Does Abundance Reflect Competitive Ability?: A Field Test with Three Prairie Grasses
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Does abundance reflect competitive ability?: A field test with three prairie grasses

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Two field experiments were conducted in a tallgrass prairie remnant to determine whether the relative abundance of three perennial grasses (*Andropogon gerardii* > *Sorghastrum nutans* > *Dichanthelium oligosanthes*) was directly related to their relative competitive ability. In the first experiment, performance of transplanted seedlings was measured in monocultures (1, 5, 10, 15 and 20 seedlings) and in pairwise species mixtures. Three different planting proportions (2:18, 10:10, 18:2 seedlings) were used for each pairwise species mixture. Neighbours reduced biomass and tiller production of seedlings significantly while survival was largely unaffected. The performance of a species grown in mixture versus in monoculture at an equivalent density did not differ significantly in almost all cases. In the second experiment, neighbours were removed experimentally from a 1 m radius around established target plants of each species. Tiller production increased significantly following neighbour removal. The three species responded about equally to neighbour removal, indicating that common and less common species were about equally suppressed by neighbours. Results of both experiments indicate that competitive ability and abundance are not significantly related for these three grasses.

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In any plant community, some species are more abundant than others. A number of researchers (e.g. Fisher 1930, Griggs 1940, Grime 1979) have suggested that a species' relative abundance in a community (i.e. species ranked from most to least common) may be directly related to its relative competitive ability (i.e. species ranked from most to least competitive). A number of studies (e.g. Grubb 1982, Roush and Radosevich 1985, Mitchley and Grubb 1986, Miller and Werner 1987, Keddy 1990) provide experimental support for a direct relationship between competitive ability and relative abundance. Yet, relative abundance and competitive ability were not directly related in two studies (Rabinowitz et al. 1984, Taylor and Aarssen 1990) involving perennial grasses. Both studies were conducted in the greenhouse and it is not clear whether results are applicable to natural environments.

To overcome this potential limitation, we recorded the outcome of competitive interactions between perennial grasses in two field experiments. Three tallgrass prairie grasses were studied to test whether their relative abundance was directly related to competitive ability (i.e. ability to respond to or affect other species). Prairie grasses were chosen for the study because one of the two laboratory studies (i.e. Rabinowitz et al. 1984) had used prairie grasses and because competition is thought to be an important determinant of prairie community structure (Tilman 1988).

Methods

Study species

The following three perennial grasses were chosen for the study: *Andropogon gerardii* Vitman, *Sorghastrum*

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nutans (L.) Nash and *Dichanthelium oligosanthes* (Schult.) Gould. Henceforth these species will be referred to by generic name only. *Andropogon* is a common grass in most mesic prairies (Weaver 1931, 1954, 1968, Curtis 1959). It is a tall, C4 perennial bunchgrass that begins growth in late April and flowers in late summer (Weaver 1954, 1968). *Sorghastrum* is also a tall, C4 perennial bunchgrass. However, this species is generally less common than *Andropogon,* with a usual cover of 1–5% in any mesic prairie community compared with >60% cover for *Andropogon* (Weaver 1931, 1954, 1968). *Dichanthelium* is normally the least common of the three grasses and usually has <1% cover in mesic prairie (Weaver 1954, 1968, Curtis 1959, Risser et al. 1981). *Dichanthelium* is a short, C3 perennial bunchgrass which flowers in early summer in contrast to the other two species (Dore and McNeill 1980).

Study site

The study was conducted in a 60-ha tallgrass prairie remnant near Windsor, Ontario, Canada (42°15′N, 83°04′W). Vegetation is dominated by a mixture of grasses and forbs (Pratt 1979). Plots for experiments were set up in a 160 m long × 30 m wide portion of a power transmission corridor that runs through the study area. The corridor has been kept free of woody plants since 1952 by periodic herbicide application and by fire. Once every six years a mixture of herbicide (2,4-D, Diphenoprop 700) and #2 furnace oil is applied to the base of any woody plants present in the corridor. Herbicide was last applied two years before the start of the present study. Fires set by children playing in the area also occur occasionally.

Parent material of soil in the study area is fine outwash sand (Hoffman 1975, cited in Pratt 1979). Average annual precipitation at Windsor airport (about 9 km from the study site) is 849 mm and monthly precipitation ranges from 50 mm in February to 89 mm in June (Environment Canada 1990, 1991). During the growing season (April–October), total precipitation was 34 mm above average in the first year of the study (1990) and about average in the second year. Average monthly air temperature ranges from −4.9°C in January to 22.2°C in July (Environment Canada 1990, 1991). During the growing season, monthly air temperature was about average in 1990 and 1.8°C higher than average in 1991.

Vegetation surveys

In August 1990, the relative abundance of the three grasses was determined along 14 30-m long by 2-cm wide line transects (10 m apart). Presence or absence of each grass species was checked in 1 m segments set up at 4-m intervals (total of 84 1-m segments). In each 1-m segment, a grass was considered present if it was directly under or over or touched the transect line. Frequency was expressed as the percentage of 1-m segments occupied by a species.

In September 1990, all species of vascular plants were censused in 16 1-m^2 quadrats. Two quadrats were randomly positioned in each of eight sampling blocks set up for experiment 2 (see below). Each quadrat was subdivided into 25 20-cm × 20-cm squares and all species rooted in each square were noted. Frequency of a particular species was calculated as the percentage of 400 squares occupied (i.e. 8 blocks × 2 quadrats × 25 squares per quadrat).

Experiment 1

Experimental design and rationale

The competitive ability of seedlings of the three grasses was determined with a randomized complete block experiment involving (a) pairwise mixtures of *Andropogon, Sorghastrum* and *Dichanthelium* seedlings, using a density of 20 seedlings per pot and three planting proportions (2:18, 10:10, 18:2 seedlings) (i.e. a replacement series) and (b) five monocultures per species (1, 5, 10, 15, and 20 seedlings per pot). Twenty seedlings per pot was the greatest density that could be planted conveniently. Monocultures were used to test the assumption that neighbours affected plant performance at the density of 20 seedlings per pot used for pairwise mixtures. A replacement series of planting proportions was used to allow comparison with results of previous studies (e.g. Rabinowitz et al. 1984). One contentious aspect of the replacement series design is that only the proportion of species in mixtures varies and not the overall density. Results, therefore, may depend of the density chosen. Cousens (1991) points out that while quantitative results of replacement series experiments may vary with density, the qualitative interpretation of which species is a better competitor is unlikely to change with density. Since the objective of the present study was only to characterize the relative competitive ability of the three grasses, a replacement series was an appropriate experimental design. Results of replacement series experiments may also be affected by differences in the size of competitors (Connolly 1986, Silvertown and Dale 1991, Grace et al. 1992). Seedlings of similar initial size were used to minimize possible plant size bias. The nine possible combinations of two species mixtures planted in three different proportions were set up along with 15 monocultures (i.e., five per species) in each of seven blocks.

Each pairwise species mixture contained a more common species interacting with a less common species because grasses of differing relative abundance were purposely chosen for the experiment. If the greater natural abundance of the more common species reflected its greater competitive ability, experimental results should show one of the following three outcomes:

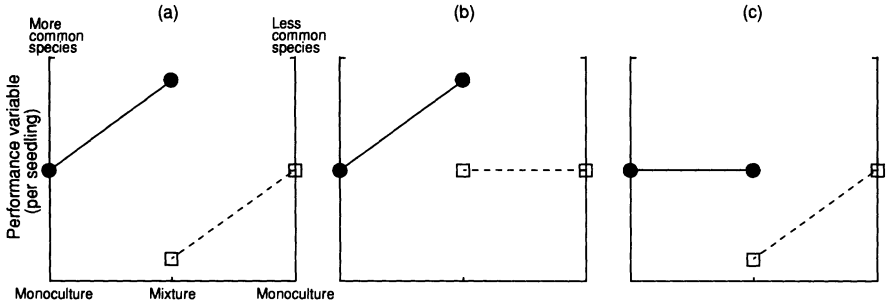

Fig. 1. Results expected if relative abundance and competitive ability are directly related. Only one of three planting proportions used for the mixture treatment is shown for ease of presentation.

1. the more common species should perform significantly better in mixture than in monoculture, while the less common species should perform significantly worse in mixture than in monoculture (Fig. 1a); 2. the more common species should perform significantly better in mixture than in monoculture, while the less common species should perform as well in mixture as in monoculture (Fig. 1b); or 3. the more common species should perform as well in mixture as in monoculture while the less common species should perform significantly worse in mixture than in monoculture (Fig. 1c). Some other pattern of response would be evident if relative abundance and competitive ability were not directly related.

Seed germination and seedling establishment

Seeds of *Dicanthelium* were collected from plants at the study site in July 1990 while seeds of *Andropogon* and *Sorghastrum* were collected in September 1990. Seeds were stored at 4°C until April 1991 to help break dormancy.

Seedlings with shoots between 10 mm and 25 mm long were planted in double pots (8.5 × 8.5 × 11 cm deep) filled with a 5:1 mix of sieved soil from the study site:coarse sand. A double pot was used to facilitate the transplanting of seedlings into field plots. The inner pot had no bottom and three 5-mm diameter holes on each side. Drainage holes in the outer pot were covered with filter paper to prevent loss of soil.

Seedlings were spaced evenly in the pot using a five row by four column planting design. In the 2:18 and 18:2 mixtures, seedlings of the minority species were surrounded by eight seedlings of the majority species. In the 10:10 mixture, seedlings were arranged in a checkerboard design to provide about equal numbers of intraspecific and interspecific neighbours. Each seedling was marked with a loose-fitting plastic ring, colour-coded to species. Rings were split to allow for expansion as the stem grew.

Seedlings were allowed to become established in the greenhouse for 4–5 weeks before they were transplanted into field plots. Any dead seedlings were replaced up to three weeks after the initial planting.

Preparation of field plots

Seven circular plots 2 m in diameter and at least 10 m apart were set up in May 1991. Aboveground vegetation within each plot was clipped and removed. Root crowns and rhizomes were removed by skimming the ground just below the surface with a small spade. To exclude animals, each plot was fenced (25-mm wire mesh, 40 cm tall). Plastic garden edging (10 cm tall) was placed at the bottom of the fence to exclude crawling invertebrates such as slugs.

Seedlings in bottomless pots were transplanted into pre-made holes about 10 cm apart in the central 0.6 m^2 of each plot. Care was taken to ensure good contact between soil at the bottom of the hole and soil in the bottomless pot. The 24 pots per plot were arranged in a five by five matrix with one hole left vacant. Pots were assigned randomly to matrix positions. Seedlings were given 75 ml water twice a week for the first two weeks after transplanting and once more in the third week.

Measurements and analysis

Transplants were harvested at ground level between 128–138 d from the start of the experiment. Plants were dried at 80°C to constant mass and weighed. The number of tillers >2 mm long was counted for each transplant.

Analysis of variance (ANOVA) for a randomized complete block design was used to test for a statistically significant effect of planting proportion (or seedling density in monocultures) on percentage survival, biomass per survivor and tiller number per survivor. Tukey's HSD test was used to compare means when ANOVA results were significant ($P < 0.05$). Data were transformed as necessary to meet ANOVA assumptions of normality of residuals and homogeneity of variance. In a few cases an extreme outlier had to be excluded to satisfy assumptions of ANOVA. The General Linear Model procedure of SAS (1985) was used for all statistical analyses.

Experiment 2

Experimental design, rationale and procedure

Effects of neighbours on older, naturally-occurring plants of the three grasses was determined using a neighbour removal experiment (cf. Aarssen and Epp 1990). For each grass, tiller production by a target plant was compared in plots with neighbouring plants left

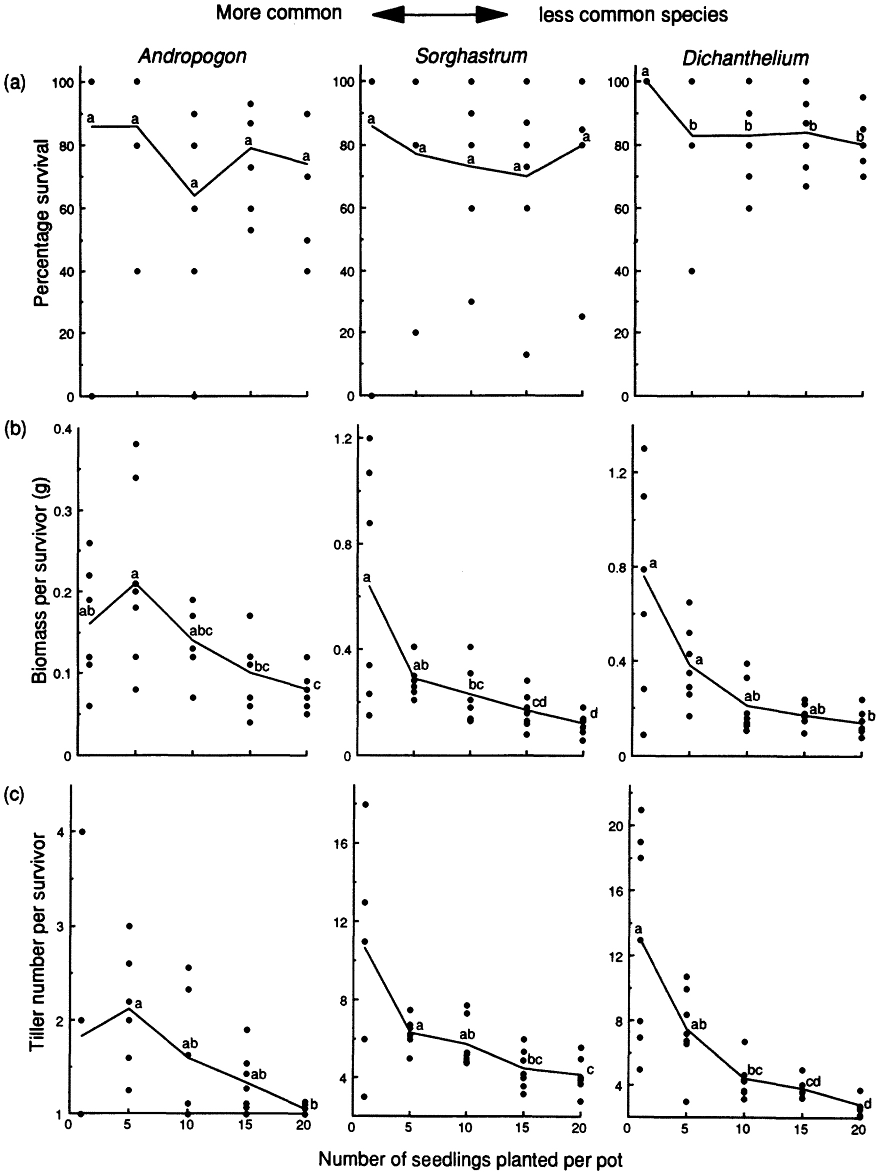

Fig. 2. Effect of planting density on (a) percentage survival, (b) biomass per survivor and (c) tiller number per survivor for seedlings of *Andropogon*, *Sorghastrum* and *Dichanthelium* in monocultures. Note that the scale on the y-axis differs between species in (b) and (c). Mean values for each of the seven blocks are shown. The line joins means for the seven blocks. Means with the same lowercase letter do not differ significantly (Tukey's HSD test, $P > 0.05$). Treatments without letters did not meet the homogeneity of variance requirement for ANOVA and were not included in the analysis.

intact (control) versus removed experimentally (neighbour removal). If a common species owed its high natural abundance to being relatively unaffected by its neighbours, removal of neighbours should have little effect on its performance. Conversely, if a less common species is low in abundance because of strong suppression by neighbours, its performance should improve significantly when neighbours are removed.

Neighbour removal experiments have been widely used to measure effects of competition from neighbours (e.g. Goldberg and Werner 1983, Keddy 1989, Aarssen and Epp 1990). Yet, their use has been criticized because nutrient supply may increase through decomposition of roots missed in the removal procedure (Campbell et al. 1991). Since decomposition simply releases nutrients that were objects of past competition, some researchers feel that this criticism is not entirely justified (Aarssen and Epp 1990). In the present study, possible confounding effects of root decomposition were less problematic because relative rather than absolute competitive ability was of interest.

Andropogon and Sorghastrum as target species

A randomized complete block experiment was set up with two treatments (i.e. control and neighbour removal) in each of eight blocks (least 5 m apart). Two plants (i.e. two isolated bunches of closely packed tillers) per species with similar basal area were chosen as target plants in each block. One of the two plants per block was randomly assigned to each experimental treatment.

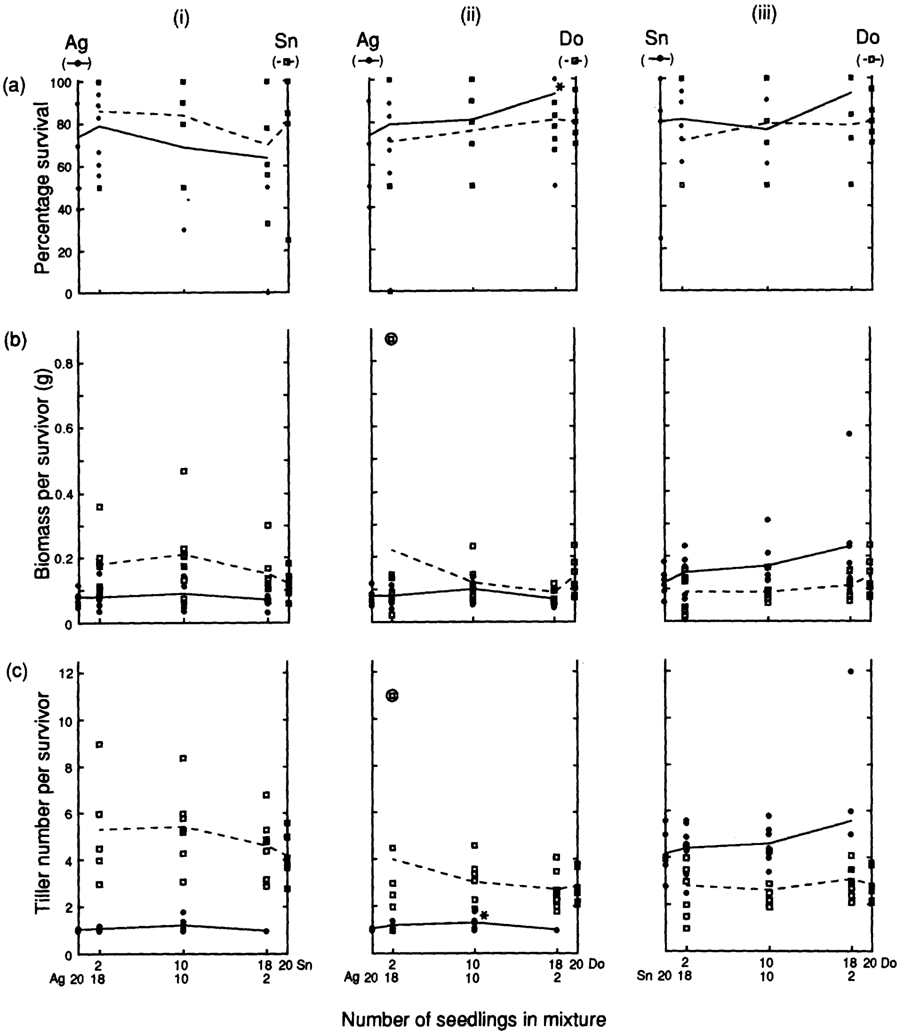

Fig. 3. (a) Percentage survival, (b) biomass per survivor and (c) tiller number per survivor in seedling mixtures of (i) *Andropogon* (Ag) and *Sorghastrum* (Sn), (ii) Ag and *Dichanthelium* (Do), and (iii) Sn and Do compared to monocultures. Mean values for each of the seven blocks are shown. The lines (solid line for species on left, broken line for species on right) join means for the seven blocks. A significant difference (Tukey's HSD, $P < 0.05$) between mean performance in mixture versus in monoculture is indicated by an asterisk. The two circled values are outliers not used in the statistical analysis.

Vegetation was left intact in the control treatment but in the neighbour removal treatment all aboveground vegetation surrounding the target plant was removed to a distance of one metre from the centre of the plant. Vegetation was clipped near the soil surface and removed. Litter was left in place. To minimize regrowth, root crowns of neighbours were removed using a spade. The order of removals was randomized over blocks and was completed between 12 June and 19 June 1990. Plots were subsequently weeded every three weeks to keep target plants free of neighbours in the neighbour removal treatment.

An initial count of tillers was completed between 21 June and 25 June 1990. Subsequent counts were made on 15–17 July and 27–29 August in 1990, and on 6–10 June, 10–12 July and 14–21 August in 1991.

Dichanthelium as target species

Dichanthelium occurred too infrequently in the eight blocks to use naturally-occurring plants for the experiment. Transplants dug from within 200 m of the study site were used instead. Transplants were planted at the centres of control and neighbour removal plots on 25 July 1990 in the same eight blocks containing target plants of the other two species. The following year, tillers of surviving transplants were counted on four dates; namely, 6–10 June, 10–12 July, 14–21 August and 13 September 1991.

Analysis

The ratio of final count of tillers: initial count of tillers was calculated for each species in both experimental treatments. The statistical significance of a difference in mean ratio values between treatments was tested with ANOVA. Ratio values were log transformed before analysis to meet ANOVA assumptions of normality and homogeneity of variance.

Live neighbour standing crop in control plots

The amount of neighbour biomass present in control plots was estimated by harvesting aboveground standing

Table 1. Mean (±1 standard error) number of tillers per target plant for three species (Sp) [*Andropogon* (Ag), *Sorghastrum* (Sn) and *Dichanthelium* (Do)] on seven sampling dates (month/day in 1990 and 1991) in neighbour removal (R) and control (C) treatments (Trt). A significant difference (Tukey's HSD, $P < 0.05$) between mean (±1 standard error) ratios of final:initial tiller number is indicated by different lowercase letters.

Sp	Trt	Number of tillers per target plant							Final: initial tiller number
		1990			1991				
		06/25	07/16	08/26	06/06	07/10	08/14	09/13	
Ag	R	90 (±11)	128 (±17)	131 (±18)	188 (±22)	192 (±18)	173 (±16)	–	2.0^{bc} (±0.2)
Ag	C	101 (±11)	114 (±14)	98 (±14)	100 (±11)	101 (±13)	89 (±13)	–	0.9^{a} (±0.1)
Sn	R	79 (±12)	108 (±18)	198 (±21)	229 (±33)	237 (±32)	283 (±31)	–	4.6^{d} (±1.1)
Sn	C	68 (±13)	88 (±21)	83 (±19)	69 (±12)	76 (±14)	74 (±14)	–	1.1^{ab} (±0.2)
Do	R	–	–	–	18 (±5)	13 (±5)	17 (±7)	30 (±11)	3.1^{cd} (±0.6)
Do	C	–	–	–	6 (±1)	4 (±1)	4 (±1)	4 (±2)	1.4^{ab} (±0.2)

crop in September 1991. Living and dead material was separated, dried at 80°C to constant mass and weighed.

Results

Vegetation surveys

Andropogon ranked first (frequency of 92%), *Sorghastrum* second (frequency of 21%) and *Dichanthelium* third (frequency of 5%) on line transects. Of the 54 species sampled in 1-m^2 quadrats, *Andropogon* (frequency of 80%) ranked first, *Sorghastrum* (frequency of 12%) ranked eighth and *Dichanthelium* (frequency of 0%) ranked last.

Experiment 1

Monocultures

The mean percentage of seedlings surviving to the end of the experiment ranged from 64 to 86% for *Andropogon,* 70 to 86% for *Sorghastrum* and 80 to 100% for *Dichanthelium* (Fig. 2a). Percentage survival did not change significantly with an increase in density from 1 to 20 seedlings per pot with the following exception; survival of *Dichanthelium* was 100% at a density of 1 seedling per pot but significantly lower (Tukey's HSD, $P < 0.05$) at densities greater than 1 seedling per pot.

In contrast, both biomass per survivor and tiller number per survivor decreased significantly (Tukey's HSD, $P < 0.05$) as plant density increased from 1 to 20 seedlings per pot (Fig. 2b, c). Mean biomass per survivor decreased from 0.21 to 0.08 g for *Andropogon,* from 0.64 to 0.12 g for *Sorghastrum* and from 0.76 to 0.14 g for *Dichanthelium.* Mean tiller number per survivor decreased from 2 to 1 tillers for *Andropogon,* from 10 to 4 tillers for *Sorghastrum* and from 13 to 3 tillers for *Dichanthelium.*

Species mixtures

Seedlings generally survived equally well in mixture and monoculture. Mean percentage survival of *Andropogon* ranged from 64 to 79% in mixture with *Sorghastrum,* and from 79 to 93% in mixture with *Dichanthelium,* compared to 74% survival in monoculture (Fig. 3a). The only significant difference (Tukey's HSD, $P < 0.05$) between *Andropogon* survival in mixture as compared to monoculture occurred in a mixture of 2 *Andropogon* plants with 18 *Dichanthelium* plants, where an average of 93% of *Andropogon* plants survived compared with 74% survival in monoculture. For *Sorghastrum,* there were no significant differences between its survival in monoculture and in any of the mixtures. Mean percentage survival ranged from 70 to 84% in mixtures with *Andropogon* and from 81 to 93% in mixture with *Dichanthelium,* compared to 80% in monocultures. Similarly, there were no significant differences in percentage survival of *Dichanthelium* seedlings in mixtures versus monoculture. Mean survival ranged from 71 to 81% in mixtures with *Andropogon* and from 71 to 79% in mixtures with *Sorghastrum,* compared to 80% in monocultures.

Biomass per survivor did not differ significantly ($P > 0.05$) between mixtures and monoculture for any of the species in any of the mixtures (Fig. 3b). Mean biomass per survivor for *Andropogon* ranged from 0.07 to 0.09 g in mixtures with *Sorghastrum* and from 0.07 to 0.10 g in mixtures with *Dichanthelium,* compared to 0.08 g in monoculture. Mean biomass per survivor for

Sorghastrum ranged from 0.15 to 0.21 g in mixture with *Andropogon* and from 0.15 to 0.23 g in mixture with *Dichanthelium,* compared to 0.12 g in monoculture. For *Dichanthelium,* the mean biomass per survivor ranged from 0.09 to 0.22 g in mixture with *Andropogon* (mean includes a single outlier of 0.87 not used in the statistical analysis; without the outlier the range is from 0.09 to 0.12), and from 0.09 to 0.11 in mixture with *Sorghastrum,* compared to 0.14 g in monoculture.

The number of tillers per survivor generally did not differ significantly ($P > 0.05$) between mixtures and monoculture for the three species (Fig. 3c). Mean tiller number per survivor for *Andropogon* ranged from 1.0 to 1.2 in mixtures with *Sorghastrum* and from 1.0 to 1.3 in mixtures with *Dichanthelium,* compared to 1.0 in monocultures. The only significant difference (Tukey's HSD, $P < 0.05$) between *Andropogon* tiller number in mixture compared to monoculture occurred in a mixture of 10 *Andropogon* plants with 10 *Dichanthelium* plants. The mean number of *Andropogon* tillers per survivor here was 1.3 in mixture and 1.0 in monoculture. Mean tiller number per survivor for *Sorghastrum* ranged from 4.6 to 5.4 in mixture with *Andropogon* and from 4.4 to 5.6 in mixture with *Dichanthelium,* compared to 4.2 in monoculture. For *Dichanthelium,* the mean tiller number per survivor ranged from 2.7 to 4.0 (mean includes a single outlier of 11 tillers not used in the statistical analysis, without the outlier the range is from 2.6 to 3.0) in mixture with *Andropogon,* and from 2.6 to 3.1 in mixture with *Sorghastrum,* compared to 2.8 in monocultures.

Experiment 2

Tillers

Tiller number increased between the start and end of the experiment in the neighbour removal treatment but showed little change in the control treatment (Table 1). Not all transplants of *Dichanthelium,* however, tolerated transplanting. Only nine of the original sixteen transplants were still alive in June 1991; namely, five plants in the neighbour removal treatment and four plants in the control treatment.

Mean ratios of final:initial number of tillers ranged from 0.9 to 4.6 (Table 1). Ratio values were significantly greater in the neighbour removal treatment than in the control treatment for each species. The effect of treatment (removal vs control) did not differ significantly among species (i.e. treatment × species term in ANOVA, $F_{2,9} = 3.16$, $P = 0.09$).

Live neighbour standing crop

Mean (±1 standard deviation) standing crop of neighbours in control plots was 637 (±158) g/m^2 for *Andropogon* plots, 732 (±178) g/m^2 for *Sorghastrum* plots and 677 (±146) g/m^2 for *Dichanthelium* plots.

Discussion

The rank order of the three test species from most to least frequent in the study area was *Andropogon, Sorghastrum, Dichanthelium.* This rank order is consistent with rank orders reported for these species at other tallgrass prairie sites (Weaver 1931, 1954, 1968, Curtis 1959, Risser et al. 1981).

Interactions among seedlings of these grasses in experiment 1 had a significant effect on their performance. In monocultures, biomass per seedling and number of tillers produced by seedlings planted 20 per pot was significantly lower than for seedlings planted 1 per pot. This reduction in seedling performance indicates that seedlings were competing for resources when planted 20 per pot. However, competitive interactions were not sufficiently intense to reduce seedling survival significantly.

For pairwise species mixtures, only two cases showed a significant improvement in performance of seedlings in mixture compared to monoculture. In both cases, seedlings of the most abundant species (*Andropogon*) performed better in mixture with a less abundant species (*Dichanthelium*). In all other cases, the less common grass was not disadvantaged (or advantaged) in any way by interactions with a more common grass. These results provide only weak evidence of a direct relationship between competitive ability and relative abundance.

Our results are largely consistent with results of greenhouse experiments by Taylor and Aarssen (1990) conducted with some old-field grasses. It is unlikely that their inability to detect a relationship between competitive ability and relative abundance was simply due to their measurement of competitive interactions in the greenhouse rather than in the field. Taylor and Aarssen (1990) proposed that competitive ability may be more a consequence of genotype than of species designation. A genotype of one species may be able to suppress some but not all genotypes of another species. Intransitive networks of competitive interactions at the genotype level could translate into roughly balanced interactions between species. This hypothesis of balanced competitive ability (see also Aarssen 1983, 1989) is supported by results obtained here for the three prairie grasses. However, our experiment was only an indirect test of this hypothesis.

Our results are not consistent with an inverse relationship between relative abundance and competitive ability reported for seedlings of prairie grasses by Rabinowitz et al. (1984). However, our results are consistent with their finding that tiller fragments of common and less common species performed equally well in mixtures and monocultures. Neither their results nor our results are consistent with a direct relationship between relative abundance and plant performance in mixtures.

If competitive interactions do affect the relative abundance of the three species tested here these interactions must occur at a later stage of plant development. If transplants has been given a longer period to interact in experiment 1, different results may have emerged. Perhaps the two tall grasses (i.e. *Andropogon* and *Sorghastrum*) would suppress the shorter grass (i.e. *Dichanthelium*). Alternatively, earlier spring growth by the C3 species (*Dichanthelium*) may allow it to suppress the two C4 species (*Andropogon* and *Sorghastrum*).

To examine species interactions at a later stage of growth, neighbours were removed from around older, naturally-occurring plants in experiment 2. The mean ratio of final:initial tiller number was significantly higher for plots where neighbours were removed than for control plots. This difference indicates that each species was suppressed to some degree by neighbours. Response to neighbour removal did not differ significantly between species (i.e. $P > 0.05$ for treatment by species interaction term in ANOVA). In other words, neighbours suppressed common and less common grasses about equally. In this case, differential effects of neighbours on established plants does not help to explain why some species are more abundant than others.

In summary, field experiments conducted with both established plants and seedlings of three grass species indicated that target plants interacted with their neighbours but there was little evidence that the more common species owes its higher abundance to being more competitive. Results of this study plus those of Rabinowitz et al. (1984) and Taylor and Aarssen (1990) indicate that the outcome of competitive interactions do not always help explain why some species are more abundant than others.

Competition is only one possible factor that may determine relative abundance (Weldon and Slausen 1986). Differential effects of herbivory (Harper 1977, Landa and Rabinowitz 1983, Gibson et al. 1990), disturbances (Grubb et al. 1982, Collins and Glenn 1988) or pathogens (Harper 1977) may play a significant role in regulating the relative abundance of these prairie grasses. Historical factors and chance events may also be important (Fowler 1990). A species may also be relatively low in abundance because of its limited reproduction (Rabinowitz et al. 1989) or because few microsites are available for regeneration (Grubb 1977) or because it arrived only recently at a particular site (Fowler 1990). The above list is not exhaustive but serves to underscore the challenge of explaining why "some species are rare, some common, some constant (even if rare or occasional only) and others sporadic" (Watt 1961).

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