

## Interactive effects of fertilization and disturbance on community structure and resource availability in an old-field plant community

Scott D. Wilson\* and D. Tilman

Department of Ecology, Evolution and Behavior, University of Minnesota, Minneapolis, MN 55455, USA

Received September 4, 1990 / Accepted in revised form June 11, 1991

**Summary.** The interactive effects of fertilization and disturbance on plant community structure and resource availability were studied by supplying four levels of nitrogen and applying four intensities of tilling to a 30 year old field in a factorial design for 2 year. Live above-ground biomass, root biomass, and litter generally increased with nitrogen supply and decreased with disturbance. Species composition varied significantly, with annuals increasing with both nitrogen and disturbance, but with perennials unaffected by nitrogen and decreased by disturbance. Species diversity decreased with disturbance, but decreased with nitrogen only in undisturbed vegetation. Root: shoot ratios decreased with added nitrogen, leaf allocation decreased with disturbance, and flowering allocation increased. Surprisingly, stem allocation was unaffected by disturbance. This result reflected a shift from vertical stems to horizontal stems as disturbance increased. Resource measurements suggested that the vegetation responded to interactions between the treatments as well as to direct treatment effects. Variation in light penetration was reduced by fertilization in undisturbed vegetation but not in tilled plots; variability was not directly affected by disturbance. The availability of nitrogen, the limiting soil nutrient, increased with fertilization but was not significantly affected by disturbance. In contrast, the ratio of ammonium to nitrate was significantly reduced by disturbance but unaffected by supply rates, suggesting that nitrogen may have had different effects under different disturbance regimes, even though its total availability was constant. While many community responses to fertilization and disturbance conformed to those reported earlier, resource and allocation measurements indicated that their interactions are not always predictable from their separate effects.

**Key words:** Fertilization – Disturbance – Interactions – Nitrogen mineralization – Old-fields

\* Present address and address for offprint requests: Department of Biology, University of Regina, Regina, Saskatchewan, S4S 0A2, Canada

General theories that attempt to account for the species composition and dynamics of ecological communities have as their major axes variation in productivity and disturbance (Connell 1978; Grime 1979; Huston 1979; Oksanen et al. 1981; Tilman 1988; Menge and Sutherland 1987). Productivity and disturbance, however, are often correlated and each can have both direct and indirect effects upon the other. Climatic factors controlling productivity also affect disturbance, as shown by the negative relationship between evapotranspiration and the frequency and intensity of forest fires (Payette et al. 1989; Clark 1989). Grazers forage most heavily in nutrient-rich areas and cause more disturbance there than in less productive sites (Huntly and Inouye 1988). Disturbance, or the removal of plant biomass (Grime 1979), can alter productivity. For example, the productivity of lakeshore vegetation is influenced by wave-driven sorting of organic matter and fine particles (Pearsall 1920; Keddy 1983). Further, fire can increase nutrients available for plant growth in the short term by removing litter which otherwise supports nutrient-demanding microbial populations (Seastedt 1988), but constant disturbance over many years can result in a long-term loss of nutrients available for use in the community (Runge 1983). Lastly, the effect of both productivity and disturbance on plants may be modified by biotic interactions, such as competition, predation and decomposition, although the magnitude and direction of such interactions remain in debate (Grime 1973; Newman 1973; Vitousek et al. 1979; Oksanen et al. 1981; Grubb 1985; Coley 1987; Thompson 1987; Tilman 1987a; Keddy 1989; Taylor et al. 1990).

Unavoidable interactions between productivity and disturbance make it difficult to study them separately in natural communities and may be one reason why attempts to go beyond descriptions of productivity-disturbance patterns to mechanisms involving resources, competition, and diversity have largely remained the domain of ecological theory (Huston 1979; Grime 1979; Menge and Sutherland 1987; Tilman 1988). This research was designed to examine interactions by varying soil resource availability and disturbance independently in a factorial

design. The relationships between them, and the mechanisms that relate them to species abundances and diversity, can then be studied. The objective of this study was to manipulate productivity and disturbance in an old field plant community and measure both the direct and interactive effects of these factors on species composition and richness, allocation patterns, life-histories, light, and soil resources.

## Methods

### *The experiment*

A factorial gradient of nitrogen supply and disturbance was established in an old field on a nitrogen poor sand plain (Field B at Cedar Creek Natural History Area, 45° 24' N, 93° 12' W, 50 km N of Minneapolis, Minnesota; see Tilman 1987b; Inouye et al. 1987a). The field has fine sand soil (Grigal et al. 1974) and was last farmed, for soybeans, in 1957. Dominant plant species include *Schizachyrium scoparium*, *Rumex acetosella*, *Lespedeza capitata*, *Solidago nemoralis*, mosses and lichens. Experiments show that nitrogen is the limiting soil nutrient in the field. Of all the nutrients (N, P, K, Ca, Mg, water) added singly or in combination, only nitrogen significantly increases community biomass and alters species composition (Tilman 1987b; 1988).

Four levels of nitrogen (N) and four of disturbance (D) were applied in a two factor design with sixteen treatments. Treatments were replicated four times with the exception of the four "corner treatments" (N1D1: no added nitrogen, no disturbance; N1D4: no added nitrogen, highest rate of disturbance; N4D1: highest rate of nitrogen addition, no disturbance; N4D4: highest rates of nitrogen and disturbance), which were replicated fourteen times. Treatments were applied to 104 plots, each 5 × 5 m, separated by 2 m corridors of undisturbed vegetation. Treatments were assigned to plots in a completely randomized design. The most important natural disturbance at the site is produced by the plains pocket gopher (*Geomys bursarius*) which is particularly active in nitrogen-rich vegetation (Inouye et al. 1987a), producing the potential for the nitrogen treatments to be confounded by disturbance. To prevent confounding of nutrient additions by disturbance from large vertebrates, the experiment was surrounded by steel netting (mesh size 1.5 cm) buried to a depth of 50 cm to exclude gophers, and by a 2 m tall fence to exclude white-tailed deer. Trapping in 1988 indicated that small mammals were not present in large numbers (Wilson and Tilman 1991).

Four levels of nitrogen were applied as commercial  $\text{NH}_4\text{NO}_3$  at 0, 2.0, 9.5, and 17  $\text{g m}^{-2} \text{ year}^{-1}$  in early May and late June in both 1988 and 1989. The following nutrients and trace elements were also added to ensure that only nitrogen was limiting:  $\text{P}_2\text{O}_5$ , 20  $\text{g m}^{-2} \text{ year}^{-1}$  as commercial 0-46-0 fertilizer;  $\text{K}_2\text{O}$ , 20  $\text{g m}^{-2} \text{ year}^{-1}$  as commercial 0-0-61;  $\text{CaCO}_3$ , 40  $\text{g m}^{-2} \text{ year}^{-1}$  as fineground commercial lime;  $\text{MgSO}_4$ , 30  $\text{g m}^{-2} \text{ year}^{-1}$  as U.S. Pure Epsom salts;  $\text{CuSO}_4$ , 18  $\mu\text{g m}^{-2} \text{ year}^{-1}$ ;  $\text{CoCO}_2$ , 15.3  $\mu\text{g m}^{-2} \text{ year}^{-1}$ ;  $\text{MnCl}_2$ , 322  $\mu\text{g m}^{-2} \text{ year}^{-1}$ ;  $\text{NaMoO}_4$ , 15.1  $\mu\text{g m}^{-2} \text{ year}^{-1}$ .

Four levels of disturbance were created by tilling with a self-propelled, rear tined rototiller. This machine allowed disturbance to be spread evenly across plots in a manner that could be repeated consistently among plots. Control plots were not tilled. Disturbed plots were tilled to a depth of 10 cm in parallel, adjacent rows. Subsequent tillings were made perpendicular to the previous until the desired cover of bare ground was achieved. Four intensities of tilling were applied, designed to produce 0, 25, 50 and 100% cover of bare ground. In practice, a single pass produced about 20–30% bare ground across all nitrogen levels, two passes produced 40–60%, and three or more passes resulted in 100% bare ground. Plots were tilled each spring as soon as the snow had melted and prior to nitrogen addition. This occurred in early April in 1988 but in early May in 1989 because of a later spring.

### *Productivity and allocation*

Above-ground primary production was determined at the peak of the growing season by harvesting standing crop on 13–14 July, 24–25 July and 11–15 August 1989 in 100 × 10 cm quadrats (50 × 10 cm in the second harvest) in each plot. Standing crop was harvested three times in order to examine temporal variation in biomass and litter. Different quadrats were harvested on each date. Quadrats were placed 1 m inside the NE corner of each plot and were separated by 20 cm. Harvested material was separated into live and dead components, dried to constant mass and weighed. The live portion of the final harvest was separated into leaves, stems and flowering parts before being dried and weighed. Root biomass was sampled using four cores (each 2.5 cm diameter, 10 cm deep) from each plot on 26 July and 22 August. Samples were taken from evenly spaced locations along a transect 1 m inside each plot. At both times cores from each plot were combined, and the roots within were washed, dried and weighed. Roots were sampled only twice because of the long time required for washing.

### *Species composition and diversity*

Species composition was determined during August 1989, at the peak of the growing season, along a transect that ran diagonally across each plot. Two quadrats (0.5 × 1 m) were placed along the transect, each 1.5 m towards the center of the plot from each end of the transect. Thus, there were two quadrats per plot. The cover of each species and bare ground was recorded using Daubenmire's scale (Mueller-Dombois and Ellenberg 1974). Sampling at this time did not miss vernal ephemerals because these species could be recognized all summer. The proportional cover of perennials, annuals and nonvascular plants (mosses and lichens) was then calculated for each quadrat. Species richness was determined as the number of species recorded, species diversity was calculated as  $H'$ , the Shannon-Wiener index, and evenness was calculated as  $J'$  (Pielou 1975).

Height of vegetation was determined in August by measuring the highest vegetation in contact with a vertical rod at four locations along a transect 1 m inside each plot. Mean height was calculated for each plot.

### *Light*

Light profiles through the vegetation of each plot were measured within 2 hours of solar noon during 2–14 August using a level 40 cm long integrating strip (Sunfleck Ceptometer, Decagon Devices). In each plot, light was measured above the vegetation, at 50, 40, 30, 20, 10, and 5 cm above the soil surface, and at four equally spaced locations on the soil surface near the center of each plot. The average light penetration to the soil surface was determined from the four measurements. Light penetration was determined as the proportion of light above the vegetation measured at each level.

### *Nitrogen*

Four soil cores (2.5 cm diameter, 10 cm deep) were taken from each plot on 25 July 1989. Cores were taken from evenly spaced locations along a transect 1 m inside each plot. The four cores from each plot were divided into two lots. Each lot was pooled and mixed, and analyzed for available soil nitrogen, in the form of nitrate and ammonium extractable with 2 M KCl, using an Alpkem Rapid Flow Analyzer. At the same time as cores were taken, measurement of nitrogen mineralization was started by placing a rigid plastic tube (2.5 cm diameter, 15 cm deep) in the soil 10 cm deep, 5 cm north of each core (Raison et al. 1987). Soil in tubes was free of above-ground vegetation. Tubes were covered with plastic cups to prevent leaching of available nitrogen by rain. Soil in tubes was collected and a core 5 cm north of each tube was also collected on 18 August. The soil from the four tubes in each plot was pooled and mixed, as were the four cores of soil from outside the tube, prior to analysis.

**Table 1.** Results (*F* values) from three factor ANOVAs for sequential samples of above-ground biomass, root biomass, litter, nitrate, ammonium, and the ammonium: nitrate ratio

Dependent variable	Effect						
	N <sup>1</sup>	D	T	N*D	N*T	D*T	N*D*T
Live above-ground biomass	24.03***	12.20***	3.60*	2.65**	0.83	2.53*	1.96*
Litter	12.52***	33.29***	4.22*	4.73***	0.66	0.86	0.90
Root biomass	0.94	8.09***	31.50***	1.40	1.99	0.93	2.02*
Soil nitrate	13.66***	2.22	3.10*	0.56	1.46	0.72	0.84
Soil ammonium	36.08***	1.29	13.67***	0.21	3.34**	0.80	0.42
Ammonium: nitrate ratio	0.91	11.48***	11.88***	2.82**	0.51	0.46	1.21

<sup>1</sup>N: nitrogen effect; D: disturbance effect; T: time effect for biomass results, sample event for nitrogen results; N\*D: nitrogen-disturbance interaction; N\*T: nitrogen-time interaction; D\*T: disturbance-time interaction; N\*D\*T: nitrogen-disturbance-time interaction  
\*  $P < 0.05$ ; \*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$

for available nitrogen. The mean of the two samples from each plot in the July sample was used as a measure of July soil nitrogen concentration, so that there was one measure of  $\text{NH}_4$  and  $\text{NO}_3$  from each plot for each sample event (soil in July, soil inside tubes in August, soil outside tubes in August).

### Analysis

Above-ground live biomass, litter, root data and available nitrogen were analyzed in three factor ANOVAs with nitrogen, disturbance and time of sample as main effects. Species abundance data, for which there were two quadrats per plot, were analyzed using three factor ANOVAs with the quadrats as a third factor nested within nitrogen and disturbance effects. Other variables were analyzed with two factor ANOVAs with nitrogen and disturbance as main effects. Contrasts among all sixteen treatments were not performed because the large number of results would be difficult to interpret. Instead, contrasts were performed only to test hypotheses of particular interest. "Corner treatments" (N1D1, N1D4, N4D1, N4D4) were highly replicated ( $N=14$ ) and were frequently contrasted in order to test for significant trends. Contrasts were also performed for other means in cases where curvilinear responses were suspected. Transformations were not used because those which reduce correlations between means and variances also remove factor interactions (Snedecor and Cochran 1980, Day and Quinn 1989), and an important objective of this study was to describe such interactions. Some data were heteroscedastic, but ANOVA results are robust in spite of heteroscedasticity in cases where sample sizes are large and dimensionality is low (Ito, 1980).

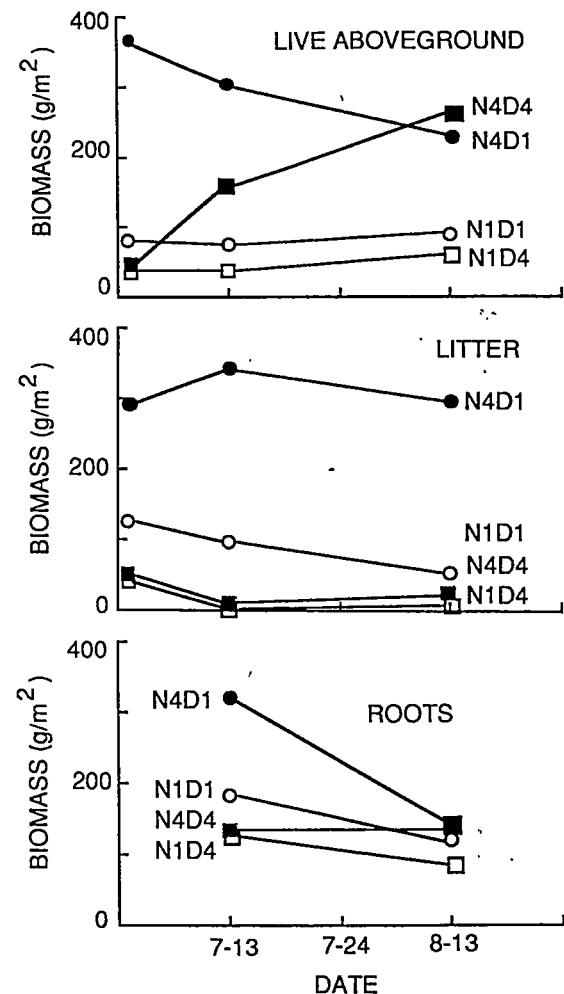
### Results

#### Productivity and allocation

Above-ground live biomass increased significantly with nitrogen availability and generally decreased with disturbance (Fig. 1, Table 1). Time of harvest showed a significant interaction with disturbance, indicating that disturbance effects were fairly large in July and relatively small in August. Live biomass increased with harvest date in most treatments but decreased over time in the most heavily fertilized, undisturbed plots.

Litter mass was significantly greater in fertilized plots and lower in disturbed plots and generally decreased with time (Table 1, Fig. 1). There was a significant interaction between nitrogen and disturbance: litter was reduced by disturbance more in fertilized plots than in unfertilized plots.

Root biomass significantly decreased with distur-



**Fig. 1.** Live above-ground biomass (top), litter (middle) and root biomass (bottom) over time in the four corners (N1D1: no added nitrogen, no disturbance; N1D4: no added nitrogen, highest rate of disturbance; N4D1: highest rate of nitrogen addition, no disturbance; N4D4: highest rate of nitrogen and disturbance) of the nitrogen - disturbance factorial gradient in 1989. ANOVA results in Table 1. Values are means of 14 replicates

bance and time but did not vary with nitrogen (Table 1, Fig. 1). A significant three-way interaction was caused by root biomass in fertilized plots declining with time only in undisturbed vegetation.

The total amount of plant biomass (above ground live biomass, litter and roots) in the last harvest increased with nitrogen and decreased with disturbance (Fig. 2; nitrogen:  $F=13.12$ ,  $P<0.001$ ; disturbance:  $F=9.86$ ,  $P<0.001$ ; interaction:  $F=1.82$ ,  $P>0.05$ ). Community root: shoot ratio decreased with increasing nitrogen, but was unaffected by disturbance and showed no effects due to an interaction between nitrogen and disturbance (Fig. 2; nitrogen:  $F=6.77$ ,  $P<0.001$ ; disturbance:  $F=0.14$ ,  $P>0.05$ ; interaction:  $F=0.21$ ,  $P>0.05$ ).

The proportion of live above-ground biomass accounted for by stems did not vary significantly within the experiment when all treatment levels were considered (nitrogen:  $F=0.80$ ; disturbance:  $F=1.40$ ; interaction:  $F=1.26$ ;  $P>0.05$ ), but contrasts among corner treatments showed that stem allocation increased significantly with nitrogen supply at both low and high levels of disturbance (Table 2). The proportion of above-ground biomass allocated to leaves varied significantly with disturbance (all treatment levels: nitrogen:  $F=0.29$ ,  $P>0.05$ ; disturbance:  $F=12.80$ ,  $P<0.001$ ; interaction:  $F=1.53$ ,  $P>0.05$ ). Pairwise contrasts of corner treatments showed that leaf allocation decreased significantly with nitrogen in undisturbed vegetation but not in disturbed plots, and decreased with disturbance in unfertilized but not in fertilized plots (Table 2). Flower allocation varied significantly with disturbance (all treatment levels: nitrogen:  $F=1.26$ ,  $P>0.05$ ; disturbance:  $F=16.69$ ,  $P<0.001$ ; interaction:  $F=1.07$ ,  $P>0.05$ ). Biomass allocated to flowers increased two to five-fold with

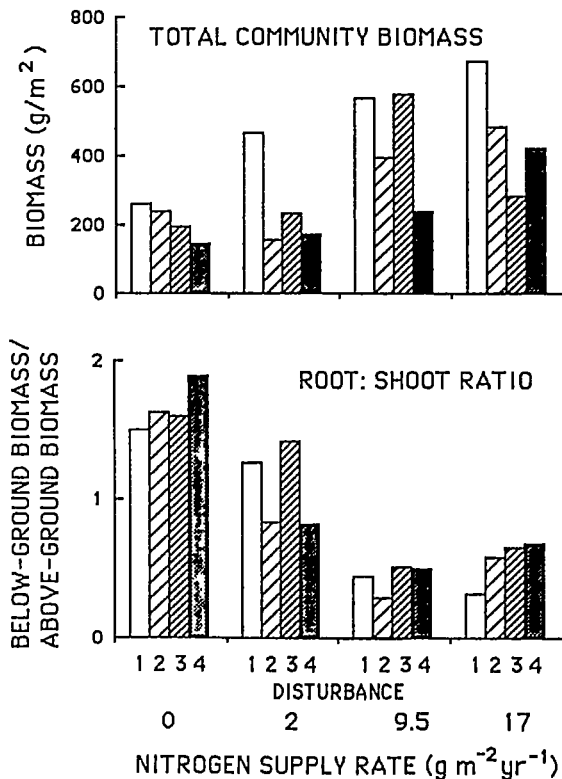


Fig. 2. Total community biomass (*top*) and root: shoot ratio (*bottom*) in all sixteen combinations of nitrogen supply rate and disturbance. There were fourteen replicates of each corner treatment (see caption for Fig. 1) and four for all others

Table 2. Means of variables describing the percent of above-ground community biomass allocated to stems, leaves and flowers in the four corners of the factorial design

Variable	Disturbance level	Nitrogen level	
		Lowest	Highest
Stem allocation	Lowest	22.6 <sup>a</sup>	36.4 <sup>a</sup>
	Highest	24.4 <sup>a</sup>	36.4 <sup>a</sup>
Leaf allocation	Lowest	71.5 <sup>a</sup>	54.7 <sup>a</sup>
	Highest	35.1 <sup>b</sup>	43.6 <sup>a</sup>
Flower allocation	Lowest	5.9 <sup>a</sup>	8.9 <sup>a</sup>
	Highest	33.3 <sup>b</sup>	20.0 <sup>b</sup>

<sup>a, b</sup> superscripts denote means not significantly different ( $P<0.05$ ) among disturbance treatments. Means joined by a common underline were not significantly different among nitrogen supply rates

disturbance (Table 2). Contrasts of corner treatments showed that flower allocation declined significantly with nitrogen supply in disturbed plots but was unaffected in undisturbed plots.

Cover of bare ground in late summer increased with disturbance ( $F=91.90$ ,  $P<0.001$ ) and decreased with nitrogen availability ( $F=53.99$ ,  $P<0.001$ ; Fig. 3). A significant interaction between main effects ( $F=7.46$ ,  $P<0.001$ ) resulted because disturbance produced more bare ground in unfertilized plots than in fertilized plots. Plots receiving intermediate rates of disturbance (D2 and D3) were similar to those receiving the highest rate of disturbance (D4) in treatments without added nitrogen

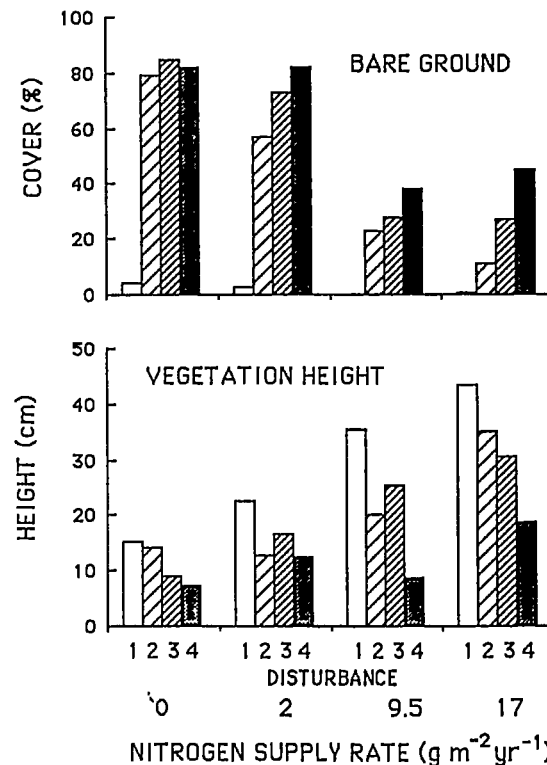


Fig. 3. Cover of bare ground (*top*) and height of vegetation (*bottom*) in all sixteen combinations of nitrogen supply rate and disturbance. There were fourteen replicates of each corner treatment (see caption for Fig. 1) and four for all others

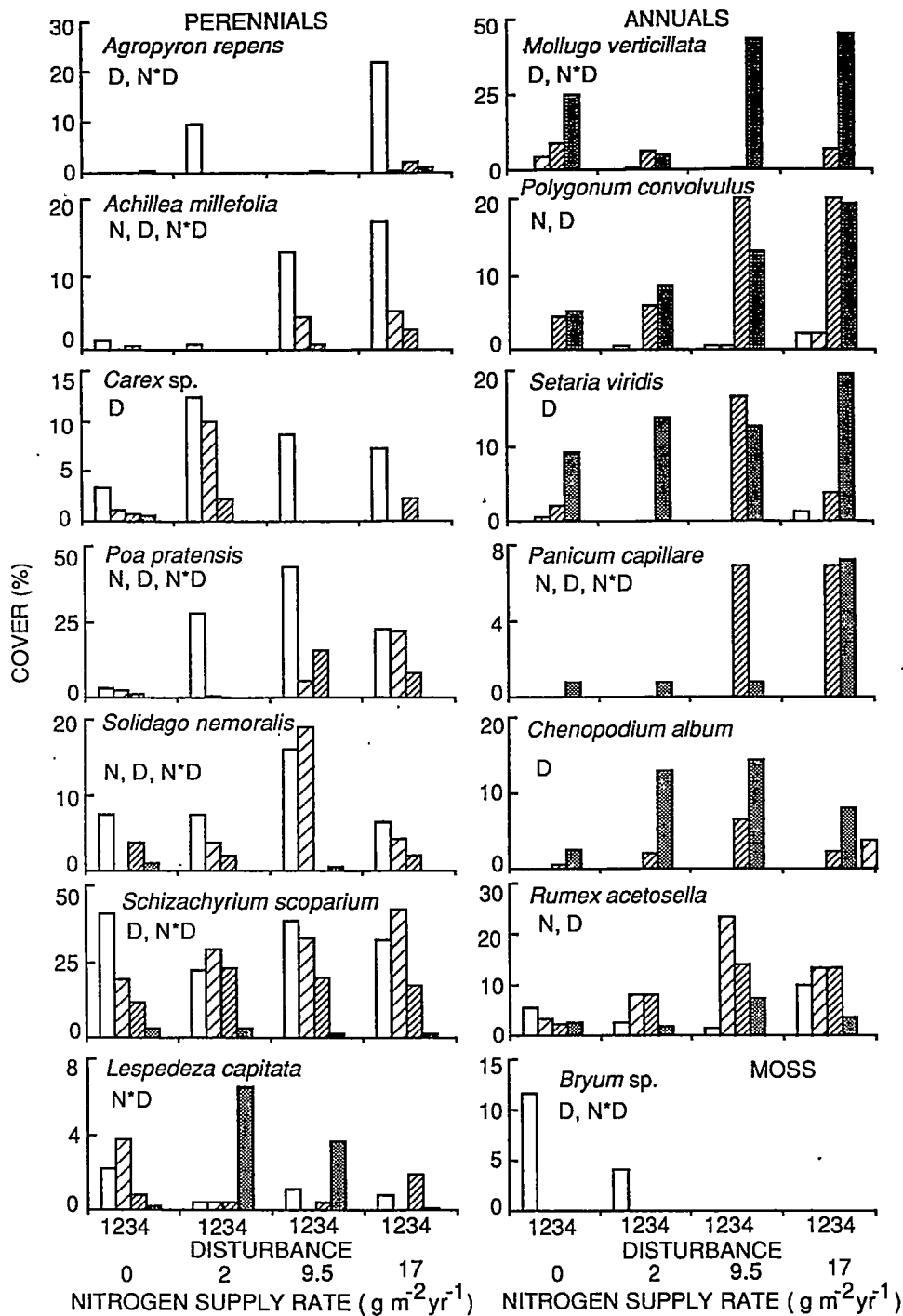


Fig. 4. Covers of common species of perennials (left), annuals (right), and moss (bottom right) in all sixteen combinations of nitrogen supply rate and disturbance. There were fourteen replicates of each corner treatment (see caption for Fig. 1) and four for all others. N: significant ( $P < 0.05$ ) nitrogen effect; D: significant disturbance effect; N\*D: significant interaction

(N1), but the four disturbance treatments formed a more even gradient in plots receiving the highest rate of added nitrogen.

Height of vegetation increased significantly with nitrogen ( $F = 12.32$ ,  $P < 0.001$ ) and decreased with disturbance ( $F = 18.55$ ,  $P < 0.001$ ; interaction:  $F = 1.63$ ,  $P > 0.05$ ; Fig. 3).

#### Species composition and diversity

Fourteen species had mean covers  $> 1\%$  across all treatments. The covers of all 14 species varied significantly

with disturbance ( $P < 0.05$ , Fig. 4). Most species also varied significantly with nitrogen or with the interaction between nitrogen and disturbance. Perennials and mosses tended to decrease with increasing disturbance whereas annuals increased (Fig. 5). Nitrogen had no direct or indirect effect on three species, *Carex* sp., *Setaria viridis*, and *Chenopodium album*. Perennials showed a variety of responses to nitrogen, annuals generally increased with nitrogen, and the moss *Bryum* sp. disappeared from fertilized plots. Several species which had no direct response to nitrogen showed a significant interaction between nitrogen and disturbance (e.g. *Agropyron repens*,

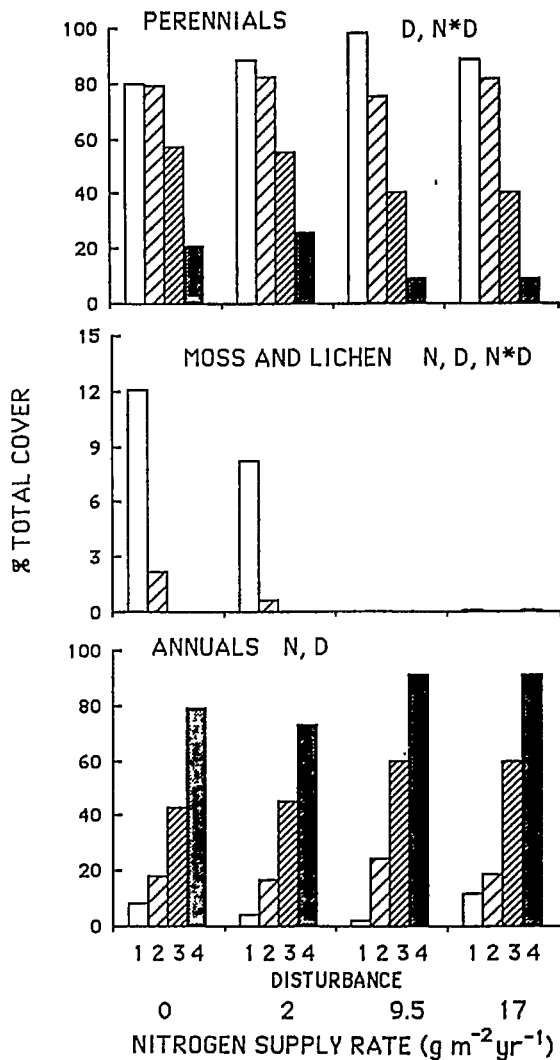


Fig. 5. Covers of perennials (top), mosses and lichens (middle) and annuals (bottom) in all sixteen combinations of nitrogen supply rate and disturbance. There were fourteen replicates of each corner treatment (see caption for Fig. 1) and four for all others. N: significant ( $P < 0.05$ ) nitrogen effect; D: significant disturbance effect; N\*D: significant interaction

Table 3. Contrasts between selected means of species covers to test for curvilinear responses to nitrogen or disturbance (Fig. 4). Contrasts are presented in pairs. The first contrast compares an intermediate treatment level with a higher treatment level possessing a lower mean value; the second pair contrasts the same intermediate

Species	First mean			Second mean			F	P
	Nitrogen level	Disturbance level	Cover (%)	Nitrogen level	Disturbance level	Cover (%)		
<i>Solidago nemoralis</i>	3	1	16.1	4	1	6.5	8.05	0.005
	3	1	16.1	1	1	7.4	6.57	0.011
	3	2	18.9	4	2	4.1	12.15	0.001
	3	2	18.9	1	2	0.0	*	
<i>Lespedeza capitata</i>	2	4	6.5	4	4	0.1	12.42	0.001
	2	4	6.5	1	4	0.2	12.01	0.001
<i>Rumex acetosella</i>	3	2	23.5	3	4	7.5	8.63	0.004
	3	2	23.5	3	1	1.5	14.68	0.001

\* Contrast could not be performed because the species' cover was 0% in all replicates

*Mollugo verticillata* and others). Some interactions between nitrogen and disturbance were the result of the complete absence of a species from a particular level of one factor. For example, *Panicum capillare* occurred only in the two most heavily disturbed treatments, whereas *Achillea millefolium* and *Poa pratensis* were eliminated from the most heavily disturbed treatment.

Most species responses appeared to be simple linear increases or decreases, but where inspection of means in Fig. 4 suggested a curvilinear response, contrasts were performed between appropriate means within two factor ANOVAs. Contrasts revealed that *Solidago nemoralis* achieved peak cover at intermediate rates of nitrogen supply in undisturbed plots (Table 3), *Lespedeza capitata* was most abundant at intermediate rates of nitrogen supply in the most disturbed plots, and *Rumex acetosella* achieved peak abundance at intermediate rates of disturbance at intermediate nitrogen supply rates (Fig. 4). Quadrat sampling as a main effect was non-significant in all cases ( $P = 0.50-1.00$ ).

The proportion of total cover accounted for by perennials decreased significantly with disturbance, and the extent of this decrease varied significantly with nitrogen supply, as indicated by the interaction (Fig. 5; nitrogen:  $F = 2.09$ ,  $P > 0.05$ ; disturbance:  $F = 187.88$ ,  $P < 0.001$ ; interaction:  $F = 2.64$ ,  $P < 0.01$ ). Cover of moss and lichens decreased with both nitrogen and disturbance (nitrogen:  $F = 4.38$ ,  $P < 0.01$ ; disturbance:  $F = 8.97$ ,  $P < 0.001$ ; interaction:  $F = 5.01$ ,  $P < 0.001$ ). Annuals responded positively to both nitrogen and disturbance (nitrogen:  $F = 4.88$ ,  $P < 0.01$ ; disturbance:  $F = 245.76$ ,  $P < 0.001$ ; interaction:  $F = 1.18$ ,  $P > 0.05$ ).

Species richness decreased significantly with disturbance and showed an interaction between nitrogen and disturbance (nitrogen:  $F = 1.26$ ,  $P > 0.05$ ; disturbance:  $F = 11.23$ ,  $P < 0.001$ ; interaction:  $F = 3.99$ ,  $P < 0.001$ ). Richness decreased significantly with nitrogen in undisturbed plots, but was consistently low in disturbed plots (Table 4). Species diversity showed the same result (nitrogen:  $F = 1.45$ ,  $P > 0.05$ ; disturbance:  $F = 8.36$ ,  $P < 0.001$ ; interaction:  $F = 2.19$ ,  $P = 0.025$ ). Evenness varied only

treatment with a lower treatment level, also with a lower mean value. Cases in which both the higher and lower treatment levels had mean values significantly lower than the intermediate level indicated nonlinear responses. Only significant results are shown

**Table 4.** Means of variables describing diversity in the four corners of the factorial design

Variable	Disturbance level	Nitrogen level	
		Lowest	Highest
Species richness	Lowest	8.3 <sup>a</sup>	4.5 <sup>a</sup>
	Highest	4.7 <sup>b</sup>	4.6 <sup>a</sup>
Species diversity	Lowest	0.67 <sup>a</sup>	0.45 <sup>a</sup>
	Highest	0.47 <sup>b</sup>	0.42 <sup>a</sup>
Evenness	Lowest	0.75 <sup>a</sup>	0.69 <sup>a</sup>
	Highest	0.72 <sup>a</sup>	0.64 <sup>a</sup>

<sup>a, b</sup> superscripts denote means not significantly different ( $P < 0.05$ ) among disturbance treatments. Means joined by common underlines were not significantly different among nitrogen supply rates

with disturbance (nitrogen:  $F = 1.10$ ,  $P > 0.05$ ; disturbance:  $F = 3.72$ ,  $P = 0.012$ ; interaction:  $F = 1.46$ ,  $P > 0.05$ ). Evenness was unaffected by nitrogen in undisturbed plots but was significantly reduced by nitrogen in disturbed plots (Table 4).

### Light

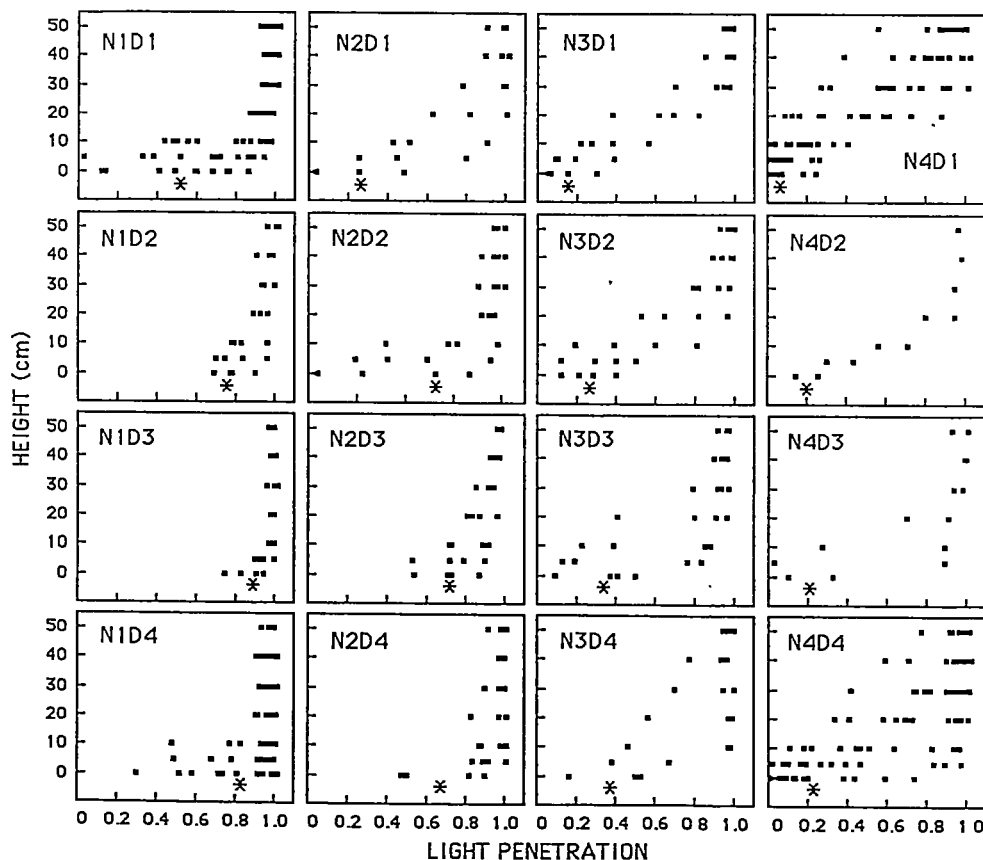
Light penetration to the soil surface decreased significantly with nitrogen supply ( $F = 35.47$ ;  $P < 0.001$ ) and increased with disturbance ( $F = 9.54$ ,  $P < 0.001$ ; interaction:  $F = 0.48$ ,  $P > 0.05$ ). In control plots, light penetration dropped to less than 80% at 10 cm above the soil

surface, whereas it was reduced to this extent at 50 cm in the most heavily fertilized plots (Fig. 6). The effect of fertilization in undisturbed vegetation (N4D1) was to produce a linear increase in light penetration with height above the soil, in contrast to the logarithmic pattern in control plots (N1D1). The same shift was found from unfertilized to fertilized plots in the most disturbed treatments (N1D4 vs. N4D4). Variability in light penetration to the soil surface was unaffected by disturbance (N1D1: std. dev. = 0.24; N1D4: std. dev. = 0.22; N4D4: std. dev. = 0.23) but was greatly reduced by fertilization of undisturbed plots (N4D1: std. dev. = 0.07). Disturbance created high levels of light penetration in both fertilized and unfertilized vegetation.

### Nitrogen

Nitrate increased significantly with nitrogen supply rate, but did not vary significantly with disturbance (Fig. 7, Table 1). Nitrate also varied significantly among the three sample events (July soil, August tubes, August soils), but the concentration of nitrate in soil inside tubes from which plant uptake and leaching had been excluded for 24 d was lower than that in the July soil sample, suggesting that nitrogen uptake by microbes equalled or exceeded that supplied by mineralization.

Ammonium increased significantly with nitrogen supply, varied among sample events, and showed a significant interaction between nitrogen supply and sample event (Fig. 7, Table 1). Contrasts between sample events,



**Fig. 6.** Light penetration through the canopy in all sixteen combinations of nitrogen supply rate and disturbance. Each point represents one measure in one replicate plot. Asterisks indicate mean light penetration at the soil surface. There were fourteen replicates of each corner treatment (N1D1, N1D4, N4D1, N4D4) and four for the others.

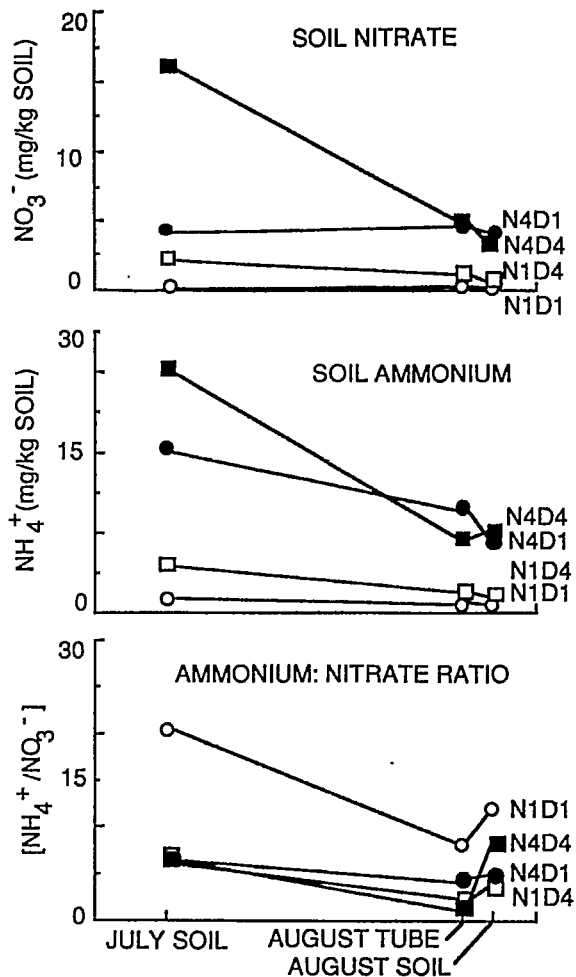


Fig. 7. Soil nitrate (top), ammonium (middle) and the ratio of ammonium to nitrate (bottom) in the soil in July, in tubes in August from which roots had been excluded, and in soil in August, in the four corners (see Fig. 1) of the nitrogen – disturbance factorial gradient. ANOVA results in Table 1. Values are means of 14 replicates

for each nitrogen supply level across all disturbance treatments, showed that this interaction was due to a greater rate of immobilization in fertilized plots than unfertilized plots: in unfertilized plots, ammonium did not vary among sample events ( $F=0.40-0.95$ ,  $P>0.05$ ), but at the highest rate of nitrogen supply, ammonium was significantly lower in August tubes and soil than in July soil ( $F=29.41$ ,  $37.96$ ,  $P<0.001$ ). Thus, microbial demand was apparently capable of immobilizing nitrogen even at the highest rate of supply. For both nitrate and ammonium, concentrations in August in soil outside tubes was generally slightly, though not significantly, lower than that inside tubes, suggesting that some plant uptake was occurring.

Disturbance had no significant effect on the availability of ammonium or nitrate (Table 1), although the concentrations of both forms of nitrogen were higher in disturbed plots than in undisturbed plots in samples taken in July (Fig. 7).

The ratio of ammonium to nitrate was consistently  $\gg 1$  (Fig. 7), decreased significantly with disturbance and

varied among sample events (Table 3). Pairwise contrasts showed that the ratio in tubes was significantly less than that in the soil in either July or August ( $F=23.69$ ,  $4.79$ ,  $P<0.05$ ), indicating that plants and microbes consumed nitrate and ammonium at different rates. The ratio of ammonium to nitrate was not affected by the rate of nitrogen supply (Table 1).

## Discussion

Nitrogen addition and disturbance produced significant effects on all aspects of community structure. Many responses were similar to those reported in previous studies. Community biomass increased with nitrogen supply rate (Tilman 1987b; Hobbs and Atkins 1988; DiTommaso and Aarssen 1989; Wilson and Shay 1990). Species richness and diversity decreased with nitrogen addition in undisturbed vegetation (Table 4), as in other grasslands (Reed 1977; Inouye et al. 1987a; Tilman 1988; Wilson and Shay 1990; Huenneke et al. 1990). Vegetation height increased, light penetration decreased, and species became separated along the nitrogen gradient (Tilman 1988). These patterns were found in both disturbed and undisturbed plots, in spite of very little overlap in species composition (Fig. 4). The similarity in response to nitrogen regardless of disturbance conformed to the fact that nitrogen availability, apart from the ammonium:nitrate ratio, was not significantly affected by disturbance (Table 1). The results suggest that nitrogen has similar effects on community structure regardless of disturbance regime and degree of species turnover. Similar results were obtained from a mediterranean-climate grassland (Huenneke et al. 1990).

The dominance of disturbed plots by annuals reflects the creation of appropriate germination conditions for these species (Gross and Werner 1982; Platt and Weis 1985; Hobbs and Atkins 1988) and the high mortality experienced by perennials. Annuals showed a slight but significant increase with nitrogen availability (Fig. 5), especially in disturbed plots, suggesting that their growth is also limited by nitrogen. Annuals disappear from undisturbed, fertilized plots at the study site after a few years (Tilman 1987b). Perennials were present at low densities in highly disturbed plots. Many perennials are capable of vegetative resprouting following disturbance, but most perennials in disturbed plots in this experiment appeared to be seedlings.

The results show that not all species had simple positive or negative relationships with nitrogen and disturbance, e.g. *Solidago nemoralis* which showed maximum abundance at intermediate rate of nitrogen availability, but only in plots receiving no or little disturbance (Table 3, Fig. 4). Other fertilization experiments at Cedar Creek show that species have curvilinear responses to nitrogen addition (Tilman 1987b), but our results show that such partitioning also occurs in disturbed vegetation, and that species partition gradients of disturbance intensity as well (Fig. 4). For example, mosses were found only in undisturbed vegetation, *Rumex acetosella* was significantly more common at the second lowest rate of distur-



bance than at the lowest or highest rates (Table 3), and most annuals were found only in disturbed plots.

The response of species diversity to disturbance was consistent with other old field studies to the extent that diversity varied significantly with disturbance (Armesto and Pickett 1985; Carson and Pickett 1990). Armesto and Pickett (1985) found that clipping increased species richness, whereas tilling in this experiment decreased richness in unfertilized vegetation and had no effect at high nitrogen availability (Table 4). The divergence in results between clipping and tilling experiments is probably due to the destruction of belowground parts by tilling. The effect of disturbance on life histories, community biomass, and diversity in this experiment was similar to that in other studies, even though the scale of disturbance greatly exceeded natural regimes for this system (Inouye et al. 1987b; Goldberg and Gross 1988).

Allocation results generally conformed to patterns from other studies. Root: shoot ratios declined with increasing nitrogen supply, as has been shown for individual plants (Hunt et al. 1987) and for communities (Tilman 1988). This occurred at all levels of disturbance, suggesting that greater root allocation was required to garner nutrients at low resource supply rates regardless of disturbance regime.

Patterns of allocation of above-ground biomass were consistent with those found for a chronosequence of succession in old fields at Cedar Creek (Gleeson and Tilman 1990). They found that root allocation was lowest in the most recently disturbed fields in the study area, and our results show that root biomass was significantly decreased by disturbance (Fig. 1). Similarly, leaf allocation was reduced in disturbed plots (Table 2), consistent with a significant successional increase in leaf allocation with time since disturbance observed by Gleeson and Tilman (1990). Flower allocation was increased by disturbance, consistent with their significant decrease in reproductive allocation with time since disturbance in natural vegetation. Further, they found that stem allocation did not increase with time since disturbance in Cedar Creek old fields, and stem allocation was unaffected by disturbance in our experiment.

Stem allocation increased about 50% with nitrogen supply in both disturbed and undisturbed vegetation (Table 2). This suggests that stem allocation was important for gathering light regardless of disturbance regime. *Mollugo verticillata* and *Polygonum convolvulus*, with a total cover of nearly 70%, were the dominant species in the most disturbed plots at the two highest rates of nitrogen supply (Fig. 4). These species have no vertical stems but are characterized by basal rosettes joined by creeping, horizontal stems in the first case and trailing stems in the second (Gleason and Cronquist 1963). Allocation to horizontal stems is presumably important in highly disturbed and fertile habitats because of the great spatial variability of light penetration to the soil surface (Fig. 6). This may account for the lack of variation in allocation to stems found along a successional sequence by Gleeson and Tilman (1990). Constant stem allocation with increasing disturbance also suggests that the results of disturbance-related allocation models are constrained

by the usual assumption in modelling that stems are strictly vertical structures (e.g. Shugart and Noble 1981, Tilman 1988). In this study, the most abundant species in highly disturbed, fertile plots had horizontal stems. Light attenuation through the canopy probably had the greatest impact on inherently short taxa, such as moss, which declined even at the lowest rate of nitrogen addition (Fig. 4). Light attenuation did not begin until 10 cm above the soil surface in control plots, but began at 30 cm above the soil in undisturbed plots receiving the lowest rates of nitrogen addition (Fig. 6: N2D1). In the most heavily fertilized, undisturbed plots (N4D1), light attenuation occurred even at 50 cm above the soil surface.

The soil concentration of available nitrogen was elevated by supplying nitrogen but was not significantly affected by disturbance (Table 1, Fig. 7). Further, there was no interaction between disturbance and nitrogen supply rate, or between disturbance, nitrogen supply and time of sample. The results suggest that disturbance had little effect on the availability of the soil nutrient limiting production in the study area (Tilman 1987b, 1988). Removal of plant biomass might be expected to cause an increase in nitrogen availability at the start of the growing season. Indeed, the concentrations of both nitrate and ammonium were higher in disturbed plots than in undisturbed plots in July (Fig. 7). The lack of a disturbance effect in this experiment probably resulted because nitrogen uptake by plants and decomposers reduced nitrogen to similar concentrations in all treatments by August. Measurements of mineralization throughout the growing season may be required to assess the full impact of disturbance on nitrogen availability.

In contrast to the results for the concentration of available nitrogen, the ratio of ammonium to nitrate varied with disturbance but not with nitrogen supply rate. The ammonium: nitrate ratio of soil varies with acidity and mean annual temperature (Runge 1983; Rorison 1987) and our results show that it is lowered by disturbance. Disturbance might reduce the ratio by mediating abiotic effects such as insolation, moisture and litter availability, or by allowing the establishment of plant species that preferentially take up ammonium and thus depress the ratio. This ratio has differential effects on species growth rates (Moore and Keratis 1971; Gigon and Rorison 1972) and may therefore be an important determinant of species composition under varying disturbance regimes. High ammonium: nitrate ratios have been hypothesized to suppress succession (Runge 1983). The high ratios found in the control plots of this experiment (Fig. 7) coincide with the slow successional sequence at the study site (Inouye et al. 1987a; Tilman 1988; Gleeson and Tilman 1990).

The concentration of available nitrogen in tubes from which plant roots and leaching had been excluded was significantly lower than that in exposed soil 24 d earlier (Fig. 7). This result suggests that instead of accumulating and potentially being available for plant growth, mineralized nitrogen was consumed by microbial populations (Seastedt 1988). Experiments using labelled nitrogen are required to confirm this mechanism. Immobilization of available nitrogen stands in contrast to

measurements of mineralization in these soils by Pastor et al. (1987a). This was probably because of the longer term of their experiment, which spanned the entire growing season, and because they used a buried-bag technique with combined soil samples, a technique predisposed to produce rates of mineralization higher than those in intact soil cores (Raison et al. 1987). Plants did consume a small, but not significant, amount of mineralized nitrogen, as indicated by the generally lower values of nitrate and ammonium outside the tubes than inside in August (Fig. 7). Killing neighbors significantly increases the amount of nutrients available for plant growth over the course of a full growing season in both disturbed (Whigham 1984) and undisturbed old fields (Tilman 1989; Wilson and Tilman 1991), indicating that uptake of nutrients by neighbor plants significantly affects the growth of individuals.

The immobilization of nitrogen by decomposers is in accordance with the extremely low nitrogen concentrations of litter of the prairie species that dominate the control vegetation (Pastor et al. 1987b; Seastedt 1988). The results suggest that, during the mid-summer period studied, the primary competitors for soil resources may not be vascular plants, but decomposers. Decomposers are presumably highly efficient nitrogen consumers because of their high surface area to volume ratios, their high relative growth rates, and their presence throughout the soil. Because plants are significant consumers of mineralized nitrogen over the course of an entire growing season (Pastor et al. 1987a; Tilman 1989; Wilson and Tilman 1991), but not during the 24 d in late summer examined here, the relative importance of decomposers as competitors for nitrogen may vary temporally (Campbell and Grime 1989). Alternatively, net immobilization of nitrogen inside tubes might be caused by the decomposition of fine roots and might not provide an accurate estimate of mineralization in intact soil. Fine root decomposition in intact soil cores inside tubes, however, had no effect on mineralization over a 130 d period (Raison et al. 1987). Further, the rate of immobilization was highest (Fig. 7: N4D4) in a treatment with relatively low root biomass (Fig. 1), which argues against a link between nitrogen immobilization and fine root decomposition.

The importance of biotic linkages, such as decomposition and competition, between resource availability and disturbance is suggested by the presence of interactions between main effects. The decrease of live above-ground standing crop over time in fertilized, undisturbed plots (Fig. 1: N4D1) and its concomitant increase in fertilized, disturbed plots (N4D4) indicates that different mechanisms controlled productivity in disturbed and undisturbed vegetation. There are a couple of obvious possibilities. The first is that microbes on accumulated litter in undisturbed plots competed with vegetation for nitrogen and stopped plant growth by mid-summer. In this case, the interaction might be caused by decomposition dynamics. The second alternative is that the perennial species which characterized undisturbed vegetation had begun to senesce by late summer whereas the annuals in disturbed plots were still growing. In this

case, the interaction would be caused by the different life-histories of the species that dominated different disturbance regimes. The dynamics of available nitrogen seem to support the latter contention. The rate of immobilization in fertilized soils was higher in disturbed plots (Fig. 7: N4D4) where plant biomass increased (Fig. 1), than it was in undisturbed plots (N4D1) where plant biomass decreased. That is, the highest rate of immobilization occurred in plots with the highest plant productivity, suggesting that differences in productivity were related more to the differences in phenology of annual and perennial species than to competition between plants and microbes for nutrients.

Experimental evidence for competition in undisturbed vegetation at Cedar Creek exists (Tilman 1989; Wilson and Tilman 1991), but the results from this experiment suggest that competition may control plant success in disturbed vegetation as well. In disturbed vegetation, evenness decreased significantly with increased nitrogen (Table 4), showing that some species increased and others declined. Since all the Cedar Creek plants examined increase in growth rate with increased nitrogen availability (Tilman 1986; Tilman and Cowan 1989), this shift in composition is probably due to competition and not simple physiological responses. Field experiments are required to examine the role of competition in disturbed vegetation, but Whigham (1984) attributed the decline of an annual in a recently abandoned field to competition.

In summary, the patterns in species composition, diversity, allocation and resource availability produced by the experiment generally reflected those produced by non-factorial experiments using fertilizer or disturbance, and those exhibited by the chronosequence of time since cultivation in the old fields of the study area. Interactive and curvilinear effects, however, indicate that interactions between each factor and biotic processes linking them also control community composition. Our results suggest that the most important of these interactions may be: 1. the lack of a significant effect of disturbance on the amount of available nitrogen, but the significant effect of disturbance on the form of available nitrogen; 2. the constant allocation to stems as disturbance varied, reflecting a shift from vertical to horizontal stems and the importance of an ability to forage for light in a horizontally patchy environment; and 3. the decrease in species evenness concomitant with no change in richness as resource availability increased in disturbed vegetation, suggesting that competition controlled species composition in disturbed plots.

*Acknowledgements.* We thank K. Grigulis for comments on the manuscript and D. Bosanko for hospitality during the field work. Supported by NSF/BSR-8806412, NSF/BSR-8811884 and the Research School of Biological Sciences, The Australian National University.

## References

- Armesto JJ, Pickett STA (1985) Experiments on disturbance in old-field plant communities: impact on species-richness and abundance. *Ecology* 66:230-240
- Campbell BD, Grime JP (1989) A comparative study of plant

- responsiveness to the duration of episodes of mineral nutrient enrichment. *New Phytol* 112:261–267
- Carson WP, Pickett STA (1990) Role of resources and disturbance in the organization of an old-field plant community. *Ecology* 71:226–238
- Clark JS (1989) Effect of long-term water balances on fire regime, north-western Minnesota. *J Ecol* 77:989–1004
- Coley PD (1987) Interspecific variation in plant anti-herbivore properties: the role of habitat quality and rate of disturbance. *New Phytol* 106 [Suppl]:251–263
- Connell JH (1978) Diversity in tropical rain forests and coral reefs. *Science* 199:1302–1310
- Day RW, Quinn GP (1989) Comparisons of treatments after analysis of variance in ecology. *Ecol Monog* 59:433–463
- DiTommaso A, Aarssen LW (1989) Resource manipulations in natural vegetation: a review. *Vegetatio* 84:9–29
- Gigon A, Rorison IH (1972) The response of some ecologically distinct plant species to nitrate- and to ammonium-nitrogen. *J Ecol* 60:93–102
- Gleason HA, Cronquist A (1963) *Manual of vascular plants of northeastern United States and adjacent Canada*. Willard Grant Press, Boston
- Gleeson SK, Tilman D (1990) Allocation and the transient dynamics of succession on poor soils. *Ecology* 71:1144–1155
- Goldberg DE, Gross KL (1988) Disturbance regimes of midsuccessional old fields. *Ecology* 69:1677–1688
- Grigal DF, Chamberlain LM, Finney HR, Wroblewski DY and Gross ER (1974) *Soils of the Cedar Creek Natural History Area*. Miscellaneous Report 123, University of Minnesota Agricultural Experiment Station, Saint Paul, Minnesota
- Grime JP (1973) Competitive exclusion in herbaceous vegetation. *Nature* 242:344–347
- Grime JP (1979) *Plant strategies and vegetation processes*. John Wiley and Sons, Chichester
- Gross KL, Werner PA (1982) Colonizing abilities of “biennial” plant species in relation to ground cover: implications for their distributions in a successional sere. *Ecology* 63:921–931
- Grubb PJ (1985) Plant populations and vegetation in relation to habitat disturbance and competition: problems of generalization. In: White J (ed) *The population structure of vegetation*. Dr W Junk, The Hague, The Netherlands, pp 595–621
- Hobbs RJ, Atkins L (1988) Effect of disturbance and nutrient addition on native and introduced annuals in plant communities in the Western Australian wheatbelt. *Aust J Ecol* 13:171–179
- Huenneke LF, Hamburg SP, Koide R, Mooney HA, Vitousek PM (1990) Effects of soil resources on plant invasion and community structure in Californian serpentine grassland. *Ecology* 71:478–491
- Hunt R, Nicholls AO, Fathy SA (1987) Growth and root-shoot partitioning in eighteen British grasses. *Oikos* 50:53–59
- Huntly NJ, Inouye RS (1988) Pocket gophers in ecosystems: patterns and mechanisms. *Bioscience* 38:786–793
- Huston, MA (1979) A general hypothesis of species diversity. *Am Nat* 113:81–101
- Inouye RS, Huntly NJ, Tilman D, Tester JR, Stillwell M, Zinnel KC (1987a) Old-field succession on a Minnesota sand plain. *Ecology* 68:12–26
- Inouye RS, Huntly NJ, Tilman D, Tester JR (1987b) Pocket gophers, vegetation and soil nitrogen along a successional sere in east central Minnesota. *Oecologia* 72:178–184
- Ito PK (1980) Robustness of ANOVA and MANOVA test procedures. In: Krishnaiah PR (ed) *Handbook of Statistics*. Vol I. North-Holland, Amsterdam, pp. 199–236
- Keddy PA (1983) Shoreline vegetation in Axe Lake, Ontario: effects of exposure on zonation patterns. *Ecology* 64:331–344
- Keddy PA (1989) *Competition*. Chapman and Hall, London
- Menge BA, Sutherland JP (1987) Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. *Am Nat* 130:730–757
- Moore CWE, Keratis K (1971) Effect of nitrogen source on growth on Eucalypts in sand culture. *Aust J Bot* 19:125–141
- Mueller-Dombois D, Ellenberg H (1974) *Aims and methods of vegetation ecology*. John Wiley and Sons, New York
- Newman EI (1973) Competition and diversity in herbaceous vegetation. *Nature* 244:310
- Oksanen L, Fretwell SD, Arrud J, Niemala P (1981) Exploitation ecosystems in gradients of primary productivity. *Am Nat* 118:240–261
- Pastor J, Stillwell MA, Tilman D (1987a) Nitrogen mineralization and nitrification in four Minnesota old fields. *Oecologia* 71:481–485
- Pastor J, Stillwell MA, Tilman D (1987b) Little bluestem litter dynamics in Minnesota oldfields. *Oecologia* 72:327–330
- Payette S, Morneau C, Sirois L, Despons M (1989) Recent fire history of the northern Quebec biomes. *Ecology* 70:656–673
- Pearsall WH (1920) The aquatic vegetation of the English Lakes. *J Ecol* 7:163–201
- Pielou EC (1975) *Ecological diversity*. John Wiley and Sons, New York
- Platt WJ, Weis IM (1985) An experimental study of competition among fugitive prairie plants. *Ecology* 66:708–720
- Raison RJ, Connell MJ, Khanna PK (1987) Methodology for studying fluxes of soil mineral-N *in situ*. *Soil Biol Biochem* 19:521–530
- Reed FC (1977) Plant species number, biomass accumulation and productivity of a differentially fertilized Michigan old-field. *Oecologia* 30:43–53
- Rorison IH (1987) Mineral nutrition in time and space. *New Phytol* 106 [Suppl]:79–92
- Runge M (1983) Physiology and ecology of nitrogen nutrition. In: Lange OL, Nobel PS, Osmond CB, Ziegler H (eds) *Physiological Plant Ecology III. Responses to the chemical and biological environment*. Springer, Heidelberg, New York, Berlin, pp. 163–200
- Seastedt TR (1988) Mass, nitrogen and phosphorus dynamics in foliage and root detritus of tallgrass prairie. *Ecology* 69:59–65
- Shugart HH, Noble IR (1981) A computer model of succession and fire response of the high altitude forests of the Brindabella Range, Australian Capital Territory. *Aust J Ecol* 6:149–164
- Snedecor GW, Cochran WG (1980) *Statistical methods*. Seventh edition. Iowa State University Press, Ames, Iowa
- Taylor DR, Aarssen LW, Loehle C (1990) On the relationship between  $r/K$  selection and environmental carrying capacity: a new habitat template for plant life history strategies. *Oikos* 58:239–250
- Thompson K (1987) The resource ratio hypothesis and the meaning of competition. *Func Ecol* 1:297–303
- Tilman D (1986) Nitrogen-limited growth in plants from different successional stages. *Ecology* 67:555–563
- Tilman D (1987a) On the meaning of competition and the mechanisms of competitive superiority. *Func Ecol* 1:304–315
- Tilman D (1987b) Secondary succession and the pattern of plant dominance along an experimental nitrogen gradient. *Ecol Monog* 57:189–214
- Tilman D (1988) *Plant strategies and the dynamics and structure of plant communities*. Princeton University Press, Princeton
- Tilman D (1989) Competition, nutrient reduction and the competitive neighbourhood of a bunchgrass. *Func Ecol* 3:215–219
- Tilman D, Cowan ML (1989) Growth of old field herbs on a nitrogen gradient. *Func Ecol* 3:425–438
- Vitousek PM, Gosz JR, Grier CC, Melillo JM, Reiners WA, Todd RL (1979) Nitrate losses from disturbed ecosystems. *Science* 204:469–474
- Whigham DF (1984) The effect of competition and nutrient availability on the growth and reproduction of *Ipomoea hederacea* in an abandoned old field. *J Ecol* 72:721–730
- Wilson SD, Shay JM (1990) Competition, fire and nutrients in mixed-grass prairie. *Ecology* 71:1959–1967
- Wilson SD, Tilman D (1991) Components of plant competition along an experimental gradient of nitrogen availability. *Ecology* 72:1050–1065