Variation in Plant Responses to Neighbors at Local and Regional Scales

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ABSTRACT: Differences in the responses of plant species to neighbors may determine their distribution among contrasting environments, but no studies have compared variation in competitive or facilitative abilities both within and among environments. We determined whether the responses of plants to interspecific interactions varied at large scales (between environments) and small scales (among sites within an environment) across a tree line. We separated the effects of above- and belowground interactions on seedlings of grasses and trees grown in prairie or forest using vegetation removals at several sites. Species interactions generally had no significant effect on transplant survival. Competition reduced seedling growth by about 33%-89% in both prairie and forest environments. Despite the strong suppression of growth by neighbors, environment and species effects contributed more to variation in transplant performance than did neighbor removals. Responses to neighbors varied among transplant species but generally did not vary significantly between environments or among sites. With vegetation removed, grasses grew significantly faster in prairie and trees grew faster in forest. Thus, in the absence of neighbors, species showed distinct preferences for the environment in which they are most abundant. In summary, the responses of grasses and woody species to neighbors did not vary significantly at either large (between environments) or small (among sites) scales. These results suggest that species responses to interspecific interactions do not vary strongly with environment or smaller-scale site effects.

Keywords: competition, competitive hierarchy, facilitation, forest, grassland, interspecific interactions.

Differences in plant responses to neighbors may influence the distribution and abundance of species along environmental gradients (Walter 1985; Rosenzweig and Abramsky

1986; Wilson and Keddy 1986; Tilman 1988; Keddy and Shipley 1989; Keddy 1990). The ability of a plant to withstand suppression by neighbors (i.e., competitive response, sensu Goldberg 1990), often varies among species (Goldberg 1996). Relatively few studies have tested for changes in the responses of species to interspecific interactions in different environments (Goldberg 1996). Like most phenotypic traits, competitive or facilitative ability probably depends on environmental conditions such as resource availability (e.g., Gulmon 1979; Eagles et al. 1982; Fowler 1982; Tilman 1984; Rice and Menke 1985; Wilson and Tilman 1995; Goldberg 1996; Greenlee and Callaway 1996; Li and Wilson 1998). Most evidence for variation in competitive response ability among environments comes from correlating patterns of species abundance in the field with species position in experimental competitive hierarchies (Connolly 1986, 1997; Keddy and Shipley 1989; Herben and Krahulec 1990; Silvertown and Dale 1991; Shipley and Keddy 1994).

Studies that have examined variation in plant responses to neighbors between environments have found that competitive responses do not vary predictably with species position in successional seres (Gerry and Wilson 1995; Wilson 1999) or with species abundance or distribution along experimental gradients of fertility and disturbance (Wilson and Tilman 1995). One reason for the weak relationship between a species distribution and its response to neighbors might be that variation in plant interactions caused by smallscale environmental heterogeneity are just as great as variation caused by differences among environments (Fowler 1990). Consistent with this idea, several field experiments have shown that small-scale (within-environment) variability in plant performance may be equal to or greater than variation among environments (e.g., Fowler 1988; Platenkamp 1991; Bell and Lechowicz 1994; Miller et al. 1995). Additionally, many models of species coexistence assume that the performance of individuals is controlled by smallscale species interactions or environmental fluctuations (Pacala 1987; Chesson 1994; Pacala and Deutschman 1995; Pacala and Levin 1997). Here, we consider "large spatial scale" to be between units of vegetation (e.g., prairie and

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forest) and "small spatial scale" to be within a unit of vegetation (e.g., sites within a forest stand; see also discussion by Underwood and Petraitis 1993; Underwood 1997). The relative importance of small- and large-scale variation in plant responses to neighbors is unknown.

At small spatial scales (i.e., among sites within a stand), plant interactions often shift from below- to aboveground with increasing community biomass, for example, along experimental fertility gradients in old fields (e.g., Wilson and Tilman 1993, 1995) and between adjacent patches of grassland and woody vegetation (e.g., Wilson 1993*a*, 1993*b*). Shifts in interactions may also occur at large spatial scales, for example, between environments, but we know of no tests of this prediction.

In this study, we asked whether the responses of grasses and trees to neighbors varied within or between prairie and forest environments. Specifically, we hypothesized that the ranking of responses for grasses and trees would be reversed between prairie and forest environments (i.e., that each plant growth form is a better response competitor in its "home" environment). We posed several questions to examine differences in plant responses to neighbors at large and small spatial scales: Does the performance of grasses and trees differ at the large scale (between environments) and at the small scale (among sites within an environment)? Here, we measure performance as transplant survival, growth, and the intensity of interspecific interactions. Do interactions among plants shift with increasing productivity at the large scale from neighbor roots in prairie to shoots in forest, as found in experiments at smaller scales?

Our experimental design also allowed us to determine the importance of neighbor effects on plant performance relative to large- and small-scale environmental effects. The distinction between the intensity (i.e., extent of suppression or facilitation by neighbors) and importance (i.e., relative contribution to variation in performance) of neighbors was made over a decade ago (Welden and Slauson 1986) but is usually not distinguished when comparing ecological processes among sites (Underwood and Petraitis 1993; Underwood 1997). Thus, we also asked, Is variation in the performance of different species controlled more by interspecific interactions than by environment or site?

Methods

Study Areas

We worked in mixed-grass prairie and boreal forest in Saskatchewan, Canada. The prairie (49°38'N, 104°11'W) was dominated by the grasses *Bouteloua gracilis*, *Carex* spp., *Agropyron* spp., and *Stipa comata*. The forest, about 450 km further north, was located at the southern edge of the

boreal forest (53°13'N, 105°41'W) and was dominated by *Populus tremuloides, Picea glauca*, and *Pinus banksiana*. Mean annual precipitation for prairie and forest study areas during 1958–1994 was 406 and 412 mm, respectively. Mean daily temperatures for prairie and forest sites, respectively, were 27.0° and 24.2°C in July and -10.6° and -13.7° C in January (Environment Canada 1993).

Experimental Design

We used a split-split plot experimental design with two environments (prairie and forest), five sites in each environment, three neighborhood treatment plots per site, three watering treatment subplots within each neighborhood plot, and four transplanted species in each neighborhood × watering treatment combination, for a total of 72 treatment combinations. Within sites, neighborhood × watering treatment combinations were replicated six times for each transplanted species (i.e., six plants per species in each subplot), giving a total of 2,160 transplants. Environment × site × neighborhood combinations formed main plots, the watering level was the split plot factor, and species was the split-split plot factor.

Five sites, each separated by at least 150 m, were located in both prairie and forest. Replication of the experiment at several sites in both prairie and forest allowed us to examine variation in neighbor effects among sites within an environment. Three neighborhood plots (10 m \times 20 m) were located within each site and were assigned to one of three neighborhood treatments. Neighborhood plots were divided into three watering treatment subplots, each randomly assigned to one of three watering treatments. Six replicate seedlings of four transplant species, two grasses and two trees, were randomly assigned to subsubplots within each watering subplot.

Experimental Treatments

Three neighborhood treatments were used to separate the above- and belowground effects of neighbors. The first treatment was "no neighbors" (NN). Roots of neighbors were excluded by inserting a plastic root exclusion tube (10 cm internal diameter, 15 cm deep) vertically into the soil until the top edge of the tube was flush with the soil surface. Neighbors rooted inside tubes were killed using the nonselective herbicide glyphosate (Roundup, Monsanto, St. Louis) 10 or more days before planting. Neighbor shoot regrowth inside tubes was removed by hand every 10 d, and shoots outside tubes were clipped monthly to eliminate shading. In forest, NN plots were located in recent clear-cuts (<2 yr old). Other competition treatments were located in undisturbed forest nearby (<50 m). In prairie, NN treatments were randomly assigned to entire

plots. The second treatment was "shoots of neighbors" (SN). This treatment is similar to the NN treatment except that neighbor shoots surrounding the tube were not clipped but allowed to grow over the tube. The third treatment was "all neighbors" (AN). Tubes were inserted and remained in the soil. Because of the size of neighbors (i.e., individual trees) in forest, no neighboring individuals were enclosed within tubes, so tubes were removed before planting to allow for tree root growth into the soil surrounding transplants.

Three watering treatments were used to simulate differences in precipitation among years. Watering levels corresponded to high, average, and low monthly precipitation amounts for Regina, Saskatchewan, which is situated between the prairie and forest study areas. Weather data for the previous 36 yr (1958-1994; Environment Canada 1996) were used to calculate mean monthly precipitation for all years (average treatment), the five wettest years (high treatment), and the five driest years (low treatment). Water was added to subplots every 10 d. Total water addition was equivalent to the mean monthly precipitation (total water addition for May-September: low = 137.0 mm, average = 260.4 mm, high = 390.1 mm). Natural precipitation to all transplants was eliminated using shelters made from transparent acrylic sheets (25 cm × 25 cm, 97% transmittance of photosynthetically active radiation). One sheet was fixed horizontally to a stake over each transplant at a height of 15 cm. Shelters did not significantly increase soil surface temperature in tubes (D. Peltzer, unpublished data).

Transplants

We measured the responses to neighbors of two grasses, Agropyron cristatum and B. gracilis, and two trees, P. glauca and P. banksiana. Hereafter, we refer to species by genus (nomenclature follows Looman and Best 1987). Bouteloua is a drought-tolerant perennial C_4 bunchgrass commonly found in mixed-grass prairie. Agropyron is a widely naturalized perennial C_3 bunchgrass. Picea is a shade-tolerant conifer found throughout the boreal forest on mesic sites. Pinus is a drought-resistant conifer found on sandy soils.

Seeds were obtained commercially (grasses: Enviroscapes, Lethbridge; trees: Saskatchewan Environment and Resource Management, Prince Albert, Saskatchewan) and planted into pots (2.5 cm diameter, 12 cm deep) containing a mixture of 6 : 1 : 1 peat : prairie : forest soils. Seedlings were thinned to one individual per pot after germination, watered to field capacity daily, and grown without supplemental light or fertilizer.

Seedlings were stored outside for 10 d during late May 1995 in preparation for planting during early June. Before planting, species were assigned randomly to tubes within watering subplots. One seedling was planted in the center of each tube during May 28–June 2. To facilitate establishment, all transplants were shaded for 2 wk using opaque plastic sheets (20 cm wide \times 40 cm tall). Grazed, damaged, or dead transplants were replaced for up to 3 wk after planting. The shoots (live and dead tissue) of all living transplants were harvested during September 15–23. Transplant roots, soil, and tubes were frozen within 3 d of harvest. Transplant roots were later washed from soil manually using a 1-mm screen. Shoots and roots were dried (70°C, 3 d) and weighed to the nearest milligram.

Growth Rates and Interaction Intensity

Transplant growth was calculated as relative growth rate (RGR) to allow for meaningful comparisons among species because plant size varied widely among taxa. Allometric relationships between initial size and biomass for all species were determined from 30 seedlings. Seedlings for allometric equations were sampled from the pool of transplants during planting and represented the range of initial transplant sizes. Size was measured as total tiller length (TTL) for grasses, height from root collar to base of apical meristem (HT) for *Picea*, and diameter of root collar (basal diameter [BD]) for Pinus at the time of planting. The allometric equations are as follows-Agropyron: total mass (g) = $(0.000859 \times \text{TTL} \text{ [mm]} (0.001745)^2$, $r^2 = 0.91$, P < .001; Bouteloua: total mass = $(0.000796 \times \text{TTL} \text{ [mm]} + 0.0457971)^2$, r^2 = 0.98, P < .001; *Picea*: total mass = 0.001794 × HT (mm) - 0.034808, $r^2 = 0.76$, P < .001; *Pinus*: total mass = $0.301385 \times BD$ (mm) - 0.14994, $r^2 = 0.87$, P < .001. Allometric equations were developed using different measurements for trees to produce the best predictive relationship (highest r^2).

Relative growth rate was calculated with the initial mass (M_i) , the final mass (M_i) , and the time interval in days (t) between biomass measurements for all harvested transplants as RGR = $(\ln M_f - \ln M_i)/t$. Only transplants that survived until the end of the growing season were included in these calculations; survivorship was examined separately.

We calculated the intensity of interspecific interactions (II) as the relative increase or reduction of transplant growth caused by neighbors. Total interaction intensity was calculated for each subplot as $II_t = (RGR_{NN} - RGR_{AN})/RGR_{NN}$, where II_t is an index of total interaction intensity, RGR_{NN} is the mean RGR of transplants in the NN treatment, and RGR_{AN} is the mean RGR for the AN treatment within a site. Similarly, shoot II (II_s) and root II (II_r) were calculated as $II_s = (RGR_r - RGR_{SN})/RGR_{NN}$, and $II_r = (RGR_{SN} - RGR_{AN})/RGR_{NN}$, where RGR_{SN} is the

mean RGR of transplants in the SN competition treatment. Before calculations of II, a constant value was added to all RGRs for all species such that the lowest RGR was 0 (i.e., the lower limit of plant performance was set to 0). Standardizing RGR in this manner eliminated spurious large positive values of II caused by negative growth.

Resource Availability

Light penetration, soil moisture, and soil available N were measured in June and August at one station in each watering subplot (n = 3 per neighborhood plot). Light penetration was measured as the proportion of incident light above the vegetation (or 50 m outside the forest canopy) that reached the substrate surface, measured using a 1×10 -cm integrating light probe (Sunfleck ceptometer, Decagon Devices, Pullman, Wash.).

Nitrogen and soil moisture were sampled in June and August in one root exclusion tube per watering treatment subplot. Three soil cores (1.9 cm diameter, 15 cm deep) were collected within each tube, pooled, and subsampled for N and water analyses. For soil available N, 10-g soil subsamples were immediately extracted in 50 mL of 0.02 M KCl and allowed to settle, and the supernatant was frozen. Total available nitrogen (sum of NO_3^- and NH_4^+) was later analyzed using an ion-selective electrode (Orion model 95-12, Boston). Soil moisture was determined gravimetrically by drying fresh soil subsamples (10 g, 70°C, 3 d) and calculating percentage of soil moisture as mass loss (water) per unit of dry soil.

Data Analysis

Transplant survivorship at the end of the experiment was tested among treatments and their interactions with likelihood ratio χ^2 tests using logistic regression (SAS Institute 1997). Differences in transplant growth rates among environments, neighborhood treatments, watering treatments, and species were examined with ANOVA. Environment × neighborhood treatment combinations formed main plots, watering treatment was the split plot factor, and species was the split-split plot factor. Environment, neighborhood treatment, watering level, and species were treated as fixed effects. Site was treated as a nested, random factor within environment. Log transformations before analyses improved the normality and homoscedasticity of the data (Zar 1984). After significant interactions in ANOVA, means were contrasted using Tukey's HSD tests. A significant interaction among environment, species, and neighborhood would suggest that neighbors affect

the performance of species differently at the large scale (between prairie and forest). A significant interaction among site, species, and neighborhood would suggest that the effects of neighbors varies at the small scale (among sites within an environment).

Watering treatments were pooled for all analyses because no significant watering treatment effects or interactions were detected for either survivorship or growth (P > .25; Wine 1964). With the watering treatment pooled, there were 18 replicate transplants for each treatment combination.

Total, root, and shoot interaction intensities were compared among environments, sites, and species using split plot ANOVA. This analysis was similar to the analysis of growth but excluded neighborhood treatment and its interactions. As for previous analyses, we also pooled watering treatments for this analysis. A significant interaction between species and environment would suggest that species responses to neighbors differ at the large scale (between forest and prairie environments). A significant interaction between species and site would suggest that species responses to neighbors differ at the small scale (among sites within environments).

Because most hypotheses of interest involve two- and three-way interactions among experimental treatments, retrospective statistical power analyses for ANOVAs of growth and interaction intensity were conducted. Power analyses revealed that our experimental design was not prone to Type II errors even for three-way interactions involving environment, neighborhood, and species (i.e., adjusted power was >0.80 in all instances).

The relative importance of all factors and their interactions was examined using the effect size for that factor or interaction (effect size $[\eta^2] = SS$ factor/[SS factor + SS residual]; Cohen 1978; e.g., Weiner et al. 1997). Effect size is a useful measure of the proportion of the variance in the dependent variable explained by a single independent variable in mixed-model ANOVAs. As for many other commonly used metrics (e.g., r^2), the null expectation is that η^2 is proportional to the degrees of freedom associated with different factors in ANOVA and should not be directly compared among terms in ANOVA. After taking this into account, comparing η^2 between treatments allows us to determine the overall importance of species responses to environment, site, and neighborhood.

Consistency in the rank order of species responses to neighbors were tested between environments and among sites within an environment using Kendall's coefficient of concordance (*W*; Statistica version 4.1, Statsoft 1994). Resource availability was analyzed using split plot ANOVA after appropriate transformations of the data (light, arcsin–square root; water, square root; nitrogen, log), similar to the analysis of interaction intensity.

Results

Survivorship

Survivorship was significantly lower in prairie than in forest (fig. 1; table 1). *Bouteloua* had almost 100% survivorship in both prairie and forest, much higher than all other transplant species. Other species had 30%–50% survivorship in prairie and about 70% survivorship in forest (fig. 1), resulting in a significant species effect and species × environment interaction (table 1). Neighbors did not affect transplant survival in either prairie or forest (table 1, neigh-



Figure 1: Survivorship $(\overline{X} + 1 \text{ SD}, n = 90)$ of the grasses *Bouteloua* (*Bou*) and *Agropyron* (*Agr*) and trees *Picea* (*Pic*) and *Pinus* (*Pin*). Transplants were grown without neighbors (*open bars*), with shoots of neighbors (*hatched bars*), or with neighbors intact (*filled bars*) in both prairie and forest. Means are calculated across sites. Lowercase letters represent significant differences between pairs of neighbor treatments. Survival was lower in prairie ($\chi^2 = 69.88$, df = 1, P < .001). Neighbors did not influence survival in either prairie or forest (neighborhood: $\chi^2 = 0.07$, df = 2, P = .993; environment × neighborhood: $\chi^2 = 1.86$, df = 2, P = .394).

Table 1: Likelihood ratios (L-R) and $P > \chi^2$ for the influence of environment (E), sites within environment (S[E]), neighborhood (N), and species (Sp) on transplant survivorship (figs. 1, 2)

Source	df	L-R χ^{2a}	$P > \chi^2$
E	1	69.88	.000
S[E]	8	73.12	.000
Ν	2	.07	.993
E × N	2	1.86	.394
$N \times S[E]$	8	36.24	.000
Sp	3	346.70	.000
Sp × E	3	96.66	.000
Sp × N	6	23.95	.001
$Sp \times E \times N$	6	18.01	.006
$Sp \times S[E]$	12	26.17	.010
$Sp \times N \times S[E]$	24	28.82	.227
Full model negative			
log likelihood		1,070.57	

^a Likelihood ratio tests are calculated as twice the difference of the log likelihoods between the full model and the model without the tested effect(s) present.

borhood and environment \times neighborhood effects not significant).

Transplant species had different responses to neighbors. Survivorship varied significantly with the interaction between species and neighborhood (table 1). Neighbors decreased the survivorship of *Pinus* in prairie (fig. 1, means contrasts: AN < SN = NN) and increased the survivorship of *Agropyron* in forest (fig. 1, means contrasts: AN =SN > NN) but did not affect the survival of *Bouteloua* or *Picea*. This produced a significant three-way interaction among species, environment, and neighborhood (table 1). Significant small-scale variation in survival (table 1, significant site effect) was due to low survivorship at one forest site (fig. 2, site 1 in the SN treatment).

Survivorship of *Agropyron* varied more among sites than did the survival of other species (fig. 2; table 1, significant species × site interaction). For example, when grown with all neighbors in prairie, average survivorship of *Agropyron* was about 75% at site 1 but only about 20% at site 2 (fig. 2, *top right*). No interaction among species, competition, and site was detected, suggesting that the effects of neighbors on survival did not vary significantly among species at the small scale (table 1).

Because survival varied strongly among species, potentially obscuring the main effects of environment, neighborhood, and site, we used separate logistic regression analyses to determine whether the survival of individual species varied with main effects. Results from these analyses were generally similar to that presented above with three exceptions. First, neighbors significantly increased the survivorship of *Agropyron* and *Picea* (lo-



Figure 2: Survivorship (mean within sites, n = 18) of the grasses *Agropyron* and *Bouteloua* and trees *Picea* and *Pinus*. Transplants were grown without neighbors, with shoots of neighbors, or with neighbors intact in both prairie and forest. Survival varied among sites ($\chi^2 = 73.12$, df = 8, P < .001) as a result of variation in the effects of neighbors and differences among species (neighborhood × site: $\chi^2 = 36.24$, df = 8, P < .001; species × site: $\chi^2 = 26.17$, df = 12, P = .010).

gistic regression: neighborhood effect, *Agropyron*; likelihood ratio [L-R] $\chi^2 = 8.41$, df = 2, P = .015; *Picea*: L-R $\chi^2 = 33.39$, df = 2, P < .001). Second, the effects of neighbors on survivorship varied between environments but only for *Pinus* (environment × neighborhood: L-R $\chi^2 = 17.99$, df = 2, P < .001). Third, neighbors affected survival differently among sites for *Bouteloua* and *Agropyron* but not for *Picea* or *Pinus* (neighborhood × site: *Bouteloua*: L-R $\chi^2 = 21.29$, df = 8, P = .006; *Agropyron*: L-R $\chi^2 = 18.71$, df = 8, P < .017; *Picea*: L-R $\chi^2 = 10.22$, df = 8, P = .250; *Pinus*: L-R $\chi^2 = 8.88$, df = 8, P = .353; see fig. 2).

Growth

Growth was significantly higher in prairie than in forest. This was caused by higher growth rates of grasses in prairie (fig. 3; table 2).

Neighbors strongly suppressed transplant growth (table 2). Growth was reduced mostly by neighbor roots in prairie

(fig. 3, relative suppression of growth in SN vs. AN neighborhoods) and by neighbor shoots in forest (fig. 3, NN vs. SN). However, the overall effects of neighbors did not vary between environments (fig. 3; table 2, neighborhood \times environment interaction not significant). Thus, the negative effects of neighbors on growth did not vary significantly at the large scale.

Grasses grew faster in prairie than in forest (fig. 3, *Bou* and *Agr*), but trees grew equally well in both environments (fig. 3, *Pic* and *Pin*), averaged across all other treatments. This resulted in a significant interaction between species and environment (table 2).

Competition reduced growth differently among species (table 2, significant interaction between species and neighborhood). Competition caused the greatest reduction in growth for *Bouteloua* but much smaller reductions in growth for trees (fig. 3). No significant interaction among species, environment, and neighborhood was observed (table 2), suggesting that species did not respond differently to neighbors between environments.



Figure 3: Growth $(\overline{X} + 1 \text{ SD}, n = 90)$ of the grasses *Bouteloua (Bou)* and *Agropyron (Agr)* and trees *Picea (Pic)* and *Pinus (Pin)*. Transplants were grown without neighbors (*open bars*), with shoots of neighbors (*hatched bars*), or with neighbors intact (*filled bars*) in either prairie or forest. Means are calculated across sites. Growth was lower in forest (environment: F = 10.46, df = 1, 4, P = .032) and in the presence of neighbors (neighborhood: F = 30.25, df = 2, 8, P < .001), but the effects of neighbors on growth did not vary between environments (environment × neighborhood: F = 3.97, df = 2, 8, P = .063).

Grasses grew fastest in prairie than in forest, and trees grew fastest in forest than in grassland but only in the absence of neighbors (fig. 3, contrast of growth vs. environment in NN treatments only—grasses: t = 10.04, df = 1,251, P < .001, growth faster in prairie; trees: t =3.59, df = 1,164, P < .001, growth faster in forest). In other words, trees and grasses had distinct preferences for forest and prairie environments, respectively.

Growth also varied significantly among sites; this was caused by variation among sites in prairie (fig. 4; table 2, significant site effect). In contrast, the effects of neighbors on growth did not vary among sites (fig. 3; table 2, neighborhood \times site interaction not significant); thus, the effects of neighbors on transplant growth did not vary significantly at the small scale.

Tree growth was more variable among sites than was the growth of grasses (fig. 4; table 2, significant species \times site interaction, e.g., AN treatment in prairie). The lack of a significant three-way interaction among species, site, and neighborhood suggests that neighbors did not suppress species differently among sites (fig. 4; table 2). Thus, there was no evidence for variation in responses to neighbors among species within an environment.

The greatest variation in growth rates was caused by differences among species (table 2, relatively large values of η^2 for species and interactions involving species). In order to test the hypothesis that plant responses to neighbors varied at large and small scales and to control for large differences in growth among species obscuring the effects of environment and site, we conducted separate ANOVAs on each species. The interactions of greatest interest for this analysis were between neighborhood and environment (large-scale differences in the effects of neighborhood and site (small-scale differences in the effects of neighborhood and site (small-scale differences in the effects of neighborhood).

The effects of neighbors differed between environments for *Bouteloua* and *Pinus* but not for *Agropyron* or *Picea* (table 3); this result was caused by *Bouteloua* and *Pinus* experiencing stronger shoot competition in forest than in prairie (fig. 3, differences between NN and SN = effects of shoot competition). No significant neighborhood × site interactions were observed, suggesting that the effects of neighbors did not vary at the small scale for any species (table 3). Thus, separate species analyses show that the effects of neighbors varied at the large scale only in some cases (i.e.,

Table 2: ANOVA results for the influence of environment (E), site within environment (S[E]), neighborhood (N), and species (Sp) on the growth of four transplant species (figs. 3, 4)

4)			
Source	df	F	η^2
E	1	10.46*	.096
S[E]	4	11.88***	.038
Ν	2	30.25***	.074
Ε×Ν	2	3.97	.013
$N \times S[E]$	8	1.50	.011
Sp	3	405.37***	.486
Sp × E	3	93.17***	.176
Sp × N	6	13.81***	.063
$Sp \times E \times N$	6	2.51	.013
$Sp \times S[E]$	12	4.41***	.038
$Sp \times N \times S[E]$	24	.94	.003
Residual error	1,212		

Note: Effect sizes (η^2) indicate the relative importance of a factor.

* P < .05.

*** P < .001.



Figure 4: Growth of the grasses Agropyron and Bouteloua and trees Picea and Pinus. Transplants were grown without neighbors, with shoots of neighbors, or with neighbors intact in either prairie or forest. Data represent mean growth rates within competition plots (n = 18). Growth varied significantly among sites (F = 11.88, df = 4, 1,212, P < .001) as a result of differences among species and not competition (neighborhood × site: F = 1.50, df = 8, 1,212, P = .150; species × site: F = 4.41, df = 12, 24, P < .001).

shoot interactions for *Bouteloua* and *Pinus*) and did not vary at the small scale in any case.

Total Interaction Intensity

Total interaction intensity (II) was similar between prairie and forest (fig. 5, split plot ANOVA: main effect of environment: F = 0.45, df = 1, 4, P = .539, $\eta^2 = 0.005$). The relatively low effect size (η^2) for environment indicates that differences in plant responses to neighbors at the large scale contributed little to variation in total interaction intensity.

Total II varied significantly among transplant species (fig. 5, species effect: F = 3.61, df = 3,70, P = .017, $\eta^2 = 0.115$). Similar to results for growth, species contributed most to variation in interaction intensity (highest value of η^2). Thus, species differed in their responses to neighbors, but environment did not significantly alter the relative responses of species.

Total II was similar among sites (fig. 6, site effect:

F = 2.26, df = 4, 70, P = .067, $\eta^2 = 0.044$). The relative low effect size (η^2) for site indicates that small-scale variation in plant interactions contributed little to variation in total interaction intensity.

Responses to neighbors varied among species at the small scale, resulting in a significant interaction between species and site (F = 2.40, df = 12, 70, P = .012, $\eta^2 = 0.126$). At one site in prairie, one species (*Pinus*) was facilitated by neighbors, producing the significant species × site effect for II. When this case was removed from the analysis, there was no significant interaction (species × site interaction: F = 1.07, df = 12, 61, P = .404, $\eta^2 = 0.006$), suggesting that small-scale variation in plant interactions may not be a general phenomenon in prairie but was driven by one species at one site.

Root and Shoot Interactions

Results for root II were similar to those for total II in all instances, but results for shoot II differed from those for

Table 3: ANOVA results for the influence of environment (E), site within environment (S[E]), and neighborhood (N) on the growth of each of four transplant species (figs. 3, 4)

Source	df	F	η^2
Bouteloua:			
Е	1	92.13***	.611
S[E]	4	3.43*	.138
Ν	2	173.09***	.439
Ε×Ν	2	13.59***	.039
$N \times S[E]$	8	1.48	.041
Error	444		
Agropyron:			
E	1	48.04***	.302
S[E]	4	2.64^{+}	.071
Ν	2	24.68***	.152
Ε×Ν	2	.48	.003
$N \times S[E]$	8	1.16	.063
Error	289		
Picea:			
E	1	.24	.611
S[E]	4	6.87***	.197
Ν	2	1.25	.015
Ε×Ν	2	1.57	.014
$N \times S[E]$	8	1.22	.063
Error	226		
Pinus:			
E	1	.26	.008
S[E]	4	12.16***	.252
Ν	2	2.56^{+}	.018
Ε×Ν	2	6.34**	.042
$N \times S[E]$	8	1.46	.074
Error	308		
Note: Effect siz	tes (η^2) is tor.	ndicate the relat	ive im-

 $^{\dagger} P < .10.$

* P < .05.

** P < .01.

*** P < .001.

total II in two instances. First, shoot II was significantly higher in forest than in prairie (environment effect: F = 8.13, df = 1, 4, P = .046, $\eta^2 = 0.126$; fig. 5). Second, species differed in their response to shoot interactions between environments (species × environment: F =7.29, df = 3, 70, P = .003, $\eta^2 = 0.076$). This was caused by facilitation of *Agropyron* and *Pinus* by neighbor shoots in prairie (fig. 5).

The rankings of species responses to neighbors were concordant between environments for total, root, and shoot interactions (fig. 5, W). Similarly, the rankings were similar among sites in forest (fig. 6). Rankings were not significantly concordant in prairie (.05 < P < .10; fig. 6), this was caused by facilitation of *Pinus* at site 3. In sum-

mary, the rankings of species responses to competition generally did not vary between environments or among sites.

Resource Availability

Neighbor removal treatments increased light penetration to about 90% in both prairie and forest. Shoots of neighbors (SN) and all neighbors (AN) treatments reduced light penetration to about 50%-75% in prairie and 10%-20% in forest (table 4). Both soil moisture and soil available N were higher in prairie than in forest (split plot ANOVA; August water, environment effect: F = 80.6, df = 1,8, P < .001; August nitrogen, environment effect: F = 74.6, df = 1, 8, P < .001). Soil moisture did not vary among neighborhood treatments, whereas soil N was lower in SN and AN neighborhoods in both environments (split plot ANOVA; August water, neighborhood effect: F = 0.63, df = 2,75, P = .535; August nitrogen, neighborhood effect: F = 7.05, df = 2, 76, P = .002; Tukey's HSD means contrasts: NN > SN = AN; table 4). Results for resource availability were similar between sampling periods (D. Peltzer and S. Wilson, unpublished results).

Discussion

Despite the overall importance of interspecific interactions, species responses to neighbors did not differ significantly at the large scale between prairie and forest. For example, competition reduced growth by 33%–89% in both environments (fig. 3), but the ranking of species responses to total, root, and shoot interactions was identical between prairie and forest (fig. 5, Kendall's *W*). These results do not support the predictions of Walter (1985) and Tilman (1988) that competitive ability varies with environment, at least for competitive response.

Plant interactions tended to shift with increasing productivity at the large scale from neighbor roots in prairie to shoots in forest (fig. 5). The intensity of total and root interactions did not differ between environments, but shoot II was significantly higher in forest than in prairie. Similar shifts from root to shoot competition were found at smaller scales between adjacent aspen (*Populus tremuloides*) forest and mixed-grass prairie (Wilson 1993*a*) and along experimental gradients of soil fertility (Wilson and Tilman 1995). Thus, there was a shift in the nature of interspecific interactions between environments even though there was no change in the ranking of species responses to neighbors.

Similar to results at the large scale, the responses of grasses and trees to neighbors did not differ at the small scale (i.e., no significant species \times site interactions ob-



Figure 5: Interaction intensity for all neighbors (*filled bars*), roots of neighbors (*heavily hatched bars*), and shoots of neighbors (*lightly hatched bars*) experienced by the grasses *Bouteloua* (*Bou*) and *Agropyron* (*Agr*) and trees *Picea* (*Pic*) and *Pinus* (*Pin*) grown in prairie and forest. Bars represent means calculated across sites (n = 15). Vertical lines are +1 SD of the mean. Positive values indicate competition, whereas negative values indicate facilitation. The ranks of species responses were similar between environments (Kendall's coefficient of concordance, *W*; **P* < .05).

served for total interaction intensity). In addition, the ranking of species responses was generally concordant among sites in both prairie and forest (fig. 6, Kendall's W); the one exception to this pattern was caused by facilitation of *Pinus* at one site in prairie rather than variation in the effects of neighbors or in species responses among sites (fig. 6). Thus, species responses to neighbors were generally consistent at both large and small scales.

No consensus has emerged as to which plant traits confer competitive or facilitative ability (Epp and Aarssen 1988; Tilman 1988; Grace 1990; Aarssen 1992; Wedin and Tilman 1993); this may be due to different traits conferring competitive effect and competitive response ability (sensu Goldberg 1990) or to these abilities varying between environments (Goldberg 1996). In this study, plant responses to neighbors differed strongly among species but generally did not vary between environments or sites for either grasses or woody plants (figs. 5, 6). Thus, our results for the intensity of interspecific interactions suggest that screening many species for those traits conferring competitive or facilitative ability is an appropriate technique to link characteristics of individual plants with their distribution and abundance (e.g., Gaudet and Keddy 1995; Grime et al. 1997).

Across all species, variation in plant responses to neighbors was greater among sites than between environments (figs. 5, 6). Significant interactions between species and site were found for survivorship, growth, and interaction intensity (tables 1, 2; fig. 6). These results were likely caused by relatively low variation in survivorship and total interaction intensity among sites for *Bouteloua* (figs. 2, 6) and relatively high variation in growth among sites for *Agropyron* (fig. 4). Taken together, these results suggest that much of the variation in species performance can



Figure 6: Total intensity of interspecific interactions experienced by transplants of the grasses *Agropyron* and *Bouteloua* and trees *Picea* and *Pinus* grown in prairie and forest. Data points represent mean interaction intensity calculated across water treatments. Positive values indicate competition, whereas negative values indicate facilitation. The ranks of species responses were similar among sites in both prairie and forest (Kendall's coefficient of concordance, *W*; [†]*P* < .10; ^{*}*P* < .05).

occur at the small scale rather than at the large scale. Similarly, Miller et al. (1995) reported that variation in the performance of a tussock grass was larger within sites than among sites in eight Texas grasslands.

Variation in species performance at the small scale may be caused by neighbors. For example, variation in survivorship among sites was caused by neighbors (table 1, significant interaction between neighborhood and site). Previous work has shown that small-scale variation in resources can be caused by the resident vegetation (Kleb and Wilson 1997). However, no study to date has linked plant effects on resource levels and heterogeneity with responses to plant interactions in natural vegetation.

In our study, the intensity of plant interactions varied most strongly with the interaction between species and site, rather than with the main effects of environment or site (see ANOVA results for total II). Furthermore, intense competition was not necessarily related to low survivorship. For example, Bouteloua experienced the most intense competition but also had the highest survivorship in all treatments (figs. 1, 5). Interactions among plants may be less important than survivorship for variation in species performance if they simply alter the performance of surviving individuals. For example, transplant survival rarely varied between neighborhoods or with interactions involving neighborhood suggesting that species interactions had little effect on survival. Further work is warranted assessing how neighbors affect different aspects of plant performance. For example, neighbor effects on survival have immediate effects on fitness and population size, whereas neighbor effects on individual growth have longer-term and poorly understood effects on plant populations (Goldberg et al. 1999). Our results for survivorship and growth (figs. 1, 3; table 2) corroborate findings from previous studies suggesting that mortality and abiotic factors can be as important as plant interactions in the establishment and performance of species (Reader 1992; Barton 1993; Reader and Bonser 1993).

Plant interactions may be less important than either large- or small-scale factors unrelated to the effects of neighborhood treatments. Neighbors strongly reduced growth, but neighborhood explained less of the variation in growth than did environment, site, or the interaction between species and environment (table 2, η^2). Neighborhood treatment strongly contributed to variation in growth only when statistical analyses were conducted on individual species (table 3). The relatively high importance of environment and site suggests that growth varied more strongly because of environmental factors operating at both large and small scales than among neighborhood treatments.

Plant growth forms performed differently at large and small scales. The growth of grasses had greater responses to environment and neighborhood treatments than did the growth of trees (table 3, environment and neighborhood effects were highly significant and had large effect sizes for grasses but not for trees). In contrast, the growth of grasses was less sensitive to differences among sites than was the growth of trees (table 3, effect sizes for site were smaller for grasses than for trees). Similarly, grass growth varied strongly between environments and tree growth varied strongly among sites. Taken together, these results suggest that different plant growth forms may respond differently to large- and small-scale factors.

Resource availability was higher in prairie than in forest but did not necessarily increase plant performance. For example, soil resources were generally two- to fivefold higher in prairie but did not result in higher growth for *Picea* or *Pinus* (table 4; fig. 3). Neighbor removals had

Date, environment, and neighborhood treatment	Light penetration (%)	Soil moisture (%)	Soil available nitrogen (µg/mg dry soil)
June:			
Prairie:			
NN	87.5 ± 3.2	25.9 ± 7.8	4.5 ± 1.6
SN	73.2 ± 14.8	27.9 ± 5.1	3.9 ± 1.9
AN	72.1 ± 14.0	26.3 ± 5.9	3.0 ± 1.5
Forest:			
NN	87.6 ± 4.9	8.9 ± 4.5	$.65 \pm .87$
SN	19.0 ± 8.7	11.0 ± 1.3	$.93 \pm 1.2$
AN	19.7 ± 9.5	13.6 ± 9.9	1.7 ± 2.3
August:			
Prairie:			
NN	91.4 ± 5.2	17.4 ± 16.7	5.2 ± 4.2
SN	63.2 ± 19.9	21.1 ± 5.5	3.4 ± 2.4
AN	54.1 ± 18.4	17.0 ± 3.2	2.2 ± 1.2
Forest:			
NN	84.7 ± 4.7	7.2 ± 3.7	$.63 \pm .63$
SN	10.4 ± 17.6	7.8 ± 2.7	.41 ± .39
AN	13.2 ± 16.6	8.8 ± 3.3	$.37 \pm .49$

Table 4: Mean (\pm 1 SD) light penetration, soil moisture, and soil available nitrogen in June and August in prairie or forest plots containing no neighbors (NN), shoots of neighbors (SN), or all neighbors (AN)

Note: Means are calculated across watering treatments and sites within an environment (n = 15).

idiosyncratic effects on soil resource availability; that is, removing neighbors did not always increase soil moisture or available N (table 4). Because resource availability was not clearly related to plant performance, other environmental or biological factors (e.g., temperature regimes, herbivory) must be regulating plant performance between environments.

Grasses and trees showed distinct preferences for prairie and forest environments. With neighbors removed, grasses grew significantly faster in prairie, and trees grew faster in forest (fig. 3). This result differs from other studies that did not find distinct preferences for environment (e.g., Keddy 1984; Wilson and Keddy 1986; Austin and Gaywood 1994). Our environments may have been sufficiently distinct to observe different physiological responses of species to abiotic factors in prairie and forest. Our results for growth and interaction intensity (figs. 3, 5) suggest that although responses to neighbors were consistent at large and small scales, physiological responses of grasses and trees differed at the large scale. Alternatively, indirect interactions (e.g., pathogens, availability of appropriate mycorrhizas, plant-soil feedbacks) may have caused the higher performance of plant growth forms in their "home" environments (e.g., Wilson and Agnew 1992; Wootton 1994; Bever et al. 1997). An unresolved question is whether these differences in growth can contribute to the location and maintenance of community boundaries.

Several lines of evidence suggest that neighbors often facilitated the performance of species. The survivorship of *Agropyron* in forest was higher with neighbors present than without neighbors (fig. 1, means contrasts). The growth of tree seedlings (*Picea* and *Pinus*) was often higher with neighbors present in prairie but generally not in forest (figs. 3, 5). These observations seem to support the views that herbaceous and woody plants coexist as a result of less intense competition between growth forms than within a growth form (Scholes and Archer 1997) and that positive interactions among plants are important and widespread (Hunter and Aarssen 1988; Callaway 1995; Callaway and Walker 1997; Bertness 1998; Levine 1999).

Long-term experiments lasting several growing seasons are appropriate for answering questions linking individuallevel species responses to population-level responses (Goldberg 1996); however, single-season removal experiments are appropriate for determining variation in plant responses to neighbors for several reasons. First, plant responses appear to be consistent among years. Single-season experiments repeated among years give similar results. For example, multiyear field experiments examining competition in Minnesota (Wilson and Tilman 1991, 1993, 1995) and Saskatchewan (Peltzer et al. 1998) old fields found no significant variation in competitive responses among years. Second, over longer periods (>1 yr), fast-growing species may reach the carrying capacity of the experimental unit sooner than slow-growing species. As a result, they could appear to be less influenced by neighbors. Lastly, we simulated amongyear differences in water by varying water supply rates threefold. In spite of the fact that water regulates both establishment and primary productivity in the northern Great Plains region (Lauenroth et al. 1978; 1994; Webb et al. 1978), it had no effect on survival or growth in our study. Thus, among-year differences in water availability would not likely change our results.

The importance of species interactions and plant effects on resources through time deserves further attention (Goldberg and Novoplansky 1997; Mitchell et al. 1999). Assessing the temporal scales over which competition operates is especially critical when addressing populationlevel questions in long-lived, perennial vegetation, that is, determining the importance of the cumulative effects of neighbors on the survival, establishment, and growth of plants. For example, Kolb and Robberecht (1996) found that root competition by bunchgrasses caused a 40%-80% increase in Pinus ponderosa seedling mortality, and decreased seedling survival by 2-3 wk. Such short-term effects of tree-grass interactions at the seedling stage are well documented (e.g., DeSteven 1991a, 1991b; Perry et al. 1994; Berkowitz et al. 1995). However, in order to have a richer understanding of how interspecific interactions contribute to the structure of natural vegetation, we need to determine the cumulative effects of species interactions and to explore how external processes such as climate modify species interactions (Archer 1995; Casper and Jackson 1997; Goldberg and Novoplansky 1997; Scholes and Archer 1997).

In summary, species responses to neighbors varied between environments and among neighborhood treatments, but the overall effects of neighbors did not vary between environments even though there was a shift from root to shoot competition between prairie and forest. The responses of grasses and trees to interspecific interactions generally did not vary at either large (between environments) or small scales (among sites). Interestingly, distinct preferences for environment were observed such that species grew faster in their "home" environment in neighbor removal treatments. The ranking of the relative responses of the four species to neighbors was consistent at both large and small scales, suggesting that interspecific interactions can be consistent across scales for herbaceous and woody plants.

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