Competitive effects of shrubs and grasses in prairie

Martin Köchy and Scott D. Wilson

We investigated the relative contributions of size and growth form (biomass allocation) to competitive effects between grasses and shrubs in western Canada for two years. We measured the effects of grasses and shrubs on each other at the population level using removal experiments in natural vegetation. In prairie where shrub abundance was low, shrubs suppressed grasses as much as grasses suppressed shrubs, even though shrubs had six times more standing crop. In adjacent brush clumps, however, where shrub standing crop was 37 times grass standing crop, shrubs suppressed grasses strongly, whereas grasses did not suppress shrubs. Shrubs reduced available soil nitrogen more strongly than grasses did, but shrubs and grasses did not differ in their effects on light or soil water. On a per-gram basis, however, shrubs had smaller effects on light, nitrogen, and water consumption than grasses did. In spite of their smaller per-gram effects on resources, the secondary growth of shrubs allowed them to accumulate more mass and height, and to eventually displace grasses. During this process, competition between the woody and the herbaceous growth form changed from symmetric to asymmetric.

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In both grasslands and forests, competition occurs across a wide range of productivity (Wilson 1991, Reader et al. 1993, Wilson 1998). Competition between plants is the product of effects on and responses to the availability of shared resources (Goldberg 1990). Competitive responses (the extent to which plants are suppressed by neighbors) differ little between trees and grasses (Wilson 1998). Competitive effects (the extent to which plants suppress their neighbors) generally increase with plant size (Grace 1985, Goldberg and Landa 1991) as an effect of successional time and community productivity (Grace 1993, Wilson 1999).

Plant size is obviously related to plant mass and, on the scale of growth forms, also to mass allocation patterns. For example, grasses are much smaller than adult trees and have a higher root:shoot mass ratio. Therefore, specific allocation patterns enable growth forms to compete better either for light or for soil resources (Tilman 1990). Competition for aboveground resources (light) is fundamentally different from competition for belowground resources (nutrients and water) because light is supplied along one spatial dimension, whereas soil resources are generally replenished along three spatial dimensions (Reynolds and Pacala 1993, Schwinning and Weiner 1998). For example, the tall stature of trees allows them to pre-empt light and their woody tissue makes them more nitrogen-efficient by positioning leaves high in the canopy with little costs in terms of N (Aerts 1995). Thus, trees may replace grasses, first, because trees have more mass, but, secondly, also because their growth form allows them to pre-empt light and use accumulated nutrients more efficiently. Grasses with their fibrous roots, however, are expected to take up more available soil resources (Caldwell and Richards 1986) and to compete successfully against short woody plants, e.g., seedlings or low shrubs.

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In contrast to hypothetical differences in competitive effect between growth forms, Goldberg and Werner (1983) proposed that species have similar competitive effects, partly because all plants require the same resources. Thus, competitive effects should be a simple function of plant size, and woody species should have greater competitive effects than grasses just because of their greater size. The relative contribution of size and growth form to competitive effects can be separated by calculating per-gram competitive effects (competitive effect divided by biomass) (Goldberg 1990). Contrasting growth forms should have similar per-gram effects if competitive effects are mostly related to mass. Differences in per-gram effects between growth forms would suggest that growth form contributes to differences in competitive effects. Thus, grasses should have larger per-gram effects on soil resources because of their fibrous roots, whereas trees should have larger per-gram effects on light because of their tall stature.

Per-gram competitive effects do not seem to differ among species with a similar growth form or among seedlings of different herbaceous growth forms (Goldberg 1987, Goldberg and Fleetwood 1987, Peart 1989, Rösch et al. 1997). However, a native summer annual had larger per-root-length effects than introduced winter annuals (Gordon and Rice 1993), established trees had larger per-gram effects than shrubs (Harrington and Johns 1990), and *Quercus* seedlings had larger per-gram shoot effects than grass seedlings (Welker et al. 1991). Thus, allocation patterns seem to contribute to competitive ability when the competitors are sufficiently different. This suggests that seedlings of woody species have little competitive advantage over grasses. As woody seedlings increase in mass and height, however, they should become more competitive due to both mass and growth form. As a result, competition between grasses and woody plants may change from symmetric to asymmetric over time.

We explored the contributions of mass and growth form to competitive effects by comparing the effects of shrubs and grasses on each other and on three important resources: light, nitrogen, and water. We also examined whether competitive effects differ between vegetation dominated by grasses and shrubs.

Methods

Location, design and site preparation

The experiment was conducted in the northern Great Plains (49°18′N, 104°38′W), 120 km south of Regina, Saskatchewan, Canada, in natural mixed-grass prairie (Coupland 1950, Looman 1980) in 1996 and 1997. We worked at the edge of stands of snowberry (*Symphoricarpos occidentalis* Hook.), a common clonal shrub in the northern Great Plains. Inside the stands, snowberry

stems are dense with a sparse grass understory. Grasses in brush were mostly *Stipa viridula* Trin., *S. spartea* Trin., and *Agropyron subsecundum* (Link) Hitchc. We call this the brush habitat. Outside the stands were sparse snowberry stems (10–30 cm tall) scattered in grassland (canopy at 10–30 cm height). It was dominated by *Stipa viridula* Trin., *S. spartea* Trin., *S. comata* Trin. & Rupr., *Bouteloua gracilis* (HBK.) Lag., *Koeleria gracilis* Pers., *Agropyron* spp., and *Poa* spp. We call this the prairie habitat.

In these two habitats, we applied four removal treatments to plots. The treatments were: intact vegetation (IV), no shrubs (NS), no grasses (NG), and no vegetation (NV). Forbs and sedges had very low cover. No other growth forms occurred. There were two intact-vegetation plots in each habitat, one serving as a reference for no-shrub and a second as an independent reference for no-grass. Thus, there were five plots in each habitat. Differences between resources levels among removal treatments allowed us to separate the effects of shrubs and grasses on each other and on resources. Plots were randomly assigned to treatment combinations within each habitat. The experiment was completely replicated at five sites within a 1-km² area.

The plots, 2 m × 2 m, were established in the first week of May 1996 by trenching to a depth of 15 cm to isolate roots within plots. Trenching was repeated in May 1997. We removed shrubs and grasses with selective herbicides in spring/early-summer (May–June). We were mostly interested in the vegetation's direct effect on soil resources (Holzapfel and Mahall 1999). Naked soil heats up more quickly and more strongly, which increases evaporation and N mineralization. Therefore, we left the dead plants in place where they continued to cast shade.

We killed shrubs with a total of 232.5 g/ha of metsulfuron (*Ally*, DuPont, Canada) in 1996 and with a total of 150.0 g/ha in 1997. Metsulfuron is a selective post-emergence systemic herbicide developed for control of herbaceous broadleaf weeds in grain crops (Ahrens 1994). It can be taken up by both roots and leaves and has been used to successfully eliminate several woody species in grassland (Derr 1989, McDaniel et al. 1991, Bowes and Spurr 1996).

We killed grasses with 190 mL/ha clethodim (*Select*, Rhône-Poulenc, Canada) and a total of 56.7 L/ha sethoxydim (*Poast*, BASF, Canada) in 1996 and with 190 mL/ha clethodim and a total of 54.0 L/ha sethoxydim in 1997 (Ahrens 1994). We killed sedges by carefully applying 3.6 g/L glyphosate (*RoundUp*, Monsanto, Canada) locally on 2 June 1997. Clethodim and sethoxydim are selective post-emergence herbicides developed for control of grasses in broadleaf crops such as canola, flax, and legumes (Ahrens 1994). They are taken up primarily through the foliage.

Metsulfuron and sethoxydim were applied repeatedly every 2–3 weeks until mortality was close to 100%. All

herbicides were sprayed in solutions containing a sur-factant (Na-hexametaphosphate, 2 g/L), blue food col-oring, and 0.25 L/m² water for the metsulfuron mixture and 1.5 L/m² water for the clethodim and sethoxydim mixtures. In brush, snowberry forms a dense canopy, so the shrub herbicide was applied to the brush canopy and the grass herbicides were sprayed on the grass below the canopy. We did not add any water to intact-vegetation plots, because the volume of added water is very low compared to monthly precipitation in May and June (50.8 and 67.3 L/m²).

Productivity and neighbor removal

Shoots and litter were harvested during 28–29 August 1996 and 4–8 September 1997. Shoots and litter were harvested in each plot from a subplot (1 m × 15 cm) ≥ 0.5 m from the plot edges. Different subplots within a plot were sampled each year.

We measured grass aboveground net primary production (ANPP) as green shoots with fresh litter, and grass standing crop as green shoots. Grass litter remains attached for ≈ 0.5 yr (Sims and Coupland 1979). In early spring, loose grass litter produced in previous years was removed by hand from subplots. Remaining attached old litter was spray-painted so that only litter produced during the current growing season was harvested each fall.

We measured shrub ANPP as the total mass of current-year shoots (herbaceous stems and twigs with their attached leaves) plus shrub litter. We measured shrub standing crop as the total mass of live shoots (woody stems + herbaceous stems with their attached leaves). Ignoring the radial growth of older stems resulted in < 5% underestimation of actual stem mass (calculated from Table 2.2 in Köchy 1999). Litter was collected in three litter traps (10 cm diameter, 5 cm deep) per plot.

After sorting, shoots and litter were dried at 70°C to constant mass and weighed. A hailstorm on 28 August 1997 removed almost all shrub leaves and many twigs. Therefore, we separated the material in the traps into leaves, current-year stems and older stems, calculated their respective mass per subplot and added the result to the mass measured in the subplots.

We assessed the effect of one growth form (neighbor growth form) on the other (target growth form) by comparing the ANPP of the target growth form in intact vegetation with the ANPP of the target growth form in vegetation where the neighbor growth form was removed.

We assessed the per-gram effect of growth forms on each other by calculating regressions of target growth form ANPP on standing crop of the neighbor growth form. Grass was considered as a target growth form in one intact-vegetation plot and in the shrub-removal plot in each habitat at each site. Shrubs were considered as a target growth form in the other intact-vegetation plot and in the grass-removal plot in each habitat at each site.

Effects of grasses and shrubs on resources

We measured light, available soil nitrogen (N) and soil water in each plot to test whether growth forms differed in their effects on resources.

Light was measured with a 40-cm integrating photo-synthetic photon flux (PPF) probe (Sunfleck Ceptome-ter, Decagon Devices, Pullman, WA, USA) 1–3 cm above the soil surface perpendicular from all plot edges and above the canopy on 18 July and 24 August 1996 and 14 July 1997, within two hours of solar noon on a cloudless day. Light measurements in 1996 did not differ significantly between July and August. Therefore, we analyzed in greater detail only 1996 data from August and restricted light measurements in 1997 to one date. In 1996 we also measured light at the top of the grass foliage canopy (≈ 30 cm above ground). Again, measurements were similar in both months and only August data is presented. On 24 August 1996, maximum PPF was 1434 μmol photons m^{-2} s^{-1} and on 14 July 1997, maximum PPF was 1723 μmol photons m^{-2} s^{-1}. We calculated light penetration for each plot as the mean of the four PPF measurements divided by the PPF above the canopy · 100%. Light attenuation by vegetation was taken as an index of light consumption and calculated as 100% – light penetration.

We collected mineral N with ion-exchange resin bags. We used this method because N uptake by resin bags likely resembles root uptake more closely than do other N extraction methods. Resin bags collect available N continuously and in relation to soil moisture conditions (Binkley and Hart 1989, Giblin et al. 1994). Insofar, our measurements should reflect the flux of available mineral N to plant roots, whereas other methods measure soil N concentrations at points of time and do not incorporate physiological availability.

Resin bags contained 2 cm³ dry mixed-bed (anionic and cationic) ion-exchange resin (AG 501-X8, BioRad, Hercules, CA, USA) with an ion-exchange capacity of 1.5 mmol/cm³ for anions and cations (Binkley and Hart 1989, Giblin et al. 1994). Bags were washed in 2 mol/L NaCl and rinsed in double-distilled water to remove dyes and background N from the resin.

Bags were inserted 10 cm into the soil on 22 May 1996 and 2 May 1997 and removed on 27 August 1996 and 28 August 1997. N was extracted from the resin in 30 mL 2 mol/L NaCl · 0.1 mol/L HCl for 1 h (Giblin et al. 1994). Nitrate and ammonium in the extract were chemically converted to ammonia whose concentration was then measured with an ion-selective electrode (Orion, Boston, MA, USA). We added known amounts

of nitrate and ammonia to unused bags to determine an extraction rate ($N_{extracted}$ (mol/L) = 0.9618 N_{added} (mol/L) + 0.0071, R^2 = 0.92, n = 48). We calculated actual N uptake of bags used in the field by applying the extraction rate equation to amounts of extracted N (Köchy and Wilson 1997).

We measured soil water gravimetrically in three pooled soil cores (2 cm diameter, 10 cm deep) collected on 27 May, 18–20 July and 27 August 1996 and on 29 May, 23 June, 14 July, and 8 September 1997. Soil from the three cores was mixed and a ≈ 40 cm^3 subsample was dried at 70°C to constant mass and weighed. Soil water is expressed as g water/g dry soil · 100%. The largest differences of soil water among plots were measured in late August 1996 and mid-July 1997. Therefore, we restricted statistical comparisons to these dates.

For each resource, we calculated relative resource consumption (RRC) of each growth form in each habitat at each site as

$$RRC_t = \frac{R_{NV} - R_t}{R_{NV} - R_{IV}} \cdot 100\%,$$

where R is resource abundance in no-vegetation plots (R_{NV}), in plots with one live target growth form (grasses or shrubs) (R_t), and in intact-vegetation plots (R_{IV}). Thus, $R_{NV} - R_t$ is the absolute consumption of resources by the target growth form. We divided absolute consumption ($R_{NV} - R_t$) by $R_{NV} - R_{IV}$, the total amount of plant-available resource, to account for differences among habitats and sites. Thus, RRC_t is a proportion of the resources available for plant uptake in each habitat and remaining differences between habitats would indicate effects of resource uptake independent of differences in habitat resource levels.

Decomposition of killed biomass is unlikely to significantly affect measured N consumption rates because both grasses and woody plants have high root turnover even as living plants (Dahlman and Kucera 1965, Caldwell and Richards 1986, George and Marschner 1996). If addition of N from decomposing root biomass was a large fraction of the soil N pool, our R_{NV} would be inflated. However, since R_t and R_{IV} are subtracted from R_{NV} in nominator and denominator, the real RRC_t would be larger and ours would be a conservative estimate.

RRC_t provides information about resource-mediated plant interactions. If the two growth forms have no effect on each other via resources, then the sum of RRC_t for both growth forms (SRRC) should be 100%. If each growth form consumes more resources in the absence of the neighbor growth form, then SRRC > 100%, indicating competition. Similarly, if each growth form consumes less resources in the absence of the neighbor growth form, then SRRC < 100%, indicating facilitation.

The per-gram effect of each growth form on resources (per-gram resource consumption) was determined by dividing RRC_t by the standing crop of the growth form in each habitat at each site.

Statistical analysis

Standing crop and ANPP data were ln-transformed, and available soil N and per-gram consumption data were square-root transformed to meet assumptions of homoscedasticity and normality for analyses of variance (ANOVA). All statistics were calculated with JMP for Macintosh (SAS Inst. 1997).

Results were examined with ANOVA for blocked-factorial designs with sites as random-effect blocks (Lorenzen and Anderson 1993), and habitat and removal treatments as fixed effects. The habitat treatments were considered randomized within each site, and removal treatments were randomized within each habitat. The error term for a fixed main or interaction effect was the effect's interaction with site (Lorenzen and Anderson 1993). The design is sometimes also called a blocked factorial split-plot design where the main plots are habitats and the split-plots are removal treatments or target growth form × neighbor-removal treatments (Snedecor and Cochran 1989). For all data we performed statistical tests separately for each year as well as for both years where year was treated as an additional factorial effect. The trends of the results were similar in each case, therefore we present results only from the second year in most cases.

We examined the effectiveness of the removal treatments by comparing, separately for grass and shrub standing crop, the four removal treatments among each other and between habitats and years with ANOVA for block-factorial designs.

We tested whether grass and shrub neighbors had different effects on grass and shrub targets using a two-factor ANOVA with target (grasses or shrubs) as one factor, and neighbor removal (intact vegetation or contrasting growth form removed) as the second factor. The removal treatments used in this analysis included the two intact-vegetation treatments, the no-shrub treatment, and the no-grass treatment. Target and neighbor removal were fixed effects and crossed with habitat (fixed effect) and site (block, random-effect), resulting in a block-factorial design.

We tested whether grasses and shrubs differed in their per-gram effects on each other by regressing grass ANPP on shrub standing crop and shrub ANPP on grass standing crop using ln-transformed data. Analyses of covariance showed that regressions did not differ significantly between habitats.

We compared the effect of the four removal treatments on resource levels with ANOVA for block-factorial designs. When habitat × removal interactions were

significant, we determined which removal treatments differed using planned orthogonal contrasts.

We tested whether resource consumption (RRC) and resource consumption per gram of biomass differed between grasses and shrubs and between habitats with ANOVA for block-factorial design. One water consumption datum was negative because water in the cleared plot (R_{NV}) was very low. Therefore, we set R_{NV} to the highest value occurring in the same habitat at the same site. One water consumption datum was $> 150\%$ because water in the intact-vegetation plot (R_{IV}) was very high. Therefore, we set $R_{IV} = R_t$, which was the same value as for the other intact plot in the same habitat.

Results

Standing crop

Standing crop varied significantly among removal treatments (Fig. 1; grasses: $F_{3,12} = 73.4$, $P < 0.0001$; shrubs: $F_{3,12} = 107$, $P < 0.0001$). Herbicides significantly reduced neighbor standing crop in plots from which either shrubs (Fig. 1; $t = 11.7$, $P < 0.0001$) or grasses (Fig. 1; $t = 6.25$, $P < 0.0001$) were removed. Herbicide applications did not reduce target standing crop in these plots (grasses: $t = 4.25$, P(one-tailed) $= 0.9994$;

shrubs: $t = 0.187$, P(one-tailed) $= 0.6$). Thus the removal treatments had the desired effects.

Shrub standing crop across removal treatments and years was significantly higher in brush than in prairie ($F_{1,4} = 11.7$, $P = 0.03$), whereas grass standing crop was significantly higher in prairie than in brush (Fig. 1; $F_{1,4} = 29.6$, $P = 0.006$).

Shrub and grass standing crop were both significantly higher in the first than in the second year (shrubs: $F_{1,4} = 24.6$, $P < 0.0001$; grasses: $F_{1,4} = 348$, $P < 0.0001$). Differences among removal treatments tended to be larger in the second year, but the removal treatment $\times$ year interaction was significant only for grasses (Fig. 1; $F_{3,12} = 4.94$, $P = 0.02$). For the sake of clarity and brevity we report further results only for the second year (1997).

Productivity and neighbor removal

In general, shrubs had significantly higher aboveground net primary productivity (ANPP) than grasses (Fig. 2; $F_{1,4} = 22.0$, $P = 0.009$). Shrub ANPP tended to be higher in brush than in prairie, whereas grass ANPP was significantly higher in prairie than in brush (Fig. 2; habitat $\times$ target growth form interaction: $F_{1,4} = 23.7$, $P = 0.008$; habitat contrasts: shrubs: $t = 2.87$, $P = 0.06$; grasses: $t = 4.02$, $P = 0.03$). Habitat had no significant main effect on ANPP ($P = 0.6$).
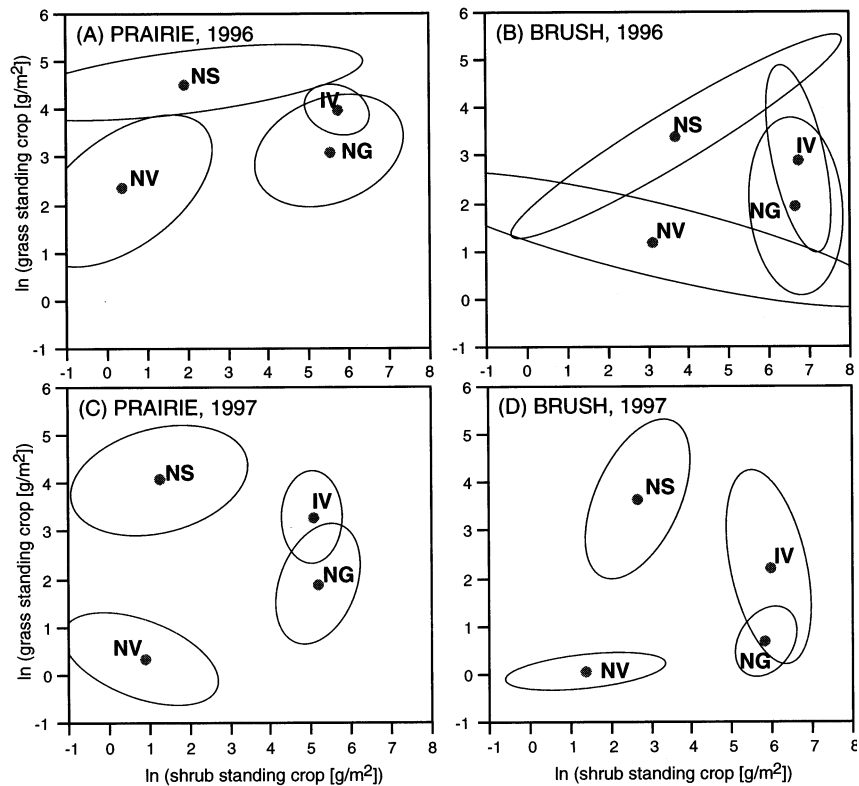

Fig. 1. Standing crop of grasses and shrubs in prairie (left) and brush (right) in 1996 (top) and 1997 (bottom) in four competition treatments: IV: intact vegetation, NS: shrubs removed, NG: grasses removed, NV: both shrubs and grasses removed. Points show means ($n = 5$), ellipses show the 95% confidence area (bivariate normal density).
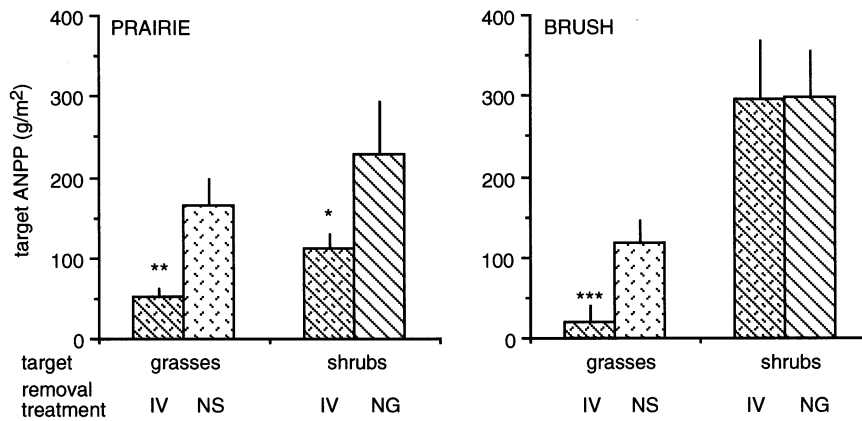
Fig. 2. Aboveground net primary productivity (ANPP) of two target growth forms (shrubs and grasses) in prairie (left) and brush (right) in three removal treatments: IV: intact vegetation, NS: shrubs removed, NG: grasses removed. Bars represent means of five sites + SE. Significant differences between removal treatments for each target growth form in each habitat are indicated by asterisks (simple linear contrasts on log-transformed data; *: $P \leq 0.05$, **: $P \leq 0.01$, ***: $P \leq 0.001$).

Removing the neighbor growth form generally increased ANPP of the target growth form (Fig. 2; $F_{1,12} = 85.5$, $P = 0.0008$). A significant interaction among habitat, target growth form and neighbor removal treatments (Fig. 2; $F_{1,4} = 20.4$, $P = 0.01$) allowed us to compare shrub and grass ANPP between intact vegetation (IV) and vegetation where one growth form had been removed, in both prairie and brush. Shrub removal (NS) significantly increased grass ANPP in both habitats (prairie: $t = 8.15$, $P = 0.001$; brush: $t = 13.6$, $P = 0.0002$). Grass removal (NG) significantly increased shrub ANPP in prairie ($t = 4.16$, $P = 0.01$) but not in brush ($t = 0.54$, $P = 0.6$), but across habitats, grass removal did not increase shrub ANPP (removal × target growth form interaction: $F_{1,4} = 11.5$, $P = 0.03$; means comparison: grass removal: $t = 1.31$, $P = 0.3$).

ANPP of both growth forms decreased across both habitats as standing crop of the contrasting growth form increased (Fig. 3; grasses: $F_{1,18} = 15.7$, $P = 0.001$; shrubs: $F_{1,18} = 7.39$, $P = 0.01$). The regression slopes did not differ significantly from each other, i.e., the regression lines can be assumed to be parallel with a common slope of -0.38 (Zar 1996). The intercept of the shrub regression was significantly higher than that of the grass regression (comparison of regression elevations, Zar 1996). Back-transformation of the log-log regressions results in grass ANPP $= 262 \cdot$ shrub standing crop$^{-0.38}$ and shrub ANPP $= 361 \cdot$ grass standing crop$^{-0.38}$, suggesting that grass standing crop had a $361/262 = 1.4$ times larger per-gram effect than shrub standing crop.

Effects of shrubs and grasses on resources

Light penetration to the grass canopy (Fig. 4A) was significantly higher in prairie than in brush ($F_{1,4} = 104$, $P = 0.0004$). Shrub removal (NS) significantly increased light penetration to the grass canopy

($t = 7.82$, $P < 0.0001$), whereas grass removal (NG) did not increase light penetration to that level (removal effect: $F_{3,12} = 38.7$, $P < 0.0001$). A significant habitat × removal interaction ($F_{3,12} = 5.62$, $P = 0.005$) occurred because shrubs had a stronger effect on light in brush than in prairie. Light penetration in cleared plots (NV) was $< 100\%$ because of remaining dead stems and litter in the plots.

Light penetration to the ground (Fig. 4B) was significantly higher in prairie than in brush ($F_{1,4} = 65.2$, $P = 0.001$) and varied significantly among removal treatments ($F_{3,12} = 188$, $P < 0.0001$). A significant interaction between habitat and removal treatment ($F_{3,12} = 3.72$, $P = 0.04$) allowed us to compare light penetration among removal treatments separately for each habitat. In both habitats, shrub and grass re-
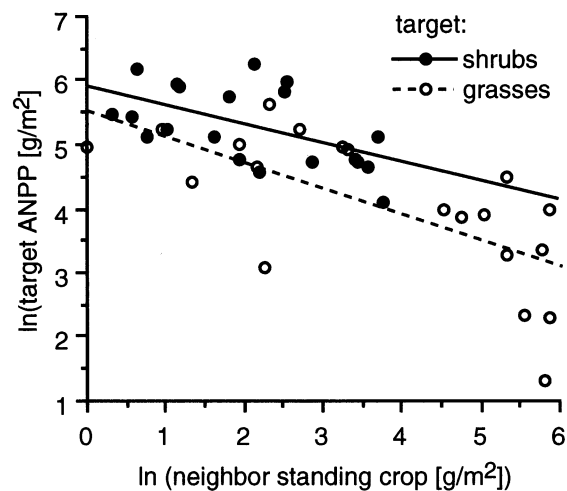

Fig. 3. Aboveground net primary productivity (ANPP) of targets (grasses and shrubs) as a function of the standing crop of the contrasting growth form. Grasses: $R^2 = 0.47$, $\ln(y) = 5.57 - 0.411 \ln(x)$; shrubs: $R^2 = 0.29$, $\ln(y) = 5.89 - 0.294 \ln(x)$.

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Fig. 4. Effect of removal treatment and habitat on (A) light penetration to the top of the grass canopy, (B) light penetration to the ground, (C) available soil nitrogen and (D) soil water. Removal treatments: IV: intact vegetation; NS: shrubs removed; NG: grasses removed; NV: both shrubs and grasses removed. Bars represent means + SE (IV: $n = 10$; NS, NG, NV: $n = 5$). A–C (significant H × R interaction): significantly different vegetation types within a habitat are indicated by different letters in both habitats, vegetation types that differ significantly between habitats are indicated by uppercase letters in the brush treatment; D: significantly different vegetation types across habitats are indicated by different letters above the bars of the prairie treatment. H: habitat, R: removal treatment; planned comparisons: *: $P \leq 0.05$, **: $P \leq 0.01$, ***: $P \leq 0.001$.
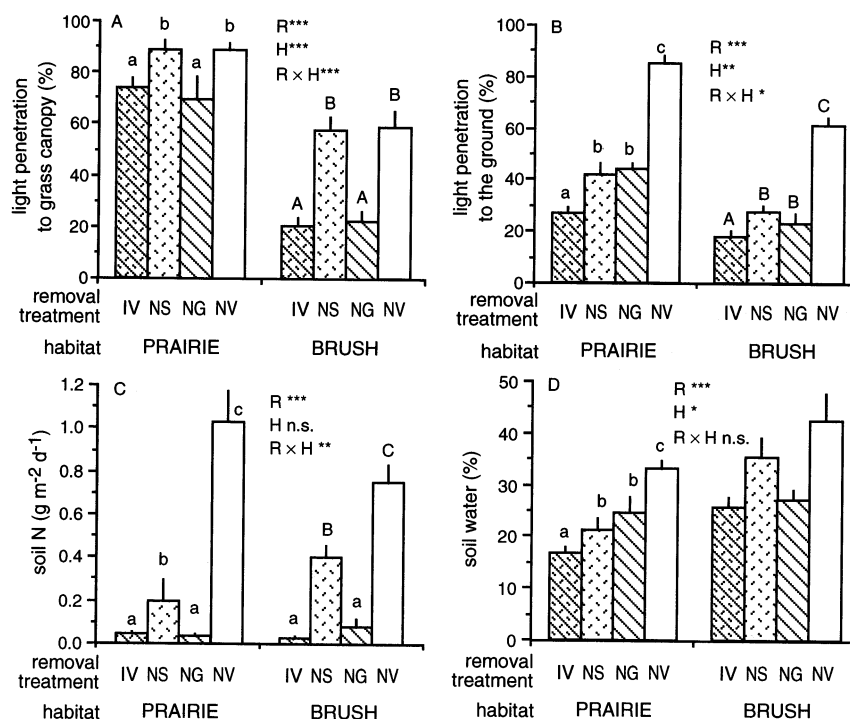
moval (NS, NG) increased light penetration similarly (prairie: $t = 2.59$, $P = 0.03$; brush: $t = 5.47$, $P = 0.0002$).

Available soil N (Fig. 4C), across habitats, varied significantly with removal treatment ($F_{3,12} = 88.4$, $P < 0.0001$). Shrub removal (NS) significantly increased available soil N ($t = 4.89$, $P = 0.0004$), but grass removal (NG) did not. Although trends among removal treatments did not differ significantly between prairie and brush ($P = 0.2$), a significant interaction between habitat and removal treatments (Fig. 4C; $F_{3,12} = 6.74$, $P = 0.007$) revealed that available soil N in vegetation without shrubs (NS) was lower in prairie than in brush ($t = 3.71$, $P = 0.004$), whereas available N in no-vegetation plots (NV) was higher in prairie than in brush ($t = 2.22$, $P = 0.048$). On the other hand, available soil N in no-grass plots (NG) and in intact vegetation (IV) did not differ significantly between habitats ($P > 0.3$).

Soil water (Fig. 4D) was significantly lower in prairie than in brush ($F_{1,4} = 21.0$, $P = 0.01$) and varied significantly among removal treatments ($F_{3,12} = 23.3$, $P < 0.0001$). Soil water was significantly lower in intact vegetation than in vegetation where one growth form had been removed ($t = 3.63$, $P = 0.003$) but did not differ between shrub and grass removal ($t = 1.08$, $P = 0.3$). There was no significant habitat × removal treatment interaction ($P = 0.1$), suggesting that removal treatments had similar effects in both habitats.

Resource uptake

Light attenuation was significantly higher in brush than in prairie (Table 1; $F_{1,4} = 9.63$, $P = 0.04$), but did not vary between growth forms.

N consumption was significantly higher in prairie than in brush (Table 1; $F_{1,4} = 18.4$, $P = 0.01$). Further, shrubs consumed significantly more N than grasses ($F_{1,4} = 33.8$, $P = 0.004$). N consumption also tended to vary with the habitat × growth form interaction effect ($F_{1,4} = 5.56$, $P = 0.08$), because N consumption by shrubs was similar in prairie and brush, whereas N consumption by grasses was lower in brush than in prairie.

Water consumption varied significantly with the habitat × growth form interaction effect (Table 1; $F_{1,4} = 43.7$, $P = 0.003$), because grasses and shrubs both consumed more water in the habitat where they dominated.

The sum of resource consumption (SRRC) was significantly greater than 100% (indicating competition) for light and nitrogen but not for water. SRRC$_{light}$ was significantly higher in brush than in prairie ($F_{1,4} = 9.63$, $P = 0.04$), whereas SRRC$_{nitrogen}$ was significantly higher in prairie than in brush ($F_{1,4} = 18.4$, $P = 0.01$), suggesting that competition in brush was strongest for light, whereas in prairie it was strongest for N.

For all resources, consumption per gram of standing crop was significantly higher for grasses than for shrubs (Table 2), but did not differ between habitats or with the habitat × growth form interaction.

Table 1. Relative resource consumption (RRC, see Methods) of grasses and shrubs in two habitats.

		Prairie		Brush	
		mean	SE	mean	SE
Light	grasses	74.4	4.8	80.2	3.4
	shrubs	70.3	3.2	86.3	3.5
	sum (SRRC)	144.7*		166.5*	
Nitrogen	grasses	89.2	9.2	49.0	6.1
	shrubs	98.7	0.8	91.8	3.2
	sum (SRRC)	187.9*		140.8*	
Water	grasses	73.1	10.8	49.6	17.2
	shrubs	48.8	9.2	87.9	8.5
	sum (SRRC)	121.9		137.5	

*: SRRC significantly $>100\%$ ($P<0.05$).

Discussion

Effects of grasses and shrubs on each other

In prairie, both shrubs and grasses were similarly suppressed by the other growth form (Fig. 2C), suggesting that competition in prairie was symmetric. Symmetric competition occurred even though shrubs had more standing crop than grasses (Fig. 1C), implying that grasses had a higher per-gram effect on shrubs than shrubs had on grasses.

In brush, shrubs strongly suppressed grasses (Fig. 2). This was not surprising since shrubs had 37 times more standing crop than grasses (Fig. 1D). In contrast, grass removal in brush had no effect on shrub ANPP (Fig. 2). Thus, competition between shrubs and grasses in brush was highly asymmetric.

Our results suggest that the interaction between grasses and shrubs is symmetric during early stages of shrub expansion into prairie, but becomes asymmetric as succession proceeds and shrub mass has accumulated. The shift from symmetric to asymmetric competition may reflect a shift from competition for soil resources in prairie to competition for light in brush (Weiner 1990, Wilson and Tilman 1991, Wilson 1993a). The shift from below- to aboveground competition also occurs in subtropical savanna where 2-yr oak seedlings compete with grasses for water and escape root competition as the oak roots extend beyond the grass rooting layer (Weltzin and McPherson 1997). Increased light competition in brush may be attributable to both higher standing crop and differences in growth form between grasses and shrubs.

Effects of shrubs and grasses on resources

Light penetration in intact vegetation was significantly higher in prairie than in brush (Fig. 4A, B). In both

habitats, shrub removal (NS) increased light penetration to the ground as much as did grass removal (NG) (Fig. 4B). This shows that, in both habitats, shrub and grass canopies reduced light to a similar degree even though shrub leaves are flat and wide, whereas grass leaves are erect and linear. However, shrubs in brush were taller than grasses. Consequently, light at the grass canopy level (Fig. 4A) and beneath (Fig. 4B) was presumably below the light saturation point of open-prairie grass species. Grasses did not pre-empt light available to shrubs because grasses are of similar height or smaller than shrubs in both habitats. Therefore, regardless of the similar effects of shrubs and grasses on light, shrubs, of course, pre-empt light because of their height.

Available soil N increased in both prairie and brush when shrubs (NS) but not when grasses were removed (NG) (Fig. 4C). This occurred presumably because of the much larger shrub mass (Fig. 1C, D; Goldberg and Werner 1983). Available N in intact vegetation did not differ significantly between prairie and brush (Fig. 4C). In contrast, available N is frequently higher under woody plants than under grasses (Callaway et al. 1991, McPherson et al. 1991, Wesser and Armbruster 1991, Wilson 1993b, Belsky 1994, Vieira et al. 1994, Wilson and Kleb 1996). The differences in our region are typically small, however, and are not always significant (Li and Wilson 1998). Available N in no-vegetation plots (Fig. 4C) was significantly higher in prairie than

Table 2. Relative resource consumption (RRC, see Methods) per gram of target standing crop.

	Grasses		Shrubs		ANOVA	
	mean	SE	mean	SE	$F_{1,4}$	P
Light	1.93	0.50	0.33	0.04	23.8	0.01
Nitrogen	1.50	0.13	0.42	0.07	20.4	0.01
Water	1.27	0.35	0.27	0.05	12.5	0.02

under brush. This may reflect higher levels of organic matter and higher rates of mineralization under prairie than forest (Dormaar and Lutwick 1966, Bettany et al. 1973, Severson and Arneman 1973, Schlesinger 1991).

Soil water was significantly lower in prairie than brush (Fig. 4D), as typically occurs in comparisons of grasses and woody plants (Callaway et al. 1991, McPherson et al. 1991, Wesser and Armbruster 1991, Belsky 1994, Vieira et al. 1994, Köchy and Wilson 1997, Li and Wilson 1998). In our system, higher soil moisture may reflect a generally lower topographic position of brush, but brush might also increase soil moisture through snow trapping (Timoney et al. 1993), hydraulic lift (Caldwell et al. 1998) or reduced evaporation (Selleck and Schuppert 1957, Mitchell et al. 1993). Soil water varied among the four removal treatments (Fig. 4D), but not between shrub and grass removal (NS, NG) treatments (Fig. 4D), suggesting that both growth forms were equally limited by water. Water uptake may be overestimated, however, because less water may have been intercepted by the remaining stems in cleared plots (NV) and more water may have entered the soil. On the other hand, reduced shade may have increased evaporation from the soil.

Resource consumption

The sum of relative resource consumption by grasses and shrubs (SRRC) was > 100% for light and N (Table 1), suggesting that grasses and shrubs competed for these two resources and that both growth forms took up belowground resources that would otherwise have been consumed by the removed neighbors. If SRRC is taken as an indicator of competition intensity, then competition in prairie was most intense for nitrogen, whereas competition in brush was most intense for light (Table 1). This contrast is typical of comparisons of herbaceous and woody communities because of the usually tall stature of woody species that pre-empts light (Tilman 1990, Wilson 1998).

Belowground competition was strongest for nitrogen (Table 1). In contrast, models of grass-shrub interactions in temperate grasslands emphasize competition for water (e.g., Sala et al. 1997, Weltzin and McPherson 1997), even though in temperate grasslands the balance of rainfall and evapotranspiration is relatively high (Walter 1984), so that N limits productivity more often than water (Tilman 1990, Wilson and Shay 1990, Peltzer et al. 1998).

In prairie, shrubs and grasses were equally tall and light levels (≈ 1000 µmol photons m^{-2} s^{-1} at grass canopy) were presumably sufficient for maximum photosynthesis of both shrubs and grasses (Redman 1971, Larcher 1984), except for the C$_4$ grass *Bouteloua gracilis*. This suggests that for C$_3$ species, light competition in prairie was low. In brush, the taller shrubs were still light saturated, but open-prairie grasses under the shrub canopy presumably experienced suboptimal photosynthesis (≈ 300 µmol photons m^{-2} s^{-1}). In summary, the contrasting responses of resources to vegetation removal suggest that competition in prairie was strongest for N, whereas in brush it was strongest for light.

Shrubs generally consumed more resources than grasses (Table 1). Comparisons with shrub and grass standing crop suggest that consumption was not a simple function of standing crop. Specifically, shrubs had 3–9 times more standing crop than grasses (Fig. 1C, D), but consumed equal amounts of light and, in prairie, less water (Table 1). Furthermore, the very high mass of shrubs relative to grasses did not correspond to the smaller differences between them in N uptake (Fig. 4C, Table 1). Therefore, differences between shrub and grass effects on resources suggest that the growth forms differed in their per-gram effects on resources.

Per-gram effects on resources

Grasses attenuated significantly more light per gram of mass than did shrubs (Table 2), because shrubs and grasses reduced light to a similar degree (Table 1), but shrubs with their woody stems had more standing crop than grasses (Fig. 1). Grasses also took up significantly more N and water per gram of mass than did shrubs (Table 2). Higher rates of N and water uptake per unit mass may also reflect the high root:shoot mass ratios of grasses relative to woody vegetation (Jackson et al. 1996).

The high resource uptake efficiency of grasses relative to shrubs may be caused by differences in allocation patterns. Grass standing crop consists only of photosynthetic leaves, whereas shrub standing crop also includes unproductive stems. Therefore, grasses can allocate photosynthates completely to resource uptake, that is, to producing new roots and leaves, whereas shrubs must allocate a portion of the photosynthates to the building and maintenance of stems. *Symphoricarpos* leaf mass is $\approx 16\%$ of standing crop (M. Köchy unpubl.). If resource uptake is divided by photosynthetic tissue mass, shrubs have higher or equal per-gram uptake than grasses. Similarly, the leaf-area to root-length ratio of forbs was larger than that of a grass in a chalk grassland (Mortimer 1992). High rates of N uptake per standing crop in grasses may also reflect the high root:shoot mass ratio of grasses (6:1, Caldwell and Richards 1986, Wilson 1993b) relative to woody vegetation (1:1 to 1:3, George and McKell 1978, Wilson 1993b). However, adding root mass to aboveground mass (assuming a root:shoot ratio of 6:1 for grasses and 1:1 for shrubs) still leaves grasses with higher per-gram effects than shrubs.

In our study, per-gram effects of established shrubs on resources were smaller than those of established grasses (Table 2) and shrub standing crop had smaller per-gram effects on grass ANPP than had grass standing crop on shrub ANPP (Figs 2, 3). In contrast, tree seedlings had higher per-gram shoot effects than grass seedlings on available soil N (Welker et al. 1991), perhaps because the tree seedlings had lower mass and a higher root:shoot ratio than the grasses.

Within the same growth form or in pot experiments, per-gram effects tend to be similar (Goldberg 1987, Goldberg and Fleetwood 1987, Peart 1989, Rösch et al. 1997), but a field removal experiment showed that established trees had twice the per-gram effect than established shrubs on herbaceous vegetation (Harrington and Johns 1990) and a native summer annual had larger per-root-length effects than introduced winter annuals on soil water potential (Gordon and Rice 1993). As far as we know, our study is the first to show that per-gram effects at the population level are lower for woody than for herbaceous growth forms.

Grass-shrub dynamics

What is the contribution of grasses to the exclusion of woody species from prairies? The responses of resources to growth-form removal suggest that competition between grasses and shrubs in prairie is strongest for N (Table 1). Thus, the ability to compete for N should be an important determinant of success in prairie. Grasses had very high N consumption per gram of mass, compared to shrubs (Table 2), because of the grasses' high root:shoot ratios and absence of woody tissues. Therefore, at equal masses, and especially in the case of young woody plants establishing among grasses, grasses may be superior competitors. However, young woody plants may endure competition by herbs (Brown et al. 1998) and accumulate biomass. Once woody species have emerged from the grass canopy, their growth rate increases dramatically (Hill et al. 1995). In established brush, shrubs are taller and reduce grass production by shading (Table 1, King 1990, Wilson 1993a, b, Li and Wilson 1998). Shading may particularly affect C_4 grasses which tend to have a higher light compensation point than shrubs (Larcher 1984). In dense brush, grasses no longer have any effect on shrub production (Fig. 2; Li and Wilson 1998).

The interaction of shrubs and grasses would be affected by factors that reduce or increase biomass of one growth form more than the other, or that would increase or reduce one of the main resources. Thus, fire, bison browsing, cattle grazing, N deposition from the atmosphere, droughts, and wet periods have different effects on shrubs and grasses and, in interaction or alone, may re-set the balance between shrubs and grasses (Archer 1996, Wilson 1998, Köchy 1999).

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