Drought and Ozone Stress Effects on Competition among Selected Prairie Grass Species and Giant Foxtail

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Additional index words. *Setaria faberi*, big bluestem, indian grass, prairie restoration, grassland ecology

Summary. Differential responses of species to environmental stress may interfere with restoration of prairie ecosystems or change community structure. The impact of increasing atmospheric ozone (O_3) concentrations and/or low water on the growth of *Andropogon gerardii* Vitm. (big bluestem) and *Sorghastrum nutans* (L.) Nash (indian grass), two common warm-season native grasses, and *Setaria faberi* Herrm. (giant foxtail), a vigorous annual weed species, were studied in replacement series. Giant foxtail grew better than either big bluestem or indian grass under all tested conditions. The leaf areas of all three species were primarily controlled by water availability. Big bluestem and indian grass accumulated biomass equally well under high water availability, but with low water, indian grass accumulated more biomass than did bluestem. Three-way analysis of variance showed biomass, leaf area, and leaf number differed among species; low water was significant in all cases except for indian grass leaf area; and the O_3 effect was significant only in the case of foxtail biomass. The interaction of O_3 concentration and low water was significant only for indian grass biomass and leaf number; the interaction of species combination and low water was significant only for big bluestem leaf area and biomass. Relative yield calculations indicated that under conditions of elevated O_3 and low water, big bluestem was the least competitive, while indian grass was most competitive. Intraspecific competition was common, each species apparently utilizing the environment in different ways. The results also suggest that giant foxtail at a low relative density may be used as a nurse species in prairie restorations as growth of big bluestem and indian grass were improved when in mixtures with foxtail.

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Prairie restoration and creation are of widespread interest, especially in locations where prairie lands have been substantially converted to other land uses (Samson and Knopf, 1996). In Illinois for example, only 0.01% of the 8.75 million ha (21.62 million acres) of prairie existing in 1820 now remain (Iverson et al., 1989). Many organizations and agencies are aggressively pursuing restoration of prairies in Illinois and other Midwestern states. Restoration efforts are also required by law after surface mining disturbance, and restoring to native grassland species is a common objective of mining companies or land agencies. Competition from weeds during establishment is a problem at sites that were formerly agricultural fields (Iverson and Wali, 1992; McClain, 1997; Schramm, 1990). A better understanding of the competitive effects among establishing native grasses and weeds is needed, so that management options favoring native species can be maximized.

The effects of competition can vary as a function of the environmental conditions influencing the organisms at the time. Successful establishment of native species can be negatively affected after short periods of low water. Weed species are generally able to survive a wider variation in moisture conditions during the critical establishment phase than native grasses (Grime et al., 1986; Harper, 1977). Slower growing natives initially have a disadvantage under water-stressed conditions as the fast-growing roots of weedy species exploit available soil moisture (Iverson, 1986; Schramm, 1990).

Tropospheric ozone (O_3) concentrations have increased rapidly during the last 50 years. In many parts of the U.S., O_3 concentrations are currently about twice as high as would exist without anthropogenic influences (Heck et al., 1984). Ambient O_3 concentrations in many areas, including the central United States where extensive prairie restoration activities are underway, can alter permeability of plant cell membranes, disrupt metabolism (Heath, 1988; Heath and Taylor, 1997), decrease foliar chlorophyll and photosynthesis, change photosynthate allocation, and suppress growth and yield (Endress and Grunwald, 1985; Heagle, 1989; Heck et al., 1988; Miller, 1988).

Most studies of the effect of atmospheric pollution on plants are performed on individual species, but in ecosystems, plants usually grow in competition with others. Ambient stresses, such as drought or O_3, may affect the structure of plant communities by altering competitive interactions (Grime et al., 1986), but only a few studies, and none recently, considered the effects of air pollutants on plant competition (Bennett and Runeckles, 1977; Miller, 1973; Smith, 1974; Treshow, 1968).

In the present experiment, we assess the competitive interaction effects among three grass species, one weed species and two species native to the Illinois tallgrass prairie, under conditions of ozone and/or low water using a single density deWit replacement series under greenhouse conditions (deWit, 1960; Harper, 1977).

Experiments using deWit replacement series provide comparative opportunities for evaluating relative performance characteristics of species in mixtures and pure cultures.

Materials and methods

This greenhouse study used a factorial experiment to assess the simultaneous effects of ozone and drought on combinations of three grass species organized as a constant density replacement series patterned after deWit (1960) and Harper (1977). Species included in

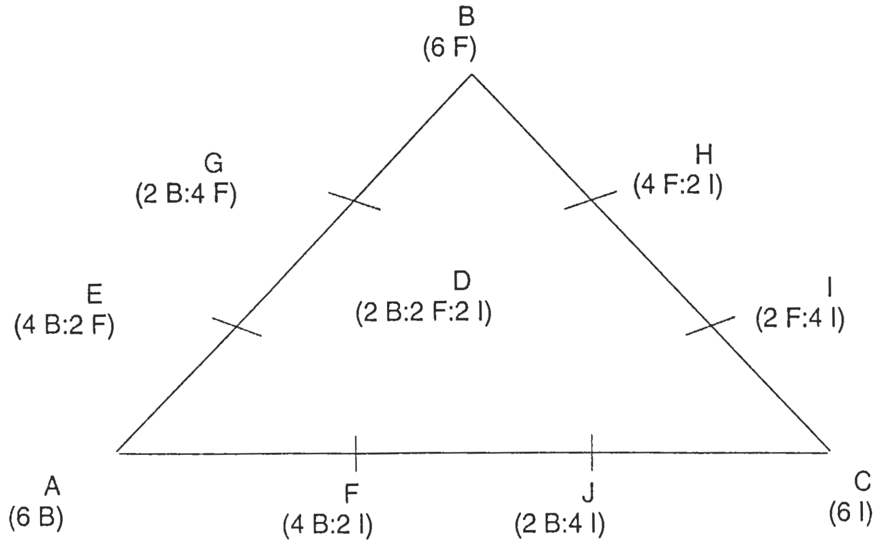

Fig. 1. Composition of the 10 experimental species mixtures and illustration of the theoretical basis for the orthogonal comparisons; B = big bluestem, F = giant foxtail, I = indian grass.

the replacement series were two native grass species commonly used in tall grass prairie restorations, *Andropogon gerardii* (big bluestem) and *Sorghastrum nutans* (Indian grass), and one exotic weed, *Setaria faberi* (giant foxtail), commonly found in prairie restoration efforts in former agricultural fields.

Seeds of each species were sown in the greenhouse on sand in flats during late April. For 11 h daily, a mist was applied for 9 s every 5 min to keep the seeds moist. After germination in mid-May, seedlings were transplanted to 15.2-cm (6-inch) diameter pots containing 800 g (28.2 oz) of a soil mix made from equal parts by volume of loam, peat moss, sand, and vermiculite. Each pot contained six seedlings spaced equidistantly around the circumference.

The constant density replacement series consisted of a total of six plants per pot, employing 10 combinations (mixtures A through J) of the three plant species (Fig. 1) with two levels of drought, three levels of ozone, and four replications for a total of 240 pots.

The two levels of low water applied to the pots beginning 12 d after transplanting were 1) control or high water level, where pots were maintained at 60% of field capacity (FC) and 2) drought stress or low water, where pots received water to only 25% of FC. Field capacity of the soil mix was determined gravimetrically to be 74.3 g water per 100 g soil (11.9 oz water per 1.0 lb soil). The level of drought stress was maintained gravimetrically by weighing each pot twice daily (before and after O_3 exposure) and adding water to the desired weight.

Pots were randomly assigned to drought and O_3 stress treatments. The O_3 treatments were randomly assigned each day to the nine exposure chambers, which were also located in the greenhouse. Plants were moved to 2-m^3 (70.6-ft^3) continuously stirred tank reactor (CSTR) chambers (Heck et al., 1978) for exposure to O_3 or nonfiltered ambient greenhouse air and then returned to the greenhouse immediately following each exposure. The air exchange rate of the CSTRs was 4.5 m^3·min^{-1} (159 ft^3/min). Ozone was generated from dry air by electric discharge with an O_3 generator (Welsbach Ozone Systems Corp., Philadelphia, Pa.) and dispensed to the chambers through rotameters. Pollutant concentrations were monitored on a time-share basis as previously described (Endress and Grunwald, 1985). Three O_3 treatments were used: 1) 58.8 ± 25.5 ng·L^{-1} (0.030 ± 0.013 ppm), the ambient air control treatment, 2) 137.1 ± 31.4 ng·L^{-1} (0.070 ± 0.016 ppm), and 3) 215.6 ± 37.2 ng·L^{-1} (0.110 ± 0.019 ppm). The latter two treatments were obtained by adding fixed increments of 78.4 and 156.8 ng·L^{-1} (0.04 and 0.08 ppm) O_3 respectively to nonfiltered ambient air. An O_3-free treatment was not included because plants in nature do not experience this condition. Ozone exposures were initiated 12 d after transplanting. Plants were exposed to the O_3 treatments for 7 h each day, 5 d per week for a total of 39 exposures.

Plants were excised at soil level at termination of the stress treatments 67 d after transplanting (90 d after seeding). Above-ground production, i.e., leaf and tiller number, leaf blade area, and fresh and dry weight of leaves and stems, was measured. Dry weights were determined after 72 h in a 65 °C (149 °F) oven.

Stress effects on the above-ground biomass, leaf area, and leaf number were analyzed by a three-way ANOVA using a completely randomized design. A series of orthogonal contrasts was constructed to permit identification of specific treatments responsible for significant differences. The contrasts for ozone concentration were 1) the ambient air concentration (control, 58.8 ng·L^{-1} (0.030 ppm) O_3) and middle (137.2 ng·L^{-1} (0.070 ppm) O_3) versus the high concentration (215.6 ng·L^{-1} (0.110 ppm) O_3) and 2) the ambient air concentration versus the middle O_3 concentration. This allowed determination of which level of ozone was responsible for an effect. The orthogonal contrasts to determine the effects for species combination were based on the triangle shown in Fig. 1, which permitted five contrasts for each species. The first was between the species in monoculture (A, B, or C) and the species in a mixture (D–J). The second was between the target species in a mixture with four plants and the target species in a mixture with only two plants using the same competitor in each mix. With big bluestem for example, the contrasts are E vs. G and F vs. J. The third orthogonal contrast was between the species in a 4:2 mixture with another species and the species in a 4:2 mixture with the third species, i.e., for big bluestem, E vs. F. The fourth contrast was the same as the third, but the species are in a 2:4 mixture, e.g., G vs. J for big bluestem. The final contrasted the mixture of three species with the species in the mixtures having only two plants present, D vs. G+J for big bluestem.

The above-ground biomass per pot was collected separately for each species and the biomass per plant determined by division. The biomass per plant was used to calculate the relative yield and competitive ratios in order to facilitate understanding of the relative competitive abilities of the three species when grown under conditions varying in O_3 and drought. The relative yield values

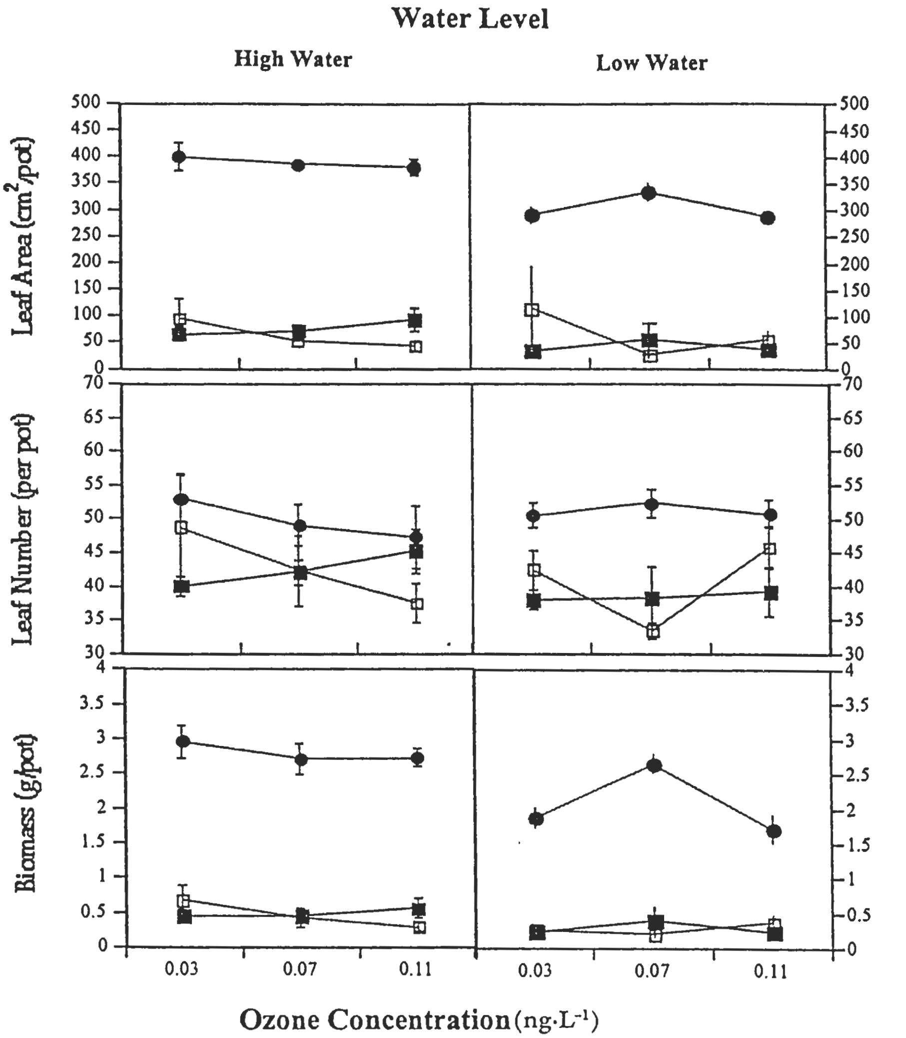

Fig. 2. Impact of ozone on leaf area, leaf number, and biomass of big bluestem (■), indian grass (□), and giant foxtail (●) grown as monocultures at two water levels. Error bars are ± 1 standard error of the mean.

and competitive ratios were calculated for each species according to the methods of Ta and Faris (1987) and Willey (1979). A competitive ratio in excess of 1 usually indicates the species is competitively superior to species grown in combination under similar conditions.

Relative yield (RY) was calculated for each species by dividing the per plant biomass for each species in a mixture by the per plant biomass of that species in monoculture: $RY_a = (Y_a \text{ in mixture}/Y_a \text{ in monoculture})$. The mean relative yield of a mixture of plant species is the average of the relative yields of each species present in the mixture: $MRY_{ab} = (RY_a + RY_b)/2$. The competitive ability of each species was determined by calculating the competitive ratio (CR) according to Ta and Faris (1987): $CR_a = [RY_a \times Za_b]/[RY_b \times Zb_a]$ where CR_a = competitive ratio of species a; RY_a = relative yield of species a; RY_b = relative yield of species b; Za_b = the proportion of species a in a mixture with species b; Zb_a = the proportion of species b in a mixture with species a.

Results and discussion

Monocultures. Shoot biomass, leaf number, and leaf area, differed between foxtail and the other species (Fig. 2). Giant foxtail developed significantly more biomass and leaf area than the other two grasses. Foxtail biomass, when grown in monoculture, was on average about five times that of the other species. Rapid seedling growth, seedling vigor, and the ability to germinate under a range of conditions (Baker, 1965, 1974) may have contributed to giant foxtail's greater biomass and weediness.

Low water caused significant biomass reductions in each of the species (Table 1; Fig. 2); bluestem and indian grass biomass were reduced by at least 50%, while foxtail maintained a higher proportion of biomass (63%) under low water. Leaf area in all species monocultures was also reduced by low water, while leaf number was not reduced (Fig. 2). The three-way ANOVA results confirmed these trends, except that the highly significant drop in leaf number due to drought was not apparent in monocultures of bluestem and foxtail (Table 1). These results indicate that biomass and leaf area for each of the species were controlled primarily by water availability in this experiment.

At low water (25% FC), the O_3 treatment in the three-way ANOVA was significant in only one instance: the biomass of foxtail where the middle O_3 treatment (137.2 ng·L^{-1} (0.070 ppm)) was stimulatory. When grown under low water in monocultures, however, the middle O_3 level was also stimulatory

Table 1. Summary of significant *P* values from three-way ANOVAs for treatment effects and their interactions.

Variable	Biomass	Leaf area	Leaves (no.)
Big Bluestem			
Water level	*P* 0.001	*P* 0.001	*P* 0.001
Species combination	*P* 0.001	*P* 0.001	*P* 0.001
Water level × species	*P* 0.05	*P* 0.05	
Foxtail			
O_3 concentration	*P* 0.01		
Water level	*P* 0.001	*P* 0.001	*P* 0.01
Species combination	*P* 0.001	*P* 0.001	*P* 0.001
Indian grass			
Water level	*P* 0.001		*P* 0.05
Species combination	*P* 0.001	*P* 0.001	*P* 0.001
O_3 × water level	*P* 0.05		
O_3 × species combination	*P* 0.05		

Table 2. Impact of species combination and water level on growth of establishing grass species at control (58.8 ng·L^{-1}, 0.030 ppm) O_3. Values are mean ± standard deviation. Species combinations refer to the 10 experimental mixtures illustrated in Fig. 1. B = big bluestem, F = giant foxtail, and I = indian grass.

		Biomass (dry g/pot)[z]			Leaf area (cm²/pot)[y]			Leaves (no.)		
Species combination	Water level	Big Bluestem	Foxtail	Indian Grass	Big Bluestem	Foxtail	Indian Grass	Big Bluestem	Foxtail	Indian Grass
D (2B:2F:2I)	High	0.15 ± 0.10	2.23 ± 0.34	0.17 ± 0.09	29.9 ± 13.4	319.6 ± 5889	35.89 ± 22.6	17.7 ± 2.3	31.0 ± 5.3	15.7 ± 3.5
	Low	0.07 ± 0.04	1.24 ± 0.61	0.10 ± 0.08	14.2 ± 11.4	232.0 ± 52.0	12.7 ± 8.3	11.4 ± 2.8	27.2 ± 3.9	12.2 ± 3.4
E (4B:2F:0I)	High	0.24 ± 0.17	2.05 ± 0.39	---	38.1 ± 29.0	297.0 ± 18.9	---	26.3 ± 6.2	32.3 ± 5.0	---
	Low	0.22 ± 0.11	0.99 ± 0.17	---	36.7 ± 23.9	186.4 ± 23.4	---	28.3 ± 5.8	29.3 ± 7.0	---
F (4B:0F:2I)	High	0.47 ± 0.13	---	0.20 ± 0.04	69.5 ± 30.0	---	24.5 ± 8.2	34.8 ± 5.1	---	16.8 ± 3.2
	Low	0.12 ± 0.04	---	0.14 ± 0.04	19.6 ± 9.8	---	23.3 ± 11.8	24.0 ± 1.4	---	14.0 ± 1.4
G (2B:4F:0I)	High	0.10 ± 0.04	2.39 ± 0.22	---	13.8 ± 8.7	350.9 ± 28.3	---	13.0 ± 2.6	41.5 ± 2.4	---
	Low	0.02 ± 0.01	1.66 ± 0.21	---	3.8 ± 1.4	261.7 ± 13.2	---	9.3 ± 1.3	38.0 ± 4.5	---
H (0B:4F:2I)	High	---	2.53 ± 0.69	0.16 ± 0.12	---	349.9 ± 69.5	22.7 ± 17.6	---	42.5 ± 6.7	15.3 ± 5.3
	Low	---	1.50 ± 0.24	0.05 ± 0.03	---	241.3 ± 17.8	13.4 ± 10.1	---	40.8 ± 5.5	12.3 ± 1.9
I (0B:2F:4I)	High	---	1.75 ± 0.69	0.28 ± 0.17	---	243.0 ± 126.1	39.6 ± 29.2	---	30.0 ± 16.0	26.0 ± 3.2
	Low	---	1.18 ± 0.46	0.12 ± 0.06	---	207.6 ± 42.7	14.1 ± 5.2	---	28.8 ± 4.2	23.0 ± 3.9
J (2B:0F:4I)	High	0.19 ± 0.16	---	0.42 ± 0.23	32.8 ± 29.5	---	57.9 ± 37.2	15.0 ± 2.5	---	34.5 ± 3.3
	Low	0.07 ± 0.05	---	0.12 ± 0.05	11.6 ± 6.9	---	18.1 ± 8.6	13.3 ± 3.3	---	25.3 ± 3.3

[z]28.35 g = 1.0 oz.
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for bluestem and foxtail (Fig. 2).

As O_3 increased from ambient levels, Indian grass biomass decreased under control water conditions, but increased when subjected to low water (Fig. 2). At the high O_3 level (215.6 ng·L^{-1} (0.110 ppm)), bluestem biomass and leaf area exceeded that of indian grass under control water, but the relationship was reversed under low water conditions (Table 2, Fig. 2). The ANOVA (Table 1) also showed the interaction of water and O_3 to be significant for indian grass, indicating again the complexity where O_3 is stimulatory under low water, but the reverse being the case under high water (control) conditions.

MIXTURES. For big bluestem growing under control water conditions, biomass was enhanced when grown in combination with indian grass relative to biomass in monoculture, but diminished when grown with foxtail (Table 2). The situation changed, however, when grown under low water: monoculture growth for bluestem was equal or superior for all combinations except in mixture E (4B:2E), in which the bluestem biomass was higher than in monoculture. However, when grown in a 2:4 ratio with foxtail (mixture G), bluestem growth was drastically reduced (Table 2). Under drought conditions, the density of foxtail (or relative density of bluestem) was very critical for the growth and establishment of bluestem.

Under control water conditions, indian grass grew better in monoculture than in mixtures. The same was true under low water, except for mixture F, comprised of two indian grass plants and four big bluestem plants. When grown in mixtures with foxtail, the biomass of indian grass was substantially reduced relative to the monoculture, regardless of the proportion of foxtail or water regime (Table 2).

The early growth of native grasses is typically below ground. The combination of below-ground growth with the weedy characteristics of giant foxtail allow the latter species to be far superior in growth compared to the two native species. Foxtail in mixtures grew better under all conditions than when in monocultures. In some instances under water stress (e.g., when there were two foxtail plants in the pot regardless of the other four plants), foxtail biomass per plant exceeded that of the monoculture under control water conditions (Table 2). This seems to suggest that intraspecific competition may be more important than interspecific competition in regulating foxtail growth (substantiation would require data from monocultures of four and two plants per pot). Alternatively, the ratios may enhance foxtail's growth.

As discussed with monocultures, the effects of O_3 were minimal in this experiment. Only foxtail biomass had a significant effect due to O_3, and indian grass had a significant interaction effect of O_3 and water for biomass and leaf number (Fig. 2). Roughly a third of the treatments showed a stimulation due to O_3, a third showed a decrease, and a third showed no effect (data not shown). Because the effects due to O_3 were so varied, it appears that the individual plant growth phenomena, including inter- and intraspecific competition as well as other genetic and cultural variations, overshadowed the effects of O_3 in this experiment. Alternatively, these species may have been insensitive to the range of O_3 levels used in these experiments.

The statistical analyses showed that species combination was always significant, water stress was usually significant (except for indian grass leaf area), and O_3 was significant only in the case of foxtail biomass (Table 1). The orthogonal contrasts showed no effect of O_3. Biomass, leaf number, and leaf area depended on whether plants were in monoculture or mixtures, whether there were two plants or four plants of the species in the mixture, the other species' identity, and how many species were in the mixture. Essentially the orthogonal contrasts demonstrated that plant growth performance depends heavily on its environment. Impacting factors include water level, other species, the number of species, the type of other species, and the proportion of the same species (abundance) in the mixture (prai-

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Table 3. Relative yields (per plant biomass in mixture per plant biomass in monoculture) of establishing-grass species mixtures. Species combinations refer to the 10 experimental mixtures illustrated in Fig. 1. B = big bluestem, F = giant foxtail, and I = indian grass.

Ozone level (ng·L^{-1})[z]	Species combination	Big Bluestem		Foxtail		Indian Grass		Mean	
		H$_2$O level							
		High	Low	High	Low	High	Low	High	Low
58.8 ± 25.5	D (2B:2F:2I)	0.97	1.18	2.26	2.00	0.74	1.11	1.32	1.43
(0.030 ± 0.013 ppm)	E (4B:2F:0I)	0.81	1.45	2.08	1.59	---	---	1.44	1.52
	F (4B:0F:2I)	1.56	0.81	---	---	0.89	1.54	1.23	1.17
	G (2B:4F:0I)	0.64	0.32	1.21	1.33	---	---	0.93	0.83
	H (0B:4F:2I)	---	---	1.28	1.20	0.70	0.55	0.99	0.88
	I (0B:2F:4I)	---	---	1.78	1.90	0.63	0.63	1.20	1.27
	J (2B:0F:4I)	1.25	0.94	---	---	0.43	0.69	1.09	0.82
137.2±31.4	D (2B:2F:2I)	0.60	0.54	2.86	1.63	0.77	1.36	1.41	1.18
(0.070 ± 0.016 ppm)	E (4B:2F:0I)	0.50	0.38	1.87	1.76	---	---	1.18	1.07
	F (4B:0F:2I)	1.88	0.50	---	---	2.10	2.18	1.99	1.34
	G (2B:4F:0I)	1.17	0.27	1.35	1.36	---	-	1.26	0.81
	H (0B:4F:2I)	---	---	1.36	1.16	0.47	0.71	0.92	0.94
	I (0B:2F:4I)	---	---	2.45	1.54	0.72	1.26	1.59	1.40
	J (B2:0F:4I)	1.13	0.64	---	---	1.01	1.76	1.07	1.20
215.6 ± 37.2	D (2B:2F:2I)	0.45	0.39	2.13	1.70	0.90	0.28	1.16	0.79
(0.110 ± 0.019 ppm)	E (4B:2F:0I)	0.53	0.99	1.98	1.64	---	---	1.26	1.32
	F (4B:0F:2I)	1.09	1.32	---	---	2.05	0.91	1.57	1.11
	G (2B:4F:0I)	0.48	1.04	1.23	1.45	---	---	0.85	1.25
	H (0B:4F:2I)	---	---	1.20	1.41	1.06	0.73	1.13	1.07
	I (0B:2F:4I)	---	---	1.19	1.84	0.60	0.83	1.60	1.33
	J (B2:0F:4I)	1.29	1.25	---	---	2.89	1.00	2.09	1.23

[z]1960 ng·L^{-1} = 1.0 ppm.

Table 4. Competitive ratios of establishing-grass species mixtures. Numbers >1 usually indicate the species is competitively superior to species grown in combination under similar conditions. Species combinations refer to the 10 experimental mixtures illustrated in Fig. 1. B = big bluestem, F = giant foxtail, and I = indian grass.

Ozone level (ng·L^{-1})[z]	Species combination	Big Bluestem		Foxtail		Indian Grass	
		H$_2$O level					
		High	Low	High	Low	High	Low
58.8 ± 25.5	D (2B:2F:2I)	0.33	0.38	1.32	0.87	0.23	0.35
(0.030 ± 0.013 ppm)	E (4B:2F:0I)	0.78	1.82	1.28	0.55	---	---
	F (4B:0F:2I)	3.47	1.05	---	---	0.29	0.96
	G (2B:4F:0I)	0.27	0.12	3.76	8.45	---	---
	H (0B:4F:2I)	---	---	3.76	4.33	0.27	0.23
	I (0B:2F:4I)	---	---	1.42	1.49	0.71	0.67
	J (B2:0F:4I)	0.67	0.69	---	---	1.49	1.46
137.2 ± 31.4	D (2B:2F:2I)	0.16	0.18	2.09	0.86	0.22	0.63
(0.070 ± 0.016 ppm)	E (4B:2F:0I)	0.53	0.43	1.88	2.32	---	---
	F (4B:0F:2I)	1.79	0.46	---	---	0.56	2.17
	G (2B:4F:0I)	0.43	0.10	2.31	9.91	---	---
	H (0B:4F:2I)	---	---	5.76	3.27	0.17	0.31
	I (0B:2F:4I)	---	---	1.69	0.61	0.59	1.64
	J (B2:0F:4I)	0.56	0.18	---	---	1.79	5.51
215.6 ± 37.2	D (2B:2F:2I)	0.14	0.20	1.58	2.54	0.35	0.13
(0.110 ± 0.019 ppm)	E (4B:2F:0I)	0.53	1.21	1.90	0.83	---	---
	F (4B:0F:2I)	1.07	2.91	---	---	0.94	0.34
	G (2B:4F:0I)	0.19	0.36	5.10	2.80	---	---
	H (0B:4F:2I)	---	---	0.44	3.85	2.26	0.26
	I (0B:2F:4I)	---	---	2.18	1.11	0.46	0.90
	J (B2:0F:4I)	0.22	0.63	---	---	4.47	1.60

[z]1960 ng·L^{-1} = 1.0 ppm.

rie). Plant performance was generally better in mixtures compared to monocultures, but there were differential effects depending on the water level and mixture type.

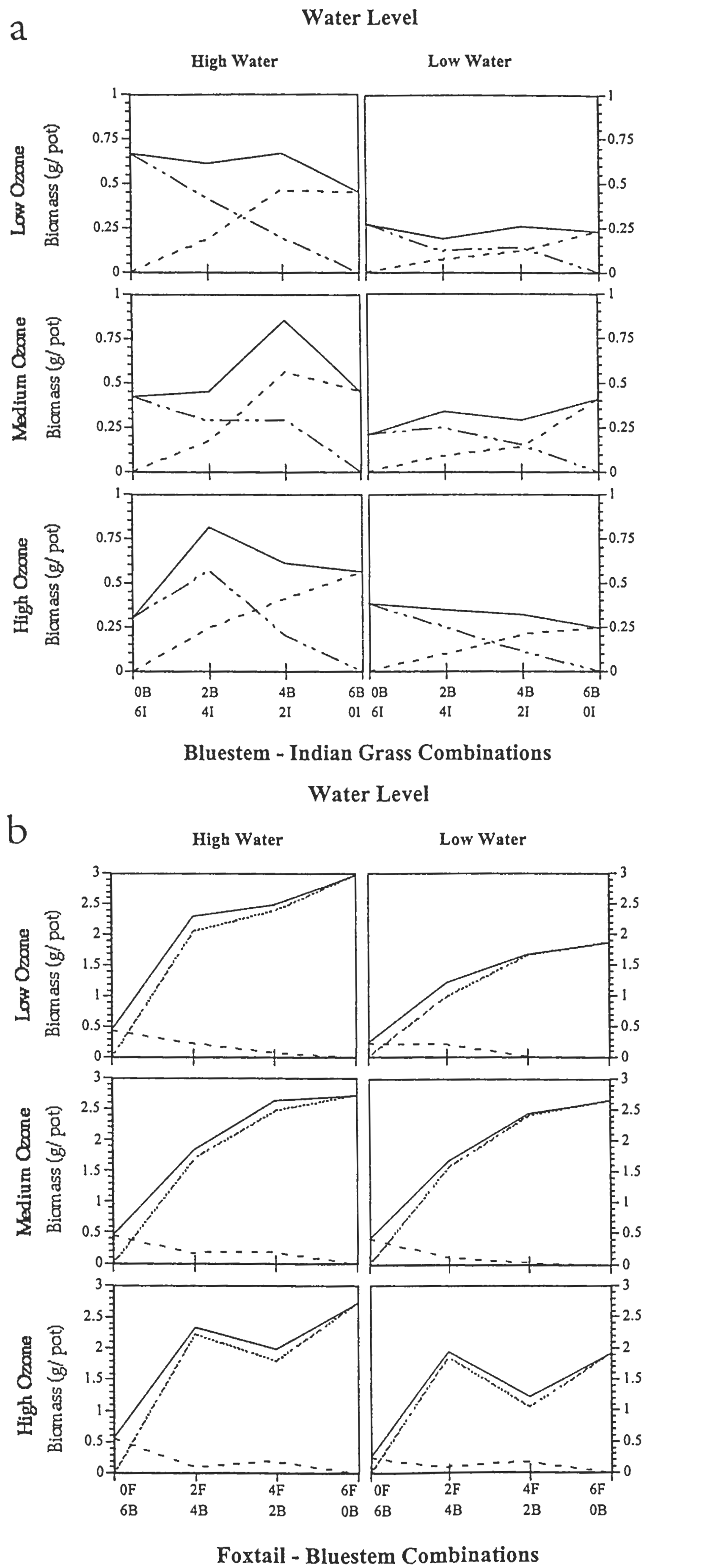
The relative yields (Table 3) and competitive ratios (Table 4) indicated that big bluestem was superior in competitive ability to indian grass under low or medium O_3 conditions, if moisture was adequate and the mixture had a higher proportion of bluestem seedlings. If, however, there was low water and/or the number of indian grass seedlings exceeded that of bluestem, the indian grass had superior competitive ability (Tables 3 and 4). Under high O_3 conditions, water level ceased to be a factor, however, and competitive superiority was gained by the species with the most seedlings. Bluestem was shown to be the least competitive, while indian grass was most competitive, under conditions of mid-ozone and low water availability. At low O_3 and water level, big bluestem had higher relative yields when in mixtures with indian grass than in monoculture, but at middle-O_3, they performed the same and at high-O_3 indian grass relative yield was more than twice what it was in monoculture (Table 3, Fig. 2).

With these two species, a 50–50 seed mix in prairie restoration may be adequate to insure establishment success for each species under a wide range of field conditions. If droughty conditions are expected, especially if combined with somewhat elevated O_3 exposures, it would be advisable to sow a higher proportion of bluestem seed.

Foxtail was competitively superior to bluestem in nearly all combinations of seedling numbers, O_3, or water level (Tables 3 and 4). The relative yield of big bluestem at the control water level was always <1.0 when grown in combination with foxtail (Table 3). Foxtail was able to quickly germinate and grow before the longer-lived, but slow-growing bluestem could establish.

In general, foxtail was a superior competitor to indian grass, for the same reasons it was superior to bluestem (Tables 3 and 4). The competitive superiority was especially profound in situations were the number of foxtail seedlings exceeded that of indian grass, at low to mid-ozone levels. The relative yield of foxtail in mixtures generally exceeded 1.0.

The results of experiments based on a replacement series of the type



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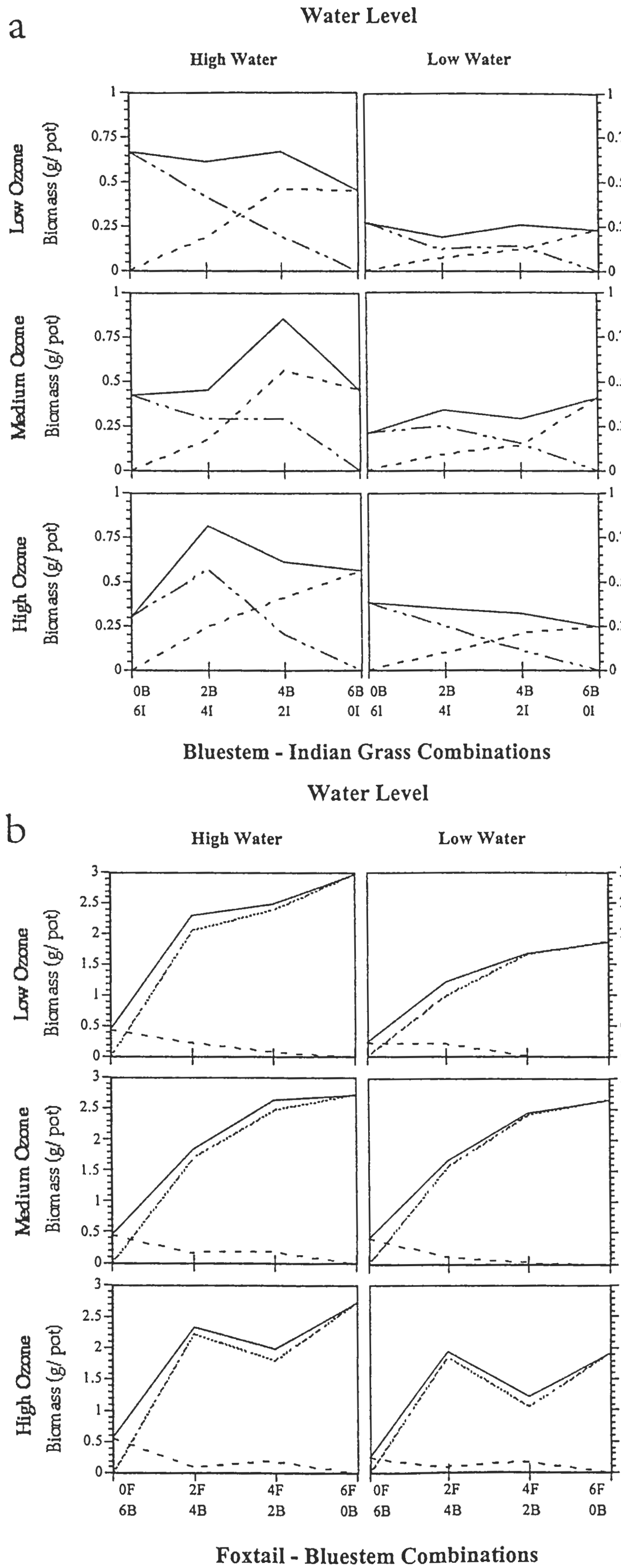
The results of experiments based on a replacement series of the type



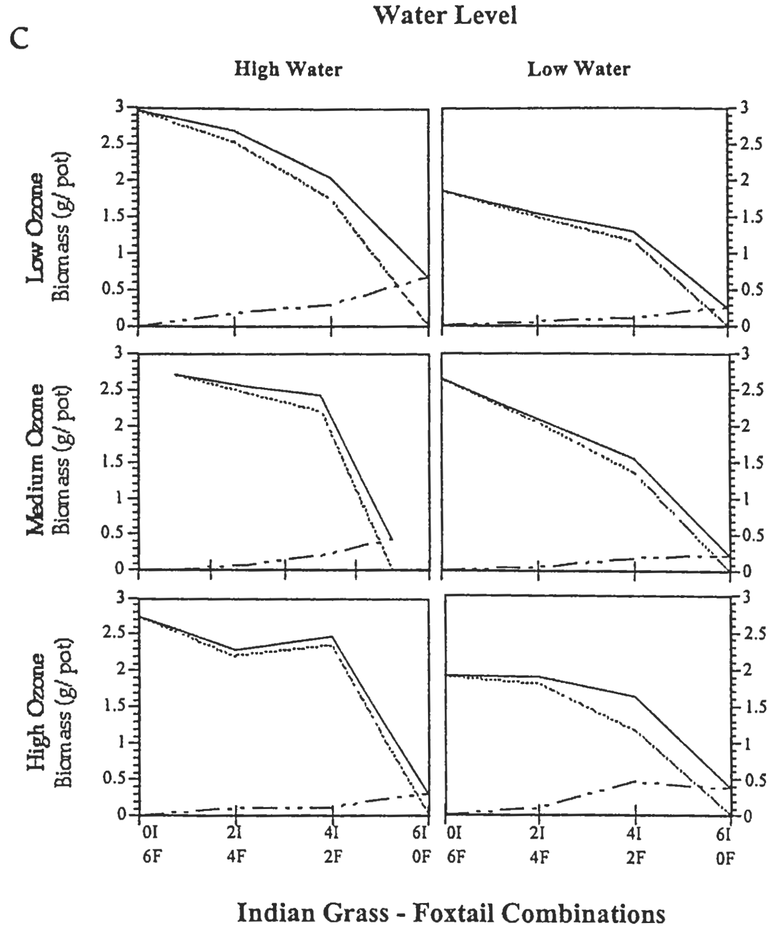


Fig. 3. deWit diagrams (biomass/pot, grams) for species combinations: (a) big bluestem (small dashes)–indian grass (long dash + dots) [mixtures A (6B:0F:0I), F(4B:0F:2I), J (2B:0F:4I), and C (0B:0F:6I)]; (b) foxtail (dots)–big bluestem (small dashes) [mixtures A (6B:0F:0I), E (4B:2F:0I), G (2B:4F:0I), and B (0B:6F:0I)]; and (c) indian grass (long dash + dots)–foxtail (dots) [mixtures B (0B:6F:0I), H (OB:4F:2I), I (0B:2F:4I), and C (0B:0F:6I)]. Solid lines are total biomass per pot. B = big bluestem, F = giant foxtail, I = indian grass. Low ozone is 58.8 ± 25.5 ng·L⁻¹ (0.030 ± 0.013 ppm); medium ozone is 137.1 ± 31.4 ng·L⁻¹ (0.070 ± 0.016 ppm), and high ozone is 215.6 ± 37.2 ng·L⁻¹ (0.110 ± 0.019 ppm).

used in this study can take any of four basic forms (Harper, 1977). In model I, the growth of two species in a mixture results in each contributing to the total yield in direct proportion to its representation in the original planting, i.e. equivalent demands on environmental resources are made by each species. This can happen in two ways: either the density is so low that there is no interference or the effect of species A on species B is precisely the same as that of B on B and the effect of B on A is the same as that of A on A. As illustrated in Fig. 3a, several big bluestem–indian grass diagrams approach the model I competitive relationship (the two species yield lines should intersect midway across the x axis and the total yield line should be straight and horizontal), especially when under water stress (Fig. 3a). Under low water, root density may be so low that moisture is extracted from separate soil volumes and the plants most likely do not interfere with one another.

Model II is exemplified most closely by the foxtail–bluestem combination under water stress and the middle O_3 level (Fig. 3b). Model II interactions are the most prevalent situation characteristic of two species that are making differential demands on the same resources, i.e. there is some difference in resource use between them. In both models I and II, the yield in mixtures is predictable from the yields in pure stands in that a straight line connecting the two monoculture yields will intersect the sums of the mixed yields. Contrary to model I, however, the intersection of the species yield lines is not midway across the x axis. The intersection of the two yield lines gives some indication of the competitive nature between the two species. The foxtail is much more capable than is bluestem of utilizing the available resources under water stress and mid-O_3 levels for the 90-d duration of the experiment.

Model III (mutual antagonism, e.g., allelopathy) occurs when neither species contributes its expected share in mixed cultures and the total yield is concave in appearance. No examples of model III were not found in this experiment.

Model IV interactions reflect mutual benefits and/or avoidance of competition. Model IV interactions in this experiment included most combinations involving giant foxtail (Fig. 3b and c), as well as the bluestem–indian grass combinations with control water and middle to high O_3 (Fig. 3a). The foxtail combinations follow this model simply because intraspecific competition exceeds that of interspecific competition for this species. More resources are demanded by an additional foxtail plant than a small bluestem or indian grass plant, so that, for example, four foxtail plants usually have nearly as much total biomass per pot (when grown with two plants of another species) as when grown in monocultures of six plants. In one instance, (foxtail–bluestem, control water, high O_3, Fig. 3b), the biomass of two foxtail plants even exceeded that of four foxtail plants, leading to an unusually shaped curve. In general, under control water, the total yield lines, for all combinations involving foxtail (Fig. 3b and c), are more convex than under water stress, indicating that, with adequate moisture, the smaller number of foxtail plants are better able to continue adding biomass per plant than when under water stress. The bluestem–indian grass combination diagrams also show a slightly greater convexity under control water, indicating an avoidance of competition in that situation (Fig. 3a). There is no clear pattern apparent due to the O_3 treatments.

These results demonstrate the competitive superiority of foxtail compared with the other two species. Big bluestem and Indian grass were competitively similar. However, one must consider the life history strategies when interpreting the results. Giant foxtail is a C4 annual, capable of rapid and massive growth on disturbed systems. Its strategy is that of a typical colonizing species, with rapid initial establishment, but short-lived in successional time. The other two species are slow-growing, long-lived, perennial species, which are the successional endpoints for the tall grass prairie. The rate of initial growth is critical to the outcome of competition among seedlings in small containers, and the rapid growth of foxtail will have depleted nutrient and water resources.

Application to prairie restoration. In most unmanaged ecosystems, plants must cope with extended periods of variability in resources such as sunlight, moisture, atmospheric CO_2, O_3 levels, etc. As typical tallgrass prairies of North America, grassland environments are characterized by seasonal periods of drought stress (Knapp, 1984; Weaver, 1954). Although differential response of individual species to increasing atmospheric O_3 concentrations may change community structure in natural ecosystems and interfere with their restoration, no major changes of competitiveness among the three species when grown under three O_3 regimes were detected.

When grown from seed, the two native grasses were competitively inferior to the nonnative foxtail under all conditions of soil moisture and O_3 used in this study. After establishment, however, it is likely that the long-lived nature of the natives would move the competitive balance in their favor. During the initial establishment phase, it would be important to minimize the amount of foxtail invading the restoration site. Their complete elimination from the site may be unnecessary as our evidence suggests that a few plants will not cause undo harm in the establishment; indeed, some tall plants may act as a nurse crop to reduce solar- and wind-enhanced evaporation from the site. However, when the density of foxtail approaches that of the planted seedlings, availability of resources for the native grasses will be reduced and their establishment hampered. The occurrence of a transition threshold where the proportion of giant foxtail to native grass alters the interaction from benefactor to competitor, and the impact of plant density on that threshold, remain to be clarified in future investigation.

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