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Competitive abilities of introduced and native grasses

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Abstract

Differences in competitive ability may explain the maintenance of existing plant populations and the invasion of new areas by plant species. We used field experiments to examine the competitive responses of *Agropyron cristatum* (L.) Gaertn., an introduced C_3 grass, and *Bouteloua gracilis* (HBK.) Lag., a native C_4 grass, and the competitive effects of *Agropyron*-dominated vegetation and successional prairie. We also tested whether the outcome of competitive interactions varied with water availability. In each vegetation type, transplants of each species were grown under two levels of competition (presence or absence of neighboring vegetation) and three levels of water availability (high, medium, or low). Transplant survival, growth, and biomass allocation patterns were measured. Water availability had no effect on the measured variables, suggesting that both species were limited by another resource. Growth rates were affected more by competition, while survival and root: shoot ratio were affected more by transplant species identity. In the successional prairie, neighboring vegetation suppressed the growth of *Agropyron* transplants less than that of *Bouteloua* transplants, suggesting that *Agropyron* has a stronger ability to resist competitive suppression in that vegetation type. The spread of *Agropyron* into surrounding vegetation may relate to its ability to resist competitive suppression. In the *Agropyron*-dominated vegetation, neighboring vegetation suppressed the growth of both species by the same extent. However, competition accounted for more variation in transplant growth in *Agropyron*-dominated vegetation than in successional prairie, suggesting that *Agropyron* has strong competitive effects which hinder plant growth and prevent other species from establishing in *Agropyron* fields.

Introduction

Human activity has altered the distribution and abundance of many species (Drake et al. 1989). Once established in new areas, introduced species can alter ecosystem structure and function, and reduce habitat for native plants and animals (Vitousek 1990).

Introduced grasses are especially adept invaders of North American grasslands (D'Antonio and Vitousek 1992). *Agropyron cristatum* (L.) Gaertn., an Asian C_3 grass, has been seeded throughout western North America because it establishes rapidly, prevents erosion, provides nutritious spring forage (Lesica and DeLuca 1996), and produces more forage than native grasses (Lawrence and Ratzlaff 1989). However, *Agropyron* also limits successional changes Looman and Heinrichs (1973), invades adjacent lands (Hull and Klomp 1967), reduces plant and animal diversity (Wilson 1989; Sutter and Brigham 1998), and alters soil chemistry (Dormaar et al. 1995; Christian and Wilson 1999).

Differences in competitive ability may explain the maintenance of existing plant populations and the invasion of new areas by plant species. Competitive ability includes the effect of competition from an individual on neighboring individuals (competitive effect) and the response of an individual to competition from neighboring individuals (competitive response; Goldberg (1990)). The paucity of native species from *Agropyron* fields (Looman and Heinrichs 1973; Wilson 1989; Christian and Wilson 1999) suggests that *Agropyron* is a strong competitor which can displace or prevent the establishment of native species. However, *Agropyron* also responds to competition: neighboring *Bromus inermis* Leyss. suppressed *Agropyron* transplants to about the same extent as it suppressed transplants of *Bouteloua gracilis* (HBK.) Lag., a C_4 grass native to the northern Great Plains of North America (Gerry and Wilson 1995).

We hypothesized that introduced and native grasses would differ in competitive ability and that these differences would be evident in their growth and biomass allocation patterns. To test this hypothesis, we used field experiments to examine the competitive responses of *Agropyron* and *Bouteloua* transplants and the competitive effects of *Agropyron*-dominated vegetation and successional prairie. Transplants were used to avoid interspecific differences in germination and establishment.

In environments with limited productivity, most competition occurs for belowground resources such as water and mineral nutrients (Casper and Jackson 1997). In the northern Great Plains, primary production is strongly correlated with precipitation (Sala et al. 1988), suggesting that water is a limiting resource in this region. In addition, interspecific differences in water use efficiency, ontogenetic patterns (Morgan et al. 1998), and response to summer drought (Frank 1994) suggest that species should respond differently to water availability. We hypothesized that water availability would affect the outcome of competitive interactions. We used high, medium, and low levels of water availability to test this hypothesis.

Methods

Study site

Grasslands National Park (49°22′N 107°53′W) is located in the mixed-grass prairie region of southern Saskatchewan, Canada. The vegetation is dominated by grasses (*Bouteloua*, *Koeleria gracilis* Pers., *Stipa comata* Trin. & Rupr.) and spikemoss (*Selaginella densa* Rydb.; nomenclature follows Barkworth and Dewey (1985) for the Triticaceae and Looman and Best (1987) for all other taxa). The region has a continental climate with average temperatures of − 7 °C in January and 27 °C in July. The average annual precipitation is 313 mm, 46% of which occurs from May through July (Environment Canada 1966–1993). Mean temperatures and precipitation levels experienced during the experiment were within one standard deviation of the long-term (1966–1993) mean.

The experiment was conducted in a field that had been cultivated and abandoned around 1940. After abandonment, part of the field was sown with *Agropyron* and part of it underwent natural succession to dominance by native grasses. As a result, the field contained two vegetation types (*Agropyron*-dominated vegetation and successional prairie) with similar disturbance histories, slopes, and aspects. Soils in the field were loam to clay loams.

Experimental design

We used root exclusion tubes to restrict the competitive interactions of the transplant to a defined area. Each tube (PVC, 10 cm diameter, 15 cm length) was hammered vertically into the ground until its upper edge was 1 cm above the soil surface. Tubes were arranged in a grid with 3 m spacing. Transplants were much smaller (final mass < 1 g) than the soil mass within each tube ($\geqslant$ 1 kg).

Vegetation types were not interspersed, so a separate factorial experiment was performed in each type. The experimental design consisted of 2 competition levels × 3 water availability levels × 2 transplant species. Treatment combinations were replicated 10 times for a total of 120 tubes per vegetation type. Treatments were randomly assigned to tubes.

Two competition levels were used: AN, with all neighbors present, and NN, with no neighbors present. Vegetation in AN tubes was not disturbed. Vegetation in NN tubes was sprayed with a 1% glyphosate [*N*-(phosphonomethyl)glycine] solution two weeks before seedlings were transplanted. Glyphosate degrades rapidly and has no residual activity. Regrowth of neighboring vegetation was continually removed by hand.

High, medium, and low levels of water availability were calculated as the monthly means of the 4 wettest, 4 median, and 4 driest summers (May to August) in the last 30 years at Val Marie, Saskatchewan (about 10 km north of the study site; Environment Canada (1966–1993)). Water was applied biweekly from May to August 1995 using historical monthly precipitation patterns (Figure 1). Natural precipitation was reduced by positioning a 20 × 20 cm piece of colorless Acrylite FF (Johnson Plastics, Winnipeg, Manitoba, Canada) 15 cm above each tube. Acrylite FF is an acrylic material that transmits 92% of light and 89% of solar energy.

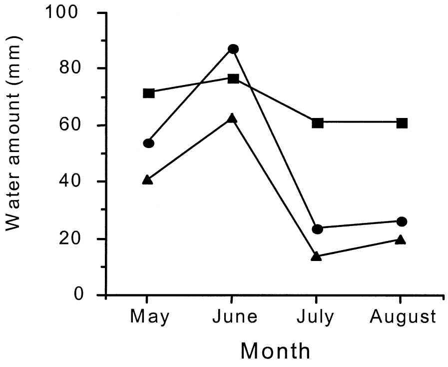

Figure 1. High (squares), medium (circles), and low (triangles) levels of water availability under which transplants were grown.

Agropyron and *Bouteloua* seeds were sown in April 1995 into pots (2.5 cm diameter, 12 cm deep) filled with a 3:1 mixture of peat and local topsoil. After germination, densities were reduced to one individual per pot. Seedlings were grown in a greenhouse at the University of Regina, where they received natural light and daily water. After 5 weeks, seedlings were moved outside for a week of hardening. In late May 1995, seedlings were brought to the study site where one individual was transplanted into the center of each tube. All transplants received 31 mm of water during transplanting and 28 mm a week later to aid establishment, and were shaded for 2 weeks after transplanting to reduce desiccation. Transplants that died within 2 weeks of planting were replaced.

Sampling methodology and analysis

Initial total transplant mass (M_i; dry weight in g) was calculated using species-specific regressions (Gerry and Wilson 1995) with total tiller length (*TTL*; mm):

$$\text{Agropyron}: M_i = [0.000859(TTL) - 0.00174]^2; r^2 = 0.91; n = 10$$

$$\text{Bouteloua}: M_i = [0.000796(TTL) + 0.00458]^2; r^2 = 0.98; n = 10$$

TTL was defined as the sum of the lengths of the longest leaf of each tiller of a transplant and was measured before transplanting. The initial transplant mass of both species was 0.024 g. The initial root: shoot ratios of *Agropyron* and *Bouteloua* were 0.99 and 1.15, respectively.

Transplants were harvested in mid-September 1995. Transplant shoots and aboveground neighboring vegetation were cut and separated, and then each tube, with the soil mass encompassed by it, was removed from the ground. After soaking each soil mass, the transplant root system was carefully teased, in its entirety, from the soil. All remaining roots were assumed to be from neighboring vegetation within the tubes. Root samples were washed to remove all soil from the surface. All vegetation samples were dried to constant mass and weighed.

The relative growth rate (*R*) of each transplant was calculated as:

$$R = [\ln(M_f/M_i)]/d$$

where M_f is final total mass, M_i is initial total mass, and *d* is the number of days between measuring *TTL* and harvest.

Final transplant root: shoot ratios (*R:S*) were calculated as:

$$R{:}S = M_r/M_s$$

where M_r is final root mass and M_s is final shoot mass.

Statistical analyses were performed using JMP statistical software (version 3.0.2; SAS Institute (1994)). Vegetation types were analyzed separately. Log-likelihood ratios tested the effects of competition, water, and species on transplant survival to harvest. Three-way analyses of variance (ANOVAs) tested the effects of competition, water, species, and all interactions on growth rate and on root: shoot ratio.

To further examine the effect of competition on transplant performance, transplant growth (i.e., M_f–M_i) was regressed on aboveground neighbor mass in AN tubes. Aboveground neighbor masses were log transformed to improve the model fit. Linear equations were fit to significant ($P = 0.05$) regressions. The 95% confidence limits of the regressions were compared to detect significant differences among regressions. For each equation, R^2 estimates the proportion of variation in transplant growth that can be accounted for by aboveground neighbor mass, the slope measures the per-gram effect of neighbors on transplant growth (Goldberg 1987), and the y-intercept predicts transplant growth in the absence of neighbors.

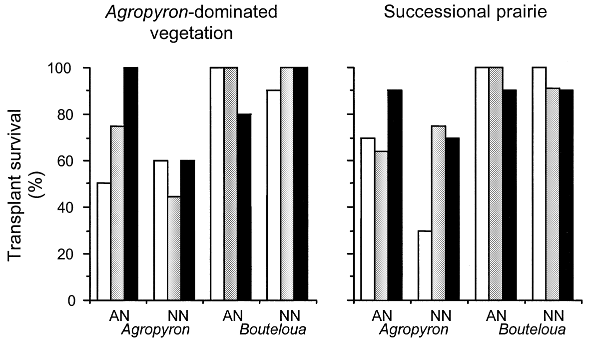

Figure 2. Mean survival of *Agropyron* and *Bouteloua* transplants in *Agropyron*-dominated vegetation and successional prairie grown with all neighbors (AN) or no neighbors (NN) and under low (open), medium (shaded), or high (dark) levels of water availability. Log-likelihood ratio results in (Table 1).

Comparison of vegetation types

The species composition of each vegetation type was assessed in late July 1995 using eight 0.5 × 1.0 m quadrats distributed around the perimeter of each study site. In each quadrat, the percent cover of bare ground, litter, and each plant species was estimated using Daubenmire's scale (Mueller-Dombois and Ellenberg 1974). The 0–5% class was broken into 0–1% and 1–5% classes to more accurately reflect the importance of smaller and infrequent plants. Species richness was calculated for each quadrat.

Shoot mass was sampled by clipping all vegetation 1 cm above the soil surface in a 0.1 m^2 area at each quadrat. Live shoots (the current year's growth) were separated from dead shoots. Root mass was sampled by pooling three soil cores (2 cm diameter, 10 cm depth) per quadrat and washing them to separate roots from soil. Live and dead roots could not be separated. Shoot and root samples were dried to constant mass and weighed. Root: shoot ratios were calculated for each vegetation type.

Differences between vegetation types were tested using Kruskal-Wallis one-way ANOVAs on ranks.

Results

Competition experiments

Variation in water availability had no effect on transplant survival (Figure 2), growth rate (Figure 3), or root: shoot ratio (Figure 4) in either vegetation type. Further, no interactions with water were significant (Table 1).

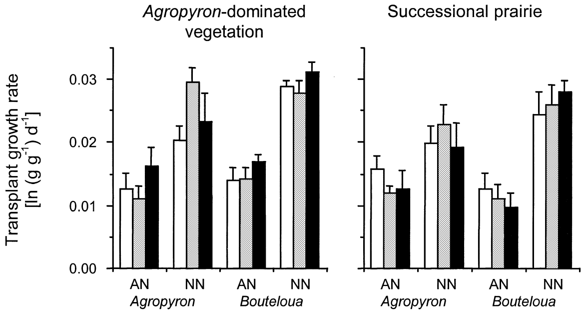

Figure 3. Mean relative growth rate (±SE) of *Agropyron* and *Bouteloua* transplants in *Agropyron*-dominated vegetation and successional prairie grown with all neighbors (AN) or no neighbors (NN) and under low (open), medium (shaded), or high (dark) levels of water availability. ANOVA results in (Table 1).

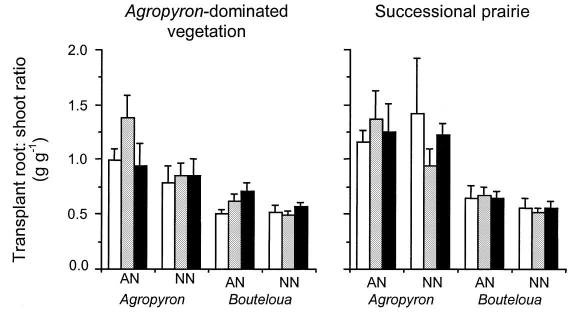

Figure 4. Mean root: shoot ratio (±SE) of *Agropyron* and *Bouteloua* transplants in *Agropyron*-dominated vegetation and successional prairie grown with all neighbors (AN) or no neighbors (NN) and under low (open), medium (shaded), or high (dark) levels of water availability. ANOVA results in (Table 1).

Transplant survival was significantly lower for *Agropyron* than *Bouteloua* in both vegetation types (Figure 2). Survival tended ($P = 0.056$) to be higher when neighbors were present in the *Agropyron*-dominated vegetation but was not affected by the presence or absence of neighbors in the successional prairie. Interactions were not tested as lack-of-fit tests indicated that including them would not improve the model fit.

Transplant growth rate was significantly lower in the presence of neighbors in both vegetation types (Figure 3). In the *Agropyron*-dominated vegetation, transplant growth rate was significantly higher for *Bouteloua* than *Agropyron* and the competition × species interaction was not significant. In the successional prairie, the presence of neighbors had a larger effect on the growth rate of *Bouteloua* than *Agropyron* transplants, producing a significant competition × species interaction. Overall, transplant growth rates were higher in the *Agropyron*-dominated vegetation than the successional prairie.

Table 1. Log-likelihood ratio results for transplant survival (Figure 2) and ANOVA results for relative growth rate (Figure 3) and root: shoot ratio (Figure 4) in *Agropyron*-dominated vegetation and successional prairie. C: competition effect; W: water effect; S: species effect. *: $P < 0.05$; **: $P < 0.01$; ***: $P < 0.001$.

Source	Survival		Relative growth rate			Root: shoot ratio		
	df	G	df	MS	*F*-Ratio	df	MS	*F*-Ratio
Agropyron-dominated vegetation								
C	1	3.663	1	36.428	95.29^{***}	1	0.702	7.52^{**}
W	2	4.220	2	0.682	1.78	2	0.131	1.40
S	1	27.573^{***}	1	2.564	6.71^{*}	1	3.488	37.34^{***}
C × W			2	0.700	1.83	2	0.132	1.42
C × S			1	0.580	1.52	1	0.190	2.03
W × S			2	0.404	1.06	2	0.155	1.66
C × W × S			2	0.899	2.35	2	0.084	0.90
Error			84	0.382		84	0.093	
Successional prairie								
C	1	2.246	1	27.317	45.49^{***}	1	0.474	3.92^{*}
W	2	1.536	2	0.050	0.08	2	0.100	0.83
S	1	18.621^{***}	1	0.565	0.94	1	6.850	56.75^{***}
C × W			2	0.627	1.04	2	0.105	0.87
C × S			1	3.523	5.87^{*}	1	0.120	0.99
W × S			2	0.095	0.16	2	0.031	0.26
C × W × S			2	0.282	0.47	2	0.057	0.47
Error			85	0.601		83	0.121	

Transplant root: shoot ratios in both vegetation types were significantly higher in the presence of neighbors and significantly lower for *Bouteloua* than *Agropyron* (Figure 4). Competition × species interactions were not significant in either vegetation type. Overall, root: shoot ratios were higher in the successional prairie than the *Agropyron*-dominated vegetation.

Transplant growth was significantly negatively correlated with aboveground neighbor mass for both species in both vegetation types (Figure 5). Regression equations did not differ from one another in slope or y-intercept. Aboveground neighbor mass explained up to 40% of the variation in transplant growth, but explained much less of the variation in *Bouteloua* than *Agropyron* growth (Figure 5: R^2 values). Per-gram effects tended to be lower for *Bouteloua* than *Agropyron* (Figure 5: slopes). Predicted and actual growth in the absence of neighbors were similar for *Agropyron* (Figure 5: y-intercepts). Predicted growth was much lower than actual growth in the absence of neighbors for *Bouteloua*.

Comparison of vegetation types

Species richness was significantly higher in successional prairie than *Agropyron*-dominated vegetation (Table 2). *Agropyron* cover was significantly higher in *Agropyron*-dominated vegetation. Covers of all other plants, of litter, and of bare ground either did not differ among vegetation types or were significantly higher in successional prairie.

Live shoot mass was significantly higher in *Agropyron*-dominated vegetation than successional prairie (Table 2). Total root mass was 3–5 times greater than live shoot mass but did not differ between vegetation types, nor did root: shoot ratio.

Discussion

Competition

The results clearly indicate that competition from neighboring vegetation reduced the growth rate and increased biomass allocation to belowground structures in both transplant species. These responses are typical of species competing for belowground resources (Casper and Jackson 1997).

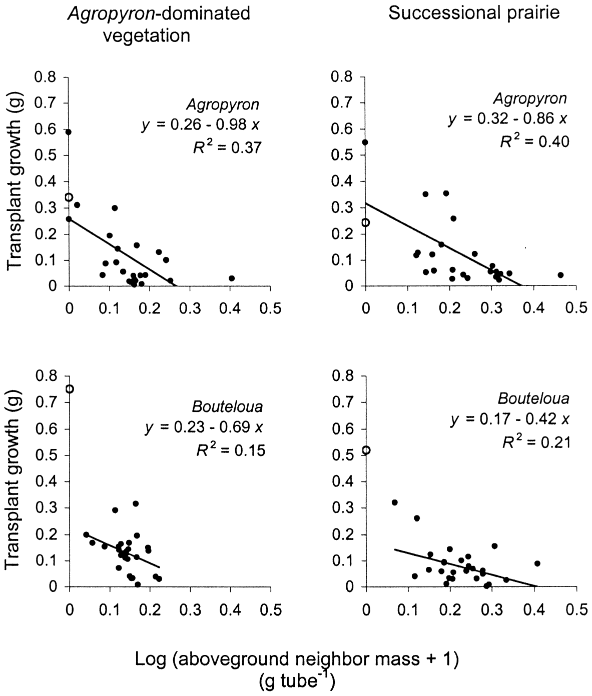

Figure 5. Growth of *Agropyron* and *Bouteloua* transplants as a function of neighbor shoot mass in all neighbor (AN) tubes in *Agropyron*-dominated vegetation and successional prairie. Data are combined across levels of water availability. Lines indicate significant (P = 0.05) regressions. Mean actual growth in no neighbor (NN) tubes, shown by the open symbol on the y-axis of each graph, was not included in the regressions.

Competitive responses varied among vegetation types. In the successional prairie, competition reduced the growth rate of *Bouteloua* by about 60% and that of *Agropyron* by about a third (Figure 3, right), indicating that *Agropyron* had a stronger ability to resist competitive suppression. In Goldberg (1990) terminology, *Agropyron* is a relatively strong response competitor in this vegetation type. The spread of *Agropyron* into native prairie (Coffin et al. 1996) may relate to its ability to resist competitive suppression. In contrast, competition in the *Agropyron*-dominated vegetation reduced the growth of both species by about half (Figure 3, left), indicating that both species were suppressed by about the same extent. Similar results have been reported when *Agropyron* and *Bouteloua* were grown with neighboring *Bromus inermis*, another introduced C_3 grass (Gerry and Wilson 1995). Thus, the ability of *Agropyron* to resist competitive suppression does not explain its dominance in fields of introduced grasses (Table 2).

Competitive effects may prevent other species from establishing in *Agropyron*-dominated vegetation. The F-ratio of the competition term (Table 1) was twice as large in *Agropyron*-dominated vegetation as in successional prairie, suggesting that *Agropyron*-dominated vegetation has strong competitive effects and that competition accounts for more variation in transplant performance in this vegetation type (Underwood and Petraitis 1993). Strong competitive effects would explain why *Centaurea diffusa* Lam., an introduced herb, invaded plots of *Agropyron* at a much lower rate than it invaded unseeded plots or plots of *Elymus junceus* Fisch. (Berube and Myers 1982).

In the absence of neighbors, *Bouteloua* transplants grew larger (Figure 5) and faster (Figure 3) than *Agropyron* transplants. The large difference between predicted and actual growth of *Bouteloua* in the absence of neighbors (Figure 5), however, indicates that even low amounts of neighbors greatly reduced the growth of *Bouteloua*. The first few neighbors appear to have a disproportionately large competitive effect on *Bouteloua*. In contrast, the predicted and actual growth of *Agropyron* in the absence of neighbors were very similar (Figure 5), suggesting that all neighbors had a proportionate effect on Agropyron. This result supports the conclusion that *Agropyron* was less suppressed by neighbors and therefore is a stronger response competitor than *Bouteloua*.

Growth was strongly affected by factors other than competition, since aboveground neighbor mass explained no more than 40% of the variation in transplant growth (Figure 5). Environmental heterogeneity may contribute to the variation in growth: species composition and amount of bare ground varied among tubes. Other factors that could affect transplant growth include genotype, initial mass, and herbivory (Goldberg 1987).

Species identity

Survival and root: shoot ratio were strongly affected by transplant species identity (Table 1). Interspecific differences reflect genetic variation but may also reflect biotic factors such as species-specific herbivory. More insect herbivory was observed on *Agropyron* than *Bouteloua* transplants (J. Bakker, personal observation), which may have contributed to the lower survival (Figure 2) and higher root: shoot ratios (Figure 4) of *Agropyron*. Similarly, the presence of neighbors may have protected transplants from herbivores (Wilson 1994), explaining the tendency for higher survival of *Agropyron* transplants in the presence of

Table 2. Species richness, cover, and biomass (mean±SE) of *Agropyron*-dominated vegetation and successional prairie in Grasslands National Park, Saskatchewan, Canada. $n = 8$ per vegetation type.

Attribute	*Agropyron*-dominated vegetation	Successional prairie	X^2
Species richness (species per 0.5 m^2)	6.4±0.7	10.1±0.6	8.25^{**}
Cover (%)			
Bare ground	30.7±6.6	17.6±4.7	2.09
Litter	7.5±2.2	7.5±2.2	0.00
Agropyron cristatum (L.) Gaertn.	31.9±3.7	0.4±0.4	13.06^{***}
Artemisia frigida Willd.	14.3±7.3	6.0±2.0	0.12
Bouteloua gracilis (HBK.) Lag.	3.9±2.4	4.2±2.4	0.03
Lichens	3.2±1.7	2.7±0.3	1.20
Stipa comata Trin. & Rupr.	0.2±0.1	10.9±7.6	6.67^{**}
Koeleria cristata (L.) Pers.	0.1±0.1	18.8±4.5	9.86^{**}
Selaginella densa Rydb.	0.1±0.1	7.5±2.8	2.14
Pascopyrum smithii (Rydb.) Löve	0.0±0.0	4.9±2.2	8.47^{**}
Poa sandbergii Vasey	0.0±0.0	1.6±0.5	6.67^{**}
Shoot mass (g m^{-2})	80.9±11.2	52.8±3.9	4.41^{*}
Root mass (g m^{-2})	240.1±31.2	248.3±31.5	0.04
Root: shoot ratio	3.3±0.6	5.2±1.1	1.33

neighbors in the *Agropyron*-dominated vegetation (Figure 2).

Over the course of the experiment, *Agropyron* allocated slightly more biomass to roots than shoots while *Bouteloua* allocated almost twice as much biomass to shoots as to roots. These differences in biomass allocation likely reflect ontogenetic patterns, as C_3 species prepare for dry, warm summer conditions by building up belowground reserves (Morgan et al. 1998).

Water availability

The absence of significant effects of water availability may relate to the timing of pulses in relation to plant phenological stage (Bilbrough and Caldwell 1997). Factors that control one stage in a plant's life history may not be critical at another stage. For example, seed germination under water stress and seedling survival under water stress are not correlated in several C_3 and C_4 grasses (Qi and Redmann 1993). In this experiment, water availability did not affect the survival, growth, or biomass allocation patterns of older transplants even though soil water availability strongly controls the germination and establishment of both transplant species (Briske and Wilson 1980; Qi and Redmann 1993; Lauenroth et al. 1994). *Bouteloua* has a high water use efficiency (Morgan et al. 1998) and is physiologically affected by small water events (Sala and Lauenroth 1982), but the growth of individual plants does not appear to be limited by water availability.

Also, processes during the interpulse interval (Goldberg and Novoplansky 1997) may have prevented the detection of significant effects of water availability. Interpulse processes include transplant moisture stress and mortality.

Although community-level production in the northern Great Plains is strongly correlated with precipitation (Sala et al. 1988), water availability was not a limiting factor in the growth or biomass allocation patterns of *Agropyron* or *Bouteloua*. Other resources such as nitrogen may have limited transplant growth (Casper and Jackson 1997). A study in North Dakota found that water availability limited *Pascopyrum smithii* (Rydb.) Löve biomass production and nitrogen availability limited *Agropyron* biomass production (Frank and Ries 1990). Interspecific differences in resource limitation help explain species coexistence and the paradoxical result that water limits community-level production but does not limit the growth of a particular species.

Vegetation types

The presence of *Bouteloua* in both vegetation types (Table 2) suggests that individuals either survived cultivation or invaded from adjacent prairie after cultivation ended. In light of the strong competitive effects of *Agropyron* (Table 1) and the fact that competition from existing vegetation greatly reduces the establishment of *Bouteloua* (Samuel and Hart 1992; Aguilera and Lauenroth 1995), it seems probable that *Bouteloua* establishment occurred before *Agropyron* was sown. Cover of *Bouteloua* was much lower in either vegetation type (4%, Table 2) than in unbroken prairie nearby (15%, Christian and Wilson (1999)), illustrating its slow recovery after disturbance (Samuel and Hart 1994; Coffin et al. 1996).

The community-level characteristics reported by this study (Table 2) correspond with those of many other studies (Hull and Klomp 1967; Smoliak et al. 1967; Looman and Heinrichs 1973; Redente et al. 1989). For example, aboveground production is higher for *Agropyron* than for native species (Lawrence and Ratzlaff 1989) and belowground production is lower (Smoliak et al. 1967) or equal (Redente et al. 1989) than in successional prairie or unbroken prairie. In addition, soil organic matter levels are reduced in *Agropyron*-dominated vegetation (Dormaar et al. 1995). Together, these results suggest that *Agropyron* exports nutrients from the soil (Dormaar et al. 1995; Lesica and DeLuca 1996) and has significant long-term ecosystem effects (Christian and Wilson 1999). Competitive ability is a significant factor contributing to the maintenance of existing *Agropyron* populations and the invasion of new areas by *Agropyron*. Therefore, *Agropyron* will continue to affect ecosystem structure and function in the northern Great Plains for the foreseeable future.

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