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 1991a, 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-
null
ment of treatments established at each site in a ran-

domized 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

× 70 cm plots located at the four corners of each block.

Neighbors were removed by applying a glyphosate her-

bicide solution (Roundup), and clipping the dead ma-

terial after 1 wk. Litter was removed by hand from the

litter removal treatments so that the soil was left un-

disturbed. 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 re-

moval plots were periodically hand-weeded during the

growing season to eliminate regrowth.

Seed additions.—Seeds of Andropogon were col-

lected from a local population in the fall of 1993 and

stored outside over winter in a plastic container to ex-

pose the seeds to winter temperature fluctuations. Seeds

were sown by hand into the treatment plots at a rate

of 1500 seeds/plot (3030 seeds/m2) in mid May 1994. B

Because the goal of this experiment was to examine

recruitment from seed in the absence of dispersal lim-

itation, a seeding rate was chosen that mimicked the

seed rain within natural stands of Andropogon (=3000

seeds/m2; 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 bio-

mass 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 transplan-
ting 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

× 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 ran-
domly selected for the experiment from a group of

≈800 healthy seedlings. The initial shoot biomass of
each seedling was estimated from a regression of seed-

ling biomass on longest leaf length (L) obtained from

a subsample of the remaining healthy seedlings (initial

transplant biomass = 0.004L − 0.011, R² = 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 ≈20 cm.

All individual transplants were watered (0.2 L/d) for eight

eight consecutive days following planting to en-
courage initial establishment. Only 16 of the 480 trans-

plants died and there were no plots where less than

three transplants survived until the end of the experi-

ment. The shoots of all surviving transplants were har-

vested in early September. Aboveground biomass of

neighbors and litter was harvested from the intact plots.

Neighbors were sorted by species to document the spe-
cies 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 exper-

imental 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, In-
corporated, Pullman, Washington). PAR measurements

were taken three times over the course of the experi-

ment 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 per-

centage PAR reaching the ground surface. Mean sea-

sonal 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: neigh-

bors and litter removed; neighbors and litter left intact.

At each sampling date, two soil cores (2.5 cm diameter

× 15 cm deep) were taken from each plot. All cores

were taken at least 10 cm away from the base of trans-

plant shoots and care was taken to minimize distur-

bance to the plots. The two cores from each plot were

composited for analysis. Subsamples (10 g) were ex-

tracted for 24 h in a 2 mol/L KCl solution, filtered, and

then analyzed colorimetrically with an Alpkem au-
toanalyzer (Alpkem Corporation, College Station,

Texas) for ammonium and nitrate. Soil nitrogen con-

centrations are expressed as the sum of extractable am-

monium and nitrate concentrations (micrograms of ni-

trogen per gram dry soil). Mean seasonal nitrogen con-
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:

\[ \text{RGR} = \frac{[\ln(B_2) - \ln(B_1)]}{(t_2 - t_1)} \]

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 \( t_1 \) and planting \( t_2 \). 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 heteroscedasticity (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:

- total effect = \((P_C - P_{NL})/P_C\)
- neighbor effect = \((P_C - P_N)/P_C\)
- litter effect = \((P_C - P_L)/P_C\)

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:

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

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>
<thead>
<tr>
<th>Source of variation</th>
<th>Effect ms/error ms</th>
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<tbody>
<tr>
<td>Among blocks</td>
<td></td>
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<tr>
<td>S</td>
<td>S/B(S)</td>
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<tr>
<td>Within blocks</td>
<td></td>
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<tr>
<td>N</td>
<td>N(N × B(S))</td>
</tr>
<tr>
<td>N × S</td>
<td>N × S/N × B(S)</td>
</tr>
<tr>
<td>L</td>
<td>L/L × B(S)</td>
</tr>
<tr>
<td>L × S</td>
<td>L × S/L × B(S)</td>
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<tr>
<td>N × L</td>
<td>N × L/N × L × B(S)</td>
</tr>
<tr>
<td>N × L × S</td>
<td>N × L × S/N × L × B(S)</td>
</tr>
</tbody>
</table>

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.
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 (Fig. 3A). 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,

<table>
<thead>
<tr>
<th>TABLE 3. Results of ANOVA for site and treatment effects on mean seasonal light penetration.</th>
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<tbody>
<tr>
<td><strong>Source of variation</strong></td>
</tr>
<tr>
<td>-------------------------</td>
</tr>
<tr>
<td>Among blocks</td>
</tr>
<tr>
<td>Site</td>
</tr>
<tr>
<td>Block</td>
</tr>
<tr>
<td>Within blocks</td>
</tr>
<tr>
<td>Neighbors</td>
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<tr>
<td>Neighbors × Site</td>
</tr>
<tr>
<td>Neighbors × Block</td>
</tr>
<tr>
<td>Litter</td>
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<tr>
<td>Litter × Site</td>
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<tr>
<td>Litter × Block</td>
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<tr>
<td>Neighbors × Litter</td>
</tr>
<tr>
<td>Neighbors × Litter × Site</td>
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<tr>
<td>Neighbors × Litter × Block</td>
</tr>
<tr>
<td>* P &lt; 0.05; *** P &lt; 0.001; NS, P &gt; 0.05.</td>
</tr>
</tbody>
</table>

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 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 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.

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>df</th>
<th>MS</th>
<th>$F$</th>
</tr>
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<tbody>
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<td>Among blocks</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Site</td>
<td>4</td>
<td>18.360</td>
<td>7.78***</td>
</tr>
<tr>
<td>Block</td>
<td>20</td>
<td>2.229</td>
<td></td>
</tr>
<tr>
<td>Within blocks</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Vegetation</td>
<td>1</td>
<td>123.884</td>
<td>73.17***</td>
</tr>
<tr>
<td>Vegetation × Site</td>
<td>4</td>
<td>0.280</td>
<td>0.16 ns</td>
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<tr>
<td>Block</td>
<td>20</td>
<td>1.693</td>
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</tr>
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</table>

*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, $P > 0.05$.}

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

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>df</th>
<th>Density</th>
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<tr>
<td></td>
<td></td>
<td>MS</td>
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<td>Among blocks</td>
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<tr>
<td>Site</td>
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<td>41.438</td>
<td>0.95 **</td>
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<td>Block</td>
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<td>Within blocks</td>
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<tr>
<td>Neighbors</td>
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<td>3659.415</td>
<td>112.52 ***</td>
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<td>Neighbors × Site</td>
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<td>18.252</td>
<td>0.56 NS</td>
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<tr>
<td>Neighbors × Block</td>
<td>20</td>
<td>32.523</td>
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<td>Litter</td>
<td>1</td>
<td>1325.331</td>
<td>43.57 ***</td>
</tr>
<tr>
<td>Litter × Site</td>
<td>4</td>
<td>322.504</td>
<td>10.60 ***</td>
</tr>
<tr>
<td>Litter × Block</td>
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<td>30.416</td>
<td></td>
</tr>
<tr>
<td>Neighbors × Litter</td>
<td>1</td>
<td>96.930</td>
<td>3.79 NS</td>
</tr>
<tr>
<td>Neighbors × Litter × Site</td>
<td>4</td>
<td>24.481</td>
<td>0.96 NS</td>
</tr>
<tr>
<td>Neighbors × Litter × Block</td>
<td>20</td>
<td>25.556</td>
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** P < 0.01; *** P < 0.001; NS, P > 0.05.

Fig. 2. (A) {Andropogon} density, and (B) total shoot biomass (mean ± 1 st) in relation to the experimental treatments (seed addition experiment). See Fig. 1 for significance levels.
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. 3B).
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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

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**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 ($n = 25$).
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 1991a). A large amount of litter can greatly reduce light penetration to the soil surface, limiting germination and seedling growth (Facelli and Pickett 1991b). Other indirect ef-

![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).](image-url)
Effects 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, interspecific interactions among target plants were possible because each experimental plot contained more than one individual target plant. Miller (1996) pointed out that because interspecific and interspecific competition may both vary along gradients, indices of competition that standardize interspecific competition by plant performance in plots where interspecific interactions are occurring may result in an insensitive measure of competition. In our study, interspecific competition was likely important in the neighbor removal plots of the seed addition experiment where Andropogon densities were quite high. If interspecific 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 C₄ 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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