Intensity of intra- and interspecific competition in coexisting shortgrass species

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Summary

1 *Bouteloua gracilis* and *Buchloë dactyloides* are dominant species in the shortgrass steppe. Previous studies have suggested that these species have similar resource requirements and, as there is no temporal segregation in growth, we suggest that competition for below-ground resources should be intense. Classical competition theory predicts that, under stable conditions, coexistence of species with similar requirements can occur if intraspecific competition is more intense than interspecific competition. We therefore compared the competitive abilities of the two species under both inter- and intraspecific conditions, another determinant of coexistence in plant communities.

2 A 3-year experiment was conducted in a small homogeneous area and a separate 2-year experiment was conducted in a larger area. In both experiments, a hexagonal planting design was used to achieve all possible combinations of species and to control plant size and neighbourhood asymmetries at the start of the experiment. Half the target plants were grown within steel cylinders to reduce below-ground competition.

3 We found similar results in the two experiments. Plant biomass and seed production were always higher in plants growing with reduced competition, although seed production was quite variable. Relative competition intensity did not differ between intraspecific and interspecific competition.

4 Our results suggest that competition between these coexisting shortgrasses is intense, but do not support the prediction of a difference between intra- and interspecific competition. We discuss alternative explanations.

Key-words: below-ground competition, coexistence, intraspecific vs. interspecific competition, shortgrasses.

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Introduction

Plant community composition results from both deterministic factors (species requirements and biotic interactions) and stochastic processes (recruitment and disturbance). Tilman (1982) suggested that 'interactions among species and of species with their environment are sufficiently strong as to establish major patterns which are discernible over such stochastic noise' (p. 4). Aarssen (1983, 1989) concluded that, in general, the coexistence of plant species results from niche requirements (i.e. resource partitioning) and relative competitive ability. Niche requirements and competitive ability of plant species have, however, rarely been studied in the same system (Goldberg & Barton 1992). We therefore evaluated the competitive abilities of two co-occurring C_4 perennial grasses whose environmental requirements are known.

Monson *et al.* (1983) proposed a model of plant co-existence for the shortgrass steppe. This was based only on temporal segregation and resource partitioning among four abundant graminoids, two of which are C_3 and two C_4, and used phenology and photosynthetic adaptation to temperature to explain the separation. Thus, the C_3 grass, *Agropyron smithii*, whose photosynthetic rates are low at high temperatures and maximum at low temperatures, grows early in the season. The other C_3 species, the sedge, *Carex eleocharis*, did not exhibit a particular

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maximum or minimum threshold for photosynthesis, compared with the other three species. Thirty per cent lower maximum photosynthesis was interpreted as indicative of a low rate of resource use, which would allow it to coexist with the other three species (Monson *et al.* 1983). There was, however, no clear temporal segregation and resource partitioning between *Bouteloua gracilis* and *Buchloë dactyloides*, both had low photosynthetic rates at low temperatures and higher rates at high temperatures, maximum values were similar, and the two species both grew preferentially during the middle to late growing season (Dickinson & Dodd 1976). We were therefore prompted to study their competitive abilities, as this could be another component contributing to coexistence.

Classical competition theory predicts that, under relatively stable environmental conditions (i.e. when there is a lack of disturbance or stress), coexistence of species with similar requirements occurs when intra-specific competition is more intense than interspecific competition (MacArthur & Levins 1967; Goldberg & Barton 1992; Tilman & Pacala 1993). Is this a valid prediction for the shortgrass steppe where competition is more intense below- than above-ground? Furthermore, this pair of species shows similarities in morphology, rooting habits and ecophysiology, and we aimed to test the hypothesis that intra- and interspecific competition will therefore be similar (Weaver & Albertson 1944; Weaver 1954; Albertson *et al.* 1966; Monson *et al.* 1983).

The performance of an individual plant can be affected by both the amount of space that surrounds it (i.e. neighbourhood area) and the identity of the neighbour species (Gurevitch *et al.* 1990; Aguilera & Lauenroth 1993b). There is also the possibility of confounding the effect of size and number of neighbours, therefore the *per capita* effect of competition must be controlled (Goldberg 1987). To avoid this weakness, which is considered to be a common problem of the few studies that compare intra- and interspecific competition (Goldberg & Barton 1992), we transplanted similar sized individuals (collections of tillers) from the field into a design which replicated the natural neighbour frequency and separation (Aguilera & Lauenroth 1993b).

Methods

STUDY SITE

We conducted two experiments at the Central Plains Experimental Range (CPER) (40°49′ N, 104°47′ W) in north-central Colorado, USA. At the CPER, *B. gracilis* accounts for 60% of plant cover and *Bu. dactyloides* is subdominant accounting for 10% of plant cover. Both these bunchgrasses reproduce by seedlings as well as vegetatively (i.e. tillers) and *Bu. dactyloides* also produces stolons. At our site, mean annual precipitation is 321 mm, mean annual temperature is 8.6 °C and mean monthly temperatures range from −5 °C in January to

22 °C in July (Lauenroth & Sala 1992; Aguilera & Lauenroth 1993a). The growing season extends from May until late September, depending on water availability. Precipitation during the 6 months of the growing season was variable during the years in which we performed the experiments, 328 mm in 1992, 160 mm in 1993 and 206 mm in 1994 (growing season mean precipitation for CPER is 192 mm, SD = 73.6, for the period 1950–80).

EXPERIMENTAL DESIGN

We conducted two experiments using the same plant distribution but differing in their size and duration. The first experiment encompassed a small area (9 m²) to maximize the probability of homogeneous soil and environmental conditions and ran for 3 years (1992, 1993 and 1994). The second experiment used a larger, more heterogeneous area (750 m²) and ran for 2 years (1993 and 1994).

In both studies, the experimental design consisted of a factorial combination of two levels of each of three variables, neighbour species, target species and competition. *B. gracilis* and *Bu. dactyloides* alternated in the role of neighbour and target species to achieve conditions of intra- and interspecific competition. We planted the target species in the centre of a hexagonal spatial arrangement with an additional border of plants, so each plant (whether target or neighbour) was surrounded by six others and the distance between centres of plants was always 14 cm. Focal plants were surrounded by an average of six neighbours in the field (Aguilera & Lauenroth 1993b), and root systems of neighbour plants begin to overlap in the steppe at an average distance of 14 cm (Coffin & Lauenroth 1991). We chose to manipulate below-ground competition because the low leaf area index in the Colorado shortgrass steppe decreases the probability of above-ground competition (Knight 1973; Lauenroth *et al.* 1978; Lauenroth & Coffin 1992). In reduced competition treatments, we planted the target plant inside a steel pipe (14.5 cm in diameter and 30 cm deep), which had been driven into the soil. Each of the eight treatments had six replications. Portions of adult plants were collected from a nearby location using a steel corer (7 cm in diameter and 15 cm in depth), such that each transplant consisted of a crown with at least nine tillers and their associated roots. For the dioecious species *Bu. dactyloides*, we optimized our estimates of seed production per plant by selecting only females as target individuals.

In the small experiment (hereafter experiment 1) all neighbour plants were planted on the same day, and were then watered to ensure establishment. Target plants and steel pipes were installed 1 month later in 1 day (early July). The identity of the target species, as well as the location of steel pipes, was randomized.

In the larger experiment (hereafter experiment 2), we randomly located six plots (blocks) and divided each into two subplots, one planted with *B. gracilis* and

the other with *Bu. dactyloides* as neighbour plants. Inside each subplot, we planted two target plants for each species, one of which grew inside a metal cylinder. The location of target species and steel pipes was randomized inside each subplot. Planting of neighbour plants occurred between June and late September. All target plants were planted on a single day in late September.

RESPONSE VARIABLES

Response variables were measured only on target plants. We estimated above-ground biomass by counting tillers per plant and using a relationship between number of tillers and dry biomass per plant for each species. The relationships were derived at each sampling date, for plants harvested from an adjacent area: r^2 values were always > 0.78. Biomass estimates for *Bu. dactyloides* included both tiller and stolon biomass. We also obtained a relationships between length of stolons and dry biomass. We used biomass to calculate relative growth rate (RGR) in each year and treatment

$$RGR = (\ln (M_2/M_1))/t, \qquad \text{eqn 1}$$

where M_2 is the biomass at the end of the growing season, M_1 is the biomass at the start of the growing season, and t is the number of days between sampling dates.

We estimated seed production per plant at the end of each growing season. We harvested the culms from *B. gracilis* and calculated the number of seeds produced per plant using a previously derived relationship between number of culms and number of viable seeds ($r^2 = 0.82$; Coffin & Lauenroth 1992). For *Bu. dactyloides*, we harvested the culms and counted the number of caryopses.

We measured light penetration at soil level midway between each target plant and one randomly selected neighbour with a Li-Cor cosine collector at noon on two cloudless days (06/15/93 and 08/04/94). We expressed light penetration as a percentage of the reading taken above the canopy.

We calculated the relative competition intensity index (RCI) from our biomass estimates using the equation

$$RCI = (M_{-C} - M_{+C})/M_{-C}, \qquad \text{eqn 2}$$

where M_{-C} is the biomass of plants growing with reduced competition and M_{+C} is the biomass of plants growing with competition (Grace 1995).

STATISTICAL ANALYSIS

Experiment 1

The factors neighbour species and target species were tested using the neighbour × target interaction as the denominator. Competition, as well as target × competition and neighbour × competition interactions, were tested using the interaction among

neighbour × target × competition as the denominator. Using the interaction terms as the denominator of the *F*-test underestimates the value of *F*, but using the residual error would overestimate it (we tested both approaches and the results did not differ; Steel & Torrie 1980). We looked at both main effects and interactions, although in general, interactions between factors were not significant. When an interaction was significant, we did not consider main effects. In the figures, we included a least significant difference (LSD) bar calculated with the residual error term to facilitate the visual comparisons of the treatments.

Experiment 2

Data were analysed as a split-plot factorial design. The effect of neighbour species (i.e. the splitting factor) was contrasted using the interaction of neighbour species × block as the denominator. Target species, competition and their interaction were tested using the type I error as the denominator. We looked at the main effects and interactions, although in general, interactions between factors were not significant. When an interaction was significant, we did not consider main effects. Simple effects and multiple comparisons were performed using LSD.

Analysis of data in both experiments was performed using SAS (SAS 1988) and repeated measures designs (MANOVA; Potvin *et al.* 1990). When time interacted with experimental factors, individual ANOVAs were performed at each sampling date. We used linear regression analysis to relate variables such as in the tiller–biomass relationship. All differences mentioned in the text are significant at $P \leq 0.05$. Data were transformed when necessary, but untransformed data are presented for ease of interpretation.

Results

EXPERIMENT 1

Target plants subject to below-ground competition from neighbours had significantly less biomass than those growing inside steel cylinders (reduced competition) on all dates for both *B. gracilis* and *Bu. dactyloides* ($P < 0.05$; Fig. 1). This effect was similar regardless of whether competition was from conspecific or heterospecific neighbours. RGR was reduced by competition only during the first 2 years ($P < 0.05$; Table 1). In 1992, neither neighbour nor target species nor the interaction of competition × neighbour and competition × target were significant, suggesting that intra- and interspecific competition caused a similar reduction in the growth of both species. In 1993, interspecific competition reduced RGR more than intraspecific competition in both *B. gracilis* and *Bu. dactyloides*, but differences were not statistically different.

Seed production was lower in plants growing with competition than in plants growing inside the tubes in all
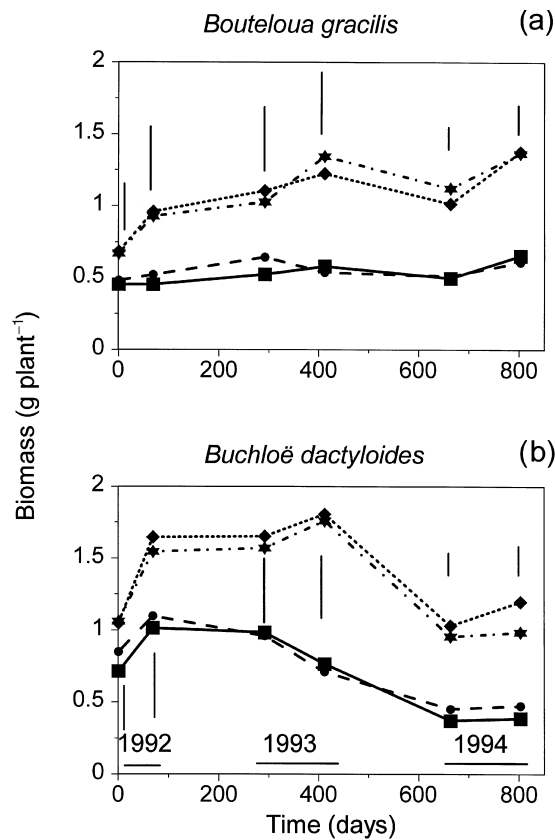
Fig. 1 Biomass per plant of *Bouteloua gracilis* (a) and *Buchloë dactyloides* (b) in experiment 1 for each of the sample dates (August and October 1992, May and September 1993, May and October 1994). For both species, the two upper lines represent the reduced competition treatments, whereas the two lower lines are with full competition. Plants growing with intra- and interspecific neighbours are represented by full and dashed lines, respectively. Bars represent the least significant difference (LSD) for each date ($P < 0.05$), calculated using the experimental error for that date.

three years ($P < 0.05$). The maximum difference due to competition occurred during 1993, when *Bu. dactyloides* produced more viable seeds than *B. gracilis*, both with and without competition ($P < 0.05$). No interaction of competition with neighbour or target species was significant (Fig. 2).

Relative competition intensity was not different for any combination of target and neighbour species, suggesting that there was no difference between intra- and interspecific competition in any of the years studied. However, time was significant, with competition intensity lower in 1992 than in either 1993 or 1994 ($P < 0.05$; Fig. 3). The fraction of light that penetrated the soil surface between plants was 93% and 91% during 1993 and 1994, respectively, suggesting that above-ground competition was negligible, even at later stages of the experiment.

EXPERIMENT 2

Competition significantly reduced biomass of both species during 1993 and 1994. Plants growing inside

Table 1 Relative growth rates (mean ± SE) of plants of *Bouteloua gracilis* and *Buchloë dactyloides* growing with competition (+C) and with reduced competition (–C) in experiment 1 (3 years) and experiment 2 (2 years). Intra- and interspecific competition treatments result from the combination of target and neighbour species. Relative growth rate was calculated using the biomass at the start and the end of the growing season of each year (equation 1). LSDs were calculated using the experimental error for each year ($P < 0.05$)

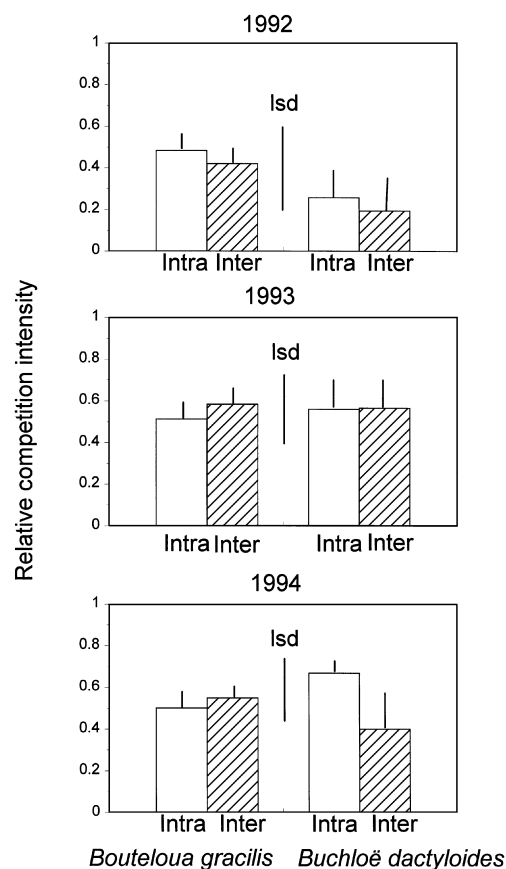| Target species:	*Bouteloua gracilis*				*Buchloë dactyloides*			
Neighbour species:	*B. gracilis*		*Bu. dactyloides*		*B. gracilis*		*Bu. dactyloides*	
Competition:	+C	–C	+C	–C	+C	–C	+C	–C
Experiment 1								
1992 (LSD: 0.0021)	–0.0003 ± 0.001	0.005 ± 0.0005	0.001 ± 0.001	0.005 ± 0.001	0.005 ± 0.001	0.007 ± 0.001	0.004 ± 0.001	0.006 ± 0.003
1993 (LSD: 0.0012)	0.001 ± 0.001	0.001 ± 0.001	–0.001 ± 0.0005	0.002 ± 0.0004	–0.001 ± 0.001	0.001 ± 0.001	–0.003 ± 0.001	0.001 ± 0.001
1994 (LSD: 0.0013)	0.002 ± 0.001	0.002 ± 0.0004	0.001 ± 0.0004	0.001 ± 0.0003	0.0006 ± 0.0007	0.001 ± 0.0007	–0.0001 ± 0.002	–0.0002 ± 0.001
Experiment 2								
1993 (LSD: 0.0052)	0.002 ± 0.002	0.006 ± 0.001	0.004 ± 0.001	0.007 ± 0.002	–0.004 ± 0.003	0.008 ± 0.001	–0.003 ± 0.003	0.002 ± 0.002
1994 (LSD: 0.0027)	0.002 ± 0.001	0.002 ± 0.0001	0.004 ± 0.001	0.004 ± 0.0005	0.002 ± 0.001	0.002 ± 0.001	–0.002 ± 0.002	0.003 ± 0.001
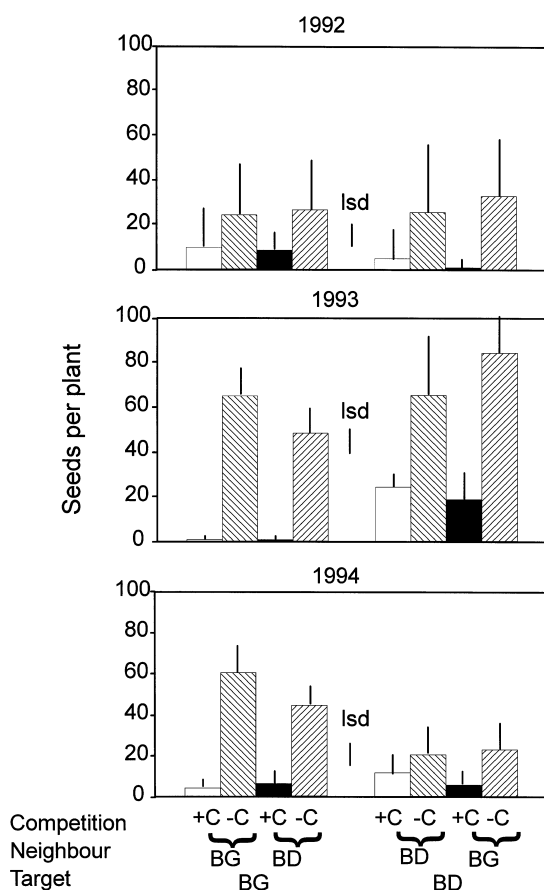
Fig. 2 Seeds per plant produced by *Bouteloua gracilis* (BG) and *Buchloë dactyloides* (BD) growing with competition (+C) and with reduced competition (−C) in the 3 years in experiment 1. Bars represent ± 1 SE. lsd bar was calculated with the experimental error for the year (*P* < 0.05).
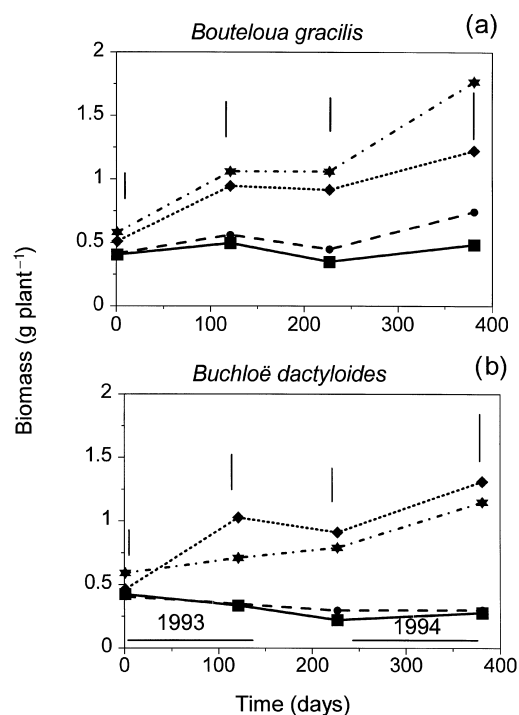

Fig. 3 Relative competition intensity for intraspecific (Intra) and interspecific (Inter) competition in *Bouteloua gracilis* and *Buchloë dactyloides* in experiment 1. Bars represent ± 1 SE. lsd bar was calculated with the experimental error for the year (*P* < 0.05).

the tubes (reduced competition) had higher biomass than plants growing with competition (*P* < 0.05 both years; Fig. 4). The lack of an effect of neighbour identity on the reduction of biomass of target plants is shown by the equal effects of intra- and interspecific competition. Relative growth rate was reduced by competition during 1993 (*P* < 0.05), but not during 1994 (*P* = 0.14) (Table 1). Intra- and interspecific competition did not differentially reduce the RGR of either species.

Seed production was reduced by competition, although the negative effect was greater in *Bu. dactyloides* than in *B. gracilis* (*P* < 0.05; Fig. 5). Over all treatments seed production per plant was higher in *B. gracilis* than in *Bu. dactyloides* in both 1993 and 1994.

There were no differences in intensity of below-ground competition between species in either year or between intra- and interspecific competition (Fig. 6). Light penetration to the soil surface was 97% and 88% during 1993 and 1994, respectively (averaged over all treatments), again suggesting that above-ground competition was negligible.
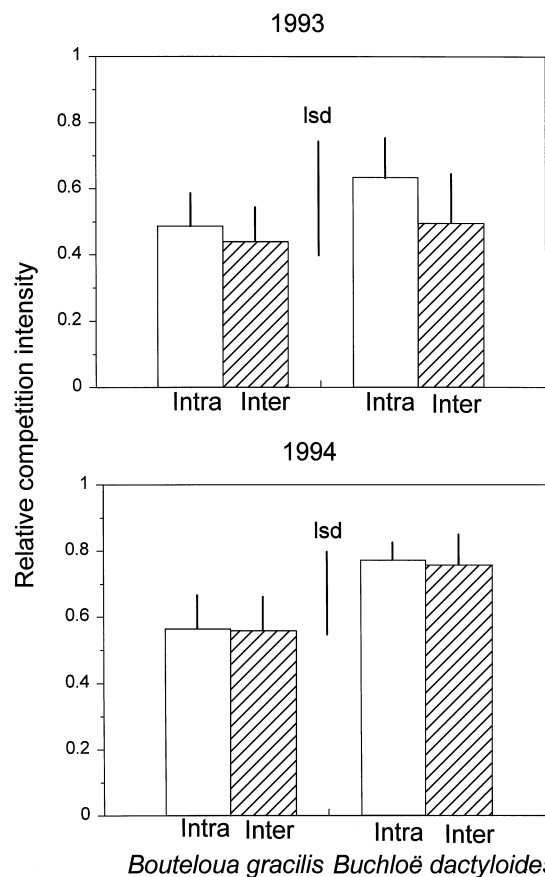

Fig. 4 Biomass per plant of *Bouteloua gracilis* (a) and *Buchloë dactyloides* (b) in experiment 2 for each of the sample dates (May and September 1993, May and October 1994). Conventions as in Fig. 1.
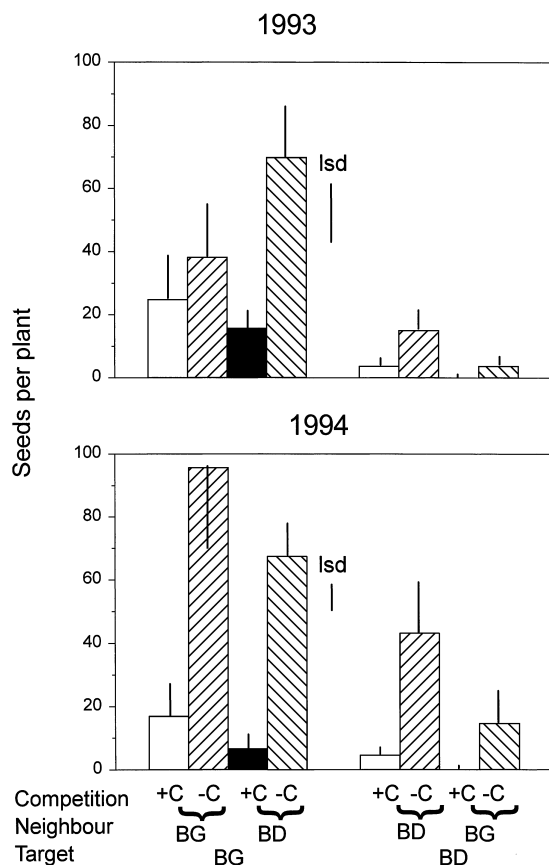
Fig. 5 Seeds per plant produced by *Bouteloua gracilis* (BG) and *Buchloë dactyloides* (BD) growing with competition (+C) and with reduced competition (−C) in the 2 years of experiment 2. Bars represent ± 1 SE. lsd was calculated with the experimental error for the year (*P* < 0.05).

Fig. 6 Relative competition intensity for intraspecific (Intra) and interspecific (Inter) competition in *Bouteloua gracilis* and *Buchloë dactyloides* in experiment 2. The bars represent ± 1 SE. lsd was calculated with the experimental error for the year (*P* < 0.05).

Discussion

In both experiments, plants growing with competition accumulated less biomass than plants growing with reduced competition, and conspecific or heterospecific neighbours had similar effects. Relative competition intensity did not differ between intra- and interspecific competition, or between species, years or experiments. Average relative competition intensity in the two experiments was 0.5. In general, our results do not support 'the classical prediction' derived from the Lotka–Volterra model that, in order for two species with similar requirements to achieve coexistence, intraspecific competition must be greater than interspecific competition (Goldberg & Barton 1992; Tilman & Pacala 1993). Our results are significant because few field experiments have compared intra- and interspecific competition (13 of 101 analysed by Goldberg & Barton 1992). Most of the previous experiments that have made this comparison may have confounded the effects of types of competition because the *per capita* effect of competition was not controlled (Goldberg & Barton 1992), whereas the initial biomass of all our *B. gracilis* and *Bu. dactyloides* plants was similar and the hexagonal design controlled for the *per capita* effect.

In general, we found that intra- and interspecific competition had the same effect on the RGR. Significant effects of competition occurred only during the first 2 years in experiment 1 and the first year in experiment 2. Although we do not have an explanation for this result, other long-term studies with grasses have found that RGR differences decreased with time, whereas differences in biomass continued (Wilson & Shay 1990; Duralia & Reader 1993). Viable seed production was more variable than biomass, but was always greater in the plants growing in tubes (reduced competition) than in the plants that grew with neighbours (competition), whereas neighbour identity had no effect. Seed production was different in the two experiments for both species with *Bu. dactyloides* being the more productive in experiment 1 and *B. gracilis* the more productive in experiment 2.

B. gracilis and *Bu. dactyloides* are dominant species in the shortgrass steppe, the driest portion of the central grassland region in North America (Lauenroth & Burke 1995; Lauenroth *et al.* 1999). Historically, it has been accepted that these species were morphologically equivalent (Weaver & Albertson 1944; Albertson *et al.* 1966) and, more recently, they have also been grouped by their similarities in ecophysiology (Monson *et al.* 1983). Results

from our study suggest that they do not differ either in their competitive abilities for below-ground resources. In the tallgrass prairie (mean annual precipitation = 849 mm), Duralia & Reader (1993) found a similar lack of differences in the competitive abilities of three native grass species (*Adropogon gerardii*, *Sorghastrum nutans* and *Dichanthelium oligosanthes*), although their relative abundances in the field and their ecophysiology and morphology did differ.

The prediction that intraspecific competition must be more intense than interspecific competition is based on the idea that a greater similarity in requirements should occur between conspecific than heterospecific neighbours (MacArthur & Levins 1967). In general, many studies whose results relate to this prediction have been performed in ecosystems in which both above-ground and below-ground competition are important, such as the wetland community in which Johansson & Keddy (1991) found that intraspecific competition was more intense than interspecific competition. By contrast, in arid and semiarid communities, intense below-ground competition is particularly important (Fowler 1986). Differences in the dynamics of resources (i.e. light and soil resources) are at the core of understanding interactions among plants in both wet and dry ecosystems. When competing for water, plants deal with a resource that has both 'the pulse phase', with high resource availability (i.e. rainfall events), and 'interpulse' intervals, with low resource availability (Goldberg & Novoplansky 1997). Competition occurs during both phases, but under different conditions soil water content can be reduced by plant absorption, evaporation and deep percolation and, because dynamics during the pulse phase may control what happens during the interpulse interval, prediction of the outcome of below-ground competition is complex. For example, during the pulse phase, plants with a high growth rate will rapidly pre-empt resources, thus reducing bare soil evaporation losses. Large plants, which are likely to have a large depletion zone, but also large water requirements, may or may not have an advantage during the interpulse phase depending on their life stage (i.e. seedling vs. adult plant). Furthermore, by reducing resource availability, fast growing plants may increase the length of the interpulse phase. In other words, traits that are an asset in a pulse phase may be a liability in an interpulse phase (Goldberg & Novoplansky 1997). Above-ground competition is, in contrast, much simpler to predict because competitive ability for light may be easily predicted from plant height. As one plant overtops another, a positive feedback develops leading to increasing differences in the growth of competing plants (Gaudet & Keddy 1988).

In conclusion, competition between dominant species of grasses in the shortgrass steppe is intense, but the identity of the neighbour plant is not important. Other factors, such as neighbourhood area may be decisive for predicting competition (Aguilera & Lauenroth 1993b). Equivalence in competitive ability arises from similarities in how plants acquire and use resources. Taub & Goldberg

(1996) found that the root systems of grasses from two contrasting ecosystems in Israel (mean annual precipitation ranged from 110 to 550 mm per year), had very low plasticity and morphological variation compared with dicots. Their results agree with the lack of difference in competitive abilities in grasses both in the shortgrass steppe (this study) and the tallgrass prairie (Duralia & Reader 1993). From a long-term perspective, equivalence between species may result from selection for competitive combining ability (Aarssen 1983) or from a random identity of neighbour plants (Hubbell & Foster 1986). The next step in understanding the current structure of the shortgrass steppe will be to assess the relative importance of other factors such as the water economy of plants, responses to herbivory, disturbance regime or recruitment dynamics.

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