PARTITIONING THE EFFECTS OF PLANT BIOMASS AND LITTER ON *ANDROPOGON GERARDI* IN OLD-FIELD VEGETATION

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Abstract. We examined the effects of living plant neighbors and litter on the performance of a native C_4 grass, *Andropogon gerardi,* at five old-field sites that differ in community biomass and soil fertility. We used plant removal experiments in which both living neighbors and litter were manipulated in a factorial arrangement of treatments over one growing season. *Andropogon* was added to treatment plots as seeds and as established transplants to examine the effects of the surrounding plant community on the recruitment and established phases of its life history.

Neighbors negatively affected *Andropogon* performance at all sites, indicating that resource exploitation by living plants was an important constraint to seedling recruitment and growth across the range of community biomass examined. Plant litter negatively affected recruitment at sites with the greatest community biomass, but had no effect on the growth of established transplants at any of the sites. The total effect of the surrounding plant community on recruitment was positively correlated with community biomass due to an increasing impact of plant litter. However, the total effect of the surrounding community on the growth of established transplants was unrelated to community biomass.

The results suggest that it may be during the recruitment phase of the life history, when seeds and seedlings are especially susceptible to the effects of both litter and living neighbors, that *Andropogon* is most sensitive to variation in community biomass. Variation in the effects of litter on recruitment may be important in regulating plant species diversity and the distribution of native C_4 grasses along old-field biomass gradients in southwest Michigan.

Key words: Andropogon gerardi; *C_4 grass; community biomass; competition; neighbor and litter effects; old fields; removal experiments.*

INTRODUCTION

Experimental field studies designed to examine variation in plant interactions among habitats or along environmental gradients often use plant removal experiments to compare the performance of target plants growing in the presence and absence of the surrounding plant community (Wilson and Keddy 1986, Wilson and Tilman 1991, 1993, Bertness and Hacker 1994, Kadmon 1995). When negative effects of the surrounding community on target plants are observed in these experiments, the effect is most often attributed to competition with plant neighbors for limiting resources (Wilson and Shay 1990, Wilson and Tilman 1991, 1993, Bonser and Reader 1995). However, in many types of vegetation, especially grassland and old-field communities, the performance of plants can also be affected by accumulated dead plant biomass or plant litter (Hulbert 1969, Goldberg and Werner 1983, Fowler 1986, Hamrick and Lee 1987, Facelli and Pickett 1991*a,* Facelli 1994). As a result, measures of competition obtained from removal experiments, and variation in these measures observed across different habitats, may reflect the effects of both living plant neighbors and litter. In this study we investigated how these two different types of effects may combine to determine the total effect of the surrounding plant community on target plants in old-field vegetation. In addition, we examined how the magnitude of these effects vary across old-field sites that differ in community biomass and soil nitrogen availability.

A number of field studies in herbaceous vegetation have shown that plant litter can significantly affect the performance of individual plants, and as a result influence the structure of plant communities. Large quantities of litter can inhibit the establishment, growth, and survival of plants, and thus contribute to low species diversity in highly productive communities (Haslam 1971, Goldberg and Werner 1983, Bergelson 1990, Carson and Peterson 1990, Tilman 1993). Other studies suggest that litter may often facilitate the establishment and growth of plants and enhance species diversity in unproductive environments by improving moisture conditions (Fowler 1986, Willms et al. 1986). As a whole, these studies suggest that the role of plant litter may vary across environments and that changes in species composition and diversity along gradients of community biomass and plant productivity may in part re-

Table 1. Community characteristics of the five study sites.

Site	Neighbor biomass (g/m²)	Litter biomass (g/m²)	Total community biomass (g/m²)	Dominant species (>5% relative biomass)	Relative biomass (%)
1	184.2 ± 24.8[a]	23.7 ± 8.0[a]	207.9 ± 31.9[a]	*Centaurea maculosa*	24.0
				Poa compressa	22.5
				Achillea millefolium	11.4
				Aster pilosis	8.7
				Rubus alleghaniensis	6.3
2	222.9 ± 15.6[a]	231.7 ± 21.6[b]	454.6 ± 33.4[b]	*Agropyron repens*	85.2
				Achillea millefolium	7.3
				Bromus inermis	6.4
3	310.8 ± 11.9[b]	216.7 ± 31.1[b]	527.5 ± 39.4[bc]	*Bromus inermis*	58.1
				Poa pratensis	10.3
				Achillea millefolium	10.1
				Agropyron repens	5.1
4	337.4 ± 20.2[b]	321.0 ± 81.0[b]	658.5 ± 73.7[c]	*Bromus inermis*	88.3
				Poa pratensis	7.5
5	598.4 ± 31.0[c]	607.1 ± 34.2[c]	1205.5 ± 48.4[d]	*Agropyron repens*	71.0
				Arrhenatherum elatius	28.3

Notes: Biomass values are presented as means ± 1 SE ($n = 5$ for each site). For each biomass type, values within a column with the same letter are not significantly different ($P > 0.05$; Tukey's HSD). Nomenclature follows Fernald (1950).

flect variation in the balance between the effects of plant neighbors and litter.

In this study, we examined the effects of living plant neighbors and litter on a single target species, the C_4 grass *Andropogon gerardi* Vitman (big bluestem), in herbaceous old fields in southwest Michigan. *Andropogon gerardi* (hereafter referred to by genus) is a dominant species in the tall-grass prairies of the United States, where it is distributed widely across gradients of soil resource availability and plant productivity (Bazzaz and Parrish 1982). *Andropogon* was a dominant species in many prairie and oak savanna communities of southwest Michigan at the time of settlement by Europeans (Gotshall 1972). However, in the current successional landscape of southwest Michigan, *Andropogon* is largely restricted to low-fertility sites, and is infrequent in the more fertile sites that are commonly dominated by nonnative C_3 grasses such as *Agropyron repens* L. Beauv. and *Bromus inermis* Leysser. The apparent poor ability of native C_4 grasses, such as *Andropogon,* to colonize and occupy fertile sites after abandonment from agriculture, is likely related to a combination of: (1) delayed seed input, due to the isolation of source populations in the landscape, and inherently low allocation to seed production (Tilman and Wedin 1991*a*); and (2) site preemption and inhibition by fast-growing C_3 grasses that are effective at rapidly colonizing and dominating fertile sites shortly after abandonment (Tilman 1987, Tilman and Wedin 1991*b*, Foster 1992). Because fire is largely absent from this landscape, effects associated with litter accumulation in the most productive sites may be important in restricting the distribution of native C_4 grasses to lower productivity sites. In this study, we addressed the following questions regarding the effects of the surrounding plant community on *Andropogon* at five old-field sites:

1) How do living plant neighbors and litter affect the recruitment and growth of *Andropogon* in old fields?

2) How do the separate effects of neighbors and litter contribute to the total effect of the surrounding plant community on *Andropogon*?

3) Do these effects vary in magnitude among the different study sites, and if so, are they correlated with aboveground community biomass?

METHODS

Study sites

This study was conducted in five herb-dominated old-field sites at the W. K. Kellogg Biological Station (KBS) of Michigan State University in southwest Michigan (Kalamazoo County; 42°24′ N, 85°24′ W). All five sites had been abandoned from row crop agriculture for at least 15 yr and were largely dominated by nonnative perennial grasses. (Table 1; Burbank et al. 1992). Naturally occurring individuals of *Andropogon* were found growing at sites 1 and 3. Soils underlying the sites are classified as sandy loam, but differ in the amount of topsoil lost to agriculture-related erosion. Assignment of site numbers (1–5) was based on a ranking of total community biomass (1 = lowest and 5 = highest biomass). In this study, we define total community biomass (or community biomass) as the sum of aboveground living plant biomass and litter biomass.

Experimental design and methods

In 1994 both seeds and seedling transplants of *Andropogon* were planted into a 2 × 2 factorial arrange-

ment of treatments established at each site in a randomized block design. The treatments included two levels of living plant neighbors (intact and removed) and two levels of plant litter (intact and removed). At all sites except site 2, two parallel rows of five 2×2 m experimental blocks were established in early May. One of the rows was used for seed additions and the other row was used for transplants. At site 2, the same block layout was used with the exception that 10 blocks were established for the transplant experiment instead of 5. In each field, the rows of blocks were separated by buffer zones of 3–6 m, and blocks within rows were separated by buffer zones ranging from 2 to 4 m.

The four experimental treatments were applied to 70 $\times$ 70 cm plots located at the four corners of each block. Neighbors were removed by applying a glyphosate herbicide solution (Roundup), and clipping the dead material after 1 wk. Litter was removed by hand from the litter removal treatments so that the soil was left undisturbed. To minimize root encroachment into the two neighbor removal treatments, plot perimeters were trenched with a flat-blade shovel to a depth of 20 cm three times during the growing season. Neighbor removal plots were periodically hand-weeded during the growing season to eliminate regrowth.

Seed additions.—Seeds of *Andropogon* were collected from a local population in the fall of 1993 and stored outside over winter in a plastic container to expose the seeds to winter temperature fluctuations. Seeds were sown by hand into the treatment plots at a rate of 1500 seeds/plot (3030 seeds/m^2) in mid May 1994. Because the goal of this experiment was to examine recruitment from seed in the absence of dispersal limitation, a seeding rate was chosen that mimicked the seed rain within natural stands of *Andropogon* ($\approx$3000 seeds/m^2; B. L. Foster and K. L. Gross, *unpublished data*). Density of *Andropogon* plants in each plot was determined in June, July, and late August by counting individuals within two randomly placed 10×20 cm quadrats. Final density determined in late August is reported here and is used throughout as a measure of *Andropogon* recruitment. In late August, all shoot biomass of *Andropogon* was harvested from each plot. In addition, aboveground biomass of plant neighbors and litter was harvested from the intact plots (neighbors and litter intact). All plant material was oven-dried at 60°C to constant mass and then weighed.

Seedling transplants.—Seedlings for the transplant experiment were obtained by germinating seeds in the greenhouse in late April 1994. Approximately 6–8 d after germination, 1000 seedlings were transferred into individual seedling plug containers (2.54 cm diameter $\times$ 10.16 cm deep) containing a 3:1:1 mixture of peat moss, commercial potting soil, and old-field soil. After 14–17 d of additional growth, 480 seedlings were randomly selected for the experiment from a group of $\approx$800 healthy seedlings. The initial shoot biomass of each seedling was estimated from a regression of seedling biomass on longest leaf length (L) obtained from a subsample of the remaining healthy seedlings (initial transplant biomass = $0.004L - 0.011$, $R^2 = 0.65$, $P < 0.0001$, $n = 100$).

In late May, four seedlings were transplanted into each 70×70 cm field plot by inserting seedling plugs into preformed holes made with a narrow-blade trowel. Within each plot, transplants were separated by $\approx$20 cm. All individual transplants were watered (0.2 L/d) for eight consecutive days following planting to encourage initial establishment. Only 16 of the 480 transplants died and there were no plots where less than three transplants survived until the end of the experiment. The shoots of all surviving transplants were harvested in early September. Aboveground biomass of neighbors and litter was harvested from the intact plots. Neighbors were sorted by species to document the species composition of each site. All plant tissue was dried and weighed as described previously.

Resource measurements

To determine how light penetration to the soil surface varied among the sites and was affected by the experimental treatments, photosynthetically active radiation (PAR) was measured above the vegetation and at the ground surface of each plot in the transplant experiment with a PAR ceptometer probe (Decagon Devices, Incorporated, Pullman, Washington). PAR measurements were taken three times over the course of the experiment at approximately monthly intervals (early June–late August). In plots where litter was left intact, light measurements were made by inserting the ceptometer beneath the litter layer. In the neighbor removal plots, measurements were made at plot edges between the hours of 1100 and 1400 when the sun was directly overhead to minimize the effects of transplants on light readings. Light penetration was expressed as the percentage PAR reaching the ground surface. Mean seasonal light penetration was calculated for each plot by averaging over the three sampling dates.

Soil nitrogen concentration (N) was also measured three times over the course of the experiment in two treatments in the seedling transplant experiment: neighbors and litter removed; neighbors and litter left intact. At each sampling date, two soil cores (2.5 cm diameter $\times$ 15 cm deep) were taken from each plot. All cores were taken at least 10 cm away from the base of transplant shoots and care was taken to minimize disturbance to the plots. The two cores from each plot were composited for analysis. Subsamples (10 g) were extracted for 24 h in a 2 mol/L KCl solution, filtered, and then analyzed colorimetrically with an Alpkem autoanalyzer (Alpkem Corporation, College Station, Texas) for ammonium and nitrate. Soil nitrogen concentrations are expressed as the sum of extractable ammonium and nitrate concentrations (micrograms of nitrogen per gram dry soil). Mean seasonal nitrogen con-

TABLE 2. Treatment effects and mean square ratios used in the mixed-model, within-subjects ANOVA. S = Sites, B(S) = Blocks within Sites, N = Neighbors, L = Litter.

Source of variation	Effect MS/error MS
Among blocks	
S	S/B(S)
Within blocks	
N	$N/N \times B(S)$
$N \times S$	$N \times S/N \times B(S)$
L	$L/L \times B(S)$
$L \times S$	$L \times S/L \times B(S)$
$N \times L$	$N \times L/N \times L \times B(S)$
$N \times L \times S$	$N \times L \times S/N \times L \times B(S)$

centrations were calculated for each plot by averaging over the three sampling dates.

Data analysis

Community biomass.—To examine whether sites differed in neighbor biomass, litter biomass, and total community biomass (sum of neighbor and litter biomass), we used one-way analysis of variance (ANOVA) and Tukey HSD tests. These analyses were performed on biomass data from the intact treatment (neighbor and litter biomass left intact).

Resources and target plant performance.—Percentage light penetration, total soil nitrogen, *Andropogon* seedling density and total shoot biomass (seed addition experiment), and transplant growth (transplant experiment) were analyzed using a mixed-model, within-subjects ANOVA (Zar 1996) with one among-subjects grouping factor (site). In this model the experimental blocks are considered to be the subjects of the analysis with the experimental treatments applied to each. Variation due to blocks within sites is considered random, while site and treatment effects are considered fixed. Error terms used to test the significance of main effects and interactions all contain the random component of variance due to blocks within sites (see Table 2). After testing the significance of the interaction terms, unplanned comparisons were used to make the appropriate comparisons of treatment means (Sokal and Rohlf 1981). Analyses of transplant growth were performed on plot mean values (mean of all surviving transplants). Relative growth rate (RGR, Chiariello et al. 1989) was calculated for each transplant as:

$$RGR = [\ln(B_2) - \ln(B_1)]/(t_2 - t_1)$$

where B_2 is the transplant biomass at harvest, B_1 is the estimated transplant biomass at planting, and $t_2 - t_1$ is the number of days growth between harvest (t_2) and planting (t_1). Light penetration data were arcsine-square-root transformed to reduce heteroscedasticity. *Andropogon* total shoot biomass and density data were log transformed and square-root transformed, respectively, to improve normality and reduce heteroscedas-

ticity (Sokal and Rohlf 1981). Untransformed data are presented in the figures.

Magnitude of community effects.—The magnitude of the effect of the surrounding plant community on *Andropogon* performance (density, total shoot biomass, and RGR of transplants) was examined using a relative community effect index (diffuse competition, Wilson and Keddy 1986; competition intensity, Wilson and Tilman 1993). This index estimates the degree to which *Andropogon* was inhibited or facilitated by the surrounding plant community by comparing plant performance in plots cleared of all plant material (neighbors and litter) to that in plots where all plant material was left intact. Positive values indicate inhibition, negative values indicate facilitation, and values of zero indicate no net effect of the surrounding community. To assess the importance of litter in contributing to the total effect of the community on *Andropogon* performance, a separate index was calculated for plots that were left intact and for plots where only litter was removed. These indices were calculated for each experimental block as:

$$\text{total effect} = (P_C - P_{NL})/P_C$$

$$\text{neighbor effect} = (P_C - P_N)/P_C$$

where P_C is plant performance in plots cleared of neighbors and litter, P_{NL} is performance in plots with neighbors and litter left intact, and P_N is performance in plots with only neighbors left intact (litter removed). An additional index was calculated to measure the effect of litter alone and was calculated as:

$$\text{litter effect} = (P_C - P_L)/P_C$$

where P_L is plant performance in plots with only litter left intact (neighbors removed).

We used one-way ANOVA and Tukey HSD tests to examine site differences for each community effect index (total, neighbor, and litter effects). We then examined correlations between each index and community biomass using linear regression in two ways. First, we analyzed the site means of each community effect index and of community biomass ($n = 5$). Second, to examine relationships across the entire range of community biomass, thus including both within- and among-site variation, we analyzed the community effect indices and community biomass measured in each individual block ($n = 25$, seed addition experiment; $n = 30$, transplant experiment). Preliminary data inspection indicated that the community effect indices tended to vary nonlinearly with community biomass. As a result, community biomass was log transformed prior to linear regression analysis. We carried out similar analyses using total soil nitrogen measured in the intact plots as the independent variable in place of community biomass. The results of these analyses were very similar, so for brevity we report only the analyses using community biomass as the independent variable. SYS-

TABLE 3. Results of ANOVA for site and treatment effects on mean seasonal light penetration.

Source of variation	df	MS	F
Among blocks			
Site	4	0.4946	52.61***
Block	20	0.0094	
Within blocks			
Neighbors	1	1.7493	164.77***
Neighbors × Site	4	0.0029	0.28 NS
Neighbors × Block	20	0.0106	
Litter	1	3.3350	297.40***
Litter × Site	4	0.1817	16.20***
Litter × Block	20	0.0112	
Neighbors × Litter	1	0.4847	49.17***
Neighbors × Litter × Site	4	0.0420	4.26*
Neighbors × Litter × Block	20	0.0099	

* $P < 0.05$; *** $P < 0.001$; NS, $P > 0.05$.

TAT statistical software (version 5.2.1; Wilkinson 1992) was used for all analyses.

RESULTS

Community biomass and species composition

Neighbor biomass, litter biomass, and total community biomass varied significantly among the five sites (neighbor biomass, $F_{4, 25} = 55.59$, $P < 0.0001$; litter biomass, $F_{4, 25} = 26.28$, $P < 0.0001$; total community biomass, $F_{4, 25} = 57.91$, $P < 0.0001$; Table 1). There was a sixfold increase in mean community biomass from site 1 to site 5. Mean litter biomass increased 25-fold across these sites and was positively correlated with community biomass ($R^2 = 0.96$, $P < 0.05$, $n = 5$). Most sites were dominated by perennial grasses. A perennial forb (*Centaurea maculosa* Lam.) and perennial grass (*Poa compressa* L.) were codominant at site 1.

Resources

Light penetration to the soil surface varied significantly among the sites, with neighbors, litter, and with interactions between litter and sites, and between neighbors and litter (Table 3, Fig. 1A). Neighbors reduced light penetration to the soil surface at all sites in plots where litter was removed, but in plots where litter was present, neighbors reduced light penetration to the soil surface only at site 1. At site 1, litter levels were so low that litter had no effect on light penetration. However, in the other four sites, light penetration in plots containing litter only was similar to that in plots containing both neighbors and litter. This suggests that light levels at the soil surface in the intact vegetation of these sites was determined more by litter than by neighbors. Mean seasonal light penetration measured in the intact plots declined logarithmically with community biomass (light penetration = −0.193 (log community biomass) + 1.315, $R^2 = 0.52$, $P < 0.0001$, $n = 25$) and mean seasonal nitrogen concentration (light penetration = −0.282 (log N) + 0.423, $R^2 = 0.51$, $P < 0.0001$, $n = 25$).

The removal of all plant material (neighbors and litter) increased mean seasonal nitrogen concentrations significantly across all sites (Table 4, Fig. 1B), ranging from 56% at site 5 to 218% at site 1. Mean seasonal nitrogen concentration measured in the intact plots was positively correlated with community biomass ($R^2 = 0.83$, $P < 0.0001$, $n = 25$).

Seed addition

Seedling recruitment.—The number of *Andropogon* seedlings that established in the plots did not differ significantly among the five sites, but did vary in response to neighbors and litter, and with the interaction between litter and sites (Table 5). Across all sites, the removal of neighbors led to a significant increase in *Andropogon* density (Fig. 2A). The significant interaction between sites and litter indicates that the degree to which litter affected *Andropogon* density varied among sites. At sites 1 and 2, litter removal had no significant effect on *Andropogon* density. However, at the three sites with the greatest community biomass (sites 3–5), the removal of litter significantly increased *Andropogon* density.

The magnitude of the total and litter effects on *Andropogon* density differed significantly among the five sites, whereas the magnitude of the neighbor effect did not (total, $F_{4, 20} = 4.97$, $P < 0.01$; neighbor, $F_{4, 20} = 0.88$, $P = 0.49$; litter, $F_{4, 20} = 3.63$, $P < 0.05$; Fig. 3A). The mean total effect on density ranged from 57% at the site supporting the lowest community biomass (site 1) to 97% at the site with the greatest community biomass (site 5), and was positively correlated with mean community biomass (Fig. 3A). The mean neighbor effect ranged from 49% at site 4 to 72% at site 2 and was not significantly correlated with mean community biomass. The mean litter effect on *Andropogon* density ranged from −30% at site 1 to 80% at site 5, and was positively correlated with mean community biomass.

There was considerable within-site variation in the magnitude of the community effects, especially at the site with the lowest community biomass (site 1; Fig. 3B). Regressions performed on data that included this variation (all blocks, $n = 25$) were consistent with those performed on site means; the community effects on seedling recruitment were correlated with community biomass only when litter was present (total and litter effects, Fig. 3B).

Total shoot biomass.—The total shoot biomass of *Andropogon* in the seed addition experiment differed significantly among the sites, and in response to neighbors and litter, and with interactions among all of these factors (Table 5). The removal of neighbors increased *Andropogon* shoot biomass at all sites, both in plots where litter was removed and in plots where litter was left intact (Fig. 2B). At sites 1 and 2, the removal of litter did not significantly affect *Andropogon* shoot biomass, either in plots where neighbors were removed or in plots where neighbors were left intact. At site 3,
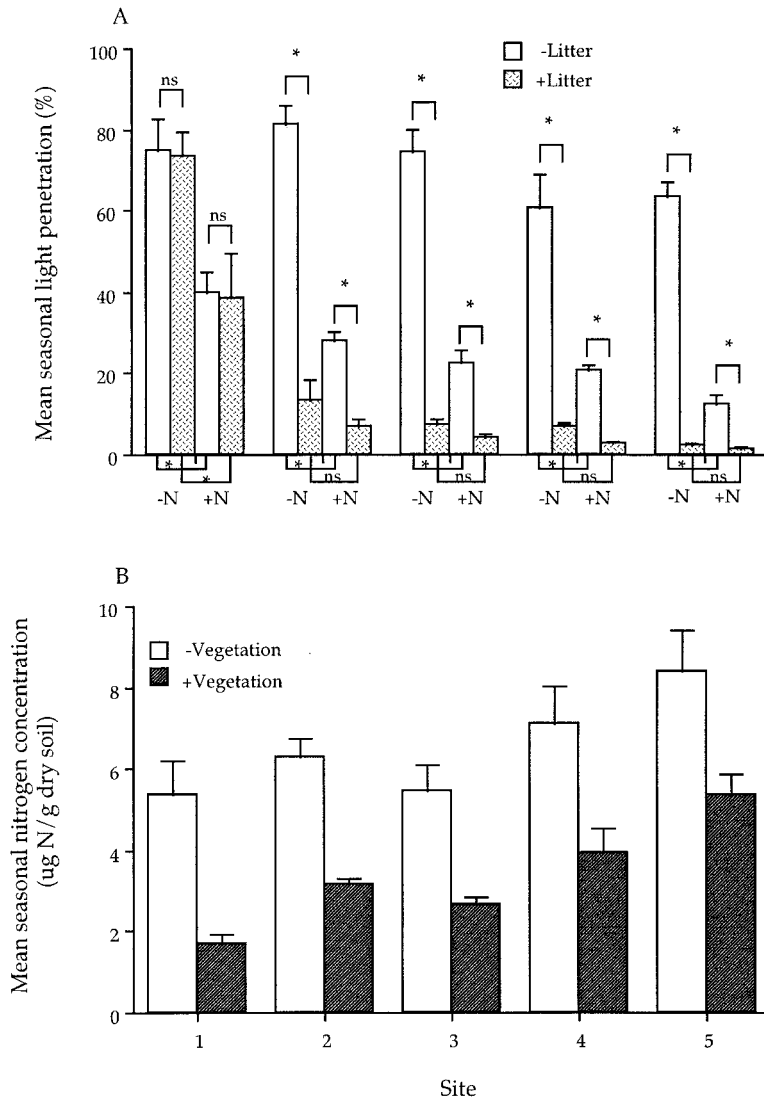
FIG. 1. (A) Mean seasonal light penetration (mean + 1 SE) in relation to the experimental treatments. Treatments with neighbors removed are indicated by −N, and treatments with neighbors left intact are indicated by +N. Brackets above and below the bars specify within-site mean comparisons made at each level of the two treatment factors (NS, $P > 0.05$; * $P < 0.05$). (B) Mean seasonal nitrogen concentrations (mean + 1 SE) in the two treatments where all vegetation (neighbors and litter) was either removed or left intact. Sites are ranked from lowest to highest community biomass.

TABLE 4. Results of ANOVA for site and treatments effects on mean seasonal soil nitrogen concentration.

Source of variation	df	MS	F
Among blocks			
Site	4	17.360	7.78***
Block	20	2.229	
Within blocks			
Vegetation	1	123.884	73.17***
Vegetation × Site	4	0.280	0.16 NS
Block	20	1.693	

Note: Nitrogen concentrations were measured only in the two treatments where all plant material (neighbors and litter) was either removed or left intact.
*** $P < 0.001$; NS, $P > 0.05$.

litter removal significantly increased *Andropogon* shoot biomass only in plots where neighbors were left intact. In contrast, litter removal significantly increased *Andropogon* shoot biomass at sites 4 and 5, both in plots where neighbors were removed and left intact.

The magnitude of all community effects on *Andropogon* shoot biomass (total, neighbor, and litter effects) differed significantly among the sites (total, $F_{4, 20} = 12.35$, $P < 0.0001$; neighbor, $F_{4, 20} = 11.83$, $P < 0.0001$; litter, $F_{4, 20} = 4.49$, $P < 0.01$; Fig. 4A). The mean total effect ranged from a low of 69% at site 1 to a high of 99% at site 5, and was positively correlated with community biomass (Fig. 4A). The mean neighbor effect ranged from 65% at site 1 to 93% at site 5, and

TABLE 5. Results of ANOVA for site and treatment effects on *Andropogon* density and total shoot biomass in the seed addition experiment.

Source of variation	df	Density		Total shoot biomass	
		MS	F	MS	F
Among blocks					
Site	4	41.438	0.95 NS	12.542	15.86***
Block	20	43.425			
Within blocks					
Neighbors	1	3659.415	112.52***	101.729	171.84***
Neighbors × Site	4	18.252	0.56 NS	9.182	15.51***
Neighbors × Block	20	32.523		0.592	
Litter	1	1325.331	43.57***	27.010	48.40***
Litter × Site	4	322.504	10.60***	8.156	14.62***
Litter × Block	20	30.416		0.558	
Neighbors × Litter	1	96.930	3.79 NS	5.732	9.67**
Neighbors × Litter × Site	4	24.481	0.96 NS	2.649	4.47**
Neighbors × Litter × Block	20	25.556		0.593	

** $P < 0.01$; *** $P < 0.001$; NS, $P > 0.05$.

FIG. 2. (A) *Andropogon* density, and (B) total shoot biomass (mean + 1 SE) in relation to the experimental treatments (seed addition experiment). See Fig. 1 for significance levels.
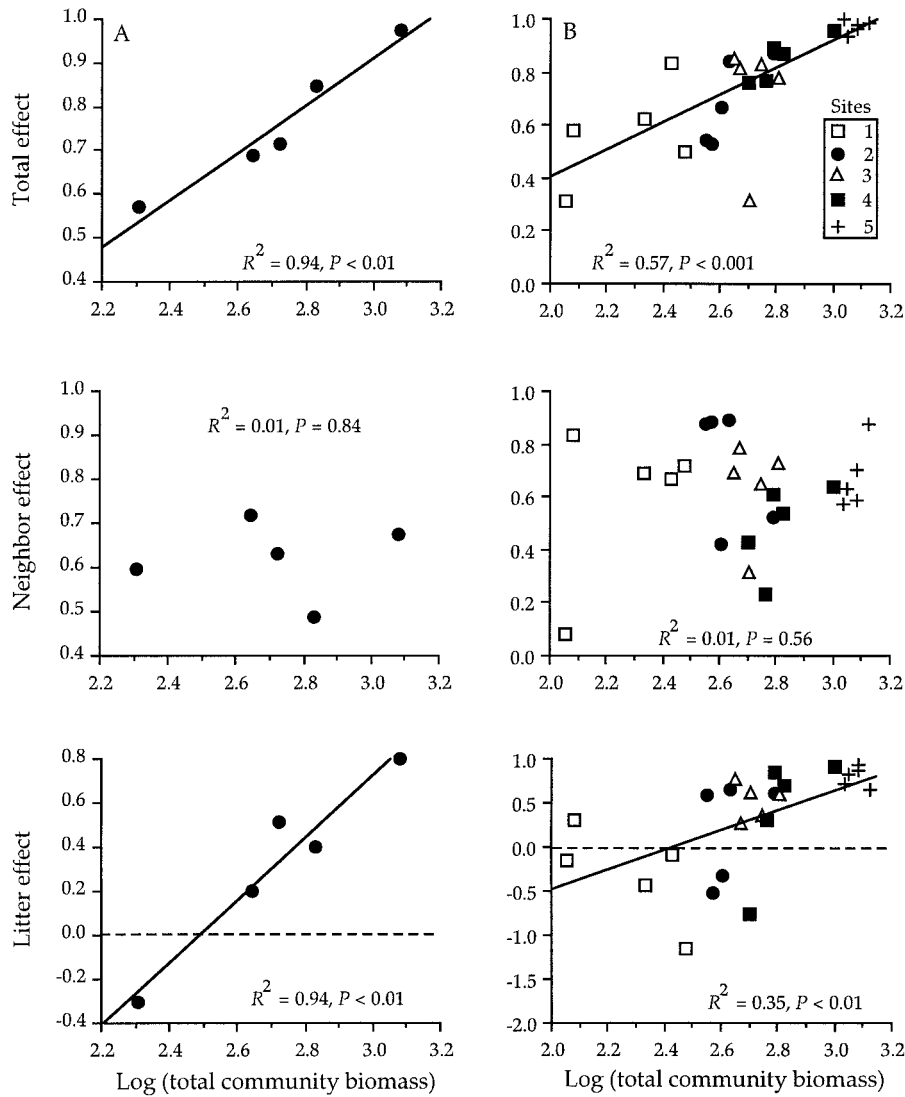
FIG. 3. Relationships between the community effects on *Andropogon* density (dependent variables) and community biomass (independent variable) in the seed addition experiment. (A) Mean community effects plotted against mean community biomass (*n* = 5). (B) Community effects calculated for all blocks plotted against block community biomass (*n* = 25).

exhibited a tendency to increase with community biomass, but the relationship was not significant. The mean litter effect on shoot biomass ranged from −41% at site 1 to 71% at site 5 and was positively correlated with community biomass.

Regressions performed on data that included within-site variation were largely consistent with those performed on site means, except that this analysis revealed a significant positive correlation between the neighbor effect and community biomass (Fig. 4B). This confirms the nonsignificant positive trend observed among site means. The observation that the neighbor effect appeared to increase with community biomass in the case of *Andropogon* shoot biomass, but was unrelated to community biomass in the case of *Andropogon* density, suggests that there may have been an increase in the

effects of neighbors on the growth of individual seedlings. However, because we did not measure the growth of individual seedlings, and because *Andropogon* shoot biomass is confounded by both recruitment and growth, we focus on the transplant experiment to better assess the effects of the surrounding community on individual plant growth.

Transplants

In the seedling transplant experiment, the RGR of *Andropogon* transplants differed among the sites, and varied in response to neighbors and litter, and with interactions between sites and neighbors, and between neighbors and litter (Table 6). The RGR of transplants responded positively to the removal of neighbors at all sites, both in the absence and presence of litter (Fig.
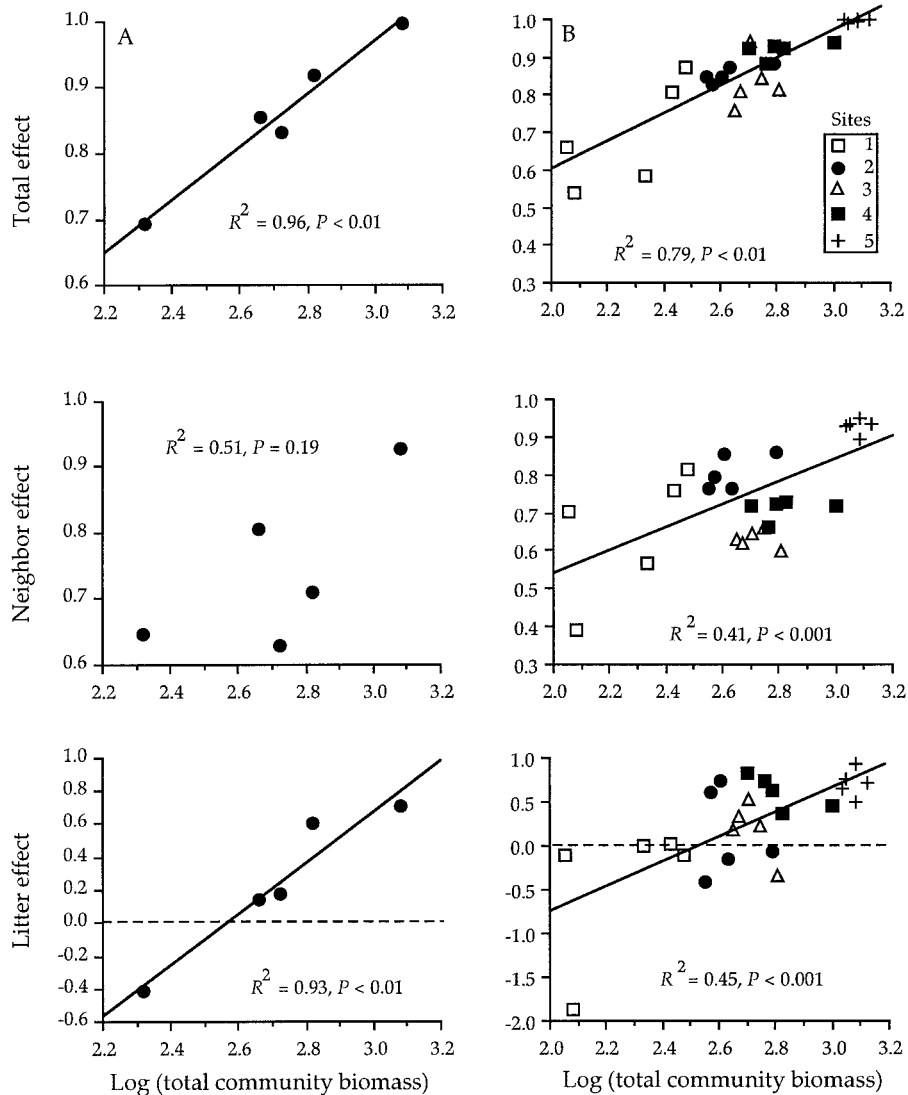
FIG. 4. Relationships between the community effects on *Andropogon* total shoot biomass (independent variables) and community biomass (dependent variable) in the seed addition experiment. (A) Mean community effects plotted against mean community biomass ($n = 5$). (B) Community effects calculated for all blocks plotted against block community biomass ($n = 25$).

5). At sites 2, 4, and 5 the removal of litter significantly increased RGR in plots where neighbors were removed, but had no effect on RGR at any of the sites where neighbors were left intact, reflecting a significant interaction between neighbors and litter.

The magnitude of the total effect on the RGR of transplants differed significantly among the five sites, whereas the magnitude of the neighbor and litter effects did not (total, $F_{4, 25} = 4.28$, $P < 0.01$; neighbor, $F_{4, 25} = 1.88$, $P = 0.15$; litter, $F_{4, 25} = 1.52$, $P = 0.22$, Fig. 6A). The mean total and neighbor effects were similar in all fields and ranged from a low of 36% (total effect) at site 5 to a high of 51% (total effect) at site 3. Neither of these effects were significantly correlated with community biomass (Fig. 6A). The mean litter effect on

transplant RGR was small relative to the total and neighbor effects, ranging from 2% at site 1 to 16% at site 5. However, the mean litter effect was positively correlated with community biomass.

There was considerable variation in the community effects on RGR within the sites (Fig. 6B). Regressions performed on data that included this variation were consistent with regressions performed on site means; the magnitudes of the total and neighbor effects were unrelated to community biomass, but the magnitude of the litter effect was positively correlated with community biomass.

DISCUSSION

In this study, living plant neighbors negatively affected all aspects of *Andropogon* performance at all

TABLE 6. Results of ANOVA for site and treatment effects on the relative growth rate (RGR) of transplants in the seedling transplant experiment.

Source of variation	df	MS	F
Among blocks			
Site	4	0.00019	12.03***
Block	25	0.00002	
Within blocks			
Neighbors	1	0.01699	1689.18***
Neighbors × Site	4	0.00005	5.25**
Neighbors × Block	25	0.00001	
Litter	1	0.00028	19.38***
Litter × Site	4	0.00002	1.68
Litter × Block	25	0.00001	
Neighbors × Litter	1	0.00026	19.25***
Neighbors × Litter × Site	4	0.00002	1.74 NS
Neighbors × Litter × Block	25	0.00001	

** $P < 0.01$; *** $P < 0.001$; NS, $P > 0.05$.

five old-field sites. This suggests that resource exploitation by living plants reduced *Andropogon* seedling recruitment and growth at all of the sites and across the entire range of community biomass and soil nitrogen availability examined. Plant litter inhibited recruitment at the sites with the greatest neighbor and litter biomass, but was of little consequence to the growth of established plants at any of the sites in the presence of both living neighbors and litter. Across sites, the total effect of the surrounding community on recruitment was positively correlated with community biomass, largely due to increasing interference by litter. However, the total effect of the community on the growth of established plants was unrelated to community biomass. These results suggest that both living plants and litter can limit the recruitment success of *Andropogon* in old fields, and that the negative impact of litter on recruitment is likely to be most pronounced at productive sites that support a continuous layer of dense litter.

Although numerous removal experiments have shown that the surrounding plant community can affect target plant performance, this study is the first to measure the separate and combined effects of living neighbors and litter on target plants across a range of environments. Although the effects of living neighbors were generally greater in magnitude than the effects of litter, litter significantly reduced the recruitment of *Andropogon* at sites with the greatest community biomass. This observation is consistent with the findings of a number of studies investigating the effects of plant litter on individual species (Werner 1975, Goldberg and Werner 1983, Fowler 1986, Hamrick and Lee 1987, Carson and Peterson 1990). Fowler (1986) and Hamrick and Lee (1987) found that, although small amounts of litter tended to enhance seedling establishment of selected herbaceous species, large amounts of litter strongly inhibited seedling establishment. Werner (1975) found that germination of the herbaceous biennial, *Dipsacus sylvestris,* was strongly inhibited by grass litter in old fields, and that the degree of this inhibition increased with litter cover. Goldberg and Werner (1983) showed that the removal of litter in the most productive areas of a 30-yr old field greatly enhanced the seedling emergence of two *Solidago* species.

There are a number of mechanisms by which a dense litter layer can inhibit the recruitment of plants from seed. Litter can act as a physical barrier, preventing the movement of seeds to the soil surface or by impeding the emergence of newly germinated seedlings (Sydes and Grime 1981, Facelli and Pickett 1991*a*). A large amount of litter can greatly reduce light penetration to the soil surface, limiting germination and seedling growth (Facelli and Pickett 1991*b*). Other indirect ef-
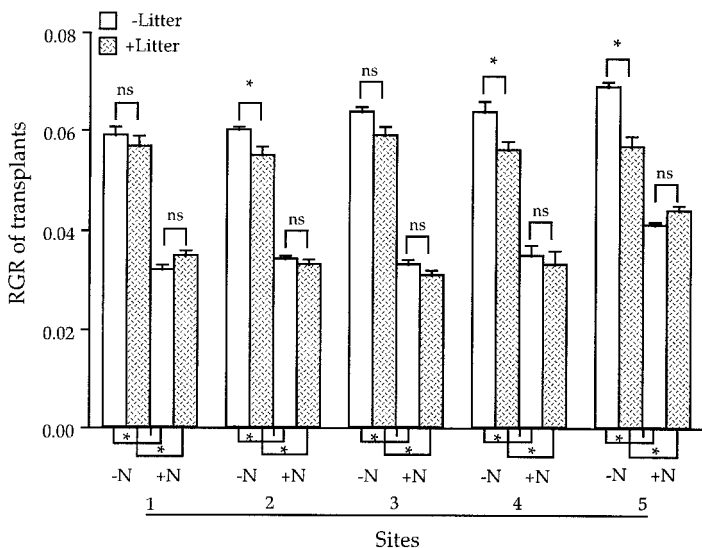

FIG. 5. Relative growth rate (RGR) of *Andropogon* transplants (mean + 1 SE) in relation to the experimental treatments. See Fig. 1 for explanation of significance levels (brackets).
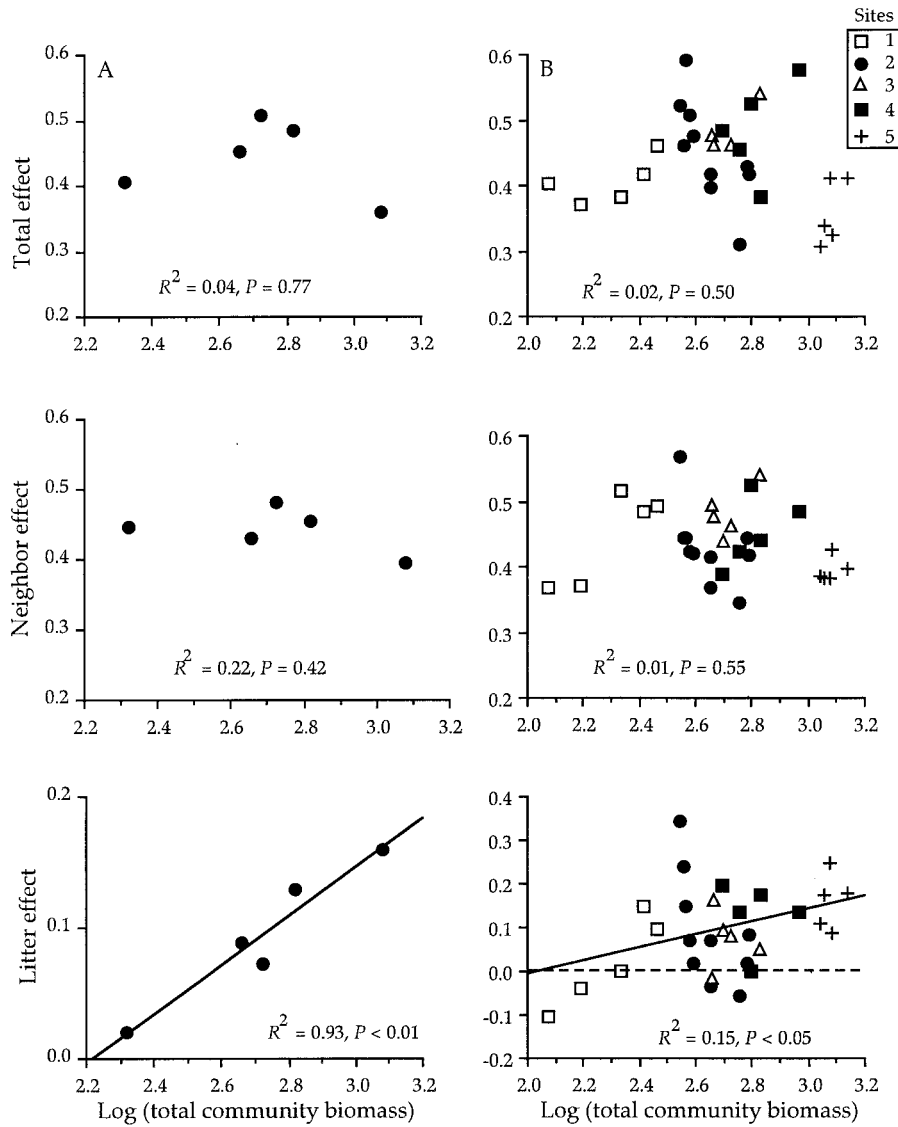
Fig. 6. Relationships between the community effects on the relative growth rate (RGR) of transplants (dependent variables) and community biomass (independent variable) in the transplant experiment. (A) Mean community effects plotted against mean community biomass ($n = 5$). (B) Community effects calculated for all blocks plotted against block community biomass ($n = 30$).

fects associated with the dark moist conditions under the litter mat, such as increased susceptibility of seedlings to fungal attack and invertebrate herbivores, have been documented (Facelli 1994).

In this study, the mechanisms by which litter inhibited seedling recruitment are not known. The fates of individual seedlings were not followed throughout the growing season, so we cannot distinguish whether the negative effects of the surrounding plant community on *Andropogon* recruitment were due to reduced germination, increased mortality, or a combination of these factors. However, field observations made over the growing season suggested that litter inhibited both germination and seedling survival at the site with the

greatest litter biomass (site 5) due to mechanical impedance. Many of the seeds added to plots containing litter at site 5, remained lodged in the litter layer throughout much of the growing season. A large number of these lodged seeds germinated in the litter, but subsequently died within a few days, likely due to the inability of roots to reach the soil. Extreme reduction of light by litter may have been an important factor limiting the emergence and growth of *Andropogon* seedlings in the sites with the greatest litter biomass. Light levels at the soil surface in the intact plots of sites 3–5 were extremely low, generally <5% of full sun (Fig. 1). Light levels in plots where only litter was present were similar, indicating that litter reduced light

levels at the soil surface to a greater degree than the living plants.

For established plants in the transplant experiment, the removal of plant litter from plots where neighbors were left intact did not lead to any significant changes in growth. This suggests that the reduced growth of established plants in these communities was due almost entirely to the exploitative effects of living neighbors rather than inhibition by litter. However, in three of the five sites (sites 2, 4, and 5) litter significantly reduced transplant growth in plots where living neighbors had been removed, accounting for the significant neighbor × litter interaction. This indicates that the observed effects of living neighbors and litter were nonadditive, suggesting that litter has the potential to reduce the growth of established plants, but that these effects are inconsequential in the intact communities due to the much stronger exploitative effects of living neighbors. The causes of reduced transplant growth in this study in plots where only litter was present is unknown.

Magnitude of plant community effects

The relative community effect indices used in this study allowed us to compare the magnitude of community effects across the different study sites. The results show that the total community effect on both the recruitment of *Andropogon* and the growth of established *Andropogon* transplants differed significantly among the sites, but that effects on recruitment were more spatially variable. Although a number of site factors may have contributed to strong site differences in the total effect on recruitment, the strong positive dependence of the total community effect index on community biomass, as well on soil nitrogen concentration (results not presented here), suggests that this variation reflects the impact of plant biomass, soil fertility, or productivity on the magnitude of plant interactions as predicted by Grime (1979) and others (Southwood 1988, Keddy 1990). Interestingly, the effect of the surrounding community on recruitment was not correlated with community biomass when litter had been removed (neighbor effect). This, and the observed positive correlation between the effect of litter alone (litter effect) and community biomass, suggests that the increase in the total effect on *Andropogon* recruitment was more the result of an increase in the interference effects of plant litter rather than an increase in the effects of living plants.

Unlike what we found for *Andropogon* recruitment, both the total and neighbor effects on established transplant growth were unrelated to community biomass. This result is inconsistent with theories of community organization that predict an increase in competition with productivity (Grime 1979, Southwood 1988, Keddy 1990). As was the case with *Andropogon* recruitment, the effect of litter alone on transplant growth, although small relative to the effect of living neighbors, increased significantly with community biomass.

Again, this appears to reflect the potential effects of litter that were not realized in the intact communities due to the much greater effects of living neighbors.

Our interpretations of the community effect indices assume that we properly standardized interspecific interactions among target plants and neighbors so as to make them comparable among the different sites. In this experiment, intraspecific interactions among target plants were possible because each experimental plot contained more than one individual target plant. Miller (1996) pointed out that because intraspecific and interspecific competition may both vary along gradients, indices of competition that standardize interspecific competition by plant performance in plots where intraspecific interactions are occurring may result in an insensitive measure of competition. In our study, intraspecific competition was likely important in the neighbor removal plots of the seed addition experiment where *Andropogon* densities were quite high. If intraspecific competition did vary among the sites in these plots, it likely increased with community biomass and soil nitrogen availability because total shoot biomass increased significantly with these factors. This would probably have led to underestimates of recruitment in the removal plots at the most productive sites due to a greater likelihood of self-thinning. If this was the case, then we may have underestimated the magnitude of community effects in the seed addition experiment at the sites with the greatest community biomass and soil nitrogen availability. Despite the possibility of an insensitive measure, we found that the total and litter effects on recruitment increased strongly with community biomass, suggesting that if anything, we underestimated the magnitude of litter interference effects on recruitment at the sites with the greatest community biomass.

The result that plant litter contributed strongly to the overall inhibitory effect of the community on the recruitment of *Andropogon* at sites with the greatest plant biomass is consistent with a number of studies showing that the accumulation of large amounts of litter can limit plant diversity in productive systems by interfering with species colonization (e.g., Carson and Peterson 1990, Tilman 1993). We suggest that theories designed to explain variation in plant interactions and species diversity along gradients in community biomass and associated gradients in productivity and soil fertility should take into account the potential impact of litter on recruitment, as well as other nonexploitative interactions that potentially occur among plants.

In addition, although our study was conducted at only five sites and over just one growing season, the results suggest that it may be during the recruitment phase of the life history, when seeds and seedlings are especially susceptible to the effects of litter, that *Andropogon* is most sensitive to variation in community biomass. If this is correct, an important implication is that the inclusion of regeneration processes in plant

competition studies may often lead to different conclusions regarding how plant interactions vary along environmental gradients compared to those based upon the responses of established plants alone. This is of particular significance because regeneration processes have often been found to be more important in determining the distribution of species in space and time than the performance of established plants (Grubb 1977, Gross and Werner 1982). These results also suggest that the distribution of native C_4 prairie grasses such as *Andropogon* along old-field biomass gradients in southwest Michigan may be more strongly constrained by limits to recruitment than by competition experienced during the established phase of the life history.

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