

Establishment, competition and the distribution of native grasses among Michigan old-fields

BRYAN L. FOSTER

W. K. Kellogg Biological Station and Michigan State University, Hickory Corners, MI 49060, USA

Summary

1 In this study the potential role of competition in influencing the distribution of three displaced native perennial grasses across complex gradients of plant productivity and species composition was investigated in Michigan old-fields. To do this plant removal and propagule addition experiments were conducted at nine old-field sites to examine the effects of living plant neighbours and litter on seedling establishment and growth of target species in relation to community biomass.

2 For two target species, *Andropogon gerardi* and *Schizachyrium scoparium*, living plant neighbours suppressed establishment from seed at most sites, and suppressed the growth of transplants at all sites.

3 Plant litter strongly inhibited the seedling establishment of both *Andropogon* and *Schizachyrium* at sites of high community biomass and litter accumulation, but had little impact on the growth rate of transplants at any of the sites.

4 The total suppressive effect of the plant community on seedling establishment and transplant growth of both *Andropogon* and *Schizachyrium* increased in magnitude in a non-linear fashion with community biomass. These effects increased in magnitude more rapidly across sites of low to medium biomass than sites of medium to high biomass.

5 The results suggest that these native grasses may be restricted to low productivity habitats within this landscape because of strong competitive interference with establishment by the existing vegetation in the most productive sites.

Keywords: *Andropogon gerardi*, biomass gradient, plant litter, *Schizachyrium scoparium*, *Sorghastrum nutans*

Journal of Ecology (1999) **87**, 476–489

Introduction

Plant ecologists have long been interested in the role of competition in influencing the distributions of species, and in determining the composition and diversity of plant communities along environmental gradients (Whittaker 1975; Werner & Platt 1976; Gurevitch 1986; Wilson & Keddy 1986; Tilman 1988; Keddy 1989; Wilson & Tilman 1991). In recent years, a number of field experiments have been conducted to test the assertion, largely attributed to Grime (1973, 1979) but made by others (Huston 1979; Southwood 1988; Keddy 1989), that the intensity or magnitude of plant competition increases along gradients of plant productivity and community biomass (Wilson & Keddy

1986; Wilson & Tilman 1991; Bonser & Reader 1995; Kadmon 1995; Twolan-Strutt & Keddy 1996). Most of these studies have examined the effects of neighbouring plants on the performance of established target plants (naturally established adult plants or large transplanted seedlings) at different positions along natural or experimental gradients in community biomass. However, few of these studies have examined the impacts of neighbouring plants on the performance of target species at the earliest life-history stages, particularly with respect to establishment from seed along biomass gradients (but see Moloney 1989; Kadmon 1995). This is somewhat surprising given that initial establishment processes are thought to be of great importance in determining the temporal and spatial distributions of plants (Grubb 1977; Harper 1977; Gross & Werner 1982; Foster & Gross 1997). Several studies indicate that it is in the early establishment stages of the life history (germination, emergence, initial root and shoot development) when

Present address: Department of Ecology, Evolution and Behaviour, University of Minnesota, St Paul, MN 55108, USA (fax 612 624 6777; e-mail foster@swan.lter.umn.edu).

plants may be most sensitive to competition and to variation in plant neighbour abundance (Grubb 1977; Weiner & Thomas 1986; Foster & Gross 1997, 1998).

In this study the impact of plant neighbours on the seedling establishment and growth of three native grasses along a complex gradient in community biomass and species composition was examined in south-west Michigan old-fields. The three target species, *Andropogon gerardi* Vitman (big bluestem), *Schizachyrium scoparium* L. (little bluestem) and *Sorghastrum nutans* L. (Indian grass), are all C₄, perennial grasses. These species represent the dominant grasses of the tall-grass prairies (Bazzaz & Parrish 1982) and were dominant components of the pre-settlement prairie and savanna communities of south-west Michigan (Gotshall 1972). In intact prairies, *Andropogon* and *Sorghastrum* are distributed widely across gradients of plant productivity, soil moisture and soil fertility, while *Schizachyrium* is typically restricted to the more xeric, infertile sites (Weaver 1954; Smeins & Olson 1970; Bazzaz & Parrish 1982).

In the current agricultural and successional landscape of south-west Michigan, these grasses are now largely restricted to low fertility, low biomass abandoned sites and are generally absent from the most productive sites that tend to be dominated by introduced C₃ grasses such as *Agropyron repens* L. Beauv. and *Bromus inermis* Leysser. Site pre-emption by such early colonizing, fast-growing grasses may interact with the poor dispersal capacity of the native grasses to prevent their re-establishment in high biomass sites following agricultural abandonment (Tilman & Wedin 1991; Foster 1992, 1996). Because fire is no longer an important factor in this landscape, litter accumulation may be particularly important in preventing the re-colonization of high biomass sites by displaced native prairie species that evolved in the presence of fire, and which may lack adaptations for establishment in dense litter (Tilman 1993; Foster & Gross 1997).

Here the results of a field experiment are reported in which seeds and transplants of the target species were added to a factorial arrangement of removal treatments at each of nine old-field sites. The treatments were designed to investigate the separate and interactive effects of living plant neighbours and plant litter on target plant performance, and consisted of two levels of living neighbours (removed and intact) and litter (removed and intact). Seeds and large seedling transplants were added to experimental plots to examine the effects of the surrounding plant community on initial seedling establishment and on the growth rates of well-established individual seedlings. This allowed an assessment of competitive effects on target plant performance at two fairly distinct stages of the life history.

The nine experimental sites used in this study were representative of the range of grass-dominated old-fields in south-west Michigan and encompassed a

complex gradient in plant productivity and species composition. Because plant production integrates abiotic and biotic characteristics of a habitat, above-ground plant community biomass (sum of living plant and litter biomass) was used as a predictor of target plant performance and of the magnitude of competition occurring along this complex gradient. With this experiment, the following specific questions were addressed regarding the role of competition in influencing the distribution of these displaced native grasses among Michigan old-fields.

1 How do living plant neighbours and litter influence seedling establishment and growth of the target species across a range of old-field sites?

2 Does seedling establishment and growth of the target species vary predictably with variation in community biomass along the complex biomass gradient?

3 Do the effects of living neighbours and litter on the target species vary predictably in magnitude with variation in community biomass?

Methods

STUDY SITES

This study was conducted in nine mid-successional grassland sites at the W. K. Kellogg Biological Station (KBS) of Michigan State University in south-west Michigan (Kalamazoo County; 42°24'N, 85°24'W). Sites were selected to encompass a wide range of community biomass common to old-fields in south-west Michigan. All nine sites had been abandoned from row crop agriculture for at least 20 years, and were dominated by perennial grasses (Table 1; Burbank *et al.* 1992). Isolated individuals of *Andropogon* were present at sites 1 and 5. *Schizachyrium* and *Sorghastrum* were not present at any of the study sites, although populations of these species were located within a kilometre of each site. Sites containing large populations of the target species were intentionally avoided so as not to confound experimental and natural seedling establishment. This also allowed investigation of the factors responsible for the absence of these species from the sites. Soils underlying the sites were classified as sandy loams in the Kalamazoo series, but differed in the degree to which the topsoil had been eroded by past agricultural activity (Burbank *et al.* 1992). Assignment of site numbers (1–9) was based on ranking of total community biomass (sum of living neighbour and litter biomass; 1 = lowest and 9 = highest biomass). Sites 8 and 9 had a history of manure application, which probably contributed to the particularly high plant productivity of these sites (Table 1).

EXPERIMENTAL DESIGN AND METHODS

In 1995 seeds and seedling transplants of the three target species were planted into a two × two factorial

Table 1 Vegetation characteristics of the nine study sites. Biomass values are shown as means \pm 1 SE ($n = 6$ for each site). Nomenclature follows Voss (1972)

Site	Living plant biomass (g m^{-2})	Litter biomass (g m^{-2})	Total community biomass (g m^{-2})	Four most abundant species	Species relative biomass (%)
1	68.8 \pm 15.2	10.4 \pm 1.5	79.2 \pm 16.1	<i>Andropogon virginicus</i> <i>Rubus alleghaniensis</i> <i>Danthonia spicata</i> <i>Solidago nemoralis</i>	50.0 13.9 9.9 5.7
2	109.6 \pm 43.7	19.6 \pm 5.9	129.2 \pm 43.2	<i>Rubus alleghaniensis</i> <i>Danthonia spicata</i> <i>Centaurea maculosa</i> <i>Andropogon virginicus</i>	27.8 17.2 14.7 11.0
3	182.3 \pm 15.1	39.1 \pm 2.3	221.4 \pm 14.8	<i>Andropogon virginicus</i> <i>Danthonia spicata</i> <i>Rubus alleghaniensis</i> <i>Desmodium rotundifolium</i>	49.8 9.8 6.0 4.8
4	259.6 \pm 27.5	91.9 \pm 23.7	351.5 \pm 50.3	<i>Agropyron repens</i> <i>Achillea millefolium</i> <i>Bromus inermis</i> <i>Melilotus alba</i>	85.2 7.3 6.4 0.1
5	348.1 \pm 17.9	235.2 \pm 50.7	583.3 \pm 54.9	<i>Bromus inermis</i> <i>Poa pratensis</i> <i>Achillea millefolium</i> <i>Achillea millefolium</i> <i>Agropyron repens</i>	58.1 10.3 10.1 10.1 5.1
6	398.8 \pm 56.2	220.4 \pm 57.5	619.2 \pm 115.7	<i>Bromus inermis</i> <i>Agropyron repens</i> <i>Poa pratensis</i> <i>Daucus carota</i>	78.0 10.3 3.8 3.2
7	745.2 \pm 105.3	397.6 \pm 42.4	1142.8 \pm 142.8	<i>Agropyron repens</i> <i>Arrhenatherum elatius</i> <i>Silene alba</i> <i>Polygonum scandens</i>	71.0 28.3 0.1 0.1
8	915.2 \pm 55.1	555.7 \pm 54.3	1470.9 \pm 102.4	<i>Bromus inermis</i> <i>Poa pratensis</i> <i>Solidago canadensis</i> <i>Agropyron repens</i>	44.2 19.1 17.4 15.4
9	1235.9 \pm 174.4	737.3 \pm 68.5	1973.2 \pm 223.8	<i>Bromus inermis</i> <i>Poa pratensis</i> <i>Agropyron repens</i> <i>Barbarea vulgaris</i>	90.6 4.9 2.5 0.1

arrangement of treatments established at each site in a randomized block design. Experimental treatments included two levels of living plant neighbours (intact and removed) and two levels of plant litter (intact and removed). At all sites, six 3×3.5 m experimental blocks were established in early May 1995 (Fig. 1). Within all sites (except sites 1 and 3), adjacent blocks were separated by buffers zones of approximately 2 m. At sites 1 and 3, blocks were separated by distances of 5–15 m. Each block contained four parallel 0.5×3 m plots separated by 0.5-m buffer areas. Each plot within each block contained six subplots, three for seed additions and three for transplants (one seed addition and one transplant subplot per target species). The three seed addition subplots (30×30 cm) were adjacent to each other at one end of the plots and were separated by buffer zones of 20 cm. The

three transplant subplots (50×50 cm) were also adjacent to each other, but had no buffer zones between them. Species were randomly assigned to both the seed addition and transplant subplots within each plot.

In early May, the experimental treatments were applied to the four 0.5×3.5 m plots located within each block. Neighbours were removed either by clipping or mowing and by applying Glyphosate herbicide solution (Roundup[®], Monsanto Inc., St. Louis, Missouri, USA.) to the regrowth a week later. Litter was removed by hand from the litter removal treatments so that the soil was left undisturbed. To minimize root encroachment into the two neighbour removal treatments, plot perimeters were trenched with a flat blade shovel to a depth of 20 cm twice during the growing season. The borders between sub-

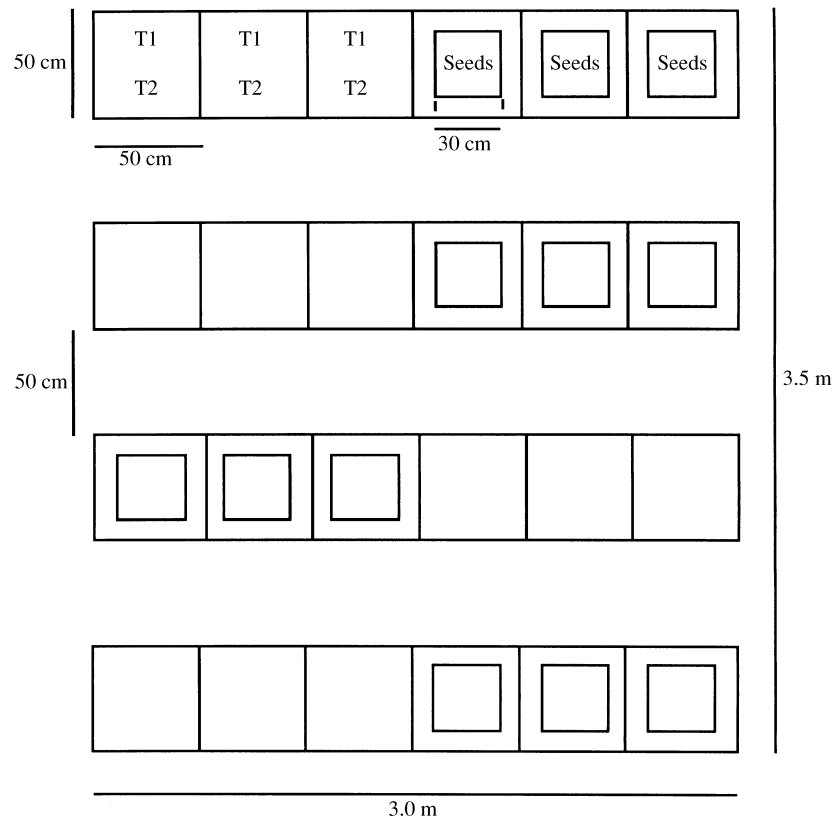


Fig. 1 Experimental block layout illustrating the arrangement of the experimental treatment plots and the transplant and seed addition subplots. T1 and T2 refer to the position of the two transplants in each transplant subplot.

plots were also trenched to prevent below-ground interactions between the different target species. Neighbour removal plots were periodically hand-weeded during the growing season to eliminate vegetation regrowth.

Seed additions

Seeds of the three target species were collected from nearby populations in the autumn of 1994 and stored over winter in an unheated garage in a metal container to expose the seeds to winter temperature fluctuations. Seeds were scattered by hand into each of the 30×30 cm subplots at a rate of 300 per subplot (3030 m^{-2}) in late May 1995. The seedlings were censused and target shoot biomass was harvested in late September 1995 to assess seedling establishment success. All plant material was oven-dried at 60°C to constant mass and then weighed.

Transplants

Seedlings of each of the target species were obtained by germinating seeds in flats in a greenhouse in mid-April 1995. Approximately 7–9 days after germination, *c.* 800 individual seedlings of each species were transferred into individual seedling containers ($2.54 \text{ cm diameter} \times 10.16 \text{ cm deep}$) containing a 3:1:1

mixture of peat moss, commercial potting soil and old-field soil. After 22–25 days of additional growth, 432 relatively large seedlings of each species were selected for the experiment. Initial shoot biomass of each of these seedlings was estimated from regressions of seedling biomass on longest leaf length obtained from subsamples of the remaining healthy seedlings (mean length of longest leaf: *Andropogon* 16.3 ± 4.6 cm, *Schizachyrium* 12.1 ± 2.9 cm, *Sorghastrum* 17.4 ± 5.2 cm).

In early June, two seedlings of each species were transplanted into their respective transplant subplots by inserting seedling plugs into holes made with a 2.54-cm diameter soil corer. Within each subplot, the two transplants were separated by *c.* 20 cm. All individual transplants were watered (0.21 day^{-1}) for 12 consecutive days following transplanting to ensure initial establishment. At sites 5, 8 and 9 most of the transplants in the neighbour removal treatments were heavily grazed by deer within 2 days of planting. The browsed transplants were replaced with new ones and a 1.5-m tall fence made from poultry netting was placed around the perimeter of the neighbour removal treatment plots at all sites to prevent further deer browsing. Fencing was not placed around the treatment plots where neighbours were left intact because the target plants growing in these plots were not being browsed. The presence of fences had no significant impact on light levels at the soil surface in any of the

sites. By the end of the experiment, only 3.7% of *Andropogon* transplants and 6.2% of *Schizachyrium* transplants had died. However, 15.3% of *Sorghastrum* transplants died, most of which were located at sites 1 and 2. In late September the shoots of all surviving transplants were harvested to measure plant growth. Transplant shoot biomass was dried and weighed to constant mass at 60 °C.

COMMUNITY BIOMASS

Above-ground biomass of living plants and litter was estimated for each site from plant material harvested from the seed addition subplots where both living plants and litter were left intact. Living plant biomass included the biomass of all species found growing in these plots, including *Andropogon*. For six of the sites, living plants were sorted by species to document species composition (Table 1). Species composition for the other three sites (4, 5 and 7) had been assessed in a previous study (Foster & Gross 1997) and data from that study are given in Table 1. Plant material from all sites was dried and weighed as described previously.

LIGHT PENETRATION

Photosynthetically active radiation (PAR) was measured in mid-June above the vegetation and at the soil surface in the transplant subplots with a PAR ceptometer probe (Decagon Devices Inc., Pullman, Washington, USA) to determine how light penetration to the soil surface varied among the sites and was affected by the experimental treatments. In plots where litter was left intact, light measurements were made by inserting the ceptometer beneath the litter layer. In the neighbour removal plots, measurements were made at plot edges at mid-day when the sun was directly overhead to minimize the impact of transplants on light readings. Light penetration is expressed as the percentage PAR reaching the ground surface.

DATA ANALYSES

Community biomass

Site differences in living plant biomass, litter biomass and community biomass (sum of living plant and litter biomass) were examined using one-way analysis of variance (ANOVA). These analyses were performed on biomass data collected from the intact treatment (living and litter biomass left intact).

Light penetration and target plant performance

Percentage light penetration, seedling density and total shoot biomass (seed addition experiments) and transplant growth (transplant experiments) were analysed using two × two factorial, randomized block

ANOVA separately for each site. In cases where the interaction between neighbours and litter was significant, contrasts among neighbour levels were compared at each level of litter, and contrasts among litter levels were compared at each level of neighbours using unplanned comparisons (Sokal & Rohlf 1981). Due to poor germination by *Sorghastrum* in a large proportion of the plots (probably due to low viability), treatment effects on density and shoot biomass were not evaluated for this species. In addition, growth rates of *Sorghastrum* transplants from sites 1 and 2 were not included in the analyses due to high transplant mortality. Analyses of transplant growth were performed on plot mean values. Relative growth rate of each transplant (RGR; Harper 1977; Hunt 1981; Chiariello *et al.* 1989) was calculated as:

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

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* and *Schizachyrium* density and total shoot biomass data were square-root and log transformed, respectively, to improve normality and reduce heteroscedasticity (Sokal & Rohlf 1981). Untransformed data are presented in the figures.

Magnitude of community effects

The magnitude of the effects of the surrounding plant community on target plant performance (density, total shoot biomass and RGR of transplants) was examined using a relative community effect index (diffuse competition, Wilson & Keddy 1986; competition intensity, Wilson & Tilman 1993). This index estimated the degree to which target plant performance was suppressed or promoted by the surrounding community by comparing plant performance in plots cleared of all plant material (neighbours 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 living plant neighbours in contributing to the total effect of the community on target performance, a separate index was calculated by comparing plant performance in cleared plots with plant performance in plots where only litter had been removed (Foster & Gross 1997). These indices were calculated for each experimental block within each field as:

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

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

where P_C is plant performance in plots cleared of all plant material (living neighbours and litter), P_{NL} is

performance in plots in the same block with neighbours and litter left intact, and P_N is performance in plots in the same block with only neighbours left intact (litter removed). An additional index was calculated to measure the effect of litter alone and was calculated as:

$$\text{Litter effect} = (P_C - P_{LIT})/P_C$$

where P_{LIT} is plant performance in plots with only litter left intact (neighbours removed).

Two-way ANOVA was used to examine site and species differences in each community effect index (total, neighbour and litter effects). High *Sorghastrum* mortality at sites 1 and 2 meant that two separate analyses were needed: (i) using data from only two species (*Sorghastrum* omitted) at all nine sites; and (ii) using data from all three species, but with sites 1 and 2 omitted.

The dependence of the target plant performance measures (density, total shoot biomass, RGR) and the community effect indices on total community biomass (as estimated from the intact plots) was examined using linear regression on site means ($n = 9$). For *Sorghastrum* response variables, regressions were performed on data from sites 3–9 only. In cases where a response variable showed evidence of non-linear dependence on community biomass, community biomass was log-transformed prior to the analyses. These data are shown in the figures untransformed with logarithmic curves presented to illustrate non-linearity. SYSTAT⁷ (SYSTAT Inc.) statistical software (version 5.2.1; Wilkinson 1992) was used for all analyses.

Results

COMMUNITY BIOMASS AND SPECIES COMPOSITION

Total community biomass and both of its components, living and litter biomass, differed significantly among sites (total: $F_{8,44} = 39.17$, $P < 0.0001$; neighbour: $F_{8,44} = 28.55$, $P < 0.0001$; litter: $F_{8,44} = 39.59$, $P < 0.0001$; Table 1). Total community biomass increased 25-fold from site 1 to site 9. Living and litter biomass increased 18- and 71-fold, respectively, from site 1 to site 9, and were positively correlated with each other ($r^2 = 0.96$, $P < 0.0001$, $n = 9$). Sites 1–3 exhibited species compositions typical of the least productive soils in the region and were dominated primarily by native species: *Andropogon virginicus* (perennial grass), *Rubus alleghaniensis* (black berry) and *Danthonia spicata* (perennial grass). In contrast, sites 4–9 were dominated by introduced perennial grasses (either *Agropyron repens* or *Bromus inermis*).

LIGHT PENETRATION

At the three sites with the lowest community biomass (sites 1–3) the removal of living neighbours sig-

nificantly increased light penetration, but removal of litter had no effect (Fig. 2). In contrast, at sites 4–9 light penetration varied significantly with neighbours, with litter, and with the interaction between the two. For these sites, contrasts among means showed that neighbour removal increased light penetration in the plots where litter had been removed, but had no significant effect where litter was left intact. At sites 4–7, contrasts indicated that litter removal increased light penetration in both the presence and absence of neighbours, while at sites 8 and 9 litter removal increased light penetration only in plots where neighbours had been removed. Mean light penetration measured in the intact plots (living neighbours and litter intact) declined logarithmically with mean community biomass ($r^2 = 0.86$, $P < 0.0001$, $n = 9$).

SEED ADDITION

Treatment effects

In the seed addition experiment, the number of *Andropogon* seedlings established in the plots was increased significantly by the removal of living plant neighbours at all nine study sites (Fig. 3a). At the two sites with the greatest community biomass (sites 8 and 9) where there were significant interactions between neighbours and litter, contrasts indicated that the removal of neighbours significantly increased *Andropogon* density, both in the absence and presence of litter. At sites 1–4, the removal of litter had no effect on *Andropogon* density. At sites 5–7, litter removal significantly increased *Andropogon* density. At sites 8 and 9, where litter biomass was greatest, litter removal increased *Andropogon* density significantly only in plots where neighbours had also been removed.

The removal of neighbours increased *Andropogon* shoot biomass significantly at all sites except the site with the lowest community biomass (site 1; Fig. 3a). At sites 5–9, where there were significant interactions between neighbours and litter, contrasts showed that the removal of neighbours significantly increased *Andropogon* shoot biomass both in the absence and presence of litter. At sites 1–4, litter removal had no effect on *Andropogon* shoot biomass. At sites 5–7, contrasts showed that litter removal significantly increased *Andropogon* shoot biomass, both in the absence and presence of neighbours. At sites 8 and 9, litter removal increased *Andropogon* shoot biomass significantly only in plots where neighbours had been removed.

In the treatment where neighbours and litter were left intact, mean seedling density of *Andropogon* declined logarithmically, while mean total shoot biomass declined linearly with total community biomass (Fig. 3a). In contrast, where neighbours and litter had been removed, both mean density and mean total shoot biomass of *Andropogon* increased logarithmically with total community biomass.

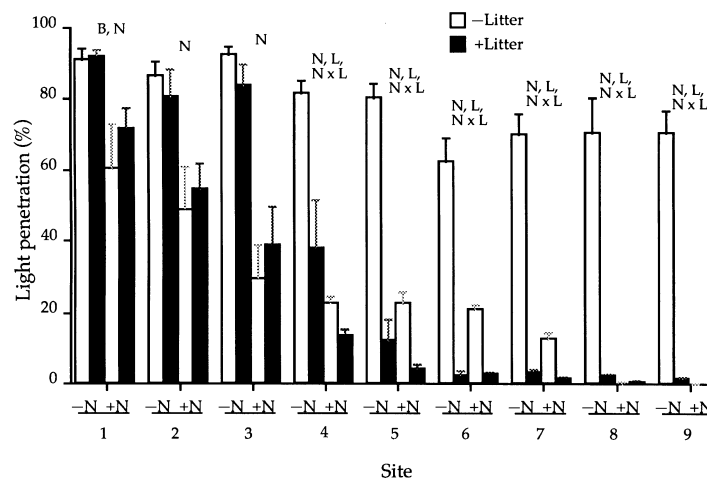


Fig. 2 Mean seasonal light penetration (mean + 1 SE) in relation to the experimental treatments. Treatments with living neighbours removed are indicated below the bars by -N, and treatments with neighbours left intact are indicated below the bars by +N. Solid bars represent treatments where litter was left intact, and open bars represent treatments where litter was removed. Letters above the bars specify the significant ($P < 0.05$) ANOVA terms (B = block effect, N = neighbour effect, L = litter effect, N \times L = neighbour by litter interaction).

The treatment responses of *Schizachyrium* in the seed addition experiment were similar to the responses of *Andropogon* (Fig. 3b). The number of *Schizachyrium* seedlings established in the plots was increased significantly by the removal of living plant neighbours at all sites except site 1. At sites 8 and 9, where there were significant interactions between neighbours and litter, the contrast showed that the removal of neighbours significantly reduced *Schizachyrium* density, both in the absence and presence of litter. At sites 1–4, the removal of litter had no effect on *Schizachyrium* density. At sites 5–7, litter removal significantly increased *Schizachyrium* density. At sites 8 and 9, litter removal increased *Schizachyrium* density significantly only in plots where neighbours had been removed.

The removal of neighbours increased *Schizachyrium* shoot biomass significantly at all sites except sites 1 and 2 (Fig. 3b). At sites 6–9, where there were significant interactions between neighbours and litter, the removal of neighbours significantly increased *Schizachyrium* shoot biomass in both the absence and presence of litter. At sites 1–4, litter removal had no effect on *Schizachyrium* shoot biomass. At site 5, litter removal significantly increased *Schizachyrium* shoot biomass. At site 6, litter removal significantly increased *Schizachyrium* shoot biomass only in plots where neighbours were present. At site 7, litter removal increased *Schizachyrium* shoot biomass in both the absence and presence of neighbours, while at sites 8 and 9, litter removal significantly increased *Schizachyrium* shoot biomass only in plots where neighbours had been removed.

In the treatment where both neighbours and litter were left intact, mean seedling density of *Schizachyrium* declined non-linearly and mean total

shoot biomass declined linearly with total community biomass (Fig. 3b). In the treatment where neighbours and litter had been removed, mean density and biomass increased non-linearly with total community biomass.

Magnitude of community effects

In the seed addition experiment, total, neighbour and litter effects on seedling density and shoot biomass differed significantly among the sites, but there were no differences among species (*Andropogon* and *Schizachyrium*) and no interaction between sites and species (Table 2, and Fig. 4). For both species, total, neighbour and litter effects on density and shoot biomass were all positively correlated with total community biomass (Fig. 4). When seedling density was analysed, the total and litter effects increased non-linearly with community biomass for both species, while for neighbour effects the relationships were best described as linear functions. All three measures of community effect (total, neighbour and litter effects) increased non-linearly with community biomass for both species when shoot biomass was analysed.

TRANSPLANTS

Treatment effects

Removal of neighbours significantly increased the RGR of *Andropogon* and *Schizachyrium* transplants at all sites (Fig. 5a,b). Removal of neighbours increased the RGR of *Sorghastrum* at sites where its responses could be tested statistically (sites 3–9; Fig. 5c). Litter removal increased the RGR of *Andropogon* and *Sorghastrum* transplants only at site 7 in plots where neighbours had been removed, and had

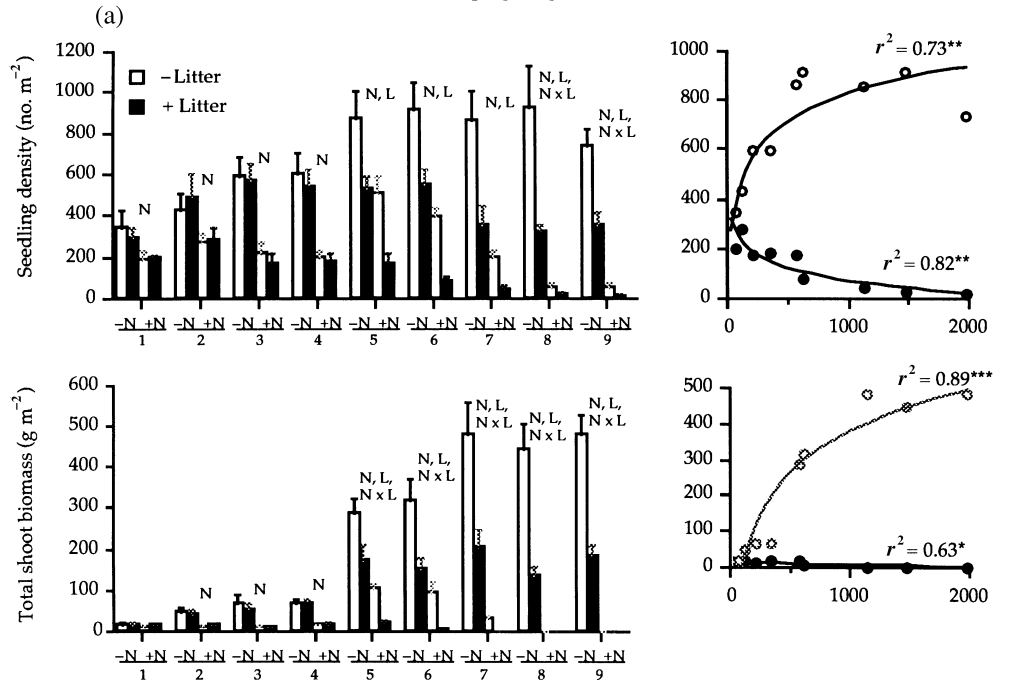
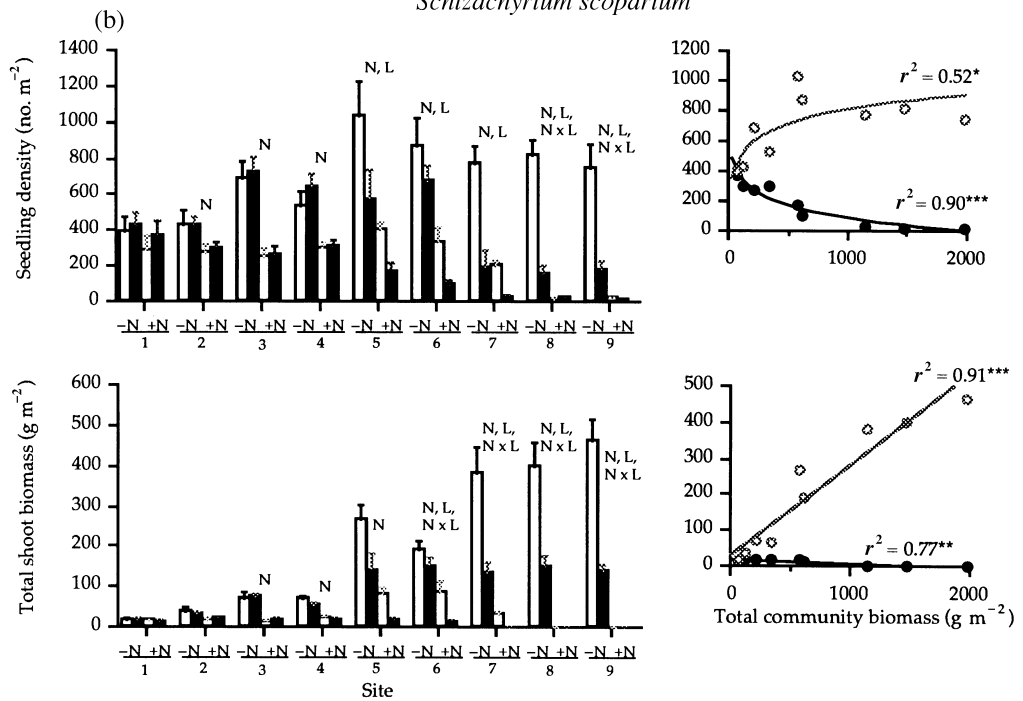
Andropogon gerardi*Schizachyrium scoparium*

Fig. 3 Density and total shoot biomass (mean \pm 1 SE) of (a) *Andropogon* and (b) *Schizachyrium* in relation to the experimental treatments in the seed addition experiment. Solid circles in the right-hand plots represent the treatment where both neighbours and litter were left intact. Open circles represent the treatment where both neighbours and litter were removed (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$).

no effect on the RGR of *Schizachyrium* at any of the sites.

Where both neighbours and litter were left intact, the mean RGR of *Andropogon* and *Sorghastrum* varied independently of community biomass, while

that of *Schizachyrium* decreased non-linearly (Fig. 5). Where neighbours and litter had been removed, mean transplant RGR increased non-linearly with total community biomass for each species.

Table 2 Results of ANOVA examining site and species differences in community effects (total, neighbour and litter effect indices) on seedling density and total shoot biomass (seed addition experiment)

Effect/source	d.f.	Density (<i>F</i> -value)	Shoot biomass (<i>F</i> -value)
Total effect			
Site	8	9.21***	10.18***
Species	1	1.52	0.01
Site × species	8	0.39	0.01
Neighbour effect			
Site	8	5.56***	10.82***
Species	1	0.01	0.01
Site × species	8	0.33	0.01
Litter effect			
Site	8	4.26***	4.22***
Species	1	0.01	0.01
Site × species	8	0.29	0.28

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Magnitude of community effects

The total effect of the plant community on the RGR of transplants varied significantly with sites, but not with species, regardless of whether or not *Sorghastrum* was included in the analyses (Table 3). However, there was a significant site by species interaction reflecting a greater total effect on *Schizachyrium* than on the other species at sites 7 and 8 (Fig. 6). The neighbour effect on transplant RGR varied significantly among sites, but litter effects did not vary significantly among sites or species (Table 3). For both *Andropogon* and *Schizachyrium*, the total and neighbour effects on RGR increased non-linearly with total community biomass (Fig. 6a,b). Litter effects on *Andropogon* and *Schizachyrium* were not correlated with community biomass. None of the three community effects on *Sorghastrum* transplants was correlated with community biomass (Fig. 6c).

Discussion

In this experiment the surrounding plant community suppressed seedling establishment (density and biomass in the seed addition experiment) and transplant growth at each study site. When the effects of neighbours and litter were separated it was found that living plant neighbours suppressed seedling establishment at most sites, and suppressed growth of transplants at all sites. Plant litter strongly inhibited seedling establishment of *Andropogon* and *Schizachyrium* at sites with the greatest community biomass, but had relatively little impact on the growth rate of transplants at any of the sites. For both seedling establishment and transplant growth, the total community effect on *Andropogon* and *Schizachyrium*, which measures the magnitude of the combined effects

of living plant neighbours and litter on these species, increased significantly with community biomass.

In the seed addition experiment there was an almost complete absence of seedling establishment in the intact plots of sites containing the highest community biomass. This finding is consistent with the hypothesis that competitive interference restricts these native grasses to unproductive habitats by preventing establishment in productive habitats. Confidence in this conclusion is strengthened by results of a separate experiment conducted over several years in some of these same fields (B. Foster, unpublished data). Although a few seedlings of *Andropogon* established from seed in the first year in intact plots at the high biomass sites, all had died by the end of the second year. In contrast, many of the plants that established in low biomass sites in the first year survived, grew and flowered by the third year.

Taken as a whole, these results are generally consistent with the biomass-dependent view of competition that predicts that the magnitude of plant competition increases with community biomass (Grime 1979; Keddy 1989). However, the strong non-linearity of these relationships indicates that the degree to which the magnitude of competition depends on community biomass may depend on the range of biomass over which effects are measured.

In a previous experiment conducted in 1994 over a more limited range of biomass (208–1205 g m⁻²) in some of the same field sites used in this study, Foster & Gross (1997) found that the total community effect on *Andropogon* seedling establishment increased with community biomass, as found in the current study. However, unlike in the current study, the total effect of the plant community on the growth of *Andropogon* transplants varied little, and was unrelated to community biomass.

To examine whether the different results observed for transplants in these two experiments could be related to the range of biomass over which effects were measured, data from the current study were re-analysed excluding data from sites that fell below the minimum level of biomass used in the previous study (sites 1 and 2 excluded). The results of these re-analyses were consistent with the previous experiment: total effects on seedling establishment of both *Andropogon* and *Schizachyrium* increased with community biomass as observed for *Andropogon* in the previous study (*Andropogon*: $r^2 = 0.78$, $P = 0.01$; *Schizachyrium*: $r^2 = 0.73$, $P = 0.01$). However, total effects on transplant growth for all three target species were not significantly correlated with community biomass over the more limited range of biomass (*Andropogon*: $r^2 = 0.48$, $P = 0.07$; *Schizachyrium*: $r^2 = 0.39$, $P = 0.14$; *Sorghastrum*: $r^2 = 0.45$, $P = 0.09$).

These comparisons suggest that detecting a positive relationship between competitive magnitude and biomass is more likely when examining wide gradients in biomass that include extremely unproductive habi-

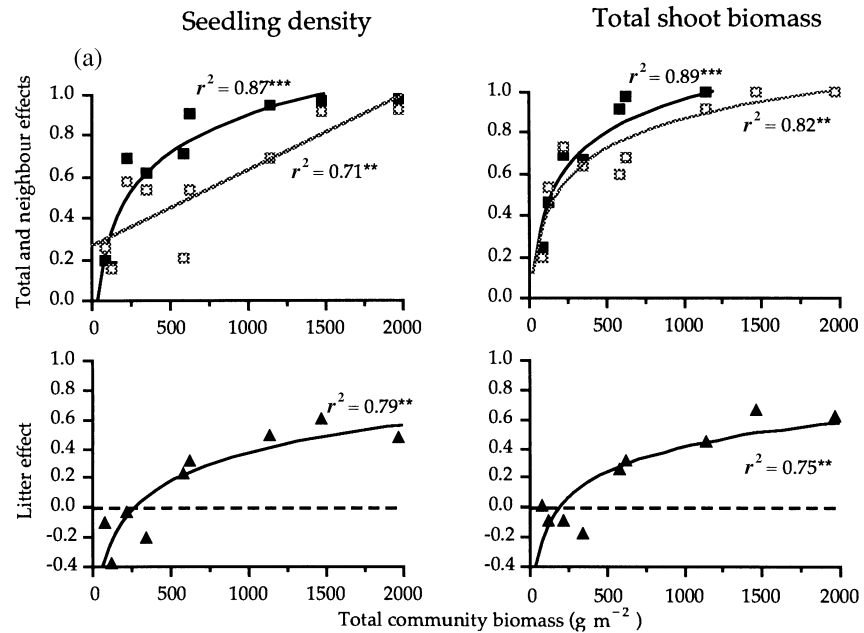
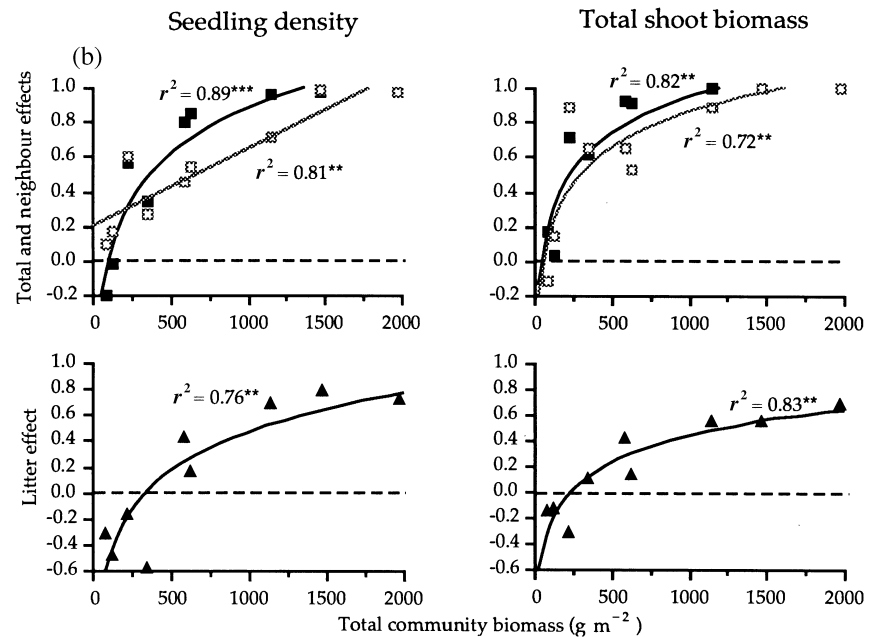
*Schizachyrium scoparium*

Fig. 4 Relationships between community effects (site means) on density and total shoot biomass (dependent variables) and community biomass (independent variable) for (a) *Andropogon* and (b) *Schizachyrium* in the seed addition experiment. Community biomass (sum of living neighbour and litter biomass) for each site was measured in plots where living neighbours and litter were left intact. Solid squares represent total community effects and the open squares represent neighbour effects (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$).

tats. Indeed, the finding in this study that the total community effect on *Sorghastrum* transplant growth was unrelated to community biomass may simply reflect the more restricted gradient over which data were available for this species. The above re-analyses also show that competitive responses to gradients in biomass may depend on the measure of target plant performance used and the stage of the life history

examined. Competitive effects on seedling establishment in the seed addition experiment were sensitive to changes in habitat quality across the entire gradient, although this sensitivity was much more pronounced across sites of low to medium biomass. In contrast, effects on the growth of established seedling transplants were sensitive to changes along this gradient only among sites of very low biomass.

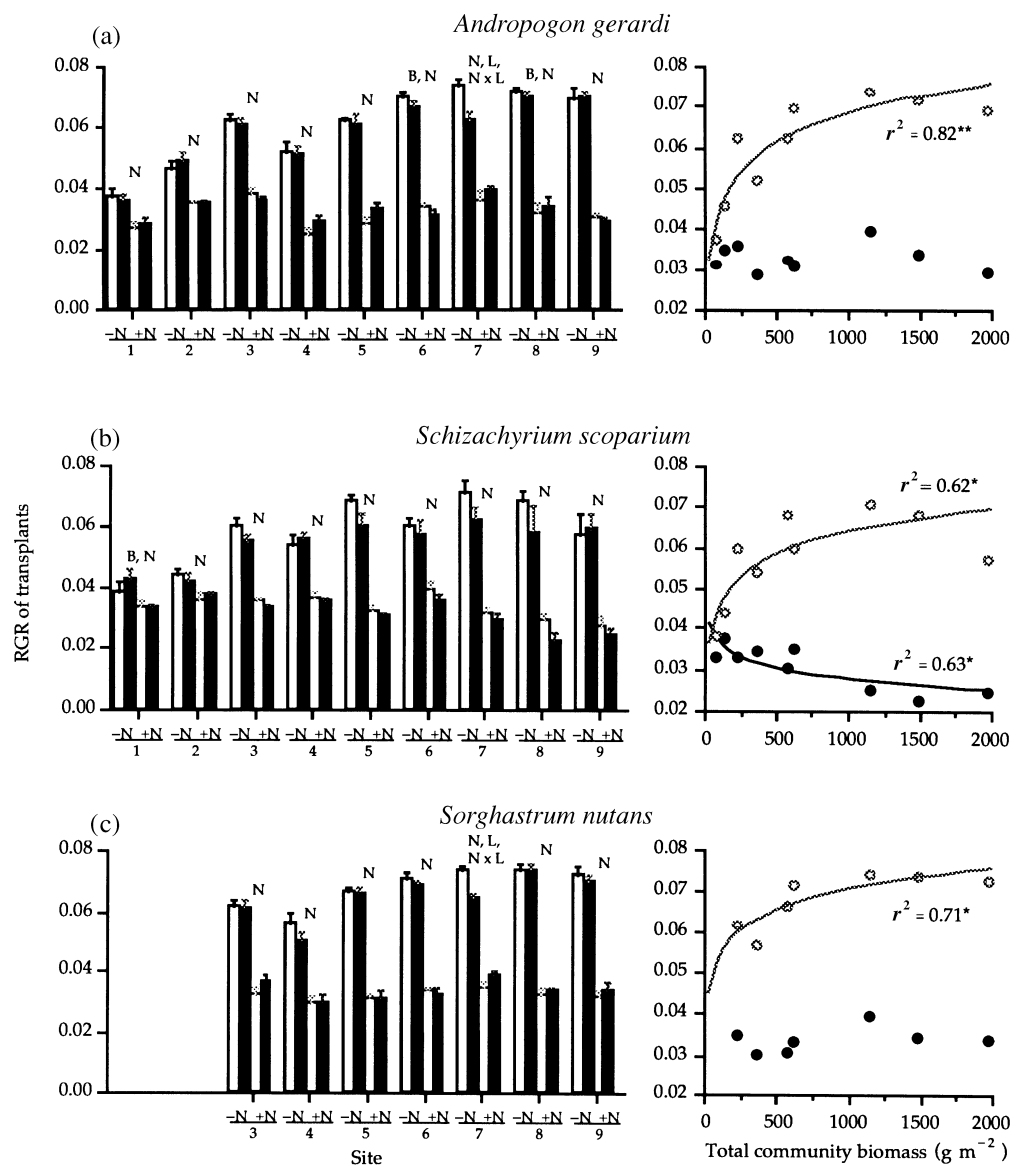


Fig. 5 RGR ($\text{g g}^{-1} \text{day}^{-1}$) of transplants (mean \pm 1 SE) in relation to the experimental treatments. Solid circles in the right-hand plots represent the treatment where both neighbours and litter were left intact. Open circles represent the treatment where both neighbours and litter were removed ($*P < 0.05$, $**P < 0.01$, $***P < 0.001$).

Although the results from the entire biomass gradient are most consistent with a biomass-dependent view of competition (Grime 1979; Keddy 1989), especially in the case of transplants, it may be more useful to consider both biomass-dependent and biomass-independent (Newman 1973; Tilman 1988) views of plant competition as being applicable across different portions of this old-field biomass gradient. Because total effects on transplants increased significantly across only a very limited range of low community biomass, the biomass-independent view may be the most relevant for all but the extremely unproductive sites.

As with most natural gradients, variation in biomass among sites in this study was accompanied by variation in species composition. The three low

biomass sites that comprised the steep portion of the non-linear community effect curves differed markedly in species composition from the remaining sites that made up the flatter portion of these curves. As a result, it is difficult to determine whether the dependence of these measures on community biomass was due to the direct effects of biomass or to some other co-varying factor, such as species composition. Indeed, the strong suppressive effects observed in this study in productive sites could be because these sites were dominated by introduced C_3 grasses. These species grow relatively fast and begin their growth earlier in the season than the native C_4 grasses, possibly pre-empting available resources before the native grasses can take advantage of them (Kemp & Williams 1980). Novel experimental approaches are needed to tease

Table 3 Results of ANOVA examining site and species differences in community effects on the RGR of transplants

Effect/source	Sites 1–9, <i>Sorghastrum</i> omitted (d.f., <i>F</i> -value)		Sites 3–9, <i>Sorghastrum</i> included (d.f., <i>F</i> -value)	
	Total effect			
Site	8	20.01***	6	6.47***
Species	1	0.09	2	0.40
Site × species	8	2.95**	12	3.11***
Neighbour effect				
Site	8	13.41***	6	4.15***
Species	1	3.70	2	3.00
Site × species	8	1.36	12	1.66
Litter effect				
Site	8	1.59	6	1.43
Species	1	0.02	2	0.01
Site × species	8	0.75	12	0.65

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

apart the relative importance of biomass and composition in determining competitive magnitude along productivity gradients (Peltzer *et al.* 1998). Nevertheless, these results indicate that community biomass can be a powerful predictor of plant performance and competitive magnitude in these communities.

SEPARATING THE EFFECTS OF LITTER FROM THE EFFECTS OF LIVING NEIGHBOURS

In this study, seedling establishment was highly sensitive to plant litter. In the absence of neighbours, the suppressive effects of litter alone increased in mag-

nitude with community biomass. In the intact communities, litter contributed strongly to the total community effect on establishment at several of the sites. Interestingly, the removal of litter at sites 8 and 9, which supported the greatest neighbour and litter biomass, led to increases in establishment only when neighbours had also been removed, while litter removal at sites of intermediate biomass (sites 5–7) increased establishment in the presence and absence of neighbours. The disparity between total and neighbour effect indices for seedling density at sites 5–7 also illustrates the suppressive impact of litter at sites of intermediate biomass. This suggests that the realized effects of litter on establishment in intact communities were greatest at sites of intermediate biomass, despite the fact that the potential effect of litter alone (in the absence of neighbours) was strong in the most productive sites (sites 8 and 9). The lack of an effect of litter removal at sites 8 and 9 in the presence of living neighbours probably reflects the negative impact of neighbours on light availability. Light penetration at sites 8 and 9 was reduced to near zero in treatments where living neighbours were left intact, regardless of whether or not litter had been removed (Fig. 2). In contrast, at sites 4–7, in treatments where neighbours were left intact, litter removal led to significant increases in light penetration at the soil surface, and this probably contributed to the positive impact of litter removal at sites of intermediate biomass.

In the seed addition experiment, negative values of the litter effect index at sites 1–4 suggest that litter facilitated seedling establishment at these sites. Several studies have shown that litter can have a positive

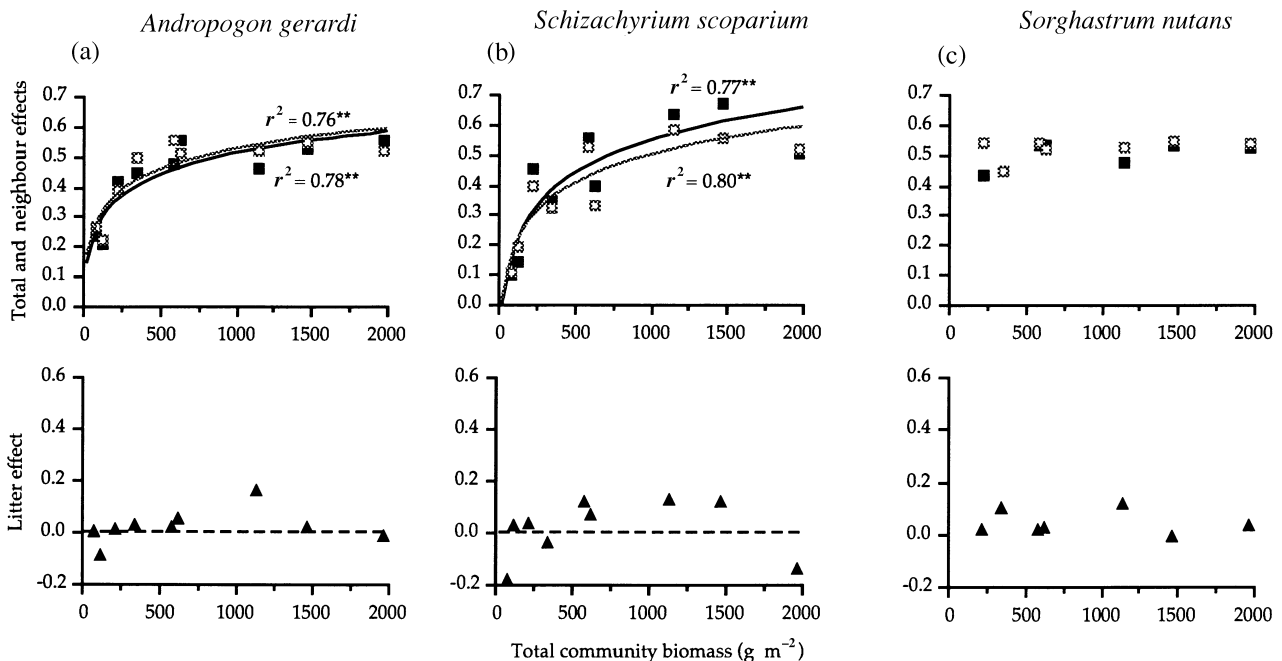


Fig. 6 Relationships between community effects on transplant RGR and community biomass. Solid squares represent total community effects and the open squares represent neighbour effects (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$).

impact on seedling recruitment, particularly in unproductive, xeric habitats where litter can ameliorate moisture stress (Fowler 1986; Willms *et al.* 1986; Suding & Goldberg 1999). However, it must be pointed out that although the mean values of the litter effect index were negative at these four sites, suggesting facilitation, there were no statistically significant effects of litter removal on seedling recruitment at these sites. The potential role of litter in facilitating seedling establishment in these unproductive habitats warrants further investigation.

The suppressive effects of plant litter on seedling establishment observed in this study are consistent with a number of other studies demonstrating negative impacts of litter on the germination, seedling emergence, growth and survival of plants (Werner 1975; Goldberg & Werner 1983; Hamrick & Lee 1987; Bergelson 1990; Facelli & Pickett 1991; Foster & Gross 1997, 1998). As seen in this study, suppressive effects of litter are usually observed at fairly high levels of litter accumulation where litter can reduce light levels at the soil surface, alter microclimate, and act as a mechanical barrier to seeds and seedlings (Facelli & Pickett 1991).

The absence of litter effects on transplants in this study may well reflect the fact that transplants were introduced into each site at a large size and were facilitated in establishment by watering during the first 12 days of the experiment. This resistance to litter effects suggests that although the initial stages of seedling establishment are strongly affected by litter, well-established seedlings that have successfully passed through the critical early establishment stages (germination and emergence) may be relatively immune to its effects, even in highly productive habitats that support large quantities of litter.

SYNTHESIS

The results of these experiments highlight the role of competition in influencing the distribution of native grasses. The data give several general insights into the nature of competition in grasslands, while raising several points relevant to the study of plant competition in the field. In combination with the findings of two other experimental studies (Shipley *et al.* 1991; Bonsor & Reader 1995), this study suggests that non-linearity in the intensity or magnitude of plant competition may be a general feature of gradients in herbaceous vegetation where there is wide variation in biomass. If this is so, then the range or extent of habitat conditions over which competition is measured in the field is critical to understanding competitive interactions in relation to habitat productivity. In fact, the strong increase in competitive magnitude observed over a short range of low values of biomass in this study suggests that it is especially important to include the most nutrient-poor, unproductive habitats in studies of this type

because the magnitude of competition experienced by plants may be particularly sensitive to small changes in habitat quality in these harsh environments.

Finally, the present study, and two others carried out in these same fields (Foster & Gross 1997, 1998), confirm the critical role of accumulated plant litter in suppressing seedling establishment and colonization in these grasslands. Understanding how plant–plant interactions influence the structure of grasslands requires knowledge of how the fitness of plants is affected by both the resource exploitative effects of their living plant neighbours and by the non-exploitative effects of plant litter.

Acknowledgements

I thank A. Porter, A. Henry and P. Moore for invaluable assistance in the field and greenhouse. I greatly appreciate K. Gross for her support and guidance throughout the course of this project. For suggestions on the manuscript I thank K. Gross, G. Mittelbach, P. Robertson, M. Klug and two anonymous referees. Support was provided by the KBS graduate Research Training Group (RTG) funded by NSF grant DIR-09113598, NSF LTER grant BSR 8702332, and a George H. Lauff Research Award. This is contribution number 882 of the W. K. Kellogg Biological Station.

References

- Bazzaz, F.A. & Parrish, J.A.D. (1982) Organization of grassland communities. *Grasses and Grassland Communities* (ed. J.R. Estes), pp. 233–254. Oklahoma State University Press, Stillwater, OK.
- Bergelson, J. (1990) Life after death: site pre-emption by the remains of *Poa annua*. *Ecology*, **71**, 2157–2165.
- Bonsor, S.P. & Reader, R.J. (1995) Plant competition and herbivory in relation to vegetation biomass. *Ecology*, **76**, 2176–2183.
- Burbank, D., Pregitzer, K.S. & Gross, K.L. (1992) *Vegetation of the W. K. Kellogg Biological Station*. Research Report Number 501. Michigan State University Agricultural Experiment Station, East Lansing, MI.
- Chiariello, N.R., Mooney, H.A. & Williams, K. (1989) Growth, carbon allocation and cost of plant tissues. *Plant Physiological Ecology* (eds J. Pearly, H.A. Mooney & P.W. Runnel), pp. 327–365. Chapman & Hall, New York, NY.
- Facelli, J.M. & Pickett, S.T.A. (1991) Plant litter: its dynamics and effects on plant community structure. *The Botanical Review*, **57**, 1–31.
- Foster, B.L. (1992) *The Role of Land Use History in Structuring an Old Field Plant Community*. Thesis, Michigan State University, East Lansing, MI.
- Foster, B.L. (1996) *Plant Competition and Diversity in Relation to Productivity in Old-Field Plant Communities*. Dissertation, Michigan State University, East Lansing, MI.
- Foster, B.L. & Gross, K.L. (1997) Partitioning the effects of plant biomass and litter on *Andropogon gerardi* in old-field vegetation. *Ecology*, **78**, 2091–2104.
- Foster, B.L. & Gross, K.L. (1998) Species richness in a

- successional grassland: effects of nitrogen enrichment and plant litter. *Ecology*, **79**, 2593–2602.
- Fowler, N.L. (1986) Microsite requirements for germination and establishment of three grass species. *American Midland Naturalist*, **115**, 131–145.
- Goldberg, D.E. & Werner, P.A. (1983) The effects of size of opening in vegetation and litter cover on seedling establishment of goldenrods (*Solidago* spp.). *Oecologia*, **60**, 149–155.
- Gotshall, T.B. (1972) The vegetation of Kalamazoo County at the time of settlement. *The Ecology of Kalamazoo County* (ed. R. Brewer), pp. 1–21. Western Michigan University Press, Kalamazoo, MI.
- Grime, J.P. (1973) Competitive exclusion in herbaceous vegetation. *Nature*, **242**, 344–347.
- Grime, J.P. (1979) *Plant Strategies and Vegetation Processes*. J. Wiley & Sons, Chichester, UK.
- Gross, K.L. & Werner, P.A. (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, P.J. (1977) The maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biological Reviews*, **52**, 107–145.
- Gurevitch, J. (1986) Competition and the local distribution of the grass *Stipa neomexicana*. *Ecology*, **67**, 46–57.
- Hamrick, J.L. & Lee, J.M. (1987) Effect of soil surface topography and litter cover on the germination, survival, and growth of musk thistle (*Carduus nutans*). *American Journal of Botany*, **74**, 451–457.
- Harper, J.L. (1977) *Population Biology of Plants*. Academic Press, London, UK.
- Hunt, R. (1981) *Plant Growth Analysis*. Edward Arnold, London, UK.
- Huston, M.A. (1979) A general hypothesis of species diversity. *American Naturalist*, **113**, 81–101.
- Kadmon, R. (1995) Plant competition along soil moisture gradients: a field experiment with the desert annual *Stipa capensis*. *Journal of Ecology*, **83**, 253–262.
- Keddy, P.A. (1989) *Competition*. Chapman & Hall, London, UK.
- Kemp, P.R. & Williams, G.J. III (1980) A physiological basis for niche separation between *Agropyron smithii* (C₃) and *Bouteloua gracilis* (C₄). *Ecology*, **61**, 846–858.
- Moloney, K.A. (1989) The local distribution of a perennial bunchgrass: biotic or abiotic control? *Vegetatio*, **80**, 47–61.
- Newman, E.I. (1973) Competition and diversity in herbaceous vegetation. *Nature*, **244**, 310.
- Peltzer, D.A., Wilson, S.D. & Gerry, A. (1998) Competition intensity along a productivity gradient in a low-diversity grassland. *American Naturalist*, **151**, 465–476.
- Shipley, B., Keddy, P.A. & Lefkovitch, L.P. (1991) Mechanisms producing plant zonation along a water depth gradient: a comparison with the exposure gradient. *Canadian Journal of Botany*, **69**, 1420–1424.
- Smeins, F.E. & Olson, D.E. (1970) Species composition and production of a native northwestern tall grass prairie. *American Midland Naturalist*, **84**, 398–410.
- Sokal, R.R. & Rohlf, F.J. (1981) *Biometry*. W. H. Freeman, New York, NY.
- Southwood, T.R.E. (1988) Tactics, strategies, and templates. *Oikos*, **52**, 3–18.
- Suding, K.N. & Goldberg, D.E. (1999) Variation in the effects of vegetation and litter on recruitment across productivity gradients. *Journal of Ecology*, **87**, 436–449.
- Tilman, D. (1988) *Plant Strategies and the Dynamics and Structure of Plant Communities*. Princeton University Press, Princeton, NJ.
- Tilman, D. (1993) Species richness of experimental productivity gradients: how important is colonization limitation? *Ecology*, **74**, 2179–2191.
- Tilman, D. & Wedin, D. (1991) Plant traits and resource reduction for five grasses growing on a nitrogen gradient. *Ecology*, **72**, 685–700.
- Twolan-Strutt, L. & Keddy, P.A. (1996) Above- and below-ground competition intensity in two contrasting wetland plant communities. *Ecology*, **77**, 259–270.
- Voss, E.G. (1972) *Michigan Flora*. Cranbrook Press, Ann Arbor, MI.
- Weaver, J.E. (1954) *North American Prairie*. University of Nebraska Press, Lincoln, NB.
- Weiner, J. & Thomas, S.C. (1986) Size variability and competition in plant monocultures. *Oikos*, **47**, 211–222.
- Werner, P.A. (1975) The effects of plant litter on germination in teasel, *Dipsacus sylvestris* Huds. *American Midland Naturalist*, **94**, 470–476.
- Werner, P.A. & Platt, W.J. (1976) Ecological relationship of co-occurring goldenrods (*Solidago*: Compositae). *American Naturalist*, **110**, 959–971.
- Whittaker, R.H. (1975) *Communities and Ecosystems*. MacMillan, New York, NY.
- Wilkinson, L. (1992) *SYSTAT: The System for Statistics*. SYSTAT, Evanston, IL.
- Willms, W.D., Smoliak, S. & Baily, A.W. (1986) Herbage production following litter removal on Alberta native grasslands. *Journal of Range Management*, **39**, 536–540.
- Wilson, S.D. & Keddy, P.A. (1986) Measuring diffuse competition along an environmental gradient: results from a shoreline plant community. *American Naturalist*, **127**, 862–869.
- Wilson, S.D. & Tilman, D. (1991) Components of plant competition along an experimental gradient of nitrogen availability. *Ecology*, **72**, 1050–1065.
- Wilson, S.D. & Tilman, D. (1993) Plant competition in relation to disturbance, fertility and resource availability. *Ecology*, **74**, 599–611.

Received 9 June 1998

revision accepted 19 November 1998