

Competitive effects of grasses and woody plants in mixed-grass prairie

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Summary

1 Variation in the competitive ability of plant species may determine their persistence and abundance in communities. We quantified the competitive effects of grasses and woody plants in native mixed-grass prairie on the performance of transplant species and on resources.

2 We separated the effects of grasses, shrubs and intact vegetation containing both grasses and shrubs by manipulating the natural vegetation using selective herbicides to create four neighbourhood treatments: no neighbours (NN), no shrubs (NS), no grasses (NG) and all neighbours (AN). Treatments were applied to 2 × 2 m experimental plots located in either grass- or shrub-dominated habitats. The effects of grasses and shrubs on resource availability (light, soil moisture, soil available nitrogen) and on the growth of transplants of *Bouteloua gracilis*, a perennial tussock grass, and *Elaeagnus commutata*, a common shrub, were measured over two growing seasons.

3 Resource availability was two- to fivefold higher in no neighbour (NN) plots than in vegetated plots (NS, NG, AN) with grasses and shrubs having similar effects. Light penetration declined linearly with increasing grass or shrub biomass, to a minimum of about 30% incident light at 500 g m⁻² shoot mass. Soil resources did not decline with increasing neighbour shoot or root mass for either grasses or shrubs, suggesting that the presence of neighbours was more important than their abundance.

4 Transplant growth was significantly suppressed by the presence of neighbours, but not by increasing neighbour shoot or root biomass, except for a linear decline in *Bouteloua* growth with increasing neighbour shoot mass in plots containing only shrubs. Competition intensity, calculated as the reduction in transplant growth by neighbours, was similar in both grass- and shrub-dominated habitats for transplants of *Bouteloua*, but was less intense in shrub-dominated habitats for the shrub *Elaeagnus*. Variation in the persistence and abundance of plants in communities may therefore be more strongly controlled by variation in the competitive effects exerted by neighbours than by differences in competitive response ability.

Key-words: competitive ability, facilitation, grassland, interspecific interactions, per-gram effects of vegetation, prairie, resource availability, seedling growth, shrub-grass competition

Journal of Ecology (2001) **89**, 519–527

Introduction

Variation in the competitive or facilitative abilities of plant species is thought to determine their persistence

and abundance in communities (Grime 1979; Tilman 1982, 1988; Walter 1985; Keddy 1989, 1990). Competitive ability can be separated into two components; competitive response and competitive effect ability (Goldberg 1990). Good response competitors are able to withstand suppression by neighbours and grow faster or survive longer at low resource levels (i.e. a good competitor *sensu* Tilman 1982 or a stress tolerator *sensu* Grime 1979). Good effect competitors are able to reduce the survival or growth of other plants and should have large per-unit (e.g. per-individual or per-gram) effects on resource availability (i.e. a good competitor *sensu* Grime 1979).

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Differences in competitive effect ability among species have been demonstrated in highly controlled environments such as glasshouse experiments (e.g. Goldberg & Fleetwood 1987; Goldberg & Landa 1991); however, surprisingly few studies have quantified the per-unit effects of different plants in the field (Goldberg 1996b; Mitchell *et al.* 1999). In this study, we determined the competitive effects of grasses and woody plants on transplant performance *in situ* by using selective herbicides to remove grasses, shrubs or all plants from mixed-grass prairie. Because interactions among plants are usually mediated through pools of relatively few limiting resources (Harper 1977; Huston & DeAngelis 1994), we also quantified the effects of grasses and shrubs on resource availability.

Previous studies suggest that woody plants may have larger competitive effects than grasses, but this may simply be caused by the higher shoot mass of shrubs and hence greater reductions in light availability (see review of Wilson 1998). The competitive effects of shrubs and trees on herbaceous plants seem obvious. For example, the canopies of woody plants shade and alter the productivity of understorey herbaceous species (Belsky 1994; Scholes & Archer 1997). In contrast, the effects of herbaceous species on established woody plants is less well understood because these interactions are largely below-ground and are thus hidden from view (Newman 1973; Casper & Jackson 1997; Wilson 1998). For example, grasses may be superior competitors for soil resources such as water and nitrogen as a result of their extensive, fine root morphology (Newman 1973; Aerts *et al.* 1991). Such effects are best documented in the forestry literature where suppression of tree seedlings by weeds is of concern (e.g. Elliott & White 1989; Glover *et al.* 1989; Mitchell *et al.* 1993, 1999).

We quantified the effects of grasses and woody plants on both resource availability and on the performance of transplants over two growing seasons. Differences in per-gram effects would suggest that the competitive effect ability of a particular neighbour is related to its growth-form or physiology (Brown *et al.* 1998; Wilson 1998). Specifically, we predict (i) that grasses will have greater per-gram competitive effects on soil resources, and (ii) that woody plants will have greater per-gram effects on light availability. We also determined whether competition is more intense within than between plant life-forms (i.e. grasses or woody plants) as this is one mechanism by which different plant life-forms can coexist (Scholes & Archer 1997).

Materials and methods

STUDY SITE

The experiment was conducted in mixed-grass prairie in southern Saskatchewan, Canada (49°38' N, 104°11' W), dominated by grasses (*Bouteloua gracilis*, *Agropyron* spp., and *Stipa comata*), several sedges (*Carex* spp.) and shrubs (*Symphoricarpos occidentalis* and *Elaeagnus commutata*)

(nomenclature follows Looman & Best 1987; this site is also described by Köchy & Wilson 2000). *Symphoricarpos* is a small, low (30–80 cm), creeping clonal shrub, which forms large clumps whereas *Elaeagnus* is a taller (50–250 cm), N-fixing shrub whose diffuse clumps are scattered throughout mixed-grass prairie in this region. Both shrubs are relatively shallow rooted with most below-ground biomass in the top 30 cm of soil (i.e. within the rooting zone of grasses) (D. Peltzer, personal observation). The climate is continental with most of the mean annual precipitation of 406 mm falling from May to July. Temperatures range from a mean daily high of 27.0 °C in July to –10.6 °C in January (Environment Canada 1993).

EXPERIMENTAL DESIGN AND PLANT REMOVAL TREATMENTS

Four removal treatments were used to assess the competitive effects of woody and herbaceous plants in mixed-grass prairie: no neighbours (NN), no grasses (NG), no shrubs (NS), and all neighbours (AN). Competition treatments were randomly assigned to plots (2 × 2 m). The edges of all plots were trenched each spring to a depth of 35 cm to eliminate below-ground competition with neighbouring vegetation. Selective herbicides were applied for 2 years prior to the experiment (i.e. in 1996 and early 1997), and again in early 1998 several weeks prior to planting seedlings. The NN treatment received sethoxydim (trade name 'Poast', total of 10.433 kg active ingredient (a.i.) ha⁻¹ at each application), metsulphuron-methyl ('Ally', 0.2325 kg a.i. ha⁻¹), and 3% glyphosate ('Round-Up', N-phosphonomethyl) solution applied at 0.75 L m⁻². The NG treatment received sethoxydim, the NS treatment, metsulphuron-methyl and the AN treatment, 2% surfactant. All treatments involved application of solutions at 0.75 L m⁻², diluted with deionized water where appropriate. All herbicides used are systemic, taken up via leaves, degrade quickly in soils (< c. 2 week) and have weak indirect effects. Glyphosate is a widely used, non-selective herbicide (Grossbard & Atkinson 1985); metsulphuron is a selective, post-emergence herbicide developed for the control of herbaceous broadleaf weeds in grain crops (Ahrens 1994), and has been used to eliminate woody plants in grasslands (Derr 1989; Bowes & Spurr 1996); sethoxydim is a selective, post-emergence herbicide used for the control of grasses in broadleaf crops such as canola, flax and legumes (Ahrens 1994).

Dead neighbour shoots and roots were not removed from NN, NG and NS plots. Although decaying plant materials are a source of carbon that may alter N availability to transplanted seedlings, work by McLellan *et al.* (1995) suggests that leaving decaying roots in place is unlikely to significantly alter the growth of transplant species. For example, nutrient mineralization from the dead roots of prairie grasses is small relative to immobilization (e.g. Seastedt 1988). This suggests that very

little of any increase in transplant growth following neighbour removal is caused by eliminating N uptake by neighbours (see discussion in Wilson & Tilman 1995).

The experiment was conducted at five sites. Sites were sufficiently large (c. 500–800 m²) to contain both grass-dominated and shrub-dominated habitats, and were separated by at least 100 m to avoid sampling contiguous patches of shrubs. There is no observable difference between these habitats in topography or soil texture; *Symphoricarpos* and *Elaeagnus* have presumably invaded into the surrounding mixed-grass prairie matrix to produce shrub-dominated areas (D. Peltzer, personal observation). Use of the two habitats provided a range of both grass and shrub biomass for the detection of per-gram competitive effects in eight competition treatment × habitat combinations. Additional replicates over a wider range of plant biomass or direct manipulation of neighbourhood densities would have improved our ability to detect differences in the per-gram effects of plants (see Goldberg & Scheiner 1993), but our sites encompassed the natural range of plant biomass in the study area and used the maximum feasible number of replicate plots.

TRANSPLANTS

The competitive effects of grasses and shrubs were quantified as the reduction in the performance of seedlings transplanted in competition plots. Seedlings of a common C₄ perennial tussock grass, *Bouteloua gracilis*, and a common clonal shrub, *Elaeagnus commutata* were grown from seeds collected at the study sites from > 20 individuals, and sown into plastic pots (2.5 cm diameter, 12 cm deep) containing a 1:5 mixture of local soil: peat moss. Several cohorts were established from late January until mid-March in each year of the experiment (1997 and 1998). Seedlings were thinned to one plant per pot at germination and grown in a greenhouse under natural light and without fertilizer. Plants were watered daily to field capacity.

Initial seedling shoot mass (g) was estimated using the following regression equations. *Bouteloua*: $(0.000577 \cdot \text{TTL} + 0.02682015)^2$, $r^2 = 0.98$, $P < 0.001$, $n = 30$, where TTL = total tiller length in mm; *Elaeagnus*: $(0.00331 \cdot \text{ht} + 0.062167)^2$, $r^2 = 0.93$, $P < 0.001$, $n = 30$, where ht = seedling height in mm just prior to planting. After one week's acclimatization outside, 10 seedlings of each species were transplanted into each competition plot during early June and tagged with coloured wire. Transplants were planted at 25-cm spacing in a 2 × 5 grid within the centre of each competition plot, and species were randomly assigned to each planting location. Transplants were immediately given 250 mL of water and shaded for 10 days using opaque plastic (30 × 40 cm). Dead seedlings were replaced for up to 3 weeks after planting. Shoots of all living transplants were harvested, dried (70 °C, 2 days), and weighed in mid-September.

GROWTH AND COMPETITION INTENSITY

The relative growth rate (RGR) of each transplant was calculated in each treatment as: $(\ln M_f - \ln M_i)/d$, where M_f is the final shoot mass, M_i is the initial shoot mass, and d is the number of days between biomass measurements. Competition intensity (CI), the proportional reduction in transplant growth caused by neighbours, was calculated as: $(\text{RGR}_{\text{NN}} - \text{RGR}_{\text{AN}})/\text{RGR}_{\text{NN}}$, where RGR_{NN} and RGR_{AN} are the growth rates for transplants in NN and AN competition treatments, respectively. Similarly, the competitive effects of shrubs and grasses were estimated using growth in the NG and NS treatments, respectively. A constant value was added to growth rates prior to calculation of CI to avoid spurious large positive values of CI due to negative growth rates in AN plots. Positive values of CI are then evidence for competition whereas negative values of CI indicate facilitation.

RESOURCE AVAILABILITY AND STANDING CROP

Light, soil moisture and soil available N were measured during the 1997 and 1998 growing seasons. Light penetration was measured in July both above the vegetation and at the soil surface at four locations within each plot using a 1 × 40 cm integrating light probe (Sunfleck ceptometer, Decagon Devices, Pullman, WA, USA). Light penetration was calculated as the mean proportion of incident light reaching the soil surface.

Soil moisture was measured gravimetrically for four pooled soil samples (2 cm diameter × 20 cm deep) collected in late July. This coincided with peak vegetation biomass and lowest seasonal water availability, i.e. the time when we would expect to see the largest cumulative effects of plants on soil resources. We also took care not to sample within 1 week of a precipitation event to avoid sampling short-term resource fluctuations.

Soil-available N was measured from May until September each year using ion exchange resin bags (3 × 3 cm). Each bag contained 2 g of wet mixed-bed ion exchange resin (AG 501-X8, Bio-Rad, Hercules, California, USA) having 1.0 mmol g⁻¹ of both anion and cation exchange capacity. Three resin bags were placed vertically in the soil about 5 cm deep in each plot in late May, removed during transplant harvest, and processed immediately (method described in Köchy & Wilson 1997 as modified by Peltzer 2001).

Standing crop was measured by harvesting all above-ground plant material within a 0.1 × 1 m quadrat in each competition plot in late July. Below-ground biomass was measured in each plot in three soil cores (10 cm diameter, 15 cm deep), encompassing the major rooting zone of both grasses and shrubs (D. Peltzer, personal observation). Cores were stored frozen in polyethylene bags until roots were manually separated from adherent soil by washing. No attempt was made to recover fine roots (< 1 mm in diameter). Standing crop and roots were dried (70 °C, 3 days) and weighed.

STATISTICAL ANALYSIS

Resource availability was analysed using split-plot ANOVA with habitat as the main-plot effect and competition treatments within habitats as the split-plot effect. Both habitat and competition factors were nested within replicate sites. Transplant growth in each year was also analysed in this way, except that the mean growth of all transplants surviving until the end of the growing season was calculated within each competition plot.

Regression analyses were used to assess the per-gram effects of grasses and shrubs. Per-gram effects of neighbours are represented by the slope of linear relationships between resource availability or transplant growth and neighbourhood biomass (Goldberg & Scheiner 1993). ANCOVA was used to analyse the effects of competition on transplant growth with neighbour biomass as the covariate. Non-proportional data were log transformed while proportional data were arcsin-square root transformed prior to each analysis (Zar 1984) to improve normality and reduce heteroscedasticity of the data. Tukey's HSD tests were used to contrast group means among competition treatments after significant ANOVA results. All data were analysed using JMP (version 3.2, SAS Institute 1997). Statistical results were similar for the 1997 and 1998 growing seasons, and only 1998 data are reported.

Results

NEIGHBOURHOOD BIOMASS

Above-ground neighbour biomass was higher in shrub-dominated than in grass-dominated habitats (Fig. 1;

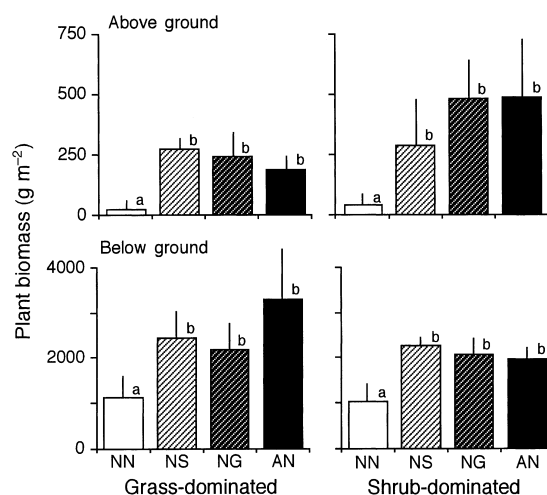


Fig. 1 Plant biomass (g m^{-2}) \pm 1 SD in four competition treatments (open bars = no neighbours present (NN); lightly hatched bars = no shrubs present (NS); heavily hatched bars = no grasses present (NG); filled bars = all neighbours present (AN)) in grass- and shrub-dominated habitats. Bars represent means across sites ($n = 5$) and different lower case letters indicate significant means contrasts among competition treatments within a habitat after significant ANOVA results using Tukey's HSD tests.

split-plot ANOVA: habitat: $F_{1,12} = 37.46$, $P < 0.001$), and in both habitats, was significantly lower in NN than other treatments (NS, NG and AN did not differ significantly, Fig. 1, means contrasts). The relatively small values in NN plots were due to residual standing litter (Fig. 1, NN). A significant two-way interaction between competition and habitat reflected the higher neighbour biomass in shrub-dominated plots for all competition treatments except NN ($F_{3,12} = 8.57$, $P = 0.003$).

Neighbour biomass was 4- to 16-fold higher below than above-ground, but showed a similar pattern in both habitats (similar in NS, NG or AN treatments, but significantly lower in NN plots; Fig. 1, means contrasts; competition: $F_{3,12} = 11.53$, $P < 0.001$; competition \times habitat: $F_{3,12} = 3.97$, $P = 0.353$). Below-ground biomass in NN plots was due to shrub roots that had not yet decomposed (D. Peltzer, personal observation). Overall, below-ground biomass was higher in the grass-dominated habitat (habitat: $F_{1,12} = 7.02$, $P = 0.021$).

EFFECTS ON RESOURCE AVAILABILITY

Light penetration ranged from *c.* 60% to 100% in total neighbour removal (NN) plots due to standing litter, and was reduced to 20–40% in all other competition treatments (Fig. 2). Light penetration was significantly lower in the shrub-dominated habitat (Fig. 2; ANOVA: habitat: $F_{1,12} = 45.51$, $P < 0.001$) and a significant interaction between competition and habitat was caused by the presence of shrubs (NG) or intact vegetation (AN) having a greater effect there ($F_{3,27} = 8.63$, $P = 0.003$).

Light penetration declined monotonously with increasing neighbour shoot mass in all competition treatments (Table 1). The per-gram reduction of light (slopes of the linear relationships between light penetration and shoot mass) was greatest for grasses (NS), intermediate for shrubs (NG), and lowest for the all neighbour competition treatment (AN); however, these differences were not significant (95% confidence intervals of the slopes overlap).

In both habitats soil moisture was *c.* 30–100% higher in NN plots (Fig. 3, competition: $F_{3,12} = 13.02$, $P < 0.001$;

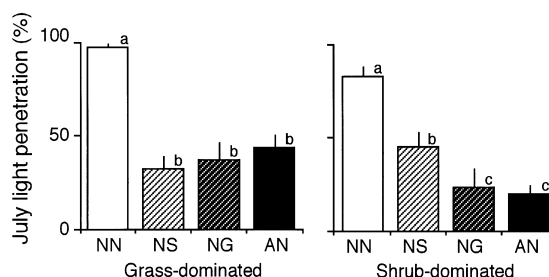


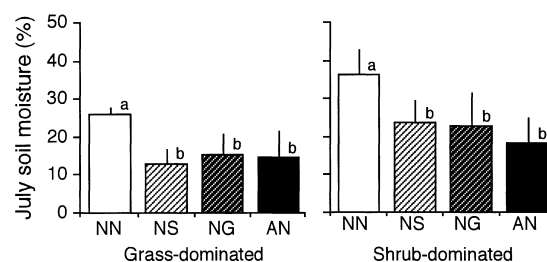
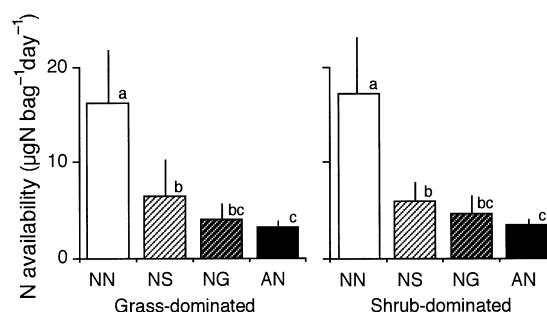
Fig. 2 Light penetration (%: means across sites \pm 1 SD, $n = 5$) in four competition treatments in both grass- and shrub-dominated habitats. Statistical conventions as in Fig. 1. Per-gram effects of neighbours on light penetration were measured as the slope of the linear relationship between light penetration and above-ground neighbour biomass (see Table 1).

Table 1 Summary for linear regressions of neighbour shoot biomass on resources and growth in three competition treatments (NS = no shrubs; NG = no grasses; AN = all neighbours; $n = 10$ for all analyses). Slope represents the per-gram effects of shoots

Dependent variable	Term	Competition treatment		
		NS	NG	AN
Light	r^2	0.659	0.595	0.714
	P	0.004	0.009	0.004
	Slope	-0.0520	-0.0501	-0.0414
Soil moisture	r^2	0.371	0.001	0.020
	P	0.082	0.931	0.695
	Slope	-0.0423	0.0014	0.0034
N availability	r^2	0.023	0.104	0.025
	P	0.673	0.363	0.533
	Slope	0.0006	-0.0010	0.0002
Growth: <i>Elaeagnus</i>	r^2	0.098	0.103	0.101
	P	0.651	0.401	0.172
	Slope	0	0	0
Growth: <i>Bouteloua</i>	r^2	0.058	0.503	0.100
	P	0.497	0.022	0.174
	Slope	0	-4.4×10^{-4}	0

habitat \times competition: $F_{3,27} = 1.58$, $P = 0.246$), but other competition treatments did not differ (means contrasts among NS, NG and AN treatments). There were no significant per-gram reductions in soil moisture by neighbours in any competition treatment (zero slopes for regressions against shoot, Table 1, or root, Table 2, biomass).

Available N in soil was two- to fivefold higher in NN competition plots than in other competition treatments (Fig. 4, competition: $F_{3,12} = 8.73$, $P = 0.002$). Plots containing both grasses and shrubs (AN) reduced N availability to a greater extent than grasses alone, but not to a greater extent than shrubs alone (i.e. N flux:

**Fig. 3** Soil moisture (%: means across sites ± 1 SD, $n = 5$) in four competition treatments in both grass- and shrub-dominated habitats. Statistical conventions as in Fig. 1. Per-gram effects of neighbours on soil moisture were measured as the slope of the linear relationship between soil moisture and neighbour biomass (shoots, Table 1, and roots, Table 2).**Fig. 4** Soil N availability ($\mu\text{g N}$ (ion exchange resin bag) $^{-1}$ day $^{-1}$): means across sites ± 1 SD, $n = (5)$ in four competition treatments in both grass- and shrub-dominated habitats. Statistical conventions as in Fig. 1. Per-gram effects of neighbours on soil available N were measured as the slope of the linear relationship between N availability and neighbour biomass (shoots, Table 1, and roots, Table 2).

AN = NG < NS; Fig. 4, means contrasts). Effects did not differ between habitats (habitat \times competition: $F_{3,27} = 0.91$, $P = 0.465$). There were no significant per-gram reductions in soil available N by neighbours in any competition treatment (zero slopes; Tables 1 & 2).

Table 2 Summary of per-gram competitive effects of neighbour roots on resources and growth in three competition treatments (conventions as in Table 1)

Dependent variable	Term	Competition treatment variable		
		NS	NG	AN
Soil moisture	r^2	0.023	0.082	0.030
	P	0.700	0.421	0.632
	Slope	-0.0032	-0.0043	-0.0008
N availability	r^2	0.129	0.207	0.166
	P	0.343	0.187	0.084
	Slope	0.0006	-0.0005	-0.0002
Growth: <i>Elaeagnus</i>	r^2	0.003	0.046	0.269
	P	0.905	0.557	0.042
	Slope	-4.2×10^{-7}	-1.0×10^{-6}	1.2×10^{-6}
Growth: <i>Bouteloua</i>	r^2	0.004	0.362	0.435
	P	0.865	0.039	0.002
	Slope	1.0×10^{-6}	-8.0×10^{-6}	2.3×10^{-6}

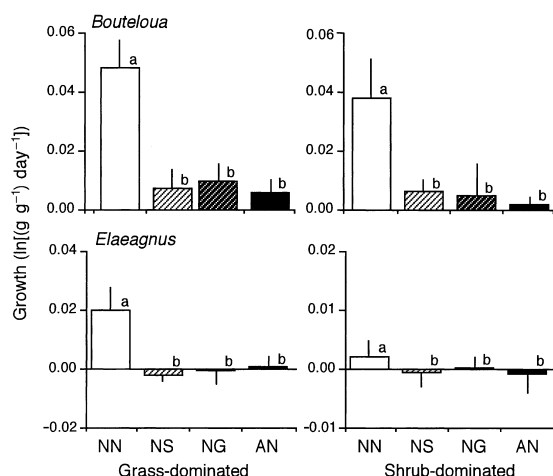


Fig. 5 Relative growth rates ($[\ln(g/g)]/d$): means across sites ± 1 SD, $n = 5$) of a grass, *Bouteloua gracilis*, and a shrub, *Elaeagnus comutata*, grown in four competition treatments in both grass- and shrub-dominated habitats. Statistical conventions as in Fig. 1. Per-gram effects of neighbours on growth were measured as the slope of the linear relationship between growth and neighbour biomass (shoots, Table 1, and roots, Table 2).

EFFECTS ON TRANSPLANT PERFORMANCE

Growth of both *Bouteloua* and *Elaeagnus* was 4- to 12-fold higher in NN plots than in other competition treatments (Fig. 5, *Bouteloua*: competition: $F_{3,12} = 100.27$, $P < 0.001$; *Elaeagnus*: $F_{3,12} = 10.89$, $P < 0.001$). Negative growth rates for *Elaeagnus* were caused by a loss of shoot mass via leaf senescence rather than by disturbance (e.g. herbivory; D. Peltzer, personal observation). Neighbours reduced transplant growth to about the same extent (Fig. 5; NS, NG and AN vs. NN competition treatments).

Growth was higher in grass-dominated habitats (*Bouteloua*: habitat: $F_{1,12} = 7.46$, $P = 0.018$; *Elaeagnus*: habitat: $F_{1,12} = 4.47$, $P = 0.056$). Competition had similar effects between habitats for *Bouteloua* (habitat \times competition: $F_{3,12} = 0.89$, $P = 0.474$), but had smaller effects for *Elaeagnus* in the shrub-dominated habitat (habitat \times competition: $F_{3,12} = 5.36$, $P = 0.014$). Neither transplant species showed a decline in growth with increasing neighbour shoot mass (ANCOVA: effect of above-ground neighbour biomass: *Bouteloua*: $F_{1,20} = 0.624$, $P = 0.439$; *Elaeagnus*: $F_{1,20} = 0.033$, $P = 0.858$).

Significant per-gram reductions in growth were rare (a single example, *Bouteloua* growing in plots containing only shrubs (NG), for both neighbour shoots and roots; Tables 1 & 2). Shrub shoots and roots suppressed growth of *Bouteloua* more than growth of *Elaeagnus* (slopes; *Bouteloua* > *Elaeagnus*). Shrub shoots suppressed growth to a greater extent than roots despite their much smaller biomass (Tables 1 & 2). Growth did not vary with biomass in other treatments except for below-ground biomass in the AN treatment (in this case a modest increase, Table 2).

Competition intensity was relatively high (c. 0.7) for most treatment combinations. *Bouteloua* experienced

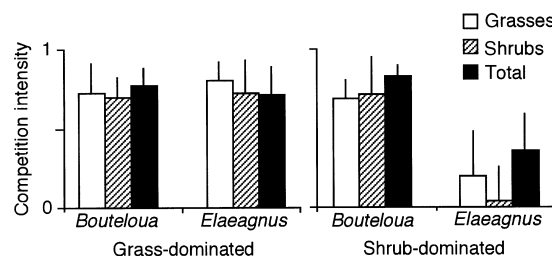


Fig. 6 Competition intensity (CI) experienced by transplants of a grass, *Bouteloua gracilis*, and a shrub, *Elaeagnus comutata*, growing in grass-dominated and shrub-dominated habitats. Bars represent mean CI across sites ($n = 5$) for each competition treatment.

intense competition regardless of neighbours or habitats (Fig. 6, habitat: CI grasses: $F_{1,4} = 0.906$, $P = 0.395$, CI shrubs: $F_{1,4} = 0.025$, $P = 0.883$, CI total: $F_{1,4} = 3.07$, $P = 0.155$). In contrast, *Elaeagnus* experienced intense competition only in the grass-dominated habitat; CI from both grasses and shrubs was reduced 2- to 10-fold in the shrub-dominated habitat (habitat: CI grasses: $F_{1,4} = 10.97$, $P = 0.030$, CI shrubs: $F_{1,4} = 11.84$, $P = 0.026$, CI total: $F_{1,4} = 8.23$, $P = 0.046$).

Discussion

COMPETITIVE EFFECTS

Competition by both grasses and shrubs strongly reduced transplant growth in grass- and shrub-dominated habitats. For example, growth of both transplant species was two- to eightfold higher in no neighbour (NN) plots than in plots containing grasses (NS), shrubs (NG), or both grasses and shrubs (AN) (Fig. 5). Although species performance generally did not decrease with increasing neighbour shoot or root biomass, there was a strong linear decrease of *Bouteloua* growth with increasing shrub shoot and root biomass (Tables 1 & 2). Effects on the performance of transplants were therefore caused mostly by the presence, but not the mass (i.e. abundance) of neighbours. Our observation that the effects of competition were similar between grass-dominated and woody-dominated habitats is consistent with several previous studies (Wilson 1993; Köchy & Wilson 2000; Peltzer & Wilson, in press).

Competition intensity (CI) experienced by the grass *Bouteloua* was similar across competition and habitat treatment combinations. In contrast, CI experienced by the shrub *Elaeagnus* was much lower in the shrub-dominated habitat (Fig. 6), suggesting that competition was less intense among woody plants. Several other studies have also observed either weak competitive interactions or facilitation among woody plants. For example, the shrub *Symphoricarpos occidentalis* competing against grasses had higher survivorship and enhanced growth when planted in intraspecific clumps rather than as individual plants (Li & Wilson 1998). Similarly, clumps of a marshland shrub, *Iva frutescens*,

facilitated intraspecific seedling establishment and survival by suppressing herbaceous vegetation and ameliorating environmental conditions (Bertness & Yeh 1994). Taken together, these findings suggest that woody plants exert strong competitive effects on herbaceous species, but not necessarily on other woody plants. This observation might explain the commonly observed phenomenon of clumped distributions or nucleation of woody plants (Yarranton & Morrison 1974), but does not seem to support the idea that herbaceous and woody plants may coexist due to less intense competition between growth-forms than within a growth-form (Scholes & Archer 1997).

Alternatively, facilitation among woody plants may offset the effects of competition. Positive interactions among plants are increasingly recognized as being important and widespread in terrestrial vegetation (see reviews by Hunter & Aarssen 1988; Bertness & Callaway 1994; Callaway 1995). Both facilitation and competition may operate simultaneously, resulting in no observed net interactions among species (Callaway 1995; Goldberg & Novoplansky 1997), or may operate differently through time. For example, Greenlee & Callaway (1996) found that the interactions between bunchgrasses and a rare mustard (*Lesquerella carinata*) were competitive in a wet, cool year but were facilitative in a dry, hot year. Distinguishing the relative importance of facilitation and competition over time deserves further consideration.

RESOURCE AVAILABILITY

Light availability decreased linearly with increasing neighbour shoot mass similarly for both grasses and shrubs (Table 1, slope: NS = NG), suggesting that above-ground biomass is more important than plant morphology for reducing light levels, at least over the range of neighbour biomass observed here (*c.* 100–800 g m⁻²). Similar patterns are found in other studies (e.g. Elliot & White 1989; Tilman & Wedin 1991; Gordon & Rice 1993).

Both soil moisture and N availability were much higher in no neighbour (NN) competition plots; for soil moisture, nearly twofold higher than all other competition treatments (Fig. 3), and for soil N, about threefold higher than in plots containing grasses (NS) and four- to fivefold higher than in plots containing shrubs (NG) or intact vegetation (AN) (Fig. 4). Thus, both grasses and shrubs decreased soil moisture and N availability to about the same extent.

Typically, very little root mass is needed to reduce soil N availability. For example, about 100 g m⁻² of root biomass reduced soil nitrate by 80% in a Minnesota grassland (Tilman & Wedin 1991; their Fig. 4). In our study, soil moisture and N availability did not vary with neighbour shoot or root mass in any competition treatment, suggesting that neither grasses nor shrubs had significant per-gram effects on soil resources (Tables 1 & 2), in contrast with their effects on light.

PLANT SIZE AND PER-GRAM COMPETITIVE EFFECTS

Many data support the prediction that variation in competitive effects is based on plant size rather than on relatively small per-gram differences among species for resource depletion (e.g. Goldberg 1987; Miller & Werner 1987; Gaudet & Keddy 1988; Mitchell *et al.* 1993). For example, Mitchell *et al.* (1999) found equivalent per-gram effects of two woody species and one grass species on light availability and soil moisture in monoculture plots. Similarly, in our study, grasses and shrubs generally had equivalent per-gram effects on both resource availability and transplant growth. A complicating factor is that plant morphology or ecophysiological traits may be more strongly related to competitive effects than are plant size or biomass. For example, plant leaf area (LAI) or specific root length (SRL) should be more strongly related to light attenuation and soil nutrient uptake, respectively, than is plant mass. Experiments exploring specific mechanisms of competition are needed to link plant traits explicitly with their predicted effects (see reviews by Goldberg 1996a and Weiher *et al.* 1999).

The weak per-gram effects of both grasses and shrubs on soil resources may be caused by several mechanisms. First, resource uptake may be uncoupled from growth, storage or standing stocks in vegetation (Chapin 1980, 1988; Chapin *et al.* 1990), suggesting that instantaneous estimates of competitive effects on resources are less appropriate than some integrated measure through time. For example, methods have been developed to determine the effects of vegetation on water availability and stress in woody plants over time (Myers 1988); analogous techniques could be used to integrate the effects of plants on light and soil nutrients. Second, resource uptake and depletion may depend on tissue turnover more than biomass (Grime 1994). This possibility could be explored using a combination of stable isotope tracers or minirhizotron techniques which link tissue turnover and quality with nutrient availability under grasses and woody plants. Third, plants may alter the temporal and spatial distribution of resources, if not their mean availability (e.g. Perry *et al.* 1994; Breshears *et al.* 1998). For example, Kleb & Wilson (1997) demonstrated that forest vegetation increases the spatial heterogeneity of soil resources more than prairie vegetation within a single growing season. Lastly, litter may have similar or even greater effects on species interactions and resource availability than do live plants (e.g. Bergelson 1990; Facelli 1994; Foster & Gross 1997; Foster 1999), suggesting that the effects of litter and live plants should be distinguished. These examples illustrate that several approaches can be used to explore the dynamic nature of competitive effects.

The importance of species interactions and plant effects on resources through time has received increasing attention (Goldberg & Novoplansky 1997; Mitchell *et al.* 1999). Assessing the temporal scales

over which competition operates is especially critical when addressing population-level questions in long-lived, perennial vegetation, i.e. determining the importance of the cumulative effects of neighbours on the establishment, survival, growth and reproduction of plants. For example, Kolb & 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 weeks. Such short-term effects of tree–grass interactions at the seedling stage are well documented (e.g. Berkowitz *et al.* 1995); however, in order to have a richer understanding of how competitive effects contribute to the structure of natural vegetation, we need to determine the cumulative effects of species interactions and explore how external processes such as climate modify species interactions (Archer 1995; De Steven 1991a,b; Perry *et al.* 1994; Casper & Jackson 1997; Scholes & Archer 1997).

Conclusion

Competition by both grasses and woody plants strongly suppressed the growth of transplants. However, competition was less intense among woody plants than among grasses, suggesting that facilitation may occur within clumps of woody plants. Resources (light, soil moisture, N availability) were all significantly higher in no neighbour (NN) competition plots than in plots containing either grasses or shrubs. Light availability decreased linearly with increases in both grass and shrub biomass, but soil resources (i.e. soil water content, N availability) did not vary with neighbour biomass. Overall, the presence of neighbour species was more important in reducing resource levels than was neighbour biomass for both grasses and shrubs. Estimates of the cumulative competitive effects of plants are needed to enhance our understanding of how species interactions contribute to vegetation structure.

Acknowledgements

We thank L. Ambrose, Z. Arbeli, H. Hager, A. Jensen and S. Yakimowski for help in the field and laboratory, S. Wilson for logistical support, two anonymous reviewers, W. Lauenroth and L. Haddon for helpful comments and editorial advice on the paper, and the Saskatchewan Prairie Farm Rehabilitation Administration for access to the study site. D.P. also wishes to thank Landcare Research *Manaaki Whenua* for providing space, tea and an excellent work environment while writing this paper. This work was supported by the Natural Sciences and Engineering Research Council of Canada.

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Received 28 March 2000

revision accepted 15 November 2000