

5. COMPETITIVE EFFECTS OF INVADING SHRUBS AND INVADED GRASSES IN THE NORTHERN GREAT PLAINS

5.1. ABSTRACT

Differences in competitive effects among species may be related both to differences in mass and differences in growth forms. I tested whether the competitive effect of invading woody species on invaded grasses and on resources was related to mass or growth form. I conducted the experiment in mixed-grass prairie in western Canada for two years. I measured the effect of woody species on grasses as the increase of aboveground net primary productivity (ANPP) of grasses when shrubs (*Symphoricarpos occidentalis*) were removed. I measured the effect of grasses on woody species as the increase of shrub ANPP when grasses were removed. In prairie where shrub invasion was recent and shrub abundance low, shrubs suppressed grasses as much as grasses suppressed shrubs, even though shrubs had 6 times more standing crop. 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. In brush, however, where shrub invasion has continued for a longer time and shrub standing crop was 37 times grass standing crop, shrubs suppressed grasses strongly, whereas grasses did not suppress shrubs. Thus, as invasion progressed, the interaction between shrubs and grasses changed from symmetric to asymmetric. On a per-gram basis, however, shrubs had

smaller effects on light attenuation, nitrogen uptake, and water uptake than grasses, suggesting that the competitive effect of invading shrubs is related mostly to shrub size. In spite of their smaller per-gram effects on resources, woody stems allow shrubs to accumulate more mass and height, and to eventually displace grasses in spite of the grasses' greater per-gram effects on resources.

5.2. INTRODUCTION

The invasion of native grasslands by woody species is a global pattern, occurring not only in subtropical savannas (Scholes & Archer 1997) but also in temperate steppes (Blackburn & Tueller 1970, Archibold & Wilson 1980, van Auken & Bush 1989, Fuller & Anderson 1993, Knight et al. 1994). Elimination of undesirable woody species from, for example, pastures is often difficult or unsuccessful (e.g., Niering & Goodwin 1974, Bragg & Hulbert 1976, Svedarsky et al. 1986, Archer 1989, Richardson et al. 1990, Harrington & Johns 1990, Bock & Bock 1992, Brown 1995, Bowes & Spurr 1996, chapter 4), showing that our knowledge about tree-grass interactions is still insufficient.

In both grasslands and forests, competition occurs across a wide range of productivity (Wilson 1991, Reader et al. 1993, Wilson 1998). Competition generally shifts from belowground to aboveground as productivity increases and the aboveground resource (light) becomes more limiting than the belowground resources (water and nutrients) (Wilson

1993a,b, Wilson & Tilman 1993, 1995). Consequently, the invasion of woody species into grasslands may be related to changes in the relative availabilities of above- and belowground resources.

Competition between plants is the product of effects on and responses to their neighbours, generally through resources (Goldberg 1990). Competitive responses (the extent to which plants are suppressed by neighbours) differ little between trees and grasses (Wilson 1998). Competitive effects (the extent to which plants suppress their neighbours) generally increase with plant size (Grace 1985, Goldberg & Landa 1991) and are often larger in more productive communities (Grace 1993, Wilson 1999). Thus, trees may replace grasses because trees can accumulate more mass.

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 & Pacala 1993, Huisman & Weissing 1994, Schwinning & Weiner 1998). Therefore, specific allocation patterns enable growth forms to compete better either for light or for soil resources (Tilman 1990). For example, the tall stature of trees allows them to preempt light and their woody tissue makes them more nitrogen-efficient. Grasses with their fibrous roots, however, may be expected to take up more available soil resources (Caldwell & Richards 1986). Thus, trees may replace grasses not only because trees have more mass, but also because their allocation pattern allows them to preempt light and use less nutrients.

Calculating per-gram competitive effects (competitive effect divided by biomass) permits the separation of the effect of size and the effect of growth form on competitive effects (Goldberg 1990). Contrasting growth forms should have similar per-gram effects if competitive effects are only related to mass. Variation in per-gram effects would suggest that growth form contributes to competitive effects. Thus, grasses are expected to have larger per-gram effects on soil resources because of their long fibrous roots, whereas trees are expected to have larger per-gram effects on light because of their tall stature.

Per-gram effects do not seem to differ among species with a similar growth form or among seedlings of different herbaceous growth forms (Goldberg 1987, Goldberg & Fleetwood 1987, Peart 1989, Rösch et al. 1997). However, a native summer annual had larger per-root length effects than introduced winter annuals (Gordon & Rice 1993), established trees had larger per-gram effects than shrubs (Harrington & 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 initially little competitive advantage over grasses. As woody species increase in mass and height, however, they should become more competitive due to mass and growth form.

I 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 (N), and water.

Second, I examined whether competitive effects change during invasion by comparing the competitive effects between shrub stands with high and low stem density.

5.3. METHODS

5.3.1. 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. I worked at the edge of snowberry stands (*Symphoricarpos occidentalis*). Inside the stands that I refer to as "brush" was dense snowberry (40-70 cm tall) with a sparse grass understorey (grass canopy at 10-30 cm height). Grasses in brush were mostly *Stipa viridula*, *S. curtisetata*, and *Agropyron subsecundum*. Outside the stands were sparse snowberry stems (10-30 cm tall) scattered in grassland (canopy at 10-30 cm height) that I refer to as "prairie". Prairie was dominated by *Stipa* spp. (including *S. comata*), *Agropyron subsecundum*, *Bouteloua gracilis*, *Koeleria gracilis*, and *Poa* spp.

In these two habitats, I applied four removal treatments to plots. Removal treatments were I: intact vegetation, i.e., no vegetation removed; S: shrubs removed (including forb removal); G: grasses removed (includes sedge removal); and SG: both shrubs and grasses removed ("cleared plot"). Forbs and sedges had very low abundance at my sites.

No other growth forms occurred. There were two intact-vegetation plots in each habitat, one serving as a reference for grasses and a second as an independent reference for shrubs. Thus, there were five plots in each habitat. Differences between vegetation and resources among plots allowed me to separate the effects of shrubs and grasses on each other and on resources.

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 to cut newly grown roots. Plots were randomly assigned to treatment combinations within each habitat. The experiment was completely replicated at five sites within a 1-km² area.

I used herbicides to remove shrubs and grasses. I used 7.5 g/ha of metsulfuron (*Ally*, DuPont, Canada) on May 27 and 75 g/ha on June 11, June 26 and July 20, 1996 and May 30 and July 3, 1997 to kill shrubs and forbs (Ahrens 1994, Bowes & Spurr 1995, 1996). I used 190 mL/ha clethodim (*Select*, Rhône-Poulenc, Canada) on May 27, 1996 and May 9, 1997 to kill annual grasses. I used 2.7 L/ha sethoxydim (*Poast*, BASF, Canada) on June 15 and 27 L/ha sethoxydim on June 26 and July 20, 1996 and May 9 and 30, 1997 to kill perennial grasses (Ahrens 1994). I carefully applied 3.6 g/L glyphosate (*RoundUp*, Monsanto, Canada) locally on June 2, 1997 to kill sedge patches. Sethoxydim and metsulfuron concentrations were increased after the first application because the initial concentration appeared to have been ineffective on visual inspection after 3 wk. Herbicide treatments were repeated until mortality was close to 100%. Dead plants remained in place and continued to cast shade.

Metsulfuron was added to ≈ 0.15 L/m² water and clethodim and sethoxydim were added to ≈ 0.75 L/m² water. A surfactant (Na-hexametaphosphate, 2 g/L) and blue food colouring were added to the mixtures. I applied the mixtures with a 12-L backpack sprayer. In prairie, herbicides were applied uniformly from above the vegetation canopy. In brush, snowberry forms a dense canopy above the grasses and therefore, metsulfuron was applied from above the brush canopy, whereas clethodim and sethoxydim were applied below the brush canopy. We did not add any water to intact plots, because the amounts of water applied with the herbicides to plots was negligibly small compared to rainfall.

5.3.2. Effects of shrubs and grasses on each other

I assessed the effect of one growth form (neighbour growth form) on the other (target growth form) by comparing the aboveground net primary production (ANPP) of the target growth form in intact vegetation with the ANPP of the target growth form in vegetation where the neighbour growth form had been removed.

I assessed the per-gram effect of growth forms on each other by calculating regressions of target growth form ANPP on standing crop of the neighbour 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.

I measured grass ANPP in plots with grasses as target growth form as the mass of current-year culms and blades with green bases plus current year's litter. Grass litter remains attached for ≈ 0.5 yr (Sims & Coupland 1979). I measured shrub ANPP in plots with shrubs as target growth form as the total mass of current-year shoots (herbaceous stems and twigs with their attached leaves) plus shrub litter from litter traps. Ignoring the radial growth of older stems resulted in $< 5\%$ under-estimation of actual stem mass (calculated from Table 2.2).

I measured grass standing crop in each plot as the mass of culms and blades with green bases. I measured shrub standing crop in each plot as the total mass of live shoots (woody stems + herbaceous stems with their attached leaves).

Shoots and litter were harvested during August 28-29, 1996 and September 4-8, 1997. Grass shoots, shrub shoots and grass litter were harvested from one $1 \text{ m} \times 15 \text{ cm}$ strip in each plot. The strip was $\geq 0.5 \text{ m}$ from the plot edge. In early spring, loose grass litter in each plot with grasses as target growth form (one half of the intact-vegetation plots and all shrub-removal plots) had been removed by hand. I did not wish to disturb the plots by tearing out attached litter, so I spray-painted the remaining attached litter. Painted litter was removed after harvest so that only litter produced during the current growing season was collected. Shrub litter was collected in three litter traps (10 cm diameter, 5 cm deep) per plot in each plot with shrubs as target growth form (one half of the intact-vegetation plots and all grass-removal plots) during the growing season each year. After sorting, shoots and

litter were dried at 70°C to constant mass and weighed. A hailstorm on August 28, 1997 removed almost all shrub leaves and many twigs. Therefore, I separated the material in the traps into leaves, current-year stems and older stems, calculated their respective mass per 0.15 m² and added the result to the mass measured in the strips.

5.3.3. Effects of grasses and shrubs on resources

I tested whether growth form effects on resources differed between habitats by comparing resource levels in each removal treatment. I assessed the per-gram effect of each growth form on resources by comparing the ratios of resource consumption:standing crop. I considered three resources: light, available soil nitrogen, and soil water.

I measured light with a 40-cm integrating photosynthetic photon flux (PPF) probe (Sunfleck Ceptometer, Decagon Devices, Pullman, Washington, U.S.A.) 1-3 cm above the soil surface perpendicular from all plot edges and above the canopy on July 18 and August 24, 1996 and July 14, 1997, within two hours of solar noon on a cloudless day. Light measurements in 1996 did not differ significantly between July and August. Therefore, I analyzed in greater detail only 1996 data from August and restricted light measurements in 1997 to one date. In 1996 I also measured light at the top of the grass foliage canopy (\approx 30 cm above ground). Again, measurements were similar in both months and only August data is presented. On 1996-08-24, maximum PPD was 1434 $\mu\text{mol photons m}^{-2}$

s⁻¹ and on 1997-07-14, maximum PPD was 1723 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$. I calculated light penetration for each plot as the mean of the four PPD measurements divided by the PPD above the canopy $\cdot 100\%$. Light attenuation by vegetation was taken as an index of light consumption and calculated as $100\% - \text{light penetration}$.

In each plot I collected mineral N with ion-exchange resin bags (3 cm \times 3 cm), each containing 2 cm³ dry mixed-bed (anionic and cationic) ion-exchange resin (AG 501-X8, BioRad, Hercules, California, U.S.A.) with an ion-exchange capacity of 1.5 mmol/cm³ for anions and cations (Binkley & Hart 1989). Thus, the total ion-exchange capacity of each bag was 3 mmol (3.3 mol/m²). Amounts of cations and anions in soil leachate and throughfall of temperate forests range from 16 to 1028 mmol m⁻² yr⁻¹ (Pastor & Bockheim 1984, Johnson & Lindberg 1992, Boxman et al. 1994). Therefore, the amount of resin was sufficient to take up all ions contained in atmospheric deposition or soil solution during the measurement period without becoming saturated. I did not treat resin against microbial attack because the effect of microbes on N capture is much smaller than the amount of N in soil solution or deposition (Binkley 1984, 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 May 22, 1996 and May 2, 1997 and removed on August 27, 1996 and August 28, 1997. The amount of N collected by the resin was assessed by removing the resin from air-dried retrieved bags and extracting the resin in 30 mL 2 mol/L NaCl \cdot

0.1 mol/L HCl (Giblin et al. 1994) for 1 h. Nitrate in the extract was converted to ammonium by reduction with TiCl_3 and ammonium was converted to ammonia by increasing the pH of the solution with 10 mol/L NaOH. The concentration of N in the extract was then measured using an ion-selective electrode (Orion, Boston, Massachusetts, U.S.A.). I added known amounts of nitrate and ammonia to unused bags to determine an extraction rate ($N_{\text{extracted}} \text{ (mol/L)} = 0.9618 N_{\text{added}} \text{ (mol/L)} + 0.0071$, $R^2 = 0.92$, $n = 48$). I calculated actual N uptake of bags used in the field by applying the extraction rate equation to amounts of extracted N (Köchy & Wilson 1997).

I calculated net N uptake in each vegetated plot in each habitat and site as [N on resin in the cleared plot] - [N on resin in each vegetated plot]. Results did not change qualitatively when uptake was standardized, i.e., divided by the resource level in cleared plots.

I measured soil water from three soil cores (2 cm diameter, 10 cm deep) per plot on May 27, July 18-20 and August 27, 1996 and on May 29, June 23, July 14, and September 8, 1997. Soil from the three cores was mixed and a $\approx 40 \text{ cm}^3$ soil subsample was dried at 70°C to constant mass and weighed. Soil water is expressed as $\text{g water/g dry soil} \cdot 100\%$. The largest differences of soil water among plots were measured in late August 1996 and mid July 1997. Therefore, I restricted statistical comparisons and calculation of net water uptake to these dates.

I calculated net water uptake in each vegetated plot in each habitat and site as [% water in the cleared plot] - [% water in each vegetated plot]. Results did not change qualitatively when uptake was

standardized, i.e., divided by the resource level in cleared plots.

5.3.4 Statistics

I examined the effectiveness of the removal treatments by comparing separately for grass and shrub standing crop the four removal treatments (I, S, G, SG) among each other and between habitats and years with analysis of variance (ANOVA) for block-factorial designs. Standing crop of both growth forms differed most strongly among removal treatments in the second year (1997, Fig. 5.1, p. 95). For all data I performed statistical tests separately for each year and as well as for both years, where year was treated as an additional factorial effect in ANOVAs and analyses of covariance (ANCOVAs). The trends of the results were similar in each case, therefore I present results only from the second year.

In order to test whether neighbour removal affected target ANPP I considered four of the removal treatments (the two intact-vegetation treatments, the shrub-removal treatment and the grass-removal treatment) as two orthogonal factors with two levels each. One factor was target growth form (shrubs or grasses) and the other factor was neighbour removal (intact vegetation or the other, neighbour growth form removed). Thus, the combination shrub target growth form - intact vegetation was represented by one intact-vegetation plot, the combination shrub target growth form - neighbours removed was represented by a grass removal

plot, the combination grass target growth form - intact vegetation was represented by the other intact-vegetation plot and the combination grass target growth form - neighbours removed was represented by a shrub removal plot. This arrangement allowed me to compare with an ANOVA for a block-factorial design the ANPP of shrubs in intact vegetation with the ANPP of shrubs without neighbours and the ANPP of grasses in intact vegetation with the ANPP of grasses without neighbours.

I 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 had shown that regressions did not differ significantly between habitats.

I compared the effect of the four removal treatments (I, S, G, SG) on light penetration, available soil N and soil water between habitats with ANOVA for block-factorial designs. When there was a significant habitat \times removal interaction, I determined which removal treatments differed between habitats by making four orthogonal contrasts (one for each removal treatment). Then I tested for each habitat which removal treatments differed from each other by using the simple or linear contrasts described in Table 5.1. When there was a significant removal treatment effect, but no significant habitat \times removal interaction, I compared removal treatments across habitats using the same contrasts (Table 5.1). Since these contrasts were planned comparisons, I used a significance level of $\alpha = 0.05$ for each comparison.

I compared light attenuation, N uptake, and water uptake per

Table 5.1. A-priori comparisons using contrasts to answer specific questions when the effect of removal treatments or the habitat \times removal treatment interaction was significant. Treatments combined for linear contrasts are bracketed. Removal treatments: I: intact vegetation, S: shrubs removed, G: grasses removed, SG: shrubs and grasses removed.

Contrast	Question
① (I, S, G) vs SG	Does vegetation affect resource levels at all? Yes \Rightarrow ②
② (S, G) vs I	Does removing a growth form affect resource levels in intact vegetation? Yes \Rightarrow ③
③ S vs G	Do grasses and shrubs have similar effects on resource levels ? Yes \Rightarrow ④ ⑤
④ S vs I	Do shrubs affect resource levels in intact vegetation?
⑤ G vs I	Do grasses affect resource levels in intact vegetation?

gram biomass among intact vegetation, grasses, and shrubs and between habitats. I calculated per-gram consumption for each plot as resource consumption divided by plot standing crop. I then compared the per-gram consumption among intact vegetation (no removal), shrubs (grass removal), and grasses (shrub removal) with an ANOVA for block-factorial design and using planned comparisons analogous to tests 3-5 in Table 5.1.

I also calculated the per-gram effects as resource consumption divided by target standing crop, i.e., instead of using plot standing crop I used shrub standing crop for shrub consumption and grass standing crop for grass consumption. These results did not differ qualitatively from the ones based on plot standing crop. Therefore, I present only results based on plot standing crop.

My experiment was completely factorial because all possible treatment combinations occurred. The results were therefore analyzed with ANOVAs for blocked-factorial designs with sites as random effect blocks (Lorenzen & Anderson 1993). Habitat and removal treatments were fixed effects. The habitat treatments were considered randomized within each site. All removal treatments, including target growth form \times neighbour-removal treatments were randomized within each habitat. The main or interaction effects of habitat and removal treatment and the main or interaction effects of habitat, target growth form, and neighbour-removal treatments were tested with their interaction effect with site as the error term in ANOVA (Lorenzen & Anderson 1993). My 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 \times neighbour-removal treatments (Snedecor & Cochran 1989).

Standing crop, ANPP, and light attenuation data were ln-transformed and available soil N data were square-root transformed to meet assumptions of homoscedasticity and normality. All statistics were calculated with JMP for Macintosh (version 3.2.1, SAS Institute 1997).

5.4. RESULTS

5.4.1. Treatment effects on standing crop

Herbicide application caused significant variation of shrub and grass standing crop among removal treatments, across habitats and years (Fig. 5.1; grasses: $F_{3,12} = 73.4$, $P < 0.0001$; shrubs: $F_{3,12} = 107$, $P < 0.0001$). Herbicides significantly reduced shrub abundance in shrub-removal plots (Fig. 5.1; S vs I: $t = 11.7$, $P < 0.0001$) and grass abundance in grass-removal plots (Fig. 5.1; G vs I: $t = 6.25$, $P < 0.0001$). Herbicides did not reduce the abundance of the remaining growth form (grass standing crop: S vs I: $t = 4.25$, $P(\text{one-tailed}) = 0.9994$; shrub standing crop: G vs I: $t = 0.187$, $P(\text{one-tailed}) = 0.6$). Herbicides significantly reduced shrub and grass standing crop in cleared plots (SG) over any other removal treatment (Fig. 5.1; simple means comparisons, SG vs I, S, G: shrubs: all $P \leq 0.02$, grasses: all $P \leq 0.001$). 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. 5.1; $F_{1,4} = 29.6$, $P = 0.006$).

Shrub and grass standing crop, across habitats and removal treatments, were each 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

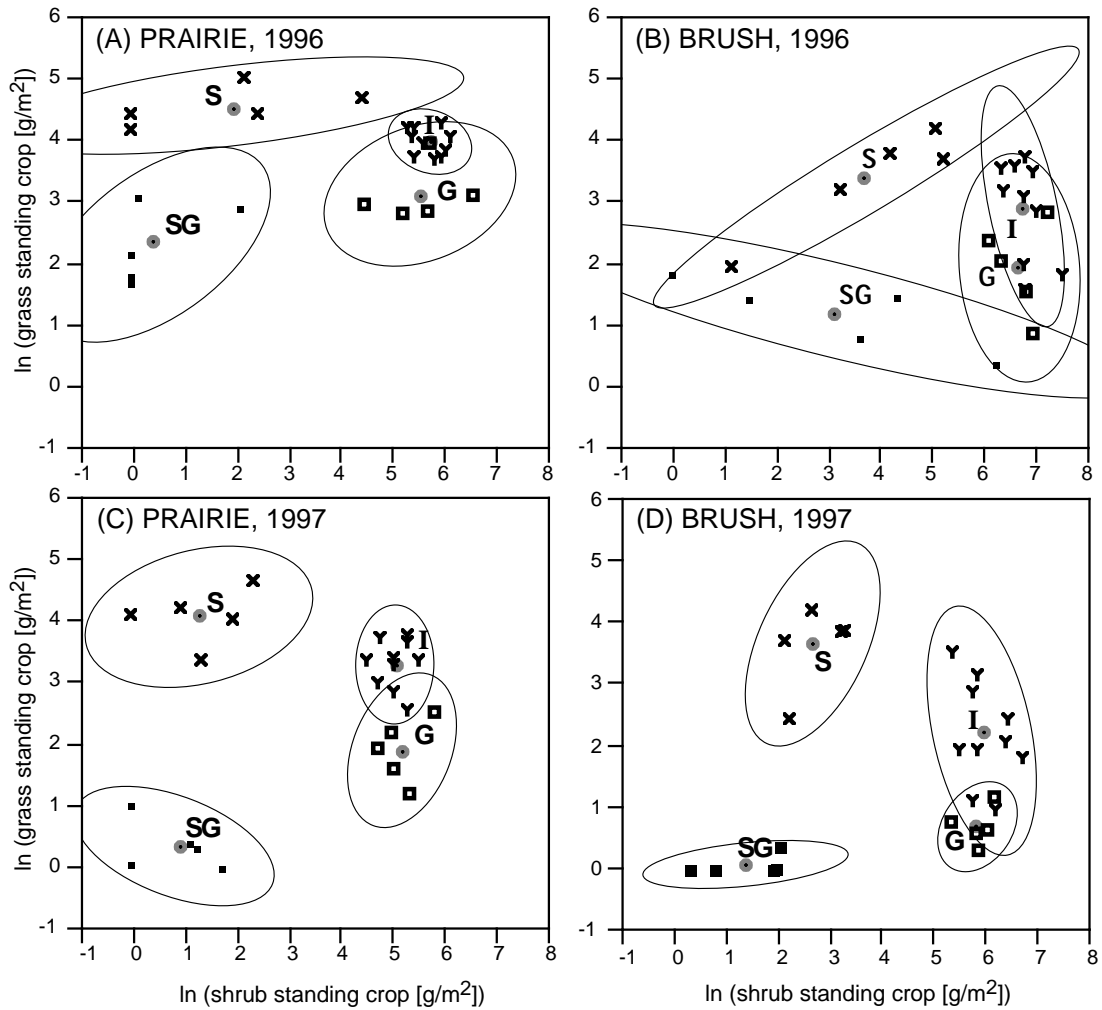


FIG. 5.1. Effectiveness of four growth form removal treatments (I, S, G, SG), based on standing crop in two habitats (prairie, brush) over two years. I (Y): grasses and shrubs at natural abundance, S (x): shrubs removed; G (□): grasses removed; SG (■): shrubs and grasses removed. Grey dots indicate the mean for each treatment. Ellipses represent the 95%-confidence area (bivariate normal density) for each group mean.

second year, but the removal treatment \times year interaction was significant only for grasses (Fig. 5.1; $F_{3,12} = 4.94$, $P = 0.02$). For the sake of clarity and brevity I report further results only for the second year (1997).

5.4.2 Effects of shrubs and grasses on each other

In general, shrubs had significantly higher aboveground net primary productivity (ANPP) than grasses (Fig. 5.2; $F_{1,4} = 22.0$, $P = 0.009$). Across neighbour-removal treatments, shrub ANPP in prairie was lower than in brush, but not significantly. Grass ANPP in prairie was significantly higher than in brush (Fig. 5.2; habitat \times target growth form interaction: $F_{1,4} = 23.7$, $P = 0.008$; prairie vs brush: shrubs: $t = 2.87$, $P = 0.06$; grasses: $t = 4.02$, $P = 0.03$). Habitat had no significant main effect on ANPP ($P = 0.6$).

Removing the neighbour growth form generally increased ANPP of the target growth form (Fig. 5.2; $F_{1,12} = 85.5$, $P = 0.0008$). A significant interaction among habitat, remaining growth form and neighbour removal treatments (Fig. 5.2; $F_{1,4} = 20.4$, $P = 0.01$) allowed me to compare means of shrub and grass ANPP between intact vegetation and vegetation where one growth form had been removed, in both prairie and brush. Shrub removal significantly increased grass ANPP in both habitats (prairie: $t = 8.15$, $P = 0.001$; brush: $t = 13.6$, $P = 0.0002$); grass removal significantly increased shrub ANPP in prairie ($t = 4.16$, $P =$

0.01) but not in brush ($t = 0.54, P = 0.6$). Across habitats, shrub removal significantly increased grass ANPP but grass removal did not increase shrub ANPP (removal \times remaining growth form interaction: $F_{1,4} = 11.5, P = 0.03$; means comparisons: shrubs: $t = 1.31, P = 0.3$; grasses: $t = 6.11, P = 0.009$).

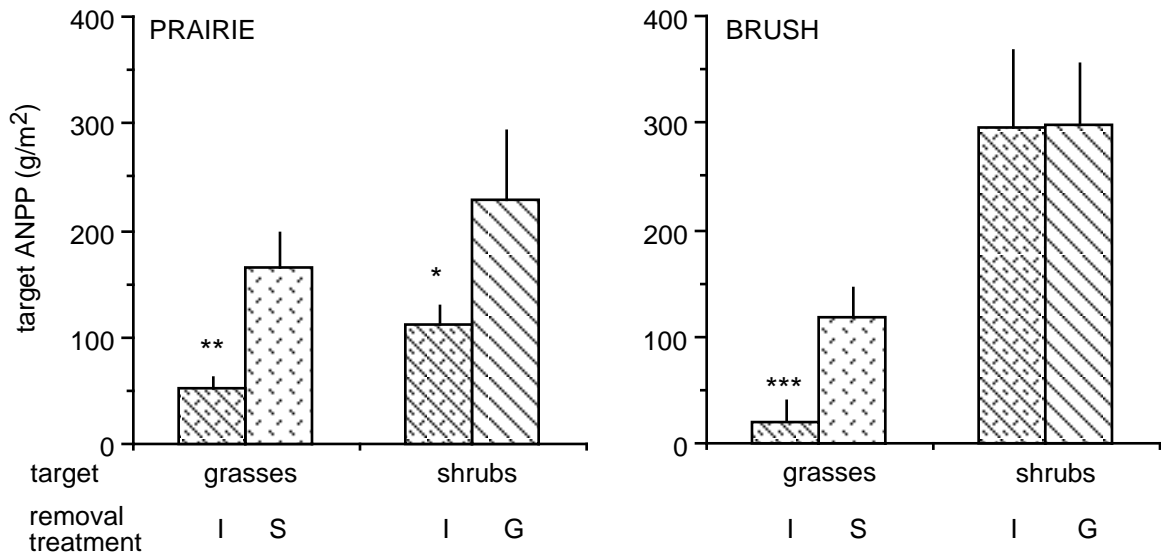


FIG. 5.2. Effect of removal and habitat treatments on aboveground net primary productivity (ANPP) of either shrubs or grasses (targets). I: intact grass-shrub vegetation; G: grasses removed; S: shrubs removed. Bars represent means of five sites + SE. Significant differences between removal treatments for each growth form in each habitat are indicated by asterisks (simple linear contrasts on log-transformed data; *: $P \leq 0.05$, **: $P \leq 0.01$, ***: $P \leq 0.001$).

ANPP of both growth forms decreased as standing crop of the contrasting growth form increased (Fig. 5.3; 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 = $262 \cdot \text{shrub standing crop}^{-0.38}$ and shrub ANPP = $361 \cdot \text{grass standing crop}^{-0.38}$, suggesting that grass standing crop had a $361/262 = 1.4$ times larger per-gram effect than shrub standing crop.

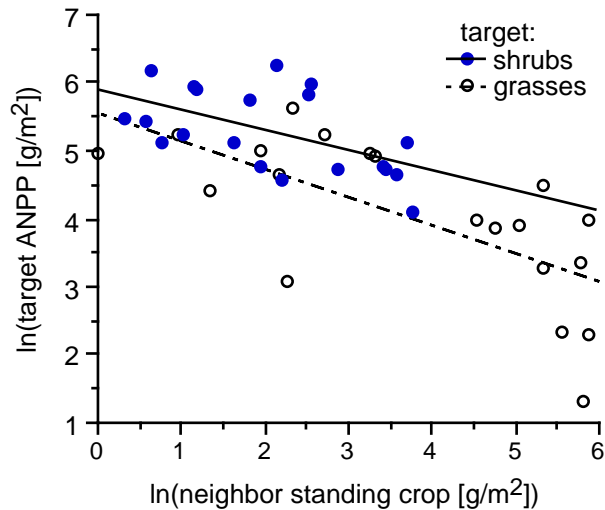


FIG. 5.3. Aboveground net primary productivity (ANPP) of targets (grasses and shrubs) as a function of the standing crop of the contrasting growth form. Grasses: $R^2 = 0.47$, $\ln(y) = 5.57 - 0.411 \ln(x)$, shrubs: $R^2 = 0.29$, $\ln(y) = 5.89 - 0.294 \ln(x)$.

5.4.3. Effects of shrubs and grasses on resources

Light penetration to the grass canopy (Fig. 5.4a) was significantly higher in prairie than in brush ($F_{1,4} = 104, P = 0.0004$). Shrub removal significantly increased light penetration to the grass canopy ($t = 7.82, P < 0.0001$), whereas grass removal did not increase light penetration to that level (removal effect: $F_{3,12} = 38.7, P < 0.0001$). A significant habitat \times 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 was <100% because of remaining dead stems and litter in the plots.

Light penetration to the ground (Fig. 5.4b), across removal treatments, was significantly higher in prairie than in brush ($F_{1,4} = 65.2, P = 0.001$) and, across habitats, 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 me to compare means of light penetration among removal treatments separately for each habitat. In both habitats, shrub and grass removal increased light penetration similarly (prairie: $t = 2.59, P = 0.03$; brush: $t = 5.47, P = 0.0002$).

Available soil N (Fig. 5.4c), across habitats, varied significantly with removal treatment ($F_{3,12} = 88.4, P < 0.0001$). Shrub removal significantly increased available soil N ($t = 4.89, P = 0.0004$), but grass removal did not. Although trends among removal treatments did not differ significantly between prairie and brush ($P = 0.2$), a significant

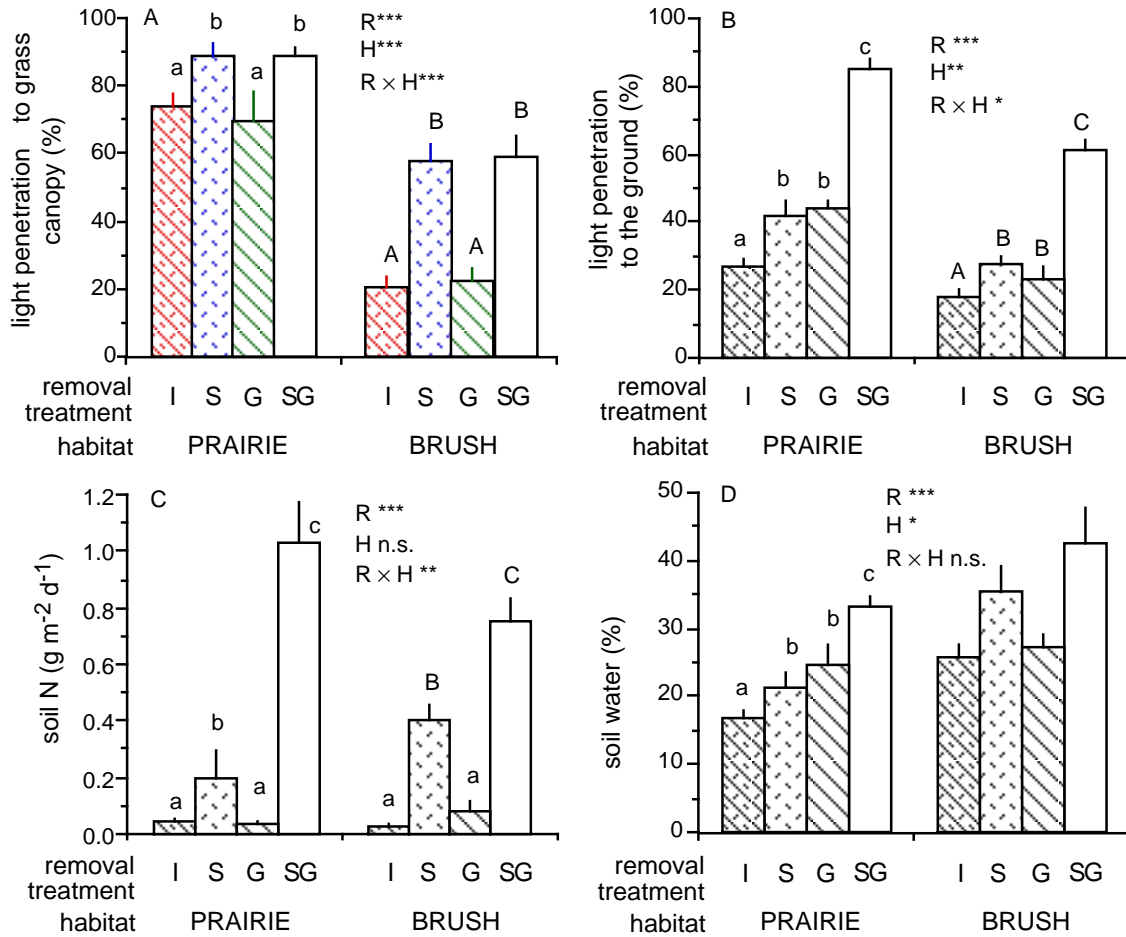


FIG. 5.4. Effect of removal treatment (R) and habitat (H) on light penetration to the grass canopy (c. 30 cm above ground) (a), to the ground (1-3 cm above soil surface) (b), available soil nitrogen (10 cm depth) (c) and soil water (0-10 cm) (d). Removal treatments: I: intact shrub-grass vegetation; S: shrubs removed; G: grasses removed; SG: shrubs and grasses removed. Bars represent means + SE (I: $n = 10$; S, G, SG: $n = 5$). For each resource, removal treatments that differ significantly from each other are marked with different letters above the bars of the prairie treatment. If $R \times H$ was significant, significantly different removal treatments within a habitat are indicated in both habitats; removal treatments that differ significantly between habitats are indicated by uppercase letters in the brush treatment. Results of ANOVA: n.s.: $P > 0.05$, *: $P \leq 0.05$, **: $P \leq 0.01$, ***: $P \leq 0.001$.

interaction between habitat and removal treatments (Fig. 5.4c; $F_{3,12} = 6.74$, $P = 0.007$) revealed that available soil N in vegetation without shrubs was lower in prairie than in brush ($t = 3.71$, $P = 0.004$), whereas available N in cleared plots (SG) was higher in prairie than in brush ($t = 2.22$, $P = 0.048$). On the other hand, available soil N in vegetation without grasses (G) and in intact vegetation (I) did not differ significantly between habitats ($P > 0.3$).

Soil water (Fig. 5.4d), across removal treatments, was significantly lower in prairie than in brush ($F_{1,4} = 21.0$, $P = 0.01$) and, across habitats, 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 \times removal treatment interaction ($P = 0.1$).

5.4.4. Per-gram effects on resources

Light attenuation (100% - light penetration in each plot) per gram standing crop (Fig. 5.5a), across habitats, varied significantly among removal treatments ($F_{2,8} = 66.3$, $P < 0.0001$). A significant interaction between habitat and removal treatments ($F_{2,8} = 9.92$, $P = 0.007$) allowed me to compare means among removal treatments separately for each habitat. Remaining grasses attenuated significantly more light

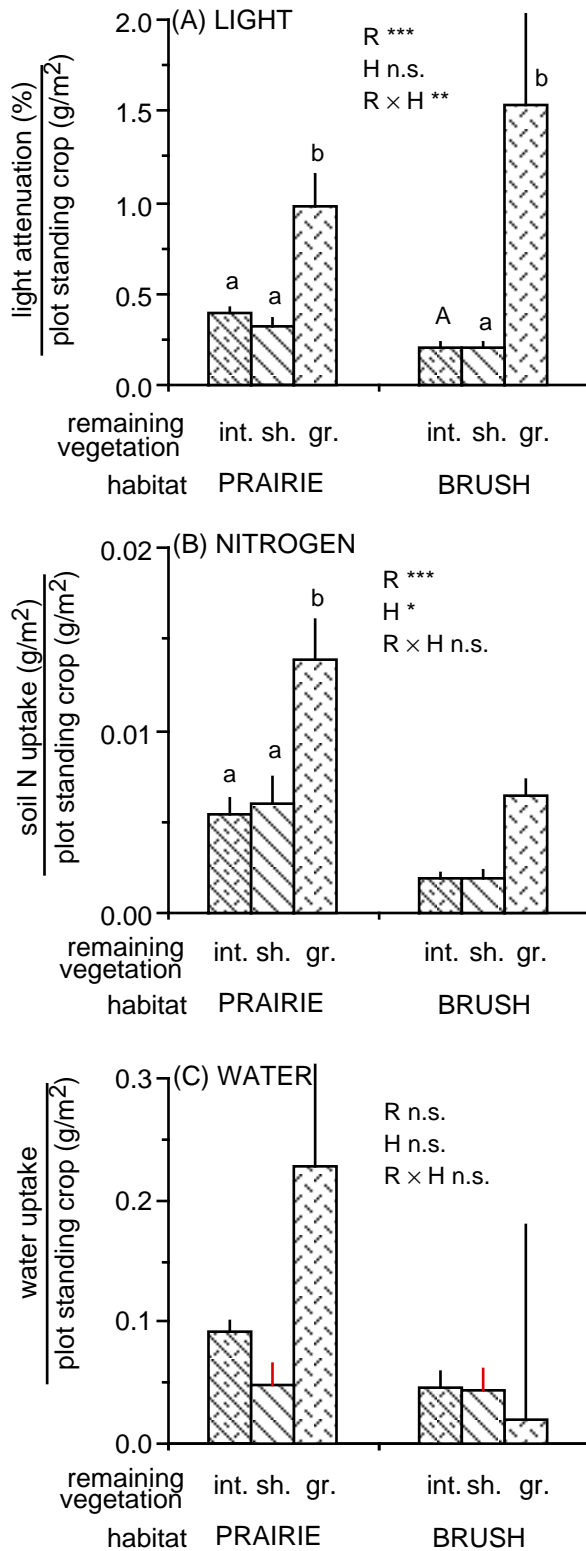


FIG. 5.5. Differences among remaining vegetation (R) and habitats (H) in light attenuation (a), soil N uptake (b) and water uptake (c) per gram standing crop. int.: intact grass-shrub vegetation; sh.: shrub vegetation (grasses removed); gr.: grass vegetation (shrubs removed). Light attenuation = 100% - light penetration (Fig. 5.4b). Soil N uptake = SOIL N in SG plots - SOIL N in I, S or G plots (Fig. 5.4c). Water uptake = SOIL MOISTURE (%) in SG plots - SOIL MOISTURE (%) in I, S or G plots (Fig. 5.4d). Bars represent means + SE (int.: n = 10; sh., gr.: n = 5). For each resource, remaining-vegetation treatments that differ significantly from each other are marked with different letters above the bars of the prairie treatment. If R x H was significant, significantly different remaining-vegetation treatments within a habitat are indicated in both habitats; remaining-vegetation treatments that differ significantly between habitats are indicated by uppercase letters in the brush treatment. Results of ANOVA: *: P ≤ 0.05, **: P ≤ 0.01, ***: P ≤ 0.001.

per gram standing crop than remaining shrubs (prairie: $t = 5.92$, $P = 0.0004$, brush: $t = 9.73$, $P < 0.0001$) or than intact vegetation (prairie: $t = 5.28$, $P = 0.0007$, brush: $t = 11.6$, $P < 0.0001$) in each habitat. In contrast, remaining shrubs did not differ significantly in their light attenuation from intact vegetation in either habitat ($P > 0.15$). Intact vegetation attenuated significantly more light per gram standing crop in prairie than in brush ($t = 5.04$, $P = 0.001$). Similarly, remaining shrubs tended to attenuate more light per gram standing crop in prairie than in brush ($P < 0.10$). In contrast, remaining grasses tended to attenuate more light per gram standing crop in brush than in prairie ($P < 0.10$). Habitat had no significant main effect on per-gram light attenuation ($P = 0.2$).

N uptake (available soil N in cleared plots minus available soil N in I, S, or G treatments) per gram standing crop (Fig. 5.5b), across removal treatments, was significantly higher in prairie than in brush ($F_{1,4} = 13.1$, $P = 0.02$) and, across habitats, varied significantly with removal treatments ($F_{2,8} = 63.0$, $P < 0.0001$). There was, however, no significant habitat \times removal treatment interaction ($P = 0.065$), therefore, I compared removal treatments across both habitats. Remaining grasses consumed significantly more available N per gram standing crop than remaining shrubs ($t = 8.86$, $P < 0.0001$) or than intact vegetation ($t = 10.7$, $P < 0.0001$). Remaining shrubs did not differ significantly in their N uptake from intact vegetation ($P = 0.6$).

Soil water uptake (% water in cleared plots minus % water in I, G, or S plots) did not vary significantly with either habitat or removal

treatments or the interaction between these two factors (Fig. 5.5c; all $P > 0.2$).

5.5. DISCUSSION

5.5.1. Effects of grasses and shrubs on each other

In prairie, shrub removal increased grass ANPP threefold, and grass removal increased shrub ANPP twofold (Fig. 5.2). Thus, in prairie, both shrubs and grasses were suppressed by the other growth form. The suppression of shrubs by grasses is surprising because shrub standing crop in prairie was six times higher than grass standing crop (Fig. 5.1 c). Thus, in prairie undergoing shrub expansion, grasses and shrubs had more or less symmetric effects. Symmetry emerged even though shrubs had much more standing crop than grasses, implying that grasses had a higher per-gram effect on shrubs than shrubs had on grasses.

In brush, shrub removal increased grass ANPP sixfold (Fig. 5.2), suggesting that shrubs strongly suppressed grasses. This was not surprising since shrubs had 37 times more standing crop than grasses (Fig. 5.1d). In contrast, grass removal in brush had no effect on shrub ANPP (Fig. 5.2), that is, grasses had a per-gram effect approaching zero. Since shrubs had a per-gram effect greater than zero, shrubs had a larger per-gram effect on grasses than grasses had on shrubs. This is the opposite of what I observed in prairie. Thus, competition between shrubs and grasses in brush was highly asymmetric.

My results suggest that the interaction between grasses and shrubs is symmetric during early stages of shrub expansion but becomes asymmetric when expansion has continued for a longer time 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 & Tilman 1991, Wilson 1993b).

5.5.2. Effects of shrubs and grasses on resources

Light penetration in intact vegetation was significantly higher in prairie than in brush (Fig. 5.4a,b). In both habitats, shrub removal increased light penetration to the ground as much as did grass removal (Fig. 5.4b). 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 and light at the grass canopy level (Fig. 5.4a) and beneath (Fig. 5.4b) 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 penetration, shrubs pre-empt light because of their size.

Available N in intact vegetation did not differ significantly between prairie and brush (Fig. 5.4c: removal I). In contrast, available N is frequently higher under woody plants than under grasses (Petranka & McPherson 1979, Miles 1985, Brady 1990, Jackson et al. 1990, Zak et al. 1990, Callaway et al. 1991, McPherson et al. 1991, Wesser & Armbruster 1991, Wilson 1993a, Belsky 1994, Vieira et al. 1994, Wilson & Kleb 1996). The differences in our region are typically small, however, and are not always significant (Li & Wilson 1998). Available N in plots from which all vegetation had been removed (Fig. 5.4c: SG removal) was significantly higher in prairie than under brush. This may reflect higher levels of organic matter and higher rates of mineralization under prairie than forest (Dormaer & Lutwick 1966, Bettany et al. 1973, Severson & Arneman 1973, Schlesinger 1991). In both prairie and brush, shrub removal significantly increased available soil N, whereas grass removal did not (Fig. 5.4c). This might simply reflect the mass difference between the two growth forms (Fig. 5.1).

Soil water was significantly lower in prairie than brush (Fig. 5.4d), as typically occurs in comparisons of grasses and woody plants (Petranka & McPherson 1979, Miles 1985, Zak et al. 1990, Jackson et al. 1990, Brady 1990, Callaway et al. 1991, McPherson et al. 1991, Wesser & Armbruster 1991, Belsky 1994, Vieira et al. 1994, Köchy & Wilson 1997). In my system, higher soil moisture probably reflects the lower topographic position of brush. Soil is also moister under woody vegetation than prairie at the same level (Wilson & Kleb 1996), suggesting that brush increases soil moisture, either through snow trapping (Timoney et

al. 1993), hydraulic lift (Caldwell et al. 1998), or reduced evapotranspiration (Selleck & Schuppert 1957, Mitchell et al. 1993). Soil water had similar effects in both habitats but varied among the four removal treatments (Fig. 5.4d). The increase of soil water, however, did not differ between shrub and grass removal (Fig. 5.4d).

Resources differed in the extent to which they were reduced by grasses or shrubs. Available N was much greater in plots from which all vegetation had been removed than in plots from which only one growth form had been removed. This suggests that the remaining growth form in each plot took up N that would otherwise have been consumed by the removed growth form, and that each exerted strong demand for N (Welker et al. 1991). For water, the available amount is the difference between the water remaining in intact-vegetation plots and in plots from which both growth forms had been removed, because the water taken up by intact vegetation may be close to the maximum that can be extracted by vegetation. Based on this, each growth form took up equal or more than half the available water (Fig. 5.4d), suggesting that, as for N, the water uptake by the remaining growth form in each plot compensated for the removal of the other growth form. In contrast to N, the demand for water by grasses was stronger in prairie than in brush, presumably because grass mass in brush was very low. Water uptake may be overestimated, however, because in plots with both growth forms removed, less water may have been intercepted by the remaining stems, therefore less water may have evaporated and more water may have entered the soil. In prairie, shrubs and grasses were equally tall and light levels ($\approx 1000 \mu\text{mol}$

photons $\text{m}^{-2} \text{s}^{-1}$ at grass canopy) were sufficient for maximum photosynthesis of both shrubs and grasses, 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 may experience suboptimal photosynthesis ($\approx 300 \mu\text{mol photons m}^{-2} \text{s}^{-1}$). 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.

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

Comparisons of the resource reductions by shrubs and grasses in neighbour-removal plots suggest that the decreases were not a simple function of standing crop. Specifically, shrubs had 3-9 times more standing crop than grasses (Fig. 5.1c,d), but attenuated as much light and took up equal amounts of water (Fig. 5.4a,b,d). Furthermore, the very high mass of shrubs relative to grasses did not correspond to the smaller differences between them in N uptake (Fig. 5.4c). Therefore, differences between shrub and grass effects on resources suggest that the growth forms differed in their per-gram effects on resources.

5.5.3. Per-gram effects on resources

Grasses attenuated significantly more light per gram of mass than did shrubs (Fig. 5.5a). This was because shrubs and grasses reduced light to a similar degree (Fig. 5.4b), but shrubs had more standing crop than grasses (Fig. 5.1) because of their woody stems. Grasses also took up significantly more N per gram of mass than did shrubs (Fig. 5.5b). Similar results as for N were found for water in prairie (Fig. 5.5c), although the results were not significant.

On a per-gram basis, grasses not only attenuated more light and took up more N than did shrubs but also more than did intact vegetation (Fig. 5.5a,b). This may simply reflect the large amounts of shrub mass removed (Fig. 5.1c,d) which made resources available for uptake, but it also suggests that grasses are physiologically able to take up far more resources in pure stands than they are able to when growing with shrubs.

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 (based on data used for Table 2.1). 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 & Richards 1986, Wilson 1993a) relative to woody vegetation (1:1 to 1:3, George & McKell 1978, Wilson 1993a). 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.

My study is probably the first to show that per-gram effects at the population level differ between growth forms but that the relative size of per-gram effects is similar across habitats. In my study, per-gram effects of established shrubs on resources were smaller than those of established grasses. In contrast, tree seedlings had higher per-gram shoot effects than grass seedlings on available soil N (Welker et al. 1991). This may be 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 & 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 & Johns 1990) and a native summer annual had larger per-root-length effects than introduced winter annuals on soil water potential (Gordon & Rice 1993).

5.5.4. Grass-shrub competition

Grasses generally consumed more resources per gram standing crop (Fig. 5.5), but grasses in brush were strongly suppressed by shrubs (Fig. 5.2). This suggests that shrubs were better competitors when their standing crop was large enough to balance the higher per-gram resource consumption of grasses, that is, when shrub mass was about 3-8 times that of grass mass (Fig. 5.5). In fact, based on the regressions of target ANPP on neighbour standing crop (Fig. 5.3), shrubs had a 1.4 times larger per-gram effect than grasses on target growth forms, or, 1.4 times more grass mass than shrub mass is needed to reduce target ANPP by one unit, at which point the grass-shrub interaction would be symmetric.

What is the contribution of grass to the exclusion of woody species from prairies? The responses of resources to growth-form removal suggest that, of the three most likely to be competed for by grasses and shrubs, N was in much higher demand in prairie than either water or light (Fig. 5.4). Thus, the ability to compete for N should be an important determinant of success in my system. Grasses had very high N uptake per gram of mass, relative to shrubs (Fig. 5.5), because of their high root:shoot ratios and absence of woody tissues. Thus, at equal masses, and especially in the case of young woody plants establishing among grasses, grasses may be superior competitors. The situation changes, however, as shrub mass increases. In prairie undergoing invasion, where shrub mass is six times that of grass (Fig. 5.1c), competition between

the growth forms is symmetric. In established brush where shrub mass is 37 times that of grass (Fig. 5.1d), competition is asymmetric because of the large mass of shrubs relative to grasses. Shrubs grow taller and shift competition from soil resources to light (King 1990, Wilson 1993a,b). This is similar to the shifts in interaction between trees and grasses in a subtropical savanna where oak seedlings initially escape root competition by grasses, then compete for water, and finally escape root competition as the oak roots extend beyond the grass rooting layer (Weltzin & McPherson 1997).

Shrub invasion can be described as a positive feedback loop (Wilson 1998). Individual shrubs that have become established in prairie have a small effect on resources because they are low and cannot preempt light and because they have small standing crop so that they acquire little N. Prairie grasses may be adapted to N limitation, but when the shrubs have grown tall enough to shade the grasses the reduction of light may severely reduce grass production (Wilson 1993a,b, Li & Wilson 1998). The effect of shrub shading may particularly affect C₄ grasses which tend to have a higher light compensation point than shrubs (Larcher 1984). The effect of grasses on shrub production appears to decrease as the shrubs grow denser. Once woody species have emerged from the grass canopy, their growth rate increases dramatically (Hill et al. 1995). In dense brush, grasses no longer have any effect on shrub production (Fig. 5.1; Li & 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, wild fires, 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, chapter 2).