

Competition and coexistence in grassland codominants: responses to neighbour removal and resource availability

Andrea M. Silletti, Alan K. Knapp, and John M. Blair

Abstract: We examined the role of interspecific competition in the regulation of abundance and coexistence of the dominant grasses in tallgrass prairie using a removal experiment with *Andropogon gerardii* Vitman and *Sorghastrum nutans* L. Nash, two of the most abundant grasses in tallgrass prairie. Plant removal treatments (using foliar herbicide), applied to 0.3-m² plots at the Konza Prairie Biological Station (northeast Kansas, USA), included removal of all *A. gerardii*, removal of all *S. nutans*, and no removal. To determine whether soil fertility altered the outcome, we included a fertilizer addition treatment (10 g N·m⁻²) fully crossed with the removal treatments. *Andropogon gerardii* removal resulted in significantly increased net photosynthesis, stomatal conductance, and tiller mass in *S. nutans*. *Sorghastrum nutans* removal had little effect on *A. gerardii*, suggesting asymmetric competition. Fertilizer significantly increased tiller mass and flowering stalk production in *S. nutans*, but had little effect on *A. gerardii*. The ability of *A. gerardii* to suppress the performance of *S. nutans* is consistent with the greater abundance of *A. gerardii* over much of the tallgrass prairie, while the ability of *S. nutans* to take advantage of increased resources may be one mechanism by which it avoids competitive exclusion. Because of the greater variability in the performance of *S. nutans* than in that of *A. gerardii*, any natural or anthropogenic alterations to this grassland that lead to shifts in dominance between these species may affect ecosystem productivity and stability.

Key words: *Andropogon gerardii*, competition, grassland, neighbour removal, photosynthesis, *Sorghastrum nutans*, tallgrass prairie.

Résumé : Les auteurs ont examiné le rôle de la compétition interspécifique dans la régulation de l'abondance et de la coexistence des herbes dominantes de la prairie de hautes herbes, dans le cadre d'une expérience d'élimination impliquant l'*Andropogon gerardii* Vitman et le *Sorghastrum nutans* L. Nash, deux des herbes les plus abondantes de la prairie haute. Les traitements d'élimination des plantes (à l'aide d'herbicide foliaire), appliqués sur des parcelles de 0,3 m², à Konza Prairie Biological Station (nord-est du Kansas, USA), incluent l'élimination totale de l'*A. gerardii*, l'élimination totale du *S. nutans*, et aucune élimination. Afin de déterminer si la fertilité du sol affecte les résultats, ils ont inclus un traitement d'addition de fertilisants (10 g N·m⁻²), complètement croisé avec les traitements d'élimination. L'élimination de l'*A. gerardii* conduit à une augmentation significative nette de la photosynthèse, de la conductance stomatale, et de la masse des talles, chez le *S. nutans*. L'élimination du *S. nutans* a peu d'effets sur l'*A. gerardii*, ce qui suggère une compétition asymétrique. Le fertilisant augmente significativement la masse des talles et la production de tiges florifères chez le *S. nutans*, mais a peu d'effet sur l'*A. gerardii*. La capacité de l'*A. gerardii* de diminuer les performances du *S. nutans* est congruente avec la plus grande abondance de l'*A. gerardii*, sur une bonne partie de la prairie de hautes herbes, alors que la capacité du *S. nutans* de tirer profit d'une addition de ressources pourrait être un des mécanismes par lesquels il évite l'exclusion par compétition. À cause de la plus grande variabilité de performance du *S. nutans* que de l'*A. gerardii*, toute altération naturelle ou anthropogène à ces prairies conduisant à un déplacement de la dominance entre ces espèces, pourrait affecter la productivité et la stabilité de l'écosystème.

Mots clés : *Andropogon gerardii*, compétition, prairie, élimination des voisins, photosynthèse, *Sorghastrum nutans*, prairie de hautes herbes.

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Introduction

Interspecific competition can regulate the abundance and diversity of coexisting plant species (Abdul-Fatih and Bazzaz 1979; Armesto and Pickett 1985; Gurevitch and Unnash 1989; Grace and Tilman 1990). In tallgrass prairie, the dominant warm season grasses, or matrix species, have strong competitive effects on the abundance and diversity of subordinate, or satellite (Hanski 1982), species of grasses and forbs (Collins 1987; Gibson and Hulbert 1987; Hartnett and Fay 1998). Consequently, factors that decrease the competitive ability of the dominant grasses, such as selective grazing or suppression of fire, may result in the competitive release of subordinate grasses and forb species (Collins 1987; Vinton et al. 1993; Hartnett et al. 1996). Less well understood are the effects of competition, if any, among the dominant grasses. While it has been suggested that interspecific competition is important among dominant grass species in these grasslands (Weaver and Fitzpatrick 1932; Hanski 1982; Hartnett and Keeler 1995; Hartnett and Fay 1998), experimental tests of this assumption are few. Those studies that have focused specifically on the dominant grasses have examined competition between species that differ in some key attribute, such as mycorrhizal dependence (Hetrick et al. 1994). Others have studied the effects of the entire plant community on a target dominant grass, which does not allow one to determine whether a particular species, or group of species, is responsible for any observed competitive effect (Tilman 1989; Durlia and Reader 1993; Foster 1999; Suding 2002).

The dominant vegetation of the tallgrass prairie of the Flint Hills of central Kansas consists of warm season (C_4) perennial grasses. Two of these grasses, *Andropogon gerardii* Vitman (big bluestem) and *Sorghastrum nutans* L. Nash (Indian grass), occur throughout the tallgrass prairie (Silletti and Knapp 2002) and are usually considered to be codominants. *Andropogon gerardii*, however, is consistently more abundant throughout this grassland (Collins and Glenn 1991; Gibson and Towne 1995). It has been stated, both historically and recently, that the similarities of these grasses in overall size, growth form, and photosynthetic pathway make them "ecological equivalents" (Weaver 1931; Weaver and Fitzpatrick 1932; Polley et al. 1992; Knapp et al. 1998). The much greater abundance of *A. gerardii*, however, suggests some fundamental differences in the interactions of these two species with their biotic or abiotic environments that allow *A. gerardii* to occur in greater abundance than *S. nutans* across the tallgrass prairie landscape. One possibility is that *A. gerardii* is more abundant because it is a stronger competitor (Durlia and Reader 1993). In this case, *S. nutans*, the weaker competitor, may avoid competitive exclusion through nonequilibrium mechanisms initiated by disturbances or driven by resource variability. Alternatively, *S. nutans* may be less abundant because of recruitment limitation or other reasons, yet persists at relatively high abundances because it is a stronger competitor than *A. gerardii* (Rabinowitz et al. 1984).

Long-term experimental manipulations of resources at the Konza Prairie Biological Station have shown that these two species respond differently to variations in availability of nitrogen (N) and water (Silletti and Knapp 2001). At the leaf

level, photosynthesis in *S. nutans* responded positively to the addition of both of these resources, while *A. gerardii* showed no response to either. In addition, a long-term correlative study revealed differences in the responses of these species to fire frequency and precipitation (Silletti and Knapp 2002). Again, the abundance of *S. nutans* was positively correlated with increased fire frequency and precipitation, while *A. gerardii* showed little or no response to any management or climatic variables. In the face of global climate change, differences in the responses of codominant species to environmental changes could have profound impacts on future community structure and ecosystem functioning (Grime 1998). Thus, it is important to understand responses of the codominant species as well as the most abundant species in an ecosystem.

We evaluated interspecific interactions between the tallgrass prairie codominants *A. gerardii* and *S. nutans* under field conditions. A removal experiment assessed the potential effects of one species on the ecophysiology, tiller growth, and reproduction of the other. Removal experiments have effectively demonstrated the occurrence and effects of competition in a field setting in a variety of ecosystems (Allen and Forman 1976; Fowler 1981; Gurevitch and Unnash 1989; Tilman 1989; Aarssen and Epp 1990; Gurevitch et al. 1992). Given the high abundance of *A. gerardii* relative to *S. nutans* and the demonstrated responsiveness of *S. nutans* to changes in resource availability, we predicted an increase in *S. nutans* performance with the removal of *A. gerardii*. Because N is one of the primary factors limiting plant productivity in tallgrass prairie (Knapp and Seastedt 1986; Turner et al. 1997), and to address the issue of whether increased resource availability increases the intensity of competitive interactions (Grime 1979; Tilman 1982), we also incorporated a N fertilization treatment into this field experiment. Given the greater leaf-level response of *S. nutans* to N documented previously (Silletti and Knapp 2001), we expected that N addition would alter competitive interactions in favor of *S. nutans* such that any response to removal of *A. gerardii* would be greater with increased N availability.

Materials and methods

Study site

We worked in the 1998 and 1999 growing seasons (May–October) at the Konza Prairie Biological Station, a 3487-ha tract of pristine tallgrass prairie in the Flint Hills of northeast Kansas, approximately 12 km south of the city of Manhattan (39°05'N, 96°35'W). Average monthly temperatures range from -2.7 °C (January) to 26.6 °C (July), and mean annual precipitation is 835 mm, with 75% falling during the growing season (Bark 1987). The site chosen for this experiment, located at the headquarters area of the Konza Prairie Biological Station, was typical of lowland areas on Konza Prairie, with high annual primary production and strong dominance by C_4 tallgrasses. We chose this particular area because it contained populations of *A. gerardii* and *S. nutans* of approximately equal size, as opposed to other areas of Konza Prairie where *A. gerardii* occurs at much higher abundances than *S. nutans* (Knapp et al. 1998). This site has been burned annually since 1991 and has not been grazed for >20 years.

Plots were established in May 1998 and treatments first applied in May to early June, after the area had been burned and regrowth of vegetation had begun. Six transects were randomly established and approximately sixteen 0.3-m² circular plots were placed along each transect at 1-m intervals. Treatments were applied to the entire 0.3-m² plot, but measurements were confined to the centre 0.1 m² of each plot, with the remaining treated area used as a buffer zone. The area was burned again in April 1999, and the same plots were used in the second year of the study.

Treatments

Treatments were assigned in a completely randomized block design, with two levels of fertilizer (addition of N fertilizer and no fertilizer added) and three levels of neighbor removal (removal of all *A. gerardii* (AR), removal of all *S. nutans* (SR), and no removal) as main effects. The six transects served as blocks, with one fertilized and one unfertilized half per block. The two factors were fully crossed, for a total of six experimental treatments: *A. gerardii* removal without fertilization (AR – N), *A. gerardii* removal with fertilization (AR + N), *S. nutans* removal without fertilization (SR – N), *S. nutans* removal with fertilization (SR + N), and plots with no vegetation removal without and with fertilizer addition (NR – N and NR + N, respectively). Each experimental treatment was applied to approximately 16 plots. Five plots per treatment were used for destructive sampling (sampling that removed plant tissue or soil from the plot during the growing season). A separate set of plots was used for nondestructive sampling. Because of a low number of tillers of the species of interest in some plots and herbicide-induced mortality of nontarget plants, we had an unequal number of plots that could be sampled nondestructively. The resulting sample sizes of nondestructively sampled plots were AR – N, $n = 10$; AR + N, $n = 11$; SR – N, $n = 9$; SR + N, $n = 10$; NR – N, $n = 9$; and NR + N, $n = 9$.

Fertilized plots received the equivalent of 10 g N·m⁻² in the form of ammonium nitrate fertilizer (NH₄NO₃). This rate of application has been shown to significantly increase production in annually burned tallgrass prairie (Turner et al. 1997). The fertilizer was hand broadcast on individual plots after vegetation removal in early June of 1998 and 1999. For the vegetation removal treatment, we applied a foliar herbicide (Roundup™, the isopropyl amine salt of glyphosate; Monsanto Corp., St. Louis, Mo.) to each expanded leaf of the target species in the plot using a small sponge, carefully avoiding herbicide contact with the soil and nontarget vegetation. After treated plants died (10–14 d), the dead above-ground tissue was clipped at ground level and removed from the plot to prevent shading of remaining plants. Removals were first performed in mid- to late May 1998 and repeated in May 1999. Plots were checked periodically throughout each summer and any re-established individuals of a target species were removed in the same way. In both years, all sampling began shortly after the vegetation removal treatment was completed.

Nondestructive sampling

Gas exchange was measured for the codominant species present in each treatment (e.g., *A. gerardii* in *S. nutans* removal plots, and both *A. gerardii* and *S. nutans* in plots with

no vegetation removal). Net photosynthesis (A_{net}) and stomatal conductance to water vapor diffusion (g_s) were measured from June to October of both years using a portable, closed system gas analysis system (LI-6200; LI-COR, Lincoln, Nebr., USA). There were five sampling dates in each year (3 July, 17 July, 12 August, 23 August, and 5 September 1998; 14 June, 25 June, 19 July, 16 August, and 2 September 1999). Five plots per treatment were randomly selected on each sample date for each species, and fully expanded leaves from one to three tillers were measured. Leaf area was determined in the field as the product of the length and width of the leaf material enclosed in the cuvette. All measurements were made at midday (1100–1500, Central Daylight Time) under full sun conditions (photosynthetic photon flux density (PPFD) >1500 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$).

Stem (tiller) densities were determined in the spring (early June) and fall (mid-October) of each growing season. Because the densities of species in a plot varied before the experiment began, we used the change in stem density over a season (fall count – spring count) as one response variable, as the absolute number of stems of a species at the end of the season was not a good indicator of treatment effects. We also examined the change in the number of tillers of each species counted in the spring of each year (spring 1999 – spring 1998) as another to examine whether treatments affected the growth of new tillers at the beginning of the second year.

Flowering stalks (inflorescence plus the stalk supporting it) of *A. gerardii* and *S. nutans* were counted in the fall of each year. Flowering stalk height from the ground surface to the top of the inflorescence was also measured.

In August 1999, light transmission through the plant canopy was quantified in all of the nondestructively sampled plots. Measurements of PPFD were taken above the plant canopy and at four locations at the soil surface with a sun-fleck ceptometer (Decagon, Pullman, Wash.). Transmission was expressed as percentage of above-canopy PPFD available at the soil surface.

After plants had begun to senesce in the fall of each growing season (mid-October), aboveground plant biomass was collected from each of the nondestructively sampled plots. Plants were clipped at ground level and sorted into the following categories: *A. gerardii* flowering stalks; other *A. gerardii* tillers; *S. nutans* flowering stalks; other *S. nutans* tillers; other grass species, sedges, forbs, and woody species; and unidentified litter. End-of-season harvests were considered a “nondestructive” measurement in this case because the next spring fire would remove all of the senesced above-ground biomass at this site. Biomass was oven-dried at 60 °C for at least 48 h, and each category was weighed separately. The harvest was performed concurrently with fall stem density counts, making it possible to calculate mean mass per stem of *A. gerardii* and *S. nutans*.

Destructive sampling

Midday leaf xylem water pressure potential (water potential, Ψ_w) was determined on the same days that gas exchange was measured. Mature upper canopy leaves were collected from one plant per species from each plot, and water potential was measured in a Scholander-type pressure chamber (PMS, Corvallis, Oreg., USA). A total of five plots per treat-

ment were measured on each sample date. At the same time, leaf tissue samples were collected from mature, upper canopy leaves of six or seven plants per species from each plot for leaf tissue chemistry analysis. Leaves were dried at 60 °C for at least 48 h and ground to a fine powder. Total carbon (C) and N concentrations of the tissue were determined by combustion and gas chromatography (Carlo-Erba NA1500, Milan, Italy). This analysis was performed for the 1999 samples only.

Soils from destructively sampled plots were sampled for inorganic N (NO_3^- and NH_4^+) availability once before the fertilizer was initially applied in 1998 (June), in midseason (August), and in late season (October) 1998. Soils were collected from all plots (including nondestructively sampled plots) in October 1999. Three cores (2 cm diameter, 10 cm deep) were taken from each plot at each sampling date. Cores were combined and sieved through 4-mm mesh to remove roots and litter and to homogenize the sample. Inorganic N was extracted from the samples using 2 mol·L⁻¹ KCl, and filtered extracts were analyzed colorimetrically for NO_3^- -N and NH_4^+ -N on an Alpkem FlowSolution auto-analyzer (OI analytical, College Station, Tex., USA).

Statistical analysis

All data were analyzed using mixed-model analysis of variance (SAS Version 8.1; SAS Institute Inc. 1999), with block as a random factor and competition and fertilization as fixed factors. We tested for the main effects of neighbor removal and fertilizer addition and for the interaction between the two. Separate analyses were done for each species. Significance was determined at the $P < 0.05$ level for all analyses. Gas exchange measurements (A_{net} , g_s , and Ψ_w) and total forb biomass showed the same patterns in both 1998 and 1999, so values were pooled across years in a single analysis of all 10 dates. Extractable NO_3^- and total N were $\log(y + 1)$ transformed before analysis to better satisfy ANOVA assumptions, as were the values for mass per tiller ($y^{-1/2}$) and percentage of tillers flowering ($\arcsin(y^{-1/2})$). ANOVA on ranks was performed on NH_4^+ data. In all other cases, raw data were used, and all of the values presented (tables and figures) are means (± 1 SE) of untransformed values.

Results

Efficacy of treatments

Herbicide successfully removed the target plant species from the experimental plots. We removed an average of 66.7 stems of *A. gerardii* in AR plots (range: 20–168), an average of 47.5% of the total number of stems in these plots (range: 14.3%–77.2%). In the SR plots, we removed a mean of 45.2 stems of *S. nutans* (range: 9–99), an average of 34.6% of the total stems in these plots (range: 5%–67.8%). In plots with no vegetation removal, an average of 40.9% of stems were *A. gerardii* and 39.8% of stems were *S. nutans*. We observed little regrowth of either species into removal plots through the experiment.

N addition effectively raised the levels of plant-available N. Before fertilization (early June 1998), there were no significant differences in inorganic N availability between plots assigned to the fertilized and unfertilized treatments (Table 1). Two months after treatment (August), levels of inor-

Table 1. Effect of fertilizer addition (ammonium nitrate equivalent to 10 g N·m⁻²) on soil inorganic N concentrations.

Nitrogen source	N concn. ($\mu\text{g}\cdot\text{g soil}^{-1}$)		df	F	P
	-N	+N			
June 1998					
NO_3^- -N	1.50 (0.39)	1.91 (0.23)	1, 18	1.78	0.1987
NH_4^+ -N	1.06 (0.18)	1.22 (0.19)	1, 18	2.87	0.1074
Total N	2.57 (0.52)	3.14 (0.35)	1, 18	1.56	0.2283
August 1998					
NO_3^- -N	0.71 (0.14)	2.08 (0.28)	1, 23	22.60	<0.0001
NH_4^+ -N	1.32 (0.18)	1.72 (0.20)	1, 23	2.25	0.1471
Total N	2.03 (0.25)	3.81 (0.40)	1, 23	16.07	0.0006
October 1998					
NO_3^- -N	0.51 (0.24)	1.39 (0.26)	1, 24	10.08	0.0041
NH_4^+ -N	0.53 (0.06)	0.87 (0.17)	1, 24	1.95	0.1753
Total N	1.04 (0.27)	2.26 (0.39)	1, 24	9.61	0.0049
October 1999					
NO_3^- -N	0.30 (0.05)	0.72 (0.07)	1, 82	26.24	<0.0001
NH_4^+ -N	1.00 (0.07)	1.07 (0.08)	1, 82	0.35	0.5565
Total N	1.31 (0.11)	1.79 (0.12)	1, 82	8.46	0.0047

Note: Values are means (± 1 SE). +N, fertilizer added; -N, no fertilizer addition; df, Satterthwaite approximate degrees of freedom (numerator, denominator).

ganic N were significantly higher in fertilized than in unfertilized plots (Table 1). The significant difference in total inorganic soil N, due mainly to differences in NO_3^- , persisted throughout the study (Table 1).

Additionally, N fertilization significantly decreased the leaf tissue C/N ratio of both species early in the second season (Table 2). The decrease was significant for the first four sample dates in *S. nutans* and the first three dates for *A. gerardii* (data not shown). The differences in both species became nonsignificant by the end of the second growing season (Table 2).

To compare the availability of resources after 2 years of treatment, we examined soil N and light transmittance at the end of the 1999 growing season. Vegetation removal had no significant effect on total inorganic soil N ($F_{[2,82]} = 0.19$, $P = 0.8312$), and there was no interaction between removal and fertilizer treatments ($F_{[2,82]} = 0.49$, $P = 0.6133$). There was no significant difference between removal treatments in NO_3^- concentrations ($F_{[2,82]} = 0.47$, $P = 0.6268$), although plots with no vegetation removal tended to have more NO_3^- than plots where *A. gerardii* or *S. nutans* had been removed (Fig. 1; top). There was no effect of removal treatments on NH_4^+ concentrations (NR = $1.01 \pm 0.1 \mu\text{g N}\cdot\text{g soil}^{-1}$; AR = $0.89 \pm 0.09 \mu\text{g N}\cdot\text{g soil}^{-1}$; SR = $0.95 \pm 0.1 \mu\text{g N}\cdot\text{g soil}^{-1}$; $F_{[2,82]} = 0.25$; $P = 0.7758$), and there were no interactions between removal and fertilization treatments for either NO_3^- ($F_{[2,82]} = 0.11$; $P = 0.9003$) or NH_4^+ ($F_{[2,82]} = 0.38$; $P = 0.6838$).

While there was no significant effect of the removal treatment on percentage of PPFD transmitted ($F_{[1,52]} = 1.11$; $P = 0.3363$), there was a trend of increasing light availability from NR to SR and AR treatments (Fig. 1; top). There was significantly less PPFD available at the soil surface in fertil-

Table 2. Effect of fertilizer (ammonium nitrate equivalent to 10 g N·m⁻²) on leaf tissue C/N ratios of *Andropogon gerardii* and *Sorghastrum nutans* during the 1999 growing season.

Species	C/N ratio		df	F	P
	-N	+N			
June 1999					
<i>A. gerardii</i>	25.7 (0.5)	21.0 (0.5)	1, 27	56.80	<0.0001
<i>S. nutans</i>	26.9 (0.7)	19.2 (0.4)	1, 26	95.36	<0.0001
September 1999					
<i>A. gerardii</i>	36.1 (1.3)	37.9 (1.0)	1, 26	0.94	0.3415
<i>S. nutans</i>	36.6 (0.6)	35.4 (1.1)	1, 26	0.28	0.4378

Note: Values are mean (± 1 SE). +N, fertilized; -N, no fertilizer addition; df, Satterthwaite approximate degrees of freedom (numerator, denominator).

Fig. 1. Effect of plant removal and fertilization treatments on available soil NO₃⁻-N and transmittance of photosynthetic photon flux density (PPFD) through the plant canopy at the end of the 1999 growing season. AR, removal of all *Andropogon gerardii* from plots; SR, removal of all *Sorghastrum nutans* from plots; NR, no vegetation removed from plots. Fertilization treatments: +N, addition of fertilizer equivalent to 10 g N·m⁻²; -N, no fertilizer addition. Bars with different letters are significantly different at $P < 0.05$. Bars represent ± 1 SE.

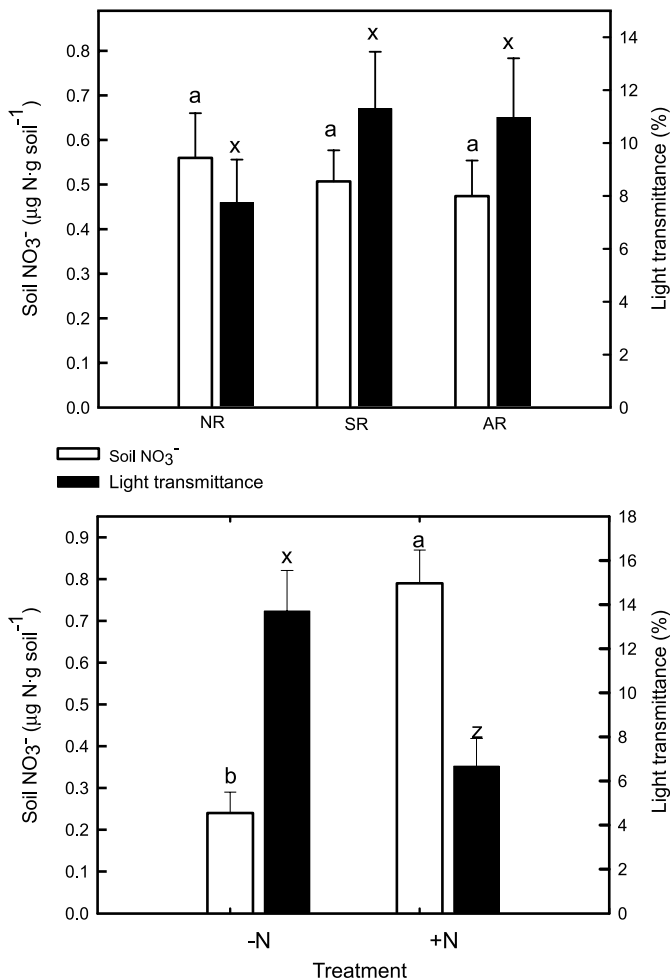


Table 3. Results of mixed-model analysis of variance on eco-physiological responses of *Andropogon gerardii* and *Sorghastrum nutans* to neighbor removal (Comp) and fertilization (Fert) treatments.

Variable	Species	Source of variation	df	F	P
A_{net}	<i>A. gerardii</i>	Comp	1184	2.11	0.1481
		Fert	1184	5.09	0.0252
		Comp \times Fert	1184	1.56	0.2136
	<i>S. nutans</i>	Comp	1188	11.08	0.0010
		Fert	1188	0.02	0.8456
		Comp \times Fert	1188	0.23	0.6356
g_s	<i>A. gerardii</i>	Comp	1184	0.95	0.3302
		Fert	1184	5.03	0.0262
		Comp \times Fert	1184	0.06	0.9542
	<i>S. nutans</i>	Comp	1188	11.00	0.0011
		Fert	1188	1.38	0.2412
		Comp \times Fert	1188	0.24	0.6276
Ψ_w	<i>A. gerardii</i>	Comp	1188	0.51	0.4781
		Fert	1188	0.05	0.8148
		Comp \times Fert	1188	0.09	0.7692
	<i>S. nutans</i>	Comp	1185	0.41	0.5241
		Fert	1185	1.49	0.2233
		Comp \times Fert	1185	0.01	0.9342

Note: df, Satterthwaite approximate degrees of freedom (numerator, denominator); A_{net} , net photosynthesis; g_s , stomatal conductance to water vapor diffusion; Ψ_w , water pressure potential.

ized than in unfertilized plots in 1999 ($F_{[1,52]} = 10.25$; $P = 0.0023$; Fig. 1, bottom).

Leaf-level responses

Because the same pattern of responses was observed in both years, eco-physiological responses were pooled across 1998 and 1999 and analyzed in a single analysis. There were no significant effects of neighbor removal or fertilization on the water potentials of either species (Fig. 2, top; Table 3). Average net photosynthesis and stomatal conductance in *S. nutans* were significantly higher in plots where *A. gerardii* had been removed (Fig. 2; Table 3), but were not significantly affected by fertilization (Fig. 2; Table 3). For *A. gerardii*, fertilizer addition had a significant effect on A_{net} and g_s (Fig. 2; Table 3), while *S. nutans* removal had no significant effect. There were no significant interactions between removal and fertilizer treatments for either species (Table 3).

Stem density

The number of *A. gerardii* tillers was highest in the spring and lowest in the fall of each year for all treatments (Fig. 3). The change in stem density over the growing season was not significantly affected by neighbor removal in 1998 ($F_{[1,29]} = 0.69$, $P = 0.4135$) or 1999 ($F_{[1,28]} = 0.41$, $P = 0.5288$) (Fig. 3). In contrast, tiller densities of *S. nutans* in all plots were lowest in the spring of each season and higher at the end of the growing season (Fig. 3). The seasonal increase in density of *S. nutans* tillers was significantly greater when *A. gerardii* was removed than with *A. gerardii* present, in both growing seasons (1998: $F_{[1,34]} = 8.07$, $P = 0.0075$; 1999: $F_{[1,34]} = 7.95$, $P = 0.0080$) (Fig. 3). Fertilization had

Fig. 2. Midday leaf xylem water pressure potentials (Ψ_w), net photosynthesis (A_{net}), and stomatal conductance to water vapor diffusion (g_s) in *Andropogon gerardii* and *Sorghastrum nutans*. Shown are the effects of addition of 10 g·m⁻² N fertilizer (+N, fertilizer addition; -N, no fertilizer added) and neighbor removal (AR, removal of all *A. gerardii* from plots; SR, removal of all *S. nutans* from plots; NR, no vegetation removed from plots). Asterisks indicate significant differences ($P < 0.05$) between treatment and control within species. Bars represent ± 1 SE.

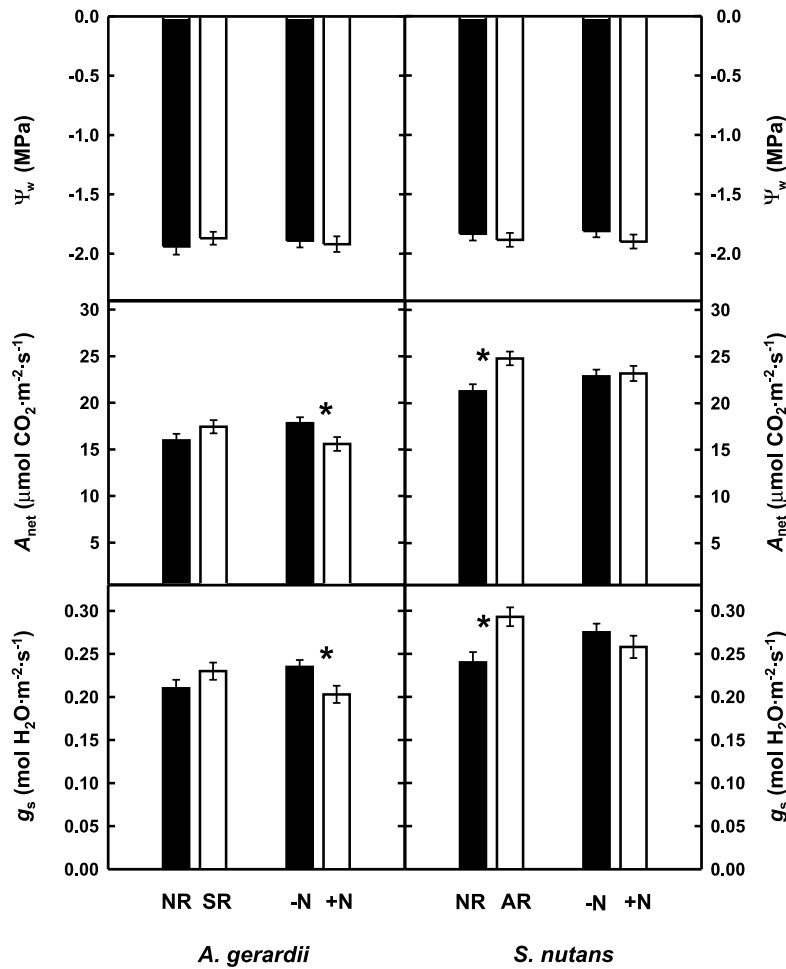


Fig. 3. Change in number of tillers per plot (0.1 m²) from earliest (spring) count for *Andropogon gerardii*, *Sorghastrum nutans*, and all stems in plots with and without neighbor removal (AR, *A. gerardii* removed from plots; SR, *S. nutans* removed from plots; NR, no vegetation removed) in the first (1998) and second (1999) growing seasons. Solid line at zero indicates no change (no. tillers in fall = no. tillers in spring). Means with different letters within species and year indicate significant differences ($P < 0.05$). Bars represent ± 1 SE.

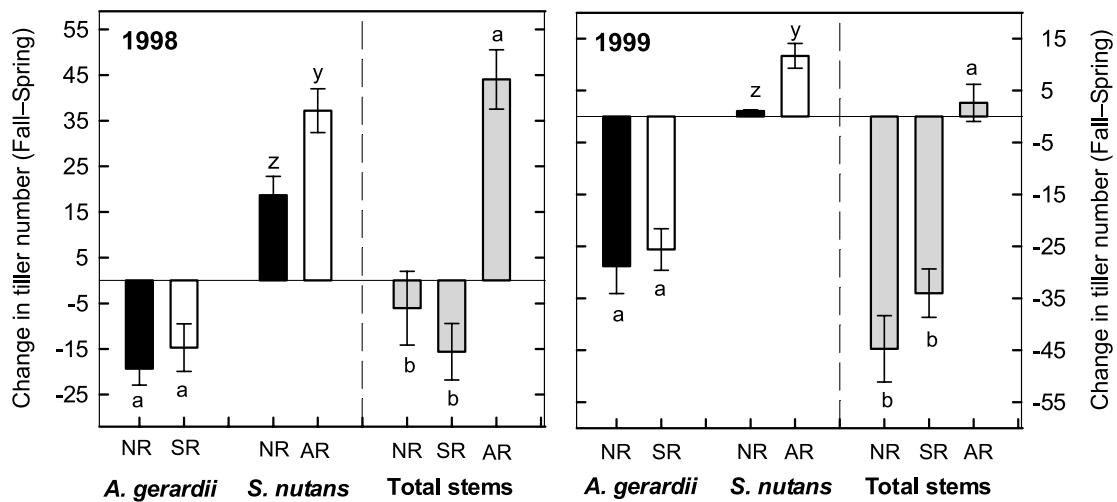
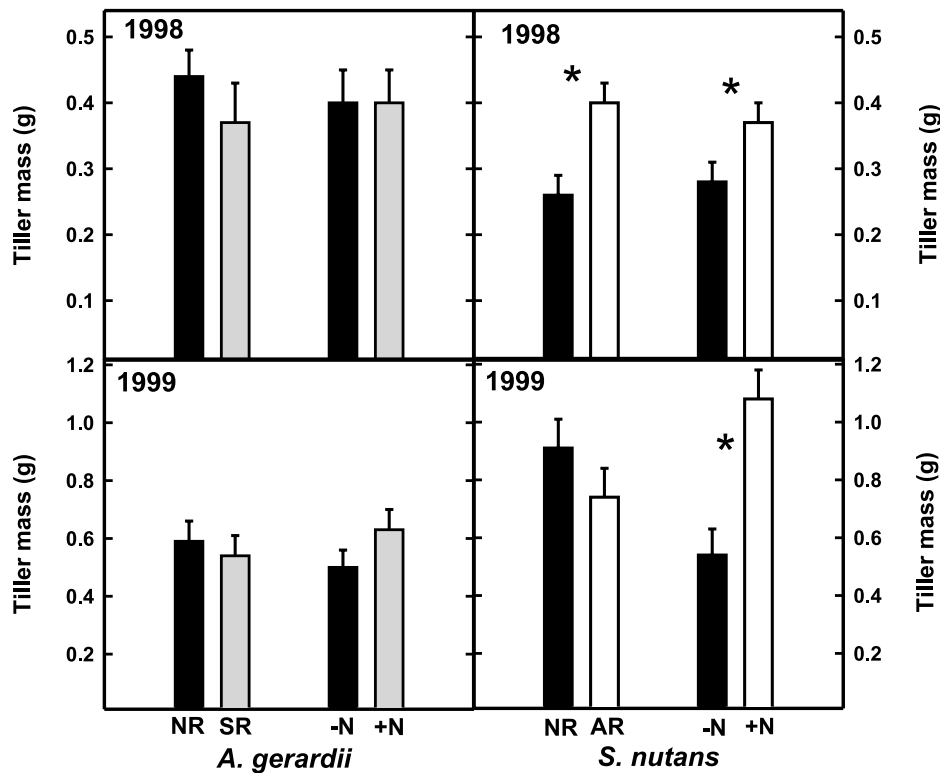


Fig. 4. Mean mass of individual tillers of *Andropogon gerardii* and *Sorghastrum nutans* in 1998 and 1999. Shown are the effects of neighbor removal (AR, removal of all *A. gerardii* from plots; SR, removal of all *S. nutans* from plots; NR, no vegetation removed from plots) and addition of 10 g·m⁻² N fertilizer (+N, fertilizer addition; -N, no fertilizer added). Asterisks indicate significant differences between treatment and control within species and year ($P < 0.05$). Bars represent ± 1 SE.



no effect on the change in tiller density of either *A. gerardii* (1998: $F_{[1,29]} = 3.49$, $P = 0.0720$; 1999: $F_{[1,28]} = 1.68$, $P = 0.2061$) or *S. nutans* (1998: $F_{[1,34]} = 0.44$, $P = 0.5099$; 1999: $F_{[1,34]} = 3.09$, $P = 0.0878$) in either year, and there were no significant interactions between the treatments.

In both growing seasons, the total number of stems of all species in a plot showed significant differences due to the removal treatment (1998: $F_{[1,47]} = 21.51$, $P < 0.0001$; 1999: $F_{[1,46]} = 27.11$, $P < 0.0001$; Fig. 3). As one could predict from the responses of the individual species, in plots where *A. gerardii* was present (SR and NR treatments), the total number of stems in a plot decreased through the growing season, while the number of stems increased through each season in the AR plots. The change in total stem density was not affected by fertilizer addition in either 1998 ($F_{[1,47]} = 0.66$, $P = 0.4193$) or 1999 ($F_{[1,46]} = 0.43$, $P = 0.5167$). We also found no significant treatment effect in either species on the change in the number of tillers counted in the spring of 1999 compared with spring 1998 (data not shown).

While these analyses show the effect of neighbor removal at natural densities, significant effects of removal for *S. nutans*, but not for *A. gerardii*, may have been due to the slightly higher average number of tillers removed in AR plots. To assess this possibility, we adjusted the responses of *S. nutans* to estimate responses for equal numbers of tillers removed in both removal treatments by multiplying the response variable by the average number of *S. nutans* stems removed divided by the average number of *A. gerardii* stems removed as a way to "proportionalize" the level of response

to removal. Analyses using these adjusted values did not alter the pattern seen at actual removal densities.

Biomass

We used average mass per individual tiller (total mass of each species divided by no. tillers counted in that plot) at the end of the growing season as the response variable to determine treatment effects at the level of the individual ramet for *A. gerardii* and *S. nutans*. In 1998, the average mass of individual tillers of *S. nutans* was significantly greater in AR plots than in NR plots ($F_{[1,34]} = 9.60$, $P = 0.0039$; Fig. 4), although this effect was not significant in 1999 ($F_{[1,34]} = 1.93$, $P = 0.1736$). Tiller mass of *S. nutans* was significantly greater in fertilized plots in both 1998 ($F_{[1,34]} = 5.55$, $P = 0.0244$) and 1999 ($F_{[1,34]} = 16.70$, $P = 0.0003$; Fig. 4). There was no significant effect of neighbor removal (1998: $F_{[1,28]} = 0.40$, $P = 0.5334$; 1999: $F_{[1,28]} = 0.02$, $P = 0.8925$) or fertilizer addition (1998: $F_{[1,28]} = 0.15$, $P = 0.7022$; 1999: $F_{[1,28]} = 2.00$, $P = 0.1684$) on the mass per tiller of *A. gerardii* in either year (Fig. 4).

Forb biomass showed the same pattern through both years, so data were pooled across 1998 and 1999, and a single analysis was used to examine treatment effects. Forb biomass was significantly greater in fertilized versus unfertilized plots during the experiment ($-N = 3.56 \pm 0.6$ g·0.1 m⁻²; $+N = 8.09 \pm 1.1$ g·0.1 m⁻²; $F_{[1,111]} = 13.11$; $P = 0.0004$), but there was no significant effect of removal of either *A. gerardii* or *S. nutans* (NR = 5.3 ± 1.1 g·0.1 m⁻²; AR =

Table 4. Flowering stalk (stalk plus inflorescence) production in *A. gerardii* and *S. nutans* for 1998 and 1999 in plots with (+N) and without (-N) addition of the equivalent of 10 g N·m⁻².

Production	<i>Andropogon gerardii</i>					<i>Sorghastrum nutans</i>				
	-N	+N	df	F	P	-N	+N	df	F	P
1998										
No. stalks / m ²	3.5 (1.9)	12.0 (4.8)	1, 28	2.61	0.1176	7.6 (3.3)	20.0 (4.6)	1, 33	4.42	0.0432
Mass/stalk (g)	2.67 (0.22)	2.24 (0.23)	1, 8	0.63	0.4500	2.98 (0.50)	2.28 (0.13)	1, 17	3.23	0.0900
Stalk height (m)	0.96 (0.03)	0.86 (0.05)	1, 8	2.21	0.1752	1.25 (0.09)	1.11 (0.05)	1, 17	3.52	0.0779
Total stalk mass (g/m ²)	9.9 (5.8)	26.3 (10.4)	1, 28	1.65	0.2090	22.4 (9.8)	46.4 (10.5)	1, 33	2.73	0.1081
% tillers flowering	1.01 (0.58)	4.62 (2.59)	1, 28	4.45	0.0439	1.32 (0.56)	2.69 (0.62)	1, 33	4.42	0.0433
1999										
No. stalks / m ²	7.6 (3.6)	13.0 (5.1)	1, 28	0.69	0.4138	38.3 (11.8)	109.5 (12.6)	1, 34	15.82	0.0003
Mass/stalk (g)	3.61 (0.60)	3.57 (0.51)	1, 10	0.13	0.7224	2.70 (0.25)	3.30 (0.18)	1, 31	3.61	0.0669
Stalk height (m)	1.16 (0.10)	1.00 (0.14)	1, 10	1.01	0.3382	1.08 (0.07)	1.18 (0.28)	1, 31	1.88	0.1801
Total stalk mass (g/m ²)	28.8 (14.7)	43.4 (15.6)	1, 28	0.36	0.5542	116.6 (40.7)	377.5 (54.4)	1, 34	13.29	0.0009
% tillers flowering	1.69 (0.78)	3.65 (1.18)	1, 28	1.22	0.2787	8.80 (2.65)	21.06 (2.32)	1, 34	15.21	0.0004

Note: Values are means (± 1 SE). df, Satterthwaite approximate degrees of freedom (numerator, denominator).

5.3 ± 1.1 g·0.1 m⁻²; SR = 6.9 ± 1.1 g·0.1 m⁻²; $F_{[2,111]} = 0.96$; $P = 0.3862$).

To test for cumulative effects of our treatments on the total biomass produced in a plot, we focused on the data from the end of the second growing season. An interaction between the fertilizer and removal treatments led to significant differences in the total biomass in each treatment ($F_{[2,53]} = 3.93$, $P = 0.0257$; Fig. 5).

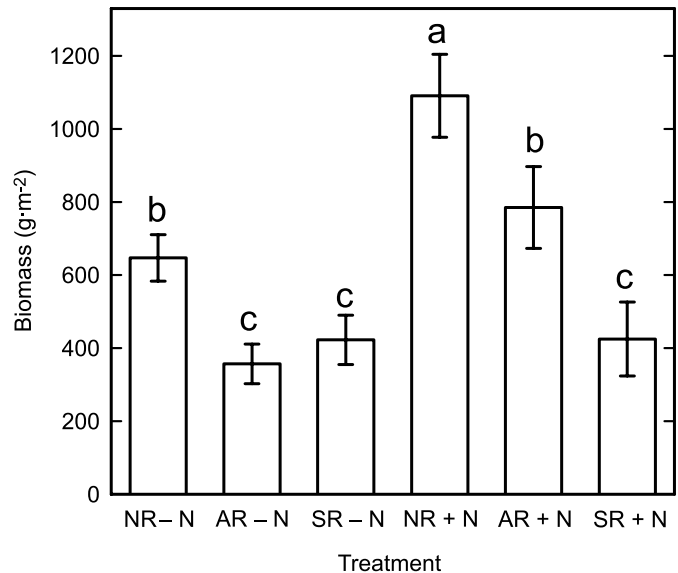
Flowering stalk production

In 1998, the number of flowering stalks of *S. nutans* was significantly higher in fertilized than in unfertilized plots, and the proportion of tillers flowering in both species was significantly higher in fertilized plots (Table 4). In 1999, fertilization significantly increased the number of flowering stalks, the total mass of flowering stalks, and the proportion of tillers flowering in *S. nutans* (Table 4). There was no significant effect of fertilization on any measured parameter of flowering stalk production in *A. gerardii* in 1999 (Table 4). Additionally, other than increasing mass per stalk in *A. gerardii* in 1998, neighbor removal did not significantly affect flowering stalk production in *A. gerardii* or *S. nutans* in either season (Table 5).

Discussion

Interspecific competition is generally regarded as an important factor structuring grassland plant communities (Hartnett and Fay 1998), but the magnitude of competitive interactions between codominant species has not been assessed. Our results suggest that asymmetric competition exists between the tallgrass prairie codominants *A. gerardii* and *S. nutans*, such that the performance of *S. nutans* at the level of the leaf and individual ramet decreased in the presence of *A. gerardii*. The opposite was not true, however, as the performance of *A. gerardii* was not affected by the removal of *S. nutans*. Asymmetric competition is common in plant communities and has been observed in removal experiments in a variety of ecosystems (Allen and Forman 1976;

Fig. 5. Mean total biomass per square metre. Data are from the end of the second growing season (1999). Bars with different letters are significantly different at $P < 0.05$. AR, removal of all *Andropogon gerardii* from plots; SR, removal of all *Sorghastrum nutans* from plots; NR, no vegetation removed from plots. Fertilization treatments: +N, addition of fertilizer equivalent to 10 g N·m⁻²; -N, no fertilizer addition. Bars with different letters are significantly different at $P < 0.05$. Bars represent ± 1 SE.



Fowler 1981; Connell 1983; Schoener 1983; Inchausti 1995; Aksenova and Onipochenko 1998).

These results are consistent with the opportunistic nature of *S. nutans* (Silletti and Knapp 2001), which may allow it to persist as a codominant with *A. gerardii* despite its competitive disadvantage. Indeed, *S. nutans* was able to take advantage of the changes in resource availability associated with removal and fertilization treatments in several ways, while *A. gerardii* was generally unresponsive to most treatments.

At the leaf level, gas exchange of *S. nutans* was higher in plots where *A. gerardii* had been removed (Fig. 2). Photo-

Table 5. Flowering stalk (stalk plus inflorescence) production in *Andropogon gerardii* and *Sorghastrum nutans* for 1998 and 1999 in plots with and without removal of one dominant species.

Production	<i>Andropogon gerardii</i>				<i>Sorghastrum nutans</i>				F	df	P	
	SR	NR	df	F	P	AR	NR	df				
1998												
No. stalks / m ²	5.00 (2.03)	9.44 (4.24)	1, 28	0.56	0.4618	13.16 (0.30)	15.56 (0.56)	1, 33	0.28	0.6022		
Mass/stalk (g)	1.78 (0.17)	2.81 (0.17)	1, 8	8.21	0.0210	2.40 (0.26)	2.61 (0.20)	1, 17	0.48	0.4996		
Stalk height (m)	0.85 (0.07)	0.93 (0.03)	1, 8	0.08	0.7859	1.16 (0.05)	1.15 (0.09)	1, 17	0.64	0.4362		
Total stalk mass (g/m ²)	8.58 (3.40)	24.6 (9.88)	1, 28	1.64	0.2108	32.15 (7.87)	38.76 (13.02)	1, 33	0.30	0.5857		
% tillers flowering	3.68 (2.82)	1.94 (0.67)	1, 28	0.23	0.6358	1.80 (0.48)	2.33 (0.74)	1, 33	<0.01	0.9721		
1999												
No. stalks / m ²	0.71 (0.32)	1.28 (0.48)	1, 28	0.69	0.4138	77.50 (14.88)	73.89 (14.71)	1, 34	<0.01	0.9729		
Mass/stalk (g)	3.97 (0.78)	3.39 (0.42)	1, 10	0.34	0.5712	3.04 (0.21)	3.04 (0.23)	1, 31	0.03	0.8532		
Stalk height (m)	1.16 (0.14)	1.04 (0.11)	1, 10	0.17	0.6902	1.15 (0.04)	1.14 (0.06)	1, 31	<0.01	0.9815		
Total stalk mass (g/m ²)	26.38 (12.06)	42.87 (16.47)	1, 28	0.49	0.4897	246.02 (51.90)	260.98 (61.82)	1, 34	<0.01	0.9961		
% tillers flowering	2.18 (1.17)	2.94 (0.86)	1, 28	0.49	0.4912	13.64 (2.67)	17.04 (3.03)	1, 34	1.39	0.2467		

Note: Values are means (± 1 SE), df, Satterthwaite approximate degrees of freedom (numerator, denominator).

synthesis rates can be viewed as an integrated measure of plant response to changes in availability of resources (water, light, nutrients, etc.) and thus is a powerful indicator of the effects of competition (Norman and Martin 1994; Gibson and Skeel 1996; Skeel and Gibson 1998). In addition, photosynthetic rates have been positively correlated with plant species abundance in tallgrass prairie (McAllister et al. 1998), suggesting that it may be possible to scale up responses observed at the leaf level to population-level responses to environmental change. We did see a response of *A. gerardii* to fertilizer addition, with both A_{net} and g_s decreasing with fertilization (Fig. 2). This effect is likely short term, as we detected no difference in these measures after 13 years of fertilization (Silletti and Knapp 2001).

At the individual plant level, average tiller mass of *S. nutans* was increased both by the removal of *A. gerardii* in the first growing season and by fertilizer addition in both years (Fig. 4). Additionally, significantly more *S. nutans* tillers were produced during the growing season in AR versus NR plots, a response not seen in *A. gerardii*. These data illustrate different tillering strategies in *A. gerardii* and *S. nutans*, which may be linked to differences in phenology and growth habits in these two grasses (McKendrick et al. 1975). Because reproduction is largely vegetative in a perennial system such as tallgrass prairie, changes in tiller dynamics directly relate to changes in resource use and thus represent an important link between population and ecosystem processes (Hartnett and Fay 1998).

The most dramatic effect of the N fertilizer treatment in this experiment was the increase in flowering of *S. nutans* in the second year of the study (Table 4). Despite the dominance of vegetative reproduction by these grasses (Hartnett and Keeler 1995), reproduction by seed can play an important role in recovery after disturbances, such as fire-induced plant mortality or animal disturbances (Risser and Johnson 1973; Foster 1999). High rates of sexual reproduction in *S. nutans* under favorable environmental conditions may be one mechanism allowing it to remain abundant in tallgrass prairie.

The observed effects of competition were the same in fertilized and unfertilized plots, suggesting that overall competitive intensity was not related to soil resource level in this instance (Tilman 1982). Other studies of competitive response of grass species have had similar results, where overall competitive interactions do not change with changes in soil fertility (DiTommaso and Aarssen 1991; Wilson and Tilman 1993). One explanation may be that as soil fertility increased, light penetration through the canopy decreased because of higher plant biomass in fertilized plots; thus one resource limitation (N) was replaced with another (light). In such a case, belowground competition for N would be replaced by aboveground competition for light, resulting in no overall change in competitive interactions (Wilson and Tilman 1993).

Within a fertilizer treatment, NR plots consistently had higher total plot biomass than either AR or SR plots. We had expected that the release of space and other resources associated with the removal of either of the two dominant grasses would result in a competitive release and increased growth of other species in the plot, as suggested by competition theory (Wardle et al. 1999). However, Smith and Knapp (2003)

noted a similar lack of response 2 years after removal of 50% of the dominant tillers in this grassland. Thus, despite the large portion of biomass removed, two growing seasons may not have allowed sufficient time for other species, mainly vegetatively reproducing perennials, to compensate for these removals.

It is important to note that these results were obtained in annually burned, ungrazed prairie. Earlier studies have shown that cover of *S. nutans* is greater in annually burned sites than in sites with a longer fire interval (Silletti and Knapp 2002). Therefore, it is possible that the responses of *S. nutans* to fertilizer and competitive release may be different in sites that are not burned as frequently. If competition with *A. gerardii* is responsible for the decrease in cover of *S. nutans* in unburned sites, we might expect that *A. gerardii* removal from unburned sites would prompt a response in *S. nutans* even greater than the one observed here. Additionally, Suding (2002) found that *A. gerardii* seedlings were increasingly affected by the presence of neighbors with increasing time since fire, suggesting that we might have observed greater response of *A. gerardii* to neighbor removal in unburned prairie. The competitive relationship seen here could also be affected by grazing, especially if there was differential selection of the two grasses by native grazers (Hendon and Briske 2002).

The increase in performance of *S. nutans* when *A. gerardii* was removed supports the prediction that interspecific competition is indeed a strong force acting between dominant, or matrix, grasses in the tallgrass prairie of North America (Gibson and Towne 1995; Duralia and Reader 1993). Overall, this experiment, along with previous studies (Silletti and Knapp 2001; Silletti and Knapp 2002), demonstrates that *S. nutans* is more responsive than *A. gerardii* to variability in climate and resources, and the opportunistic nature of *S. nutans* may be one characteristic that helps *S. nutans* avoid competitive exclusion by the more competitive grass, *A. gerardii*.

These results highlight the importance of studying not only the most abundant species in an ecosystem, but also the less abundant codominants (Grime 1998), since natural and anthropogenic changes have the potential to reorder species dominance in ecosystems (e.g., Berendse et al. 1987; Bobbink and Wilems 1987). In the case of such a reordering, trait differences in codominant species could have significant effects on ecosystem structure and (or) functioning (Grime 1998). For example, if climate changes in North American grasslands lead to increased abundance of the more responsive *S. nutans* relative to *A. gerardii*, greater variability in ecosystem productivity may result, as well as changes in the invasibility of the ecosystem (Smith and Knapp 1999) and species-specific effects on belowground processes (Wedin and Tilman 1990; Hobbie 1992).

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References

- Aarssen, L.W., and Epp, G.A. 1990. Neighbor manipulations in natural vegetation: a review. *J. Veg. Sci.* **1**: 13–30.
- Abdul-Fatih, H.A., and Bazzaz, F.A. 1979. The biology of *Ambrosia trifida* L. Influence of species removal on the organization of the plant community. *New Phytol.* **83**: 813–816.
- Aksenova, A.A., and Onipchenko, V.G. 1998. Plant interactions in alpine tundra: 13 years of experimental removal of dominant species. *Ecoscience*, **5**: 258–270.
- Allen, E.B., and Forman, R.T. 1976. Plant species removals and old-field community structure and stability. *Ecology*, **57**: 1233–1243.
- Armesto, P.A., and Pickett, S.T.A. 1985. Experiments on disturbance in old-field plant communities: impact on species richness and abundance. *Ecology*, **65**: 1705–1712.
- Bark, L.D. 1987. Konza Prairie Research Natural Area, Kansas. *In* The climate of long term ecological research sites (Occasional Paper 44). *Edited by* D. Greenwood. Institute for Arctic and Alpine Research, University of Colorado, Boulder, Colo. pp. 45–50.
- Berendse, F., Oudhof, H., and Bol, J. 1987. A comparative study on nutrient cycling in wet heathland ecosystems. I. Litter production and nutrient losses from the plant. *Oecologia (Heidelb.)*, **74**: 174–184.
- Bobbink, R., and Willems, J.H. 1987. Increasing dominance of *Brachypodium pinnatum* (L.) Beauv. in chalk grasslands: a threat to a species rich ecosystem. *Biol. Conserv.* **40**: 301–314.
- Collins, S.L. 1987. Interaction of disturbances in tallgrass prairie: a field experiment. *Ecology*, **68**: 1243–1250.
- Collins, S.L., and Glenn, S.M. 1991. Importance of spatial and temporal dynamics in species regional abundance and distribution. *Ecology*, **72**: 654–664.
- Connell, J.H. 1983. On the prevalence and relative importance of interspecific competition: evidence from field experiments. *Am. Nat.* **122**: 661–696.
- DiTommaso, A., and Aarssen, L.W. 1991. Effect of nutrient level on competition intensity in the field for three coexisting grass species. *J. Veg. Sci.* **2**: 513–522.
- Duralia, T.E., and Reader, R.J. 1993. Does abundance reflect competitive ability? A field test with three prairie grasses. *Oikos*, **68**: 82–90.
- Foster, B.L. 1999. Establishment, competition and the distribution of native grasses among Michigan old-fields. *J. Ecol.* **87**: 476–489.
- Fowler, N. 1981. Competition and coexistence in a North Carolina grassland. *J. Ecol.* **69**: 843–854.
- Gibson, D.J., and Hulbert, L.C. 1987. Effects of fire, topography, and year-to-year climate variation on species composition in tallgrass prairie. *Vegetatio*, **72**: 175–185.
- Gibson, D.J., and Skeel, V.A. 1996. Effects of competition on photosynthetic rate and stomatal conductance of *Sorghastrum nutans*. *Photosynthetica (Prague)*, **32**: 503–512.
- Gibson, D.J., and Towne, G. 1995. Dynamics of big bluestem (*Andropogon gerardii*) in ungrazed Kansas tallgrass prairie. *In* Proceedings of the 14th North American Prairie Conference, 12–16 July 1991, Kansas State University, Manhattan, Kansas. *Edited by* D.C. Hartnett. Manhattan, Kans.
- Grace, J.B., and Tilman, D. 1990. Perspectives on plant competition. Academic Press, Inc., San Diego, Calif.

- Grime, J.P. 1979. Plant strategies and vegetation processes. John Wiley and Sons, Ltd., New York.
- Grime, J.P. 1998. Benefits of plant diversity to ecosystems: immediate, filter, and founder effects. *J. Ecol.* **86**: 902–910.
- Gurevitch, J., and Unnasch, R.S. 1989. Experimental removal of a dominant species at two levels of soil fertility. *Can. J. Bot.* **67**: 3470–3477.
- Gurevitch, J., Morrow, L.L., Wallace, A., and Walsh, J.S. 1992. A meta-analysis of competition in field experiments. *Am. Nat.* **140**: 539–572.
- Hanski, I. 1982. Dynamics of regional distribution: the core and satellite species hypothesis. *Oikos*, **38**: 210–221.
- Hartnett, D.C., and Fay, P.A. 1998. Plant populations: patterns and processes. In *Grassland dynamics: long-term ecological research in tallgrass prairie*. Edited by A.K. Knapp, J.M. Briggs, D.C. Hartnett, and S.L. Collins. Oxford University Press, New York. pp. 81–100.
- Hartnett, D.C., and Keeler, K.H. 1995. Population processes. In *The changing prairie: North American grasslands*. Edited by A. Joern and K.H. Keeler. Oxford University Press, Oxford, UK. pp. 82–99.
- Hartnett, D.C., Hickman, K.R., and Fischer Walter, L.E. 1996. Effects of bison grazing, fire, and topography on floristic diversity in tallgrass prairie. *J. Range Manage.* **49**: 413–420.
- Hendon, B.C., and Briske, D.D. 2002. Relative herbivory tolerance and competitive ability in two dominant:subordinate pairs of perennial grasses in a native grassland. *Plant Ecol.* **160**: 43–51.
- Hetrick, B.A.D., Hartnett, D.C., Wilson, G.W.T., and Gibson, D.J. 1994. Effects of mycorrhizae, phosphorus availability, and plant density on yield relationships among competing tallgrass prairie grasses. *Can. J. Bot.* **72**: 168–176.
- Hobbie, S. 1992. Effects of plants on nutrient cycling. *Trends Ecol. Evol.*, **7**: 336–339.
- Inchausti, P. 1995. Competition between perennial grasses in a Neotropical savanna: the effects of fire and of hydric-nutritional stress. *J. Ecol.* **83**: 231–243.
- Knapp, A.K., and Seastedt, T.R. 1986. Detritus accumulation limits productivity of tallgrass prairie. *Bioscience*, **36**: 662–668.
- Knapp, A.K., Briggs, J.M., Blair, J.M., and Turner, C.L. 1998. Patterns and controls of aboveground net primary production in tallgrass prairie. In *Grassland dynamics: long-term ecological research in tallgrass prairie*. Edited by A.K. Knapp, J.M. Briggs, D.C. Hartnett, and S.L. Collins. Oxford University Press, New York. pp. 193–221.
- McAllister, C.A., Knapp, A.K., and Maragni, L.A. 1998. Is leaf-level photosynthesis related to plant success in a highly productive grassland? *Oecologia (Heidelb.)*, **117**: 40–46.
- McKendrick, J.D., Owensby, C.E., and Hyde, R.M. 1975. Big bluestem and Indiangrass vegetative production and annual reserve carbohydrate and nitrogen cycles. *Agro-Ecosystems*, **2**: 75–93.
- Norman, F., and Martin, C.E. 1994. Growth, photosynthesis, water relations, and competition of the old-field species *Abutilon theophrasti*, *Ambrosia trifida*, and *Helianthus annuus* grown under controlled conditions. *Photosynthetica (Prague)*, **30**: 361–371.
- Polley, H.W., Norman, J.M., Arkebauer, T.J., Walter-Shea, E.A., Gregor, D.H., Jr., and Bramer, B. 1992. Leaf gas exchange of *Andropogon gerardii* Vitman, *Panicum virgatum* L., and *Sorghastrum nutans* (L.) Nash in a tallgrass prairie. *J. Geophys. Res.* **97**: 18 837–18 844.
- Rabinowitz, D., Rapp, J.K., and Dixon, P.M. 1984. Competitive abilities of sparse grass species: means of persistence or cause of abundance. *Ecology*, **65**: 1144–1154.
- Risser, P.G., and Johnson, F.L. 1973. Carbon dioxide exchange characteristics of some prairie grass seedlings. *Southwest. Nat.* **18**: 85–91.
- SAS Institute Inc. 1991. SAS Version 8.1 [computer program]. SAS Institute Inc., Cary, N.C.
- Schoener, T.W. 1983. Field experiments on interspecific competition. *Am. Nat.* **122**: 240–285.
- Silletti, A.M., and Knapp, A.K. 2001. Responses of the codominant grassland species *Andropogon gerardii* and *Sorghastrum nutans* to long-term manipulations of nitrogen and water. *Am. Midl. Nat.* **145**: 159–167.
- Silletti, A.M., and Knapp, A.K. 2002. Long-term responses of the grassland dominants *Andropogon gerardii* and *Sorghastrum nutans* to changes in climate and management. *Plant Ecol.* **163**: 15–22.
- Skeel, V.A., and Gibson, D.J. 1998. Photosynthetic rates and vegetative production of *Sorghastrum nutans* in response to competition at two strip mines and a railroad prairie. *Photosynthetica (Prague)*, **35**: 139–149.
- Smith, M.D., and Knapp, A.K. 1999. Exotic plant species in a C₄-dominated grassland: invisibility, disturbance, and community structure. *Oecologia (Heidelb.)*, **120**: 605–612.
- Smith, M.D., and Knapp, A.K. 2003. Dominant species maintain ecosystem function with non-random species loss. *Ecol. Lett.* **6**: 509–517.
- Suding, K.N. 2002. The effect of spring burning on competitive ranking of prairie species. *J. Veg. Sci.* **12**: 849–856.
- Tilman, D. 1982. Resource competition and community structure. Princeton University Press, Princeton, N.J.
- Tilman, D. 1989. Competition, nutrient reduction and the competitive neighborhood of a bunchgrass. *Funct. Ecol.* **3**: 215–219.
- Turner, C.L., Blair, J.M., Scharz, R.J., and Neel, J.C. 1997. Soil N and plant responses to fire, topography, and supplemental N in tallgrass prairie. *Ecology*, **78**: 1852–1843.
- Vinton, M.A., Hartnett, D.C., Finck, E.J., and Briggs, J.M. 1993. Interacting effects of bison (*Bison bison*) grazing and plant community composition in tallgrass prairie. *Am. Midl. Nat.* **129**: 10–18.
- Wardle, D.A., Bonner, K.I., Barker, G.M., Yeates, G.W., Nicholson, K.S., Bardgett, R.D., Watson, R.N., and Ghani, A. 1999. Plant removals in perennial grasslands: vegetation dynamics, decomposers, soil biodiversity, and ecosystems properties. *Ecol. Monogr.* **69**: 535–568.
- Weaver, J.E. 1931. Who's who among the prairie grasses. *Ecology*, **7**: 623–632.
- Weaver, J.E. and Fitzpatrick, T.J. 1932. Ecology and relative importance of the dominants of tallgrass prairie. *Bot. Gaz.* **93**: 113–150.
- Wedin, D.A., and Tilman, D. 1990. Species effects on nitrogen cycling: a test with perennial grasses. *Oecologia (Heidelb.)*, **84**: 433–441.
- Wilson, S.D., and Tilman, D. 1993. Plant competition and resource availability in response to disturbance and fertilization. *Ecology*, **74**: 599–611.

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