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Competitive abilities of native grasses and non-native (*Bothriochloa* spp.) grasses

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INTRODUCTION

North American grasslands continue to be destroyed by expansions of agricultural fields, development, and urban sprawl (Samson and Knopf 1994). In Kansas alone, tallgrass prairie has declined approximately 83% (i.e., 6.9 to 1.2 million ha; Samson and Knopf 1994). Another threat to these native plant communities is the accidental and deliberate introductions of non-native species (Smith and Knapp 1999; Grace et al. 2002). Approximately 60 non-native grass, forb, and woody plant species have been identified as causing concern in the central grasslands (Grace et al. 2002).

Old World Bluestems (OWB; *Bothriochloa spp*.) are one group of non-native, perennial, warm-season grasses that have begun to raise concerns in the central and southern Great Plains (Smith and Knapp 1999; Grace et al. 2002; Reed et al. 2005; Harmoney and Hickman 2004). These grasses were introduced from Europe and Asia in the 1920s (Celarier and Harlen 1955), because of their purported superiority to native grasses (Coyne and Bradford 1985a). Anecdotal evidence in the 1950s suggested OWB were weedy and negatively affected biodiversity (Harlen et al. 1958), and recent studies regarding grassland bird and rodent communities support this claim (Sammon and Wilkins 2005; Hickman et al. 2006).

Superior competitive ability has been suggested as an important plant mechanism by which non-native plant species successfully invade foreign habitats (Baker 1965, 1974; D'Antonio and Vitousek 1992; Sakai et al. 2001). Non-native plant species might be released from constraints of their native environment (i.e., predators and pathogens) allowing individuals of a species in an alien environment to be taller, more vigorous, and produce more seeds than they would in their native environments (Crawley 1987; Blossey 1999; Willis et al. 2000; Stastny et al. 2005). Potentially, this release could enhance the competitive ability of the non-

native species and subsequently promote displacement of native species (e.g., Busch and Smith 1995). In contrast, the competitive ability of native species might be a major defense protecting native habitats from invasion (Crawley 1987; Tilman 1997).

Studies on OWB primarily have focused on forage potential rather than invasion potential. In native pastures invaded by OWB it has been suggested that the native grass species might be selectively grazed by cattle (*Bos taurus*) (Berg and Sims 1984; Harmoney and Hickman 2004), potentially allowing OWB to experience a competitive advantage over the palatable native grasses (Briske 1991; Anderson and Briske 1995). A recent publication (Reed et al. 2005) suggests that OWB might be invading native tallgrass prairie preserves because of their ability to assimilate carbon and specifically nitrogen more efficiently than native grass species. Therefore, our research objectives were to compare the competitive ability (i.e., effect and response) of two OWB species with three warm-season, perennial native grasses.

A target-neighbor design (Goldberg and Fleetwood 1987; Hartnett et al. 1993) was selected in order to reduce environmental variability (Freckleton and Watkinson 2000), assess specific plant characteristics involved in competition (Tilman 1987b), and reduce the threat of escape of the non-native species (Mack 1996). The target-neighbor experiment also allowed for the calculation of both competitive response, the capacity of a species to avoid suppression by another species, and competitive effect, the ability of one species to suppress another species (Goldberg and Fleetwood 1987; Goldberg and Landa 1991). Specifically our questions were 1) do neighbor species type and density significantly affect growth of the target species relative to the control, and 2) do the responses of the target species differ significantly from one another in the presence of the same neighbor species. We hypothesized growth parameters of OWB target individuals would not be affected by the presence of native grass species. We also hypothesized

that OWB neighbors would inhibit growth parameters of native target grass species. We predicted that if our hypotheses were correct, interspecific competition of OWB neighbors would significantly reduce growth parameters of the target native grass species.

METHODS

Experimental Design

Research was conducted from June to September 2003 in a NEXUS (NEXUS Corporation, Northglenn, CO) greenhouse on the Fort Hays State University campus, Hays, KS (38°52'19"N, 99°20'23"W). Greenhouse thermostat was set at 21ºC daytime temperature and 19ºC nighttime temperature, however, daytime temperatures reached as high as 35ºC. The shade cloth was open daily from 0600 h to 1000 h.

Composited native loam soil (62 ppm NO_3^-, 49 ppm P, 357 ppm K, and a pH of 7.6) was collected from the Fort Hays State University Farm, Hays, KS. The non-sterilized soil was sieved through a fine screen (1-cm mesh) to reduce introduction of roots and other plant material into the potting media, and 3.8 L of sieved soil were placed in 4.4-L black plastic pots. In May 2003 seeds of the five warm-season grasses used in our study (Table 1) were germinated in sterile vermiculite. Scientific names and origin are found in Table 1.

Similar sized seedlings (approximately 2 cm in height) were used to initiate the study as follows: a single individual of the target species was transplanted the first week of June 2003 into the middle of the pot and neighbors were placed equidistant around the target at assigned densities (i.e., 0, 2, 4, and 8). To examine effects of both interspecific and intraspecific competition, all pair-wise comparisons among the five plant species were established at all densities. Six replications of each target-neighbor combination were established for a total of 480

pots. To assess competitive interactions, control pots contained only one individual of the target species. All pots were watered daily with a stream adapter. Pots were arranged in a complete randomized block design, on six greenhouse benches. To maintain target-neighbor densities, seedlings that died during the first two weeks of the study were replaced. Pots were removed from the study if death of any seedling occurred two weeks after the beginning of the study. Eight weeks into the study, all pots were fertilized with approximately 350 mL of a commercial fertilizer prepared per label instructions (Miracle-Gro; 20 N: 20 P: 20 K; Scotts Company, Marysville, OH).

At the end of 16 weeks, height (cm) of the tallest vegetative tiller of each plant was measured and aboveground plant material was clipped at 1-cm height. Belowground biomass was harvested by teasing roots of the target species apart from the neighbor individuals and thoroughly washing the roots by using a screen and a fine mist of water. Both aboveground and belowground structures were placed into separate bags (i.e., one for the single target species, and one for all the neighbors), placed in a drying oven (60°C) for at least 48 hours and weighed to the nearest mg.

Statistical Analysis

All statistical analyses were performed by using SPSS statistical package (version 11.5.0, SPSS Incorporated, Chicago, IL). Normal distribution of data was assessed by a Kolmogorov-Smirnov goodness of fit test. Parameters not normally distributed or with unequal variances were appropriately log, squared, or square root transformed.   Statistical significance level used in analysis was $p \leq 0.05$.

Competitive effect was assessed as follows: a multiple analysis of covariance (MANCOVA) was used for each target species to determine if target vegetative tiller height,

aboveground, and belowground biomass at the 16th week differed significantly with neighbor type and neighbor density. If the MANCOVA was significant, a linear regression was conducted to determine if as density increased the growth parameters also increased. If the amount of variation in the data set, according to the adjusted r-squared value, was greater than 0.30 then an analysis of variance (ANOVA) was conducted on the residuals followed by a Tukey HSD (Highly Significant Difference) to determine where significant differences were located between types of neighbor species. If the variation explained was less than 0.30 then the covariate density was eliminated and a multiple analysis of variance (MANOVA) was performed followed by a Tukey HSD.

To calculate competitive response, target aboveground biomass was divided by the mean target aboveground biomass of the control. This proportion was used to detect a significant response of aboveground biomass among all target species when grown with the same neighbor. The same procedure was used to calculate competitive response of target belowground biomass. A MANOVA was performed on target aboveground and belowground biomass for neighbors *Bothriochloa bladhii* and *Schizachyrium scoparium*. An ANOVA was performed on target aboveground biomass for neighbor *Andropogon gerardii*. If significance was obtained by the MANOVAs and ANOVAs, a Tukey HSD was performed to assess the significant differences among the target species. A Kruskal-Wallis test (Zar 1999) was used because equal variances could not be obtained for neighbors *A. gerardii* target belowground biomass, *Bouteloua curtipendula* target aboveground and belowground biomass, and *Bothriochloa ischaemum* target aboveground and belowground biomass followed by a non-parametric Tukey's test (Zar 1999). As a result of multiple analyses for neighbors *A. gerardii*, *B. curtipendula*, and *B. ischaemum*, a Bonferroni correction was calculated using the new significance level: $p \leq 0.025$ ($^{0.05}/_2$).

RESULTS

Competitive effect results for the MANCOVAs are presented in table 2. The neighbor density was not significant or had a low r-squared value for all the species except *S. scoparium*, therefore the following results are MANOVAs. The results for *S. scoparium* are from the Tukey HSD test. Competitive effect results are on a per target species basis, with significance only reported if neighbor species were significantly different from the control (i.e., zero density with no competition occurring). Competitive response results are on a per neighbor species basis.

Competitive Effect:

Target *A. gerardii*

Significant differences were found between the species of the neighbor and vegetative tiller height (F = 9.0, p < 0.001), aboveground biomass (F = 6.7, p < 0.001), and belowground biomass (F = 4.6, p = 0.001) of *A. gerardii*. Vegetative tiller height of target *A. gerardii* was significantly lower relative to the control in the presence of all neighbor species (*A. gerardii*, p = 0.001; *B. bladhii*, p < 0.001; *S. scoparium*, p = 0.002; *B. curtipendula*, p < 0.001; and *B. ischaemum*, p < 0.001; Table 3). Aboveground biomass of *A. gerardii* was significantly reduced relative to the control in the presence of all neighbor species (*A. gerardii*, p = 0.049; *B. bladhii*, p = 0.001; *S. scoparium*, p = 0.015; *B. curtipendula*, p < 0.001; and *B. ischaemum*, p < 0.001; Table 4), whereas, belowground biomass of *A. gerardii* was significantly lower with neighbor species *B. bladhii* (p = 0.027), *B. curtipendula* (p = 0.001), and *B. ischaemum* (p = 0.002; Table 5) compared with the control.

Target *B. bladhii*

The species of the neighbor significantly influenced vegetative tiller height (F = 8.3, p < 0.001), aboveground biomass (F = 6.9, p < 0.001), and belowground biomass (F = 10.0, p <

0.001) of *B. bladhii*. Vegetative tiller height of *B. bladhii* was significantly lower with neighbors *B. bladhii* (p = 0.015), *B. curtipendula* (p = 0.014), and *B. ischaemum* (p = 0.015; Table 3) in comparison to the control. Aboveground biomass of *B. bladhii* was significantly lower with neighbor species *B. bladhii* (p = 0.021), *B. curtipendula* (p = 0.012), and *B. ischaemum* (p = 0.010; Table 4) compared with the control. Belowground biomass of *B. bladhii* was significantly lower than the control with neighbors *B. bladhii* (p = 0.001), *B. curtipendula* (p < 0.001), and *B. ischaemum* (p < 0.001; Table 5).

Target *S. scoparium*

Vegetative tiller height of *S. scoparium* was significantly lower with all neighbor species types except *S. scoparium* compared with the control (*A. gerardii*, p = 0.009; *B. bladhii*, p < 0.001; *B. curtipendula*, p = 0.008; and *B. ischaemum*, p = 0.022; Figure 13).

Aboveground biomass of *S. scoparium* was significantly lower with neighbors *B. bladhii*, (p = 0.010), *B. curtipendula* (p = 0.002), and *B. ischaemum* (p = 0.002; Figure 15) than the control. Belowground biomass of *S. scoparium* was significantly lower with neighbors *B. bladhii*, (p = 0.013), *B. curtipendula* (p = 0.001), and *B. ischaemum* (p = 0.008; Figure 16) than the control.

Target *B. curtipendula*

The species of the neighbor did not significantly influence vegetative tiller height (F = 1.4, p = 0.239) or aboveground biomass (F = 2.2, p = 0.058) of *B. curtipendula* (target), but belowground biomass was significantly influenced (F = 4.2, p = 0.002). Belowground biomass of *B. curtipendula* was significantly lower than the control when the neighbor species were *B. bladhii* (p = 0.020), *B. curtipendula* (p = 0.021), and *B. ischaemum* (p = 0.043; Table 5).

Target *B. ischaemum*

The species of the neighbor significantly influenced vegetative tiller height (F = 6.9, p < 0.001), aboveground biomass (F = 5.6, p < 0.001), and belowground biomass (F = 4.1, p = 0.002) of *B. ischaemum*. Vegetative tiller height of *B. ischaemum* was significantly lower when surrounded by neighbor species *B. bladhii* (p = 0.019; Table 3). Aboveground biomass of *B. ischaemum* was significantly lower when surrounded by neighbor species *B. bladhii* (p = 0.043; Table 4). Belowground biomass of the target was not significantly different from the control compared to any of the neighbor species type.

Competitive Response:

All species showed a significant competitive response (Table 6). The results of the post hoc Tukey's tests are described below.

Neighbor *A. gerardii*

Aboveground biomass for target *S. scoparium* was significantly lower (p < 0.001) compared with all other target species (*A. gerardii*, p = 0.006; *B. bladhii*, p < 0.001; *B. curtipendula*, p = 0.004; and *B. ischaemum*, p = 0.002; Table 7). Belowground biomass of target *S. scoparium* was significantly lower compared with target species *B. bladhii* (p < 0.05), *B. curtipendula* (p < 0.05), and *B. ischaemum* (p < 0.05; Table 8).

Neighbor *B. bladhii*

B. bladhii significantly lowered aboveground biomass of *S. scoparium* compared with targets *A. gerardii* (p = 0.001), *B. bladhii* (p = 0.002), *B. curtipendula* (p < 0.001), and *B. ischaemum* (p = 0.004; Table 7). Belowground biomass of target *S. scoparium* was significantly lower compared with targets *A. gerardii* (p < 0.001), *B. curtipendula* (p = 0.021), and *B. ischaemum* (p = 0.001; Table 8).

Neighbor *S. scoparium*

S. scoparium significantly reduced aboveground biomass of target *S. scoparium* compared with all other target species (*A. gerardii*, p < 0.001; *B. bladhii*, p < 0.001; *B. curtipendula*, p < 0.001; and *B. ischaemum*, p < 0.001). The presence of neighbor *S. scoparium* significantly increased aboveground biomass of *B. curtipendula* compared with target *S. scoparium* (p < 0.001) and significantly decreased aboveground biomass of *B. curtipendula* compared with target *B. ischaemum* (p = 0.019). Neighbor *S. scoparium* significantly increased aboveground biomass of target *B. ischaemum* compared with targets *A. gerardii* (p = 0.013), *B. bladhii* (p = 0.020), *S. scoparium* (p < 0.001), and *B. curtipendula* (p = 0.019; Table 7).

In the presence of neighbor *S. scoparium*, belowground biomass of target *B. ischaemum* was significantly greater than targets *B. bladhii* (p = 0.005), *S. scoparium* (p < 0.001), and *B. curtipendula* (p = 0.008) grown with *S. scoparium*. Neighbor *S. scoparium* significantly increased belowground biomass of targets *B. curtipendula* and *B. bladhii* (p = 0.006; p = 0.008) compared with target *S. scoparium* and significantly decreased belowground biomass of targets *B. curtipendula* and *B. bladhii* (p = 0.008; p = 0.005) compared with target *B. ischaemum*. Neighbor *S. scoparium* significantly lowered belowground biomass of target *S. scoparium* compared with all other target species (*A. gerardii*, p < 0.001; *B. bladhii*, p = 0.008; *B. curtipendula*, p = 0.006; and *B. ischaemum*, p < 0.001; Table 8).

Neighbor *B. curtipendula*

B. curtipendula significantly lowered aboveground biomass of *S. scoparium* compared with targets *B. bladhii* (p < 0.05), *B. curtipendula* (p < 0.05), and *B. ischaemum* (p < 0.05). Aboveground biomass of target *A. gerardii* was significantly lower compared with *B.*

curtipendula (p < 0.05; Table 7). Belowground biomass of *S. scoparium* was significantly

lower compared with *B. curtipendula* (p < 0.05) and *B. ischaemum* (p < 0.05; Table 8).

Neighbor *B. ischaemum*

 B. ischaemum significantly reduced aboveground biomass of *S. scoparium* in comparison

with targets *B. bladhii* (p < 0.05), *A. gerardii* (p < 0.05), *B. curtipendula* (p < 0.05), and *B.*

ischaemum (p < 0.05; Table 7). Belowground biomass of *S. scoparium* was significantly lower

compared with all other target species (*A. gerardii*, p < 0.05; *B. curtipendula*, p < 0.05; and *B.*

ischaemum, p < 0.05; Table 8) except *B. bladhii*.

DISCUSSION

 Research has indicated successful invasion of a plant species into an area is partially

dependent on competition with individual plants already present in the habitat (Turner 1985;

Berlow 1997; D'Antonio et al. 2001). Several researchers have suggested invasive plant species

are competitively superior to native species (e.g., Baker 1965, 1974; Newsome and Noble 1986;

D'Antonio and Mahall 1991; D'Antonio and Vitousek 1992; Blossey and Nötzold 1995;

Londsdale 1999; Sakai et al. 2001), resulting in competitive exclusion of the native species.

 We found the non-native *B. bladhii* and *B. ischaemum* to competitively inhibit some

growth parameters of all native grass species included in our study, supporting our hypothesis

that the non-native grasses would negatively affect the native grasses. *B. bladhii* inhibited at

least one growth characteristic of each of the three native species. *B. bladhii* reduced vegetative

tiller height of *S. scoparium* and *A. gerardii* by as much as 47% and 53%, respectively. The

belowground biomass of target *B. curtipendula* was significantly lower in the presence of *B.*

bladhii, but aboveground growth was not affected. *B. bladhii* showed strong intraspecific

competition, in that it competitively inhibited itself in all growth parameters measured. *B.*

ischaemum, as the neighbor, significantly reduced all growth parameters of the natives *A. gerardii* and *S. scoparium*. Belowground biomass of *B. curtipendula* also was reduced. These results suggest that *B. ischaemum* is a superior competitor when grown in close proximity to the native grass species studied.

Unlike *B. bladhii*, *B. ischaemum* did not show significant intraspecific competition. Connell (1983) determined when intraspecific competition occurs, the plant species no longer has the ability to adequately compete interspecifically. Therefore, we hypothesize *B. ischaemum*. was able to compete more successfully in our study with the native grass species than *B*. bladhii because of the lack of intraspecific competition. Results of our study also indicate most of the native species did not competitively inhibit growth of either OWB species. *A. gerardii* and *S. scoparium*, showed no competitive effect on OWB. In contrast, *B. curtipendula*, as the neighbor, was a significant competitor given that growth parameters of the target species, *B. bladhii*, *A. gerardii*, and *S. scoparium* were all significantly reduced. Based on these results, we hypothesize that in native grasslands dominated by *B. curtipendula*, the competitive ability of *B. curtipendula* might prevent establishment and spread of *B. bladhii* and *B. ischaemum*.

B. bladhii and *B. ischaemum* were successful belowground competitors because both inhibited root production of all native species included in our study. Other pot studies have found that competition for water and nutrients (i.e., belowground competition) were of greater significance than aboveground competition (Eagles 1972; Weiner 1986, 1990) potentially because of limited space.

S. scoparium consistently had a significantly lower response to each of the neighbor species compared with all other target species, suggesting that this native grass species would be

more greatly affected by the presence of an OWB than the other native species studied
(Goldberg and Fleetwood 1987; Goldberg and Landa 1991). *B. ischaemum* was the only target
species to respond positively to a neighbor species, *S. scoparium*. The positive response of *B.
ischaemum* was not predicted by our original hypotheses. Aboveground and belowground
biomass of *B. ischaemum* were increased by 118% to 122%, respectively when grown with *S.
scoparium*. Tremmel and Bazzaz (1993) conducted a target-neighbor study and proposed that
the target plant would have to exhibit morphological and physiological plasticity that would
allow it to compensate for resource acquisition by neighboring plants. Neighbor *S. scoparium*
promoted the growth of *B. ischaemum*, which might be because of aboveground and
belowground morphologic plasticity showed by *B. ischaemum* that provided it with the ability to
overcome the effects of the *S. scoparium* neighbor on resource acquisition.

Callaway and Ashehoug (2000) suggested that plants in alien environments can realize
more of their fundamental niche because natural competitors are not present; thus, these plants
have the ability to become formidable competitors to native grass species. This reasoning, when
combined with the results of our study, suggests that non-native OWB are competitively superior
to the three native grasses, supporting anecdotal evidence of OWB invasions into native
grasslands of the Central and Southern Great Plains. OWB characteristics found in common
with known invasive species (Baker 1965, 1974; Newsome and Noble 1986; D'Antonio and
Vitousek 1992; Blossey and Nötzold 1995; Lonsdale 1999; Sakai et al. 2001) include: 1)
smaller seed size than native plant species (Coyne and Bradford 1985b); 2) plastic morphological
traits that allow adjustment to water and nitrogen deficiencies (Coyne and Bradford 1985a;
Szente et al. 1996; Reed et al. 2005); 3) rapid growth to reach sexual maturity before native grass
species (Harmoney and Hickman 2004); 4) readily breaking off at the lower node (Schmidt and

Hickman 2006); and 5) competitive superiority to three native grass species. Based on the results of this study and previous published research, we propose that OWB pose a significant invasive threat to the native grasslands of the Central and Southern Great Plains.

The goal of our greenhouse study was to quantitatively assess competition among OWB and native grasses under favorable, controlled conditions. To more fully understand the competitive interactions among OWB species and the native grass species used in our study, a field study should be performed testing these hypotheses. In addition, an additional greenhouse study should be conducted to assess potential shifts in competitive interactions in the presence of limited resources and selective herbivory.

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Table 1 - Species descriptions of grasses used in this study

Species	**Description**	**Origin/Importance**
Andropogon gerardii Vitman (big bluestem)	C_4 perennial reproduces asexually by rhizomes and sexually by seed	United States; Dominant in the tallgrass prairie of North America, also found in the mixed-grass prairie; forage for large ungulates, cover for wildlife
Schizachyrium scoparium (Michx.) Nash (little bluestem)	C_4 perennial bunchgrass, reproduces by seed and short rhizomes	United States; Dominant in the mixed-grass prairie of North America, also found in the tallgrass prairie; highly drought tolerant, good forage material, cover for wildlife
Bouteloua curtipendula (Michx.) Torr. (sideoats grama)	C_4 perennial bunchgrass, reproduces by rhizomes	United States; Dominant in the mixed-grass prairie of North America, also found in the tallgrass prairie; highly tolerant of drought and over-grazing, highly palatable, seeds utilized by songbirds and small mammals
Bothriochloa bladhii (Retz.) S.T. Blake [=*Bothriochloa caucasica* (Trin.) C.E. Hubb.] (Caucasian bluestem)	C_4 perennial bunchgrass, reproduces seeds via apomixis	Eurasia; Found in mixed- and tallgrass prairies in North America after being planted; used for erosion control, forage quality limited
Bothriochloa ischaemum (L.) Keng (yellow bluestem)	C_4 perennial bunchgrass, reproduces seeds via apomixis	Eurasia; Found in mixed- and tallgrass prairies in North America after being planted; forage quality limited

Table 2. Competitive effect results of the MANCOVAs, Simple Linear Regressions, and residual ANOVAs for each species vegetative tiller height (VTH), target aboveground biomass (TAG), and target belowground biomass (TBG).

Andropogon gerardii

	Neighbor Species	Neighbor Density	Simple Linear Regression					
			adjusted r^2	F value	p value	equation		
MANCOVA	F = 2.2, p = 0.009	F = 5.4, p = 0.002						
VTH	F = 6.6, p < 0.001	F = 11.8, p = 0.001	0.247	29.5	< 0.001	y = 56.536 - 3.358x		
TAG	F = 4.9, p = 0.001	F = 12.9, p = 0.001	0.200	22.2	< 0.001	y = -0.126 - 0.066x		
TBG	F = 3.5, p = 0.007	F = 3.8, p = 0.056						

Bothriochloa bladhii

	Neighbor Species	Neighbor Density	Simple Linear Regression			
			adjusted r^2	F value	p value	equation
MANCOVA	F = 3.6, p < 0.001	F = 3.1, p = 0.030				
VTH	F = 7.7, p < 0.001	F = 7.9, p = 0.006	0.100	10.5	0.003	y = 72.521 + 1.820x
TAG	F = 5.9, p < 0.001	F = 3.7, p = 0.057				
TBG	F = 8.7, p < 0.001	F = 4.5, p = 0.037	0.088	9.3	0.002	y = 0.015 + 0.032x

Schizachyrium scoparium

	Neighbor Species	Neighbor Density	Simple Linear Regression				ANOVA (residuals)	
			adjusted r^2	F value	p value	equation	F value	p value
MANCOVA	F = 4.7, p < 0.001	F = 24.1, p < 0.001						
VTH	F = 5.4, p < 0.001	F = 35.5, p < 0.001	0.356	50.2	< 0.001	y = 39.697 - 2.200x	5.9	< 0.001
TAG	F = 10.3, p < 0.001	F = 41.9, p < 0.001	0.447	74.7	< 0.001	y = 0.136 - 0.107x	7.9	< 0.001
TBG	F = 9.9, p < 0.001	F = 35.6, p < 0.001	0.418	66.5	< 0.001	y = 0.085 - 0.088x	7.9	< 0.001

Bouteloua curtipendula

	Neighbor Species	Neighbor Density
MANCOVA	F = 1.8, p = 0.038	F = 1.9, p = 0.139

Bothriochloa ischaemum

	Neighbor Species	Neighbor Density	Simple Linear Regression			
			adjusted r^2	F value	p value	equation
MANCOVA	F = 2.6, p = 0.001	F = 5.7, p = 0.001				
VTH	F = 6.9, p < 0.001	F = 10.8, p = 0.001	0.114	11.6	0.001	y = 84.059 - 2.264x
TAG	F = 5.6, p < 0.001	F = 15.3, p < 0.001	0.135	15.3	< 0.001	y = 0.626 - 0.060x
TBG	F = 4.1, p = 0.002	F = 9.1, p = 0.003	0.083	9.3	0.003	y = 0.144 - 0.038x

Table 3. Effect on vegetative tiller height of target species with different neighbor species. Target effects are expressed as a mean value in grams ± S.E. Values within the same column with the same letter are not significantly different from one another.

	TARGET				
	big bluestem	Caucasian bluestem	little bluestem	sideoats grama	yellow bluestem
NEIGHBOR					
Control	71.5 ± 3.1^a	79.9 ± 4.9^a	50.5 ± 4.1^a	69.8 ± 9.9^a	85.5 ± 1.0^a
big bluestem	48.0 ± 5.6^b	75.1 ± 4.2^a	28.1 ± 3.8^b	62.4 ± 6.5^a	79.5 ± 1.7^a
Caucasian bluestem	40.9 ± 4.8^b	57.8 ± 4.3^b	25.1 ± 2.2^b	57.0 ± 4.1^a	61.4 ± 1.4^b
little bluestem	50.4 ± 6.0^b	71.9 ± 5.5^a	34.1 ± 2.1^a	63.5 ± 5.9^a	87.8 ± 1.3^a
sideoats grama	28.4 ± 5.5^b	54.4 ± 4.4^b	27.9 ± 2.2^b	60.1 ± 4.2^a	64.4 ± 1.6^a
yellow bluestem	35.0 ± 3.5^b	57.5 ± 5.4^b	28.8 ± 3.6^b	57.1 ± 4.0^a	80.3 ± 1.7^a

Table 4. Effect on aboveground biomass of target species with different neighbor species. Target effects are expressed as a mean value in grams ± S.E. Values within the same column with the same letter are not significantly different from one another.

	TARGET				
	big bluestem	Caucasian bluestem	little bluestem	sideoats grama	yellow bluestem
NEIGHBOR					
Control	1.128 ± 0.249^a	4.443 ± 0.600^a	2.722 ± 0.586^a	5.247 ± 0.696^a	4.599 ± 0.541^a
big bluestem	0.697 ± 0.280^b	2.584 ± 0.431^a	0.849 ± 0.217^a	3.381 ± 0.517^a	3.048 ± 0.631^a
Caucasian bluestem	0.399 ± 0.199^b	1.551 ± 0.405^b	0.490 ± 0.246^b	2.350 ± 0.444^a	2.121 ± 0.419^b
little bluestem	0.841 ± 0.326^b	2.154 ± 0.383^a	0.717 ± 0.249^a	3.231 ± 0.564^a	5.422 ± 0.584^a
sideoats grama	0.228 ± 0.174^b	1.146 ± 0.319^b	0.367 ± 0.173^b	2.466 ± 0.458^a	2.596 ± 0.520^a
yellow bluestem	0.359 ± 0.158^b	1.009 ± 0.250^b	0.460 ± 0.175^b	2.292 ± 0.528^a	2.824 ± 0.525^a

Table 5. Effect on belowground biomass of target species with different neighbor species. Target effects are expressed as a mean value in grams ± S.E. Values within the same column with the same letter are not significantly different from one another.

	TARGET				
	big bluestem	Caucasian bluestem	little bluestem	sideoats grama	yellow bluestem
NEIGHBOR					
Control	1.031 ± 0.180^a	2.333 ± 0.379^a	2.722 ± 0.480^a	3.294 ± 0.533^a	1.520 ± 0.266^a
big bluestem	0.734 ± 0.319^a	1.238 ± 0.297^a	0.849 ± 0.240^a	2.243 ± 0.421^a	1.272 ± 0.385^a
Caucasian bluestem	0.443 ± 0.197^b	0.739 ± 0.270^b	0.490 ± 0.226^b	1.296 ± 0.361^b	0.815 ± 0.254^a
little bluestem	0.871 ± 0.322^a	1.074 ± 0.278^a	0.717 ± 0.230^a	2.007 ± 0.455^a	1.853 ± 0.321^a
sideoats grama	0.284 ± 0.192^b	0.554 ± 0.200^b	0.366 ± 0.149^b	1.258 ± 0.319^b	0.988 ± 0.288^a
yellow bluestem	0.418 ± 0.171^b	0.536 ± 0.177^b	0.460 ± 0.180^b	1.391 ± 0.382^b	1.170 ± 0.290^a

Table 6 - Competitive response results of ANOVA (F value) and Kruskal-Wallis (H value) tests

Neighbor	Target	Biomass	Test	Test statistic	p value
big bluestem	big bluestem Caucasian bluestem little bluestem sideoats grama yellow bluestem	aboveground	ANOVA	F = 6.7	< 0.001
big bluestem	big bluestem Caucasian bluestem little bluestem sideoats grama yellow bluestem	belowground	Kruskal-Wallis	H = 16.9	0.005
Caucasian bluestem	big bluestem Caucasian bluestem little bluestem sideoats grama yellow bluestem	aboveground	ANOVA	F = 6.4	< 0.001
Caucasian bluestem	big bluestem Caucasian bluestem little bluestem sideoats grama yellow bluestem	belowground	ANOVA	F = 6.2	< 0.001
little bluestem	big bluestem Caucasian bluestem little bluestem sideoats grama yellow bluestem	aboveground	ANOVA	F = 15.5	< 0.001
little bluestem	big bluestem Caucasian bluestem little bluestem sideoats grama yellow bluestem	belowground	ANOVA	F = 12.6	< 0.001
sideoats grama	big bluestem Caucasian bluestem little bluestem sideoats grama yellow bluestem	aboveground	Kruskal-Wallis	H = 32.5	< 0.001
sideoats grama	big bluestem Caucasian bluestem little bluestem sideoats grama yellow bluestem	belowground	Kruskal-Wallis	H = 26.3	< 0.001
yellow bluestem	big bluestem Caucasian bluestem little bluestem sideoats grama yellow bluestem	aboveground	Kruskal-Wallis	H = 30.0	< 0.001
yellow bluestem	big bluestem Caucasian bluestem little bluestem sideoats grama yellow bluestem	belowground	Kruskal-Wallis	H = 30.2	< 0.001

Table 7. Aboveground target species responses with the same neighbor species. Target responses are expressed as a percentage of the mean value of the target divided by the control ± 1 S.E. Values within the same row with the same letter are not significantly different from one another.

NEIGHBOR	TARGET				
	big bluestem	Caucasian bluestem	little bluestem	sideoats grama	yellow bluestem
big bluestem	66.59 ± 23.16^a	73.76 ± 40.89^a	24.09 ± 23.08^b	63.05 ± 45.47^a	65.55 ± 43.41^a
Caucasian bluestem	42.27 ± 16.27^a	42.77 ± 29.35^a	13.4 ± 16.70^b	45.35 ± 37.41^a	46.12 ± 34.32^a
little bluestem	66.53 ± 22.66^{ab}	59.40 ± 34.60^{ab}	21.05 ± 20.34^c	61.16 ± 43.45^b	117.89 ± 54.89^a
sideoats grama	22.83 ± 13.56^{bc}	32.69 ± 27.22^{ab}	10.43 ± 14.31^c	47.94 ± 38.47^a	56.45 ± 37.98^{ab}
yellow bluestem	31.87 ± 14.13^a	28.02 ± 24.45^a	11.49 ± 15.46^b	43.58 ± 39.04^a	60.21 ± 40.36^a

Table 8. Belowground target species responses with the same neighbor species. Target responses are expressed as a percentage of the mean value of the target divided by the control ± 1 S.E. Values within the same row with the same letter are not significantly different from one another.

| | **TARGET** | | | | |
NEIGHBOR	big bluestem	Caucasian bluestem	little bluestem	sideoats grama	yellow bluestem
big bluestem	69.99 ± 22.70^{ab}	64.77 ± 28.36^{a}	31.5 ± 23.15^{b}	66.98 ± 37.14^{a}	83.64 ± 28.19^{a}
Caucasian bluestem	52.48 ± 17.34^{a}	37.21 ± 20.27^{ab}	17.65 ± 16.81^{b}	39.80 ± 27.77^{a}	53.65 ± 21.28^{a}
little bluestem	75.83 ± 22.10^{ab}	54.05 ± 24.42^{b}	26.34 ± 19.96^{c}	60.46 ± 34.23^{b}	121.96 ± 32.09^{a}
sideoats grama	31.19 ± 15.15^{ab}	28.60 ± 18.84^{ab}	13.48 ± 14.28^{b}	38.93 ± 27.47^{a}	64.99 ± 24.42^{a}
yellow bluestem	40.57 ± 15.24^{a}	27.28 ± 17.86^{ab}	16.93 ± 16.46^{b}	42.43 ± 30.52^{a}	75.28 ± 25.94^{a}