Competition, facilitation, and the distribution of *Schizachyrium scoparium* along a topographic-productivity gradient

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Abstract: In this study, neighbor-removal and propague-addition experiments were conducted along a natural topographic-productivity gradient in Kansas grassland to investigate the impact of plant neighbors on recruitment, survival, and growth of a widespread native grass (*Schizachyrium scoparium* L.). Plant neighbors had contrasting effects on *Schizachyrium* that depended on the stage of the life history considered, the measure of plant performance examined, and the position of the local habitat along the complex topographic-productivity gradient. Germination of *Schizachyrium* was strongly suppressed by plant neighbors at high productivity, but facilitated by neighbors at low productivity. Final recruitment (final seedling density in seed addition plots) was facilitated by neighbors in low productivity sites, resulting in differential recruitment success in the presence of neighbors along the productivity gradient. Although transplant survival was also facilitated by plant neighbors in unproductive sites, transplant survival varied independently of productivity in the presence of neighbors. Despite positive effects on transplant survival, neighboring plants strongly suppressed the growth of surviving transplants, with the magnitude of suppression varying independently of productivity. The results suggest that despite strong neighbor effects on established plants, facilitation of seedling recruitment may play a particularly important role in regulating the re-colonization potential and the spatial distribution of *Schizachyrium* in successional grasslands. The findings support the view that events occurring during the earliest establishment phases of the life history can be of primary importance in regulating species distribution along environmental gradients.

Keywords: competition, facilitation, topographic-productivity gradient, *Schizachyrium scoparium*.

Introduction

Elucidating the role of species interactions in regulating plant distribution and species composition along environmental gradients is a fundamental goal in plant ecology (Grime, 1979; Gurevitch, 1986; Tilman, 1988; Huston, 1994). Over the past two decades, there has been great emphasis in the literature on the importance of resource competition along gradients of nutrient availability, productivity, and community biomass in plant communities (Wilson & Keddy, 1986; Tilman, 1988; Goldberg & Barton, 1992). Numerous neighbor-removal experiments have been conducted in the field to test the hypothesis of Grime (1979) that competition intensity increases along gradients of productivity or community biomass (Wilson & Keddy, 1986; Kadmon, 1995; Wilson & Tilman, 1995; Twolan-Strutt & Keddy, 1996; Foster, 1999). However, it has become increasingly apparent that the abundance and distribution of plants along natural environmental gradients are often influenced by a balance of competitive and facilitative interactions (Callaway, 1994; Callaway & Walker, 1997; Holmgren, Scheffer & Huston, 1997; Li & Wilson, 1998). A large body of research indicates that competitive interactions among plants predominate in habitats characterized by low levels of environmental stress, while facilitative interactions are most common in habitats where environmental stress is severe (Grime, 1979; Fowler, 1988; Berntness & Callaway, 1994).
In nature, broad gradients in productivity and community biomass generally reflect an underlying gradient in stress (salt stress, water stress, nutrient stress, extreme temperatures, disturbance, exposure, etc.; Grime, 1979; Huston, 1994; Callaway & Walker, 1997). As a result, the magnitude and relative importance of competition and facilitation across broad landscape gradients may vary predictably among habitats in relation to measures of productivity or community biomass (Callaway & Walker, 1997). The relative importance of competition and facilitation may also vary strongly depending on life stage of the focal species (Morris & Wood, 1989; Callaway & Walker, 1997). Particularly in severe environments, the effect of established neighbors on focal plant performance may shift from facilitative during the recruitment phase of the focal plant's life history to competitive during the established phase (McAuliffe, 1984; Morris & Wood, 1989; Greenlee & Callaway, 1996; Callaway & Walker, 1997).

In this study I examined positive and negative effects of plant neighbors on the performance of a native grass across a natural topographic-productivity gradient in successional grassland. The target species, Schizachyrium scoparium L. (little bluestem), is a perennial, C_{4} grass that is a dominant component of the upland prairies of Kansas and is widespread throughout the midwestern U.S.A. (Bazazz & Parish, 1982). At the landscape scale, Schizachyrium is commonly restricted to fairly xeric sites along well-drained ridges and hill-slopes and generally declines in abundance as one moves down slope to more mesic and productive areas (Weaver, 1954; Crockett, 1964; Smeins & Olsen, 1970; Bazazz & Parrish, 1982). The distribution of Schizachyrium along topographic-productivity gradients in tall grass prairie is presumably the result of this species' limited ability to compete with neighboring plants in high-productivity sites coupled with its high capacity to compete and/or to tolerate environmental stresses in low-productivity sites (Weaver, 1954; Bazazz & Parrish, 1982; Tilman, 1987; Welden & Tilman, 1993). In the context of successional grasslands on abandoned agricultural land in Kansas, the capacity of Schizachyrium to recolonize from seed and to persist as established plants in productive lowland sites after abandonment may be even more limited than in intact prairies. This is because productive successional grasslands are often dominated by introduced C_{3} grasses that have a capacity to pre-empt resources very early in the growing season (Waller & Lewis, 1979; Kemp & Williams, 1980; Foster & Gross, 1997).

Here I report the results of a neighbor-removal and propagule-addition experiment carried out in successional grassland in northeastern Kansas. The objectives of the study were to (i) test the hypothesis that the intensity of competition experienced by Schizachyrium increases with productivity along a complex, natural landscape gradient; (ii) examine how the response of Schizachyrium to plant neighbors may depend on the measure of plant performance used and life history stage; and as a result (iii) elucidate the role of plant-plant interactions in regulating the re-colonization potential and distribution of Schizachyrium along complex topographic-productivity gradients in successional grassland. In this experiment, seeds and seedling transplants of Schizachyrium were added to neighbor-removal and control plots positioned along a natural topographic-productivity gradient. Both seeds and relatively large seedling transplants were added to field plots in order to assess the effects of plant neighbors at two fairly distinct stages of the life history. Seed additions evaluate the impact of neighbors on germination and initial recruitment from seed. Transplant additions evaluate the impact of neighbors on survival and growth of already established seedlings.

**Methods**

**Study site**

This experiment was conducted from early May to early October 2000 at the Nelson Environmental Studies Area (NESA) of the University of Kansas. NESA is located within the prairie-forest ecotone of northeastern Kansas, 12 km north of the city of Lawrence (Jefferson County; 39°03'N, 95°12'W). The experiment was carried out within a 20-ha successional grassland that is dominated by perennial grasses: Bromus inermis Leyss. (introduced C_{3} grass); Festuca arundinaceae Schreb. (introduced C_{3} grass); and Poa pratensis L. (introduced C_{3} grass). The field site is undergoing succession following abandonment in 1984 from use as a hay field and is currently being colonized by native plants from a nearby prairie remnant. Invading native prairie species, which are present at low abundance on unproductive upland ridges within the site, include Schizachyrium scoparium L. (C_{4} perennial grass); Sorghastrum nutans L. (C_{4} perennial grass); Silphium integrifolium Michx. (perennial forb); and Asclepias verticillata L. (perennial forb). Topography within the site is undulating, forming the typical ridge-to-swale geomorphology of the region. Uplands include convex ridges and hill-slopes. Lowlands are gently concave, forming minor swales along ephemeral drainages (Kettle & Whittemore, 1991). Soils are a combination of Pawnee clay loam and Grundy silty clay loam (montmorillonitic, mesic Aquic Argiudolls). Vegetation standing crop varies considerably across the site, ranging from as low as 88 g m^{-2} on upland ridges to as high as 734 g m^{-2} in low swales associated with ephemeral drainages.

**Experimental procedure**

In spring 2000, seeds and transplants of Schizachyrium were planted into 20, 2.3-m × 3.8-m planting blocks distributed throughout the 20-ha study area. Planting block locations were distributed across the 20-ha site using a stratified approach designed to strike a balance between the need to sample across a wide range of productivity and the need to minimize spatial autocorrelation among planting blocks. Stratification was achieved by delineating 5 micro-watersheds within the study area and then placing 4 blocks within each. Within each micro-watershed, blocks were distributed randomly, subject to the constraint that no two blocks could be placed within 10 m of each other. This approach assured that the blocks of similar productivity were well dispersed across the entire study area. After the planting blocks were established and marked, the relative elevation of each was measured using standard survey procedures.

In mid-April, a 4 × 4 grid of 16, 20-cm × 20-cm transplant plots was established on one side of each planting block. Plots within each 4 × 4 grid were separated by
buffers strips of 0.5 m. On the opposite side of each planting block, two 0.5-m × 0.5-m seed addition plots were established. The two seed-addition plots within each block were separated from the adjacent 4 × 4 grid of transplant plots and from each other by 1-m buffer strips.

Within each block, aboveground vegetation was removed in late April from eight randomly selected transplant plots and one randomly selected seed addition plot by applying glyphosate herbicide (Roundup®) and removing plant material one week later. To prevent drift of herbicide outside of the plots, a cardboard barrier (40 cm height) was placed around the perimeter of the plots before spraying. To minimize root encroachment into the neighbor-removal plots, plot perimeters were trenched three times with the growing season with a flat-blade shovel to a depth of approximately 20 cm. The neighbor-removal plots were regularly hand weeded throughout the growing season.

• Seed additions: Seeds of Schizachyrium were collected in November 1999 from a nearby prairie remnant and then stored outside during the winter in a plastic container. In early May 2000, three hundred seeds of Schizachyrium were added by hand to each of the seed-addition plots. A week after sowing, it became apparent from thorough inspections of every seed-addition plot that virtually all the Schizachyrium seeds that had been added to the neighbor-removal plots had been blown away due to windy and dry conditions. As a result, seeds were re-sown into the neighbor-removal plots (additional 300 seeds) eight days after the original sowing. Prior to re-sowing, the few Schizachyrium seeds that remained in the no-neighbor plots from the first sowing were removed by hand. Several steps were taken to reduce the loss of re-sown seeds in the no-neighbor plots. First, just prior to re-sowing, the surface soil in each no-neighbor plot was watered and then lightly scarified with a garden tool. Seeds were then added and gently pressed into the moist soil by hand to hold them in place. The plots with neighbors present received the same amount of water as the no-neighbor plots. Schizachyrium seeds were not re-sown into the plots with neighbors present because numerous seeds from the original sowing were observed on the ground surface in these plots. Although Schizachyrium seeds were observed to be abundant in the vegetated plots, I cannot rule out the possibility that some of these seeds were blown out of the plots during the windy conditions at the time of first sowing, producing somewhat variable seedling rates among the plots. Schizachyrium germination and seedling density were monitored bi-weekly throughout the growing season in all seed-addition plots. On each census date, newly germinated seedlings were marked with color-coded toothpicks. Data from the seed-addition plots are reported as percent germination (fraction of seeds that germinated during the experiment; early May–early October 2000) and final seedling density (seedling density recorded at the end of the growing season).

• Transplants: Schizachyrium seedlings were obtained for the transplant portion of the study by germinating seeds in flats in the greenhouse in early April 2000. Four to five days after germination, 640 seedlings were transplanted into individual seedling containers that had been filled with a 3:1 mixture of commercial planting medium and old-field soil. After 18 days of additional growth in an outdoor lath house, 320 seedlings were selected for transplantation. Before planting in the field, initial biomass of each seedling was estimated from a regression of seedling biomass on longest leaf length (mean leaf length: 9.98 ± 2.56 cm) obtained from the destructive harvest of extra seedlings (biomass = 0.0006 leaf length + 0.0049, r² = 0.61, P < 0.001, n = 32).

In early May, the seedlings were transplanted singly into the center of the 20-cm × 20-cm field plots by inserting seedling plugs into holes made with a 2.54-cm diameter soil sampler. After planting, each seedling was watered for five days (0.2 L day⁻¹) to encourage establishment. Within the first week of planting, 67 transplants either died or were heavily damaged by rodent herbivory. Dead and heavily damaged transplants were replaced from a stock of extra seedlings and then watered for five days. The transplant plots were visited every two weeks throughout the growing season to survey for mortality and evidence of further herbivory. Transplant herbivory was scored on a three-point scale: 1) no evidence of herbivory; 2) light herbivory, signified by small holes in leaves or small pieces of leaves removed; and 3) heavy herbivory, signified by loss of whole leaves or whole plants clipped off at the ground.

In early October, the shoots of surviving transplants were harvested by clipping at the ground surface. Roots were harvested by moistening the soil in the plots and hammering a 10-cm-diameter, 20-cm-deep steel pipe into the ground to extract a core of soil around each transplant. Roots were then separated from soil by soaking the cores in a surfactant solution (5% sodium hexametaphosphate) for 24 hours and then washing the soil away over a screen. Although this method does not obtain the entire root system, it does obtain a large portion of the coarse roots, which likely makes up a substantial fraction of the root biomass. After harvesting, all plant material was dried for 5-7 days at 70°C and weighed.

• Standing crop biomass and resources: In July 2000, aboveground plant standing crop was harvested within each block by clipping vegetation in a 0.1-m × 2.3-m strip in the buffer area between the seed addition and transplant plots. Biomass was separated into living and litter components, dried at 70°C to constant mass and weighed. Light availability was estimated for each block by measuring photosynthetically active radiation (PAR) above and below the plant canopy using an Accupar light interception device (Decagon Devices Inc., Pullman, Washington). Light readings were taken between 10 AM and 2 PM on clear days in May, July, and August 2000. Readings were taken nearby (within 0.5 m) of each block, but outside of the experimental plots. Light availability was expressed as a percentage of PAR reaching the ground surface, averaged across the three sampling periods. Gravimetric soil moisture was measured in May, June, and September 2000, three days after rain in each case. On each sampling date, two 2.54-cm × 10-cm deep soil cores were taken within each block, inside the buffer area between the seed addition and transplant plots. The two soil cores from each block were mixed together for analysis. Soil moisture values (%) for each sampling date were converted to relative moisture values and then averaged across sampling dates before analysis. Relative moisture values for each sampling date were calculated by dividing individual block values by the maximum value occurring among the blocks.
DATA ANALYSES

To characterize the complex topographic-productivity gradient, simple correlation analyses were used to examine interrelationships between relative elevation and the four productivity variables measured in each block: standing crop biomass; litter biomass; relative soil moisture; light penetration. Principle components analysis (PCA) was then used to reduce the correlation matrix of productivity variables to form a composite index of productivity that could be used as an independent variable in subsequent analyses (see Results).

For examining variation in germination and recruitment from seed (seed-addition plots) and transplant performance (survival and growth in the transplant plots), the data conform to a within-subjects analysis of covariance (ANCOVA; Zar, 1974). In this analysis, each block was considered to be the subject of analysis, with two treatments (plant neighbors present, plant neighbors absent) applied to each block. The continuous productivity index derived from PCA (PCA axis 1; see Results) was included in the analysis as a covariate to examine whether the effects of neighbors on target plant performance varied along the complex productivity gradient.

Transplant survival was calculated for each block as the proportion of transplants in a treatment that survived to harvest. Seedlings that experienced heavy levels of herbivory were not included in calculations of survival and growth. Relative growth rate (RGR; Harper, 1977; Hunt, 1981) of each surviving transplant was calculated as

\[ RGR = \frac{\ln(B_t) - \ln(B_i)}{(t_f - t_i)} \]

where \( B_t \) is the transplant biomass (roots plus shoot) at harvest, \( B_i \) is the estimated transplant biomass at planting, and \( t_f - t_i \) is the time interval in days between planting and harvest. Analyses of RGR were performed on within-block mean values. Within-block averaging resulted in two mean RGR values per block: one for transplants growing in the presence of neighbors and one for transplants growing in the absence of neighbors. Mean RGR in the absence of neighbors was not calculated for one of the blocks due to 100% transplant mortality.

The intensity of plant neighbor effects on Schizachyrium performance (germination, transplant survival, transplant growth) was measured using the log response ratio (ln RR; Goldberg et al., 1999; Hedges, Olkin & Curtis, 1999). The log response ratio measures the degree to which neighboring plants suppress or facilitate target-plant performance by comparing performance in plots where neighbors have been removed to that in plots where neighbors have been left intact. Positive values indicate competition and negative values indicate facilitation. The log response ratio is calculated as

\[ \ln RR = \ln \left( \frac{P_{NR}}{P_{NI}} \right) \]

where \( P_{NR} \) is target plant performance in plots where neighbors have been removed and \( P_{NI} \) is performance in plots where neighbors have been left intact. The log response ratio is mathematically related to the relative competition intensity index (RCI = [\( P_{NR} - P_{NI} \)/\( P_{NR} \); Wilson & Keddy, 1986; Wilson & Tilman, 1991]. I use ln RR in this study because this metric has been shown to be symmetrical for competition and facilitation (Goldberg et al., 1999). The dependence of ln RR on the productivity index (PCA axis 1) was examined using regression.

All statistical analyses were performed using SPSS statistical software (version 8.0). To meet the assumptions of ANOVA, arcsine square-root transformations were applied to the germination and survival data, while Log transformations were applied to the transplant growth data.

**Results**

CHARACTERIZATION OF THE PRODUCTIVITY GRADIENT

Standing crop, litter biomass, and relative soil moisture were all significantly negatively correlated with relative elevation (Table I). In contrast, light penetration was significantly positively correlated with relative elevation. Standing crop, litter biomass, and light penetration were all significantly intercorrelated. The first principle component (PC1) derived from a PCA on the four productivity variables (standing crop, litter biomass, light penetration, and relative soil moisture) explained 70.5% of the total variance in the data and was strongly correlated with relative elevation (\( r = -0.88; P < 0.001 \)). Light penetration was negatively loaded on PC1, while standing crop, litter biomass, and relative soil moisture were all loaded positively (Table II). As a result, increasing PC1 scores can be interpreted as a gradient of increasing block productivity.

SEED ADDITION PLOTS

Germination of Schizachyrium seeds over the course of the growing season varied significantly with neighbor removal, with block productivity (PC1), and with the interaction between neighbor removal and productivity (Table III). The interaction between neighbor removal and productivity reflects a suppressive effect of plant neighbors on germination at high productivity, but a tendency towards facilitation at low productivity (Figure 1). In the presence of neighbors, germination declined significantly with increasing block productivity, while in the absence of neighbors, germination was uncorrelated with productivity (Figure 1a). Competition intensity measured using germination (ln RR, germination) increased significantly with block productivity, reflecting a

| Standing crop | Litter | Relative moisture
<table>
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<tbody>
<tr>
<td>-0.83</td>
<td>0.76</td>
<td>0.36</td>
</tr>
<tr>
<td>-0.40</td>
<td>0.76</td>
<td>-0.59</td>
</tr>
<tr>
<td>0.81</td>
<td>-0.76</td>
<td>-0.69</td>
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<td>-0.27</td>
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TABLE I. Correlation matrix (Pearson coefficients) illustrating the relationships among productivity variables and relative elevation. Coefficients in bold are statistically significant (\( P < 0.05 \)).

| Standing crop | Litter | Relative moisture
<table>
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<tbody>
<tr>
<td>0.95</td>
<td>0.81</td>
<td>0.52</td>
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<td>-0.85</td>
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TABLE II. Loadings of the four productivity variables on the first principle components axis (PC1). PC1 explained 70.5% of the variance in the data matrix.
TABLE III. Results of ANCOVA examining the effects of plant neighbors on *Schizachyrium* germination. Productivity (PC1) is analyzed as a covariate.

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>df</th>
<th>Mean square</th>
<th>F-value</th>
<th>Significance</th>
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<td><strong>WITHIN-BLOCK EFFECTS</strong></td>
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<tr>
<td>Neighbors</td>
<td>1</td>
<td>0.220</td>
<td>14.7</td>
<td>&lt;0.001</td>
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<tr>
<td>Neighbors × Productivity (PC1)</td>
<td>1</td>
<td>0.100</td>
<td>6.7</td>
<td>0.019</td>
</tr>
<tr>
<td>Error</td>
<td>18</td>
<td>0.015</td>
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<tr>
<td><strong>BETWEEN-BLOCK EFFECTS</strong></td>
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<tr>
<td>Productivity (PC1)</td>
<td>1</td>
<td>0.230</td>
<td>8.2</td>
<td>0.01</td>
</tr>
<tr>
<td>Error</td>
<td>18</td>
<td>0.028</td>
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FIGURE 1. a) Relationship between germination and productivity (PC1) in the presence of neighbors (solid circles and regression line) and absence of neighbors (open circles); b) Relationship between competition intensity on germination (In RR<sub>germination</sub>) and productivity.

shift from facilitation at low productivity to competitive suppression at high productivity (Figure 1b).

In the absence of plant neighbors, seedlings that had emerged during the growing season all died before the final census in October. As a result, ANOVA could not be used to evaluate variation in seedling recruitment (seedling density at the end of the growing season). In the final census, low densities of *Schizachyrium* seedlings were recorded in many of the vegetated plots, indicating facilitation of recruitment. Seedling recruitment in the presence of neighbors ranged from 0 to 23 seedlings per plot, but was generally greatest in low productivity blocks (negative relationship between seedling density and PC1; Figure 2).

**TRANSPLANT PLOTS**

- **Herbivory:** During the course of the growing season 41 transplants were heavily damaged by rodent herbivores and were thus excluded from calculations of survival and the analyses of growth. Heavy damage was independent of experimental treatment (18 transplants in plots with neighbors present; 23 transplants in plots with neighbors absent), as assessed using the Wilcoxon paired-samples test ($z = -1.21$, $P > 0.05$). The greatest number of transplants excluded from analysis for any given treatment in any block was three. An additional 33 transplants were lightly damaged and were included in the analysis because (1) the light damage was distributed independently of the experimental treatments (19 transplants in plots with neighbors present; 14 transplants in plots with neighbors absent; Wilcoxon test: $z = -0.97$, $P > 0.05$); and (2) damage per block was distributed independently of block productivity, as assessed using Spearman rank correlation (neighbors present: $r_s = -0.13$, $P > 0.05$; neighbors absent: $r_s = -0.10$, $P > 0.05$). Therefore, variation in plant performance associated with minor herbivory was assumed to be a component of random error rather than a function of treatment or productivity.

- **Transplant survival:** In the absence of neighbors, 56% of the transplants survived to the end of the growing season, while 88% survived in the presence of neighbors (Figure 3). Most of the transplant mortality occurred within two distinct periods during the growing season: during the first 35 days following planting (May 4 to June 7); and later in the season between day 91 (August 2) and day 120 (August 31; Figure 3). Transplant survival measured on a per-block basis varied significantly among blocks with neighbor removal, with block productivity (PC1), and with the interaction between neighbor removal and productivity (Table IV). The interaction between neighbor removal and productivity reflects a positive effect of plant neighbors on transplant survival that diminished in importance with increasing block productivity (Figure 4). In the presence of neighbors, within-block transplant survival ranged from 67 to 100% and varied independently of block productivity. In the neighbor-removal plots, transplanted survival ranged from 0 to 100% and increased significantly with productivity (Figure 4a). Competition intensity measured using survival (In RR<sub>survival</sub>) was negative (indicating facilitation) for all but three blocks and increased significantly with block productivity (Figure 4b).

- **Transplant growth:** Mean RGR varied significantly with neighbor removal (Table V; Figure 5a). However, mean RGR did not vary significantly with block producti-
TABLE IV. Results of ANCOVA examining the effects of plant neighbors on *Schizachyrium* transplant survival. Productivity (PC1) is analyzed as a covariate.

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>df</th>
<th>Mean square</th>
<th>F-value</th>
<th>Significance</th>
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<td>WITHIN-BLOCK EFFECTS</td>
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<td>Neighbors</td>
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<td>Error</td>
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<td>Productivity (PC1)</td>
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<tr>
<td>Error</td>
<td>18</td>
<td>0.076</td>
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**Figure 3.** Survivorship curves for transplants grown in the presence of neighbors (solid circles) and absence of neighbors (open circles).

**Figure 4.** a) Relationship between transplant survival and productivity (PC1) in the presence of neighbors (solid circles) and absence of neighbors (open circles and regression line). b) Relationship between competition intensity on survival (\(\ln RR_{survive}\)) and productivity.

**Figure 5.** a) Relationship between transplant growth (RGR, g g\(^{-1}\) day\(^{-1}\)) and productivity (PC1) in the presence of neighbors (solid circles) and absence of neighbors (open circles). b) Relationship between competition intensity on transplant RGR (\(\ln RR_{RGR}\)) and productivity.

**Table V.** Results of ANCOVA examining the effects of plant neighbors on *Schizachyrium* transplant growth (RGR, g g\(^{-1}\) day\(^{-1}\)). Productivity (PC1) is analyzed as a covariate.

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<tr>
<th>Source of variation</th>
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<tr>
<td>Neighbors</td>
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<tr>
<td>Error</td>
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<td>BETWEEN-BLOCK EFFECTS</td>
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<tr>
<td>Productivity (PC1)</td>
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<td>0.706</td>
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<tr>
<td>Error</td>
<td>17</td>
<td>0.421</td>
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**Discussion**

In this study, plant neighbors had contrasting effects on the performance of *Schizachyrium* that depended on the stage of the life history considered, the measure of plant performance examined, and the position of the local habitat along the complex topographic-productivity gradient. Germination of *Schizachyrium* was strongly suppressed by
plant neighbors at high productivity, but was facilitated at low productivity. Final recruitment (final seedling density in the seed addition plots) and transplant survival were facilitated by plant neighbors, primarily in unproductive sites. Despite positive effects on transplant survival, neighboring plants strongly suppressed the growth of the surviving transplants, with the magnitude of this suppression varying independently of productivity.

The role of facilitation in regulating the performance of individuals and the distribution of species along environmental gradients has received a great deal of attention in recent years (Callaway, Nadkarni & Mahall, 1991; Bertness & Callaway, 1994; Bertness & Hacker, 1994; Hacker & Gaines, 1997). Furthermore, it is clear from a number of studies that facilitative and competitive interactions can combine in complex ways to regulate plant performance and distribution in some plant communities (Bertness & Shumway, 1993; Callaway & Walker, 1997; Holmgren, Scheffer & Huston, 1997; Holzapfel & Mahall, 1999; Pugnaire & Luque, 2001). Facilitation has been found to occur most frequently in harsh environments where habitat amelioration by resident organisms can be particularly important in regulating the recruitment of other species (Archer et al., 1988; Fowler, 1988; Bertness & Callaway, 1994; Greenlee & Callaway, 1996). I interpret the results of the current study as being consistent with this generalization, showing that positive effects of neighbors on germination, final recruitment from seed, and transplant survival were most prevalent in unproductive upland ridges, presumably due to a greater potential for neighbor-amelioration of water stress in those sites. Although total rainfall was near normal during the year of this study, the growing season was punctuated with several extremely hot and dry periods. Moisture stress experienced by germinated seedlings and established transplants in the absence of neighbors may have been most pronounced during dry periods on the unproductive and xeric upland ridges. That neighbor amelioration of water stress could be a mechanism of facilitation in this study is supported by a separate neighbor-removal experiment conducted nearby in the same year showing that grass neighbors within low-productivity sites facilitated the survival of first-year elm seedlings in unirrigated plots, but not in irrigated plots (Foster & Ross, unpubl. data).

The strong competitive effect of neighbors on transplant growth in this study appears to contradict the results obtained for transplant survival. How can plant neighbors inhibit growth, while at the same time facilitating survival? On the surface it seems logical that if water stress induces higher rates of plant mortality in the absence of neighbors, such a stress would also manifest itself as reduced growth among the surviving transplants in the absence of neighbors. It is possible that transplant growth in this study was temporarily facilitated by neighbors during hot and dry periods of the growing season when water stress was most intense and when many of the transplants died. However, the measure of relative growth obtained in this study for surviving individuals was integrated across unfavorable and favorable periods and reflects the balance of competition and facilitation experienced over the entire growing season. The presence of net competitive effects on transplant growth in this experiment necessarily means that any periods of stress conducive to facilitation of growth would have been exceeded by benign conditions conducive to neighbor inhibition. The facilitation of survival observed in this study, then, likely reflects the inability of susceptible individuals growing in the absence of neighbors to survive relatively discrete periods of intense water stress (1-3 weeks), thus preventing them from taking advantage of the prevailing benign conditions.

Although this study was not designed to assess the impacts of animals on the target species, it is clear that herbivory must play a large role in regulating plant performance at the study site. Of the 320 Schizachyrium seedlings planted, 23% suffered some measure of herbivory, and a number of the more heavily damaged transplants died as a result. Although I found no detectable tendency of herbivory to vary with treatment or as a function of productivity, it appears likely that herbivory is an important constraint on Schizachyrium establishment in this grassland. Further experimentation is needed to test the relative impact of herbivory and competition on plant establishment and growth along environmental gradients.

**COMPETITION INTENSITY AND PRODUCTIVITY**

The hypothesis that competition intensity increases with productivity (Grime, 1979; Huston, 1979; Keddy, 1989) was only partially supported by this study. The intensity of competition on germination increased strongly with productivity, suggesting that resident plant neighbors pose a strong resistance to initial seedling emergence in the most productive microsites. The results for germination should be viewed with some caution. As discussed in the methods section, I cannot completely rule out the possibility that effective seedling rates were slightly greater in the no-neighbor plots at the beginning of the experiment because of methodological problems. However, even if initial seedling rates differed between the treatments, the interpretation that plant neighbors suppressed germination in the highest-productivity plots would remain robust. This is because the seedlings present in the vegetated plots throughout the experiment (pers. observ.), there was virtually no germination from among these seeds in the highest-productivity blocks. Because measurable numbers of seeds germinated in the absence of neighbors in the high-productivity blocks, it is reasonable to conclude that germination failure at high productivity in the vegetated plots was the result of competitive suppression or some other indirect impact of vegetation. Despite these effects on germination, none of the seeds that germinated in the absence of neighbors produced seedlings that survived to the final census, resulting in a net facilitative effect of neighbors on seedling recruitment that was most pronounced in low-productivity sites.

Many experimental studies testing the relationship between competition intensity and productivity have focused on the growth responses of target transplants to surrounding plant neighbors (Gurevitch, 1986; Wilson & Shay, 1990; Wilson & Tilman, 1991; Bonsor & Reader, 1995; Twolan-Strutt & Keddy, 1996; Peltzer, Wilson & Garry, 1998; Foster, 1999). Results from these studies are conflicting and provide little consensus except that transplant experiments conducted on natural productivity gradients do tend to show a positive relationship between competition...
intensity for growth and productivity more often than experiments conducted on fertilization gradients (Goldberg & Barton, 1992). The results of the current study do not fit this tendency. Here, effects of neighbors on transplant growth along a broad natural gradient were strongly inhibitive, but uncorrelated with productivity. One possible reason for this is that in this study, unlike many natural productivity gradients, dominant-species composition and growth form did not vary substantially from low to high productivity. Most plots were dominated by hay grasses (Bromus inermis and Festuca arundinacea) that were likely planted uniformly across the site years earlier. It has been suggested that effects of turnover in dominant-species composition, rather than direct effects of productivity, might explain positive correlations between competition intensity and productivity where they occur (Goldberg & Barton, 1992; Peltzer, Wilson & Gerry, 1998; Foster, 1999). In support of this possibility, DiTommaso and Aarssen (1991) and Peltzer, Wilson and Gerry (1998) found that competition intensity in grasses did not vary with productivity along experimental fertility gradients where species composition was held constant. The current study, which found no relationship between competition intensity for transplant growth and productivity, is complementary to the studies of DiTommaso and Aarssen (1991) and Peltzer, Wilson and Gerry (1998) because it provides a rare example of a substantial gradient in productivity within natural or semi-natural vegetation that is accompanied by little change in the identity of dominant species of growth form.

Implications for the distribution of Schizachyrium

What do the results of this study indicate, if anything, about the processes regulating the re-colonization potential and distribution of Schizachyrium along gradients of productivity in this successional grassland? Although single-year competition experiments are limited in scope, the results do suggest that processes occurring during the initial establishment phases of the life history (germination and initial seedling establishment) are perhaps more critical than at later stages (growth and survival of established seedlings). Results from the seed-addition portion of this study suggest that the probability of successful recruitment from seed in the presence of plant neighbors, although generally low, is likely to be greatest in relatively low-productivity sites because of facilitation in unproductive sites and a limited potential to germinate in high productivity sites. Studies in Michigan grassland have also shown that initial seedling recruitment of Schizachyrum and other native C_4 grasses tends to be greatest within low-productivity habitats and that productive habitats are highly resistant to recruitment (Foster & Gross, 1997; Foster, 1999). Mechanisms of resistance in the Michigan studies appear to be intense competition for light and inhibition of seedling recruitment by abundant litter in productive locations. In this study, the lack of Schizachyrum recruitment from seed in the presence of neighbors within the highest productivity blocks cannot be attributed to competition because there was no recruitment observed at all in the absence of neighbors. In the year of this study at least, sites of high potential productivity were apparently inhospitable to recruitment by seed both in the presence and absence of neighbors. The lack of recruitment from seed in the absence of neighbors was likely due to the desiccation of the sensitive seedlings during the hottest and driest periods. Although numerous seeds germinated within many of the no-neighbor plots, particularly after rainfall events (pers. observ.), none of the resulting seedlings survived to the end of the growing season. These results indicate that facilitation of seedling recruitment likely plays a particularly important role in determining the re-colonization potential and thus the spatial distribution of Schizachyrium along gradients of productivity in successional grassland. Unlike germination and recruitment from seed, the growth of established transplants in the presence of neighbors did not change with productivity in this study, and the effects of competition on transplant growth, although strong, were just as intense at low productivity as at high productivity. Although transplant survival was facilitated by neighbors at low productivity, survival did not vary with productivity in the presence of neighbors. This suggests that the probability of survival past the initial recruitment stages may be relatively constant across this gradient. The findings of this study are consistent with the view that events occurring during the earliest establishment phases of the life history (germination, emergence, seedling recruitment) are of primary importance in regulating species distribution along environmental gradients (Grubb, 1977; Gross & Werner, 1982; Foster, 1999). Another generalization that may be made by this study is that the magnitude and sign of plant-plant interactions for some aspects of plant performance may change dramatically over relatively short distances within communities and along local environmental gradients.

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Literature cited


