FACILITATION AMONG WOODY PLANTS ESTABLISHING IN AN OLD FIELD

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Abstract. Trees and shrubs establishing in grasslands frequently occur in clumps associated with increased soil moisture and N availability. We tested whether the presence of conspecifics or enhanced soil resources increased the growth and survivorship of a shrub (*Symphoricarpos occidentalis*) and a tree (*Picea glauca*) in the presence of the perennial grass (*Bromus inermis*). Rhizomes of *Symphoricarpos* and seedlings of *Picea* were transplanted into plots either singly or with four conspecific neighbors, and with grass neighbors present or removed. Half the plots received additional water, N, and shade to simulate a forest environment. Roots and shoots of transplants were harvested after two growing seasons. Soil moisture and available N were lowest at high transplant density, and highest in the simulated-forest environment and in treatments where grass was removed. Transplant survivorship was generally enhanced in plots where grasses were removed and in the simulated-forest environment. *Picea* survivorship was reduced by grasses in plots without resource manipulations but was unaffected by grasses in the simulated-forest environment, suggesting that the simulated-forest environment enhanced the ability of *Picea* to compete with grasses. *Picea* growth, however, was reduced by conspecific neighbors in all cases. For *Symphoricarpos,* conspecific neighbors significantly decreased growth rates with grasses absent but significantly increased growth rates with grasses present. Thus the direct effect of high density in monoculture was to reduce *Symphoricarpos* growth, but the indirect effect of high density in the presence of grass was to facilitate *Symphoricarpos* growth. In summary, conspecific neighbors increased the growth rate of *Symphoricarpos* in competition with grass, and a simulated-forest environment enhanced the ability of *Picea* to survive in the presence of grasses. The results support the idea that contagious distributions of woody species invading grasslands enhance woody plant establishment.

Key words: Bromus inermis; *competition; facilitation; feedback; indirect effects;* Picea glauca; *plant density; soil water;* Symphoricarpos occidentalis.

INTRODUCTION

Woody plants in nonforested areas are frequently clumped (Bailey and Wroe 1974, Yarranton and Morrison 1974, Archer et al. 1988, Kellman and Kading 1992, Magee and Antos 1992, Teague and Smit 1992, Thiery et al. 1995, Milne et al. 1996). Clumps probably reflect seed dispersal patterns and vegetative spread (Payette and Filion 1985, Thiery et al. 1995, Greene and Johnson 1996), as well as the patchy distribution of suitable establishment sites (Kullman 1995). Whatever their initial cause, clumps of woody vegetation may initiate environmental changes associated with positive feedbacks (Wilson and Agnew 1992). Positive feedback occurs when a change in one part of a system influences a second part in such a way as to induce further change in the first part (DeAngelis et al. 1986). Positive feedbacks between plants and soil are frequently suggested as possible mechanisms underlying vegetation change (Berendse et al. 1989, Armand 1992,

Vetaas 1992, Bertness and Callaway 1994, Wilson 1998) but, outside wetlands (Berendse et al. 1989, Bertness and Yeh 1994, Srivastava and Jefferies 1996), such suggestions have received little experimental attention.

Trees establishing in grassland in clumps may generate positive feedback by increasing soil resource availability. Possible mechanisms include the capture of fog (Wilson and Agnew 1992), rain (Weathers et al. 1995), snow (Payette and Filion 1985), or airborne mineral nutrients (Kellman 1989, Lovett 1992), sheltering nutrient-depositing animals (Wimbush and Forrester 1987, Archer et al. 1988, Belsky 1994), litter deposition (Van Cleve et al. 1983, Facelli and Pickett 1991, Hobbie 1992), or symbiotic N fixation (Chapin et al. 1994). Soils under shrubs or trees tend to have more moisture and available N than soils under adjacent grassland (Petranka and McPherson 1979, Miles 1985, Brady 1990, Jackson et al. 1990, Zak et al. 1990, Callaway et al. 1991, McPherson et al. 1991, Wesser and Armbruster 1991, Belsky 1994, Vieira et al. 1994, Köchy and Wilson 1997). Invading trees are associated with lower organic matter in northern prairie soils (Dormaar and Lutwick 1966, Bettany et al. 1973, Severson and Arneman 1973), possibly because of enhanced min-

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TABLE 1. Available N and soil moisture in prairie and forest ~20 km E of the study site.

Variable	Prairie	Forest	Reference
Soil moisture (%)	5–22	12–19*	Wilson 1993*a*
	5–7	9–11**	Wilson and Kleb 1996
	10–11	9–11	Kelb and Wilson 1997
	12	16***	Köchy and Wilson 1997
Available N (mg N/kg soil)	3–13	5–15*	Wilson 1993*a*
	5–8	5–14**	Wilson and Kelb 1996
	2–3	2–4	Kleb and Wilson 1997
Standing crop (g/m^2)	112	7467**	Wilson 1993*a*

Notes: Means differ between prairie and forest at: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. Ranges are across sample dates (Wilson 1993*a*, Kleb and Wilson 1997) or experimental treatments (Wilson and Kleb 1996). Mean soil moisture across all sample dates in Wilson (1993*a*) was higher in forest.

eralization rates. Environments with high rates of N mineralization may support more standing crop, causing shoot competition to increase in importance (Wilson 1993*a*, 1998), and allowing trees with high stem allocation to better resist competition from grasses (Werner and Harbeck 1982, Tilman 1988, Magee and Antos 1992).

The direct effects of high tree density might be expected to result in decreased growth for individual trees. Conversely, indirect effects could increase individual growth via suppression of neighboring grasses (Miller 1994). We examined these alternatives, and evaluated possible positive feedback mechanisms related to changes in light and soil conditions. Our specific objectives were to test (1) whether growing woody seedlings at high density would increase their ability to compete against grasses, and (2) whether woody plants in a simulated forest environment were less suppressed by grasses than those in an old-field environment.

METHODS

We worked in an old field at the University of Regina, Regina, Saskatchewan (50°26′ N, 104°40′ W) on Dark Brown Chernozemic soil (Agriculture Canada 1992). We conducted the experiment in an old field rather than native prairie because prairie remnants are small and scarce in our region due to cultivation. The field was likely cultivated for several decades until it was planted with the introduced perennial grass *Bromus inermis* (nomenclature follows Looman and Best, 1987), probably in the 1960s. The grass was cut annually for hay until 1991 when it was set aside for research. The vegetation in our experiment was nearly all *B. inermis* (Gerry and Wilson 1995:276).

Average temperatures are $-18°C$ in January and $19°C$ in July (Environment Canada 1982). The mean annual frostless period is 114 d. Mean monthly temperatures during the experiment differed from 30-yr mean monthly temperatures by $<3.5°C$ (Environment Canada, *unpublished data*). Average annual precipitation is 384 mm. Mean monthly rainfall during the experiment was similar to the 30-yr mean, except for

June 1994 and August 1995, when rain was about twice the monthly mean.

Our experiment had four factors, each with two levels: density (one or five transplants), environment (grassland or simulated-forest), grass (present or removed), and transplant species (*Symphoricarpos occidentalis* or *Picea glauca*). There were 40 replicates of each treatment combination with grass present and 20 replicates of each treatment with grass removed, for a total of 480 plots. Replication was higher for the grass-present treatment because we expected higher transplant mortality in this treatment. Each treatment was applied to a plot surrounded by a solid galvanized steel tube (15 cm diameter, 15 cm deep) hammered into the ground in early April 1994. The top of the tube was level with the soil surface. The tube ensured that plant roots interacted and it facilitated root harvest. Plots were separated by 1 m north–south and by 0.5 m east–west so that shades (see next paragraph) did not affect adjacent plots. Treatments were randomly allocated to plots. The experiment ran from spring 1994 until fall 1995.

The grassland level of the environment treatment received no resource manipulation. The simulated-forest level of the environment treatment was designed to reflect the higher levels of soil moisture, available N, and shade associated with forests (Table 1). Precipitation was supplemented in both years by 300 mm/yr, an amount about equal to the mean growing-season precipitation. Water was applied weekly: 10% in June, 40% in July, 40% in August, and 10% in September. This temporal pattern reflected seasonal variability in soil moisture in nearby natural forest (Wilson 1993*a*). N was supplied at 5 g N·m^{-2}·yr^{-1} as commercial urea (NH_2CONH_2). N was applied in both years, with 30% in late May, 50% in late June, and 20% in late July. Similar to water, N availability was designed to follow average seasonal patterns. N was supplied with the last weekly water addition each month. Plots were shaded with 50% shade cloth (45 cm wide, 40 cm high) held vertically by two stakes (Fig. 1). The bottom of the cloth was 10 cm above the ground, 10 cm south of each plot. This arrangement shaded plots without interfering
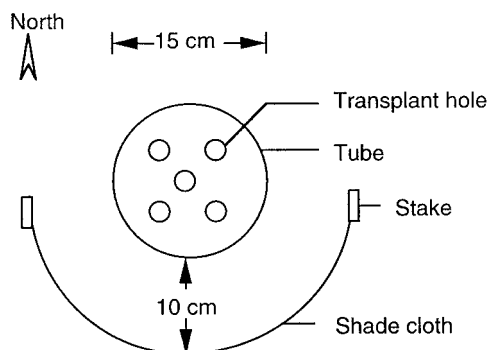
Fig. 1. Arrangement of one plot. Each plot was surrounded by a steel tube (15 cm diameter) driven into the ground with its top flush with the soil surface. Five holes (2 cm diameter) were made in the enclosed soil to receive transplants of woody species. Shade cloth was used only for plots in the simulated-forest environment.

with rain. Fog and dew are uncommon in our dry climate and were probably not influenced by the shades. Shades were removed between September and April so that they would not affect snow accumulation.

Vegetation in plots with grass present was not manipulated. Vegetation in the grass-removal plots was sprayed with glyphosate, a rapidly decomposing, systemic herbicide, in late May 1994. Vegetation within 10 cm of grass removal plots was clipped monthly to prevent shading. Grass mass in June 1994 was 797 ± 344 g/m^2 (mean $\pm$ 1 SD, $N = 30$); height was 21.1 cm ± 5.4.

The two transplant species were chosen for their contrasting growth forms. *Symphoricarpos* is a common rhizomatous shrub 50–100 cm tall that forms circular clones up to 10 m diameter in prairie. It also surrounds individual aspen stands (Coupland 1950) and is the dominant understory species in aspen stands (Kleb and Wilson 1997). *Symphoricarpos* rhizomes were collected in May 1994 from natural prairie 20 km east of the experiment. *Picea* is a dominant tree of boreal forest north of the study site and is interspersed with native prairie in parts of southern Saskatchewan (Zoltai 1975, Pielou 1991). *Picea* seedlings frequently occur in prairie in even-aged clumps ~5 m in diameter, which appear to establish from seed (S. Wilson, *personal observation*). *Picea* seedlings were obtained from a nursery ~400 km north of Regina. Initial *Picea* height was 12.5 ± 2.3 cm (mean $\pm$ 1 SD).

Initial transplant mass was estimated using regression equations relating mass to size, developed from 30 individuals of each species. For *Symphoricarpos,* initial dry rhizome mass (R_d) was predicted from fresh rhizome (R_f) mass (g) ($R_d = -0.0379 + 0.4879R_f$, $r^2 = 0.98$, $P < 0.01$). Initial *Symphoricarpos* mass was 1.01 ± 0.64 g (mean $\pm$ 1 SD). For *Picea,* initial dry shoot (S) and root (R) mass (g) was calculated from stem height (H, cm; $1/S = -0.2726 + 9.8970/H$, $r^2 =$ 0.66, $P < 0.01$; $R = 0.0435H^{1.0791}$, $r^2 = 0.60$, $P < 0.01$). Initial *Picea* mass was 2.66 ± 0.71 g.

Five *Symphoricarpos* rhizomes or *Picea* seedlings were transplanted into each plot of the high density treatment; one transplant was in the center of each plot and the remaining four were planted around it (Fig. 1). One transplant was planted in the center of each low density plot, and four holes surrounding the transplant were made in the same position as the extra transplants in the high density treatment. The extra holes were filled with soil. Transplants were protected from sunlight for the 1st wk by placing shade cloth (50% shade, 40 cm high, 30 cm wide) on the south side of each plot. Seedlings were transplanted in early June 1994, just after the usual date of last frost. During the following 2 wk, dead transplants were replaced with new ones in their original positions.

Picea height was measured in late October 1994 and early April 1995 to determine whether density influenced growth over winter. We measured from ground level to the highest green needle and estimated overwinter growth using the regression equations relating mass to height.

We established 30 additional plots with grass present but without woody targets, in order to measure the performance of grass in the absence of targets. Half the plots were assigned to the simulated-forest treatment to allow us to test the hypothesis that grass is more suppressed by woody plants in this environment.

Soil moisture and available N were sampled on 23 October 1994, and 2 May, 12 June, and 11 August 1995. Sample dates were at least 5 d after rainfall or water addition. One soil sample (2.5 cm diameter, 10 cm deep) was taken from each of 10 randomly chosen plots in each treatment combination on each sampling date. A 10-g subsample was extracted in 50 mL 0.02 mol/L KCl for 6 h and the supernatant was frozen until analysis for available N (sum of ammonium and nitrate) using an ion selective electrode (Orion, Boston, Massachusetts). The remainder of each soil sample was dried to determine water content.

Transplants and grass inside tubes were harvested in early September 1995. Belowground parts were washed and transplants were separated from grass. We measured the root mass (including rhizomes) and shoot mass of transplants and grass in each plot after drying plant material to constant mass at 70°C. Mean transplant mass was determined for the high density plots. Root : shoot ratios were determined for transplants and grass. Transplant relative growth rates (RGR) were calculated as: RGR = $[\ln(M_2/M_1)]/d$ where M_1 is initial biomass, M_2 is final biomass, and d is the length of the growth period in days.

We used three-way contingency table analyses to determine whether survivorship varied with density, environment, or grass removal for each transplanted species. Analysis of variance (ANOVA) was used to examine the effects of density, environment, grass, and

FIG. 2. Survivorship of transplants of a shrub (*Symphoricarpos*) and a tree (*Picea*) grown in an old field for two summers at a density of 1 or 5 transplants per plot, in the environment of the grassland unmanipulated (Gra) or modified to simulate forest (For), with grass present (Pre) or removed (Rem).
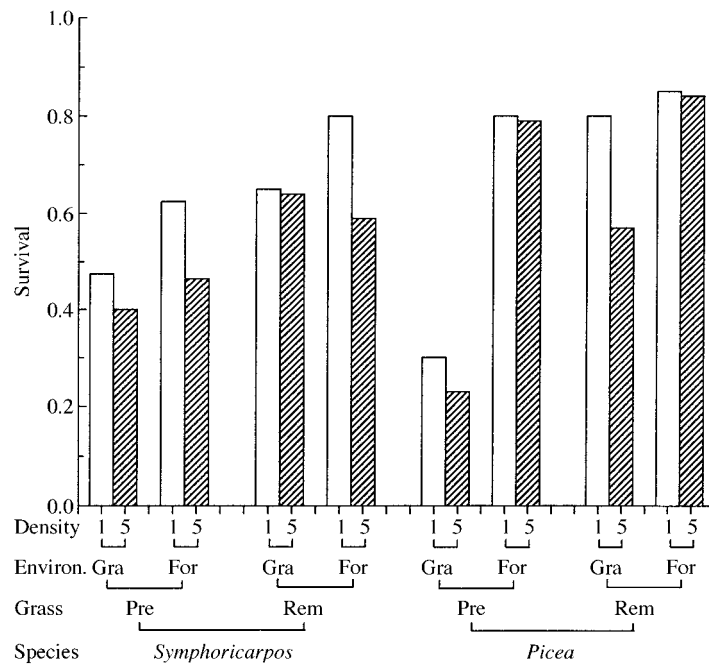
transplant species on transplant growth, root mass, shoot mass, and root : shoot ratios. We analyzed mean values from the high density treatments. Because growth accounts for initial differences in size among transplants, we used growth to test our hypotheses.

ANOVA involving all four factors was also used to examine soil water and N content on each sample date. Data were examined for normality and heteroscedasticity and transformed where necessary.

The response of grass to transplant density, environment, and transplant species was examined with three-way ANOVA. It was not possible to compare grass performance in these treatments with grass performance with no transplants present because this case had only one level of transplant density (0). Therefore, the response of grass biomass and root : shoot ratios to the presence of transplants was examined with two-way ANOVA with environment and target species (none, *Symphoricarpos*, or *Picea*) as main effects. This analysis used data pooled from the two density treatments because the previous analysis showed that transplant density had no significant effect on grass performance.

RESULTS

Competition

Survivorship of *Symphoricarpos* did not vary significantly with any treatment ($\chi^2 = 4.45$, $P > 0.1$), but tended to be higher in the simulated-forest environment and with grass removed (Fig. 2). Survivorship of *Picea* was generally high but did not vary significantly with any factor (Fig. 2; $\chi^2 = 8.98$, $0.05 < P < 0.1$). The results for *Picea* were probably near significant because

survivorship was much lower in the grassland environment with grass present than in any other treatment (Fig. 2). The data suggest that grass decreased *Picea* survivorship in the grassland environment more than in the simulated-forest environment.

Transplant growth rates varied significantly with all main effects (Table 2; see Table 3 for the number of replicates used in analyses). Growth rates were generally lower at high transplant density, higher in the simulated-forest environment, higher in plots with grass removed, and generally higher for *Picea* than *Symphoricarpos* (Fig. 3).

Interactions were of particular interest for testing our hypotheses (Table 2). The significant three-way interaction among density, grass removal, and species allowed us to test the hypothesis that the response of transplants to grass varied with density and between transplant species. We compared means between density treatments at each level of grass treatment for each transplant species (Fig. 4A). Means were compared across environments since there was no four-way interaction involving environment (Table 2). With grass removed, growth rates were significantly reduced at high density for both transplanted species (Fig. 4A). *Picea* growth was also decreased at high density with grass present. *Symphoricarpos* growth rates, however, were significantly greater at high density with grass present. Thus, the growth of one woody species in the presence of grass was significantly enhanced at high density.

Growth rates also varied significantly with the three-way interaction among density, environment, and grass removal (Table 2). This allowed us to test the hypoth-

TABLE 2. F values for the effects of transplant density (D), environment (E), grass removal (G), and transplant species (S) on transplant growth, shoot mass, root mass, and root : shoot ratio (R : S), and on available N and soil water measured four times. In all cases df = 1.

Effect	Growth	Shoot mass	Root mass	R:S	Soil available N			
					Oct	May	Jun	Aug
D	19.18***	53.78***	79.30***	4.88*	2.58	7.08**	1.25	2.92
E	28.11***	60.68***	44.52***	0.02	27.98***	0.47	54.15***	2.59
G	88.93***	58.22***	41.70***	24.23***	53.48***	115.60***	47.90***	4.03*
S	8.13**	552.30***	21.76***	63.75***	3.18	1.87	2.92	2.84
$D \times E$	3.53	16.09***	18.07***	1.5	4.79*	1.6	6.14*	1.99
$D \times G$	6.97**	14.79***	9.05**	1.56	0.74	6.26*	4.59*	0.14
$D \times S$	7.27**	22.90***	1.02	4.68*	0.01	1.49	10.95**	1.18
$E \times G$	2.06	9.02**	16.61***	0.57	21.43***	0.61	31.97***	5.56*
$E \times S$	0.77	20.28***	1.17	0.02	4.82*	1.97	0.3	3.52
$G \times S$	11.16***	7.44**	0.03	23.86***	0.9	2.26	0.42	0
$D \times E \times G$	7.53**	11.94***	15.24***	2.38	0.06	0.81	11.00**	0.1
$D \times E \times S$	0.34	2.76	0.08	1.53	1.4	0.13	4.56*	0.23
$D \times G \times S$	6.57*	1.44	0.18	1.55	0.25	3.21	6.44*	1.93
$E \times G \times S$	2.76	0.00	0.61	0.61	1.74	1.19	0.25	1.27
$D \times E \times G \times S$	0.1	1.05	0.07	2.41	0.35	0.58	3.1	5.45*

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

esis that, for both transplant species considered together, transplants were more suppressed in the grassland environment than in the simulated-forest environment. Growth was significantly reduced by grass at both densities in both environments (Fig. 4B), suggesting that the ability of woody plants to resist suppression from grasses was not enhanced in the simulated-forest environment. The significant interaction was probably attributable to the highest growth rates occurring with grass removed in the simulated-forest environment at low density.

Overwinter growth of *Picea* was significantly higher in plots without grass (Fig. 5) but did not vary significantly with any other factor. Overwinter growth was not consistently higher at high density, so there was no

evidence that conspecific neighbors improved overwinter performance.

Transplant shoot and root mass followed patterns similar to that of growth (Table 3), being greater for *Picea* than *Symphoricarpos,* greater with grass removed, greater in the simulated-forest environment, and greater at low density than high. The significant interaction among density, grass removal, and target species that occurred for growth did not occur for mass (Table 2), probably because initial differences in transplant size tended to increase variance and decreased our ability to detect interactions.

Transplant root : shoot ratios were slightly but significantly lower at high density than at low (Fig. 6; Table 2). Root : shoot ratios did not vary significantly

TABLE 3. Shoot and root mass (mean ± 1 SD) of *Symphoricarpos* and *Picea* grown with grass neighbors present (Pre) and removed (Rem), in the environment of the grassland unmanipulated (Gra) or modified to simulate forest (For), at a density of 1 or 5 transplants per plot.

Species	Grass	Environ.	Density	Shoot mass (g)	Root mass (g)	N
Picea	Pre	For	1	4.13 ± 2.24	1.96 ± 1.00	32
			5	3.02 ± 1.23	1.48 ± 0.58	40
		Gra	1	2.71 ± 1.90	1.56 ± 1.01	22
	Rem		5	1.92 ± 0.96	1.05 ± 0.43	19
		For	1	7.21 ± 2.93	3.48 ± 1.71	17
			5	3.52 ± 1.42	1.74 ± 0.72	20
		Gra	1	3.79 ± 1.44	1.69 ± 0.70	16
			5	2.84 ± 1.29	1.47 ± 0.62	18
Symphoricarpos	Pre	For	1	0.14 ± 0.19	1.44 ± 0.99	28
			5	0.17 ± 0.15	0.75 ± 0.31	38
		Gra	1	0.12 ± 0.37	1.29 ± 1.25	32
			5	0.12 ± 0.12	0.76 ± 0.22	34
	Rem	For	1	1.90 ± 1.26	3.17 ± 1.71	16
			5	0.56 ± 0.31	1.16 ± 0.41	20
		Gra	1	0.40 ± 0.40	1.43 ± 0.76	14
			5	0.34 ± 0.12	0.95 ± 0.25	18

  Notes: N is the number of plots with surviving transplants used in analyses of growth and mass (Table 2). There were initially 40 replicates of all treatment combinations with grass present and 20 with grass removed.

TABLE 2. Extended.

Soil water content			
Oct	May	Jun	Aug
0.23	6.11*	4.76*	20.11***
4.26*	254.50***	5.42*	291.48***
2.24	8.77**	19.29***	1.73
7.81**	21.08***	0.66	0.02
1.28	3.66	0.58	0.12
0.01	10.24**	0.03	0.11
3.85	19.44***	1.4	0.04
0.27	11.90***	0.44	2.06
1.13	2.43	7.26**	19.10***
0.53	104.50***	0.2	0.16
1.3	11.21***	0.05	0.1
10.06**	4.49*	2.07	2.92
1.85	11.38***	1.4	1.81
0.06	117.81***	0.02	0.16
3.07	12.18***	1.56	0.36

between environments. Root:shoot ratios were significantly higher in the presence of grass, and significantly higher for *Symphoricarpos* than *Picea* (note the different scales for each species in Fig. 6). The highly significant interaction between grass removal and transplant species reflected the greater sensitivity of *Symphoricarpos* to the presence of grass; *Symphoricarpos* root:shoot ratios were more than doubled by the presence of grass, while *Picea* was unaffected.

Mass of grass neighbors in plots with surviving transplants was significantly higher in the simulated-forest environment (Fig. 7A) but did not vary significantly with transplant density or species. Similarly, grass biomass was not significantly reduced by the

presence of transplants (Fig. 7B), but was higher in the simulated-forest environment. Grass root:shoot ratios did not vary significantly with any factor (Fig. 7C).

Resources

Soil moisture varied significantly with all four main effects on at least one sample date (Table 2). Soil moisture was significantly lower at high transplant density on three dates (Fig. 8). Moisture was significantly higher in the simulated-forest environment on all dates. Moisture was significantly higher in plots with grass in May but significantly lower in June. Moisture was significantly higher under *Picea* in October 1994 but significantly lower in May 1995. In summary, soil moisture was consistently lower at high transplant density, and higher in the simulated-forest environment.

Available N varied significantly with density only in May (Table 2), when N was lower at high density (Fig. 9). Simulated-forest plots had significantly more N than control plots in October 1994 and June 1995. Grass removal significantly increased N on each date. Transplant species did not differ significantly in their effects on available N.

DISCUSSION

High transplant density significantly enhanced the ability of *Symphoricarpos* to compete against grasses (Fig. 4A). In the absence of grass, *Symphoricarpos* grew better at low than high density. In contrast, with grass present, *Symphoricarpos* growth rates at high density were twice those at low density. The results suggest that the direct effect of high *Symphoricarpos* density, measured in plots without grass, was to decrease *Symphoricarpos* growth, whereas the indirect

FIG. 3. Growth rates (mean + 1 SD; measured as $[\ln (M_2/M_1)]/d,$ where M_1 is initial biomass, M_2 is final biomass, and d is length of the growth period in days) of *Symphoricarpos* and *Picea* grown at a density of 1 or 5 transplants per plot, in the environment of the grassland unmanipulated (Gra) or modified to simulate forest (For), with grass present (Pre) or removed (Rem). ANOVA results are given in Table 2.
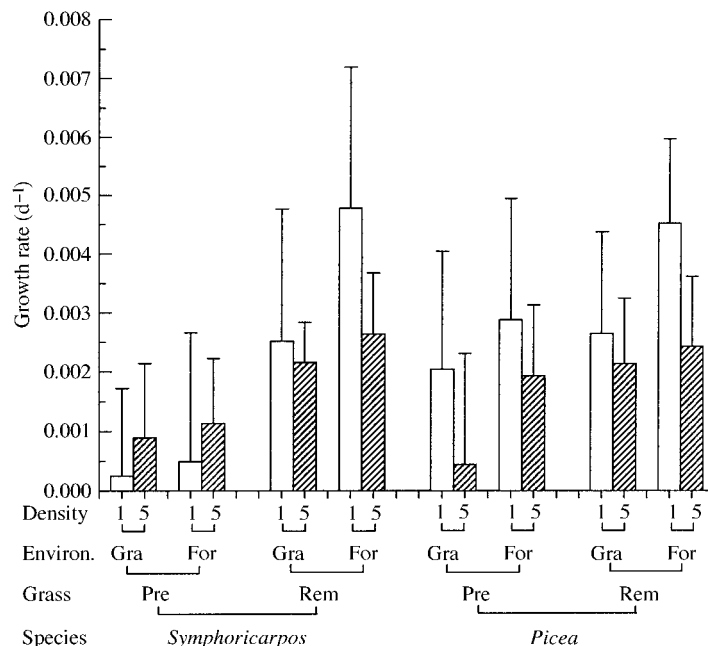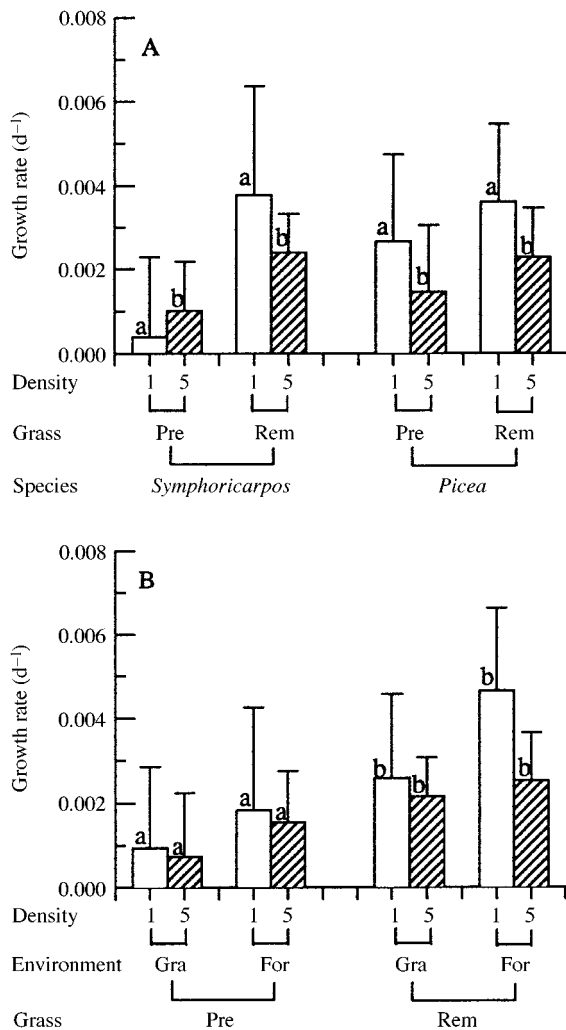
FIG. 4. (A) Growth rates (mean + 1 SD; see Fig. 3) of *Symphoricarpos* and *Picea* grown at a density of 1 or 5 transplants per plot, with grass present (Pre) or removed (Rem). Means were calculated across two environment treatments (Fig. 3), in accordance with the significant three-way interaction among density, grass, and transplant species, and the lack of a four-way interaction involving environment (Table 2). Lowercase letters are for means contrasts between density levels at each level of grass removal for each target species. (B) Growth rates (mean ± 1 SD) of woody transplants grown at densities of 1 or 5 transplants per plot, in the environment of the grassland unmanipulated (Gra) or modified to simulate forest (For), with grass present (Pre) or removed (Rem). Means were calculated across two transplanted species (Fig. 3), in accordance with the significant three-way interaction among density, environment, and grass, and the lack of a four-way interaction involving species (Table 2). Lowercase letters are for means contrasts between grass removal levels at each level of density and environment.

effect of high density in the presence of grass was to increase *Symphoricarpos* growth. *Symphoricarpos* growth was enhanced by conspecific neighbors in the presence of grass (Fig. 3), but final mass was lower with conspecific neighbors (Table 3). The reason for
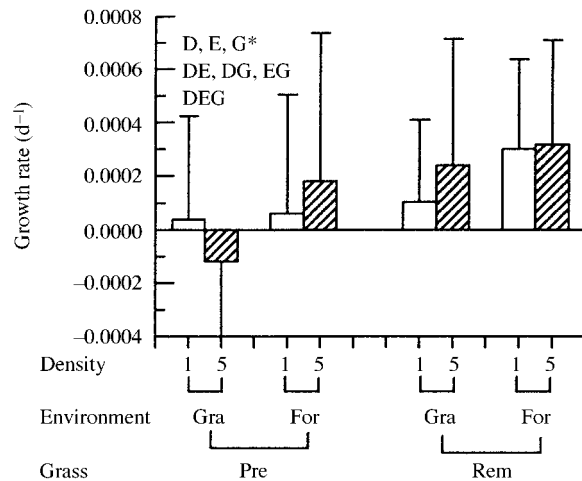

FIG. 5. Growth rate (mean + 1 SD; see Fig. 3) of *Picea* during winter at a density of 1 or 5 transplants per plot, in the environment of the grassland unmanipulated (Gra) or modified to simulate forest (For), with grass present (Pre) or removed (Rem). D, E, G: ANOVA results for main effects (density, environment, grass) and interactions (*$P < 0.05$).

this apparent discrepancy is the lower survival rate with conspecific neighbors (Fig. 2) which caused us to re-place transplants early in the experiment. Replacement transplants were smaller than those used initially. Indirect positive effects were also found for perennial old-field species in a removal experiment by Miller (1994), but he found that positive effects only mitigated negative effects, so that net effects were negative. We may have found positive net effects because of the difference in growth forms between *Symphoricarpos* and its grass neighbors, or because we measured the response of transplants instead of populations.

In contrast, *Picea* growth was not facilitated at high density, possibly because of intense intraspecific competition. Total *Picea* mass at high density was ~1500 g/m² whereas grass mass was ~900 g/m² (Fig. 7A). *Symphoricarpos* mass at high density was ~250 g/m². Similarly, *Picea* shoots may have influenced each other from the start of the experiment, whereas *Symphoricarpos* rhizomes without shoots were probably most affected by grass. Thus *Symphoricarpos* was probably most affected by competition from grass whereas *Picea* was most affected by intraspecific competition, and this may account for decreased *Picea* growth at high density regardless of the presence of grass.

Competition from grass significantly decreased transplant growth (Fig. 3), but transplants had no significant effect on grass mass (Fig. 7B), reflecting the typical asymmetrical effects of established vegetation on seedlings (Goldberg 1990). In contrast, *Symphoricarpos* at high density had positive effects on the growth of conspecifics in the presence of grass, suggesting that high-density *Symphoricarpos* had some kind of negative effect on grass, even though grass mass was not significantly reduced. Spatial variation

FIG. 6. Root : shoot ratios (mean + 1 SD) of *Symphoricarpos* and *Picea* grown at a density of 1 or 5 transplants per plot, in the environment of the grassland unmanipulated (Gra) or modified to simulate forest (For), with grass present (Pre) or removed (Rem). Root : shoot ratios of *Symphoricarpos* have been divided by 10. ANOVA results are given in Table 2.
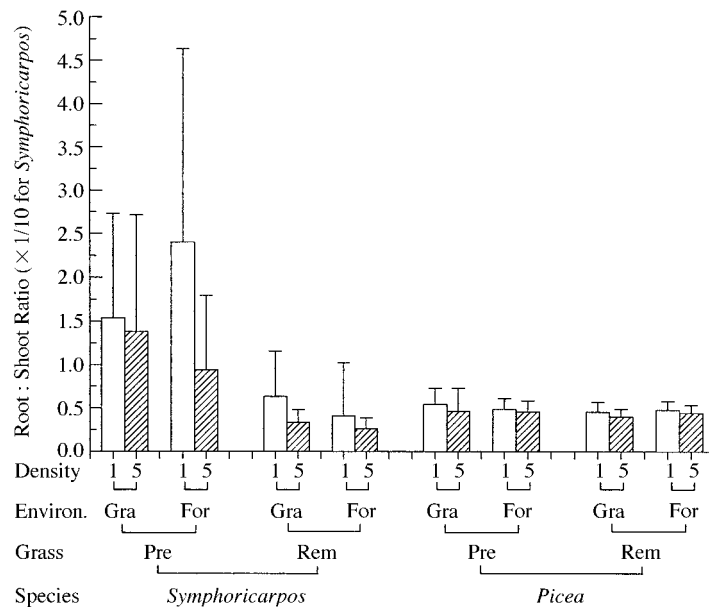
may have made the small reductions of grass mass in the presence of woody transplants (Fig. 7B) nonsignificant. Alternatively, grass may have responded to increased transplant density by decreasing physiological activity, benefiting *Symphoricarpos* without decreasing grass biomass.

Woody plants might be expected to be less suppressed in the simulated-forest environment if competitive abilities vary among environments (Walter 1985, Tilman 1988). Survivorship data supported this idea, with *Picea* survivorship lowest in the grassland environment with grass present but high in the simulated-forest environment with grass present (Fig. 2). Although the simulated-forest environment appeared to enhance the ability of *Picea* to survive in the presence of grasses, growth data did not support variation in competitive abilities. Growth of *Picea* was suppressed by grasses in both environments (Fig. 3), as was the growth and survivorship of *Symphoricarpos*. Similarly, there was no evidence that the ability of transplants to affect grass varied with environment (Fig. 7A). Changes in competitive abilities among environments may occur only for some species at some stages of their life history.

Winter winds have been suggested as a factor excluding trees from treeless areas (Kullman 1995), so trees at high density might provide some shelter and enhance individual growth. Density, however, had no effect on overwinter growth (Fig. 5). Grasses suppressed trees even in winter, as was found above an alpine tree line (Egerton and Wilson 1993).

Removal experiments suggest that competition in our old field is entirely below ground (Gerry and Wilson 1995, Peltzer et al. 1998). Experiments with herbaceous transplant species indicate that competition shifts from

roots to shoots as nutrients increase and light decreases (Wilson and Tilman 1995). As a consequence, the total effect of competition varies little along such gradients. We observed this in our experiment: transplant growth rate showed no significant interaction between environment and grass removal (Table 2), suggesting that competition suppressed transplants to about the same extent in both environmental treatments. Transplant root : shoot ratios may also have reflected changes in root and shoot competition. Root : shoot ratios were significantly higher with grass present (Table 2, Fig. 6), reflecting intense root competition. In contrast, root : shoot ratios were significantly lower at high transplant density (Table 2, Fig. 6), reflecting increased stem allocation due to light competition.

Competitive effects of grasses on *Picea* survivorship appeared to be most intense in the grassland environment: survivorship was high in the forest environment regardless of grass neighbors, but was cut in half in the grassland environment when grass neighbors were present (Fig. 2). In contrast, the survivorship of *Symphoricarpos,* with a much higher root : shoot ratio (Fig. 6), was unaffected by grass neighbors. Similar patterns emerged from comparisons of species with contrasting root : shoot ratios grown with and without neighbors in natural grassland and woody vegetation in experiments nearby (Wilson 1993*a*) and close to an alpine treeline (Wilson 1993*b*): plants with low root : shoot ratios are most susceptible to competition from grass.

Transplant survivorship was never promoted by the presence of grass (Fig. 2), in contrast to many studies which show that neighbors increase survivorship while decreasing subsequent growth (Callaway 1995). Positive neighbor effects on survivorship are often attributable to protection from grazers. There may have been
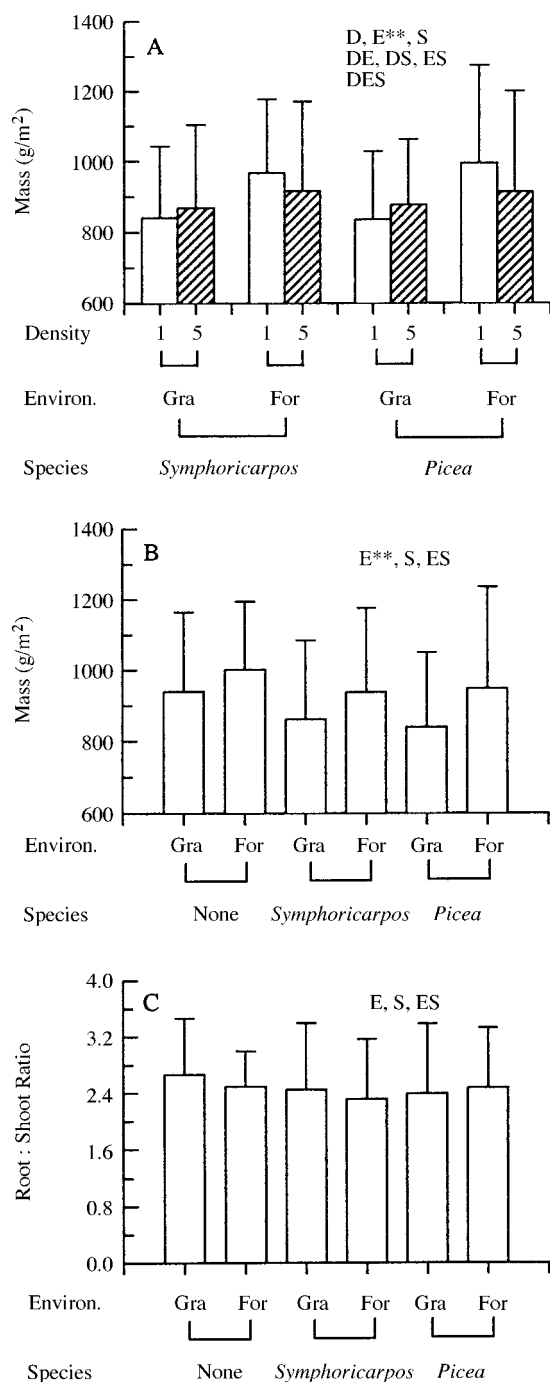
FIG. 7. (A) Mean grass mass at two densities of transplants, in the environment of the grassland unmanipulated (Gra) or modified to simulate forest (For), for two transplant species. D, E, S: ANOVA results for main effects (density, environment, transplant species) and interactions (**$P <$ 0.01). (B) Mean grass mass in the environment of the grassland unmanipulated (Gra) or modified to simulate forest (For), for plots with no woody species transplanted, or with transplants of Symphoricarpos or Picea. (C) Mean grass root: shoot ratios in the environment of the grassland unmanipulated (Gra) or modified to simulate forest (For), for plots with no woody species transplanted, or with transplants of Symphoricarpos or Picea.
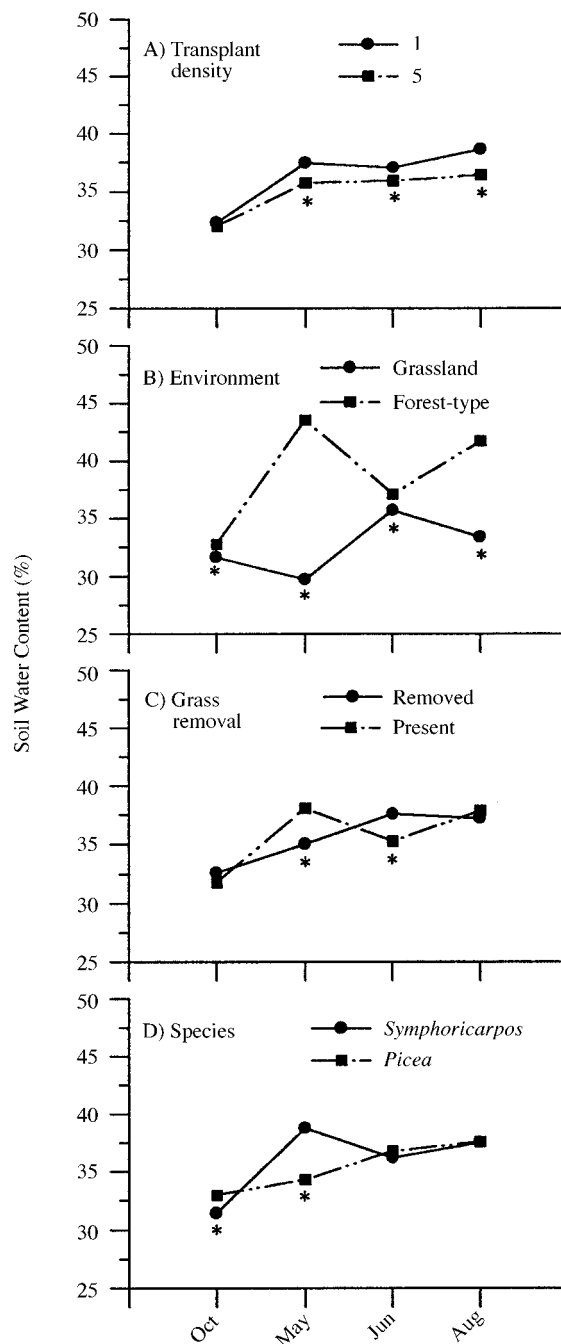
FIG. 8. Mean soil water content for both levels of each of the four main effects: (A) transplant density, (B) environment, (C) grass removal, and (D) transplant species. Asterisks (*) denote significantly different means for each date ($P <$ 0.05; ANOVA results are given in Table 2).

few grazers of Picea and Symphoricarpos at our experimental site, so that the net effect of neighbors on transplant survival was negative. Survivorship might have been lower if we had used smaller transplants.

Resource measurements indicated that our environmental treatment succeeded in creating simulated-for-
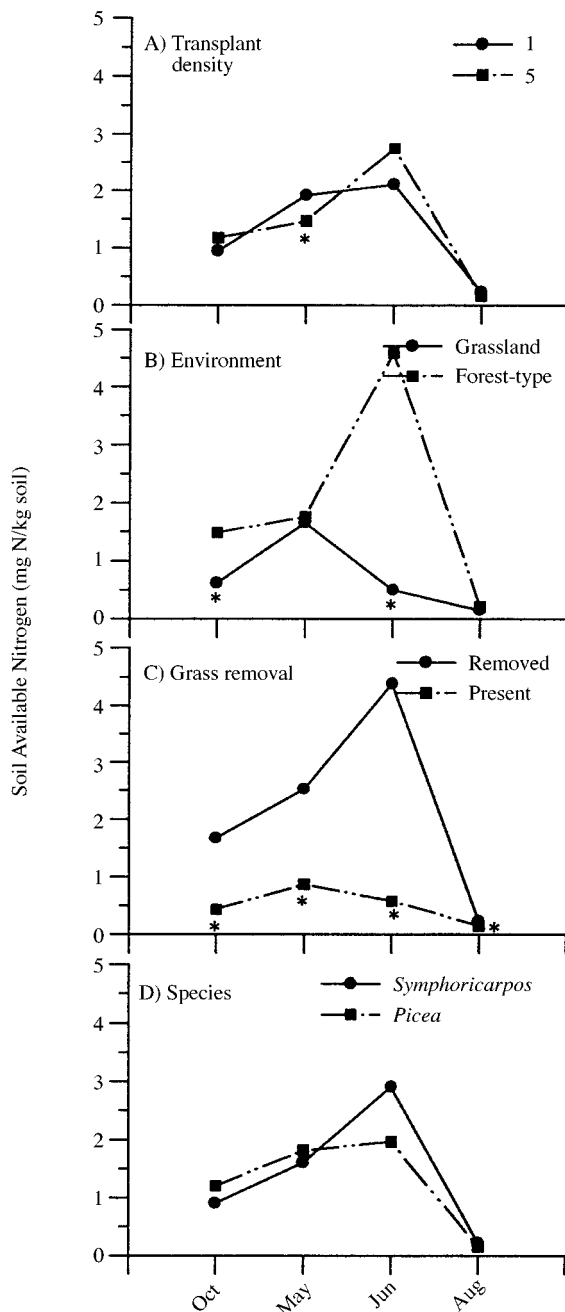
FIG. 9. Mean soil available N (sum of ammonium and nitrate) for both levels of each of the four main effects: (A) transplant density, (B) environment, (C) grass removal, and (D) transplant species. Asterisks (*) denote significantly different means for each date ($P < 0.05$; ANOVA results are given in Table 2). N was added in May, June, and July.

est conditions. Soil water was significantly higher on all sample dates (Fig. 8), consistent with observed higher soil moisture in forest than prairie (Table 1). Soil moisture was higher in our experiment than in nearby prairie, probably because the prairie is a remnant on sandy soil unsuitable for agriculture. Soil avail-

able N was significantly higher in the simulated-forest treatment on two sample dates (Fig. 9), consistent with higher soil N in forest than in prairie (Table 1). Soil N was lower in the experimental old-field than in nearby prairie, probably because of cultivation (Burke et al. 1995).

Both transplant growth and grass biomass were significantly higher in the simulated-forest environment (Figs. 3, 7A). Survivorship also tended to be higher in the simulated-forest environment (Fig. 2). In contrast, the root : shoot ratios of both transplants and grass were not affected by the environment treatment (Table 2, Figs. 6, 7C). Root : shoot ratios usually decrease as soil resources increase (Wilson 1988). This may not have occurred in our experiment because the environment treatment was relatively modest in scale.

We hypothesized that woody plants at high density might initiate positive feedback by enhancing soil moisture and N mineralization, but the results showed the opposite pattern. Soil moisture was always lower at high transplant density (Fig. 8) and soil available N was lower at high density on the single date when it varied significantly between density levels (Fig. 9). The transplants in our experiment had simple uptake effects on resources. More frequent measurements of soil water and more integrative measurements of available N (e.g., mineralization rates) might produce a more accurate picture of woody effects. Alternatively, woody seedlings may have had no positive effect on available N in our experiment because there is relatively little organic matter remaining to be mineralized in previously cultivated soils (Burke et al. 1995). The experiment might detect effects if it were conducted on undisturbed prairie soil with more organic matter. Lastly, more time might be required.

The lack of positive effects on soil resources caused by our transplants contrasts with results from large trees surrounded by grasses and with trees invading grasslands, both of which tend to be associated with higher soil moisture and N availability (Vetaas 1992, Ko and Reich 1993, Wilson 1993a, Belsky 1994). There may be a gradient of effects of woody plants on soil resources, with simple uptake (negative) effects caused by young, small woody plants and positive effects caused by mature trees. Our seedlings were clearly closer to the small end of the gradient. Maximum total transplant mass in our experiment was ~1500 g/m², whereas tree mass in nearby forest is ~7500 g/m² (Table 1). The mass of woody plants, and the time, required for effects on soil resources to change from negative to positive remains to be determined.

Regardless of short-term resource effects, our experiment suggests that indirect positive effects of conspecific neighbors can enhance the ability of woody plants to establish in grasslands. The results also support models invoking positive feedbacks during the invasion of grasslands by woody plants. Implications of positive feedbacks for natural area management include

the possibility that invasions will be irreversible while feedbacks continue.

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