INTERSPECIFIC COMPETITION AND RESOURCE PULSE UTILIZATION IN A COLD DESERT COMMUNITY

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Abstract. In desert ecosystems a large proportion of water and nitrogen is supplied in rain-induced pulses. It has been suggested that competitive interactions among desert plants would be most intense during these pulse periods of high resource availability. We tested this hypothesis with three cold desert shrub species of the Colorado Plateau (*Gutierrezia sarothrae*, *Atriplex confertifolia*, and *Chrysothamnus nauseosus*), which differ in their distribution of functional roots. In a three-year field study we conducted a neighbor removal experiment in conjunction with simulated 25-mm precipitation events and the addition of a nitrogen pulse in either spring or summer. We measured predawn water potential (Ψ), gas exchange, leaf $\delta^{15}N$, carbon isotope discrimination (Δ), and growth of target plants for the duration of the study. We found that *G. sarothrae* used resource pulses to a larger extent than *A. confertifolia*, which has more functional roots at depth. In all species, the addition of a water or nitrogen pulse did not significantly affect maximal rates of photosynthesis or branch growth. Contrary to our initial hypothesis, we did not find that pulse use was reduced by the presence of neighboring plants. Nevertheless, there was strong evidence for competitive interactions, which were more likely mediated by water at depth than by nitrogen. In the more deep-rooted species *A. confertifolia*, neighbor removal affected Ψ, gas exchange, Δ, percentage of carbon, and growth. *G. sarothrae*, which has a much smaller proportion of roots at depth, was less affected by the removal of neighboring shrubs, and not at all when only predominantly shallow-rooted herbaceous species were removed.

These results suggest that shrubs in this cold desert community may primarily compete for water in deeper soil layers, where water depletion is slow and dominated by plant water uptake. There appeared to be little competition for water in shallow soil layers, where depletion is fast and dominated by evaporation.

Key words: Atriplex confertifolia; Chrysothamnus nauseosus; Colorado Plateau; desert; Gutierrezia sarothrae; neighbor removal; plant competition; resource pulses; stable isotopes; water uptake.

INTRODUCTION

Whether or not competition for belowground resources occurs in arid land ecosystems, and the extent to which it affects the structure and dynamics of desert communities are topics of a continuing debate (Shreve 1942, Fonteyn and Mahall 1981, Fowler 1986, Casper and Jackson 1997, Goldberg and Novoplansky 1997). Shreve (1942) was the first to suggest that desert plants may not compete because stressful physical conditions would result in plant densities too low to interfere with the soil resources of their neighbors. More recently, some experimental studies involving plant neighborhood analysis and neighbor removal experiments demonstrated that interspecific competition, particularly for water, frequently occurs in desert communities (Fonteyn and Mahall 1981, Ehleringer 1984, Fowler 1986, Casper and Jackson 1997, but see Sala et al. 1989). In light of conflicting experimental results, a useful approach might be

to ask when and under what circumstances desert plants compete for belowground resources.

In arid land ecosystems, resource supply typically occurs in pulses after rainstorm events such that plants experience brief periods of relatively high resource availability followed by possibly long interpulse periods with low resource supply and high stress conditions (Noy-Meir 1973, Schimel and Parton 1986, Gallardo and Schlesinger 1992). As resource supply fluctuates, one can expect that competitive interactions among species also vary. Goldberg and Novoplansky (1997) developed a theoretical framework that incorporates the resource dynamics of pulse-driven systems into the predictions of competitive interactions among species. They suggest that belowground resource competition is most intense during pulse periods, and therefore, that the extent of competitive interactions is a function of pulse frequency. If interpulse periods are long, plant growth and survival are more likely to be dependent on the plant's ability to survive stressful conditions than on their competitive ability (Goldberg and Novoplansky 1997).

In this study, we examined the competitive interaction among species of a cold desert shrub community

in relation to the pulsed supply of soil resources. In this ecosystem, pulses of water and nitrogen occur predominantly in shallow soil layers, while soil moisture availability at depth is less dynamic and only changes seasonally (Caldwell 1985, Smith et al. 1997). Many desert shrubs develop root systems with roots in the surface layer and at depth to use both water sources (Jackson et al. 1996). There are, however, large differences in the proportional use of the two water sources and the extent of pulse use (Ehleringer and Dawson 1992, Lin et al. 1996, Ehleringer et al. 1997, Gebauer and Ehleringer 2000). We expected that differences in pulse use would affect the extent to which competitive interactions modified the physiological performance and growth of species.

For this experiment, we selected three shrub species with contrasting rooting patterns. Our hypothesis was that among the three species, *Gutierrezia sarothrae*, which has the largest proportion of roots in the surface layers, would be most affected by the application of water pulses and/or the removal of shallow-rooted neighbors, while neighbor removal would have no effect on the water status and growth of the deepest rooted species, *Chrysothamnus nauseosus*. For *Atriplex confertifolia*, which has a water-use pattern intermediate between *G. sarothrae* and *C. nauseosus*, we expected a smaller response to a water pulse and neighbor removal than for *G. sarothrae*. We expected, however, that all three species would use nitrogen pulses in the shallow soil, since nitrogen is most concentrated near the soil surface and declines exponentially with depth (Charley 1975, Evans and Ehleringer 1994). By comparing the effect of water and nitrogen pulses and their interactions with neighbor removal on plant physiological performance and growth, we expected to gain insight into the relative importance of water vs. nitrogen limitations, and the extent and timing of competitive interactions.

Study Area and Methods

Study area and target species

This study was conducted in the Needles District of Canyonlands National Park in southern Utah, USA (38°19′ N, 109°78′ W, elevation 1460 m). The climate in the area is characterized by cold winters (mean temperature in January is −2.3°C) and hot summers (mean temperature in July is 25.6°C). Annual precipitation averages 215 mm, but shows high year-to-year variability (Ehleringer 1994). The area has a rainy season in winter and summer, with 36% of the annual precipitation occurring during the monsoon summer months (June–September). During the three years of this study, summer precipitation was 68% (1996), 131% (1997), and 86% (1998) of the long-term average (Fig. 1).

Study species were *Chrysothamnus nauseosus*, *Atriplex confertifolia*, and *Gutierrezia sarothrae*. *C. nauseosus* (rubber rabbit brush) is a winter deciduous 1–2 m tall perennial shrub that produces deep root sys-
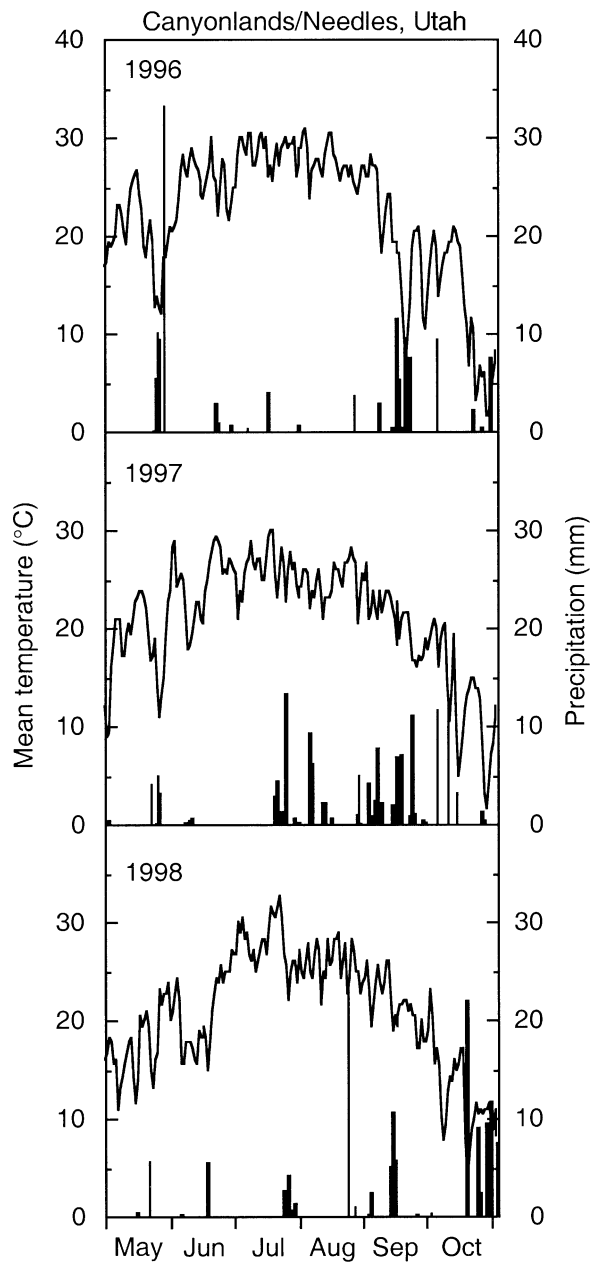

Fig. 1. Mean temperature (line graphs) and daily precipitation (bar graphs) in the summer growing seasons of 1996–1998 at the Needles District of Canyonlands National Park, Utah. The weather station is ~8 km west of the North Six-shooter site and 6 km southeast of the Lower Jump Off site.

tems and predominantly utilizes soil moisture at depth (Donovan and Ehleringer 1994). *A. confertifolia* (shadscale) is an evergreen 0.3–0.8 m tall perennial shrub that makes relatively little use of the soil moisture pulses in the surface layer. *G. sarothrae* (broom snakeweed) is a winter deciduous 0.1–0.7 m tall subshrub that has the largest proportion of its root system composed of shallow, fibrous roots, but that also grows roots at depth (Wan et al. 1993). *C. nauseosus* and *A.*

TABLE 1. Target species, biomass of neighbors removed around target species (mean ± 1 SE), and timing of the water or nitrogen pulse application at the two sites in the study area.

Target species, by site	Neighbors removed (g/m²)		Water pulse	Nitrogen pulse
	Woody perennials	Herbaceous plants		
North Sixshooter (BLM land)				
A. confertifolia	43.9 ± 7.2	19.5 ± 1.8	spring/summer	spring/summer
G. sarothrae	113.6 ± 18.1	12.9 ± 2.4	spring/summer	spring/summer
Lower Jump Off (NPS land)				
G. sarothrae	...	15.6 ± 2.8	...	spring/summer
C. nauseosus	13.25 ± 3.0	4.3 ± 1.2	...	spring/summer

Note: BLM, Bureau of Land Management; NPS, National Park Service.

confertifolia are able to grow in saline soils (Sandquist and Ehleringer 1995). *G. sarothrae* and *C. nauseosus* have C_3 photosynthesis, while *A. confertifolia* has C_4 photosynthesis.

Two study sites were chosen ~15 km apart. The North Sixshooter (NSS) site was located on Bureau of Land Management land, which was occasionally used for cattle grazing during winter months. The Lower Jump Off (LJO) site was located within the Canyonlands National Park, and cattle grazing had not occurred there since the establishment of the park in 1962. The main effect of grazing on ecosystem function is the reduction of the cryptobiotic crust cover, which diminishes the primary source of N input into these ecosystems (Evans and Belnap 1999). At the NSS site we studied *A. confertifolia* and *G. sarothrae* (Table 1). The general vegetation at the NSS site included the shrubs *Coleogyne ramosissima*, *Atriplex confertifolia*, *Gutierrezia sarothrae*, and *Ephedra torreana*, and the perennial grass species *Hilaria jamesii* and *Oryzopsis hymenoides*. At the LJO site, we studied *C. nauseosus* and *G. sarothrae* (Table 1). *C. nauseosus* plants grew together with *Sarcobatus vermiculatus*, *Atriplex confertifolia*, and *Hilaria jamesii*. The vegetation associated with *G. sarothrae* was a mixture including *Juniperus osteospermum*, *Coleogyne ramosissima*, *Oryzopsis hymenoides*, and *Hilaria jamesii*. The soils at both sites consisted of fine, sandy loams, moderately calcareous, with little horizon development. Soils in the *A. confertifolia* stand at the NSS site and *C. nauseosus* stand at the LJO site were more saline than the soils of both *G. sarothrae* stands.

Functional root distribution of target species

To determine the functional root distribution of each of the target species at the study sites, we measured the hydrogen-stable isotopes in stem water to determine the proportional use of shallow and deeper water sources. Stem water was extracted from fully suberized branches taken randomly from 4 to 6 shrub canopies at regular intervals throughout the 1997 growing season. In addition, we determined the extent and the dynamics of pulse utilization of *A. confertifolia* and *G. sarothrae* in spring and summer 1997 by simulating a

25-mm precipitation event with water isotopically enriched to a δD value of ~200‰. The water was applied above each plant with a sprinkler system at a rate slow enough to avoid run-off, similar to the method described in Lin et al. (1996) and Gebauer and Ehleringer (2000). Pulse utilization was determined by collecting stem samples in regular intervals until 7 d after the precipitation event, and determining the δD of the xylem water. Immediately upon collection, all stem samples were placed in sealed glass vials wrapped in parafilm and kept frozen until the extraction of xylem water by cryogenic vacuum distillation from stem samples (Ehleringer and Osmond 1989). For the hydrogen isotope analysis, ~2 μl of the extracted water was reduced with Hayes zinc to hydrogen gas in an evacuated Pyrex tube at 500°C (modified from Coleman et al. 1982). Hydrogen gases were analyzed with an isotope ratio mass spectrometer (see section *Measurement of plant responses*). The proportion of enriched irrigation water taken up by the plant was calculated using a linear mixing model (Dawson and Ehleringer 1993).

Treatments

Treatments included the removal of neighbors, a summer or spring water pulse, and a summer or spring nitrogen pulse (Table 1). We chose similarly sized target plants within an area of ~0.5 ha in spring 1996. The basal canopy radius from the center of the plant was 0.14 m, 0.25 m, and 0.75 m for *G. sarothrae*, *A. confertifolia*, and *C. nauseosus*, respectively. Because of size differences among the different target species, we adjusted the circular plot size for the treatment application to a radius of 1.0 m, 1.5 m, and 2.0 m around the center of the target plants of *G. sarothrae*, *A. confertifolia*, and *C. nauseosus*, respectively. Plots originally contained 3–20 woody perennials and 30–180 perennial or annual grass tillers. Neighbors, which can make use of pulses, were removed from half of the randomly selected target plants. At the NSS site and for *C. nauseosus* at the LJO site, neighbors removed comprised all those woody perennials (*Coleogyne ramosissima*, *G. sarothrae*, *A. confertifolia*, and *Ephedra torreana*) and herbaceous plants (*Oryzopsis hymenoides* and *Hilaria jamesii*) that have functional roots in the surface layer (Table 1). For *G. sarothrae* at the

LJO site, we only removed herbaceous plants (Table 1). The selection of plant species that were removed was based on hydrogen isotope ratios in stem water (Ehleringer et al. 1991; J. R. Ehleringer, *unpublished data*). We did not remove *Bromus tectorum* because it is mainly active during the winter months (November–May). Neighbors were removed by manually clipping the aboveground biomass of woody shrubs or by pulling herbaceous perennials within plots. Care was taken to minimize soil disturbance. To estimate the amount of neighboring biomass, we collected the plant material separately for woody and herbaceous perennials, and determined the dry mass of removed aboveground material (Table 1). Any regrowth was regularly removed throughout the three years of the experiment.

Target plants with and without neighbors received resource pulses either in spring (May 1997 and May 1998) or in summer (August 1996, August 1997, and July 1998) (Table 1). At the NSS site, water and N pulses were applied in four different pulse treatment combinations per season: controls receiving no water or N pulse, a treatment receiving a water pulse and no N pulse, a treatment receiving no water pulse and a N pulse, and a treatment receiving both a water and a N pulse. At the LJO site, water pulses were omitted to reduce the disturbance of National Park land, resulting in two pulse treatments per season: a control treatment receiving no N pulse, and a treatment receiving a N pulse (Table 1).

The N pulse was added as a NH_4NO_3 solution sprayed onto the plots. The addition rate was 1 g/m^2 of NH_4NO_3 per pulse, which is within the range of NH_4NO_3 annually mineralized by an intact cryptobiotic crust (West and Skujins 1977, Evans and Belnap 1999). For the water pulse, we simulated a 25-mm precipitation event with sprinklers using nonlabeled well water. The water pulse, which saturated soils to a depth of 20–25 cm, was applied after the N pulse to facilitate the transport of nitrogen into the root zone.

Each treatment combination occurred once per block in a randomized, complete block design, with six blocks each for *C. nauseosus* and *A. confertifolia*, and with nine blocks for *G. sarothrae*, at both sites. As *G. sarothrae* is a relatively small shrub, we randomly chose different subsets of four to six blocks on each sampling date to minimize the impact of destructive measurements. The block arrangement was based on small differences in surface slope and drainage patterns.

Measurement of plant responses

Predawn xylem water potential (Ψ) and maximum photosynthetic and stomatal conductance rates were measured three days after the application of the water or N pulse. In addition, Ψ was measured in the spring and fall throughout the experiment (1996–1998). The Ψ was measured with a Scholander-type pressure chamber (PMS Instruments, Corvallis, Oregon, USA). Maximum photosynthesis and stomatal conductance were measured using a LiCor 6200 portable closed photosynthesis system (LiCor Instruments, Lincoln, Nebraska, USA). All gas exchange measurements were made between 0830 and 1100, when photosynthetic photon flux density (PPFD) was >1500 μmol·m^{-2}·s^{-1} and prior to midday stomatal closure. Leaf temperatures generally ranged between 30° and 35°C. In *G. sarothrae* and *C. nauseosus*, photosynthetic rates and stomatal conductance are presented based on the sum of photosynthetic leaf and stem areas. Projected leaf and/or stem areas were measured using a leaf area meter (LiCor 3100 Area Meter, LiCor Instruments, Lincoln, Nebraska, USA).

In 1997 and 1998, we determined growth nondestructively by measuring the increase in the branch length of terminal twigs. Three twigs per plant were tagged and repeatedly measured throughout the growing season.

Leaves for ^{15}N, ^{13}C, percentage of N and percentage of C analysis were collected at the end of each growing season (1996–1998) from several locations within the canopy and mixed to a single bulk sample. Leaves were dried at 70°C for 48 h and ground with mortar and pestle to a fine powder. Samples of 2 mg were combusted in a Carla Erba elemental analyzer (CE Instruments, Milan, Italy) directly coupled to an isotope ratio mass spectrometer operating in a continuous flow mode (Delta S, Finnigan MAT, San Jose, California, USA). Carbon, nitrogen, and hydrogen isotope ratios are expressed in the δ notation in parts per thousand (‰) as

$$\delta = (R_{sample}/R_{standard} - 1) \times 1000‰$$

where R is the molar ratio of heavy to light isotopes (D/H, ^{15}N/^{14}N, ^{13}C/^{12}C). The standard is Standard Mean Ocean Water (SMOW) for hydrogen, atmospheric air for nitrogen, and Pee Dee Belemnite (PDB) for carbon. Carbon isotope discrimination (Δ) was calculated from leaf carbon isotope ratios using a carbon isotope ratio of −8‰ for atmospheric carbon dioxide (Farquhar and Richards 1984).

Data analysis

Data were analyzed separately for each site, season, and species. A four-way analysis of variance was used to assess the effect of water pulse, nitrogen pulse, presence of neighbors, and blocks on measured plant variables of each species. When the error term was not normally distributed, or the variances were not equal, arcsine or log transformations were used to comply with ANOVA assumptions. For each treatment combination and species the variable means are presented over 4–6 replicates.

RESULTS

Isotopic composition of stem water and pulse use

After the start of summer rains in late July 1997 (Fig. 1), hydrogen isotopes (δD) in stem water became increasingly enriched until October (Fig. 2). This increase was greater in *G. sarothrae* than in *A. confertifolia* or *C. nauseosus*, indicating that *G. sarothrae*
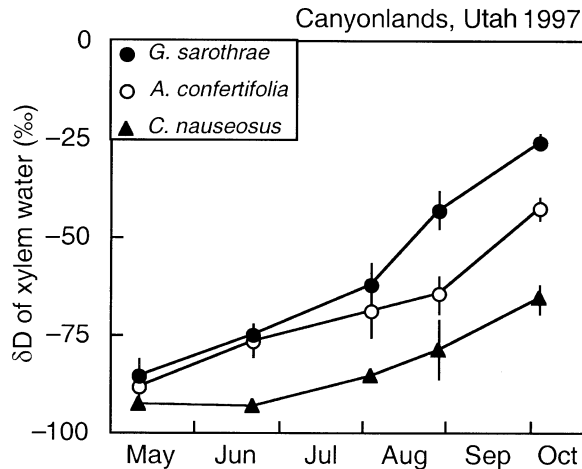
FIG. 2. Seasonal change in δD values of stem water of *G. sarothrae* (solid circles), *A. confertifolia* (open circles), and *C. nauseosus* (solid triangles) growing at the study sites for 1997 (mean ± 1 SE, $n = 5–6$).

had the largest proportion of functional roots in the surface layers. In a separate experiment we determined that in spring, and particularly in summer, pulse water contributed more to the stem water in *G. sarothrae* than in *A. confertifolia* (Fig. 3). During the first five days after watering in the summer, *G. sarothrae* derived 60% of its stem water from the water pulse, while *A. confertifolia* increased the pulse use from <10% in the first three days to 20–28% between day 5 and 7. Predawn xylem water potentials (Ψ) in *A. confertifolia* and *G. sarothrae* increased in response to the water addition only during the summer, and more so in *G. sarothrae* than in *A. confertifolia* (Fig. 4). This improvement in

water status was independent of the presence of neighbors, as the interaction term of the ANOVA was always nonsignificant (Table 2). At the North Sixshooter site (NSS site) Ψ was overall more negative in *A. confertifolia* than in *G. sarothrae*, indicating the presence of salt in the soil (Fig. 4). In the deep-rooting species *C. nauseosus* at the Lower Jump Off site (LJO site), Ψ decreased relatively little during the summer (never below -2.6 MPa) (Fig. 5). By contrast, minimum Ψ in the shallow-rooted species *G. sarothrae* at LJO decreased to less than -6 MPa in 1996 and 1998.

Leaf $\delta^{15}N$ increased by 1‰ to 2.5‰ (measured as parts of ^{15}N per thousand parts of N) in *A. confertifolia* and *G. sarothrae* at both sites when the N pulse was applied during the summer, and in some years when it was applied in spring (Fig. 6). The change in leaf $\delta^{15}N$ was also independent of the presence of neighbors, as the interaction term of the ANOVA was again nonsignificant (Table 2). In *C. nauseosus* we only observed nonsignificant increases in leaf $\delta^{15}N$ values with the application of N pulses. Control plants of *G. sarothrae* had lower leaf $\delta^{15}N$ values than control plants of *A. confertifolia* and *C. nauseosus* (Fig. 6). Leaf $\delta^{15}N$ values in *G. sarothrae* were higher overall at the NSS site (3.05‰) than at the LJO site in the national park (1.81‰).

The summer water pulse resulted in a significant increase in stomatal conductance in *G. sarothrae* in 1996 and 1998 (Fig. 7). Trends in the photosynthetic rates were similar, but nonsignificant. In *A. confertifolia* photosynthesis was only slightly and nonsignificantly lower in plants that received a summer pulse. Nitrogen pulses had no significant effects on leaf gas exchange of any species (data not shown). Neither the water pulses nor the nitrogen pulses affected leaf carbon discrimination (Δ) or percentage of leaf carbon (data not
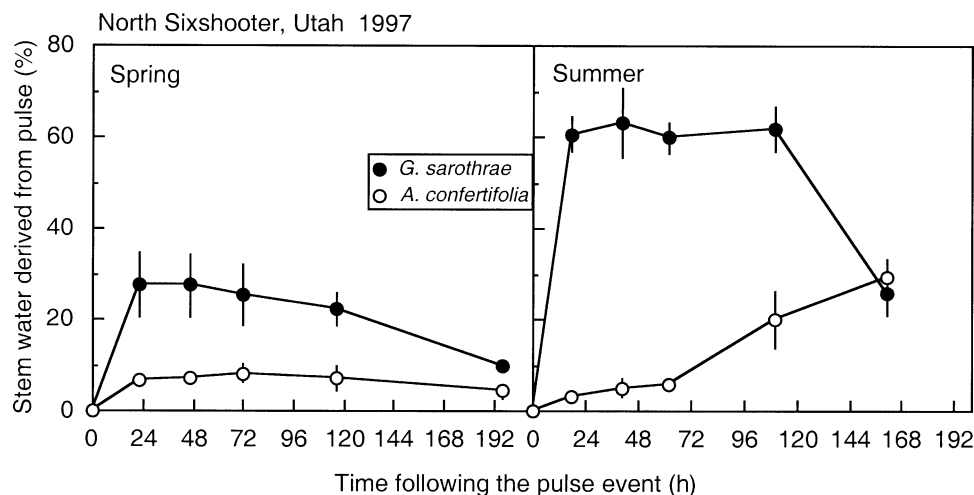

FIG. 3. Comparison of pulse water uptake by *A. confertifolia* (open circles) and *G. sarothrae* (solid circles) (mean ± 1 SE, $n = 4$) following the application of 25 mm of isotopically enriched water ($\delta D = 200‰$). The proportion of enriched irrigation water taken up by the plant was calculated using a linear mixing model (Dawson and Ehleringer 1993). The apparent sudden decline in the pulse water fraction in *G. sarothrae* in summer was due to a natural rain event, which diluted the deuterium label of water near the soil surface and did not reflect an actual decline in pulse water uptake.
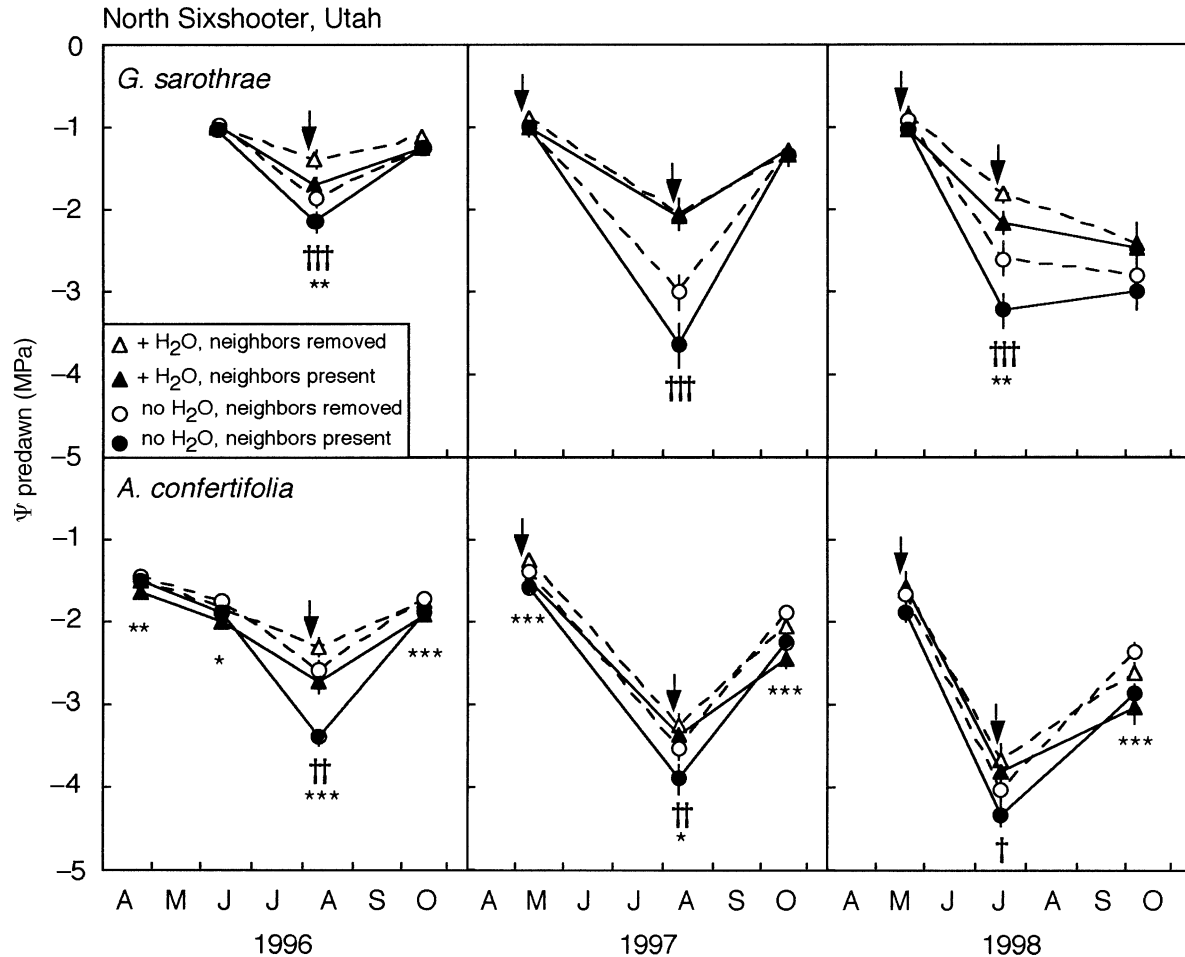
FIG. 4.   Seasonal changes in predawn xylem water potential (mean $\pm$ 1 SE, $n = 4$–5) in response to the application of a 25-mm simulated rain event (triangles) and the removal of neighbors (open symbols) in *A. confertifolia* and *G. sarothrae* at the North Sixshooter site. Arrows indicate the application of the water pulse. Significant results of the ANOVA are indicated for the main effects for water (†) and competition (*) (see also Table 2): * or † indicate $P < 0.05$; ** or †† indicate $P < 0.01$; and *** or ††† indicate $P < 0.001$.

shown). In *A. confertifolia*, the water pulse treatment had a significant effect on growth in 1997 (Fig. 8). Growth was, however, highest in control plants, which did not receive any water pulse.

Competitive interactions

The removal of neighbors significantly increased the Ψ of *A. confertifolia* throughout the first two years of the experiment (1996, 1997) and in fall 1998 (Fig. 4, Table 2). In contrast, the removal of competitors significantly affected Ψ of *G. sarothrae* only during the summers of 1996 and 1998, when plants experienced greater water stress. At the LJO site, the removal of only herbaceous shallow-rooted neighbors did not affect the Ψ of *G. sarothrae* (Fig. 5). The removal of shallow-rooted shrubs and herbaceous neighbors did not affect the deep-rooting species *C. nauseosus*.

The removal of neighbors did affect leaf ^{15}N in the shallow-rooted species *G. sarothrae*, but only at the LJO site in 1997 (Fig. 6), when plants did not experience much water stress during the summer (Fig. 5). In all other instances, leaf ^{15}N was not significantly affected by the removal of neighbors.

In 1996, the removal of neighbors significantly increased stomatal conductance in both *A. confertifolia* and *G. sarothrae* at the NSS site (Fig. 7). Photosynthetic rates followed similar trends, but were significantly increased only for *A. confertifolia* in 1996. At the LJO site, the removal of neighbors affected neither stomatal conductance nor photosynthetic rates of either target species (data not shown).

Leaf carbon discrimination (Δ) and carbon concentrations were only affected by the removal of neighbors in *A. confertifolia*, but not in *C. nauseosus* and *G. sarothrae* (Figs. 9 and 10). In each year of the study, leaf Δ in *A. confertifolia* significantly decreased by >0.5‰,

TABLE 2. ANOVA *F* values indicating, for *A. confertifolia* and *G. sarothrae* at the North Sixshooter site, treatment, and block effects on summer Ψ measurements three days after the application of the pulse, and on leaf $\delta^{15}N$ at the end of the growing season.

|	Ψ			$\delta^{15}N$		
Source	1996	1997	1998	1996	1997	1998
A. confertifolia						
Block	3.01*	11.0***	0.84	0.33	10.1***	4.21
H_2O	7.10**	9.94**	5.42*	1.23	1.10	1.83
Neighbors	20.9***	4.21*	0.71	0.32	0.04	0.08
N	0.42	1.08	0.27	7.49**	36.5***	5.90**
H_2O × Neighbors	1.09	0.12	1.05	0.07	2.20	0.60
H_2O × N	1.60	1.59	0.76	0.02	0.85	1.89
N × Neighbors	0.27	1.04	2.95	0.23	1.00	1.61
H_2O × N × Neighbors	0.82	0.52	0.01	0.01	2.51	1.79
G. sarothrae						
Block	2.94*	0.72	0.58	0.46	1.19	1.32
H_2O	16.1***	19.9***	10.7**	1.21	0.82	2.01
Neighbors	7.31**	2.36	3.29	0.03	1.25	1.70
N	0.92	2.80	0.30	16.5***	15.0***	25.9***
H_2O × Neighbors	0.88	1.23	0.15	1.06	2.30	1.25
H_2O × N	0.16	1.32	0.18	0.04	0.86	0.05
N × Neighbors	1.85	1.53	0.06	0.06	1.16	1.14
H_2O × N × Neighbors	0.76	0.47	0.01	0.05	0.34	0.92

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.
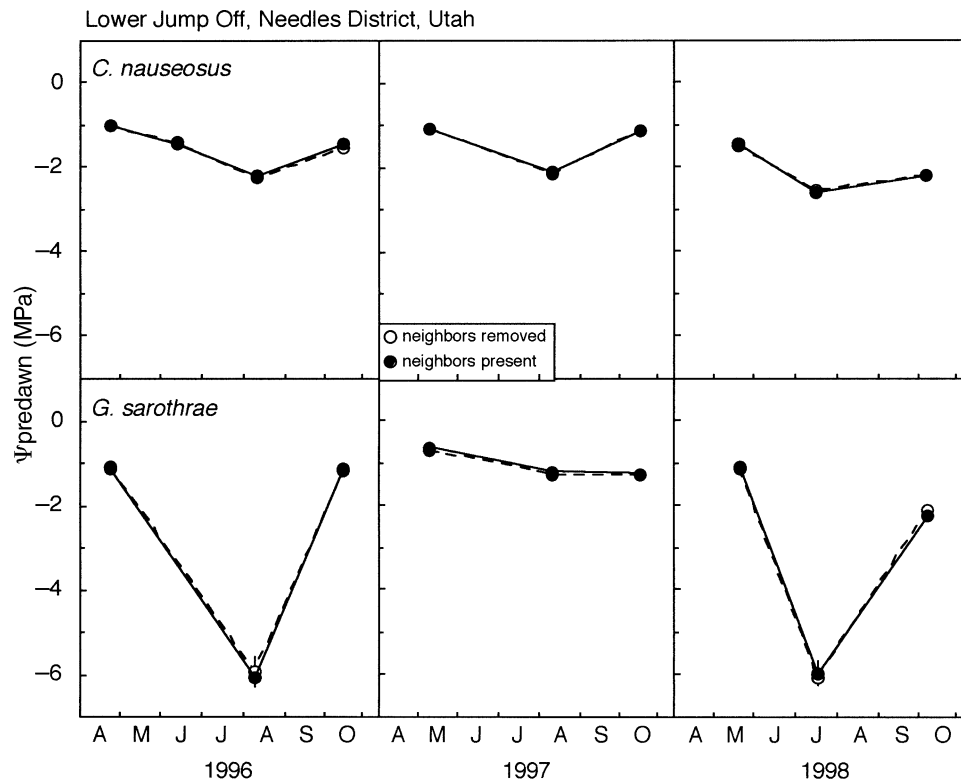
FIG. 5. Changes in predawn xylem water potential (mean ± 1 SE, *n* = 5) in response to the removal of neighbors (open circles and dashed lines) in *C. nauseosus* and *G. sarothrae* at the Lower Jump Off site (lines and symbols nearly overlap). Data for the nitrogen pulse treatments were pooled as the ANOVA indicated a nonsignificant nitrogen effect. The effect of neighbor removal was nonsignificant ($P > 0.05$) throughout the study.
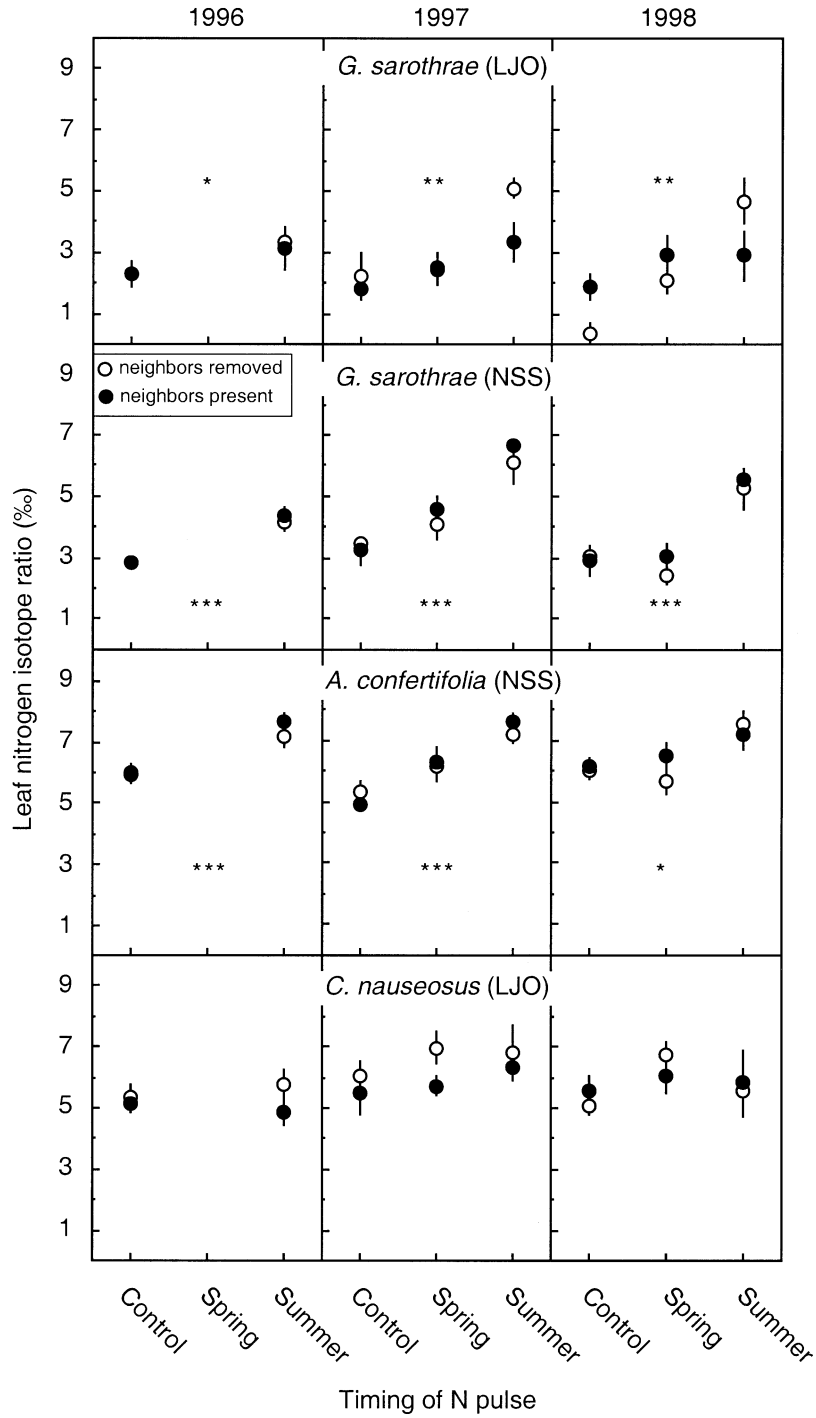
FIG. 6. Changes in leaf $\delta^{15}N$ ratios (mean $\pm$ 1 SE, $n = 4-5$) in response to the application of a nitrogen pulse in spring or summer and the removal of neighbors (open circles) in *A. confertifolia* and *G. sarothrae* at the North Sixshooter site, and *C. nauseosus* and *G. sarothrae* at the Lower Jump Off site. Significant results of the ANOVA are indicated for the main effects for nitrogen (*) (see also Table 2): Data for the water pulse treatments at NSS were pooled, as the ANOVA indicated a nonsignificant effect of water pulse applied in either spring or summer (Table 2).
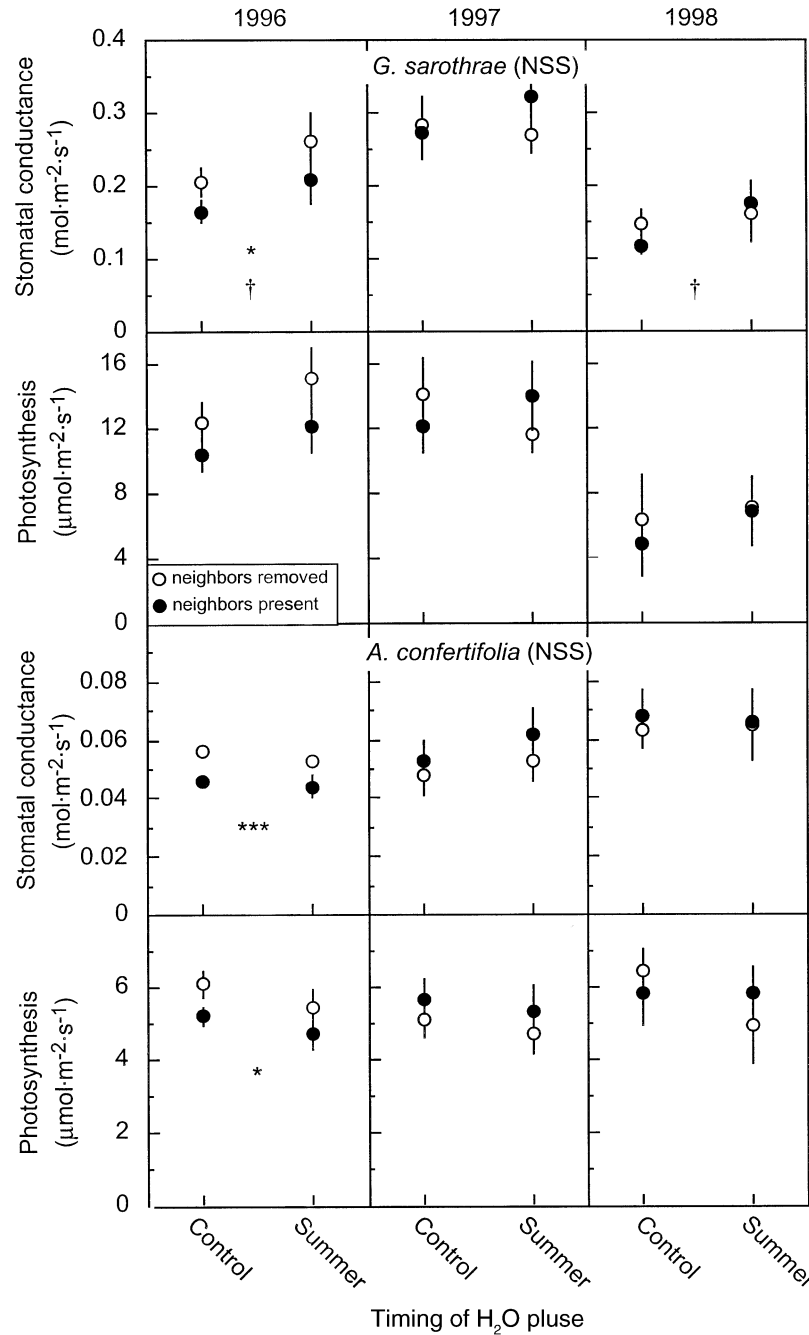
*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

FIG. 7. Changes in stomatal conductance and maximum photosynthetic rates (mean ± 1 SE, $n = 5$) in response to the application of a 25-mm summer water pulse and the removal of neighbors (open circles) in *A. confertifolia* and *G. sarothrae* at the North Sixshooter site. Significant results of the ANOVA are indicated for the main effects for water (†) and competition (*) as the interaction terms were nonsignificant: * or † indicate $P < 0.05$, and *** indicates $P < 0.001$. Data for the nitrogen pulse treatments were pooled, as the ANOVA indicated a nonsignificant nitrogen effect.

and carbon concentrations decreased by >1% when neighbors were removed.

Neighbor removal also significantly increased growth in *A. confertifolia* in 1997 and 1998 (Fig. 8). In *G. sarothrae*, neighbor removal significantly in-

creased growth only in 1998 at the NSS site (Fig. 8), but not in 1997 or at the LJO site, where only shallow-rooted herbaceous plants were removed (Fig. 11). Neighbor removal did not significantly affect growth in *C. nauseosus* (Fig. 11).
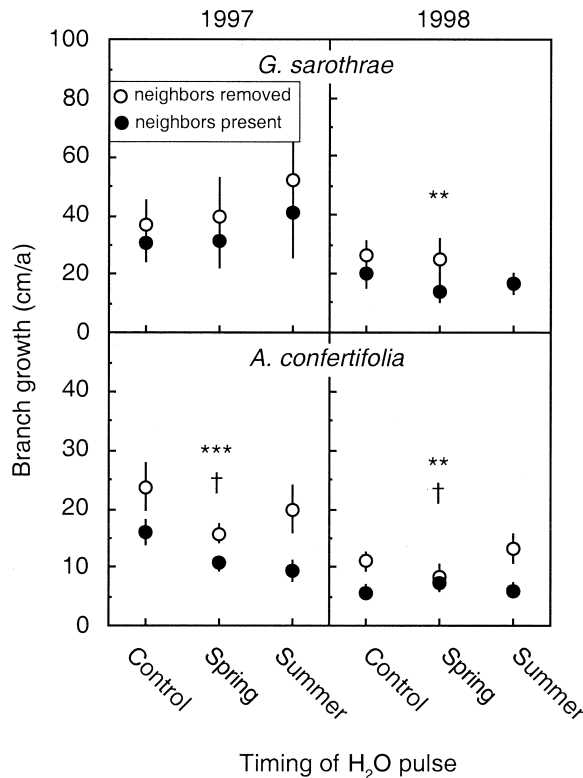
FIG. 8. Changes in the length of tagged branches (mean ± 1 SE) in response to the application (''a'') of a 25-mm water pulse in spring or summer and the removal of neighbors (open circles) in *A. confertifolia* and *G. sarothrae* at the North Sixshooter site. Significant results of the ANOVA are indicated for the main effects for water (†) and competition (*) as the interaction terms were nonsignificant: † indicates $P < 0.05$, ** indicates $P < 0.01$, and *** indicates $P < 0.001$. Data for the nitrogen pulse treatments were pooled, as the ANOVA indicated a nonsignificant nitrogen effect.

DISCUSSION

In Colorado Plateau plant communities, as in many other desert ecosystems, a large proportion of the annual water supply occurs in relatively short pulses during spring and summer rain events (Noy-Meir 1973, Ehleringer et al. 1999). One would therefore expect that plants that strongly rely on these water pulses would also strongly compete for them (Goldberg and Novoplansky 1997). However, our experiments did not support this initial expectation. The presence of neighbors with roots in the surface layers did not significantly interfere with the use of resource pulses even in *G. sarothrae*, a plant which uses pulses to a large extent (Fig. 3). Positive effects of neighbor removal on physiology and growth were only observed when the removed plants included shrubs that also had roots at depth. In addition, competitive effects were more strongly expressed in *A. confertifolia*, which has a larger proportion of functional roots at depth compared to *G. sarothrae*, even though more biomass was removed

from the neighborhoods of *G. sarothrae* plants (Table 1). The deepest-rooted shrub of this study, *C. nauseosus*, was not affected by the removal of neighbors. We conclude that in this Colorado Plateau shrub community, competition for pulsed resources in shallow soil layers is weak or nonexistent, and that competition for stored water in deeper soil layers may be more important in mediating interactions among shrubs.

Pulse use

Like most other shrub species in this desert community, both *A. confertifolia* and *G. sarothrae* have roots present in surface layers and at depth (Ehleringer et al. 1991, Wan et al. 1993, Lee and Lauenroth 1994, Jackson et al. 1996). *G. sarothrae* has, however, proportionally more functional roots in the upper soil layer than *A. confertifolia*, because it showed the largest increase in stem δD after the onset of summer rains (Figs. 1 and 2), which have distinctly higher hydrogen isotope ratios than winter rains (Lin et al. 1996). In addition, *G. sarothrae* made more use of water pulses (Fig. 3) and showed larger seasonal changes in Ψ during the summer months than *A. confertifolia* (Fig. 4). By contrast, *C. nauseosus* derived most water from a deeper soil horizon than either *G. sarothrae* or *A. confertifolia*, where water availability remains more constant throughout the year (Manning and Barbour 1988, Flanagan et al. 1992, Donovan and Ehleringer 1994), explaining the relatively small variation in Ψ throughout the year (Fig. 5).

G. sarothrae and *A. confertifolia* used the water pulse to a larger extent in summer than in spring (Figs. 3 and 4). In spring, soil moisture levels are relatively high throughout the soil profile due to recharge by winter rains (Caldwell 1985), and plants experience relatively little water stress. Since the entire root system has access to soil moisture, water uptake from shallow roots contributes much less to the total amount of water taken up than in summer, when the soil is drier below the shallow soil layer wetted by rain (Gebauer and Ehleringer 2000, Schwinning and Ehleringer 2001).

The differences in the distribution of functional roots between *G. sarothrae*, *A. confertifolia*, and *C. nauseosus* were also indicated by the increasing enrichment in leaf $\delta^{15}N$ in control plants (Fig. 6), as $\delta^{15}N$ in the soil profile typically increases from the surface layers downward (Nadelhoffer and Fry 1994, Högberg 1997). However, other factors can also contribute to a variation in leaf $\delta^{15}N$ (Handley and Raven 1992, Nadelhoffer and Fry 1994, Högberg 1997, Michelsen et al. 1998). We found that *G. sarothrae* at the NSS site had higher leaf $\delta^{15}N$ values (by 1.24‰) at the LJO site (Fig. 6). This enrichment is likely to reflect the disturbance of the microbiotic crust outside the boundaries of the National Park and the associated increased gaseous N losses from the ecosystem (Evans and Belnap 1999).

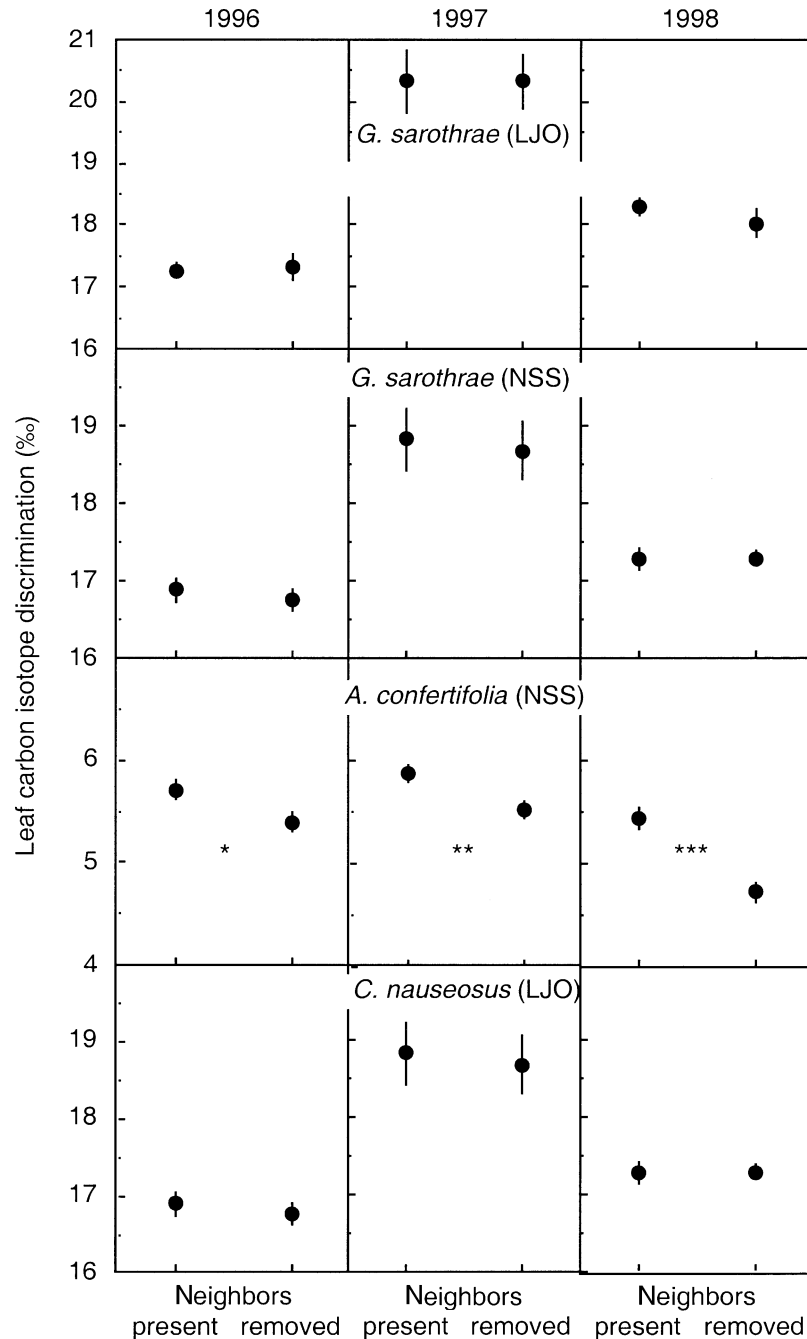We observed that *A. confertifolia* and *G. sarothrae* not only took up water from the summer pulse, but also

FIG. 9. Changes in leaf carbon discrimination (Δ) (mean ± 1 SE) in response to the removal of neighbors in *A. confertifolia* and *G. sarothrae* at the North Sixshooter site, and in *C. nauseosus* and *G. sarothrae* at the Lower Jump Off site. Significant results of the competition effect are indicated. Data for the nitrogen and the water pulse treatments were pooled, as the ANOVA indicated a nonsignificant nitrogen or water pulse effect, respectively.
*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

nitrogen, as leaf $\delta^{15}N$ increased in plants which received an N pulse (Fig. 6). It is important to note that the nitrogen added to the plots was not labeled with ^{15}N, and several mechanisms may explain the apparent ^{15}N enrichment of applied nitrogen. Gaseous N losses by volatilization or denitrification can be substantial in

desert ecosystems (Peterjohn and Schlesinger 1990, Schlesinger and Peterjohn 1991), leading to considerable ^{15}N enrichment (Nadelhoffer and Fry 1994, Högberg 1997). In addition, repeated mineralization and immobilization of nitrogen associated with high microbial turnover could explain a large enrichment in
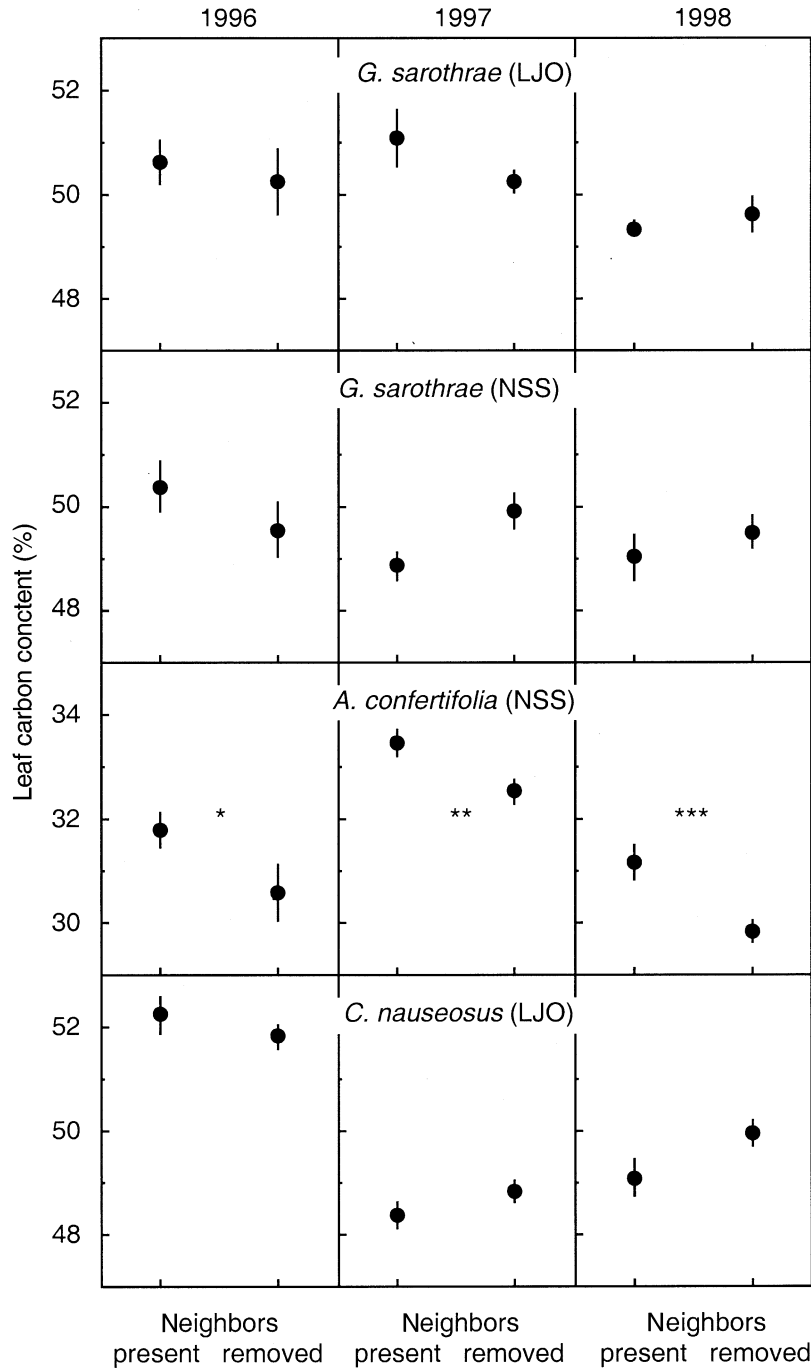
FIG. 10. Changes in leaf carbon concentrations (mean ± 1 SE) in response to the removal of neighbors in *A. confertifolia* and *G. sarothrae* at the North Sixshooter site, and *C. nauseosus* and *G. sarothrae* at the Lower Jump Off site. Significant results of the competition effect are indicated. Data for the nitrogen and the water pulse treatments were pooled, as the ANOVA indicated a nonsignificant nitrogen or water pulse effect, respectively.

*P < 0.05; **P < 0.01; ***P < 0.001.

[15]N (Nadelhoffer and Fry 1994). Because we do not know to what extent the enrichment of added nitrogen by soil processes varied throughout the growing season, it is possible that shrubs may have utilized N pulses also in spring, even though we did not always detect

this as differences in leaf δ^{15}N. A previous N pulse study using $^{15}NH_4^{15}NO_3$ showed that five cold desert shrub species from the Colorado Plateau did utilize N pulses in spring (Gebauer and Ehleringer 2000).

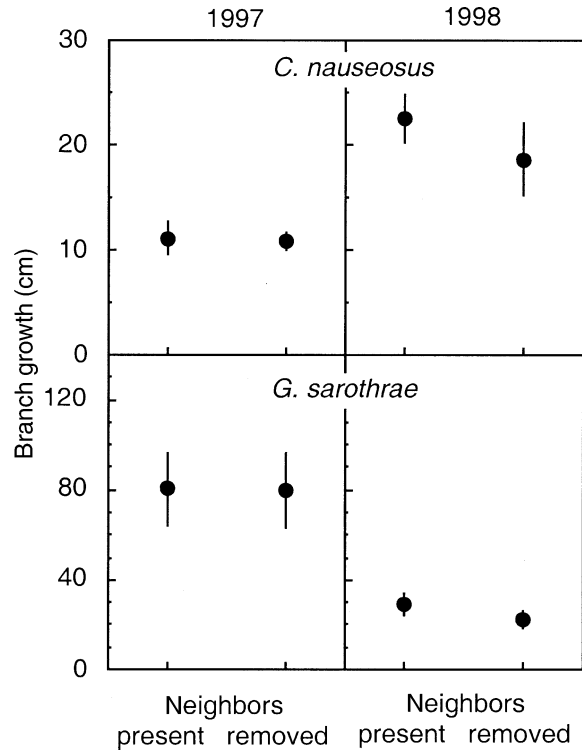We found that significant water or nitrogen pulse

FIG. 11.   Changes in the length of tagged branches (mean ± 1 SE) in response to the removal of neighbors in *G. sarothrae* and *C. nauseosus* at the Lower Jump Off site. Competition effects were nonsignificant throughout the study. Data for the nitrogen pulse treatments were pooled, as the ANOVA indicated a nonsignificant nitrogen effect.

uptake did not necessarily result in significantly increased carbon gain or growth (Figs. 7 and 8). This supports earlier studies showing that rainstorms need to be larger than 25 mm to trigger significant increases in photosynthesis and growth in many desert plants (Beatley 1974, Ehleringer et al. 1999). On the Colorado Plateau, however, fewer than 8% of the annual rainstorm events are >25 mm (Ehleringer et al. 1999).

Competitive interactions

The neighbor removal experiment showed that shrubs did not compete for resource pulses. In both *A. confertifolia* and *G. sarothrae*, the extent of pulse use was not affected by neighboring shrubs, as the interactions between resource pulse addition and neighbor removal were always nonsignificant (Table 2). There is, however, strong evidence for competitive interactions among shrubs of this desert community, and it appears more likely that shrubs compete for water than for nitrogen. In *A. confertifolia*, throughout the growing season, Ψ was generally higher in shrubs where neighbors were removed (Fig. 4), which resulted in an increase in stomatal conductance and photosynthetic rates during the summer of 1996 (Fig. 7). By contrast, leaf $\delta^{15}N$ were generally not affected by the removal

of neighbors (Fig. 6), and nitrogen addition did not affect photosynthesis or growth. Furthermore, throughout the experiment, leaf carbon isotope discrimination (Δ) in *A. confertifolia* was increased when neighboring shrubs were present (Fig. 9). This is consistent with studies showing that Δ values in C_4 plants often increase with greater environmental stress (Bowman et al. 1989, Sandquist and Ehleringer 1995) due to an increase in the CO_2 leakiness of the bundle sheath (Farquhar 1989). This in turn, is associated with greater energetic costs to the plants (Ehleringer and Pearcy 1983). We observed that in 1996 and 1997 growth in *A. confertifolia* was significantly lower in plants when neighbors were present. Growth dilution in *A. confertifolia* without neighbors may account for decreases in leaf carbon concentrations (Fig. 10).

In contrast to our initial hypothesis, response to neighbor removal was overall less strong in *G. sarothrae* than in *A. confertifolia*, although in proportion to the treatment area, more biomass was removed from around *G. sarothrae* plants at the NSS site (Table 1). In addition, independent of the extent of water stress during a particular year, we found responses to neighbor removal only at the NSS site, where we had removed shrubs and herbaceous species around *G. sarothrae* plants. In contrast, at the LJO site, the removal of only predominantly shallow-rooted herbaceous species did not affect any of the measured response variables. Thus, it appears that the removal of functional roots at depth was responsible for relieving competitive pressure, and not the presence of functional shallow roots.

Overall, *O. nauseosus* was not affected by the removal of neighbors, indicating that this species may avoid competition for water, because roots penetrate below the rooting depth of other shrub species. Manning and Barbour (1988) also found that the removal of neighboring shrubs did not affect Ψ in *C. teretifolius*.

Our result that competitive interactions among plants in desert communities may primarily occur at depth rather than in the surface layers is supported by other competition studies (Kadmon and Shmida 1989, Reichenberger and Pyke 1990, Briones et al. 1998). For example, Reichenberger and Pyke (1990) used root exclusion experiments to assess root competitive interactions among different desert grass species. They found that in perennial grass species, seedling growth and survival increased significantly with greater depth of root exclusion. Further evidence also comes from a study on a desert grass species (*Stipa capensis*) in which the size of the simulated rainstorms was manipulated in combination with a neighbor removal experiment (Kadmon and Shmida 1989). The study showed that competition intensity among plants significantly increased with larger simulated rainstorms (80 mm vs. 30 mm), presumably because more water penetrated deeper into the soil profile.

A spatiotemporal perspective on competition in arid land

Noy-Meir (1973) pointed out that in desert ecosystems, the dynamics of soil water availability is closely linked to location within the soil horizon. In the shallow soil horizon, water availability is dependent on short-term recharge and depletion. The occurrence of resource pulses, which last hours to days, is restricted to shallow soil layers (Sala et al. 1989). In deeper soil layers, the dynamics of water availability is governed more by longer term processes, such as seasonal rainfall patterns and seasonal fluctuation in plant activities (Schlesinger et al. 1987, Reynolds et al. 1999). Only a series of rain events or rainstorms during cooler seasons can infiltrate into deeper soil horizons. Another critical difference between soil layers is that water in the shallow soil is depleted by plant water uptake and soil surface evaporation, while water at greater depth is almost entirely depleted by plant uptake (Sala et al. 1981, Schlesinger et al. 1987). Goldberg and Novoplansky (1997) argued that the strength of competition depends strongly on the degree to which plants govern rates of resource depletion relative to physical processes. The dynamics of water availability in shallow soil layers is governed by physical processes and not by plant uptake, while at depth, plant water uptake dominates soil water depletion. Therefore, one would predict that competition for deeper soil water dominates plant interactions in desert ecosystems (Cohen 1970). This is what we found in our experiments. Thus, contrary to Goldberg and Novoplansky (1997), we suggest that competition for pulsed resources is relatively unimportant for structuring sparsely vegetated desert communities, unless water pulses are large enough to penetrate into deeper soil layers.

Our results have important implications for how desert communities may respond to predicted changes in precipitation patterns. Predicted early climate-change events include an increase in the variance of summer monsoon and winter precipitation, and the frequency of extreme precipitation events. Our results suggest that the competitive balance of desert communities will be affected more by changes in winter precipitation than in summer precipitation, corresponding to the difference in the depth of recharge. Evidence for this prediction comes from a study in southeastern Arizona, which found that the expansion of woody perennials can be explained by unusually wet winters, and not by variation in summer rainfall (Brown et al. 1997).

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