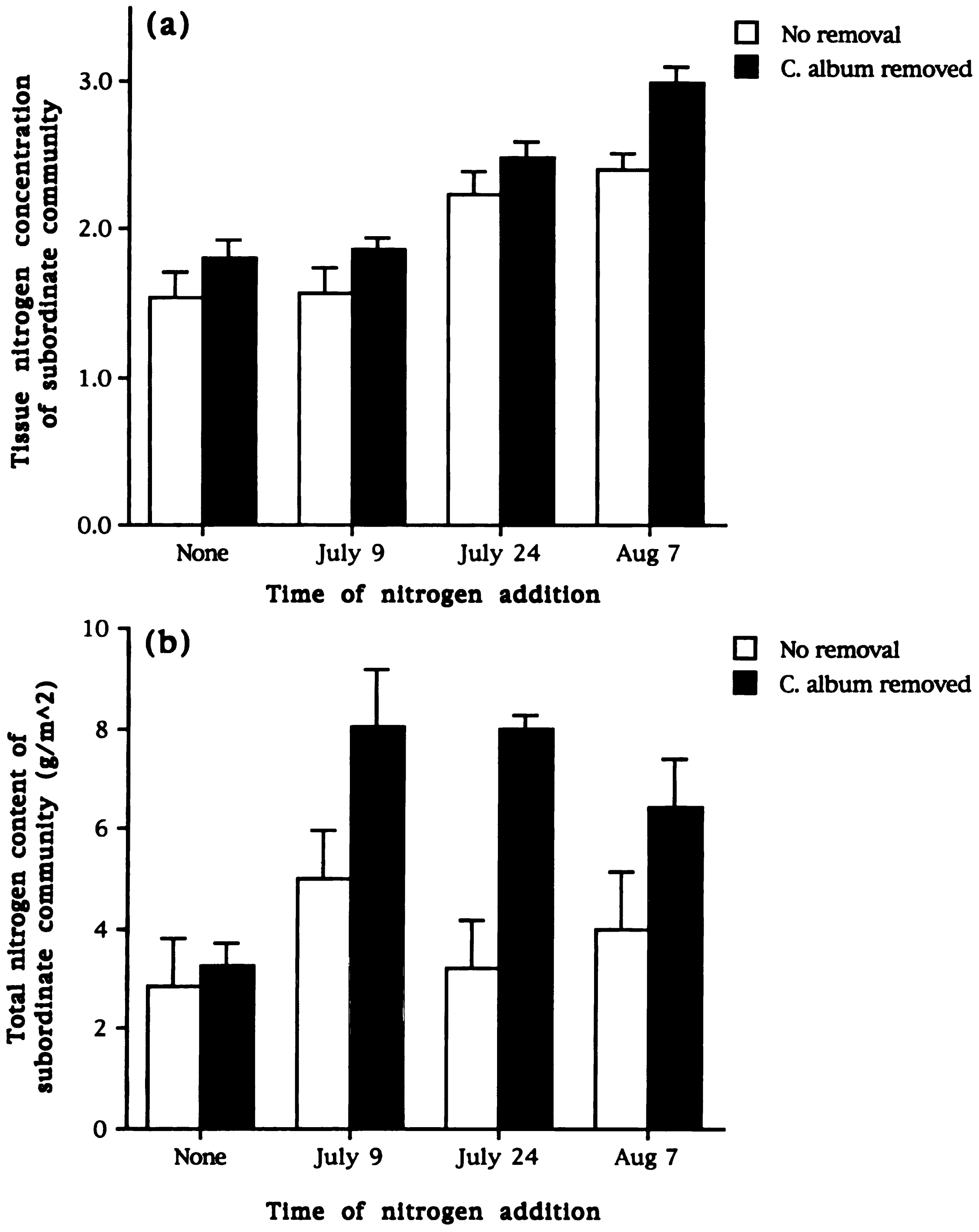


Figure 10. Tissue nitrogen concentration (a) and total nitrogen content (b) of the subordinate plant community in response to removal of the dominant species and time of nitrogen addition.

concentration of the subordinate community increased as the nitrogen addition came later in the season (Figure 10a).

Tissue nitrogen concentrations of individual species declined with species biomass in both the control and mid-season nitrogen addition plots (Figure 11). In both the control and nitrogen addition treatment, tissue nitrogen concentrations leveled off above a species biomass of 100 g/m2, suggesting that the species of large biomass were able to convert added nitrogen to biomass. This suggestion is supported by two results. First, the higher elevation of the curve for the nitrogen addition treatment indicates that most species across the range of biomass values increased nitrogen acquisition with the mid-season nitrogen addition. Second, most of the species increased nitrogen concentrations when nitrogen was added mid-season (Figure 12a). That is, most of the species are above the dotted line where tissue nitrogen concentrations of individual species are equivalent in the control and nitrogen addition treatment (Figure 12a). However not all species in the community were able to allocate the acquired nitrogen to growth and increase their total nitrogen content. The canopy-dominant species increased their total nitrogen content disproportionately to the sub-canopy and ground-layer species (Figure 12b).

Summary of results

The effect of the dominant species on subordinate community biomass, community structure, and nitrogen acquisition varied with the time of the nitrogen pulse. The effects of C. album removal and the time of nitrogen addition on evenness and diversity (Figure 5a - c) were consistent with their effects on the biomass (Figure 2a - c) and nitrogen uptake patterns (Figures 9 and 10) of the dominant species and the subordinate community. When

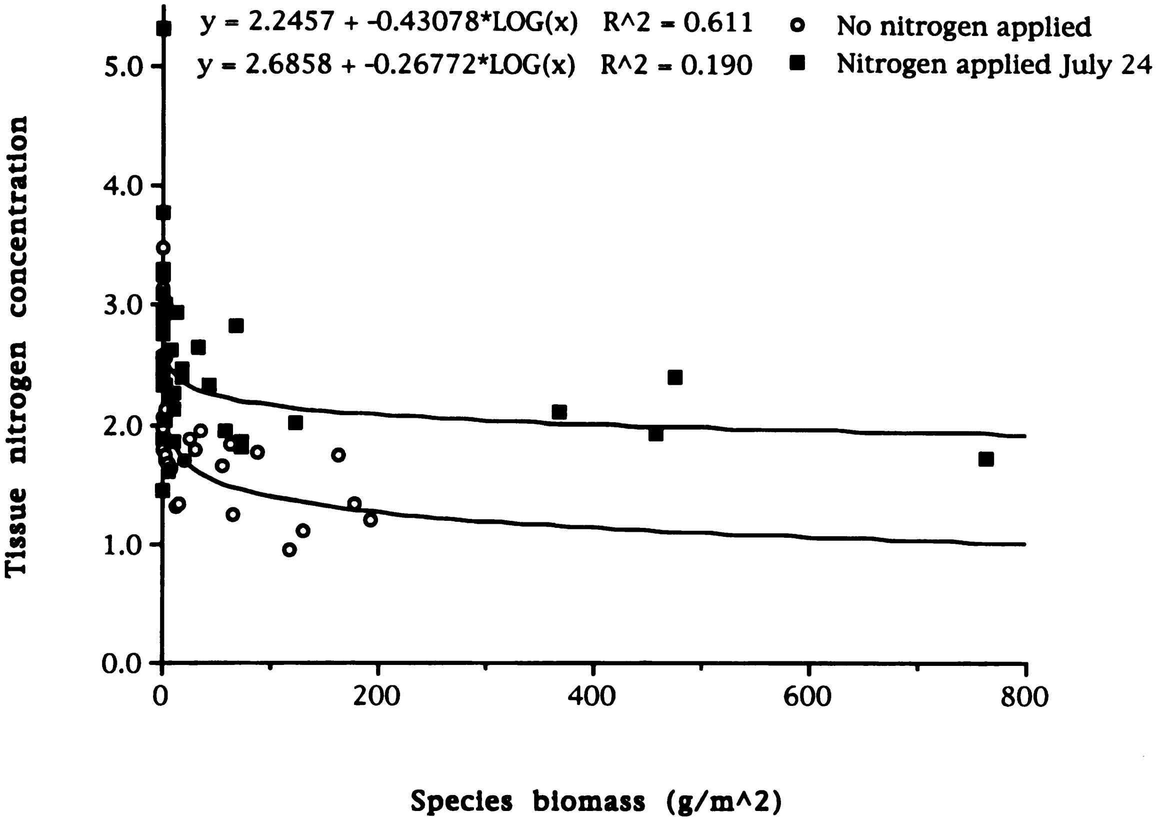
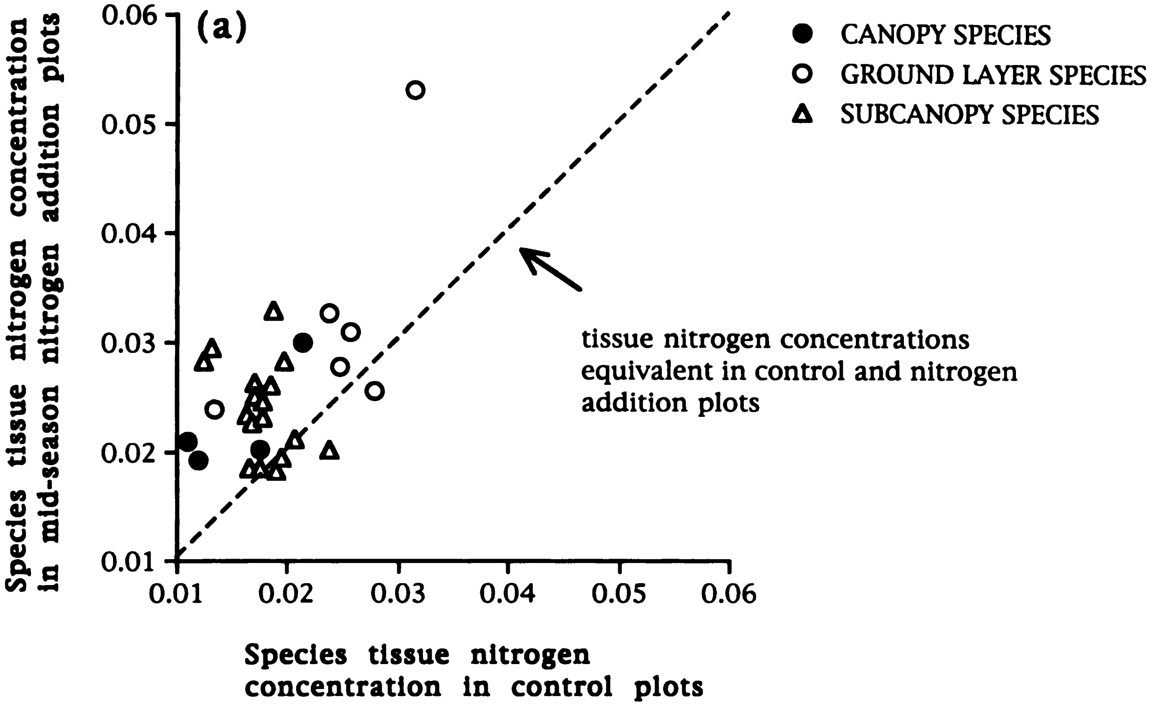


Figure 11. Relationship between tissue nitrogen concentration and species biomass in control plots and mid-season (July 24) nitrogen addition plots.



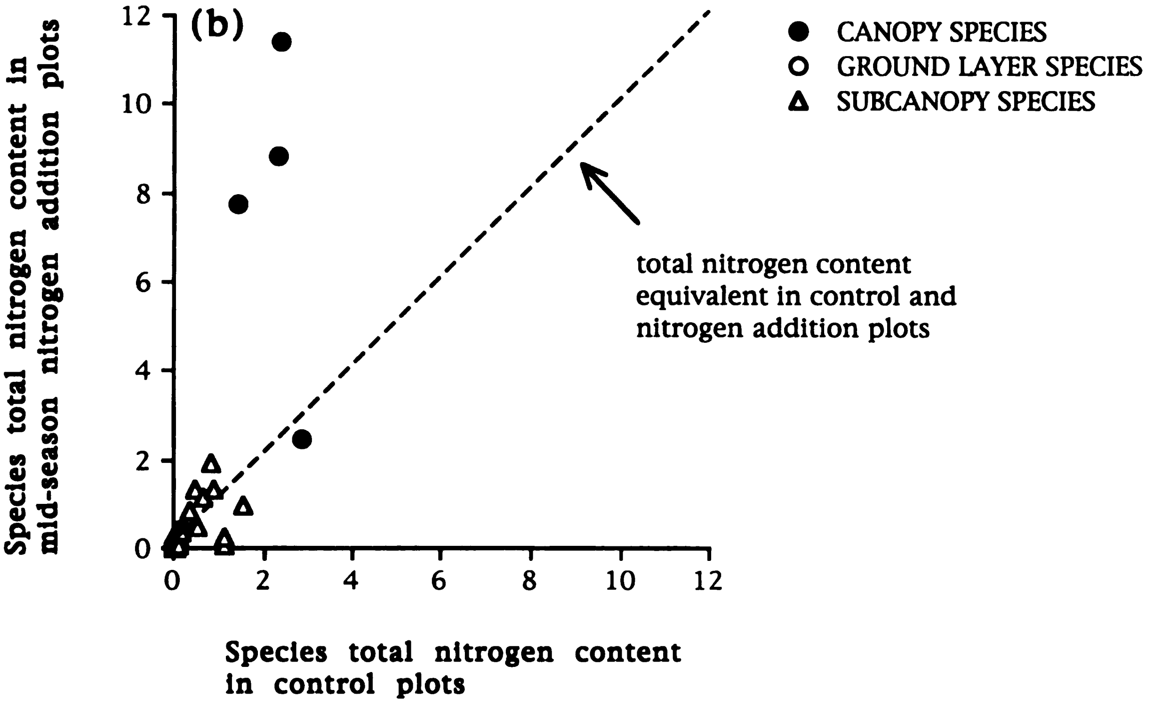


Figure 12. Relationship between (a) tissue nitrogen concentration of species in control and mid-season (July 24) nitrogen addition plots, and (b) total nitrogen content of species in control and mid-season (July 24) nitrogen addition plots.

nitrogen was added early in the season, both *C. album* and the members of the subordinate community increased in biomass and nitrogen content relative to the unfertilized control. Likewise, when nitrogen was added early in the season, the removal of *C. album* had a small effect on evenness and diversity. When nitrogen was added mid-season, however, the *C. album* response was disproportionately greater than that of the subordinate community: *Chenopodium album* increased tissue nitrogen concentration, total nitrogen content, and biomass relative to the subordinate community. The tissue nitrogen concentration of the subordinate community increased relative to the unfertilized control, but the added nitrogen was not allocated to growth when the dominant species was present. When the dominant was removed, the subordinate community was able to respond to a mid-season nitrogen addition by increasing tissue nitrogen concentrations, total nitrogen content and biomass. Likewise, the competition intensity indices and the magnitude of the effect of *C. album* on evenness and diversity were greatest when nitrogen was added mid-season. When nitrogen was added late in the season, the dominant species increased biomass, tissue nitrogen concentration, and total nitrogen content. The subordinate community increased tissue nitrogen concentrations significantly with the late-season nitrogen addition, but did not allocate the acquired nitrogen to growth (i.e. biomass and total nitrogen content did not increase). When *C. album* was removed, the subordinate community increased tissue nitrogen concentrations, biomass, and total nitrogen content in response to the late-season nitrogen addition. With the late-season nitrogen addition, the competition intensity indices and the magnitude of the effect of the dominant species were smaller than in the mid-season nitrogen addition treatments.

DISCUSSION

Community biomass responses and nitrogen acquisition

To my knowledge, this is the first field study that explicitly tests the impact of within-season variation in the time of a soil resource pulse on the competitive interactions and consequences for diversity in a terrestrial plant community. These results show that the time of a nitrogen addition determines the magnitude of the competitive effect of the dominant species on subordinate community structure, biomass, and resource acquisition. When the dominant species was present and nitrogen was added early in the growing season, both the dominant species and the subordinate community could acquire the additional nitrogen and convert it to a significant increase in biomass. However, when nitrogen was added later in the growing season (late July or early August) only the dominant species, C. album, could increase in biomass; the subordinate community did not increase in biomass. When the dominant species was removed, the subordinate community increased biomass in both the early- and mid-season nitrogen addition treatments. These results are consistent with the hypothesis that, with increased fertility, the magnitude of the competitive effect of the dominant species on the subordinate community increases (Grime 1987).

The difference in the response of the dominant species and subordinate community to nitrogen addition may have been influenced by the degree to which a biomass/height hierarchy had developed among species when the nitrogen pulse was added. Early in the growing season, the plant community had not developed a distinct canopy, sub-canopy, and ground layer. Thus, the biomass dominant (C. album) and subordinate species were likely of more equal size than later in the season, and thus more equivalent competitors (Miller and Werner 1987). By mid-season (late July), there may have been a more developed biomass/height hierarchy in the community, allowing the dominant species to have disproportionate access to resources and consequently a larger competitive effect on the subordinate community. A more detailed examination of the physiognomy and phenology of the growth of species in this community would be required to confirm this assumption. Miller (1987) has shown that early advantages in emergence or growth may become magnified through the growing season in these annual old-field communities. Several studies of the response of old-field plant communities to increased nutrient availability have shown that diversity and evenness peaked early in the growing season (May or June) and declined as the season progressed (Bakelaar and Odum 1978, Wakefield and Barrett 1979, Hyder and Barrett 1986, Carson and Barrett 1988, Carson and Pickett 1990), supporting the suggestion by Miller and Werner (1987) that competitive interactions may be weak early in the season and then increase later in the season when plants begin to overlap spatially. These patterns may be characteristic of fertile sites where light competition will be important due to overlap of species canopies and disproportionate growth of the dominant species and where asymmetric competitive interactions would preclude a more even representation of species during the whole growing season.

One consequence of the seasonal development of a competitive hierarchy in this plant community is that the resources limiting canopy and sub-canopy species changed over the growing season. The patterns of nitrogen acquisition suggest that early in the season the whole plant community was nitrogen-limited. The analysis of tissue nitrogen demonstrated that the dominant and subordinate species responded similarly to a nitrogen pulse early in the season by increasing growth, tissue nitrogen concentrations, and total nitrogen content. Later in the season, however, as the canopy closed, the subordinate community was limited by light and the dominant species was only limited by nitrogen. When nitrogen was added mid-season, the dominant species acquired the added nitrogen and allocated it to growth. The subordinate community was able to acquire some of the mid-season nitrogen addition, but, because of light limitation, it could not allocate it to growth. Consequently, tissue nitrogen concentration of the subordinate community was significantly higher in the mid-season nitrogen addition than in the unfertilized control. However, when the dominant species, C. album, was removed the subordinate community could respond to the mid- and late season nitrogen addition by increased nitrogen uptake and growth. The data on light penetration to the soil surface in these plots in early August (between the mid- and late season nitrogen addition) support the conclusion that growth of C. album controlled light levels to the subordinate community. On August 1 light penetration was significantly lower in the early-season nitrogen addition plots than in the mid-season nitrogen addition plots when C. album was present.

The patterns of nitrogen acquisition in this study are consistent with the results of Carson and Pickett (1990) showing a shift in resource limitation from nitrogen early in the growing season to water and then light later in the growing season in a Solidago-dominated old-field. These results clarify the interpretation by Goldberg and Miller (1990) that addition of a resource limiting early in the season (nitrogen) will reduce diversity more than addition of a resource limiting later in the season (water). They suggested that early season nitrogen addition would lead to earlier canopy closure and greater mortality due to light limitation. Indeed, early nitrogen addition did lead to earlier canopy closure in this study. However, the early season nitrogen addition was acquired by both dominant and subordinate species and allocated to biomass. Though early nitrogen addition may lead to earlier canopy closure, more species in the community would be able to increase in biomass if the growth phenologies among species were relatively synchronous and the nitrogen addition came before a dominance hierarchy was established.

The importance of position in the canopy for resource acquisition was further demonstrated by the difference in nitrogen acquisition by a single species, C. album, when it was a canopy dominant and a ground layer subordinate member of the community. When C. album was the subordinate member of the community, it increased tissue nitrogen concentrations significantly in response to nitrogen addition but did not allocate the acquired nitrogen to above-ground biomass, suggesting that it was light-limited. When it was the canopy-dominant species, it increased nitrogen concentration in response to nitrogen addition and it allocated the nitrogen acquired to growth. Hence, when C. album was a canopy-dominant, it had higher total nitrogen content in nitrogen addition plots than control plots.

The decline in the ability of the plant community to increase biomass in response to the late-season nitrogen pulse may have been due to harvesting the plants before they could allocate nitrogen to growth. The tissue nitrogen concentration of both the dominant species and the subordinate community at harvest increased as the nitrogen addition came later in the season. The plants clearly were able to take up the late-season nitrogen addition, but could not convert it to biomass, probably because they were harvested before they could do so. The dominant species and subordinate species appeared to be physiologically capable of taking up added nitrogen at each of these three stages in their phenology.

Diversity and community structure

The effect of the dominant species on subordinate species biomass and nitrogen acquisition had important consequences for diversity and community structure. These results are consistent with the predictions of the "resource richness hypothesis" (Grime 1979, Huston 1979, Tilman 1982) that the negative effect of the dominant species, C. album, on the subordinate species performance should be correlated with a reduction in the diversity indices. These results are also partially consistent with the prediction that the impact of the dominant species on the diversity indices should be greater in nitrogen addition treatments than in the control plots.

Removal effects. - In this study, the removal of the dominant species resulted in a small, but significant, increase in species richness. There were one to two more species in the community when C. album was removed. However, the removal of the dominant species had a stronger impact on biomass evenness than on species richness. Thus, the Shannon diversity index increased significantly when C. album was removed. It appears that, within a single growing season, the removal of the dominant species had a stronger effect on the distribution of biomass across species than on the net recruitment and mortality of species. Chenopodium album may have been removed too late in the season and a canopy established too rapidly for new species to germinate and grow. In addition, it may take several generations for responses in recruitment and mortality of species to manifest. Within a single season, however, rearrangement of the biomass hierarchy after removal of the dominant species may create the conditions for differential recruitment and mortality in following years. The effects of the removal of C. album are consistent with other studies that have demonstrated an increase in richness, evenness, or diversity after removal of the dominant species (Abul-

Fatih and Bazzaz 1979, Armesto and Pickett 1985, Keddy 1989b, Gurevitch and Unnasch 1989). The effects of the removal of C. album contrast with studies where the removal of the dominant species resulted in either no change or a decline in species diversity (Pinder 1975, Allen and Forman 1976, Hils and Vankat 1982). The studies in which species diversity did not respond to the removal of a dominant species were conducted in older fields or in younger fields dominated by biennials, where the dominant species accounted for a small proportion of total community biomass. In contrast, species diversity increased upon removal of the dominant species in young fields and in a 7-year field, where the dominant species accounted for more than 80 percent of the total community biomass. Similarly, in my study, C. album accounted for 75 to 90 percent of community biomass.

Time of nitrogen addition. - In this study, the response of diversity and community structure to the time of nitrogen addition differed depending on whether the dominant species was present in the community. When C. album was present, the time of nitrogen addition had no significant impact on species richness. The range of standing crop created by nitrogen addition to an already fertile site may not have been sufficient to produce a response in species richness. Moore and Keddy (1989) have demonstrated that richness and standing crop were unrelated within community types. However, over a wide range of standing crops that included different types of communities, there was a curvi-linear relationship between richness and standing crop. In addition, the effects of nitrogen addition on species richness may not manifest in a single season.

However, the nitrogen addition significantly reduced biomass evenness, and this effect was strongest when nitrogen was added mid-season. Consequently, the Shannon diversity index also was lower when nitrogen was added, and it was lowest when nitrogen was added mid-season. Thus, like the removal treatment, the time of nitrogen addition appeared to have a stronger effect on the distribution of biomass across species than on the net recruitment or mortality of species. The strongest decline in evenness and diversity occurred with the mid-season nitrogen addition where C. album biomass doubled and the subordinate community biomass did not change. These results are consistent with the hypothesis that the disproportionate increase in the growth of the dominant species when fertility increases leads to a decline in community diversity (Grime 1979, 1987) and with the results of the experiment by Gurevitch and Unnasch (1989) where the effect of the removal of the dominant species, Dactylis glomerata, on richness and evenness was stronger in fertilized plots than in control plots. However, this study shows that the seasonal time of the nitrogen pulse was crucial in determining the magnitude of the effect of the dominant species at higher fertility levels.

When the dominant species was removed, the time of nitrogen addition had no significant impact on species richness. The effect of time of nitrogen addition on evenness in the subordinate community was similar to, but weaker than, the effect of nitrogen addition when the dominant was present. Thus, there appeared to be more equitable access to the nitrogen pulses applied at all times during the season when the dominant was removed. Consequently, when the dominant was removed there was no significant change in the Shannon diversity index with different times of nitrogen addition. This pattern is consistent with the result that, when the dominant was removed, the subordinate community doubled in biomass in response to both early- and mid-season nitrogen addition.

Thus, in this experiment, dominance by Chenopodium album led to a decline in evenness and diversity with increasing fertility. When C. album was removed, no single species consistently replaced it as the dominant species. Several C3 dicots (Abutilon theophrasti and Ambrosia artemisiifolia), a C4 dicot (Amaranthus retroflexus), and several C4 grasses (Panicum dichotomiflorum, Setaria faberi, Setaria lutescens, Setaria viridis, and Cyperus esculentus) all responded positively to the early nitrogen addition. Chenopodium album has several traits that may contribute to its disproportionate growth in response to nitrogen addition. First, C. album is an early-emerging, fast growing, C3 dicot (Chapin 1980, Miller 1987, Grime 1988) potentially achieving an early size advantage. Second, C. album is capable of consuming nitrogen in excess of the immediate needs for growth. My results showed that the total nitrogen content of C. album increased 4- to 5-fold while its biomass increased by about 2-fold in response to nitrogen addition. Third, Chenopodium album has a tall, erect growth form with the potential to branch profusely above ground, thereby depleting light to shorter plants. However, I do not suggest that C. album is the only species that could function as the biomass dominant and reduce the subordinate community performance and diversity in this type of community. In a nearby annual old-field community, where Ambrosia artemisiifolia, was the numerical and biomass dominant and C. album was a sub-dominant species, water addition reduced the diversity of the community (Goldberg and Miller 1990).

Magnitude of competition intensity and mechanisms of plant competition

The results of this experiment are consistent with the hypothesis that increasing competition intensity along a gradient of increasing nutrient availability and plant biomass leads to a decrease in species diversity (Grime 1973, 1979, Huston 1979, Southwood 1988, Keddy 1989a, Campbell et al. 1991b).

However, in this annual old-field community, the seasonal time of nitrogen addition and presumably the stage of development of the species biomass hierarchy influenced the magnitude of the increase in competition intensity caused by fertilization. The indices of competition intensity were greatest when nitrogen was added at mid-season, and smaller when nitrogen was added early or late in the growing season. The intensity of competition from the dominant species was greatest at the time of nitrogen addition when the dominant species most severely reduced evenness, diversity, and subordinate community biomass. These results are consistent with the few studies that report an increase in competition intensity with increasing productivity (Wilson and Keddy 1986, Reader and Best 1989). However, these results contrast with the larger number of recent studies that demonstrate no relationship between fertility or productivity and competition intensity (Gurevitch et al. 1990, Wilson and Shay 1990, Wilson 1991, Wilson and Keddy 1991, Wilson and Tilman 1991a, 1993, and Campbell and Grime 1992). There are at least two explanations for these differences in results. These explanations clarify some of the conflict in the literature about the magnitude of competition intensity and mechanisms of plant competition along productivity gradients.

First, most of the studies on competition intensity (Wilson and Shay 1990, Wilson 1991, Wilson and Keddy 1991, Wilson and Tilman 1991a, 1993, Reader and Best 1989, and Reader et al. 1994) measure either absolute or relative competition intensity as the effect of all neighbors on the performance of a single target. However, implicit in the hypothesis for the mechanism underlying the negative relationship between diversity and fertility is the idea that asymmetric competition from one or several dominant species (Allen and Forman 1976, Grime 1987, Miller and Werner 1987, Carson and Pickett 1990) leads to reduced recruitment, growth, and reproduction of subordinate species. To develop an index and experimental design that is more consistent with the logic of this hypothesis, the removal of the dominant species at different fertility levels may be a more appropriate experimental design. The design in this study measures the effect of a single dominant species on the performance of the subordinate community rather than the effect of the entire community on a single individual. Using a single target individual may exaggerate the competition intensity relative to the effect of a dominant species on the subordinate community. The whole plant community may have a stronger competitive effect (sensu Goldberg and Werner 1983, Goldberg 1990) on a single target individual than a dominant species has on the subordinate community. Alternatively, the ability of the subordinate community to respond (sensu Goldberg and Werner 1983, Goldberg 1990) to a dominant species may be stronger than the response ability of a single target individual to the whole plant community. If either of these alternatives is true, then the magnitude of competition intensity in this and other studies may not be comparable. The approach of removing the dominant species may be appropriate under conditions where asymmetric interactions are likely to occur (i.e. in plant communities where light is limiting). Miller and Werner (1987) have demonstrated that competitive interactions in a similar annual old-field plant community located 1 km from this LTER site were primarily asymmetric. The result observed in my study that competition intensity was significantly correlated with the biomass of C. album supports the conclusion that asymmetric competition from the dominant species is important in determining community structure and diversity in this annual old-field community.

Second, the range of fertility and biomass levels in this and other studies may differ substantially. The early-successional old-fields in southwestern Michigan where these experiments were conducted may represent a gradient from moderate to high fertility, whereas the Cedar Creek site in Minnesota (Wilson and Tilman 1991a, 1993) and the North American prairie site in Saskatchewan (Wilson and Shay 1990) may represent a gradient from lower fertility to moderate fertility. In addition, the rate of nitrogen addition in this experiment was twice that applied by Wilson and Tilman (1991a, 1993) and four times that applied by Wilson and Shay (1990) and these studies were conducted in perennial grass-dominated communities. However, the above-ground biomass gradient in my study (200 - 1100 g/m^2) was comparable to that in Wilson and Tilman (1991a) (400 - 1200 g/m^2) and Wilson and Tilman (1993) (10 - 1000 g/m^2), but not with that in Wilson and Shay (1990) (100 - 450 g/m^2).

Wilson and Tilman (1991a, 1993) demonstrated that below-ground competition intensity decreased and above-ground competition increased along a nutrient gradient. As a result of this negative correlation between above- and below-ground competition intensity, total competition intensity remained constant as nutrient availability increased. In this study, the fertility gradient may represent a gradient of primarily increasing above-ground competition. The subordinate plant community in the presence of the dominant species was able to acquire added nitrogen, but when the addition came mid- or late season, the subordinate community did not allocate the additional nitrogen to growth. This suggests that nitrogen addition increased competition intensity for light. The trade-offs in above- and below-ground competition intensity that Wilson and Tilman (1991a, 1993) observed may not have occurred in my study where competition intensity increased when nitrogen was applied. Competition intensity may increase with fertility only in fertile sites where there can be strong and increasing competition for light.

Finally, the nitrogen acquisition results observed in this study and the patterns of nitrogen acquisition by plants of different life-histories described by Pate (1983) provide a possible explanation for why resource demand and acquisition by roots and shoots, and thus, above- and below-ground competition intensity, in an annual plant community may not be as tightly linked as suggested by Grime (1994). Pate (1983) describes several patterns of nitrogen acquisition in annuals from numerous plant families in Australia. Several of the families that he describes, including Chenopodiaceae, Amaranthaceae, Polygonaceae, occur in this Michigan old-field plant community. According to Pate (1983) some annuals have shoot-dominated nitrogen assimilation. They transport nitrate via the xylem and store nitrate reserves in the shoot later reducing it to amino compounds in the leaves. Pate (1983) suggests that root demand for nitrogen can be satisfied by phloem transport of reduced nitrogen from the shoot to the roots. This mechanism of nitrogen uptake and assimilation would result in a decoupling of the demands of the root and shoot within a season. Early season nitrogen uptake can be stored as nitrate and converted to biomass later in the season when soil nitrogen has been severely depleted. However, competition with other plants will alter the potential allocation of nitrogen uptake to growth. If light availability declines significantly as it did in this study, subordinate plants will store the nitrogen taken up early in the season or in response to a pulse and not allocate it to growth. The time scale (within and between seasons) over which plants integrate their depletion of resources and their response to resource depletion (sensu Goldberg 1990) may complicate predictions about whether above- and/or below-ground resource competition predominates in productive plant communities.

CHAPTER 3

EFFECT OF TIME OF NITROGEN ADDITION ON COMMUNITY STRUCTURE AND RESOURCE AVAILABILITY IN AN OLD-FIELD PLANT COMMUNITY

INTRODUCTION

Increasing attention is being paid to the patterns of exploitation of spatial and temporal resource heterogeneity by plants (Campbell and Grime 1989, Naeem and Colwell 1991, Caldwell and Pearcy 1994) and the role of spatial and temporal heterogeneity in maintaining species coexistence (review by Tilman and Pacala 1993). Several studies have demonstrated the importance of temporal variation in resources for plant performance. Yearly fluctuations in rainfall favored different species in different years in a coastal dune grassland (van der Maarel 1981). Chapin and Shaver (1985) found that the relative abundances of tundra species depended on annual variation in environmental conditions (temperature, nutrients, and light). Carson and Pickett (1990) demonstrated that three subcanopy species in a New Jersey old-field were limited by different resources at different times of the season and that the severity of resource limitation varied from year to year. They suggested that resource heterogeneity could maintain species coexistence. Relatively little attention has been paid to the consequences of within-season temporal variation in resource availability for community structure in terrestrial plant communities. This study examines the effects of varying the within-season time of nitrogen addition on diversity, community structure, and resource availability of an early successional (second-year) old-field.

Community level responses to within-season temporal variation in resource availability might be expected because plant species vary in the time of emergence, growth, flowering, fruiting, and senescence within a season (Swieringa and Wilson 1972, Mellinger and McNaughton 1975, Reed 1977). Differences in growth phenology can affect resource demands and resource depletion patterns of different species. Their response to resources may depend on the time of resource addition relative to their development status

(Mengel and Kirkby 1978, Watson 1984, Benner and Bazzaz 1985, 1988), and relative to the development of the biomass hierarchy among individuals or species (Benner and Bazzaz 1987, Chapter 2). I am aware of only two studies in natural plant communities that have explored community level consequences of within-season temporal variation in resource availability. In an annual old-field plant community, Reed (1977) showed that a single large pulse of nitrogen early in the season reduced diversity more than the same total amount of nitrogen applied in smaller presses over the growing season. However, the magnitude and time of nutrient pulses were confounded in that experiment. In a species removal experiment (Chapter 2), I varied only the time of nitrogen addition to an annual plant community while keeping the magnitude of nitrogen addition constant. The dominant species reduced biomass evenness and diversity most with the mid-season (early July) nitrogen addition, suggesting that the degree of development of the biomass hierarchy influenced the response of dominant and subordinate species to nitrogen addition. In this study, the seasonal time of nitrogen addition was varied in a second-year old field, because it has a greater number of growth forms, life history types (annuals, biennials, and perennials), and growth phenologies than a first-year annual old-field plant community. The pattern of development of a biomass hierarchy and consequently the response to time of nitrogen addition may differ from that in an annual old-field.

The objectives of this study were: (1) to document the growth phenologies of individual species in a second-year old-field plant community and the seasonal development of plant community structure, (2) to explore the effects of varying the within-season time of nitrogen addition on diversity, community structure and biomass, (3) to document the effect of the plant community on seasonal patterns of resource availability, and (4) to link seasonal patterns of resource availability with patterns of community structure.

METHODS

Study site

The study was conducted from May to August of 1993 in a second-year abandoned old-field at Michigan State University's W. K. Kellogg Biological Station in southwestern Michigan (42° 24' N latitude, 85° 23' W longitude). The old-field is one in a chronosequence of 1-hectare fields planted to soybeans and abandoned in sequential years since 1989. The field in this study was planted to soybean (Glycine max (L.) Merr.) in May 1991 with no fertilizer application, and was abandoned in the fall after the soybean harvest. The vegetation was dominated by summer annuals (Abutilon theophrasti, Amaranthus retroflexus, and Chenopodium album) in 1992 and by Conyza canadensis (horseweed) with a diverse mixture of winter annuals, biennials, perennials, and summer annuals during the summer of 1993 when this study was conducted. The soil is of the Kalamazoo series (fine-loamy, mixed, mesic).

Experimental design

The experimental design included 6 treatments (no nitrogen addition and nitrogen added at five different times during the growing season) replicated four times (24 treatment plots). The treatments were arranged in a completely randomized design using 1-m^2 plots (0.5 x 2.0 m) separated by a 1 m buffer on each side. Nitrogen was applied in a single pulse at 32 g N/m^2 as dry ammonium nitrate pellets (320 kg N/acre, typical of fertilizer levels for corn production in this region) on either May 11, May 26, June 17, July 8, or July 26. The times of nitrogen addition were chosen to include periods where different plant life history groups would be actively growing.

West of each treatment plot was a paired 0.5 x 2.0 m plot which I refer to as a phenology plot. All of the vegetation was sampled from four replicates of the phenology plots on the day that nitrogen was added to the paired treatment plots. The vegetation samples from the phenology plots were used to estimate above-ground community biomass, species diversity, and community structure at the time when the nitrogen was added to the treatment plots and to document the seasonal development of community structure in this field. All of the above-ground plant biomass was harvested from the control and nitrogen addition treatment plots on August 16 by clipping stems 1 cm above the soil surface. Plant samples from the phenology plots and the final harvest of the treatment plots were separated by species, dried at 60°C, and weighed to ± 0.01 g.

Species richness was calculated as the number of species per plot. The Shannon diversity index was calculated as $H' = - \sum p_i (\log p_i)$, where p_i is the proportion of biomass accounted for by species i. The Pielou index of biomass evenness was calculated as $J = H' / H_{max}$, where H_{max} = log of species richness. Species richness, evenness and diversity were calculated per plot, and are expressed as the mean of four replicates. Evenness and diversity were calculated based on biomass rather than numbers of individuals because biomass has been shown to be a good predictor of competitive ability in plants (Gaudet and Keddy 1988 and references therein; review by Goldberg and Barton 1992).

Soil sampling and nitrogen analysis

Soil was sampled from the experimental plots on June 2, June 16, July 6, and July 22 for analysis of mineral nitrogen availability (NO_3-N + NH_4-N) and for laboratory incubations to determine potential nitrogen mineralization rate. Soil sampling dates were chosen to follow the dates when nitrogen was added to the treatment plots. Soil sampling dates were constrained by seasonal rainfall patterns which influenced whether the soil was moist enough to be able to sample the appropriate depth (10 cm) or dry enough to pass easily through the soil sieve. Three 2.5-cm diameter, 10-cm deep soil cores were collected from random locations in each experimental plot. The three cores were composited and passed through a 2-mm sieve. A 5-g sample of soil was extracted in 50 ml of 2M KCL for analysis of the initial mineral nitrogen content. The extracts were shaken for 1 minute and left at room temperature for 24-hours before filtering through a 1-micron Gelman (Ann Arbor, MI, USA) glass filter. Filtered sample extracts were stored in 7-ml plastic vials at 4°C until analyzed for nitrate and ammonium concentrations. About 25 g of the remaining soil was placed in a loosely capped 50 ml Qorpak bottle. These samples were incubated at 25°C and 80% relative humidity for 28 days and then subsampled and extracted as for the initial soil samples. Gravimetric soil moisture content was determined for each composite sample by drying soil subsamples at 105°C for 48 hours. Soil moisture as a measure of resource availability was calculated as a percent of dry soil mass. Soil moisture for correcting the nitrogen content of soil extracts was calculated as a percent of wet soil mass.

The soil extracts were analyzed colorimetrically for nitrate and ammonium using an Alpkem Segmented Flow Analyzer (Model 3550). The NO_3-N and NH_4-N concentrations of the extracts were corrected for variation in initial soil moisture and are expressed as ug NO_3-N or NH_4-N per gram dry soil. Available soil nitrogen is expressed as the sum of initial NO_3-N and NH_4-N concentrations. Potential mineralization rate (ug mineral-N/ g soil/ day) was calculated as the difference between the mineral-N (NO_3-N + NH_4-N) concentrations of initial and post-incubation soil subsamples divided by 28 days.

Light measurements

The effect of the plant community on light availability at the soil surface was measured on May 13, May 20, June 16, June 23, July 15, and August 13 using a 40-cm long integrating light probe (Sunfleck PAR ceptometer, Decagon Devices Model SF-80, Pullman, WA). The dates of light measurements were constrained to cloudless days between 11:00 and 13:00 and to follow the dates of nitrogen addition. Photosynthetically active radiation (PAR) was measured above the plant canopy and 1 cm above the soil surface with the light probe oriented north-south along the center of the 2-m length of the plot. Light penetration is expressed as the percent of PAR above the plant canopy penetrating to 1 cm above the soil surface. One light reading was taken per plot and treatment levels of light penetration are expressed as the mean percent light penetration over four replicate plots.

Statistical analyses

Analysis of variance (ANOVA) of the effect of time of nitrogen addition on each variate was performed using the GLM procedure in SAS version 6 (1989). The error term was the replicate x time of N addition interaction term. Analysis of variance was performed on log-transformed plant biomass data. Percent light penetration values were arcsin square root transformed before analysis of variance. The GLM procedure was also used to perform correlations and regressions.

RESULTS

Seasonal patterns of community biomass, diversity, and structure

Total community biomass in the unfertilized phenology plots peaked in early May, then declined and increased again to 337 g/m^2 by mid-August (Figure 13). Mean species richness increased from 15 to 20 species early in the season, and then declined slightly throughout the growing season to 18 species by mid-August (Figure 14a). There was a turnover of species composition as well as a change in species richness over the growing season (Figure 14a and Table 7). The decline in richness and biomass in May corresponds to the decline of winter annuals in the community and an increase in the biomass and species richness of biennials, perennials, and summer annuals as the growing season progressed (Figure 13 and 14a). Annual and perennial monocots were less common than dicots throughout the season. The species biomass evenness index increased early in the season from 0.38 to 0.67, and then declined throughout the season to 0.49 (Figure 14b). The seasonal pattern of species biomass diversity reflected the richness and evenness patterns, peaking in May at 2.0 and then declining to 1.4 by mid-August (Figure 14c).

The peak in total community biomass in May corresponded to the early peak in richness, evenness and diversity. Early in the season there was a positive correlation between community biomass and the three diversity measures. As the season progressed total community biomass increased and the diversity measures declined, creating a negative association between community biomass and diversity. This pattern suggests that a biomass hierarchy developed during the growing season and that increasing biomass of the dominant species resulted in a decline in the three diversity measures. The dominant species, Conyza canadensis, increased from 3 percent of community biomass in May to 51 percent of community biomass in mid-August.

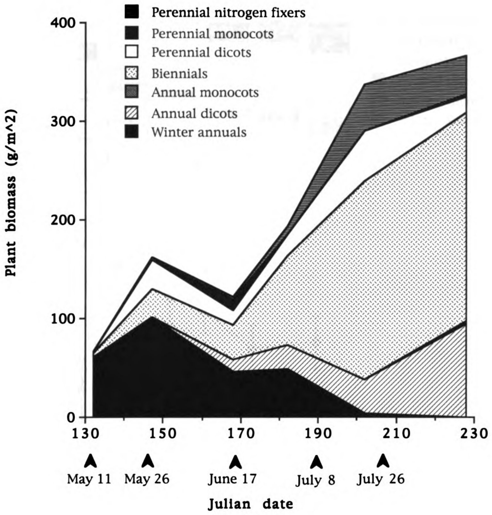


Figure 13. Seasonal pattern of above-ground biomass production of different life history groups in a second-year Michigan old-field (arrows indicate time of nitrogen addition).

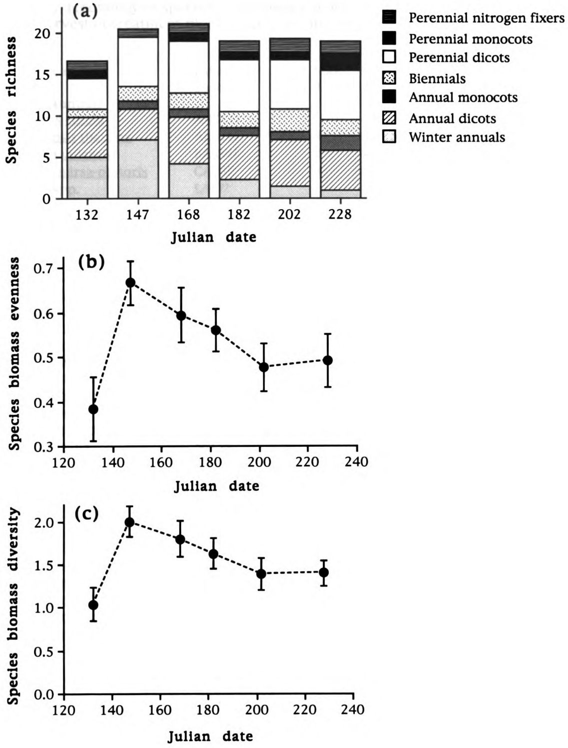


Figure 14. Seasonal patterns of a) species richness, b) biomass evenness, and c)biomass diversity in a second-year Michigan old-field.

Table 7. Frequency of species in phenology plots (maximum = 4 plots) and final harvest of treatment plots (August 16, maximum = 24 plots).

Scientific name	Bayer code	May 12	May 27	June 17	July 1	July 21	August 16
Winter annuals							
Anthemis cotula	ANTCO			2			
Arabidopsis thaliana	ARBTH	4	4				
Barbarea vulgaris	BARVU	2	4	3	4	4	24
Capsella bursa-pastoris	CAPBP	1	3				
Lactuca spp.	LAC??					1	
Lactuca serriola	LACSE		1	1	1	1	1
Lepidium campestre	LEPCA		2	3			
Lepidium densiflorum	LEPDE		2				
Lepidium virginicum	LEPVI	1					
Malva neglecta	MALNE				1		1
Stellaria media	STEME	4	4	4	2		
Veronica officinalis	VEROF	4	4	3	1		
Veronica peregrina	VERPG	4	4	1			
Summer annual grasses							
Panicum capillare	PANCA				1	1	3
Panicum dichotomiflorum	PANDI					1	6
Poa annua	POAAN						1
Setaria lutescens	SETLU		2	2	3	1	15
Setaria viridis	SETVI						2
Summer annual dicots							
Abutilon theophrasti	ABUTH	4	4	4	4	4	16
Amaranthus retroflexus	AMARE			2		2	1
Ambrosia artemisiifolia	AMBEL	4	4	4	4	4	24
Chenopodium album	CHEAL	4	4	4	4	4	24
Oxalis stricta	OXAST	1		4	4	4	24
Polygonum aviculare	POLAV			3	4	4	21
Polygonum persecaria	POLPE	2			1		9
Polygonum pensylvanicum	POLPY	4	3				1
Polygonum spp.	POLSPP			1			
Biennials							
Cirsium altissimum	CIRAL			1			
Cirsium vulgare	CIRVU		1				2
Erigeron anuus	ERIAN		4	4	4	4	22
Conyza canadensis	ERICA	3		3	4	4	24
Potentilla norvegica	PTLNO					2	
Verbascum thapsis	VESTH		2			1	3
Perennial grasses							
Agropyron repens	AGRRE			2			2
Dactylis glomerata	DACGL	2					
Juncus tenuis	IUNTE						1

Table 7 (cont'd).

Perennial grasses (cont'd)							
Poa compressa	POACO			2	1	1	5
Perennial dicots							
Achillea millefolium	ACHMI						2
Aster spp.	ASTPI						9
Cerastium vulgatum	CERVU	4	2	4	4	4	16
Unidentified composite	COM??		4	2			
Daucus carota	DAUCA		1		1		9
Hieracium spp.	HIE??	1					
Medicago lupulina	MEDLU					2	6
Medicago sativa	MEDSA						1
Silene alba	MELAL		1	1		2	2
Plantago lanceolata	PLALA					1	1
Potentilla argentea	PTLAG	2	4	4	4	3	24
Potentilla recta	PTLRC		1	1	2		5
Rumex crispus	RUMCR	2	1	2	3	1	10
Rumex obtusifolius	RUMOB		1	1			
Solanum nigrum	SOLNI						1
Solidago canadensis	SOOCA	1	2	4	4	4	24
Taraxacum officinale	TAROF	1	3	2	3	3	10
Specularia biflora	TJDBI					1	
Specularia perfoliata	TJDPE		2				
Viola spp.	VIO??		1	2	2	4	2
unidentified woody spp	WOODY	4	1	2	2	1	14
Perennial nitrogen fixers							
Trifolium hybridum	TRFHY				1		
Trifolium pratense	TRFPR						6
Trifolium repens	TRFRE	2	4	4	4	4	24

Effect of time of nitrogen addition on total community biomass, species richness, diversity and evenness

Total community biomass in the nitrogen addition treatments was twice that of the control for all five times of nitrogen addition (Figure 15). Community biomass in nitrogen addition plots was significantly greater than the control plots for all times of nitrogen addition except the last addition on July 26 (Table 8). Total community biomass increased most relative to the control when nitrogen was added mid-season on June 17, and the magnitude of biomass response to nitrogen declined when nitrogen was added later on July 8 and July 26. Total community biomass accumulation in the phenology plots was beginning to level off by mid-July (Figure 13); lower productivity may thus explain the weaker response of community biomass to nitrogen added later in the season.

There was no significant effect of the time of nitrogen addition on species richness at harvest ($F_{5,18} = 0.38$, $p = 0.85$; Figure 16a). Species biomass evenness was lower in the nitrogen addition treatments than in the control, but the effect of time of nitrogen addition was not statistically significant ($F_{5,18} = 1.35$, $p = 0.29$; Figure 16b). There was little variation in species biomass evenness with the time of nitrogen addition. The change in the diversity index reflected the change in the evenness index (Figure 16c). Species biomass diversity declined with each time of nitrogen addition relative to the control, but the effect of time of nitrogen addition was not significant ($F_{5,18} = 1.61$, $p = 0.21$; Figure 16c).

Responses of the dominant species and subordinate community

The clear biomass dominant in this community was _Conyza_ _canadensis_, a tall, erect, leafy-stemmed biennial (Figure 17). The biomass of _Conyza_

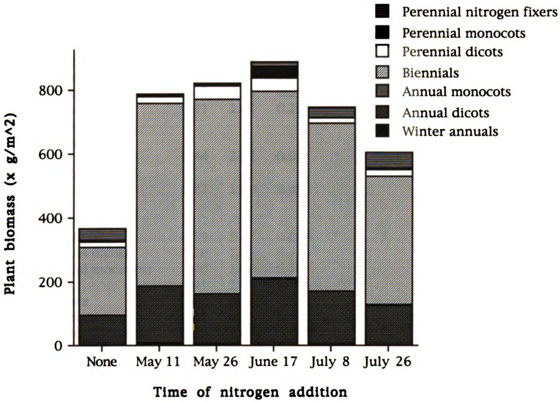


Figure 15. Above-ground plant community biomass by life history groups at harvest in control (no nitrogen added) and 5 times of nitrogen addition treatments in a second-year Michigan old-field.

Table 8. Results of analysis of variance for time of nitrogen addition on community biomass, species richness, biomass evenness, and biomass diversity (numerator df = 5, error df = 18). Dunnett's t-test was used to test for significant differences between the control and each time of nitrogen addition (* = significant at alpha = 0.05, df 18).

	ANOVA			Dunnett's t-test				
Variable	r^2	F	p	None v May 11	None v May 26	None v June 17	None v July 8	None v July 26
Community variables								
Total community biomass	0.63	6.06	0.002	*	*	*	*	
Species richness	0.10	0.38	0.85					
Biomass evenness	0.27	1.35	0.29					
Biomass diversity	0.31	1.61	0.21					
Dominant species (Conyza canadensis) biomass	0.44	2.82	0.05	*		*	*	
Subordinate community biomass	0.22	1.00	0.45					
Life history groups								
Winter annuals	0.59	5.17	0.004	*	*			
Summer annual dicots	0.26	1.26	0.32					
Summer annual monocots	0.40	1.90	0.16					
Biennials	0.41	2.49	0.07			*		
Perennial dicots	0.04	0.15	0.98					
Perennial monocots	0.20	0.17	0.91					
Perennial nitrogen fixers	0.80	13.95	0.0001	*	*	*		
Common species								
Barbarea vulgaris	0.65	6.79	0.001	*	*			
Ambrosia artemisiifolia	0.26	1.24	0.33					
Chenopodium album	0.13	0.53	0.74					
Oxalis stricta	0.39	2.31	0.09					
Potentilla argentea	0.16	0.66	0.66					
Solidago canadensis	0.10	0.40	0.84					
Trifolium repens	0.89	28.13	0.0001	*	*	*		

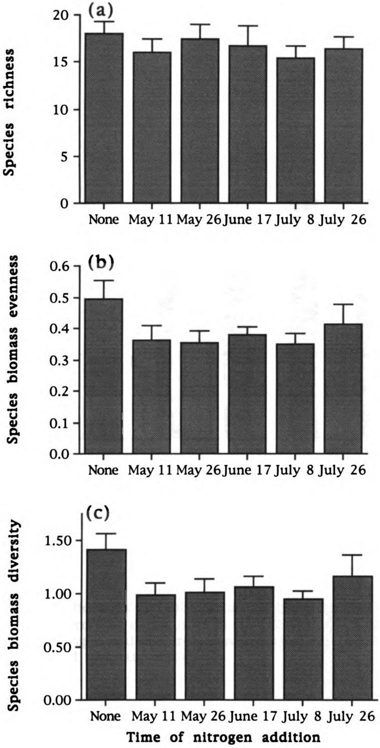


Figure 16. Species richness (a), species biomass evenness (b), and species biomass diversity (c) at harvest in control plots (no nitrogen added) and 5 times of nitrogen addition treatments in a second-year Michigan old-field (error bar = 1 standard error).

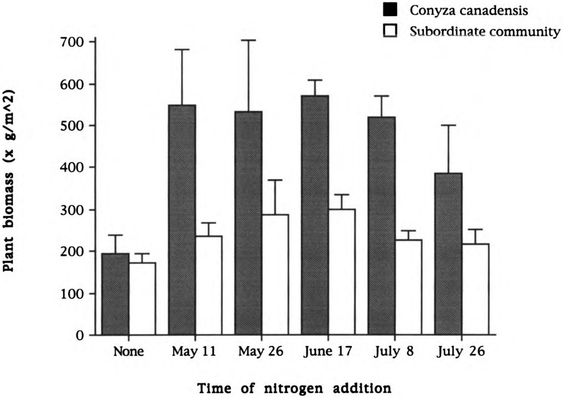
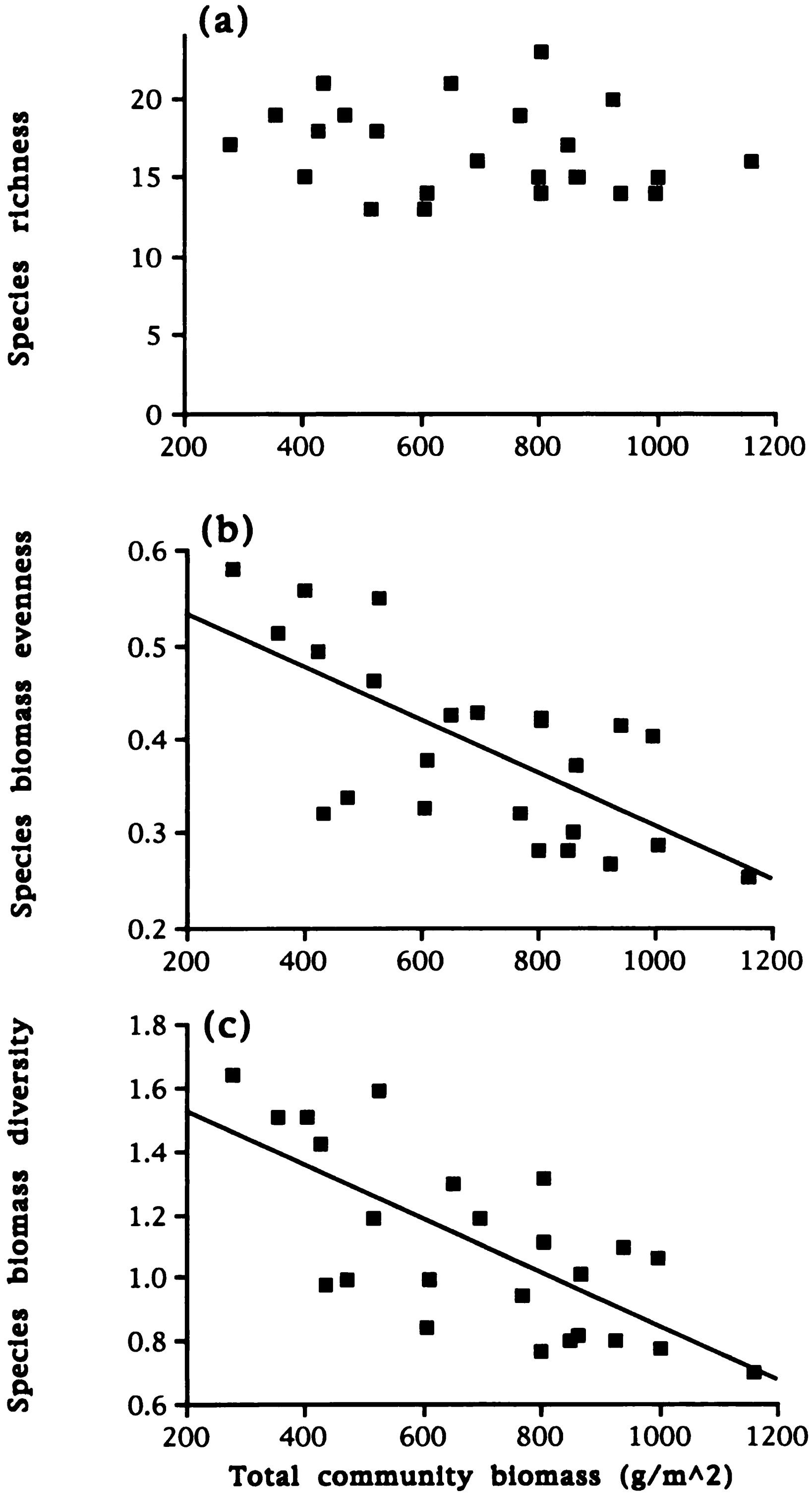


Figure 17. Above-ground biomass of the dominant species, Conyza canadensis, and the subordinate community in control plots (no nitrogen added) and 5 times of nitrogen addition treatments in a second-year Michigan old-field (error bar = 1 standard error).

canadensis doubled in response to each time of nitrogen addition (Figure 17). The effect of nitrogen addition on C. canadensis biomass was significant on the first (May 11), third (June 17), and fourth (July 8) nitrogen addition (Table 8). The magnitude of biomass response to the second (May 26) addition was as large as the response to other times of nitrogen addition, but there was too much variation in biomass with the second nitrogen addition to detect a difference. The subordinate community had a much smaller biomass response to the nitrogen additions than the dominant species (Figure 17). The biomass of the subordinate community was slightly higher in nitrogen addition plots than in the control plots, but the effect was not significant for any time of nitrogen addition (Table 8).

The reduction in evenness and diversity with nitrogen addition may have been a result primarily of the disproportionate increase in the biomass of the dominant species, Conyza canadensis. Species richness was not significantly related to total community biomass (Figure 18a) or to the biomass of C. canadensis (Figure 19a). However, community structure was closely related to total community biomass and the biomass of C. canadensis. Both evenness and diversity declined with increasing total community biomass (Figure 18b and c) and increasing biomass of C. canadensis (Figure 19b, c). The r^2 values for the regression of evenness and diversity on the biomass of C. canadensis (0.67 and 0.72, respectively) were higher than the r^2 values for the regression of evenness and diversity on total community biomass (0.47 and 0.50, respectively), suggesting that the biomass of the dominant species, C. canadensis, explained variation in evenness and diversity better than did total community biomass. The negative relationship between the biomass of C. canadensis and the measures of evenness and diversity suggest that increasing fertility, accompanied by increased biomass of the dominant



r2 = 0.05
F = 1.12
p = 0.30

r2 = 0.47
F = 19.18
p = 0.0002

r2 = 0.50
F = 22.08
p = 0.0001

Figure 18. Relationship between total community biomass per plot and a) species richness, b) species biomass evenness, and c) species biomass diversity.

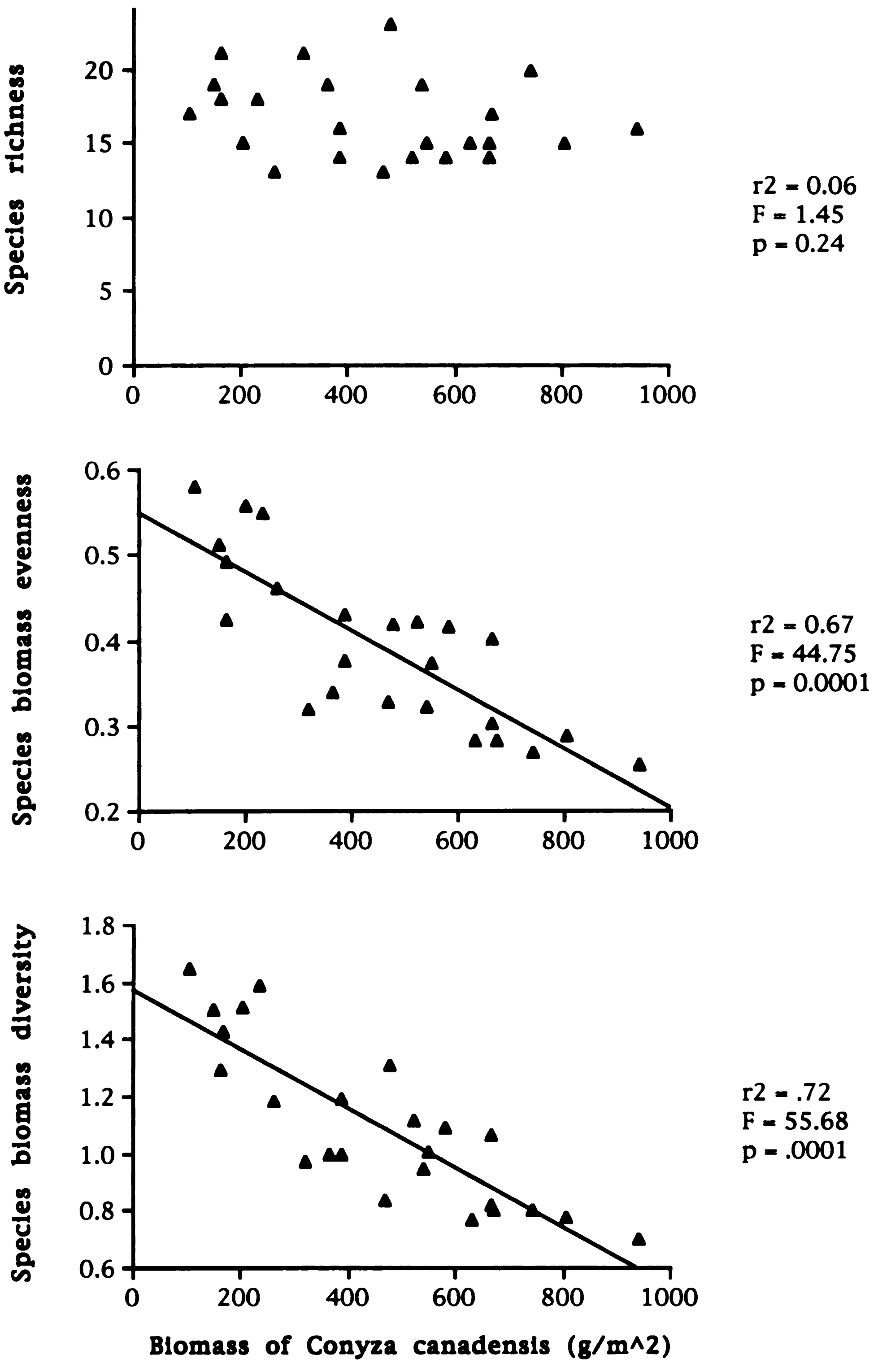


Figure 19. Relationship between biomass of the dominant species, Conyza canadensis, per plot and a) species richness, b) species biomass evenness, and c) species biomass diversity.

species, leads to decreased diversity in this plant community, but that there was not sufficient power to detect the effect of nitrogen statistically in the ANOVA in Table 8.

Responses of life history/growth form groups and individual species to the time of nitrogen addition

Although the effects of time of nitrogen addition on richness, evenness, and diversity were not significant, the response of several life history groups and individual species to the time of nitrogen addition varied significantly. The effect of time of nitrogen addition on the biomass of life history groups was significant for winter annuals, biennials, and perennial nitrogen fixers (Table 8). The biomass of winter annuals at harvest was significantly greater in the first and second nitrogen addition treatments than in the control (Figure 15, Table 8), but their biomass in later nitrogen addition treatments was not significantly greater than the control. The biomass of biennials increased significantly over the control only with the third nitrogen addition. The biomass of perennial nitrogen fixers decreased significantly relative to the control in the first, second, and third nitrogen addition treatments, but not with the fourth and fifth nitrogen addition. These differences among life history/growth form groups may have offset each other at the final harvest, resulting in no significant effect of time of nitrogen addition on the indices of species diversity and community structure. Because the diversity and evenness indices are based on the proportional biomass of individual species and because the growth phenology of species within life/history growth form groups varied (Table 7), I expected to find that individual species within life history/growth form groups differed in their response to the time of nitrogen addition.

Seven species in addition to the dominant species, *Conyza canadensis*, were chosen to analyze individual species responses to the time of nitrogen addition. These species were chosen because they were abundant in all replicates of all treatments (n = 24) and because they represent the most frequent and abundant life history/growth form groups in this community.

The effect of the time of nitrogen addition on the biomass of *Barbarea vulgaris*, a winter annual, was significant (Table 8). The biomass of *B. vulgaris* increased significantly in response to the first and second nitrogen addition, but not to the later nitrogen additions (Figure 20). The biomass of *Ambrosia artemisiifolia*, a tall erect summer annual, increased in response to all times of nitrogen addition (Figure 20), though the biomass response was not statistically significant (Table 8). *Ambrosia* was able to reach the canopy in this community and was the same height as *C. canadensis* during the growing season. There was no significant effect of time of nitrogen addition on the biomass of another erect summer annual, *Chenopodium album* (Table 8). In this plant community, *C. album* was common in the subordinate community but did not make it to the canopy. It accounted for only 1 to 4 percent of community biomass at harvest. The effect of time of nitrogen addition on the biomass of *Oxalis stricta*, a low-growing summer annual, was marginally significant (Table 8). *Oxalis stricta* tended to increase in biomass with the later nitrogen additions, but did not respond to the first two early nitrogen additions (Figure 20).

The effect of time of nitrogen addition on the biomass of two perennial species, *Potentilla argentea* and *Solidago canadensis*, was not significant (Table 8). However, these species provide examples of the response of two perennials with different growth forms and phenologies in this community. *Potentilla argentea*, has a short spreading growth form, and was an abundant member of

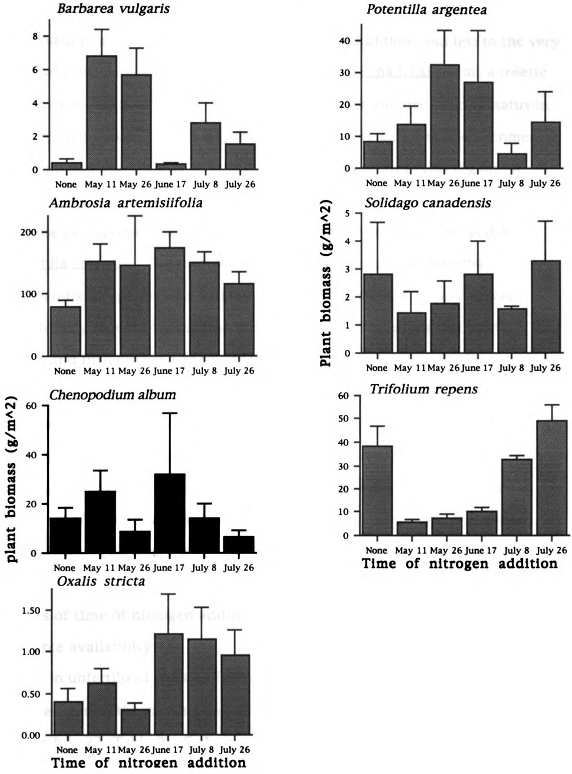


Figure 20. Above-ground biomass of seven common species in control plots and nitrogen addition treatments in a second-year Michigan old-field plant community (error bar = 1 standard error).

the subordinate community throughout the growing season (Table 7). It responded more to the second and third nitrogen additions and less to the very early and very late additions (Figure 20). *Solidago canadensis* forms a rosette and then develops to an erect growth form. It never attained canopy status in this growing season, though it grows to a height of at least 1 m and becomes the dominant species later in later successional old-fields in this region. It tended to be suppressed by nitrogen additions early in the season and did not increase in response to any times of nitrogen addition (Figure 20) as did *Potentilla argentea*. The response of *Trifolium repens*, a low-growing, nitrogen-fixing species, was striking (Table 8). Its biomass at harvest was significantly reduced by the first three nitrogen additions and not by the fourth and fifth nitrogen additions (Figure 20). This variation in the responses of life history/growth forms and several individual species suggests that the position in the canopy and time of active growth relative to the development of the biomass hierarchy may influence access to resources and plant growth in this plant community. The absence of a response in the measures of community structure (evenness and diversity) obscured these individual species responses.

Effects of time of nitrogen addition on seasonal patterns of resource availability

In unfertilized plots, soil mineral nitrogen levels (NO_3-N + NH_4-N) declined during the growing season from 3.3 ug/g soil on June 2 to 2.5 ug/g soil on July 22 (Table 9). Soil ammonium concentrations in unfertilized plots were 2 to 4 times higher than soil nitrate concentrations throughout the growing season (Table 9). In this community experimental nitrogen addition at different times of the growing season provided a transient increase in

Table 9. Seasonal patterns in average soil nitrate and ammonium concentrations (ug N/g soil) in control (no nitrogen addition) and nitrogen addition treatments in a second-year Michigan old-field.

Time of soil sample	June 6		June 16		July 6		July 22	
	NO_3-N	NH_4-N	NO_3-N	NH_4-N	NO_3-N	NH_4-N	NO_3-N	NH_4-N
Time of N addition								
No N	1.2	2.1	0.4	1.4	0.4	1.7	0.7	1.8
May 11	44.1	43.5	12.3	10.8	1.2	2.3	1.3	1.8
May 26	50.4	44.4	16.5	17.0	0.2	1.7	0.8	1.8
June 17	2.7	2.0	0.8	1.5	4.4	7.1	0.5	3.1
July 8	1.8	2.3	0.8	1.7	0.9	2.2	32.8	34.8
July 26	1.2	2.1	0.3	1.9	0.2	1.4	0.9	1.5

available soil nitrogen. Addition of 32 g/m^2 of ammonium nitrate to the experimental plots increased mineral nitrogen availability by an order of magnitude (Figure 21, May 11 and 26 additions). By the end of the season, however, nitrogen levels had declined to similar levels in the control and early season nitrogen addition treatments, suggesting that plants could deplete soil nitrogen to similar levels in unfertilized control plots and fertilized treatment plots or that the losses of nitrogen to plant uptake, leaching, denitrification

and microbial immobilization were equivalent in both control and nitrogen addition treatments.

The patterns of mineral nitrogen levels in Figure 21 suggest that the plant community was depleting soil nitrogen faster in the middle of the growing season (June) than early in the growing season (May). When plots were fertilized early in the season (May 11) total mineral nitrogen in these plots was 87.6 ug N/g soil within 23 days after the ammonium nitrate addition. In contrast, later in the season (mid-June addition) the plant community drove soil mineral nitrogen to 7.1 ug N/g soil within 19 days after adding ammonium nitrate. This assumes that losses of nitrogen to leaching, denitrification, and microbial immobilization were minimal relative to plant uptake.

Potential nitrogen mineralization rates declined between June 2 and July 22 regardless of the time of nitrogen addition (Figure 22). Thus, both nitrogen availability and the rate of nitrogen supply declined during the growing season. The nitrogen mineralization rate of plots fertilized on July 8 was greater than the control on July 22, suggesting that the microbial community may have been nitrogen-limited in mid-July.

Soil moisture in the control and treatment plots increased from June 2 to June 16 and then decreased by July 22 (Figure 23). By the July 6 and 22

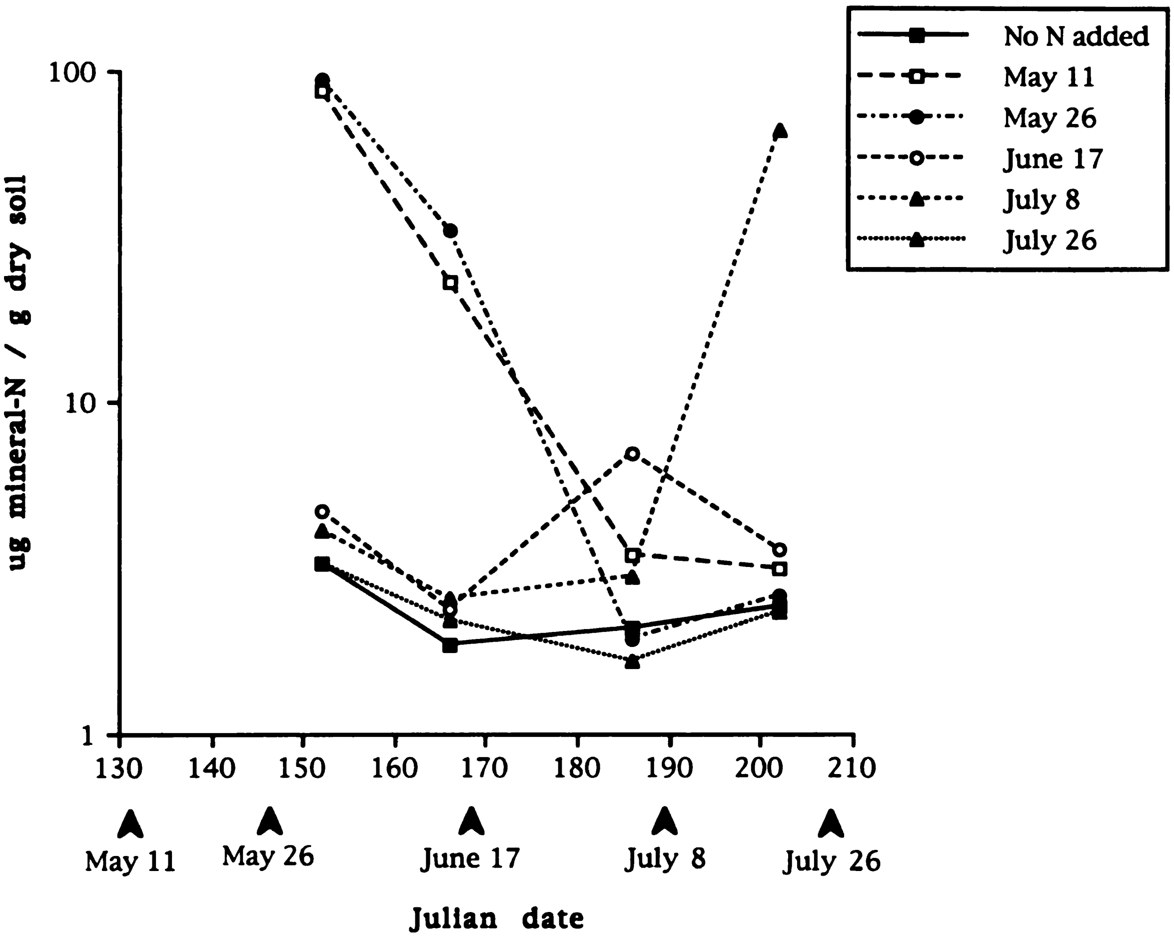


Figure 21. Seasonal patterns of mineral nitrogen levels (NO_3-N + NH_4-N) in control plots and 5 times of nitrogen addition treatments in a second-year Michigan old-field. Arrows indicate time of nitrogen addition. Note the log scale on the y-axis.

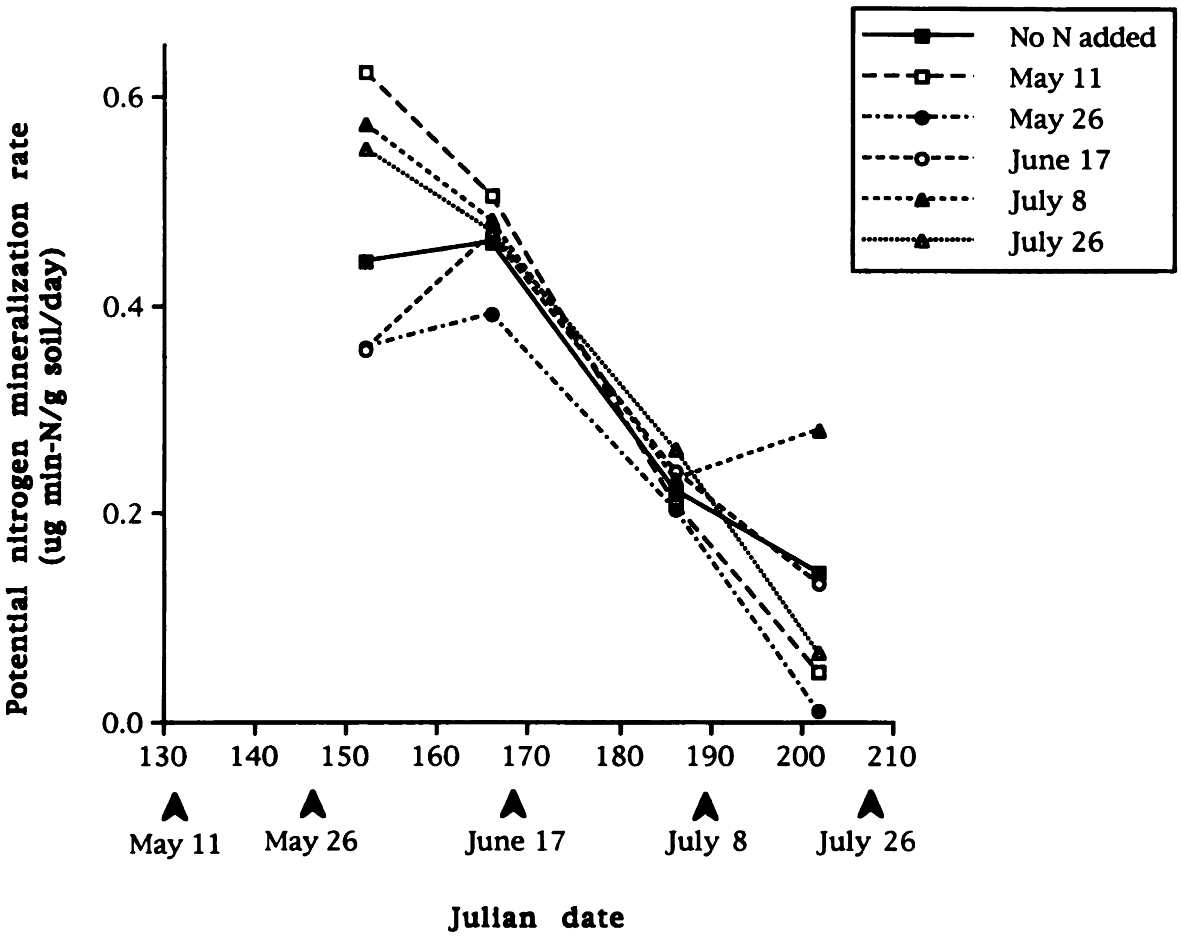


Figure 22. Seasonal patterns of potential nitrogen mineralization rate in control plots and 5 times of nitrogen addition treatments in a second-year Michigan old-field. Arrows indicate time of nitrogen addition.

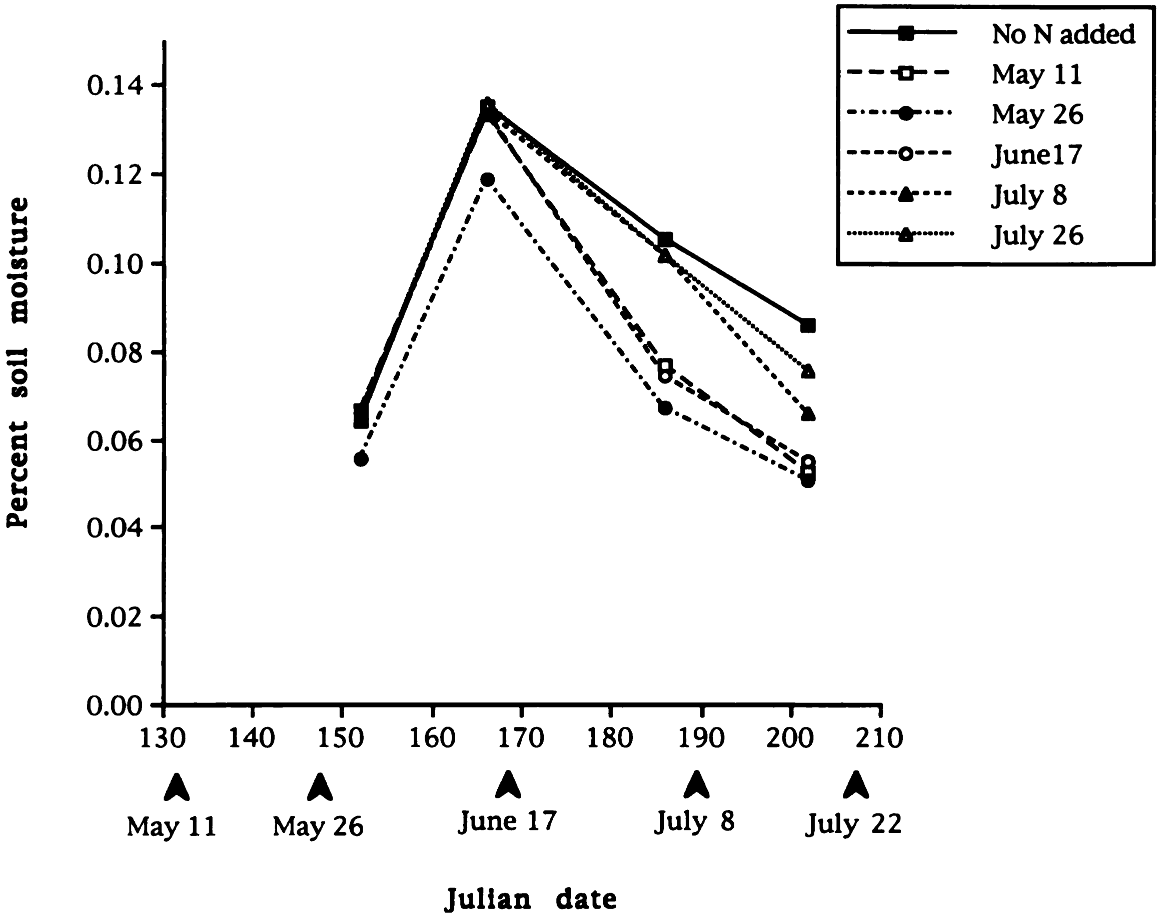


Figure 23. Seasonal patterns of soil moisture in control plots and 5 times of nitrogen addition treatments in a second-year Michigan old-field. Arrows indicate time of nitrogen addition.

sampling date, soil moisture was lower in plots fertilized early in the season on May 11, May 26 and June 17 than in control plots and the treatments fertilized later in the season. This suggests that soil moisture was depleted more in plots that had higher plant biomass.

Percent light penetration to the soil surface declined from a grand mean of 80% in mid-May to 19% in mid-August (Figure 24). The most rapid light depletion in control plots occurred between mid-June and mid-July when above-ground plant productivity was greatest (Figure 13). The time of nitrogen addition influenced the rate, magnitude, and timing of light depletion. Light was depleted earlier, more rapidly, and to a lower level in plots with early nitrogen additions (May and June) than in the control plots (Figure 24). The earlier in the season that nitrogen was applied the earlier in the season light penetration to the soil surface was depleted. The rank of percent light penetration to the soil surface on June 23 corresponded to the time of nitrogen addition up to that time; light was depleted to the lowest level when nitrogen was added May 11. It is important to note that although there were effects of the time of nitrogen addition on light penetration at mid-season (June 16 and 23), light levels were depleted to similar levels in all treatments by mid-July and remained low until the last measurement in mid-August.

DISCUSSION

The results of the phenology study showed that: 1) a species biomass hierarchy developed, 2) species diversity and evenness declined , and 3) species composition changed during the growing season in this second-year old-field. These patterns create the potential for variation in response of community structure to the time of nitrogen addition. The nitrogen addition

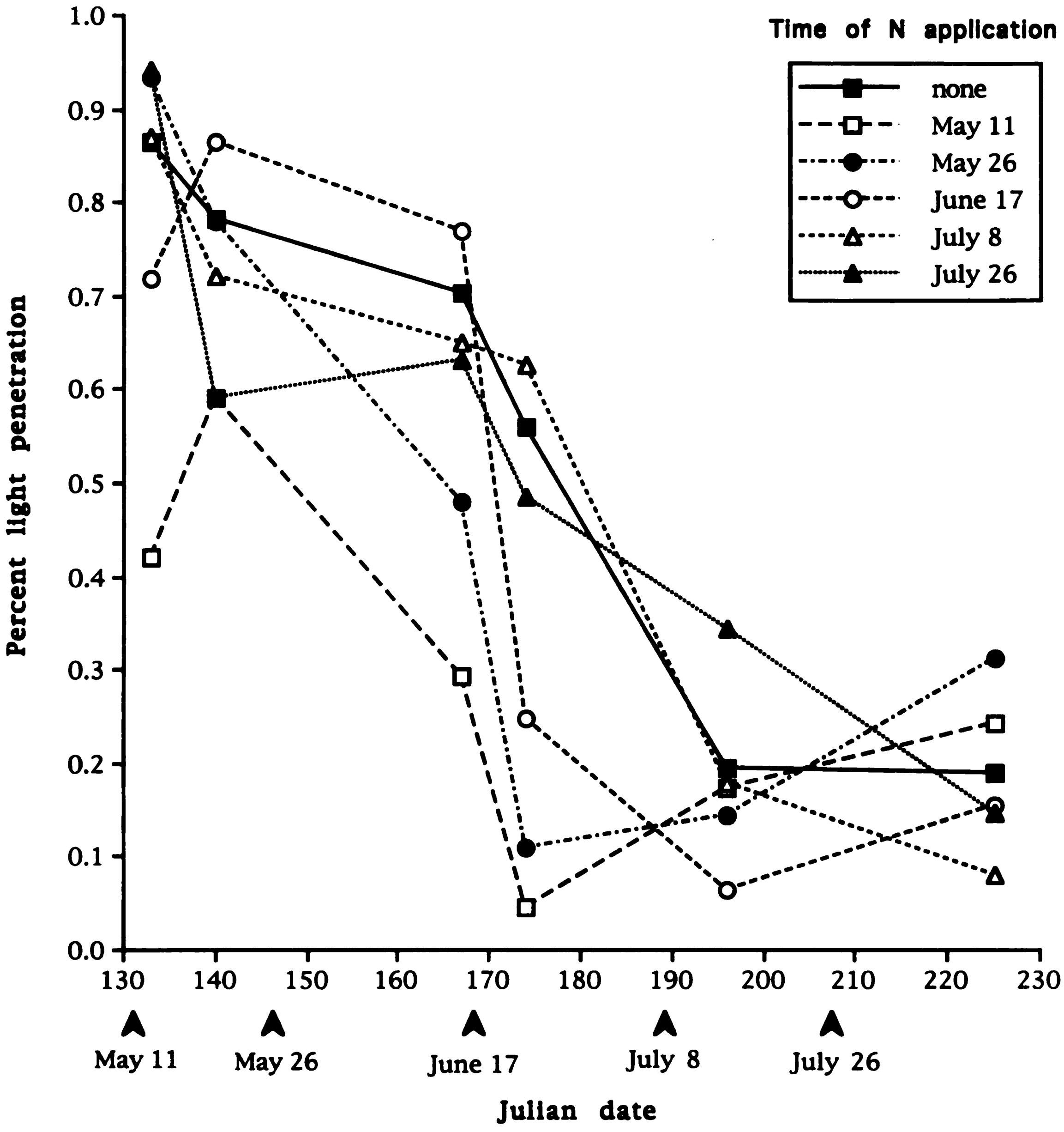


Figure 24. Seasonal patterns of light penetration to the soil surface in control plots and 5 times of nitrogen addition treatments in a second-year Michigan old-field. Arrows indicate time of nitrogen addition.

study showed that: 1) species richness, evenness, and diversity at the final harvest did not vary significantly with the time of nitrogen addition, 2) *Conyza canadensis*, a tall biennial, dominated community biomass and was associated with the reduction in biomass evenness and diversity, 3) variation in the response of individual life history/growth form groups and individual species to the time of nitrogen addition did occur and obscured changes in the diversity indices, and 4) although there are transient nitrogen addition treatment effects on mineral nitrogen levels, *nitrogen mineralization rates?*, and light levels, these resource levels decline to the same low levels in control plots and nitrogen addition plots by the end of the season.

Seasonal development of community structure

From mid- to late May species richness, evenness, and diversity increased with increasing total community biomass. After this early season peak, species richness, evenness, and diversity declined as total above-ground community biomass increased until the final harvest in mid-August. The observed seasonal decline in species biomass evenness demonstrates that a biomass hierarchy developed in this plant community during the growing season. Biomass was more equitably distributed across species early in the season than late in the season. Similar patterns of decline in species evenness over the growing season have been observed in other old-field studies (Bakelaar and Odum 1978, Wakefield and Barrett 1979, Hyder and Barrett 1986, Carson and Barrett 1988). Because individual plant biomass is an important plant trait determining competitive ability, (Gaudet and Keddy 1988, review by Goldberg and Barton 1992), the seasonal development of the biomass hierarchy among species may influence the strength of competitive interactions and the ability of different members of the community to respond to a nutrient pulse. Miller and Werner (1987) suggested that competitive interactions may be less intense earlier in the season when plants are small and do not overlap spatially. If the degree of development of a biomass hierarchy determines access to resources or success in converting resources to biomass, then the subordinate species may have better access to added nutrients earlier in the season than later in the season when dominance (in height and/or biomass) by a few species is well established.

Species composition also changed seasonally in this plant community. Winter annuals dominated early in the season and biennials, perennials, and summer annuals later in the season. Within these life history groups, there was also variation in the growth phenology of species. The results of the phenology study describe a community with the potential of species to respond to a nutrient pulse depending on the stage of their growth phenology and the development of the biomass hierarchy of competitors.

Effects of time of nitrogen addition on community structure

In this study applying nitrogen at different times of the growing season caused an increase in soil resources at different stages of development of the plant biomass hierarchy. Although nitrogen addition reduced biomass evenness and diversity in this community, the time of the nitrogen addition did not influence species richness, biomass evenness, or biomass diversity. This suggests that the degree of development of the biomass hierarchy as documented in the phenology study did not influence the overall response of community structure to the time of nitrogen addition. However, community level measures of diversity and structure, such as the Shannon diversity index and the Pielou evenness index do not account for changes in species composition or changes in rank abundance of species in a community (Heske et. al 1993).

Although the time of nitrogen addition did not influence diversity and community structure it did influence the final biomass of life history/growth form groups and individual species. The response of life history/growth form groups and individual species can be related to their growth phenology and their position in the developing biomass hierarchy. Winter annuals, and Barbarea vulgaris in particular, increased biomass significantly with the early season nitrogen additions. These positive responses corresponded to the time of active growth of winter annuals in this community and with a relatively poorly developed biomass hierarchy early in the season (i.e. high evenness). Light availability was high in early May and the summer annuals and biennials had just begun to increase in biomass. The response of winter annuals to the early nitrogen additions was probably larger than indicated by the final harvest because most of the winter annuals appeared to increase biomass in response to early nitrogen additions but they did not persist to the final harvest.

The perennial species were subordinate members of the community for most of the growing season in this second-year old field. As a group, perennial dicots did not respond significantly to the time of nitrogen addition. The responses of Potentilla argentea, a perennial dicot, to the time of nitrogen addition were similar to those of Barbarea vulgaris, a winter annual. Potentilla argentea tended to increase in biomass relative to the controls in response to early season nitrogen additions but not to later nitrogen additions. Potentilla argentea appeared in the phenology samples early in the season before a canopy of Conyza canadensis and summer annuals developed. Thus, P. argentea may have been able to respond to nitrogen additions before becoming light limited by the canopy later in the season.

In contrast, another perennial, *Solidago canadensis*, did not increase in biomass relative to the control in response to nitrogen addition and tended to be suppressed by early season nitrogen additions. Though *Solidago canadensis* has a tall erect growth form as an adult and often dominates old-field communities later in succession (Bazzaz 1990), as a juvenile in early successional fields it has a rosette growth form and a relatively slow growth rate (Bazzaz 1990). It did not appear frequently in the phenology samples until mid-June. Thus, due to its growth phenology and subordinate position in the biomass hierarchy at this stage of succession *Solidago canadensis* could not turn added nitrogen into biomass within this growing season. However, because it can store nitrogen acquired this season in structural roots, it does have a growth advantage early the following growing season (Bazzaz 1990).

Among the subordinate community, *Trifolium repens*, a low-growing nitrogen-fixing perennial, showed the strongest biomass response to the time of nitrogen addition. The final biomass of *T. repens* was significantly lower in the first three nitrogen addition treatments than in the control plots. However, *T. repens* biomass was equivalent in the two later nitrogen addition treatments and in the control plots. The final biomass of *T. repens* increased as nitrogen additions came later in the season. *Trifolium repens* grew early in the season before the summer annuals, biennials, and perennials emerged, and it has an extended period of growth following flowering early in the season. Early nitrogen additions may have increased the growth and competitive effect of *Conyza canadensis* and some of the taller subcanopy species on *T. repens*. Nitrogen-fixing species tend to be shade intolerant. Thus, delaying nitrogen additions may have delayed the effect of the dominant species on *T. repens* by delaying the depletion of light near the soil surface. This correlation between light availability, growth of the dominant and, growth of *T. repens* would need to be tested by experimentally removing canopy species. However, the response of *T. repens* in this study is consistent with the dominance of nitrogen fixers in low nutrient high light conditions and a decline in their abundance in high nutrient low light conditions (Tilman 1982).

In this study it appears that the variation in growth phenology and position in the biomass hierarchy led to different responses among species and life history/growth form groups to the time of nitrogen addition. The responses of individual species to the time of nitrogen addition appear to have offset each other, resulting in no effect of the time of nitrogen addition on the indices of diversity and community structure. This result contrasts with a study in a newly abandoned old-field plant community dominated by summer annuals where the seasonal time of nitrogen addition influenced the biomass evenness and diversity of the community at harvest (Chapter 2). Germination and growth in the first-year old-field dominated by annuals was relatively synchronous compared to the second-year old-field in this study. There was no winter annual component in the annual old-field community because they were removed by plowing and discing in early May. Biennials and perennials were also rare in the summer annual community. Thus, there was little opportunity for early growing and late growing species to offset each other in their responses to the time of nitrogen addition. The members of the competitive hierarchy in the annual old-field were established early and maintained throughout the growing season.

Seasonal patterns of resource availability

To my knowledge this is the first study of the effects of the time of nitrogen addition on above- and below-ground resource availability measured at several times during the growing season in a natural plant community. Most studies have measured resource availability late in the season near the time of harvest of the plant biomass and have been able to show significant effects of nutrient additions or disturbance on light or soil nitrogen levels (e.g. Tilman 1987, Goldberg and Miller 1990, Wilson and Tilman 1991a, 1991b). However, the seasonal variation in both light, mineral nitrogen availability, and nitrogen supply rate in this study demonstrates that single measurements of resource availability within a season do not adequately describe resource availability and may obscure the effects of experimental treatments on resource availability. Wilson and Tilman (1993) also found seasonal variation in light penetration and mineral nitrogen availability in a nitrogen-poor sand plain in Minnesota.

Mid-season levels of light penetration to the soil surface declined when nitrogen was added to this plant community. By late July, however, light penetration to the soil surface was similar in fertilized and control plots. Thus, if light measurements had been taken only at the end of the growing season, the conclusion would have been that nitrogen addition had no effect on light availability at the soil surface. The patterns of light availability in this study contrast with those of Tilman (1984, 1987) and Wilson and Tilman (1993), where the unfertilized plant community did not deplete light availability as low as did the fertilized community by September and October. In the Minnesota sand plain, light penetration to the soil surface declined when nitrogen was added but the difference between fertilized and unfertilized plots was maintained from mid-July through October. The vegetation on the Minnesota sand plain has lower biomass and height than the vegetation in the old-field in this study. Thus, the unfertilized sand plain vegetation may not deplete light availability to the levels observed in the unfertilized plots in this study. Light availability at the soil surface in unfertilized plots in the Tilman (1984) study was 87% of light availability above the canopy in July. In the Wilson and Tilman study (1993) light penetration to the soil surface was 35-45% of incident radiation. In contrast, mean light penetration in August in unfertilized plots in this Michigan old-field site was much lower (19%).

This study also demonstrated the direct link between the time of nitrogen addition and the timing of light depletion. Delaying nitrogen addition delayed the depletion of light availability at the soil surface. Early season nitrogen addition lead to an earlier, more rapid, and a greater magnitude of light depletion than later season nitrogen additions. It appears that if nitrogen is added when the plant community growth rate is highest, then light is depleted more rapidly.

Mineral nitrogen concentrations (= resource availability) and potential nitrogen mineralization rates (= resource supply rate) declined during the growing season in both fertilized and unfertilized plots. While the nitrogen additions increased mineral nitrogen availability immediately following the addition, nitrogen levels were depleted to the same low level in fertilized and control plots by July. Assuming that losses to leaching, denitrification, and microbial immobilization were minimal, these results indicate that the plant community could take up the added nitrogen rapidly and that increased soil fertility by adding ammonium nitrate was maintained only over brief periods. Thus, these different times of nitrogen addition functioned as pulses of resource availability in this plant community.

Several studies have shown that mineral nitrogen availability and nitrogen mineralization vary seasonally in grasslands (Davy and Taylor 1974, 1975, Gupta and Rorison 1975, Taylor et al. 1982), sand dunes, and old-fields (Robertson and Vitousek 1981). But few studies in natural plant communities have documented mineral nitrogen levels (Wilson and Tilman 1993) or nitrogen mineralization rates (Pastor et al. 1987) over the growing season in fertilized and control plots. Wilson and Tilman (1993) also found that, by September and October, nitrogen was depleted to about 1 ug/g soil in both fertilized and control plots in a Minnesota sand plain. This demonstrates the potential for soil nitrogen levels to be depleted to the same low levels in habitats of differing productivity and the potential for nitrogen to become more limiting to plant productivity as the growing season progresses. Pastor et al. (1987) also found that nitrogen mineralization varied with month of the year, but that nitrogen additions did not affect nitrogen mineralization rates except in the oldest field (>100 yr).

CHAPTER 4

RESPONSE OF A SPECIES BIOMASS HIERARCHY TO EXPERIMENTAL TREATMENTS: A GRAPHICAL AND STATISTICAL METHOD

INTRODUCTION

There is a growing interest in evaluating the influence of competitive interactions among species at the community level (Goldberg 1994). However, there is a lack of experimental designs and analytical approaches to examine the response of many individual species to an experimental treatment. There are numerous indices available to ecologists for evaluating the impact of experimental treatments or environmental perturbations on species diversity and community structure (Magurran 1988). For example, species richness can be used to evaluate whether the number of species present in a community responds to a treatment. Diversity indices, such as the Shannon (H') and Brillouin (HB) indices, incorporate the number of species and their relative abundance. The Pielou evenness index quantifies how evenly abundance (in biomass or numbers) is distributed across species. To measure convergence and divergence in community composition, similarity indices, such as the Sorenson or Jaquard indices, are commonly used. Log abundance curves can be used to detect whether the proportional abundance of dominant or subordinate species changes with treatment. Rank statistics, such as Kendall's coefficient of rank correlation, can test whether the order of species abundance remains constant in response to the treatment. However, the identity of individual species is lost in all of these analyses of species diversity and community structure. An experimental treatment may result in no change in the species richness, the Shannon index or the Pielou evenness index, while changes do occur in individual species rank abundance (Samson et. al 1992, Heske et. al 1993). None of these community level indices allow us to examine individual species abundance responses in a multi-species context. Nor do they permit a determination of whether the responses of species to a treatment are dependent on some characteristic of the species.

In this chapter, I describe a graphical and statistical method to address two null hypotheses about the response of a species abundance hierarchy to an experimental treatment or an environmental perturbation. The first null hypothesis is that there is no change in the hierarchy of species abundance in response to an experimental treatment. The second null hypothesis is that the magnitude and direction of the response of species to a treatment is independent of their abundance in the control (or pre-perturbation treatment).

The question of whether the absolute or relative response is more appropriate for measuring species response to competition has raised a major controversy in the literature in recent years (Campbell and Grime 1992, Grace 1993, Wilson and Tilman 1993, Goldberg 1994, Reader et. al 1994). This problem extends to measuring the response of species to any experimental treatment or environmental perturbation. The absolute and relative responses of species to a treatment may differ and lead to conflicting results and conclusions. For example, species A may increase from 0.5 in the control to 1.0 in the treatment, and species B may increase from 5.0 to 5.5. The absolute responses of the two species are equivalent (0.5), but the response of species A relative to the control value (100%) is larger than that of species B (10%). It is not yet clear theoretically when to use absolute or relative changes in abundance. We are only beginning to accumulate empirical patterns of absolute and relative responses of species to competition in the literature. Therefore, in this chapter, I calculate both the absolute and relative measures of species responses to an experimental treatment.

Specifically, I examine the response of species in old-field communities to nitrogen additions. The importance of biomass as a predictor of competitive ability and the potential for asymmetric and transitive competitive interactions suggest that the species responses to nitrogen additions should be dependent upon the biomass of the species in the control. The biomass of a species is an important predictor of competitive ability in plants (Miller and Werner 1987, Gaudet and Keddy 1988 and references therein, review by Goldberg and Barton 1992). On a population level, Wiener and Thomas (1986) concluded that asymmetric competition is common in plant monocultures and leads to size hierarchies in annual plant populations (Weiner and Solbrig 1984 and Weiner 1985). On a community level, Miller and Werner (1987) showed that, in an annual old-field plant community, competitive interactions were primarily asymmetric. Keddy and Shipley (1989) reviewed eight published experiments and found that pairwise interactions were asymmetric and that competitive interactions were transitive (for competing species A, B, and C, if the effect of A on B > the effect of B on A, and the effect of B on C > the effect of C on B, then the effect of A on C > the effect of C on A).

The graphical and statistical method described in this chapter addresses three specific questions about species responses to nitrogen addition in old-field plant communities. First, does the hierarchy of species abundances in the control plots remain constant when nitrogen is added at different times of the growing season? Second, does the magnitude and direction of species responses to the nitrogen addition depend on the abundance of the species in the control (i.e. do more abundant species have a larger response to the nitrogen addition than do rare or less common species)? Third, are the patterns of absolute and relative responses to nitrogen addition similar among species of different abundance? In this chapter, I first present a graphical and statistical approach to testing the second null hypothesis. Then I test the efficacy of this method using data from a species removal and nitrogen addition experiment in a newly abandoned old-field (Chapter 2) and a nitrogen addition experiment in a second-year old-field (Chapter 3).

METHODS

Testing rank correlation of species abundances

I used Kendall's coefficient of rank correlation in this analysis to test the first hypothesis of whether the rank order of species is the same in the control and treatment plots. The mean species biomass values across four replicates within a treatment were ranked in descending order. The CORR procedure in SAS version 6 (SAS 1989) was used to test for correlations between the rank order of species abundance in control plots and nitrogen addition treatments. Only species that were present in both the control and nitrogen addition treatment within a comparison were used in the correlation analysis.

Graphical and statistical analysis

To test the second null hypothesis that the magnitude and direction of species biomass responses to the nitrogen addition are independent of the abundance of the species in the control plots, the absolute biomass response to the nitrogen addition treatment was plotted against the mean species biomass in the control (see example in Figure 25). The absolute biomass response is $\Delta B = B_t - B_c$, where B_t is the mean biomass of the species in the treatment, and B_c is the mean biomass of the species in the control. Only the species that are present in both the control and treatment are included in the regression. Thus, this method is most appropriate for situations where species composition in the control and treatment are similar and the communities are relatively species rich so that there are a sufficient number of data points for a regression.

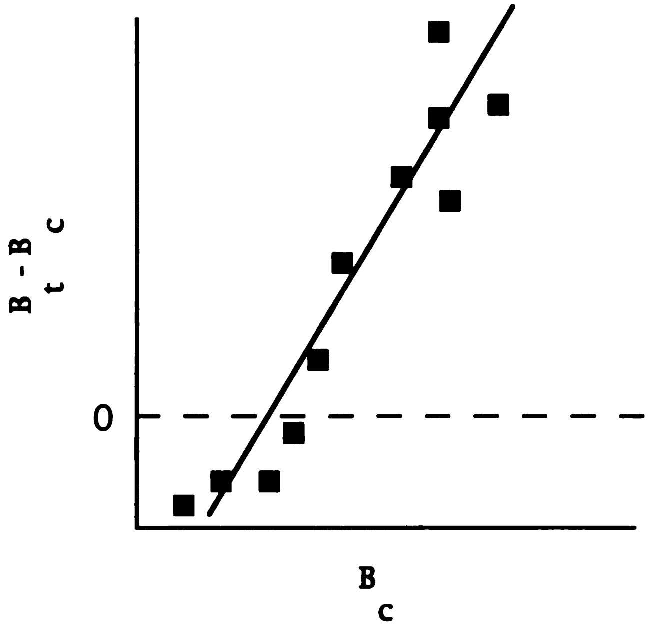


Figure 25. Absolute biomass response to an experimental treatment. Each point represents a single species. The dashed line represents no change in species abundance in response to the treatment. Points above the dashed line represent species that increased in response to the treatment; points below the line represent species that decreased in response to the treatment. The solid line is the fitted regression line through the data.

The null hypothesis that the species biomass responses to the treatment are independent of their biomass in the control plots is the line of slope = 0, indicated by a dashed line in Figure 25. The y-intercept may be greater than or equal to zero. Points above the dashed line in Figure 25 represent species that increase in biomass in response to the treatment. Points below the dashed line represent species that decrease in biomass in response to the treatment. The slope of the fitted regression line, a solid line in Figure 25, indicates whether the magnitude and direction of species biomass responses to the treatment are dependent on their biomass in the control plots. The criterion for rejecting the null hypothesis is provided by the standard regression analysis testing whether the slope and y-intercept are different from zero.

Several examples of potential absolute biomass responses are illustrated in Figure 26. The dashed line represents the null hypothesis. In Figure 26a, the slope of the regression, represented by a solid line, equals zero and the intercept is significantly greater than zero. The interpretation of this response is that species of all abundances in the control plots increased in biomass by the same absolute amount in response to the treatment and this response was independent of the biomass of the species in the control. In Figure 26b, the y-intercept = 0, and the slope of the regression is significantly greater than zero. The interpretation of this response is that the absolute response of species to the treatment was dependent on their abundance in the control plots. Species of all abundances in the control plots increased in biomass in response to the treatment, but the absolute responses of the more abundant or dominant species were larger than that of the least abundant species. In Figure 26c, the slope of the regression is significantly greater than zero, and the y-intercept is significantly less than zero. In this case, the absolute responses of the species are dependent on their biomass in the

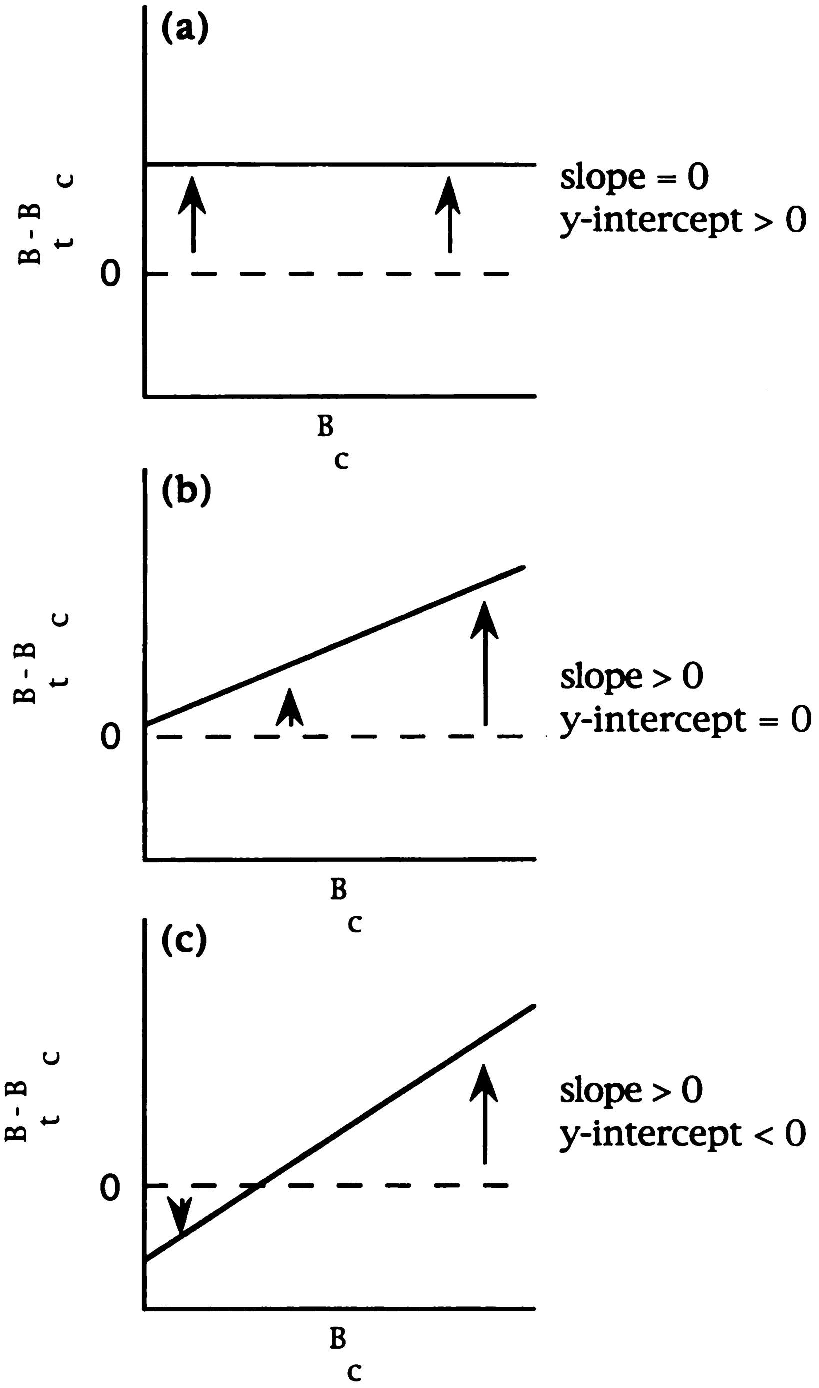


Figure 26. Potential responses of species to an experimental treatment. The dashed line represents the null hypothesis and the solid line represents the fitted regression line. In (a), all species increase in biomass in response to the treatment and the magnitude of their response is independent of their biomass in the control. In (b), the biomass of species of all abundances increased and species of larger biomass in the control have larger magnitudes of response in the treatment. In (c), species of low abundance in the control decrease in biomass and species of high abundance in the control increase in biomass in response to the treatment.

control. However, the more abundant or dominant species increase in biomass and the least abundant species decrease in biomass in response to the treatment.

The r^2 value of the fitted regression line indicates the degree of random variation of species responses to the treatment. A small r^2, associated with a large amount of scatter, indicates that the magnitude and/or direction of the response of different species to the treatment varied randomly with respect to their abundance in the control plots. Various response patterns could produce a low r^2 value. For example, all of the species responses to the treatment could be positive, but the magnitudes of response could vary independently of the biomass of species in the control plots. Or, the responses could be both positive and negative, but vary randomly with respect to abundance in the control plots.

To test whether the relative biomass response of species to the treatment is dependent on the biomass of species in the control, the relative biomass response, $\%\Delta B$, can be calculated by dividing the absolute biomass response by the biomass of the species in the control, $(B_t - B_c) / B_c$. Figure 27 shows several potential relative biomass responses that are analogous to the responses in Figure 26. In Figure 27a the subordinate species have a larger relative biomass response than the dominant species. Although species of all abundances in the control increase by the same absolute amount (Figure 26), the absolute response is a larger proportion of subordinate species biomass. The slope is less than zero and the y-intercept is greater than zero. In Figure 27b, the relative biomass response to the treatment is equal for species of all abundances in the control. The slope = 0 and the y-intercept is positive. Whether the slope = 0 in this case depends on the magnitude of the slope of the response in Figure 27b. In Figure 27c the relative response is large and

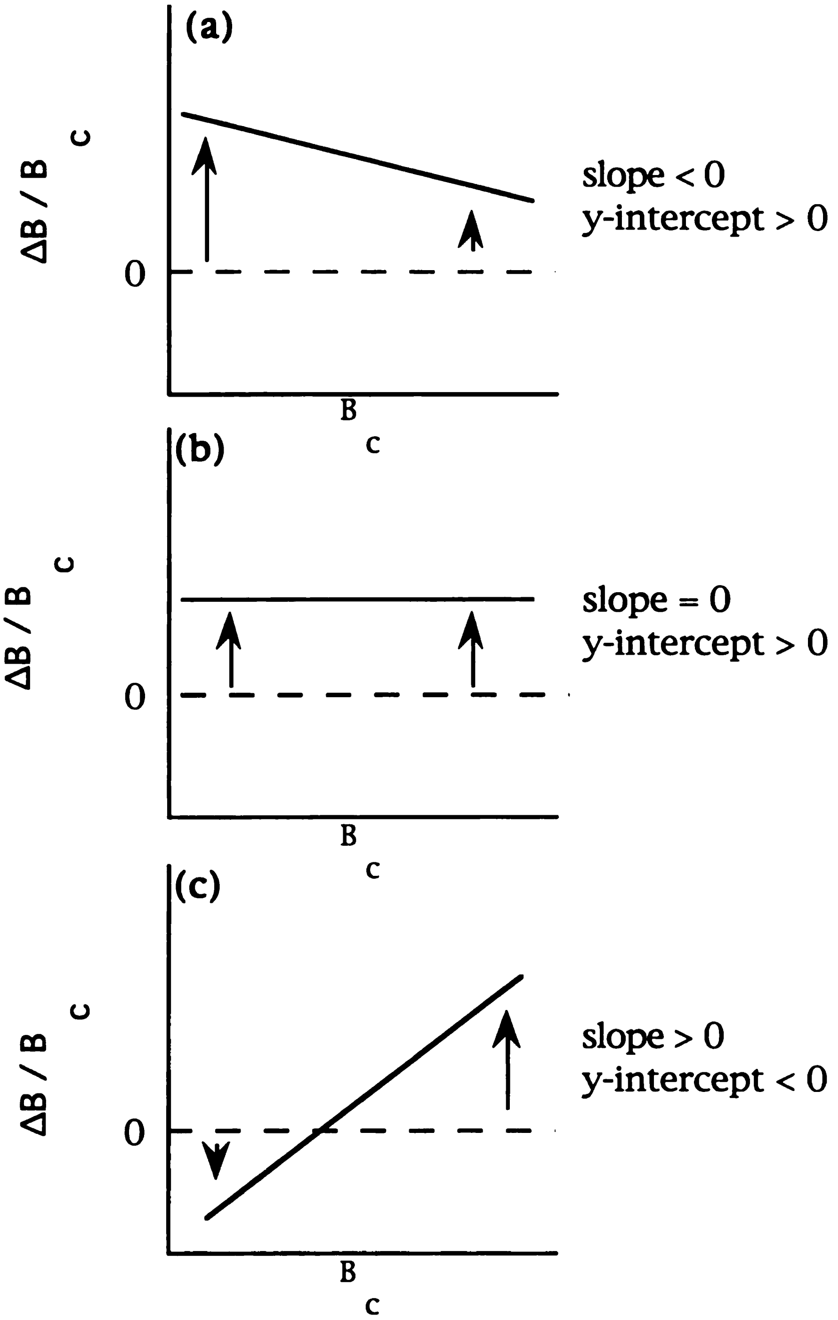


Figure 27. Potential relative responses of species to an experimental treatment. The dashed line represents the null hypothesis and the solid line represents the fitted regression line. In (a), all species increase in biomass in response to the treatment and the magnitude of their relative response is larger for species of lower abundance in the control than for species of higher abundance. In (b), the biomass of species of all abundances increases and species of all abundances in the control have equivalent or almost equivalent relative biomass responses. In (c), species of low abundance in the control have a large negative relative biomass response and species of high abundance in the control have a large positive relative biomass response to the treatment.

negative for species of low abundance in the control plots and large and positive for species of high abundance. The slope of the response is positive and the y-intercept is negative.

Field experiments

The data used to test the efficacy of this graphical and statistical method are from two field experiments conducted in a newly-abandoned old field and a second-year old-field at Michigan State University's W. K. Kellogg Biological Station in southwestern Michigan (Chapter 2 and 3, respectively). The soils, land-use history of the sites, and the details of the field experimental designs are described in Chapters 2 and 3. In summary, the experimental design for the study in a newly abandoned field at the Long Term Ecological Research (LTER) site in agricultural ecology included 4 blocks X 2 species removal levels (no removal, removal of the dominant species, Chenopodium album) X 4 times of nitrogen addition (none and 0, 2, and 4 weeks after removing C. album). The treatments were arranged in a complete randomized block design using 1 m^2 plots (2 m X 0.5 m). Chenopodium album was removed between July 6 and 8, 1992 by pulling or clipping seedlings. Nitrogen was applied in a single pulse at 32 g N/m^2 ammonium nitrate (320 kg/ha, typical of fertilizer levels for corn in this region) 0, 2, and 4 weeks after removing C. album. This experimental design produced 6 pairs of comparisons of species biomass: control v. early (July 9), mid- (July 24) and late (August 7) season nitrogen addition with C. album present, and control v. early, mid-, and late season nitrogen addition with C. album removed experimentally. The response of the plant community to a nutrient pulse was measured as above-ground biomass at harvest on August 21 two weeks after the final nitrogen addition. The plants were harvested by clipping the stems at the soil surface. Plants were separated by species, dried at 60°C, and weighed to ± 0.01 g.

The experimental design in the second-year old-field included 6 treatments (no nitrogen addition and nitrogen added at five different times during the growing season) replicated four times (24 treatment plots). The treatments were arranged in a completely randomized design using 1-m^2 plots (0.5 x 2.0 m) separated by a 1 m buffer on each side. Nitrogen was applied in a single pulse at 32 g N/m^2 as dry ammonium nitrate pellets on either May 11, May 26, June 17, July 8, or July 26, 1993. All of the above-ground plant biomass was harvested from the control and nitrogen addition treatment plots on August 16 by clipping stems 1 cm above the soil surface. Plant samples from the phenology plots and the final harvest of the treatment plots were separated by species, dried at 60°C, and weighed to ± 0.01 g.

The correlation and regression analyses were conducted using the CORR and GLM procedures, respectively, in SAS version 6 (SAS 1989). Only data points for species that were present in both the control and treatment comparison were used in the analyses.

RESULTS

Annual old-field: Relationship between species frequency and abundance

Only species that were present in both the control and the nitrogen addition treatment within a comparison were used in the correlation and regression analyses. In the annual old-field, the species that were excluded because they appeared in only one of the pair in a comparison tended to be species of low mean biomass and low frequency (Table 10). There was a significant positive correlation between the mean biomass of species and their frequency across replicates (Pearson $r = 0.35$, $p = 0.0001$). The replicates over the large spatial area of this experiment occur over a 50-hectare area of the

Table 10. Number of replicates out of four in which species were present and their mean biomass (g/m^2) in parentheses.

	C. album present				*C. album* removed			
Species	No N added	+N July 9	+N July 24	+N August 7	No N added	+N July 9	+N July 24	+N August 7
Abutilon theophrasti	4 (24.3)	4 (39.1)	4 (20.8)	4 (27.8)	4 (27.6)	4 (70.8)	4 (46.5)	4 (33.6)
Amaranthus retroflexus	4 (42.8)	4 (35.5)	4 (32.9)	4 (44.8)	4 (50.5)	4 (82.5)	4 (135.6)	4 (37.8)
Ambrosia artemisiifolia	1 (40.6)	1 (64.7)	1 (30.7)	1 (22.3)	1 (21.2)	1 (85.9)	1 (14.6)	1 (52.5)
Apocynum cannabinum	2 (.39)	1 (.05)	1 (.52)	3 (5.7)	2 (.29)	1 (.06)	3 (.74)	
Asclepias syriaca		1 (1.1)	1 (2.0)					
Barbarea vulgaris	1 (.05)		1 (.16)	1 (.04)	1 (.06)	1 (.29)	1 (.12)	1 (.59)
Chenopodium album	4 (258.9)	4 (481.2)	4 (515.3)	4 (363.4)	3 (1.6)	4 (8.6)	4 (8.9)	4 (4.0)
Cyperus esculentus			1 (.04)	1 (6.2)	1 (.82)	1 (38.5)	1 (2.1)	1 (.52)
Digitaria sanguinalis	4 (9.4)	2 (31.8)	4 (17.9)	2 (19.2)	4 (15.8)	3 (8.0)	4 (58.7)	4 (20.9)
Echinochloa crus-galli		1 (1.5)	1 (.24)	1 (2.5)	1 (.89)	1 (.41)	1 (1.7)	
Lactuca canadensis		1 (.06)		2 (8.3)	1 (3.6)		1 (.54)	
Lactuca serriola					1 (2.5)			
Silene alba	1 (.12)			1 (1.8)			1 (.15)	
Oxalis stricta	2 (.06)		2 (.27)		1 (.3)	1 (.09)	1 (.29)	1 (.66)
Panicum capillare		1 (.15)	1 (.02)	1 (.02)	2 (.13)			1 (.15)
Panicum dichotomiflorum	4 (13.6)	4 (9.2)	4 (15.2)	4 (9.7)	3 (14)	4 (16.4)	4 (18.1)	4 (43.4)
Polygonum persicaria		1(.07)		1 (.34)	1 (.41)	1 (.44)	1 (.98)	1 (.56)
Potentilla norvegica				1 (.008)			1 (.003)	1 (.02)
Rhus typhina						1 (.07)		
Rumex acetosella				2 (.71)	2 (.52)			1 (.60)
Rumex crispus	1 (.20)	1 (.1)					1 (.44)	
Rumex obtusifolius	1 (3.7)		1 (4.5)					1 (.25)
Setaria faberi	1 (29.5)	1 (112.3)	2 (1.2)	1 (.14)	1 (7.8)	2 (39.0)	1 (18.1)	
Setaria lutescens	2 (13.7)	2 (43.2)	1 (17.9)	1 (11.9)	1 (28.0)	2 (53.5)	2 (19.9)	1 (23.3)
Setaria viridis			1 (.20)		1 (.25)	1 (35.1)		1 (.05)
Solanum nigrum		2 (.2)	2 (.19)		1 (.09)	1 (.28)	2 (.62)	
Stellaria media			1 (.10)	1 (.06)	1 (3.5)	2 (.25)	2 (1.1)	1 (.28)
Taraxacum officinale	4 (.64)	2 (.04)	2 (.37)	3 (.54)	4 (3.7)	4 (2.1)	4 (2.9)	4 (2.0)

Table 10. (cont'd)

Trifolium hybridum					1 (.18)			
Trifolium pratense								1 (.91)
Trifolium repens	1 (.49)	1 (.03)				1 (.05)	1 (.11)	1 (.36)
unidentified woody biomass			1 (.14)					

LTER site at KBS. There is considerable variation in species composition in these annual old-fields (Gross and Huberty, in prep). Thus, several rare species with patchy distributions at the 50-hectare scale did not appear consistently in the experimental plots. Between 6 and 12 species with mean biomass ranging from 0.003 to 8.3 g/m^2 were excluded from the six comparisons leaving 12 to 18 species in common for each comparison (Table 11). The values used in the correlations and regressions are the mean biomass of the species across four replicates. Thus, a species is represented once in each of the correlation and regression analyses.

Annual old-field: Correlations of species rank abundance

Within a single growing season, the overall biomass hierarchy of species was maintained when nitrogen was added to the annual plant community at different times during the growing season. The Kendall tau-b correlations between the rank abundance of species in the control and nitrogen addition treatments were significant when the dominant species, Chenopodium album, was present and when it was removed experimentally (Table 12). Therefore, the first null hypothesis that the rank of species abundances does not change with nitrogen additions can be accepted.

Although the rank abundance of species did not change with nitrogen additions, the correlation analysis does not show whether species of different abundances in the control plots responded positively or negatively to the nitrogen additions or whether the magnitude of the response was dependent on species abundance.

Table 11. Number of species occurring in both the control and nitrogen addition treatments that were included in the correlation and regression analyses, and number of species that were excluded because they did not appear in both the control and the nitrogen addition treatment.

Treatments compared	No. of species present in both treatments of comparison	No. of species excluded
C. album present		
Control v. N added July 9	12	9
Control v. N added July 24	13	11
Control v. N added August 7	12	12
C. album removed		
Control v. N added July 9	18	6
Control v. N added July 24	18	8
Control v. N added August 7	16	10

Table 12. Spearman and Kendall tau-b correlation coefficients for rank of species mean biomass in control and nitrogen addition plots.

Variables	N	Spearman correlation coefficient	p	Kendall tau-b correlation coefficient	p
C. album present					
Control v. N added July 9	12	0.85	0.0005	1.64	0.004
Control v. N added July 24	13	0.90	0.0001	0.79	0.0002
Control v. N added August 7	12	0.75	0.005	0.64	0.004
C. album removed					
Control v. N added July 9	18	0.73	0.0007	0.54	0.002
Control v. N added July 24	18	0.89	0.0001	0.74	0.0001
Control v. N added August 7	16	0.80	0.0002	0.58	0.002

Annual old-field: Absolute biomass responses

In an absolute sense, the positive response to the nitrogen additions was larger for the dominant species than for the less abundant species in the annual old-field (Figure 28). When the dominant species, Chenopodium album, was present, the slopes of the regressions of species biomass in each of the three nitrogen addition treatments against species biomass in the control plots were significantly greater than zero (Table 13). Chenopodium album, represented by the isolated data point in the upper right of Figures 28a-c, was abundant in the control plots and had a large absolute response to the nitrogen addition. Consequently, it exerted a large influence on the regression.

The dominant species, C. album, accounted for a large proportion of community biomass in this study and had the greatest absolute increase in biomass in response to the nitrogen additions. Consequently, the data is not bivariate normally distributed when C. album is included in the analyses. When C. album was excluded from the regression analyses (Figure 29), the results and interpretations of the regressions were different from those in Figure 28. When nitrogen was added early in the season, the magnitude of the positive response of species tended to increase with their abundance in the control plots (Figure 29a). However, the slope of the relationship was not significantly different from zero (Table 13). Thus, the response was qualitatively similar to the results in Figure 28a. When nitrogen was added at mid-season, the absolute change in biomass was negative for species of greater than 20 g/m^2 in the control and positive for species of less than 20 g/m^2 in the control (Figure 29b). The slope was significantly less than one and the y-intercept was not significantly different from zero (Table 13). This result and interpretation differs radically from that in Figure 28b and illustrates the

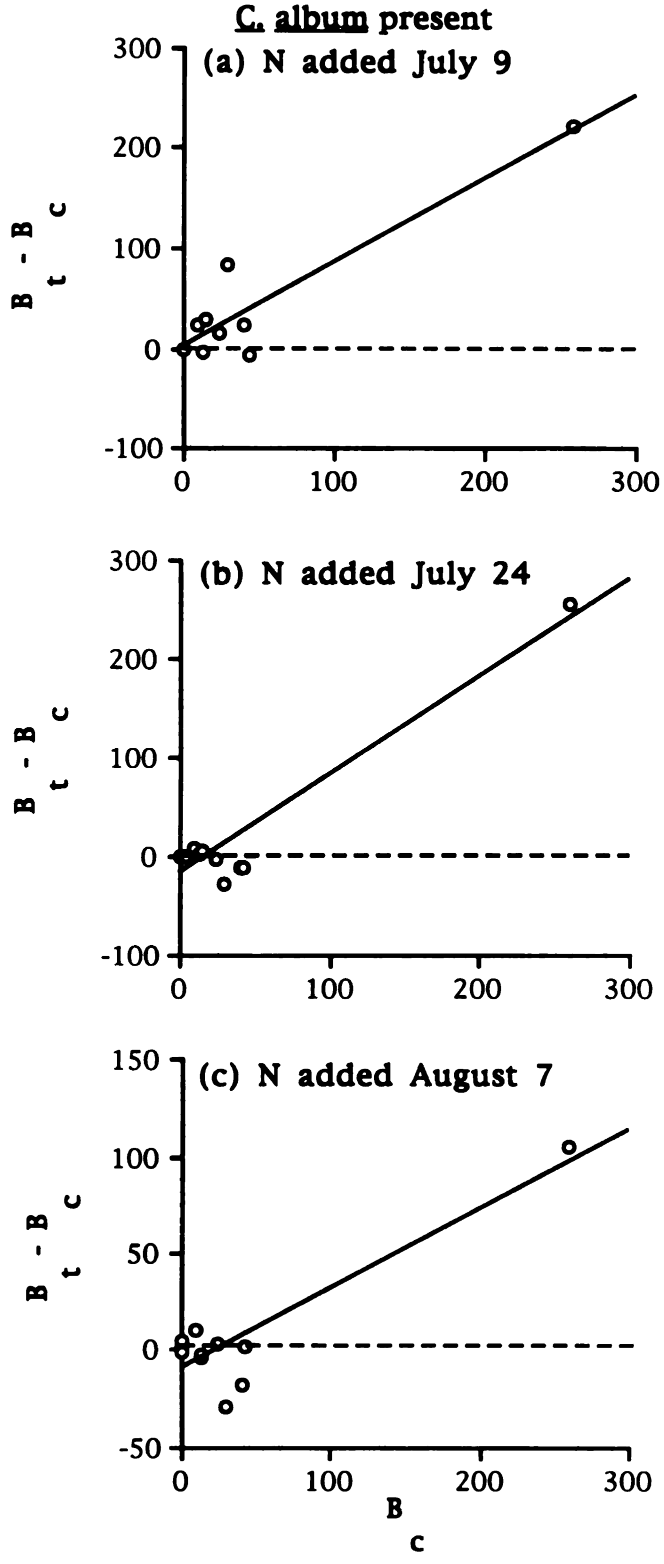


Figure 28. Absolute species biomass responses to a) early, b) mid-, and c) late season nitrogen addition with C. album present in the community (dashed line = null hypothesis; solid line = fitted regression line).

Table 13. Regression statistics for the relationship between mean biomass of species in control plots (no nitrogen added) and the change in mean biomass between treatment (nitrogen added at different times of the growing season) and control plots (absolute response, see Methods). Only species that occurred in both control and treatment are included in the regression analyses. Values in boldface indicate that the slope or y-intercept differs significantly from zero. The corresponding plots appear in Figs. 4, 5, 6.

Treatment comparison	N	model p	r^2	slope	p for slope	y-intercept	p for intercept
C. album present							
Control v. N added July 9	12	0.0001	0.87	**0.84**	0.0001	1.4	0.86 ns*
Control v. N added July 24	13	0.0001	0.90	**0.99**	0.0001	**-16.5**	0.04
Control v. N added August 7	12	0.0001	0.79	**0.41**	0.0001	-8.5	0.13 ns
C. album present, but excluded from regression analysis							
Control v. N added July 9	11	0.29	0.12	0.56	0.29	5.6	0.63 ns
Control v. N added July 24	12	0.03	0.40	**-0.38**	0.03	2.6	0.42 ns
Control v. N added August 7	11	0.11	0.26	-0.35 †	0.11	2.8	0.54 ns
C. album removed							
Control v. N added July 9	18	0.04	0.24	**0.74**	0.04	7.5	0.19 ns
Control v. N added July 24	18	0.001	0.50	**1.14**	0.001	-3.0	0.54 ns
Control v. N added August 7	16	0.98	0	0	0.98	3.3	0.38 ns

* ns = not significant

† marginally not significant

C. album present, but excluded from regression analysis

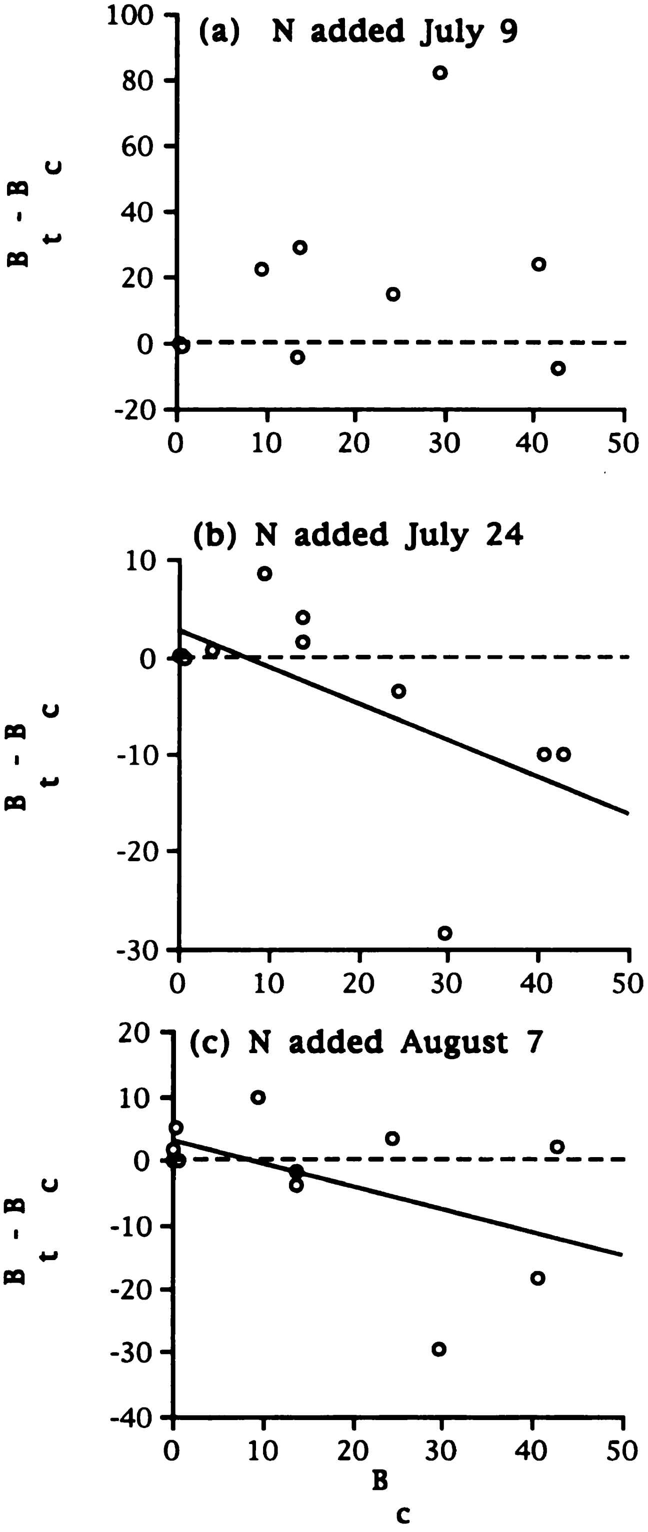


Figure 29. Absolute species biomass responses to a) early, b) mid-, and c) late season nitrogen addition with C. album present in the community but excluded from the regression analysis (dashed line = null hypothesis; solid line = fitted regression line).

influence that one species with a strong response can have on the regression results and interpretation. When nitrogen was added late in the season, the slope was only marginally different from zero and the y-intercept was zero (Figure 29c and Table 13), suggesting that the negative response to nitrogen additions was larger for the more abundant species.

When C. album was removed experimentally, the more abundant species had a larger absolute increase in biomass in the early and mid-season nitrogen addition treatments than did the less abundant species (Figure 30a, b). The slopes of the regressions of absolute response against the biomass of species in control plots were significantly greater than zero for the early and mid-season nitrogen addition (Table 13). The slope was not significantly different from zero when the dominant species was removed and nitrogen was added late in the season (Figure 30c, Table 13), indicating that the response to late season nitrogen additions was independent of the abundance of the species in the control plots.

Annual old-field: Relative biomass responses

The relative biomass response to nitrogen addition was independent of the abundance of the species in the control plots for all three comparisons when C. album was present in the plots and included in the regression analyses (Figure 31). The slopes and the y-intercepts were not significantly different from zero (Table 14). The relative response of the C. album, the only species with mean biomass greater than 100 g/m2 in the control plots, was positive in the early and mid-season nitrogen addition (Figure 31a, b). However, the direction and magnitude of relative biomass responses among species with mean biomass less than 100 g/m2 in the control plots were highly variable. Consequently, when C. album was present in the community and

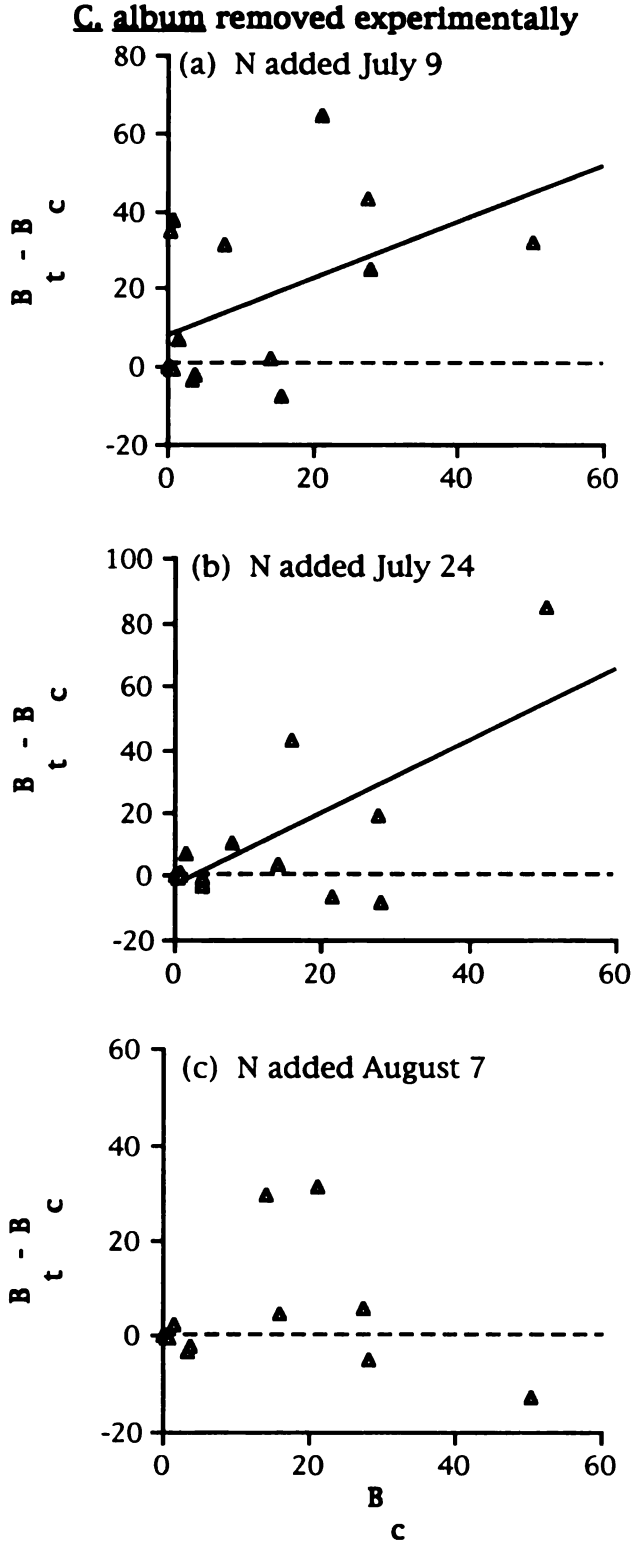


Figure 30. Absolute species biomass responses to a) early, b) mid-, and c) late season nitrogen addition with C. album removed from the community (dashed line = null hypothesis; solid line = fitted regression line).

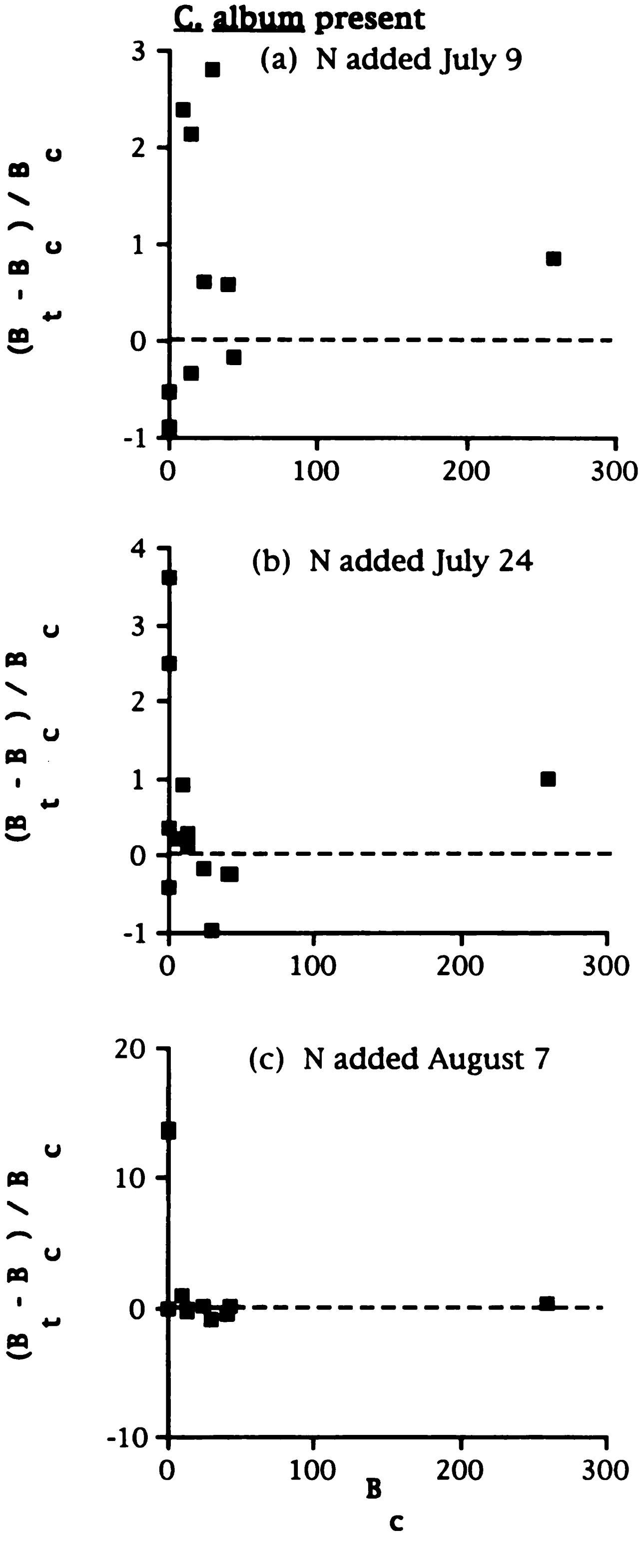


Figure 31. Relationship between the biomass of species in the control plots and the relative change in mean biomass of species with a) early, b) mid-, and c) late season nitrogen addition and C. album present in the community (dashed line = null hypothesis; solid line = fitted regression line).

Table 14. Regression statistics for the relationship between mean biomass of species in control plots (no nitrogen added) and the relative change in mean biomass between treatment (nitrogen added at different times of the growing season) and control (relative response, see Methods). Only species that occurred in both control and treatment are included in the regression analyses. Values in boldface indicate that the slope or y-intercept differs significantly from zero. The corresponding plots appear in Figs. 7, 8, and 9.

Treatment comparison	N	model p	r^2	slope	p for slope	y-intercept	p for intercept
<u>C. album</u> present							
Control v. N added July 9	12	0.60	0.03	0	0.60	0.35	0.46 ns*
Control v. N added July 24	13	0.96	0.0003	0	0.96	0.55	0.20 ns
Control v. N added August 7	12	0.51	0.05	0	0.51	2.8	0.15 ns
<u>C. album</u> present, but excluded from regression analysis							
Control v. N added July 9	11	0.26	0.14	0	0.26	-0.09	0.89 ns
Control v. N added July 24	12	0.06	0.31	**-0.05**	0.06	**1.2**	0.03
Control v. N added August 7	11	0.12	0.25	-0.17 †	0.12	**5.2**	0.05
<u>C. album</u> removed							
Control v. N added July 9	18	0.39	0.05	0	0.39	16.3	0.12 ns
Control v. N added July 24	18	0.56	0.02	0	0.56	1.4	0.02
Control v. N added August 7	16	0.52	0.03	0	0.52	1.1	0.15 ns

* ns = not significant

† marginally not significant

included in the regression analysis, the value of its relative response exerted disproportionate influence on the regression.

When C. album was excluded from the regression analysis, the direction and magnitude of the relative biomass response to the early season nitrogen addition was independent of the species biomass in the control plots (Figure 32a, Table 14). When nitrogen was added mid-season, the slope was significantly negative, and the y-intercept was significantly greater than zero (Figure 32b and Table 14). The relative response of species of less than 20 g/m^2 in the control plots was positive and the relative response of species of more than 20 g/m^2 was negative. The slope was negative and marginally not significant when nitrogen was added late in the season (Figure 32c, Table 14). The analysis excluding C. album in Figure 32 illustrates the influence of the dominant species on the regressions in Figure 31.

When C. album was removed from the community experimentally, the relative biomass responses to nitrogen addition were independent of the biomass of the species in the control (Figure 33, Table 14). The direction and magnitude of relative responses to each time of nitrogen addition were highly variable. The positive relative responses tended to be larger and more variable than the negative relative responses.

Second-year old-field: Absolute biomass responses

In the second-year old-field the absolute biomass response to each time of nitrogen addition was positive and larger for species of greater biomass in the control plots (Figure 34). The slopes were significantly greater than zero and the y-intercepts were not significantly different from zero (Table 15). As had been observed in the annual-field, the dominant species in the second-year old-field, Conyza canadensis (a tall, densely leaved composite), accounted

C. album present, but excluded from regression analysis

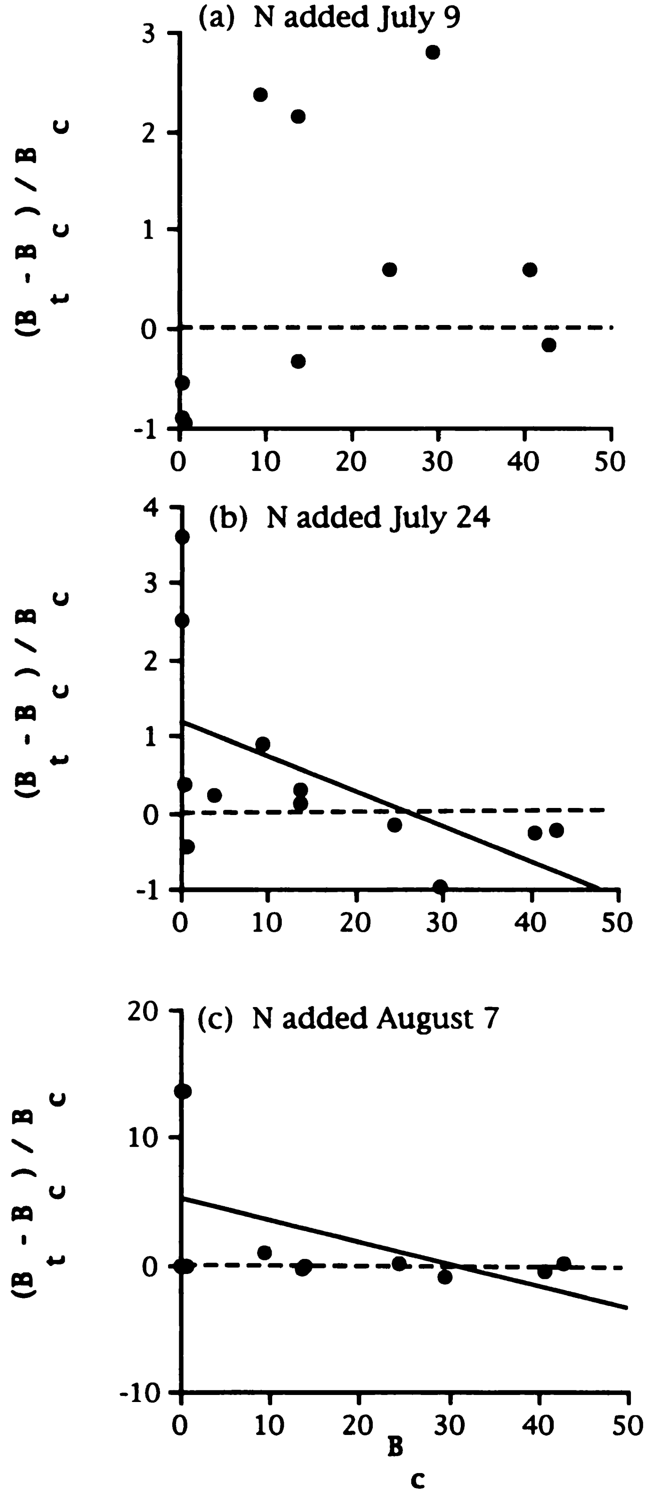
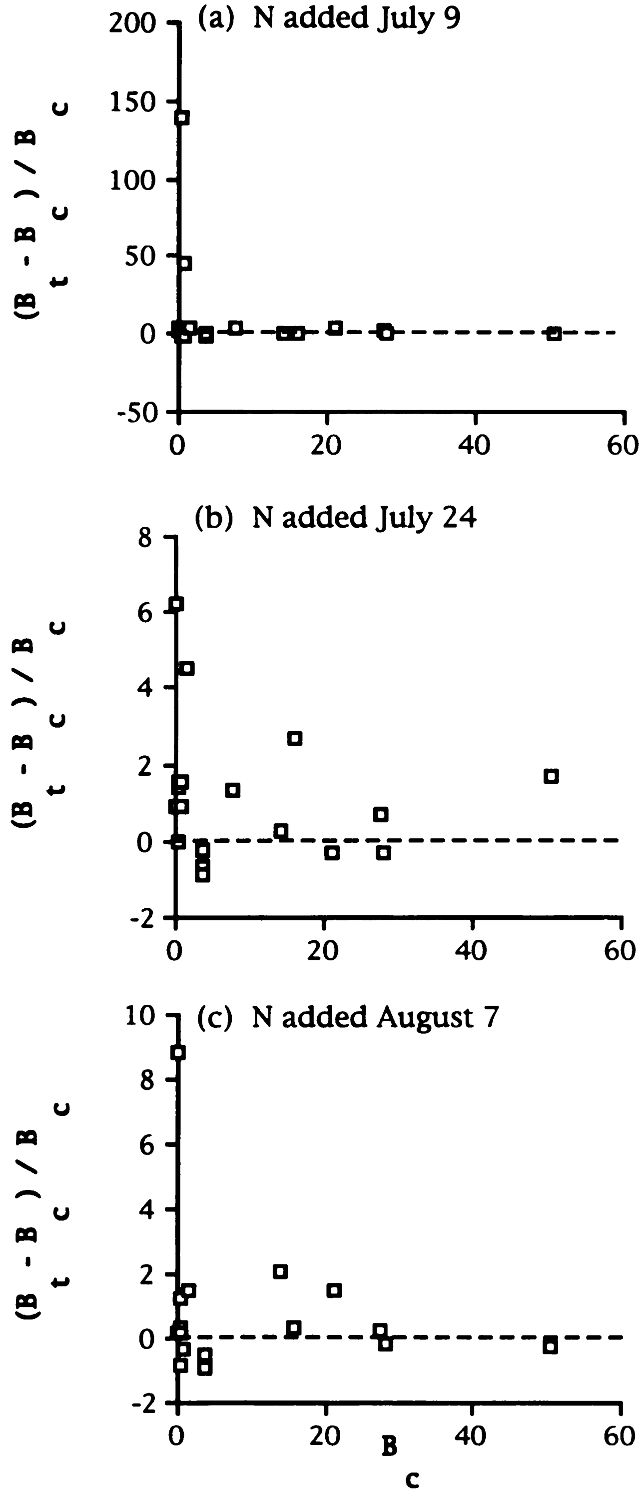


Figure 32. Relative species biomass response to a) early, b) mid-, and c) late season nitrogen addition with C. album excluded from the regression analysis (dashed line = null hypothesis; solid line = fitted regression line).



C. album removed

Figure 33. Relationship between the biomass of species in the control plots and the relative change in mean biomass of species with a) early, b) mid-, and c) late season nitrogen addition and C. album removed from the community (dashed line = null hypothesis; solid line = fitted regression line).

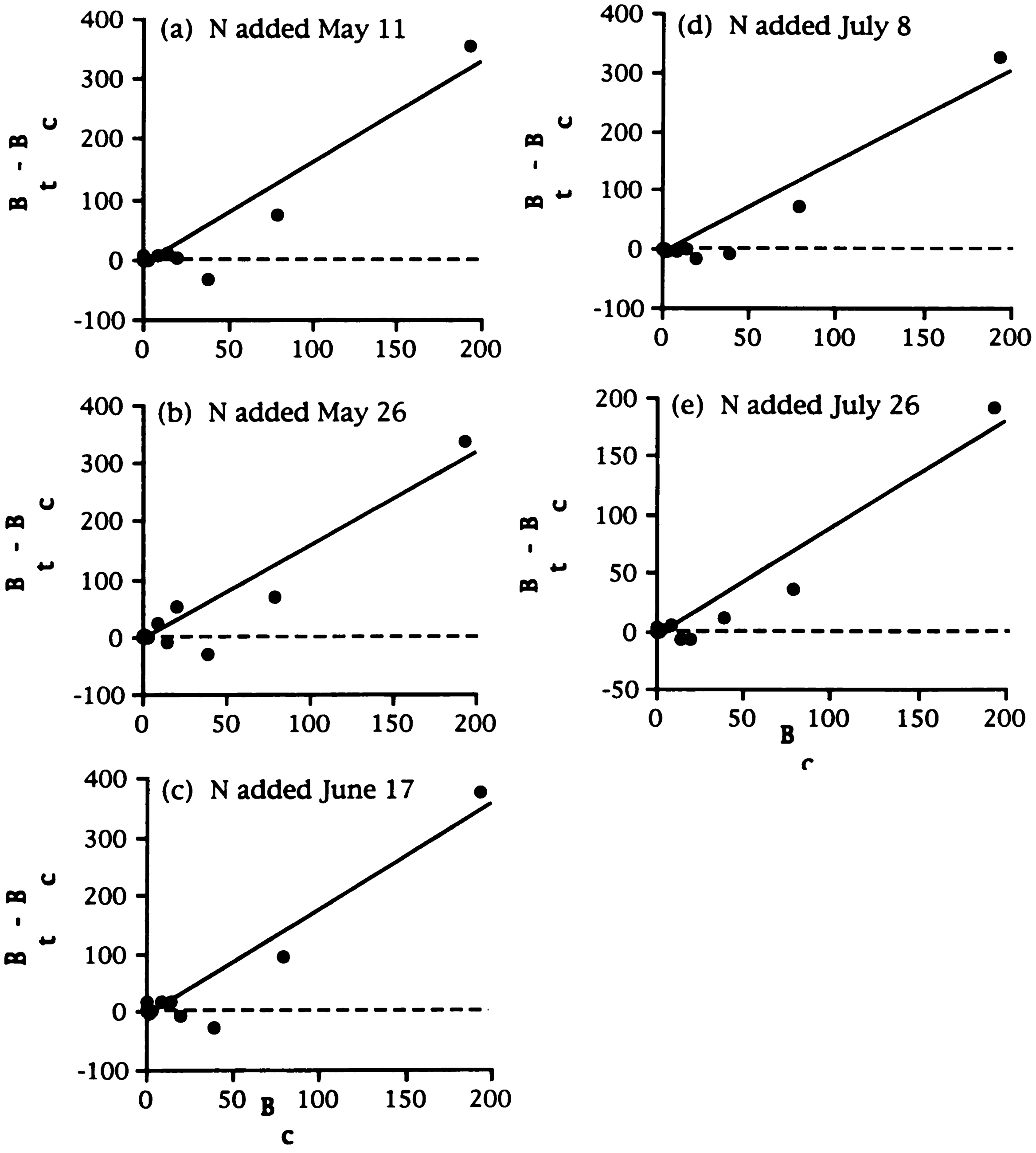


Figure 34. Absolute species biomass responses to 5 times of nitrogen addition in a second-year old-field in southwestern Michigan (dashed line = null hypothesis; solid line = fitted regression line).

Table 15. Regression statistics for the relationship between mean biomass of species in control plots (no nitrogen added) and the change in mean biomass between treatment (nitrogen added at different times of the growing season) and control plots (Absolute response, see Methods) in the second-year old field. Only species that occurred in both control and treatment are included in the regression analyses. Values in boldface indicate that the slope or y-intercept differs significantly from zero. The corresponding plots appear in Figures 10 and 11.

Treatment comparison	N	model p	r^2	slope	p for slope	y-intercept	p > T for intercept
Conyza canadensis included in regression analysis							
Control v. N added May 11	22	0.0001	0.89	**1.68**	0.0001	-8.6	0.16
Control v. N added May 26	21	0.0001	0.88	**1.61**	0.0001	-6.4	0.32
Control v. N added June 17	25	0.0001	0.90	**1.79**	0.0001	-6.2	0.25
Control v. N added July 8	21	0.0001	0.92	**1.57**	0.0001	-9.3	0.07 †
Control v. N added July 26	23	0.0001	0.92	**0.91**	0.0001	-4.3	0.10
Conyza canadensis excluded from regression analysis							
Control v. N added May 11	21	0.002	0.40	**0.61**	0.002	-1.8	0.60
Control v. N added May 26	20	0.008	0.33	**0.63**	0.008	0.2	0.97
Control v. N added June 17	24	0.0003	0.46	**0.82**	0.0003	-0.7	0.84
Control v. N added July 8	20	0.0001	0.60	**0.69**	0.0001	-3.4	0.22
Control v. N added July 26	22	0.0001	0.71	**0.39**	0.0001	-1.2	0.30

* ns = not significant

† marginally not significant

for a disproportionate share of community biomass. None of the species except C. canadensis had a mean biomass greater than 100 g/m^2. As a result, the data were not bivariate normally distributed and the dominant species may have had disproportionate influence on the regression.

When C. canadensis was excluded from the regression analyses, the absolute biomass responses were dependent on the biomass of the species in the control for each time of nitrogen addition (Figure 35). The slopes were significantly positive and the y-intercepts did not differ from zero (Table 15). The values for the slope and r^2 were lower when C. canadensis was excluded from the regression analyses than when it was included (Table 15), illustrating the influence of the large positive response of the dominant species on the regressions.

Second-year old-field: Relative biomass responses

The relative biomass response was independent of the biomass of the species in the control for each time of nitrogen addition when C. canadensis was included in the regression analysis (Figure 36, Table 16) and when it was excluded (Figure 37, Table 16). The magnitudes of the relative responses were much smaller and less variable for species of biomass greater than 10 g/m^2 in the control than for species less than 10 g/m^2. The positive relative responses of the species of very low biomass were larger and more variable than the negative relative responses.

DISCUSSION

Consequences of spatial variability of species distributions

The variability of species frequency and abundance on a 50 hectare scale in the annual old-field study created several challenges for the analysis

Conyza canadensis excluded from the analysis

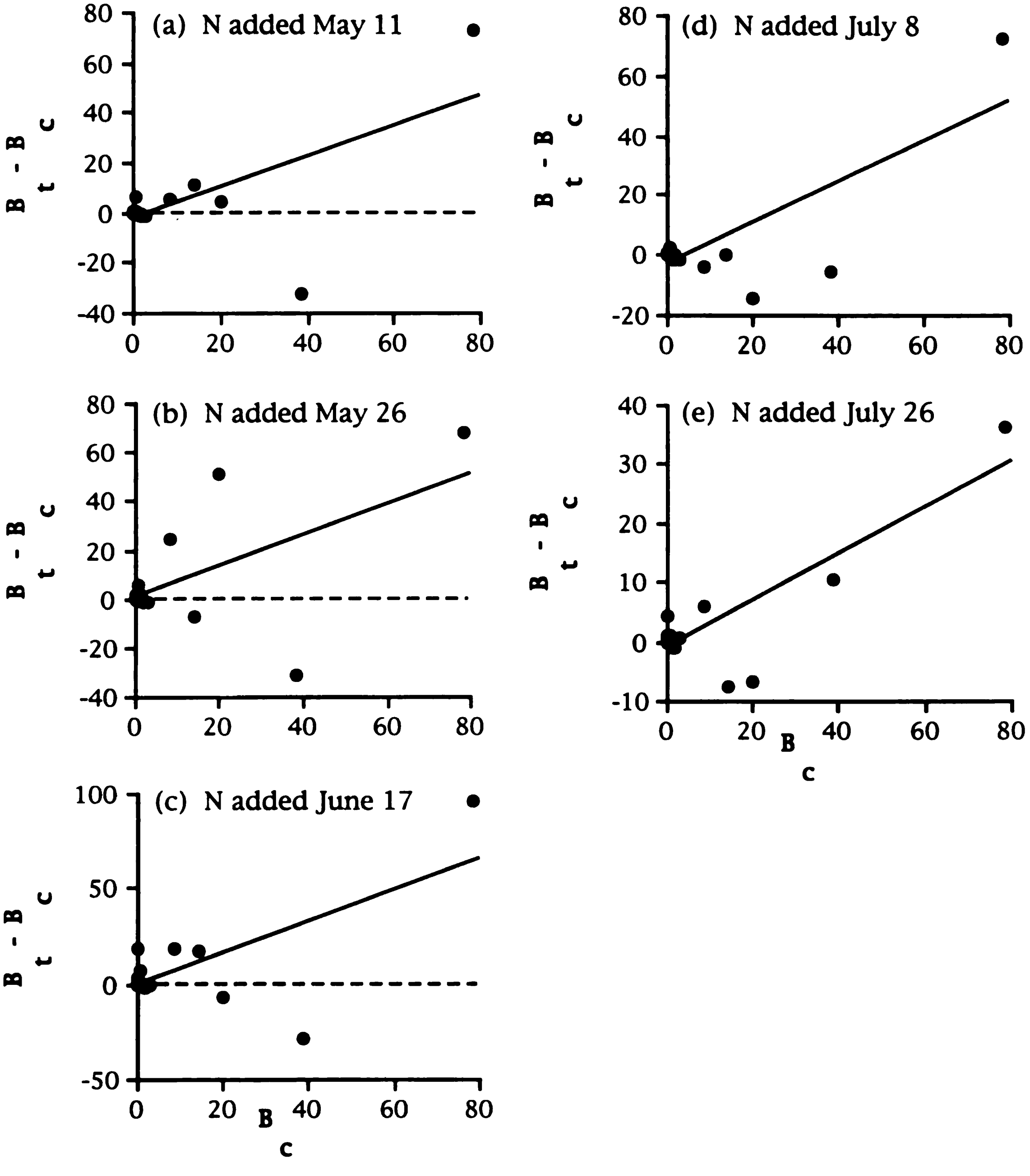


Figure 35. Absolute species biomass responses to 5 times of nitrogen addition in a second-year Michigan old-field. The dominant species, Conyza canadensis, is excluded from the regression analysis (dashed line = null hypothesis; solid line = fitted regression line).

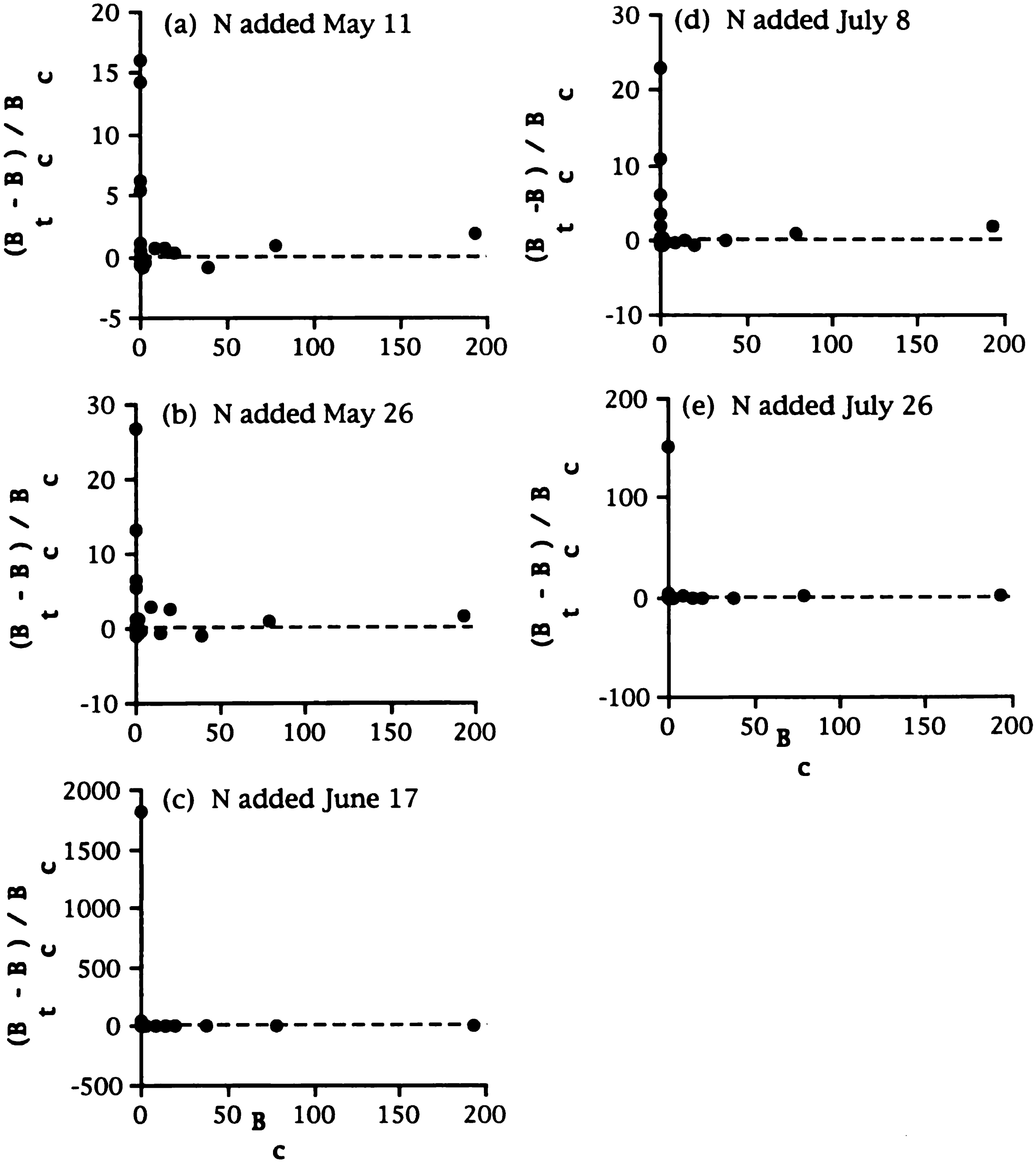


Figure 36. Relationship between the biomass of species in the control plots and the relative change in mean biomass of species at 5 times of nitrogen addition in a second-year Michigan old-field. (dashed line = null hypothesis; solid line = fitted regression line).

Table 16. Regression statistics for the relationship between mean biomass of species in control plots (no nitrogen added) and the relative change in mean biomass between treatment (nitrogen added at different times of the growing season) and control (Relative response, see Methods) in the second-year old-field. Only species that occurred in both control and treatment are included in the regression analyses. Values in boldface indicate that the slope or y-intercept differs significantly from zero. The corresponding plots appear in Figures 12 and 13.

Treatment comparison	N	model p	r^2	slope	p for slope	y-intercept	p > T for intercept
Conyza canadensis included in regression analysis							
Control v. N added May 11	22	0.74	0.006	-0.008	0.74	2.2	0.06 †
Control v. N added May 26	21	0.66	0.01	-0.01	0.66	3.07	0.06 †
Control v. N added June 17	25	0.71	0.006	-0.7	0.71	86.1	0.28
Control v. N added July 8	21	0.71	0.008	-0.01	0.71	2.4	0.09 †
Control v. N added July 26	23	0.70	0.007	-0.06	0.70	8.4	0.25
Conyza canadensis excluded from regression analysis							
Control v. N added May 11	21	0.49	0.02	-0.04	0.49	2.4	0.05 †
Control v. N added May 26	20	0.50	0.03	-0.06	0.50	3.3	0.06 †
Control v. N added June 17	24						
Control v. N added July 8	20	0.50	0.03	-0.05	0.50	2.6	0.08 †
Control v. N added July 26	22	0.64	0.01	-0.2	0.64	9.1	0.25

* ns = not significant

† marginally not significant

Conyza canadensis excluded from the analysis

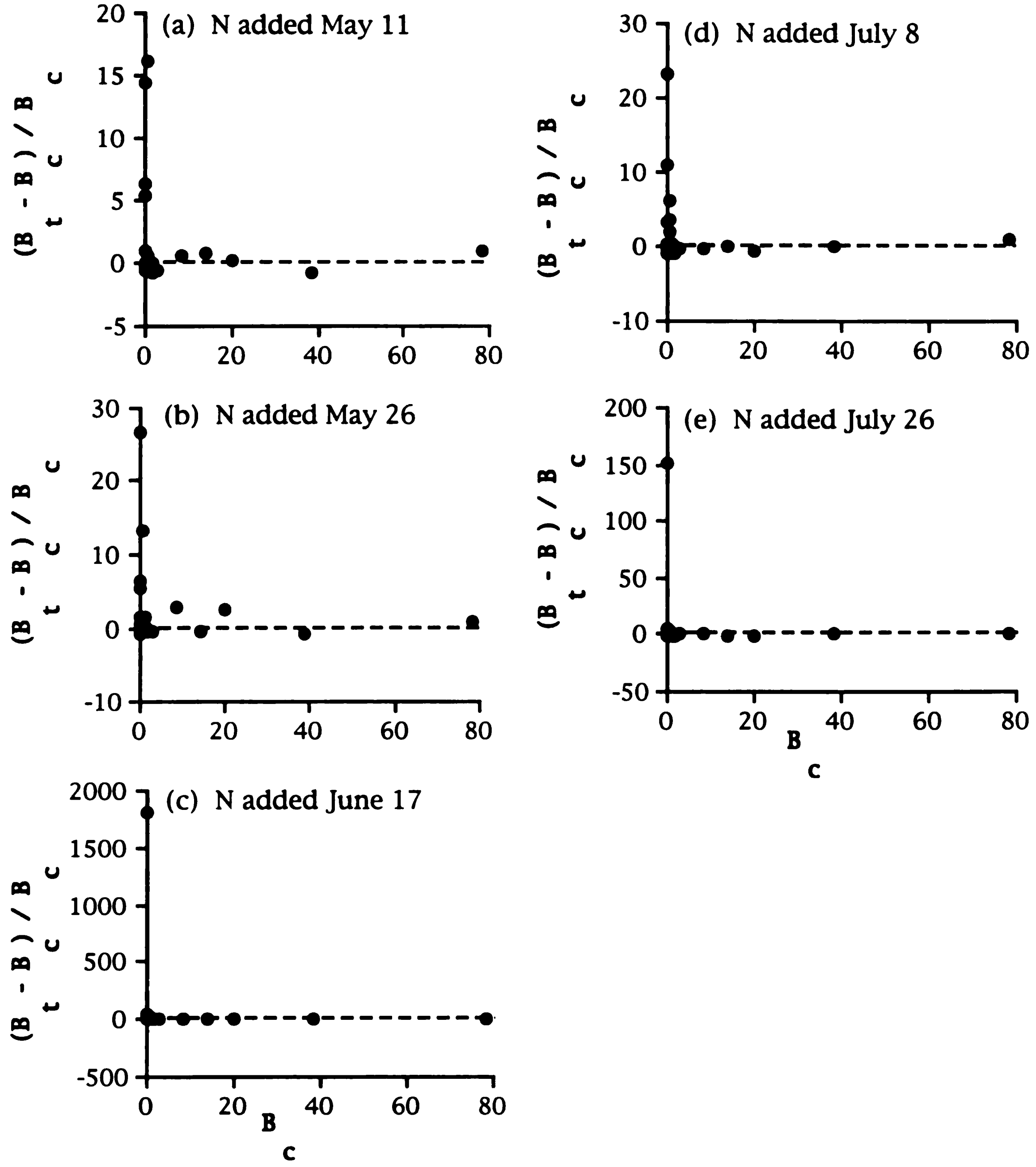


Figure 37. Relationship between the biomass of species in the control plots and the relative change in mean biomass of species at 5 times of nitrogen addition in a second-year Michigan old-field. The dominant species, _Conyza canadensis_, is excluded from the regression analysis (dashed line = null hypothesis; solid line = fitted regression line).

and interpretation. Several species did not occur in both the control and nitrogen addition treatments when mean species biomass was calculated. Several species were locally abundant at the one hectare scale, but not frequent at the 50 hectare scale (*Setaria spp.* and *Ambrosia artemisiifolia*) and so did not appear in all 4 replicates of the treatments. Several species were of low abundance at the one hectare scale, and low frequency across replicates, particularly the early colonizing perennials, such as *Apocynum cannabinum* and *Silene alba*. In general, the frequency and abundance of species was positively correlated (Pearson r = 0.35 and p = 0.0001).

One consequence of species not appearing in all replicates of all treatments is that the sample size, and thus the power of the regression analysis, is reduced. Between 6 and 12 species were excluded from the regression analysis because they were not present in both the control plots and nitrogen addition treatments within a comparison. One way to increase the degrees of freedom is to plot species responses in each replicate separately. However, this could create pseudo-replication because each species would be represented by more than one data point in the regression analysis.

A second consequence of some species appearing in only a subset of replicates is that the mean biomass response may be a poor estimate of the performance of the species. The behavior of *Setaria faberi* provides a good example of a species that occurred infrequently on a 50 hectare scale, but was locally abundant on a one hectare scale, and displayed a large negative response to the nitrogen additions. Its response may have been the result of sampling bias in either the control or treatment plots. Consequently, *Setaria faberi* was an anomalous data point in Figures 29b and 29c, and may have exerted disproportionate influence on the fitted regression lines.

Responses of the species biomass hierarchy to nitrogen additions

Each of the correlations between rank of species abundance in control and rank of species abundance in the nitrogen addition treatment was significant indicating that the general order of species abundance remained constant within a growing season when nitrogen was added to the annual community. Thus, we can accept the first null hypothesis that, in general, there was no change in the species biomass hierarchy with any of the times of nitrogen addition. Mitchley and Grubb (1986) also found a constancy of rank order of plant species abundances across a site, between years, and between sites in a chalk grassland.

The second null hypothesis addressed whether the direction and magnitude of the species biomass response to nitrogen addition depended on the biomass of the species in the control plots. The slope of the relationship between the absolute and relative responses of species biomass depended on the time of nitrogen addition and whether C. album was present or removed from the community. When nitrogen was added early in the season there was at least a tendency for species of greater biomass in the control plots to have larger absolute responses to the nitrogen addition whether C. album was present or not (Figures 29a and 30a). The absolute and relative biomass responses to the early nitrogen addition suggest that a competitive hierarchy was not well established early in the season (Miller and Werner 1987). Species of all abundances could increase biomass (in an absolute and relative sense) in response to the early season nitrogen addition.

When nitrogen was added later in the season (late July and early August), subordinate species of higher biomass in the control plots had a larger negative absolute response to the nitrogen addition than species of lower biomass. The slope of the relationship between absolute and relative species response and species abundance in the control plots was significantly negative. Presumably, this was a result of the stronger competitive effect from C. album when nitrogen was added at mid-season. The dominant species, C. album, doubled in biomass and reduced species diversity and evenness most with the mid-season nitrogen addition (Chapter 1). When C. album was removed experimentally, the absolute responses of the remaining species to the mid-season nitrogen addition were generally positive and the magnitude of the absolute response increased significantly with species biomass in the control plots (Figure 30b). The relative responses were also generally positive (Figure 33b), but the slope was not significantly different from zero.

In contrast to the annual community, the slopes for absolute responses to nitrogen addition in the second-year old-field were always significantly positive (Figure 35), and the slopes for the relative responses were never significantly different from zero (Figure 37).

Absolute and relative responses

The magnitude of absolute responses tended to be larger among species of high mean biomass in the control plots than species of low biomass. The magnitude of relative responses tended to be higher among species of low biomass in the control plots than species of high biomass. This is consistent with the statement by Goldberg (1994) that the measure of relative change in species abundance is more sensitive to changes in rare species than is the measure of absolute change in abundance.

Analogies to other approaches

This graphical method is analogous to statistical and graphical approaches in population biology that analyze genetic covariation between performance of genotypes in different environments (Via and Lande 1985, Shaw and Platenkamp 1993). These population methods compare the performance of genotypes in different environments to determine whether the direction and magnitude of response to environmental change is the same among genotypes. In this analysis of species responses in a community, the mean species biomass response is analogous to the genotype response in population genetics analyses. The species response surfaces in this study are the result of the ability of the species to respond to the nitrogen additions and the changes in competitive interactions when nitrogen is added.

In community ecology, Pinder (1975) used a similar graphical method to illustrate the response of net productivity of subordinate forb species as a group to the removal of a dominant grass species, but he did not extend his graphical approach to evaluate species level responses. Silander and Antonovics (1982) used perturbation response diagrams to examine the responses of species abundances to the removal of a dominant species. The size of the circles in the diagrams were proportional to the abundance of species in the control and species removal treatments. However, it is difficult to discern from the perturbation response diagrams in Silander and Antonovics (1982) whether the species responses were related to their abundance in the control plots.

This approach of looking at the relationship between species performance in two environments is also analogous to the ecosystem level approach used by Hendrickson et. al (1988 a, b) to quantify changes in the water chemistry of lakes between 1974/75 and 1986 in the Thousand Lake Survey in Norway. They plotted water chemistry parameters of the lakes in 1974/75 (pH, nitrate, sulfate, aluminum) against the parameters in 1986, looking for responses to changes in industrial emissions.

CHAPTER 5

SUMMARY AND CONCLUSIONS

The species removal and nitrogen addition experiment in the annual old-field demonstrated that competition intensity from the dominant species varied with the time of nitrogen addition. The dominant species reduced subordinate community biomass, evenness, and diversity most when nitrogen was added mid-season (late July). When nitrogen was added early in the growing season, both the dominant species and subordinate community increased tissue nitrogen concentration, growth and total nitrogen content. When nitrogen was added later in the season (late July or early August), the dominant species increased tissue nitrogen concentration, growth, and total nitrogen content. The subordinate community increased tissue nitrogen concentration, but not growth and total nitrogen content. The degree of canopy development appears to determine the ability of dominant and subordinate species to acquire added nutrients and allocate them to increased growth rather than storage, and thus, influences the magnitude of the effect of the dominant species on diversity and community structure.

This pattern of response to nitrogen addition may be typical of habitats where plant productivity is high, where a distinct canopy, sub-canopy, and ground-layer can develop, and light limitation increases during the growing season. The patterns of response to the time of nitrogen addition may differ substantially in a habitat with lower fertility and productivity and shorter vegetation or where a distinct canopy, sub-canopy, and ground layer do not develop.

The extension of these results to the effects of natural patterns of nutrient pulses must be done with care. The amount of the experimental nitrogen pulse was very large, equivalent to the amount of nitrogen mineralized during the entire growing season in these soils. The nutrient pulses that occur in spring when microbial activity increases following snow melt ("vernal dam") and during the growing season following rainfall events are much smaller in magnitude than the nitrogen pulses described in Chapter 2 and 3. We need more information about the consequences of natural temporal variation in nutrient availability for competitive interactions and community structure in terrestrial plant communities. However, I would predict that in the annual community, the subordinate community would be able to acquire and allocate nitrogen made available by microbial activity early in the season better than nitrogen mineralized later in the season.

The decline in biomass evenness during the growing season in the second-year old-field study demonstrated the development of a biomass hierarchy. While there were seasonal changes in species composition and abundance, there was a clear biomass dominance by Conyza canadensis. This dominant species increased biomass disproportionately to the subordinate community in response to each time nitrogen addition. Although biomass evenness of the community declined with each time nitrogen addition, the magnitude of the effect did not vary with time of nitrogen addition as it did in the annual old-field. Rather, life-history/growth form groups and individual species in the subordinate community varied in their response to the time of nitrogen addition. These individual responses appeared to compensate for each other and thus, evenness and diversity did not vary with the time of nitrogen addition in the second-year old-field. The variation in growth phenologies of component species is greater in the second-year old-field with winter annuals, biennials, and perennials than in the annual old field consisting primarily of summer annuals.

The second-year old-field represents a transition between dominance by annual species in the first year following abandonment from agriculture and dominance by perennial species three to five years following abandonment. Many of the ultimate dominant herbaceous species, such as Solidago canadensis and Aster species colonize fields at this stage of succession. Understanding the mechanisms of plant competition in this transitional community is crucial to understanding how annual species are lost and perennial species come to dominate as succession proceeds in this region. The experiment in the second-year old-field demonstrated the potential for variation in competitive interactions during the growing season. Plants that establish or grow at different times of the growing season will likely be confronted with different amounts and species of competitors and with different availabilities of above- and below-ground resources. This may influence their success in persisting for longer periods in these successional communities.

The seasonal patterns of resource availability demonstrated that nitrogen addition to the second-year old-field led to reduced light penetration to the soil surface. At mid-season light penetration was lower and soil nitrogen availability was higher in the nitrogen addition treatments than the control. However, by August light penetration and nitrogen availability were at the same low levels in the control and nitrogen addition plots. Few field studies have documented seasonal patterns of resource availability in terrestrial plant communities. The effects of competitors and experimental treatments on resource availability are usually measured only at the end of the experiment. In the second-year old-field, the effect of nitrogen additions on resource availability was apparent early and mid-season but not at the end of the season. Monitoring seasonal patterns of resource availability will be important for understanding which resources limit plant productivity and for untangling the mechanisms of plant competition.

The graphical and statistical method demonstrated that the slope of the relationship between the absolute and relative responses of species to nitrogen addition in the annual old-field and the biomass of the species in the control plots depended on the time of nitrogen addition. The slope was not significant when nitrogen was added early in the season in the annual old-field, when the hierarchy among species was not established and species of all abundances in the control plots increased biomass. However, the slope was significant and negative when nitrogen was added mid- or late season. Species of higher abundance in the control plots decreased in biomass and species of low abundance increased in biomass. The negative slope was the result of competition from the dominant species; the slope was positive when *C. album* was removed from the community and nitrogen was added mid-season. In contrast to the annual old-field, the slope of the relationship between absolute biomass response to nitrogen addition and the biomass of species in the control plots was always positive. This result suggests that the effect of *Conyza canadensis* and *Chenopodium album* on the biomass hierarchy differed. In both studies, the absolute response was larger for species of high abundance in control plots than for species of low abundance. The relative response was larger for species of low abundance than for species of high abundance. This pattern suggests that measures of absolute response are more sensitive changes in rare species, and measures of relative response are more sensitive to changes in abundant or dominant species.

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