

## WATER AND NITROGEN UPTAKE PATTERNS FOLLOWING MOISTURE PULSES IN A COLD DESERT COMMUNITY

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**Abstract.** Variation in the ability to utilize pulses of both water and nitrogen (N) is one possible mechanism allowing the coexistence of species in the cold desert community on the Colorado Plateau. We simulated 25-mm precipitation events and used stable isotope tracers (<sup>2</sup>H and <sup>15</sup>N) to follow water and N uptake patterns in six dominant perennials (*Artemisia filifolia*, *Coleogyne ramosissima*, *Cryptantha flava*, *Ephedra viridis*, *Quercus havardii*, and *Vancoveria stylosa*) at different times of the growing season. Water pulse utilization varied on a seasonal basis and was to some extent different among species during the summer. Carbon isotope discrimination was negatively related to both plant use of moisture in upper soil layers and foliar N concentration. Species that were similar in water pulse utilization patterns differed in the natural abundances of <sup>15</sup>N, suggesting partitioning in N sources. All species were able to utilize N pulses after rain events, but there were temporal differences in the responses among species. We also found that water and N uptake in shallow roots do not necessarily occur simultaneously. *Artemisia*, *Cryptantha*, and *Quercus* showed significant uptake of both water and N from the upper soil layers. In contrast, *Coleogyne* and *Ephedra* showed the capacity to utilize the water pulse, but not the N pulse. *Vancoveria* only took up N. The results indicate that different parts of the root system may be responsible for the acquisition of water and N. Our results also suggest that N and water partitioning could contribute to the coexistence of species in highly variable environments such as the Colorado Plateau desert system.

**Key words:** Colorado Plateau (USA); desert perennials; nitrogen uptake patterns; pulse utilization; resource partitioning; stable isotopes; water uptake patterns.

### INTRODUCTION

In arid and semiarid ecosystems, soil resources are typically available for plant uptake only during pulses following precipitation. Nitrogen mineralization and nutrient movement to the root surface are high when soil moisture levels increase following precipitation events (Noy-Meir 1973, Schimel and Parton 1986, Gallardo and Schlesinger 1992, Cui and Caldwell 1997). High soil resource availability is restricted to infrequent pulse events and plants may be forced to share the same resources, resulting in strong competitive interactions. The ability to rapidly capture water and nutrients may influence competitive relationships or the accumulation of sufficient resources for survival during long periods of low resource availability (Goldberg and Novoplansky 1997). On the other hand, competitive interactions among desert species could be reduced if soil resources were partitioned in time, space, or form (e.g., nitrate vs. ammonium) (Bratton 1976, Fitter 1986, McKane et al. 1990, Reynolds et al. 1997).

Belowground resources in arid lands not only change greatly during short-term pulses after rain events, but can be very heterogeneous in both time and space on

larger scales (Caldwell 1994, Ehleringer 1994, Schlesinger et al. 1996, Ryel et al. 1996). For example, plants growing on the Colorado Plateau can experience high year-to-year variability in precipitation (Ehleringer 1994). Precipitation is divided between winter and summer storms (Houghton 1979), with winter precipitation recharging much of the soil profile. As the summer season progresses, most of the soil profile dries, but rain storms increase soil moisture in the upper soil layers for a short time (Kemp et al. 1997; R. Gebauer, unpublished data). As a result, a disjunct soil moisture distribution is often found during the summer, with high soil moisture availability in shallow and deep layers, separated by a drier soil layer. Most Colorado Plateau plant species are dormant during cold winter months and make little immediate use of increased soil moisture availability. Succulents and a few herbaceous species rely entirely on the acquisition of surface soil moisture derived from summer rain events (Ehleringer et al. 1991). Perennial shrubs often develop a dimorphic root system, where deeper roots tap a more reliable water source at depth (Ehleringer and Dawson 1992, Lin et al. 1996). Therefore, water is to some extent partitioned spatially among different lifeforms and competitive interactions may be reduced (Sala et al. 1989, Casper and Jackson 1997, Ehleringer et al. 1997). Among species of the same life form, the zones of water

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TABLE 1. Characteristics of cold desert community species in the Colorado Plateau of southern Utah.

Species	Growth form	Leaf longevity	Flowering
<i>Coleogyne ramosissima</i>	shrub	drought deciduous	April–August
<i>Artemisia filifolia</i>	shrub	winter deciduous	August–October
<i>Quercus havardii</i>	shrub	winter deciduous	April–June
<i>Ephedra viridis</i>	shrub	evergreen†	July–August
<i>Vancleavea stylosa</i>	shrub	winter deciduous	July–August
<i>Cryptantha flava</i>	perennial forb	evergreen	May–July

† Carbon gain in photosynthetic stems.

uptake generally show greater overlap (Rundel and Nobel 1991, Ehleringer and Dawson 1992). It has been argued that spatial differences in water uptake patterns alone may be insufficient to allow the stable coexistence of a large number of species of the same life form (Scholes and Archer 1997).

After water availability, nitrogen (N) is the most important factor limiting productivity in arid land ecosystems (Noy-Meir 1973, Fisher et al. 1987, Gutierrez and Whitford 1987). In contrast to soil moisture with a bimodal distribution after summer rain events, N availability is highest in the upper soil layers and declines strongly with depth (Charley 1975, Evans and Ehleringer 1994, Stark 1994). One may expect that the largest fraction of N required by desert plants is taken up by roots growing in the shallow soil layers following pulse events. Relatively little is known, however, about the short-term N uptake patterns of different desert species. Great Basin desert species were generally capable of utilizing the N pulse in spring (Bilbrough and Caldwell 1997). A reduction in competitive interactions among species might then be achieved by either temporal differences in N uptake activity of surface roots or by utilizing different forms of N (Fitter 1986, McKane et al. 1990, Nadelhoffer et al. 1996). In grassland systems, when N uptake was compared between spring, summer, and fall, species showed temporal differences in N acquisition (McKane et al. 1990).

In this study, we compared the in situ ability of six dominant species (five woody shrubs, one herbaceous perennial) of a cold desert community on the Colorado Plateau to utilize water and N pulses during different times of the growing season. In May, July, and September, we simulated 25-mm rain events and used stable isotope tracers ( $^2\text{H}$  and  $^{15}\text{N}$ ) to follow water and N uptake patterns. We asked whether niche separation among species of this cold desert community would become more distinct when N utilization patterns were considered in addition to the utilization of different water sources. We also examined whether species which depend more heavily on rain events have higher water use efficiencies to compensate for exposure to long, dry periods between rain pulses.

#### MATERIALS AND METHODS

The study site was located in Arches National Park in southern Utah (38°46' N, 110°07' W, elevation 1585

m). The cold desert vegetation at the study site was dominated by perennial shrubs including *Coleogyne ramosissima*, *Ephedra viridis*, *Artemisia filifolia*, *Vancleavea stylosa*, and *Quercus havardii*. Soils consisted of alluvial sands and no caliche layer was observed to a depth of 1 m.

Long-term precipitation records from nearby Moab, Utah show a mean annual precipitation of 220 mm. Precipitation is bimodal, with 32% of the precipitation occurring during the summer months (June–September). Summer precipitation during the two years of this study was 71% (1996) and 178% (1997) of the long-term means.

The experiments were conducted in July 1996 and May, July, and September 1997 on five dominant perennial shrub species (*Quercus havardii* Rydb., *Ephedra viridis* Cov., *Artemisia filifolia* Torr., *Coleogyne ramosissima* Torr., and *Vancleavea stylosa* (Eastw.) Greene) and the most dominant herbaceous perennial species (*Cryptantha flava* (A. Nels.) Payson) (Table 1). The treatments were applied on 1 and 2 July, 1996, 17 and 18 May, 17 and 18 July, and 17 and 18 September, 1997. Three different treatments were randomly assigned to six replicates per species: a control treatment receiving no supplemental precipitation and no addition of  $^{15}\text{N}$ , a treatment receiving a 25-mm precipitation event and no addition of  $^{15}\text{N}$ , and a treatment receiving a 25-mm precipitation event and the addition of  $^{15}\text{N}$ . For the  $^{15}\text{N}$  treatment, 1.5 L of 0.264 mol/mL  $^{15}\text{NH}_4^{15}\text{NO}_3$  (10% enriched) was homogeneously added by spraying the solution onto the soil surface within a radius of 1.5 m surrounding the main stem of the perennial shrubs. Because *Cryptantha flava* is considerably smaller than the perennial shrubs, the  $^{15}\text{N}$  label was only added to a radius of 0.5 m (but with the same amount of label per unit area). The addition rate of the  $^{15}\text{N}$  tracer was sufficiently low to avoid N fertilization of plants. However, as an additional caution a nonenriched  $^{14}\text{NH}_4^{14}\text{NO}_3$  solution was added to control plants and plants receiving only a 25-mm precipitation event. After N was added to the soil surface, plants received the 25-mm precipitation event in a manner similar to that described in Lin et al. (1996). Local well water was isotopically enriched with heavy water ( $\text{D}_2\text{O}$ ) to reach a  $\delta\text{D}$  value of  $\sim 0\text{‰}$  in 1996 and  $\sim +200\text{‰}$  in 1997. The precipitation was applied above each plant

with a sprinkler system at a rate slow enough to avoid run off.

Leaves for  $^{15}\text{N}$  analysis were sampled one day before and several times after the application of the  $^{15}\text{N}$  tracer. Leaves were collected from several locations within the canopy and mixed to a single bulk sample for stable isotope analysis. Leaves were dried at  $75^\circ\text{C}$  for 48 h and ground with mortar and pestle to a fine powder. For the  $^{15}\text{N}$ ,  $^{13}\text{C}$ , and N concentration analyses, 2-mg samples were combusted on an elemental analyzer linked in line with an isotope ratio mass spectrometer (model delta S, Finnigan MAT, San Jose, California, USA). For determination of water source and surface root uptake, woody stem samples (5–7 cm long) were collected from different branches within the shrub canopy removed as far as possible from transpiring leaves. For the herbaceous perennial, *Cryptantha flava*, samples of the main root were collected. Samples were collected one day before, and three and five days after the watering treatment. Immediately upon collection, stem samples were placed in sealed glass vials wrapped in parafilm. Samples were kept frozen until the extraction of xylem water by cryogenic vacuum distillation from stem samples (Ehleringer and Osmond 1989). For the hydrogen isotope analysis  $\sim 2 \mu\text{L}$  of the extracted water was reduced with Hayes zinc to hydrogen gas in an evacuated Pyrex tube at  $500^\circ\text{C}$  (modified from Coleman et al. 1982). Hydrogen gases were analyzed with an isotope ratio mass spectrometer.

Hydrogen, carbon, and nitrogen isotope ratios are expressed in  $\delta$  notation in parts per thousand (‰) as:

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

where R is the molar ratio of heavy to light isotopes (D/H,  $^{15}\text{N}/^{14}\text{N}$ ,  $^{13}\text{C}/^{12}\text{C}$ ). The standard is Standard Mean Ocean Water (SMOW) for hydrogen, atmospheric air for nitrogen, and PDB for carbon. Carbon isotope discrimination ( $\Delta$ ) was calculated from leaf carbon isotope ratios using a carbon isotope ratio of  $-8\text{‰}$  for atmospheric carbon dioxide (Farquhar and Richards 1984).  $\Delta$  values provide a long-term estimate of the ratio of intercellular to ambient  $\text{CO}_2$  concentrations ( $C_i/C_a$ ) which in turn can be related to water use efficiency ( $A/g$ ), where A refers to assimilation and g refers to stomatal conductance (Farquhar et al. 1982). The proportion of enriched irrigation water taken up by the plant was calculated using a linear mixing model (Dawson and Ehleringer 1993). In September 1997, there were heavy rainfall events after watering the plants. Based on deuterium ratios of the upper soil layer in the soil profile 10 d after the treatment, we determined the dilution of irrigation water by rain to adjust the  $\delta\text{D}$  value of source water of surface roots. Differences in plant biomass and N pool size and microbial immobilization can affect the extent of  $^{15}\text{N}$  enrichment in leaves (Nadelhoffer and Fry 1994, Buchmann et al. 1995). Because shrubs could not be harvested we determined the occurrence of N uptake only by evaluating whether the

$^{15}\text{N}$  enrichment between  $^{15}\text{N}$  labeled plants and plants with no  $^{15}\text{N}$  addition was significantly different from zero. However, within a species seasonal comparisons could be made because individuals were chosen within a small range of plant sizes.

Predawn xylem water potentials were measured with a pressure chamber (PMS Instruments, Corvallis, Oregon, USA). To express N concentrations on an area basis, leaf areas were measured using a leaf area meter (LiCor Incorporated, Lincoln, Nebraska, USA).

Two-way analyses of variance were performed to assess effects of species and season on measured plant variables. Species differences within season were determined with Scheffé's multiple comparison test (Day and Quinn 1989). Significance was determined at the 5% level, all percentages were arcsine transformed before analysis, and means were expressed with standard errors.

## RESULTS

### Water pulse utilization

There were significant seasonal and species differences in the water pulse utilization after a rain event (Fig. 1, Table 2). In May, all species derived  $<10\%$  of their stem water from the simulated precipitation event and there was no difference among species (Fig. 1). In July and September species generally obtained a larger fraction of stem water from the precipitation event and we found clear differences in the extent of pulse utilization among species. In July, the maximum fraction of stem water taken up by shallow roots was 50–55% in *Coleogyne* and *Artemisia*, followed by *Quercus* and *Ephedra* with 25–30%. Water pulse utilization was  $<10\%$  in *Vanclavea* and *Cryptantha*. The ranking of species in their ability to utilize water from a rain event changed between July and September as the maximum fraction of stem water derived from the upper soil layers increased in *Quercus* and *Vanclavea* to 65% and 40% respectively, but decreased in *Artemisia* to 39%. In all the other species, utilization of the rain event was similar between July and September.

Species also differed in the short-term dynamics of the deuterium signal in stem water (Fig. 1). In *Artemisia* and *Quercus* the fraction of stem water derived from the simulated rain event declined strongly between day 3 and 5. This dilution of the deuterium signal suggested, that after a rain event both species switched back quickly to uptake of deeper, unlabelled soil moisture sources. By contrast, the dilution of the deuterium signal between day 3 and 5 was small or nonexistent in *Coleogyne*, *Cryptantha*, and *Vanclavea*. In *Ephedra* the larger fraction of stem water derived from the upper soil layers was measured on day 5, indicating a slow response to a water pulse.

Interannual comparison of surface water uptake in July for all species showed good agreement between 1996 and 1997 ( $r^2 = 0.807$ ,  $P < 0.001$ ) (Fig. 2). In

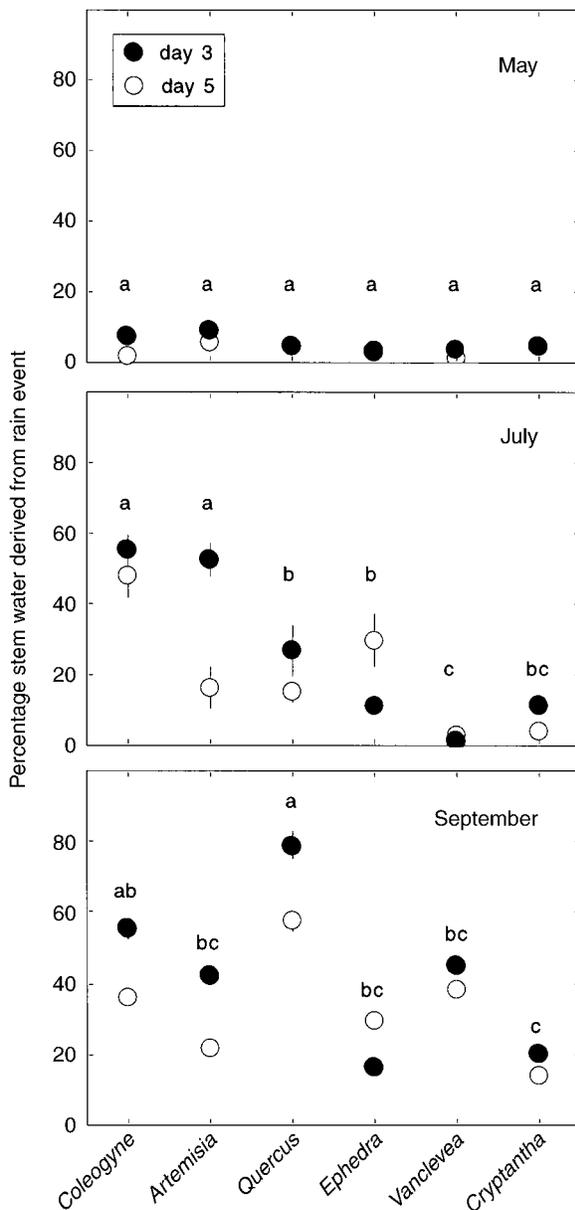


FIG. 1. Seasonal comparison of rain pulse utilization in 1997 by six perennial cold desert species. The percentage of stem water derived from the 25-mm rain event is shown as closed circles for day 3 and as open circles for day 5 (mean  $\pm$  1 SE,  $n = 6$ ). Significant differences ( $P < 0.05$ ) among means within season are indicated by differing lowercase letters.

1997, *Artemisia* had higher a fraction and *Cryptantha* had a lower fraction of stem water supplied by surface roots than in 1996.

#### Predawn water potentials and carbon isotope discrimination

The seasonal maximum and minimum predawn xylem water potentials ( $\Psi$ ) were used as an indicator of average soil water potentials experienced by plant spe-

cies (Fig. 3). *Coleogyne* and *Ephedra* had consistently lower  $\Psi$  than the other species. During the growing season  $\Psi$  of *Coleogyne* and *Ephedra* decreased strongly by  $\sim 5$  MPa and  $\sim 4$  MPa to a minimum  $\Psi$  of  $-6.0$  MPa and  $-5.1$  MPa, respectively. *Quercus*, *Artemisia*, *Cryptantha*, and *Vancleavea* had similar patterns of water deficits, with  $\Psi$  ranging at its maximum between  $-0.35$  MPa and  $-0.67$  MPa and dropping to a value of  $-2.5$  MPa to  $-3.4$  MPa in midsummer.

Carbon isotope discrimination ( $\Delta$ ) values indicated significant differences in water use efficiencies ( $A/g$ ) among species (Table 3). *Cryptantha* and *Vancleavea* had highest  $\Delta$  values (20.1 and 19.6‰) suggesting the lowest  $A/g$ . *Quercus*, *Artemisia*, and *Coleogyne* had intermediate  $\Delta$  values and *Ephedra* had the lowest  $\Delta$  value. Carbon isotope discrimination values were negatively related to plant use of surface soil moisture during summer ( $r^2 = 0.43$ ,  $P < 0.001$ ). There was also a negative relationship between carbon isotope discrimination and foliar N concentration ( $r^2 = 0.54$ ,  $P < 0.001$ ) (Fig. 4). *Ephedra* is the only species in our study with carbon assimilation occurring mainly in stems and it was the only gymnosperm. When *Ephedra* was excluded from the analysis, the relationship between  $\Delta$  values and stem water derived from upper soil layers or N concentrations improved considerably ( $r^2 = 0.94$ ,  $P < 0.001$  and  $r^2 = 0.77$ ,  $P < 0.001$ , respectively).

#### $^{15}\text{N}$ natural abundances and N pulse utilization

Comparisons of  $^{15}\text{N}$  natural abundances in leaves among species indicate that *Ephedra* and *Quercus* may have utilized different N sources than the four other species (Table 3). *Ephedra* had the highest leaf  $\delta^{15}\text{N}$  values ( $+1.8 \pm 0.3\text{‰}$ ), while in leaves of *Quercus*  $\delta^{15}\text{N}$  values were significantly depleted ( $-4.9 \pm 0.3\text{‰}$ ). *Cryptantha*, *Vancleavea*, *Coleogyne*, and *Artemisia* showed intermediate leaf  $\delta^{15}\text{N}$  values ranging from  $-1.2$  to  $+0.0\text{‰}$ .

Changes of leaf  $\delta^{15}\text{N}$  after the application of a  $^{15}\text{N}$  label were used to determine N pulse utilization of shallow roots after a rain event. Temporal changes in July 1996 showed that leaf  $\delta^{15}\text{N}$  values in *Cryptantha* increased considerably within three days, while increases in leaf  $\delta^{15}\text{N}$  values of *Vancleavea* and *Artemisia* were considerably smaller but significant ( $P < 0.01$ ) (Table 4 and Fig. 5). With the exception of *Cryptantha*, leaf  $\delta^{15}\text{N}$  values did not change further after two weeks following the rain event. Increases in leaf  $\delta^{15}\text{N}$  values in *Quercus*, overall, were small, but leaf  $\delta^{15}\text{N}$  levels two weeks following the application were significantly higher than at the beginning of the experiment ( $P < 0.05$ ). By contrast, leaf  $\delta^{15}\text{N}$  values of *Coleogyne* and *Ephedra* did not change significantly during the sampling period ( $P > 0.05$ ).

For the seasonal and species comparisons in 1997, the change in  $\delta^{15}\text{N}$  is shown for only 14 d after the simulated rain event, since the ranking of species re-

TABLE 2. Effects of species and season on resource utilization after a rain pulse. See Figs. 1 and 5 for means and standard errors.

Source	Fraction of stem water derived from rain event				Change in leaf $\delta^{15}\text{N}$			
	df	MS	F	P	df	MS	F	P
Species	5	0.434	17.5	0.0001	5	49.4	13.7	0.0001
Season	2	2.709	109.2	0.0001	2	9.8	2.7	0.0721
Species $\times$ Season	10	0.278	11.9	0.0001	10	31.9	8.9	0.0001
Error	138	0.025			90	3.6		

mained the same as during the initial sampling period. In July 1997, soil labeling with enriched  $^{15}\text{N}$  tracer resulted in the same ranking patterns among species as in July 1996. The leaf-level  $^{15}\text{N}$  changes were, however, ten times smaller (Figs. 5 and 6). Overall, there were species differences in the seasonal pattern of N pulse utilization during 1997. *Artemisia*, *Vanclavea*, and *Quercus* were able to utilize N pulses throughout the entire growing season as leaf  $^{15}\text{N}$  were significantly enriched (Fig. 6). The enrichment in  $\delta^{15}\text{N}$  in *Vanclavea* was highest in May. *Coleogyne* and *Ephedra* also showed spring uptake, but appeared to have no significant N uptake activity by surface roots in July or September ( $P > 0.05$ ). In contrast, *Cryptantha* was the only species which exhibited no significant N uptake in May, but large changes in July and September.

DISCUSSION

*Seasonal and species differences in water pulse utilization*

In semiarid or arid regions, perennial woody species generally have greater rooting depths than annuals or herbaceous perennials and are able to utilize water sources in deeper soil layers (Sala et al. 1989, Ehleringer et al. 1991, Canadell et al. 1996, Scholes and Archer 1997, Weltzin and McPherson 1997). These studies describe a relatively distinct pattern of soil moisture partitioning, which may promote the coex-

istence of different life forms. However, woody species also exhibit wide variations in their utilization of soil moisture from the upper soil layers (Ehleringer et al. 1991, Flanagan et al. 1992, Lin et al. 1996). In this study, woody species derived between 1% and 79% of their stem water from a simulated 25-mm rain event. On the Colorado Plateau, this is a large rain event, which would be expected to occur only 1–2 times during the entire summer monsoon season (Houghton 1979). Therefore, measured water pulse utilization represents a maximum estimate for species responses in this cold desert community.

In contrast to some species of the pinyon–juniper community on the Colorado Plateau (Ehleringer et al. 1997), species in our study showed limited year-to-year variation in the capacity to take up summer moisture, even though the total amount of summer precipitation differed substantially between years. We observed, however, distinct seasonal differences in the utilization of soil moisture from the upper soil layers. Early in the growing season, each of these species derived relatively little water from the simulated rain event (<10% of the stem water). In July and September, we generally observed a greater relative moisture uptake from the upper soil layers. In spring, due to recharging

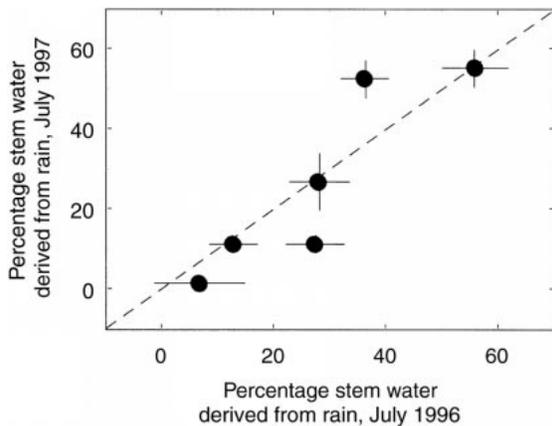


FIG. 2. Interannual comparison of rain pulse utilization between July 1996 and July 1997 (mean  $\pm$  1 SE).

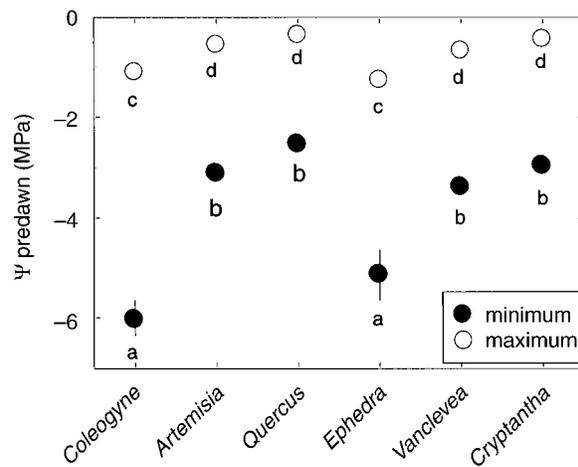


FIG. 3. Seasonal minimum (closed circles) and maximum (open circles) predawn xylem water potential (mean  $\pm$  1 SE,  $n = 5$ ) of the six perennial cold desert species. Significant differences ( $P < 0.05$ ) among means within season are indicated by differing lowercase letters.

TABLE 3. Foliar carbon discrimination ( $\Delta$ ) and  $\delta^{15}\text{N}$  values of six perennial cold desert species.

Species	$\Delta$ (‰)	$\delta^{15}\text{N}$ (‰)
<i>Coleogyne</i>	17.11 $\pm$ 0.14 <sup>b</sup>	-0.71 $\pm$ 0.19 <sup>bc</sup>
<i>Artemisia</i>	17.31 $\pm$ 0.23 <sup>b</sup>	0.04 $\pm$ 0.14 <sup>c</sup>
<i>Quercus</i>	17.80 $\pm$ 0.10 <sup>b</sup>	-4.94 $\pm$ 0.34 <sup>a</sup>
<i>Ephedra</i>	16.26 $\pm$ 0.13 <sup>a†</sup>	1.78 $\pm$ 0.31 <sup>d†</sup>
<i>Vanclaveva</i>	19.50 $\pm$ 0.11 <sup>c</sup>	-0.53 $\pm$ 0.12 <sup>bc</sup>
<i>Cryptantha</i>	20.10 $\pm$ 0.14 <sup>c</sup>	-1.19 $\pm$ 0.14 <sup>b</sup>

Notes: Significant differences ( $P < 0.05$ ) among species are indicated by differing superscript letters. Values are means  $\pm$  1 SE.

†  $\Delta$  and  $\delta^{15}\text{N}$  were measured in photosynthetic stems.

by winter rains, soil moisture levels are relatively high throughout the soil profile (Caldwell 1985; R. Gebauer, unpublished data). All species reached relatively high  $\Psi$  and water was unlikely to be limiting for plant activity. Since the entire root system had access to water, active roots in shallow soil layers may have contributed relatively little to the plant's water uptake. Later in the growing season when water loss by evapotranspiration results in extremely dry soils throughout most of the profile, competition for water among species is likely to be more intense. Thus, during summer, soil moisture partitioning may be more important for the maintenance of species diversity than in spring, when soil moisture availability is high. Our results show that species differences in the ability to utilize rain events became more apparent in July and September. There was, however, considerable overlap in water pulse utilization. We can identify three species clusters based on response patterns to the simulated rain event and the degree of water stress experienced during the summer months: (1) *Artemisia*, *Quercus*, and *Vanclaveva*, (2) *Coleogyne* and *Ephedra*, and (3) *Cryptantha*.

*Artemisia*, *Quercus*, and *Vanclaveva* showed the capacity to both extensively utilize water pulses after rain events and to take up soil moisture stored at depth. In

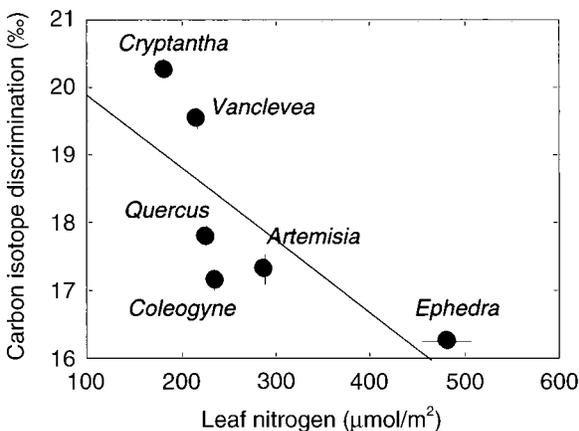


FIG. 4. Relationship between carbon isotope discrimination and nitrogen concentrations among different species (mean  $\pm$  1 SE,  $n = 34$ –36).

TABLE 4. Changes in  $\delta^{15}\text{N}$  values in stems of six perennial cold desert species in response to a rain event and after the application of an  $^{15}\text{N}$  label in July 1996 (means  $\pm$  1 SE,  $n = 4$ ).

Species	Change in $\delta^{15}\text{N}$ (‰)
<i>Coleogyne</i>	0.46 $\pm$ 0.50 <sup>NS</sup>
<i>Artemisia</i>	4.28 $\pm$ 0.81 <sup>**</sup>
<i>Quercus</i>	3.50 $\pm$ 1.58 <sup>NS</sup>
<i>Ephedra</i>	0.37 $\pm$ 0.57 <sup>NS</sup>
<i>Vanclaveva</i>	4.76 $\pm$ 1.82 <sup>*</sup>
<i>Cryptantha</i>	206.5 $\pm$ 73.9 <sup>†</sup>

<sup>NS</sup>  $P > 0.05$ , <sup>\*</sup>  $P < 0.05$ , <sup>\*\*</sup>  $P < 0.01$ .

†  $\delta^{15}\text{N}$  was measured in roots.

*Artemisia* and *Quercus* the presence of active roots in the upper soil layers is indicated by considerable uptake of moisture from the simulated rain in July and September. On the other hand, the reduction of deuterium in stem water between days 3 and 5 indicates that both species switched back relatively quickly to deeper soil moisture sources. Additional evidence for access to soil moisture at depth was the relatively small decreases in  $\Psi$  throughout the summer. Similarly  $\Psi$  in *Vanclaveva* decreased relatively little during the summer. However, in contrast to *Artemisia* and *Quercus*, *Vanclaveva* only utilized rain pulses in September. Lin et al. (1996) observed similar patterns in *Vanclaveva* and suggested that high soil temperatures may have affected water uptake capacity of shallow roots.

The second cluster, *Coleogyne* and *Ephedra*, utilized a relatively large proportion of soil moisture from summer rain pulses, but exhibited large decreases in  $\Psi$  during the summer. These patterns imply that both species were unable to effectively switch from use of surface moisture to water sources at depth (Lin et al. 1996). For these species, there was also no dilution of the deuterium signal in stem water in July between days 3 and 5. In fact, the fraction of *Ephedra*'s stem water derived from the rain event increased between days 3 and 5. This delayed response to the simulated rain event

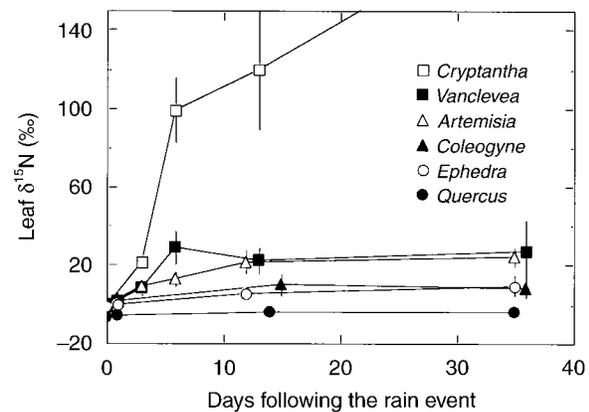


FIG. 5. Temporal changes in leaf  $\delta^{15}\text{N}$  of different species after the application of an  $^{15}\text{N}$  label in July 1996 (means  $\pm$  1 SE,  $n = 6$ ).

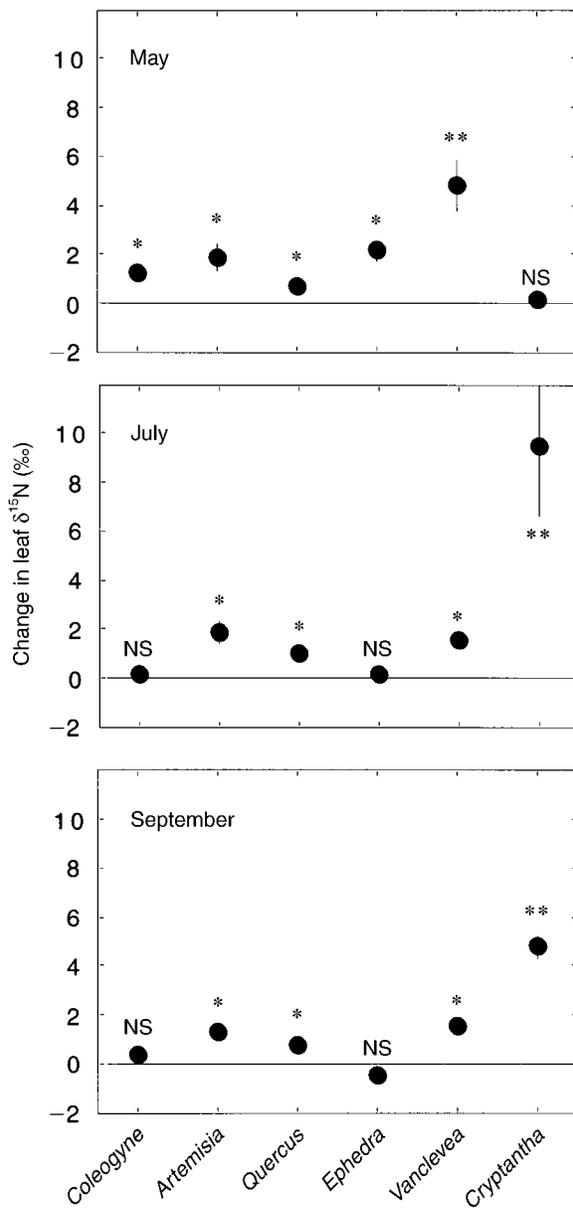


FIG. 6. Seasonal comparison of nitrogen pulse utilization in 1997 by six dominant perennial species of a cold desert community at Arches National Park, Utah. Changes in leaf  $\delta^{15}\text{N}$  between unlabelled and  $^{15}\text{N}$  enriched plants (mean  $\pm$  1 SE) are shown for 14 d after the application of the  $^{15}\text{N}$  label. Changes significantly different from zero are indicated by \*  $P < 0.05$  and \*\*  $P < 0.01$ .

might be a result of low rates of water transport through the plant. As a gymnosperm, *Ephedra* has different hydraulic architecture than the other species (Sperry et al. 1994, Tyree et al. 1994) and low transpirational flux rates (Comstock and Ehleringer 1992). It is also possible that the delay in water uptake in *Ephedra* was associated with a time lag required for new root growth (Nobel 1994). Such a delayed utilization of a rain event could place *Ephedra* into a competitive disadvantage

with other species, which are able to deplete moisture sources faster than *Ephedra*.

*Cryptantha*, the only herbaceous perennial in our study, made limited use of increased moisture availability in the upper soil layers, but as indicated by the maintenance of relatively high  $\Psi$ , had access to soil moisture at depth. This water uptake pattern was different than most other herbaceous species, which generally rely more strongly on water uptake from upper soil layers (Ehleringer et al. 1991).

The significant negative relationship between leaf carbon isotope discrimination ( $\Delta$ ) and the proportional water uptake from the upper soil layers indicated that species with a high fractional utilization of water pulses in upper soil layers had a greater water use efficiency ( $A/g$ ) than species with access to a more reliable water source at depth. Similar relationships between  $\Delta$  values and utilization of shallow soil moisture have been found in other plant communities (Flanagan et al. 1992, Valentini et al. 1992). It is consistent with Walter's hypothesis (1979) that when considerable overlap in functional root systems exists among species, differences in  $A/g$  may in part contribute to the coexistence of those species (Walker et al. 1981, Scholes and Archer 1997). Low stomatal conductances, greater photosynthesis, or the combination of both can lead to increases in  $A/g$  (or decreases in  $\Delta$  values) (Ehleringer et al. 1993). We also found a high correlation between  $\Delta$  values and leaf N concentrations among species, suggesting that carbon discrimination responded to differences in photosynthetic capacity. The correlations of  $\Delta$  values, water pulse utilization and N content indicates that N use patterns affected carbon and water relationships of different plant species. Thus, even during times when water was the primary factor limiting plant activity, N partitioning among species may influence species coexistence.

#### Natural abundances of $^{15}\text{N}$

$\delta^{15}\text{N}$  values of plant tissues were quite different among species. For example, *Ephedra* (1.8‰) was enriched in  $^{15}\text{N}$  relative to the other species, while *Quercus* (-4.9‰) was considerably depleted. Variations in natural abundances of  $\delta^{15}\text{N}$  of plant tissues have been attributed to several factors, including (1) soil transformations of N (N fixation, turnover by microbial mineralization/immobilization), (2) the soil depth from which N is taken up, (3) the form of soil N used (organic N,  $\text{NH}_4^+$ ,  $\text{NO}_3^-$ ), and/or (4) influences of mycorrhizal symbiosis (Handley and Raven 1992, Nadelhoffer and Fry 1994, Högberg 1997, Michelsen et al. 1998). Because of the complexity in N pathways and the interactions between these factors, it is often difficult to link observed variations in natural abundances of  $^{15}\text{N}$  values to a specific mechanism (Nadelhoffer and Fry 1994, Högberg 1997). Of the species studied *Quercus* is the only species with an ectomycorrhizal association (J. Trappe, *personal communication*). This may

TABLE 5. Summary of resource uptake patterns in response to a rain event in 1997.

Species	May		July		September	
	H <sub>2</sub> O	N	H <sub>2</sub> O	N	H <sub>2</sub> O	N
<i>Artemisia</i>	–	*	++	*	+	*
<i>Quercus</i>	–	*	+	*	++	*
<i>Cryptantha</i>	–	NS	+	*	+	*
<i>Coleogyne</i>	–	*	++	NS	++	NS
<i>Ephedra</i>	–	*	+	NS	+	NS
<i>Vanclavea</i>	–	*	–	*	++	*

Notes: Water uptake is indicated as (–), (+), or (++) when stem water derived from the rain event was <10%, 10–40%, or >40%, respectively. N uptake is indicated in terms of whether changes in leaf  $\delta^{15}\text{N}$  were significant (\*,  $P < 0.05$ ) or were not significantly different from zero (NS,  $P > 0.05$ ).

be a contributing factor to the large  $^{15}\text{N}$  depletion found for this species. Nevertheless, the large differences in  $\delta^{15}\text{N}$  among species supports the hypothesis that the soil N pool is to some extent partitioned among species. It has been suggested that differences in  $\delta^{15}\text{N}$  correlated with the absence or presence of mycorrhizal association may reflect uptake of different forms of N, rather than fungal discrimination against  $^{15}\text{N}$  (Michelsen et al. 1998). In our study, species which were similar with respect to their utilization of water sources (e.g., *Ephedra* and *Coleogyne* or *Quercus* and *Artemisia*) may be differentiated from each other with respect to N sources.

#### *N pulse utilization need not to be related to water pulse utilization*

In arid and semiarid ecosystems, N availability is highest in surface layers and declines strongly with depth (Charley 1975, Virginia and Jarrell 1983, Evans and Ehleringer 1994), which can result in intense competition for N among species during infrequent pulse events. The results of the  $^{15}\text{N}$  labeling experiment showed that all dominant species of this cold desert community utilized the N pulses in the upper soil layers. There were, however, seasonal differences in N pulse utilization among species. *Coleogyne* and *Ephedra* did take up N from surface layers in May, but not in July and September. In contrast, *Cryptantha* did not utilize the surface N pool in May, but did so in July and September. *Artemisia*, *Quercus*, and *Vanclavea* took up N from the upper soil layers throughout the year. Similar to the results of our study, McKane et al. (1990) found temporal differentiation in N uptake among species of an old field plant community.

One conclusion of this study is that water and N uptake do not necessarily occur simultaneously. In July, in particular, when resources were most constrained, we found distinctly different N and water utilization patterns among species (Table 5, Figs. 1 and 6). Only *Artemisia*, *Quercus*, and *Cryptantha* showed significant water and N uptake from the upper soil layers. However, at this time *Cryptantha* derived only a small fraction of its transpirational water from the water pulse.

*Coleogyne* and *Ephedra* had the capacity to utilize the water pulse but not the N pulse. Shallow roots in *Vanclavea* only took up N.

Most theoretical and experimental studies of root activity and below-ground resource competition assume that water and N uptake in different roots occur together (e.g., Casper and Jackson 1997). To our knowledge, few studies have tested the assumption of simultaneous N and water uptake. Schulze and Bloom (1984) showed that N uptake rates in hydroponically grown tomato plants were independent of water uptake rates (as measured by transpiration rates). A comparison of two perennial grass species of the Great Basin Desert showed that water uptake recovered rapidly following drought in both grasses, while N uptake was fully restored in only one of the species (Bassirrad and Caldwell 1992). One possibility to explain water without significant N uptake in *Coleogyne* and *Ephedra* might be that N acquisition requires considerable amounts of energy (Clarkson 1985, Chapin 1988). Even though both species remained photosynthetically active during the summer months (R. Gebauer, unpublished data), it is likely that due to the reduced leaf area, whole plant carbon gain might not have been sufficient to offset the uptake costs of N. A possible mechanism for the observed resource uptake pattern in *Vanclavea* is that hydraulic conductances in shallow roots were relatively small compared to deeper growing roots. Differences in hydraulic conductivities between tap and lateral roots have been shown for proteaceous species (Pate et al. 1995). Despite the relatively low water flux rates in the shallow roots, N uptake and transport are likely to be maintained as has been shown for corn (Tanner and Beevers 1990).

The idea that parts of the integrated root system can serve different functional roles was discussed by Waisel and Eshel (1991). Our results show that in addition to distinguishing among different functional (e.g., storage, anchorage, and transport or resource acquisition), it is important to recognize that different parts of the root system can be acquiring different essential resources, in this instance water and N. Our results also have important implications for understanding competition and coexistence of species. Trade-offs in the ability to capture resources are unavoidable (Tilman 1982, 1988) and differential water and N utilization suggest a mechanism by which species of this cold desert community could be favored differentially under conditions of highly variable resource availability. The challenge ahead is to understand the consequences of variability in resource utilization on long-term interactions of plants under field conditions.

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## LITERATURE CITED

- Bassirirad, H., and M. M. Caldwell. 1992. Temporal changes in root growth and N-15 uptake and water relations of 2 tussock grass species recovering from water stress. *Physiologia Plantarum* **86**:525–531.
- Bilbrough, C. J., and M. M. Caldwell. 1997. Exploitation of springtime ephemeral N pulses by six Great Basin plant species. *Ecology* **78**:231–243.
- Bratton, S. P. 1976. Resource division in an understory herb community: responses to temporal and microtopographic gradients. *American Naturalist* **110**:679–693.
- Buchmann, N., E. -D. Schulze, and G. Gebauer. 1995. N-15-ammonium and N-15-nitrate uptake of a 15 year old *Picea abies* plantation. *Oecologia* **102**(3):361–370.
- Caldwell, M. M. 1985. Cold deserts. Pages 198–212 in B. F. Chabot and H. A. Mooney, editors. *Physiological ecology of North American plant communities*. Chapman and Hall, New York, New York, USA.
- Caldwell, M. M. 1994. Exploiting nutrients in fertile soil microsites. Pages 325–348 in M. M. Caldwell and R. W. Pearcy, editors. *Exploitation of environmental heterogeneity by plants*. Academic Press, San Diego, California, USA.
- Canadell, J., R. B. Jackson, J. R. Ehleringer, H. A. Mooney, O. E. Sala, and E. Schulze. 1996. Maximum rooting depth of vegetation types at the global scale. *Oecologia* **108**:583–595.
- Casper, B. B., and R. B. Jackson. 1997. Plant competition underground. *Annual Review of Ecology and Systematics* **28**:545–570.
- Chapin, F. S. 1988. Ecological aspects of plant nutrition. *Advances in Mineral Nutrition* **3**:161–191.
- Charley, J. L. 1975. Mineral cycling in rangeland ecosystems. Pages 215–256 in R. E. Sosebee, editor. *Rangeland plant physiology*. Society of Range Management, Denver, Colorado, USA.
- Clarkson, D. T. 1985. Factors affecting mineral nutrient acquisition by plants. *Annual Review of Plant Physiology* **36**:77–115.
- Coleman, M. L., T. J. Shepard, J. J. Durham, J. E. Rouse, and G. R. Moore. 1982. Reduction of water with zinc for hydrogen isotope analysis. *Analytical Chemistry* **54**:993–995.
- Comstock, J. P., and J. R. Ehleringer. 1992. Plant adaptations in the Great Basin and Colorado Plateau. *Great Basin Naturalist* **52**:195–215.
- Cui, M., and M. M. Caldwell. 1997. A large ephemeral release of nitrogen upon wetting of dry soil and corresponding root responses in the field. *Plant and Soil* **191**:291–299.
- Dawson, T. E., and J. R. Ehleringer. 1993. Isotopic enrichment of water in the “woody” tissue of plants: implications for water source, water uptake and other studies which use stable isotope composition of cellulose. *Geochimica et Cosmochimica Acta* **57**:3487–3492.
- Day, R. W., and G. P. Quinn. 1989. Comparisons of treatments after an analysis of variance in ecology. *Ecological Monographs* **59**:433–463.
- Ehleringer, J. R. 1994. Variations in gas exchange characteristics among desert plants. Pages 361–392 in E.-D. Schulze and M. M. Caldwell, editors. *Ecophysiology of photosynthesis*. Springer-Verlag, Berlin, Germany.
- Ehleringer, J. R., and T. E. Dawson. 1992. Water uptake by plants—perspectives from stable isotope composition. *Plant, Cell and Environment* **15**:1073–1082.
- Ehleringer, J. R., R. D. Evans, and D. Williams. 1997. Assessing sensitivity to change in desert ecosystems—a stable isotope approach. Pages 223–237 in H. Griffiths, editor. *Stable isotopes*. BIOS Scientific Publishers, Oxford, UK.
- Ehleringer, J. R., A. E. Hall, G. D. Farquhar. 1993. Stable isotopes and plant carbon/water relations. Academic Press, San Diego, California, USA.
- Ehleringer, J. R., and C. B. Osmond. 1989. Stable isotopes. Pages 281–300 in R. W. Pearcy, J. R. Ehleringer, H. A. Mooney, and P. W. Rundel, editors. *Plant physiological ecology: field methods and instrumentation*. Chapman and Hall, New York, USA.
- Ehleringer, J. R., S. L. Phillips, W. F. S. Schuster, and D. R. Sandquist. 1991. Differential utilization of summer rains by desert plants. *Oecologia* **88**:430–434.
- Evans, R. D., and J. R. Ehleringer. 1994. A break in the nitrogen cycles in aridlands: evidence from  $\delta^{15}\text{N}$  of soils. *Oecologia* **94**:314–317.
- Farquhar, G. D., M. H. O’Leary, and J. A. Berry. 1982. On the relationship between carbon isotope discrimination and the intercellular carbon dioxide concentration in leaves. *Australian Journal of Plant Physiology* **9**:121–137.
- Farquhar, G. D., and R. A. Richards. 1984. Isotopic composition of plant carbon correlates with water-use efficiency of wheat genotypes. *Australian Journal of Plant Physiology* **11**:539–552.
- Fisher, F. M., J. C. Zak, G. L. Cunningham, and W. G. Whitford. 1987. Water and nitrogen effects on growth and allocation patterns of creosote bush in the northern Chihuahuan Desert. *Journal of Range Management* **41**:387–391.
- Fitter, A. H. 1986. Spatial and temporal patterns of root activity in a species-rich alluvial grassland. *Oecologia* **69**:594–599.
- Flanagan, L. B., J. R. Ehleringer, and J. D. Marshall. 1992. Differential uptake of summer precipitation among co-occurring trees and shrubs in a pinyon–juniper woodland. *Plant, Cell and Environment* **15**:831–836.
- Gallardo, A., and W. H. Schlesinger. 1992. Carbon and nitrogen limitations of soil microbial biomass in desert ecosystems. *Biogeochemistry* **18**:1–17.
- Goldberg, D., and A. Novoplansky. 1997. On the relative importance of competition in unproductive environments. *Journal of Ecology* **85**:409–418.
- Gutierrez, J. R., and W. G. Whitford. 1987. Chihuahuan desert annuals: importance of water and nitrogen. *Ecology* **68**:2032–2045.
- Handley, L. L., and J. A. Raven. 1992. The use of natural abundance of nitrogen isotopes in plant physiology and ecology. *Plant, Cell and Environment* **15**:965–985.
- Högberg, P. 1997.  $^{15}\text{N}$  natural abundance in soil–plant systems. *New Phytologist* **137**:179–203.
- Houghton, J. G. 1979. A model for orographic precipitation in the north central Great Basin. *Monthly Weather Review* **107**:1462–1475.
- Kemp, P. R., J. F. Reynolds, Y. Pachepsky, and J. L. Chen. 1997. A comparative modeling study of soil water dynamics in a desert ecosystem. *Water Resources Research* **33**:73–90.
- Lin, G., S. L. Phillips, and J. R. Ehleringer. 1996. Monsoonal precipitation responses of shrubs in a cold desert community on the Colorado Plateau. *Oecologia* **106**:8–17.
- McKane, R. B., D. F. Grigal, and M. P. Russelle. 1990. Spatiotemporal differences in  $^{15}\text{N}$  uptake and the organization of an old field plant community. *Ecology* **71**:1126–1132.
- Michelsen, A., C. Quarmby, D. Sleep, and S. Jonasson. 1998. Vascular plant  $^{15}\text{N}$  natural abundance in heath and forest tundra ecosystems is closely correlated with presence and type of mycorrhizal fungi in roots. *Oecologia* **115**:406–418.
- Nadelhoffer, K. J., and B. Fry. 1994. Nitrogen isotope studies in forest ecosystems. Pages 22–44 in K. Lathja and R. Michener, editors. *Stable isotopes in ecology*. Blackwell, Oxford, UK.

- Nadelhoffer, K. J., G. Shaver, B. Fry, A. Giblin, L. Johnson, and R. McKane. 1996.  $^{15}\text{N}$  natural abundances and N use by tundra plants. *Oecologia* **107**:386–394.
- Nobel, P. S. 1994. Root–soil responses to water pulses in dry environments. Pages 285–304 in M. M. Caldwell, and R. W. Pearcy, editors. *Exploitation of environmental heterogeneity by plants*. Academic Press, San Diego, California, USA.
- Noy-Meir, I. 1973. Desert ecosystems, environment and producers. *Annual Review of Ecology and Systematics* **4**:25–41.
- Pate, J. S., K. W. Dixon, and G. Orshan. 1995. Hydraulic architecture and xylem structure of the dimorphic root system of Southwest Australian species of Proteaceae. *Journal of Experimental Botany* **46**:907–915.
- Reynolds, H. L., B. A. Hungate, F. S. Chapin III, and C. M. D'Antonio. 1997. Soil heterogeneity and plant competition in an annual grassland. *Ecology* **78**:2076–2090.
- Rundel, P. W., and P. S. Nobel. 1991. Structure and function in desert root systems. Pages 349–378 in D. Atkinson, editor. *Plant root growth: an ecological perspective*. Blackwell Scientific Publications, Cambridge, UK.
- Ryel, R. J., M. M. Caldwell, and J. H. Manwaring. 1996. Temporal dynamics of soil spatial heterogeneity in sagebrush–wheatgrass steppe during a growing season. *Plant and Soil* **184**:299–309.
- Sala, O. E., R. A. Golluscio, W. K. Lauenroth, and A. Soriano. 1989. Resource partitioning between shrubs and grasses in the Patagonian steppe. *Oecologia* **81**:501–505.
- Schimel, D. S., and W. J. Parton. 1986. Microclimatic controls on nitrogen mineralization and nitrification in short-grass steppe soils. *Plant and Soil* **93**:347–357.
- Schlesinger, W., J. A. Raikes, A. E. Hartley, and A. F. Cross. 1996. On the spatial pattern of soil nutrients in desert ecosystems. *Ecology* **77**:364–374.
- Scholes, R. J., and S. R. Archer. 1997. Tree–grass interactions in savannas. *Annual Review of Ecology and Systematics* **28**:517–544.
- Schulze, E. D., and A. J. Bloom. 1984. Relationship between nitrogen influx and transpiration in radish and tomato. *Plant Physiology* **76**:827–828.
- Sperry, J. S., K. L. Nichols, J. E. M. Sullivan, and S. E. Eastlack. 1994. Xylem embolism in ring-porous, and coniferous trees of northern Utah and interior Alaska. *Ecology* **75**:1736–1752.
- Stark, J. M. 1994. Causes of soil nutrient heterogeneity at different scales. Pages 255–284 in M. M. Caldwell and R. W. Pearcy, editors. *Exploitation of environmental heterogeneity by plants*. Academic Press, San Diego, California, USA.
- Tanner, W., and H. Beevers. 1990. Does transpiration have an essential function in long-distance ion transport in plants? *Plant, Cell and Environment* **13**:745–750.
- Tilman, D. 1982. *Resource competition and community structure*. Princeton University Press, Princeton, New Jersey, USA.
- Tilman, D. 1988. *Plant strategies and the dynamics and structure of plant communities*. Princeton University Press, Princeton, New Jersey, USA.
- Tyree, M. T., S. D. Davis, and H. Cochard. 1994. Biophysical perspectives of xylem evolution: Is there a tradeoff of hydraulic efficiency for vulnerability to dysfunction? *IAWA Journal* **15**:335–360.
- Valentini, R., G. E. S. Mugnoza, and J. R. Ehleringer. 1992. Hydrogen and carbon isotope ratios of selected species of a Mediterranean macchia ecosystem. *Functional Ecology* **6**:627–631.
- Virginia, R. A., and W. M. Jarrell. 1983. Soil properties in a mesquite-dominated Sonoran desert ecosystem. *Soil Science Society of America Journal* **47**:138–144.
- Waisel, Y., and A. Eshel. 1991. Multifunctional behavior of various constituents of one root system. Pages 39–52 in Y. Waisel, A. Eshel, and U. Kafkafi, editors. *Plant roots: the hidden half*. M. Dekker, New York, New York, USA.
- Walker, B. H., D. Ludwig, C. S. Holling, and R. M. Peterman. 1981. Stability of semi-arid savanna grazing systems. *Journal of Ecology* **69**:473–498.
- Walter, H. 1979. *Vegetation of the earth and ecological systems of the geo-biosphere*. Springer, Berlin, Germany.
- Weltzin, J. F., and G. R. McPherson. 1997. Spatial and temporal soil moisture resource partitioning by trees and grasses in a temperate savanna, Arizona, USA. *Oecologia* **112**:156–164.