3. WATER AVAILABILITY AND COMPETITION IN THE NORTHERN GREAT PLAINS

3.1. ABSTRACT

I examined the response of grass and shrub standing crop to water availability in a natural, arid grassland in the northern Great Plains, Canada. Water availability was manipulated during the hot season (late June-early September) by excluding rain and supplying water at levels corresponding to precipitation amounts in dry, wet, and average years. Competition between grasses and shrubs was manipulated by removing grasses or shrubs with a herbicide. Low water supply significantly reduced total standing crop when grasses and shrubs interacted but not in the absence of competition. The general effect of water supply on standing crop was small, suggesting that water limitation during a single hot season was of little importance for vegetation structure. The effect of water supply did not differ between open prairie and within shrub clones, suggesting that similar mechanisms operate in both habitats.

3.2. INTRODUCTION

Temperate grasslands are thought to be mostly controlled by precipitation or water availability (Walter 1984, Lauenroth & Sala 1992, Paruelo et al. 1993, Briggs & Knapp 1995). However, herbaceous vegetation in oak savanna in Minnesota was limited by water in only one out of eight years which was a major drought year (Tilman 1990) and there is little evidence that water availability affects competition between prairie plants (Fowler 1986, Wilson 1988a). Thus, water availability may have strong effects on competition only in years with very high or low precipitation. Furthermore, competition in temperate grasslands may also be little affected by water availability because the ecosystem is dominated by one growth form and therefore species responses may be similar (Taub & Goldberg 1996).

Prairie grasses and prairie shrubs differ strongly in growth form. Grasses with their high root:shoot mass ratio should be better competitors for soil water than woody species with their low R:S ratio (Tilman 1988). Shrubs, on the other hand, often have deeper roots than grasses and therefore may be less affected by grass competition for soil water (Sala et al. 1989). Therefore, shrubs and grasses should differ strongly in their response to water availability. Still, even woody plants and grasses appear to differ in their response only in years of extreme low or high precipitation (Cable 1969, Golluscio et al. 1998).

The most abundant shrub in the northern Great Plains, snowberry, *Symphoricarpos occidentalis*, grows in dense clones. Clones appear to be denser in depressions or on north-facing slopes, suggesting that snowberry is responding to water availability (Pelton 1953). Due to shading, evaporation inside clones may be lower and water supply may have a smaller effect on competition than outside, allowing the shrubs to displace grasses. Higher soil moisture also accelerates N mineralization (Myers et al. 1982) and may therefore increase competitiveness of shrubs.

I examined the response of prairie vegetation to water availability by comparing the standing crop of grasses and shrubs at three levels of water supply. I hypothesized that low water supply would decrease the standing crop of shrubs more than that of grasses, whereas high water supply would increase the standing crop of shrubs more than that of grasses. I also hypothesized that when grasses and shrubs grow together the amount of water available to each growth form would be lower. Therefore, low water supply should affect grasses and shrubs more strongly when they grow together than when they grow without the other growth form. Finally, I tested whether the responses of grasses and shrubs vary with habitat.

3.3. METHODS

The experiment was carried out in mixed-grass prairie (Coupland 1950) dominated by *Stipa* spp., *Agropyron subsecundum*, *Bouteloua gracilis*, *Koeleria gracilis*, and *Poa* spp. in the northern Great Plains, 120 km south of Regina, Saskatchewan, Canada (104° 38'W, 49° 18'N). The prairie at this site includes *Symphoricarpos occidentalis* (snowberry) clones (95% snowberry cover inside the clone) with a sparse undergrowth of grasses and sedges. I refer to these clones as brush habitat, in contrast to the prairie habitat outside the clones where young snowberry stems have 10-20% cover. Soils are dark-brown solonetzic on clayey loam.

I applied two factors (water supply and growth-form removal) with three levels each in a factorial design to plots in each habitat. Nine plots were randomly located within the brush habitat and nine plots were randomly located in the prairie habitat. Brush and prairie plots (40 cm diameter) were established when the soil had thawed in May 1995 by trenching 10-15 cm deep to confine roots within plots. Roots of *Symphoricarpos* and of grasses were concentrated in the upper 15 cm of the soil (*personal observation*). Root uptake of most species at our site is greatest at 0-15 cm depth (Johnson 1960). The plot perimeter was lined with 1.5 mm thick, 10 cm deep plastic (lawn edging). All prairie plots contained snowberry stems and all brush plots contained grass.

To test the effect of water supply on shrub and grass growth I manipulated water supply in plots from June 22 to September 9, 1995 by excluding rain and watering by hand. Rain was excluded from all plots

	month			
water supply rate	June	July	August	September
low	25	35	22	34
average	72	61	42	36
high	117	114	53	61

Table 3.1. Monthly water supply rates (L/m^2) in the three water supply treatments.

with clear plastic tents (93% PAR penetration). The tents had a triangular base and one open side to allow air circulation. The closed tent sides faced the dominant wind directions on rainy days (SE, NW; Environment Canada 1986-1994). There were three water supply rates: low, average and high (Table 3.1). The monthly amount of water was related to monthly precipitation at Regina during the 1958 - 1994 period (Environment Canada 1958-1994). The low water supply of a month was calculated as the mean precipitation of the same month of the five driest years. The average water supply of a month was calculated as the mean precipitation of the same month of all years. The high water supply of a month was calculated as the mean precipitation of the same month of the five wettest years. The plots were watered three times per month with one third of the monthly rate.

To determine the response of grasses and shrubs to water supply, I applied three removal treatments (intact vegetation, shrubs removed, or grasses removed). Shrubs and grasses were removed by carefully painting a fast decaying herbicide (glyphosate, RoundUp) with a sponge or paint brush on shrub or grass leaves on 28 May (2.5% dilution), and again on 6 June, 1995 (3.0% dilution).

One plot was randomly assigned to each water supply rate $\times$ removal combination, resulting in nine plots per habitat or 18 plots per site. Sites were c. 100 m^2, comprising bush and prairie habitat. The experiment was replicated at 10 sites for a total of 180 plots.

In each plot I determined standing crop of grasses and shrubs non-destructively during 5-16 June and 9-23 September, 1995. Grass standing crop was determined with a point-frequency counting frame (Mueller-Dombois & Ellenberg 1974). The number of pins (2.5 mm diameter, spacing 2 × 6 cm) intersecting with leaves of grasses or herbs were multiplied with a regression equation ($\sqrt{m}$ = 2.089 intersections/pin + 0.6976, $R^2 = 0.608$, $n = 38$) to calculate grass mass (m). The regression equation was based on using the frame on one 30 × 30 cm^2 patch in the prairie and brush habitat at each site (total 20 patches) on 18 June and 15 September, 1995. Two patches were eliminated from the regression because they were outliers causing a negative intercept. Grasses and herbs in the patches were cut 1 cm above the ground, dried at 105°C until mass was constant, and weighed.

Shrub standing crop was determined by measuring the diameter of all shrub stems in all prairie and brush plots and applying a regression equation. I measured the diameter at the thinnest portion within 3-4 cm height with calipers (accuracy 0.01 mm). The regression ($m = 0.3174d^2 - 0.7097d + 0.4458$, $R^2 = 0.984$) was based on the diameter (d(mm)) and aboveground mass (m(g)) of 20 shrubs harvested outside the plots on 18 June, 1995. Shrubs were cut 1 cm above the ground, dried at 105°C until mass was constant, and weighed. Diameters measured in September were generally smaller than those measured in June, presumably because I measured the diameter at the visually thinnest stem portion within 3-4 cm height in June but measured at actually thinner portions of the stem within 3-4 cm height in September. As a result, growth rates were apparently negative and I present only results based on September measurements.

The design of the experiment was block-factorial with site as a random factor and habitat, water supply and growth-form removal as fixed factors. Variation in standing crop (sum of grass and shrub) was examined with analysis of variance (ANOVA). To increase homogeneity of variances and normality, mass was ln-transformed. All ANOVAs were calculated with JMP for Macintosh 3.2.1 (SAS Institute 1997). Total rather than grass and shrub standing crop was used in ANOVA, because shrub and grass standing crop in intact plots were measured in the same plots and were therefore not independent.

3.4. RESULTS

Standing crop varied with habitat and removal treatment in a foreseeable way due to the much higher physical density of woody shrubs than herbaceous grasses. Thus, standing crop, across all other treatments, was significantly higher in brush than in prairie (Fig. 3.1; $F_{1,9} = 24.5$, $P = 0.0008$). Total standing crop in intact vegetation was higher than in grass-removal plots which was higher than in shrub-removal plots (Fig. 3.1; $F_{2,18} = 59.6$, $P < 0.0001$). A significant habitat × removal interaction (Fig. 3.1; $F_{2,18} = 103$, $P < 0.0001$) revealed that total standing crop in shrub-removal plots was higher in prairie than in brush, whereas total standing crop in grass-removal plots and in intact vegetation was higher in brush than in prairie. In both habitats, grass mass in shrub removal treatments was significantly less than in intact vegetation (*t*-tests, $P < 0.05$). This difference, however, was present already in June. Water availability had no significant main or interaction effect on total standing crop.

Grasses and shrubs in removal plots showed leaf damages that may have been caused by dryness due to high evaporation or by herbicide drift. Therefore, to detect an effect of water supply on total standing crop, I restricted the data set to plots with intact vegetation. The ANOVA showed that water supply had a significant effect on standing crop (Fig. 3.2; $F_{2,18} = 5.07$, $P = 0.02$). Standing crop at high water supply was not significantly different from that at average water supply, which, however, was significantly higher than that at low water supply

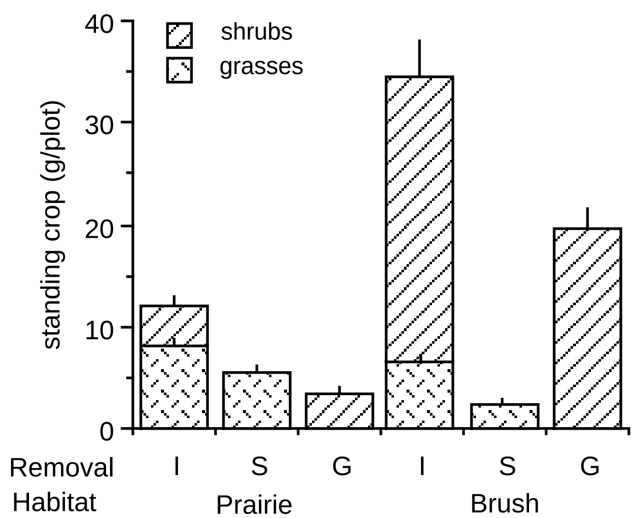

FIG. 3.1. Effect of habitat and growth-form removal on standing crop of grasses and shrubs. I: intact vegetation, none removed, S: shrubs removed, G: grasses removed. Bars indicate means (across water supply treatments) + 1 SE ($n = 9$).

(simple contrast: t = 2.45, P = 0.02). As for the complete data set, standing crop was significantly higher in brush than in prairie ($F_{1,9}$ = 43.2, P = 0.0001). There was no significant water supply × habitat interaction (P = 0.14).

I tested with the restricted data set whether grasses and shrubs differed in their response to water supply by separating grass and shrub mass and adding growth form as an additional fixed, completely factorial effect to the ANOVA. The effect of water supply across all other treatments was no longer significant (P = 0.06) and did not interact with any other factor. As for the complete data set, standing crop, across removal and water supply treatments was significantly higher in brush than in prairie ($F_{1,9}$ = 64.1, P < 0.0001, Fig. 3.1: Removal: "I" treat-

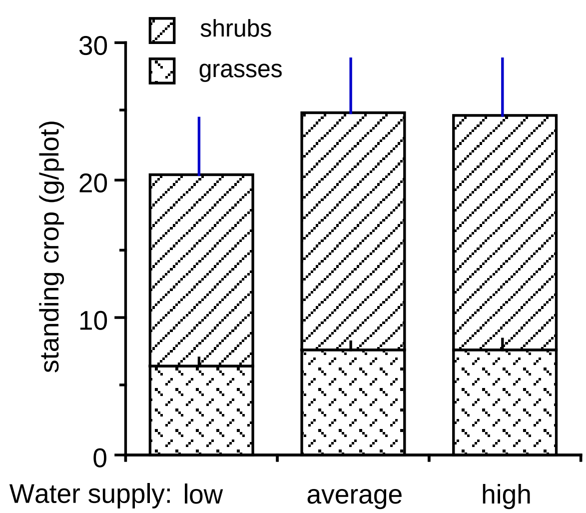

FIG. 3.2. Effect of water supply on standing crop of grasses and shrubs in intact vegetation (no-removal treatment). Bars indicate means (across habitats) + 1 SE (n = 20).

ments). A significant habitat × growth form interaction ($F_{1,9}$ = 78.3, P < 0.0001), however, showed that grass standing crop did not differ significantly between habitats, whereas shrub standing crop was significantly lower in prairie than in brush (simple contrasts: t = 11.1, P < 0.0001; Fig. 3.1: Removal: "I" treatments).

3.5. DISCUSSION

Low water supply significantly reduced total standing crop (Fig. 3.2), but only in intact vegetation. This was mainly due to lower shrub production (Fig. 3.2), presumably because snowberry with its broad, thin leaves is more susceptible to drought than the prairie grasses with their coarse, narrow leaves. In addition, roots of grasses and snowberry are concentrated in the upper soil layers (Johnson 1960, George & McKell 1978) so that plants of both growth forms would directly compete for the available water. This is similar to the grass-shrub interaction in a West African humid savanna (Le Roux et al. 1995) where grasses and shrubs compete for the same water. In other grasslands, shrubs take up water from deeper soil layers than grasses do and therefore woody plants in those grasslands are less affected by low water supply (Knoop & Walker 1985, Weltzin & McPherson 1997, Golluscio et al. 1998).

High water supply in my experiment did not significantly increase total standing crop (Fig. 3.1), perhaps because shrub growth at average and high water supply is more limited by nitrogen than by water.

This is supported by very low N availability under grass-shrub vegetation at one site where N availability was measured by resin extraction (chapter 5.3.3) to explore the method's sensitivity for competition experiments. Water supply in shrub and grass removal plots may have had no significant effect on standing crop because available water and nitrogen were not growth-limiting in the absence of competitors. Total standing crop may also have varied little with water supply because plant growth, especially growth of woody plant, may be strongly influenced by moisture conditions in the preceeding year (Bailey & Wroe 1974) or by moisture very early in the growing season, i.e., before the application of my treatments. It may also be necessary that water deficits accumulate over several years before there is a measurable effect on shrub or grass growth. For example, several years of below-average precipitation on the northern Great Plains during the 1930s severely reduced basal cover of the dominant grass species (Albertson & Tomanek 1965). The general effect of water on plant growth may also have been small because growth was mostly completed before the application of the water treatments. Snowberry is reported to end growth in mid-June (Kirby & Ransom-Nelson 1987). The dominant prairie grasses in the region flower in mid-June to early July (*personal observation*, Johnson 1960). This suggests that although the dry season in the northern Great Plains is in July and August (Walter & Lieth 1967) the effect of water availability on growth may be stronger during the time of peak growth in spring.

Woody and grass transplants showed little response to water availability also in other competition experiments at the same location, at a location 200 km W and at a location 400 km N of my sites in the same year (J. D. Bakker and D. A. Peltzer, pers. comm.). In these experiments, water availability was also manipulated with rain shelters and controlled water supply. The congruence of results suggests that water is rarely a growth-limiting resource in the northern Great Plains. This is in line with long-term results in an oak savanna in Minnesota where water was growth-limiting in only one out of eight years (Tilman 1990).

Standing crop did not vary with the interaction of water supply and habitat, suggesting that habitat-related variables like soil structure or litter cover had little effect on water availability. This might indicate that the correlation of shrub density with depressions and north-facing slopes may not be linked to consistently higher soil moisture but to flushes of higher soil moisture, e.g. in spring, whereas during the rest of the year, N is the limiting resource (Seastedt & Knapp 1993).

Typically, shrubs and grasses compete for resources, and shrub removal increases grass growth (Scholes & Archer 1997, Li & Wilson 1998, Wilson 1998, chapter 5). Shrub removal in this experiment, however, did not increase grass growth. This may be due to herbicide drift or due to shrubs outside the plots growing roots into the plots.

In conclusion, only very low water supply had a significant effect on grass-shrub interaction in temperate grassland and reduced total standing crop. This suggests that water becomes only rarely a growth-limiting resource for both grasses and shrubs in the northern Great Plains in the later part of the growing period.