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## Water and nitrogen dynamics in an arid woodland

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**Abstract** Arid environments are characterized by spatial and temporal variation in water and nitrogen availability. Differences in  $\delta^{15}\text{N}$  and  $\delta\text{D}$  of four co-occurring species reveal contrasting patterns of plant resource acquisition in response to this variation. Mineralization potential and nitrogen concentration of surface soils associated with plant canopies were greater than inter-canopy locations, and values decreased with increasing depth in both locations. Mineralization potential and nitrogen concentration were both negatively correlated with soil  $\delta^{15}\text{N}$ . The spatial variation in soil  $\delta^{15}\text{N}$  caused corresponding changes in plant  $\delta^{15}\text{N}$  such that plant  $\delta^{15}\text{N}$  values were negatively correlated with nitrogen concentration of surface soils. Plants occurring on soils with relatively high nitrogen concentrations had lower  $\delta^{15}\text{N}$ , and higher leaf nitrogen concentrations, than plants occurring on soils with relatively low nitrogen concentrations. Two general temporal patterns of water and nitrogen use were apparent. Three species (*Juniperus*, *Pinus* and *Artemisia*) relied on the episodic availability of water and nitrogen at the soil surface.  $\delta^{15}\text{N}$  values did not vary through the year, while xylem pressure potentials and stem-water  $\delta\text{D}$  values fluctuated with changes in soil moisture at the soil surface. In contrast, *Chrysothamnus* switched to a more stable water and nitrogen source during drought.  $\delta^{15}\text{N}$  values of

*Chrysothamnus* increased throughout the year, while xylem pressure potentials and stem-water  $\delta\text{D}$  values remained constant. The contrasting patterns of resource acquisition have important implications for community stability following disturbance. Disturbance can cause a decrease in nitrogen concentration at the soil surface, and so plants that rely on surface water and nitrogen may be more susceptible than those that switch to more stable water and nitrogen sources at depth during drought.

**Key words** Cryptobiotic crust · Desert ecology · Nitrogen cycle · Stable isotopes · Water source

### Introduction

Understanding patterns of plant resource acquisition and plant tolerance to resource limitation is crucial for the interpretation of community dynamics and stability in the face of anthropogenic change. Several resource limitations often interact to decrease plant productivity (Chapin et al. 1987). In arid regions, productivity is clearly limited by water stress, but productivity is also limited by nitrogen, and nitrogen addition alone (Fischer et al. 1988), or in addition to supplemental watering (Ettershank et al. 1978; Sharifi et al. 1988; Miller et al. 1991), can increase plant growth.

Disturbance can cause spatial heterogeneity in soil nitrogen concentration. In the Chihuahuan Desert of North America, disturbance has caused a shift in species composition from grassland to shrubs (Schlesinger et al. 1990). Nutrients are localized under shrubs, and soil fertility decreases between shrubs due to erosion and gaseous nitrogen loss (Schlesinger et al. 1990). Disturbance can also increase spatial variability in semi-arid woodlands of the southwestern United States. Soils are covered by a cryptobiotic crust composed of cyanobacteria, lichens, moss, and fungi (Harper and Marble 1988). Nitrogen fixation by the

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lichens and cyanobacteria in the cryptobiotic crust is a primary source of nitrogen input (Evans and Ehleringer 1993). Nitrogen fixation does not occur following disturbance (Belnap 1993), but organic matter decomposition and gaseous loss continue causing lower soil nitrogen concentrations in disturbed areas.

Water availability in most arid regions is episodic, with drought alternating with periods of relatively high soil moisture following precipitation. Many species tolerate drought by abscising leaves, lowering stomatal conductance, and maintaining cell turgor (Schulze 1986; Turner 1986). However, other species avoid severe water stress by using more stable water sources located at depth in the soil (Ehleringer et al. 1991; Flanagan et al. 1992). The response of species to increases in soil water following drought can be variable; annuals, succulent perennials, and herbaceous perennials often use surface soil water following rain, but many woody perennials continue to rely on the more stable water sources found at depth (Ehleringer et al. 1991; Flanagan et al. 1992).

Patterns of water use can have a direct impact on plant nitrogen dynamics. Spatial variation in soil nitrogen is common in arid environments; soil nitrogen concentrations are highest at the soil surface and decrease rapidly with depth (Charley and West 1977; Burke 1989; Evans and Ehleringer 1993). A trade-off may therefore be expected between nitrogen and water acquisition. Plants that tolerate drought and respond to increases in water availability at the soil surface would have access to soil with relatively high nitrogen concentrations, while species that avoid drought by obtaining water at depth may have to rely on soil with relatively low nitrogen concentrations.

Variation in the  $\delta^{15}\text{N}$  and  $\delta\text{D}$  of plant nitrogen and water, respectively, provides a means to address specific hypotheses concerning plant resource acquisition. The isotopic composition of soil nitrogen varies due to differences in nitrogen inputs into the soil and subsequent fractionation during mineralization and gaseous nitrogen loss (Nadelhoffer and Fry 1988). Spatial variation in the isotopic composition of soil water exists because of seasonal differences in the isotopic composition of precipitation, fractionation during evaporation of water from the soil, and differences in isotopic composition between soil water and ground water (Ehleringer and Dawson 1992). Isotopic fractionation does not occur during nitrogen (Mariotti et al. 1982; Yoneyama and Kaneko 1989) or water (White et al. 1985; Dawson and Ehleringer 1991) uptake by roots, and so differences in the isotopic composition of nitrogen or water between plants reflects the use of different resource pools within the soil (Virginia and Delwiche 1982; Shearer et al. 1983; White et al. 1985; Garten 1993).

This study examines (1) plant nitrogen dynamics associated with spatial variation in soil nitrogen and (2) the potential trade-off between contrasting temporal

patterns of nitrogen and water use. The study site is a semi-arid woodland that has been the location for past studies of plant water use (Flanagan et al. 1992) and soil nitrogen dynamics (Evans and Ehleringer 1993). Soil nitrogen concentration is heterogeneous at the soil surface due to disturbance of the cryptobiotic crust, and there is a strong negative correlation between soil  $\delta^{15}\text{N}$  and nitrogen concentration (Evans and Ehleringer 1993). The dominant species have contrasting patterns of water use (Flanagan et al. 1992). One shrub (*Artemisia tridentata*) and one tree (*Pinus edulis*) species respond readily to precipitation following drought, while a second shrub species (*Chrysothamnus nauseosus*) continues to use more stable water sources at depth. The response of a second tree species (*Juniperus osteosperma*) is variable. We addressed three questions. First, do spatial differences in nitrogen concentration cause differences in the amount of nitrogen that is potentially available for plant assimilation? Second, do spatial patterns of plant  $\delta^{15}\text{N}$  correlate with soil  $\delta^{15}\text{N}$ , and therefore with soil nitrogen concentration? Third, do trade-offs exist between temporal patterns of water and nitrogen acquisition?

## Material and methods

The study site was located near Coral Pink Sand Dunes State Park (latitude  $37^{\circ}03'$ , longitude  $112^{\circ}45'$ ) in south-central Utah, USA. This site is adjacent to plots used in previous studies (Flanagan and Ehleringer 1991; Flanagan et al. 1992). The soils are aeolian deposits; development of soil horizons was not apparent, and fine roots were not observed below 25 cm.

Five plots, separated by at least 50 m, were established on 18 March 1991. One individual plant of *Juniperus*, *Pinus*, and *Chrysothamnus* was tagged in each plot for measurement throughout the study. Two individuals of *Artemisia* were tagged in each plot: one located under the *Juniperus* canopy and a second located in the open spaces between tree canopies. Hereafter, intra-canopy location refers to tree (*Juniperus* or *Pinus*) canopies, while inter-canopy refers to locations between the tree canopies.

### Soil nitrogen and water

Soil samples for nitrogen and water analysis were collected throughout the growing season. Samples for the intra-canopy were collected beneath the *Juniperus* 0.5 m from the canopy edge. Two inter-canopy locations were sampled: 0.5 m from the primary stem of the *Artemisia*, and a bare area at least 1 m from any plant. Two subsamples were gathered from each location and subsamples were combined for all analyses. Samples were collected at depths of 0–0.1 m, 0.15–0.25 m, 0.45–0.55 m, and 0.95–1.05 m, using a soil auger. Depths refer to mineral soil and do not include litter layers. Litter, when present, consisted of loose plant material.

Each soil sample was divided into three fractions at the time of collection. The first was placed into a 25 ml screw-top vial, sealed with parafilm, and frozen on dry ice for later analysis of the isotopic composition of hydrogen within soil water. The second fraction, for  $\text{NH}_4^+$  and  $\text{NO}_3^-$  analysis, was placed in a sample tin, sealed with electrical tape, and frozen on dry ice. The third fraction, for determination of soil moisture, was placed in a sample tin, sealed with electrical tape, and stored in a cooler on ice. A fourth fraction was

collected in March for determination of total soil nitrogen and for potential mineralization experiments. This fraction was collected into a sample tin, sealed with electrical tape, and stored on ice.

Soils samples for  $\text{NH}_4^+$  and  $\text{NO}_3^-$  analyses were stored in the laboratory at  $-30^\circ\text{C}$ . Inorganic nitrogen was extracted in 5:1 (v/w) 2 M KCl after passing the soil through a 2 mm sieve. The  $\text{NH}_4^+$  in the extract was measured using an autoanalyzer (Model CFA-200, Scientific Instruments, Hawthorne, NY, USA). Devarda alloy was then added to the extract to reduce  $\text{NO}_3^-$  to  $\text{NH}_4^+$  (Keeney and Nelson 1982), and the  $\text{NH}_4^+$  concentration again determined. The amount of  $\text{NO}_3^-$  was taken to be the difference between the final and initial  $\text{NH}_4^+$  concentrations.

Total soil nitrogen was determined in duplicate for each sample by Kjeldahl analysis. Soil samples (ca. 2 g DW) were passed through a 2 mm sieve, combined with 4 ml 18 M  $\text{H}_2\text{SO}_4$ , 1.5 g  $\text{K}_2\text{SO}_4$ , and 50 mg  $\text{CuSO}_4 \cdot 5\text{H}_2\text{O}$ , heated at  $100^\circ\text{C}$  for 1 h, followed by heating at  $350^\circ\text{C}$  for 6 h on a block digester (Model AD-40, Scientific Instruments, Hawthorne, NY, USA). The  $\text{NH}_4^+$  in the digest was determined using the autoanalyzer.

Over small gradients, total soil nitrogen concentration may not accurately indicate the potential for soils to produce nitrogen available for plants (Binkley and Vitousek 1989), and so mineralizable nitrogen determined from anaerobic incubations was used as an index of potential plant-available nitrogen (Keeney 1982; Binkley and Vitousek 1989). Duplicate samples were sealed in 25-ml vials under waterlogged conditions and incubated for 14 days at  $40^\circ\text{C}$  (Keeney 1982). The  $\text{NH}_4^+$  in each sample was measured using the autoanalyzer before and after the incubation, following extraction with 2 M KCl. Mineralizable nitrogen was calculated as the difference between the final and initial  $\text{NH}_4^+$  concentrations.

Samples for determination of soil moisture were divided into three subsamples. Soil moisture was measured gravimetrically after drying each subsample at  $75^\circ\text{C}$  for at least 48 h.

#### Plant nitrogen and water

Leaf samples for analysis of nitrogen isotopic composition were collected from each of the tagged plants throughout the year. Leaf material was gathered from all sides of the canopy, and samples were divided into the current year's new growth and growth that occurred during the previous year. Leaf samples were also gathered from *Senecio spartioides*, a shallow-rooted herbaceous perennial, during May. All leaf material was dried at  $75^\circ\text{C}$  for at least 48 h and then ground.

Xylem pressure potentials for all individuals were measured before dawn on each date using a pressure chamber (Model 1000, PMS Instrument Company, Corvallis, Ore., USA). Two measurements were made for each plant. Stem samples were collected on each date for measurement of the isotopic composition of hydrogen within xylem water. Collection procedures followed Flanagan et al. (1992).

#### Isotopic analysis

The isotopic composition of nitrogen within leaf and soil samples were analyzed following Evans and Ehleringer (1993). The isotopic composition of hydrogen within soil and plant water was analyzed following Flanagan et al. (1992). All isotope ratios were determined on a mass spectrometer (Delta S, Finnigan MAT, San Jose, Calif. USA). Isotope ratios are expressed in delta ( $\delta$ ) notation as

$$\delta X = \left( \frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) \times 1000\text{‰}$$

where X is either nitrogen or hydrogen, and R refers to the ratio of the heavier to the lighter isotope for the sample and standard. The standard used for  $\delta^{15}\text{N}$  is atmospheric nitrogen, and the standard for  $\delta\text{D}$  is standard mean ocean water (SMOW).

#### Statistical analysis

The slopes and intercepts of correlation equations were tested following Neter et al. (1985). Potential mineralization (depth  $\times$  location), plant  $\delta^{15}\text{N}$  (age  $\times$  date), and plant xylem pressure potentials and  $\delta\text{D}$  (date  $\times$  species) were analyzed as a two-factor factorial within a randomized block experimental design. Soil inorganic nitrogen,  $\delta\text{D}$ , and soil moisture were analyzed as a three-factor (depth  $\times$  location  $\times$  date) factorial within a randomized block experimental design. Comparison between inter- and intra-canopy locations, and species comparisons were analyzed as a single factor within a randomized block experimental design. All statistical comparisons were made using full and reduced regression models (Neter et al. 1985). Mean values were compared using a Waller-Duncan multiple range test.

## Results

### Soil nitrogen

Mineralizable nitrogen exhibited considerable spatial variation within the soil (Fig. 1). Mineralizable nitrogen was greatest in surface soils in intra-canopy locations, and values were over 55% greater than inter-canopy locations. Mineralizable nitrogen was not significantly different between inter-canopy soils at any depth. Mineralizable nitrogen decreased significantly with depth for all locations: from 11.3 to  $1.8 \mu\text{g NH}_4^+\text{-N g}^{-1}$  under *Juniperus* canopies, and from 7.2 to  $1.8 \mu\text{g NH}_4^+\text{-N g}^{-1}$  for soils in the inter-canopy.

Mineralizable nitrogen was dependent upon total soil nitrogen concentration at all locations (Fig. 2). Neither the slopes ( $P = 0.4334$ ) nor intercepts ( $P = 0.6047$ ) of the correlation equations were significantly

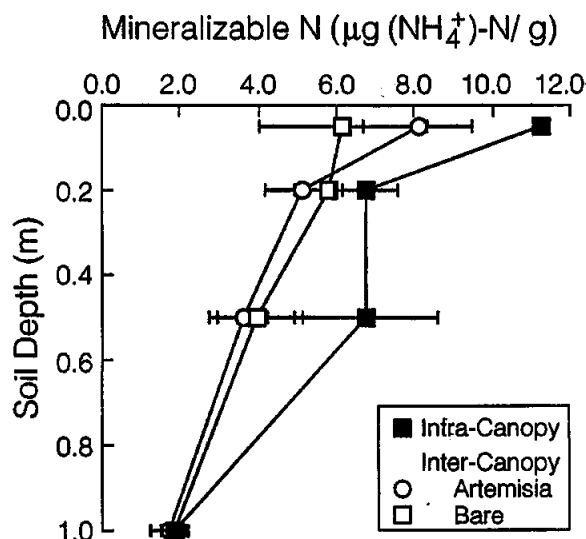


Fig. 1 Mineralizable nitrogen for soils located beneath *Juniperus osteosperma* in the intra-canopy, or in bare areas or adjacent to *Artemisia tridentata* in the inter-canopy. Soil depth is distance below the surface of the mineral soil. Each point is the mean ( $\pm$  SE) of three values

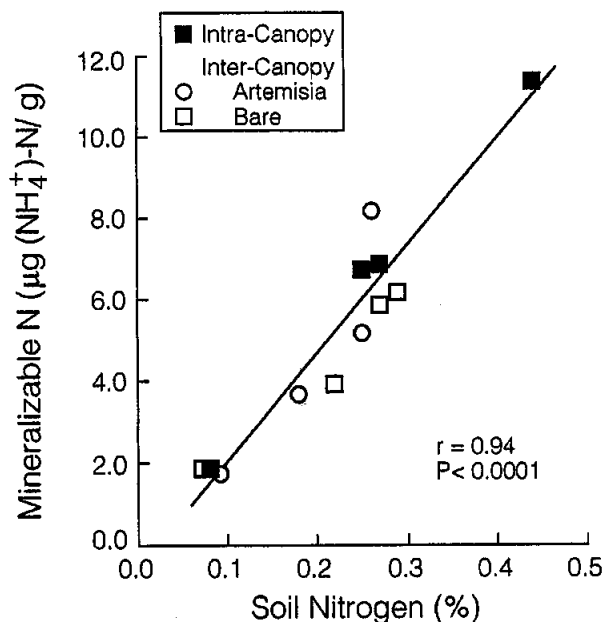


Fig. 2 The relationship between mineralizable nitrogen and total soil nitrogen for soils located beneath *Juniperus osteosperma* in the intra-canopy, or in bare areas or adjacent to *Artemisia tridentata* in the inter-canopy. Each point is the mean of three observations for a single depth at a location. The statistical correlations for the three locations are not significantly different

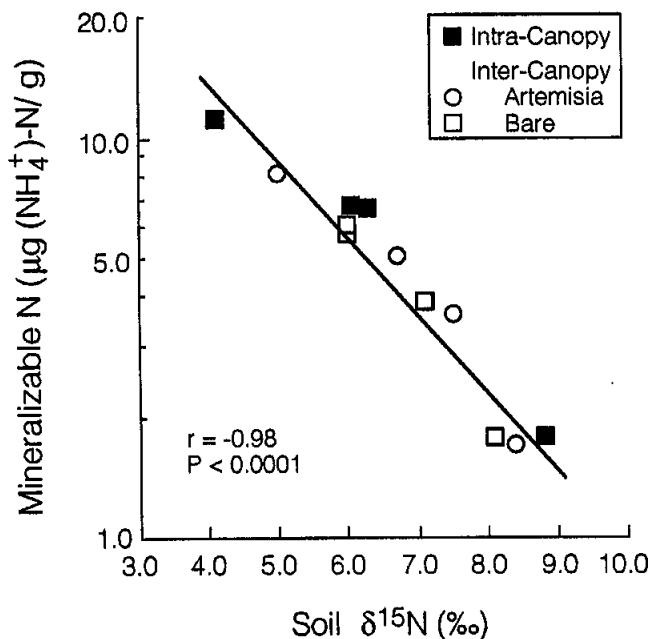


Fig. 3 The relationship between mineralizable nitrogen and total soil  $\delta^{15}\text{N}$  for soils located beneath *Juniperus osteosperma* in the intra-canopy, or in bare areas or adjacent to *Artemisia tridentata* in the inter-canopy. The statistical correlations for the three locations are not significantly different

different, indicating that the relationship between mineralizable nitrogen and total soil nitrogen was identical for all locations at the site. The relationship between mineralizable nitrogen and total soil nitrogen was positive and the intercept was not significantly different from zero ( $P = 0.4391$ ).

Mineralizable nitrogen was also strongly correlated with the  $\delta^{15}\text{N}$  of total soil nitrogen for all locations (Fig. 3). As with total soil nitrogen, neither the slopes ( $P = 0.5231$ ) nor intercepts ( $P = 0.4391$ ) were significantly different among locations. This indicates that the potential to produce plant-available nitrogen was directly correlated with the  $\delta^{15}\text{N}$  of total soil nitrogen, regardless of spatial location.

Soil inorganic nitrogen concentration varied both spatially and temporally (Fig. 4). Surface soils in the intra-canopy had significantly greater total inorganic nitrogen concentrations than inter-canopy soils during May. Inorganic nitrogen concentrations in the intra-canopy were over 150% greater than soils located in either inter-canopy location, and this difference can almost entirely be attributed to higher concentrations of  $\text{NO}_3^-$ . Inorganic nitrogen concentrations did not differ between locations below 0.1 m depth. Soil in the intra-canopy also had significantly greater inorganic nitrogen concentrations during July, but concentrations for all depths and locations were generally less than  $2.0 \mu\text{g N g}^{-1}$ .

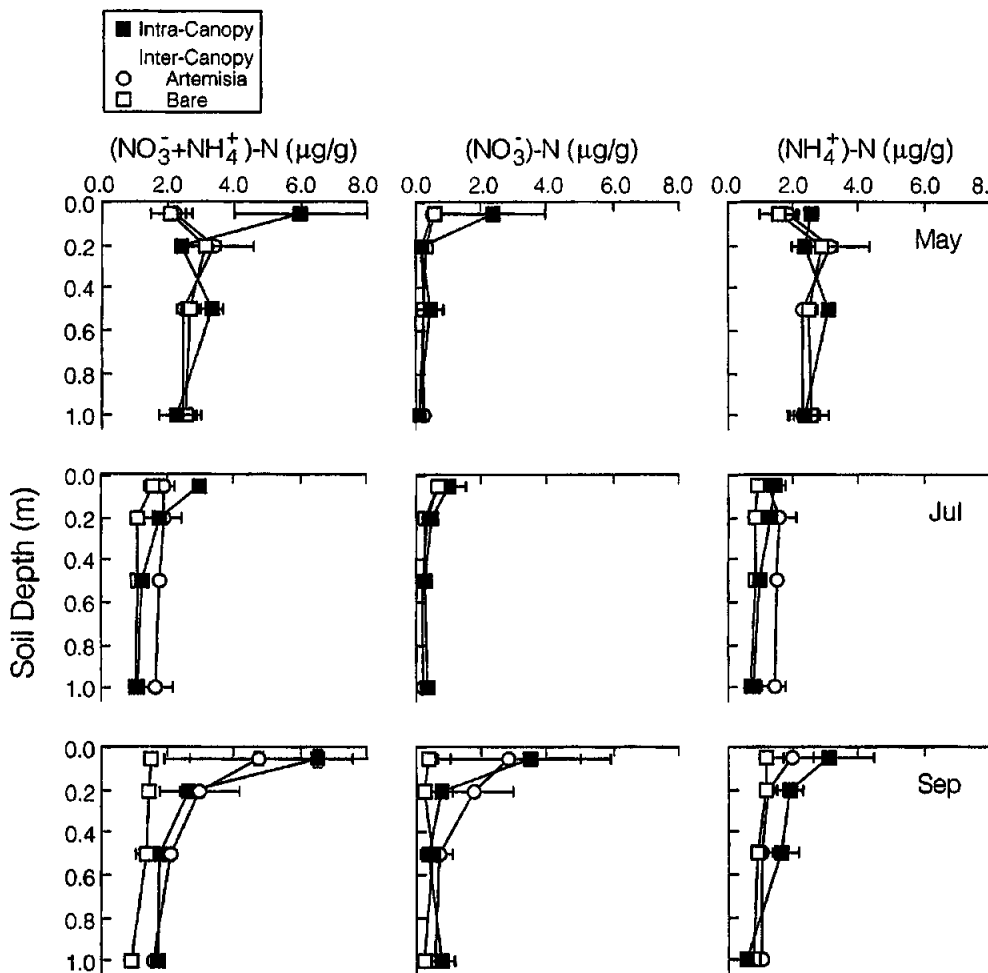
The greatest inorganic nitrogen concentrations occurred during September shortly after a rain storm. Surface soils under *Juniperus* ( $6.5 \mu\text{g N g}^{-1}$ ) in the intra-canopy and adjacent to *Artemisia* ( $4.7 \mu\text{g N g}^{-1}$ ) in the inter-canopy had greater total inorganic nitrogen concentrations than soils located in the bare spaces ( $1.5 \mu\text{g N g}^{-1}$ ), due to higher concentrations of  $\text{NO}_3^-$ .  $\text{NH}_4^+$  concentrations were also greatest under *Juniperus* canopies.

#### Plant nitrogen

The  $\delta^{15}\text{N}$  of the dominant plant species was significantly different between locations (Table 1). The mean  $\delta^{15}\text{N}$  of plants located in the intra-canopy was 0.9‰, compared to 2.7‰ for plants located in the inter-canopy. The  $\delta^{15}\text{N}$  was not significantly different between plants in the inter-canopy spaces. *Juniperus* did have significantly lower  $\delta^{15}\text{N}$  values than other species in intra-canopy locations, but no other species were significantly different ( $\bar{x} = 1.1\text{‰}$ ).

The  $\delta^{15}\text{N}$  of *Artemisia* and *Juniperus* foliage did not vary seasonally (Fig. 5). The mean  $\delta^{15}\text{N}$  values for all measurements were 0.3‰ for *Juniperus*, and 1.1‰ and 2.6‰ for *Artemisia* in the intra- and inter-canopy locations, respectively.  $\delta^{15}\text{N}$  of *Pinus* did vary between sampling dates:  $\delta^{15}\text{N}$  values in September and March

**Fig. 4** Inorganic nitrogen concentrations during May, July, and September for soils located beneath *Juniperus osteosperma* in the intra-canopy, or in bare areas or adjacent to *Artemisia tridentata* in the inter-canopy. Soil depth is distance below the surface of the mineral soil. Each point is the mean ( $\pm$  SE) of three observations



were significantly greater than values in May. However, this difference was less than 0.6‰. *Chrysothamnus* leaves exhibited the greatest seasonal change in  $\delta^{15}\text{N}$ . Values increased throughout the year, from 2.6‰ after leaf flush in May to over 4.5‰ in September.

In no instance did  $\delta^{15}\text{N}$  differ between different aged leaves for any species (Fig. 5). The maximum difference was 0.3‰ for *Juniperus* in July, and all other differences were less than 0.2‰. The  $\delta^{15}\text{N}$  value for *Juniperus* leaf litter underneath the tree canopies ( $\bar{x} = 0.4$ ‰) was not significantly different from *Juniperus* foliage ( $\bar{x} = 0.3$ ‰).

#### Plant and soil water

Xylem pressure potentials exhibited contrasting patterns among species throughout the year (Fig. 6). Xylem pressure potentials were above  $-0.8$  MPa for *Artemisia*, *Juniperus*, and *Pinus* during May, and declined to a low of  $-2.1$  MPa for *Pinus* and *Artemisia*, and  $-2.8$  MPa for *Juniperus*, during August. Xylem

pressure potentials for all three species increased above  $-1.0$  MPa following rain in September. In contrast to other species, xylem pressure potentials of *Chrysothamnus* did not change significantly throughout the year ( $\bar{x} = -0.7$  MPa).

Soil moisture was not significantly different between locations at any time during the year, and so values are presented as means of inter- and intra-canopy locations. Soil moisture increased with depth during May and July (Fig. 7); soil moisture at 1.0 m was 3.2% in May and 1.7% during July. Soil moisture at 0.05 m was 0.3% on both dates. Soil moisture at 1 m continued to decline through the summer and values decreased to 1.1% during September. A rainstorm saturated the upper 0.5 m of the soil 2 days prior to sampling during September, and soil moisture increased to 4.5% in the upper 0.25 m of the soil.

The  $\delta\text{D}$  of soil water also did not differ between canopy locations throughout the year: the maximum difference was during July at 1 m depth, when the  $\delta\text{D}$  of soils under the *Juniperus* canopy was 8‰ less than soils in the inter-canopy spaces.  $\delta\text{D}$  did not vary with depth

**Table 1** The  $\delta^{15}\text{N}$  of the dominant plant species near Coral Pink State Park during May. *Intra-canopy* indicates plants associated with tree (*Pinus* or *Juniperus*) canopies, and *inter-canopy* refers to plants located between tree canopies

| Species                        | Intra-canopy  | Inter-canopy  |
|--------------------------------|---------------|---------------|
| <i>Juniperus osteosperma</i>   | $0.2 \pm 0.3$ |               |
| <i>Pinus edulis</i>            | $1.0 \pm 0.3$ |               |
| <i>Artemisia tridentata</i>    | $1.1 \pm 0.3$ | $2.7 \pm 0.4$ |
| <i>Chrysothamnus nauseosus</i> |               | $2.6 \pm 0.5$ |
| <i>Senecio spartioides</i>     | $1.1 \pm 0.1$ | $2.9 \pm 0.4$ |

during May ( $\bar{x} = -111\text{‰}$ ). The  $\delta\text{D}$  of soil water varied with depth during July, as  $\delta\text{D}$  at 0.2 m increased to  $-99\text{‰}$ .  $\delta\text{D}$  values were not significantly different between other depths ( $\bar{x} = -111\text{‰}$ ). The rainstorm during September caused significant increases in  $\delta\text{D}$  in the top 0.5 m of the soil. Soil water  $\delta\text{D}$  increased to  $-57\text{‰}$  in the top 0.25 m of the soil, and to  $-95\text{‰}$  at 0.5 m.  $\delta\text{D}$  at 1 m was  $-98\text{‰}$  during September.

The  $\delta\text{D}$  of xylem water exhibited contrasting patterns throughout the season among the four species (Fig. 7).  $\delta\text{D}$  did not differ between species during May ( $\bar{x} = -108\text{‰}$ ). The stem water  $\delta\text{D}$  of *Pinus* and *Juniperus* were not significantly different in July ( $\bar{x} = -105\text{‰}$ ). *Artemisia* had significantly lower  $\delta\text{D}$  ( $-114\text{‰}$ ) than either tree species. Both *Artemisia* and *Pinus* responded to rain in September. The  $\delta\text{D}$  values increased to  $-59$  and  $-61\text{‰}$  for *Artemisia* and *Pinus*, respectively. However, *Chrysothamnus* did not respond to the rain during September. The response to summer rain by *Juniperus* individuals was not uniform; one group of individuals all had stem-water  $\delta\text{D}$  values less

than  $85\text{‰}$  ( $\bar{x} = -95\text{‰}$ ), while another had values greater than  $60\text{‰}$  ( $\bar{x} = -58\text{‰}$ ).

### Artemisia comparison

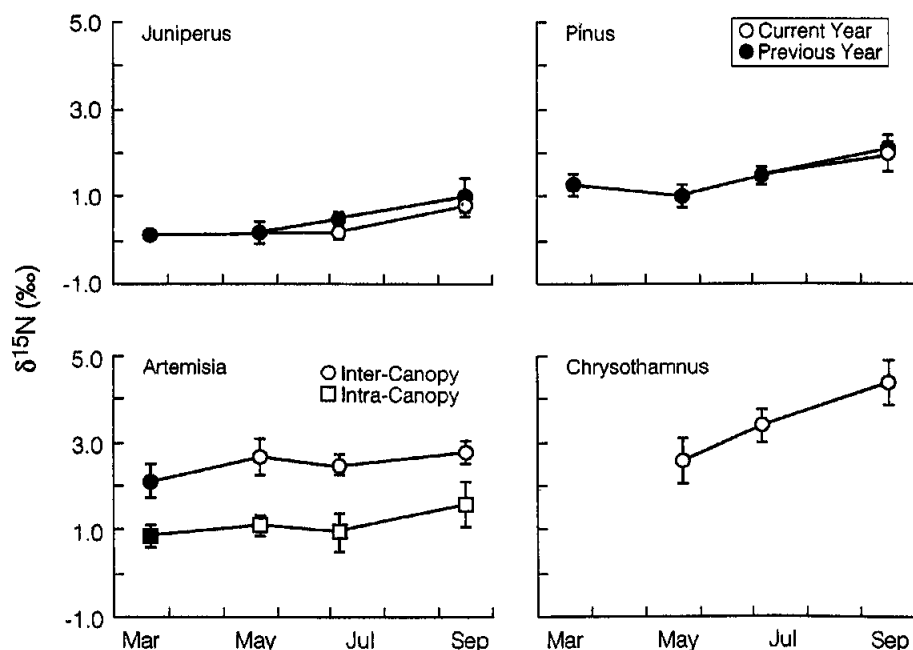
*Artemisia* was the only species that occurred in both intra- and inter-canopy locations. Nitrogen concentrations of plants in the intra-canopy location were over 20% greater than those in the inter-canopy location, and this corresponded to a 1.6‰ difference in leaf  $\delta^{15}\text{N}$  (Table 2). The nitrogen concentrations of soil in the intra-canopy location were over 60% greater than those in the inter-canopy locations, corresponding to a 1.9‰ difference in  $\delta^{15}\text{N}$ . Xylem pressure potentials and stem-water  $\delta\text{D}$  were not significantly different between plants growing in the two locations (Table 2).

## Discussion

### Spatial patterns

Plant  $\delta^{15}\text{N}$  values directly reflect spatial variability in soil  $\delta^{15}\text{N}$ . Direct comparisons between soil and plant  $\delta^{15}\text{N}$  are not valid because fractionation may alter the  $\delta^{15}\text{N}$  of plant-available nitrogen compared to organic nitrogen (Shearer and Kohl 1986; Nadelhoffer and Fry 1988). However, the  $\delta^{15}\text{N}$  values of species at each location closely match that of *Senecio*. The roots of this herbaceous species were observed only in the top 20 cm of the soil, and so *Senecio* serves as a "reference plant" (*sensu* Shearer and Kohl 1986) for the  $\delta^{15}\text{N}$  of plant-available nitrogen at this depth. The similarity in  $\delta^{15}\text{N}$

**Fig. 5** The  $\delta^{15}\text{N}$  of the dominant species near Coral Pink State Park. Each point is the mean ( $\pm$  SE) of five observations



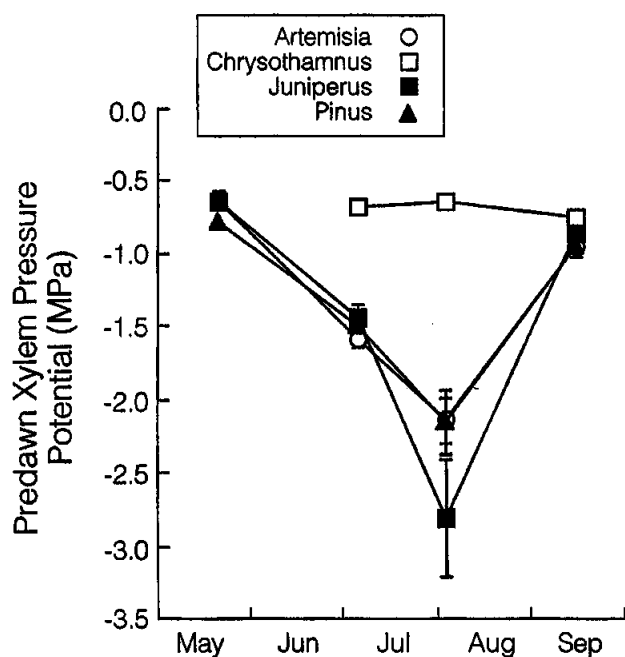


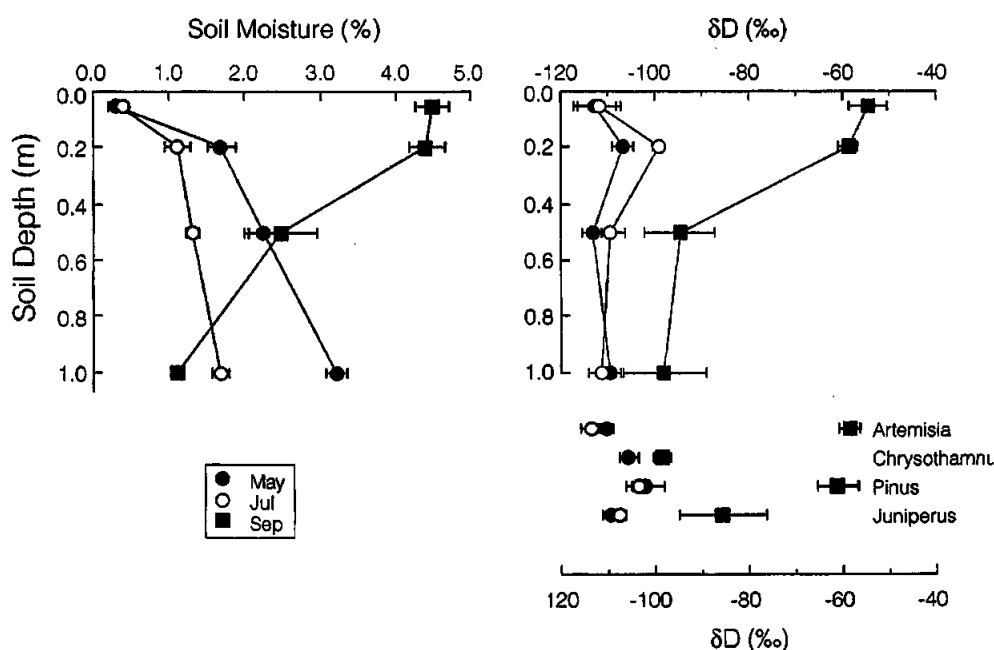
Fig. 6 The xylem pressure potential before dawn of the dominant species near Coral Pink State Park. Values for *Artemisia tridentata* are from shrubs in the inter-canopy locations. Leaves of *Chrysothamnus nauseosus* were not present during May. Each point is the mean ( $\pm$  SE) of five observations

between *Senecio* and the woody perennials at each spatial location suggests that in spring, all species were preferentially using nitrogen from the top 20 cm of the soil.

The  $\delta^{15}\text{N}$  of the plant-available inorganic nitrogen pool can be modified relative to the organic nitrogen pool by mineralization, nitrification, immobilization, and gaseous nitrogen loss (Nadelhoffer and Fry 1994), and the fractionation associated with each can be significant (Shearer and Kohl 1986; Handley and Raven 1992). Fractionation during mineralization is likely to be the controlling factor for the pattern observed here. The differences between the  $\delta^{15}\text{N}$  of inorganic nitrogen as estimated using *Senecio* and that of soil organic nitrogen was alike for inter- ( $-3.1\%$ ) and intra-canopy ( $-3.0\%$ ) locations, and both values are similar to earlier estimates of discrimination during net mineralization ( $-1.8\%$ ) (Evans and Ehleringer 1993).

The increase in soil  $\delta^{15}\text{N}$  as nitrogen concentration decreases follows a Rayleigh Distillation model (Evans and Ehleringer 1993). This model predicts that decomposition and subsequent gaseous nitrogen loss will cause a decrease in soil nitrogen concentration, and fractionation during these processes will increase the  $\delta^{15}\text{N}$  of residual soil nitrogen (Nadelhoffer and Fry 1994). Nitrogen input from decomposition of the cryptobiotic crust ( $\delta^{15}\text{N} = -0.4\%$ ) will cause the  $\delta^{15}\text{N}$  of undisturbed soils to remain relatively low at the soil surface, but nitrogen input does not continue in disturbed locations resulting in lower nitrogen concentrations and greater  $\delta^{15}\text{N}$  as decomposition continues. The importance of the cryptobiotic crust was apparent in the  $\delta^{15}\text{N}$  values of plants in the intra-canopy locations. The  $\delta^{15}\text{N}$  of species in arid regions that derive a significant amount of nitrogen from nitrogen fixation will approach  $0\%$  (Shearer et al. 1983), while the  $\delta^{15}\text{N}$  of species not capable of nitrogen fixation is usually

Fig. 7 Percentage soil moisture, and the  $\delta\text{D}$  of soil and plant water near Coral Pink State Park. Soil moisture and  $\delta\text{D}$  were not significantly different between locations, and values were grouped for each depth on a sampling date. Soil depth is distance below the surface of the mineral soil. Each point represents the mean ( $\pm$  SE) of 10 observations for soil  $\delta\text{D}$ , 15 observations for soil moisture, and 5 observations for plant  $\delta\text{D}$



**Table 2.** Characteristics of *Artemisia tridentata* and soils in the inter- and intra-canopy locations. Soil values are for the 0–0.10 m depth. *ns* no significant difference, *XPP* predawn xylem pressure potential

|                           |           | Intra-canopy    | Inter-canopy    | Significance |
|---------------------------|-----------|-----------------|-----------------|--------------|
| <i>Artemisia</i>          |           |                 |                 |              |
| $\delta^{15}\text{N}$ (‰) |           | 1.1 $\pm$ 0.3   | 2.7 $\pm$ 0.4   | $p < 0.0001$ |
| N (%)                     |           | 2.9 $\pm$ 0.2   | 2.4 $\pm$ 0.2   | $p < 0.0001$ |
| $\delta\text{D}$ (‰)      | July      | –114 $\pm$ 2    | –119 $\pm$ 4    | <i>ns</i>    |
|                           | September | –59 $\pm$ 2     | –62 $\pm$ 5     | <i>ns</i>    |
| XPP (MPa)                 | July      | –1.9 $\pm$ 0.1  | –2.1 $\pm$ 0.2  | <i>ns</i>    |
|                           | September | –1.1 $\pm$ 0.1  | –1.0 $\pm$ 0.1  | <i>ns</i>    |
| Soil                      |           |                 |                 |              |
| $\delta^{15}\text{N}$ (‰) |           | 4.1 $\pm$ 0.0   | 6.0 $\pm$ 0.0   | $p < 0.0001$ |
| N (%)                     |           | 0.44 $\pm$ 0.03 | 0.29 $\pm$ 0.07 | $p < 0.0001$ |

greater than 5‰ (Shearer et al. 1983; Ehleringer et al. 1992). However, the  $\delta^{15}\text{N}$  of all species in intra-canopy locations approached 0‰, even though none are capable of nitrogen fixation.

Mineralization potential was strongly correlated with soil  $\delta^{15}\text{N}$ . Mineralization rates are determined by available substrate, temperature, and moisture. In the experiments presented here, temperature and moisture were held constant, and so differences were directly related to nitrogen concentration. Soil  $\delta^{15}\text{N}$  is also mechanistically linked to soil nitrogen concentration, and so the correlation between  $\delta^{15}\text{N}$  and mineralization potential is not unexpected. This relationship suggests that plant  $\delta^{15}\text{N}$  values may reflect the potential for the nitrogen source to produce plant-available nitrogen. This was apparent for *Artemisia*. Individuals growing intra-canopy had lower  $\delta^{15}\text{N}$  values and higher leaf nitrogen concentrations than individuals in the inter-canopy. *Artemisia* often responds to an increase in available nitrogen by increasing leaf nitrogen concentration (Doescher et al. 1990). An increase in leaf nitrogen is significant, because leaf photosynthetic rates are often strongly correlated with leaf nitrogen concentration (Field and Mooney 1986), and maximum photosynthetic rates are directly related to leaf nitrogen concentration in *Artemisia* (Delucia and Schlesinger 1991), *Pinus* (Lajtha and Barnes 1991), and *Juniperus* (Marshall et al., In press).

The inter-specific differences in plant  $\delta^{15}\text{N}$  values within a location were small ( $< 0.4\text{‰}$ ), except for *Juniperus* growing in intra-canopy locations ( $> 0.8\text{‰}$ ). Differences in mycorrhizal associations between species can cause similar differences in plant  $\delta^{15}\text{N}$  values: Högborg (1990) observed that species with VA (vesicular arbuscular) mycorrhizae had  $\delta^{15}\text{N}$  values that were 1–2.5‰ less than trees with ecto-mycorrhizae. However, all species in this study are associated with VA mycorrhizae, except for *Pinus*, whose association is ecto-mycorrhizal (M. Allen, personal communication). The differences in  $\delta^{15}\text{N}$  observed between *Juniperus* and the other species may instead be explained by the distribution of hyphae within the soil. The hyphae of mycorrhizae associated with *Juniperus* intermix with

the cryptobiotic crust, while those of *Artemisia*, *Pinus*, and *Chrysothamnus* are distributed below the crust (M. Allen, personal communication). This distribution may explain the differences in plant  $\delta^{15}\text{N}$  values; hyphae of *Juniperus* are located closer to cryptobiotic crust and therefore would utilize nitrogen from organic matter that had undergone less decomposition than that found slightly deeper in the soil.

### Temporal patterns

Temporal patterns of nitrogen acquisition were closely tied to patterns of water use. All species had similar xylem pressure potentials and  $\delta\text{D}$  during May. The uniformity of soil water  $\delta\text{D}$  precludes any estimation of active zones of water uptake, but the similarity in  $\delta^{15}\text{N}$  between *Senecio* and the other species indicates all were acquiring nitrogen from near the soil surface. Two patterns of response to water deficits were observed as soils dried during July. The xylem pressure potentials and  $\delta\text{D}$  of *Pinus*, *Artemisia*, and *Juniperus* all changed in response to the episodic availability of water at the soil surface. In contrast, *Chrysothamnus* apparently switched to a more constant water source at depth in the soil; xylem pressure potentials did not change during drought, and no response was observed to increased soil water following rain during September. This is the same pattern observed in previous years at this site (Flanagan and Ehleringer 1991; Flanagan et al. 1992).

The temporal availability of plant-available inorganic nitrogen near the soil surface is likely to be episodic.  $\text{NO}_3^-$  and  $\text{NH}_4^+$  concentrations were low during July, but this may result from plant uptake rather than low availability (Binkley and Vitousek 1989). The pattern of soil water  $\delta\text{D}$  suggests low availability. The increase in  $\delta\text{D}$  at 0.2 m is characteristic of fractionation during evaporation and movement of water through the soil (Barnes and Allison 1988). The point of the maximum  $\delta\text{D}$  value is where most evaporation is taking place (Barnes and Allison 1983), because fractionation during evaporation causes



water to become isotopically heavier over time. Water moves above this point as a vapor by diffusion, while water transport below this maximum is via liquid transport toward the evaporating surface (Barnes and Allison 1983). Water movement primarily in the vapor phase would not be conducive to diffusion of nutrients to the root (Nye and Tinker 1977).

The  $\delta^{15}\text{N}$  values of *Pinus*, *Artemisia*, and *Juniperus* suggest that these species continued to rely on episodic periods of nitrogen availability at the soil surface. *Pinus* and *Juniperus* complete vegetative growth, and *Artemisia* reproductive growth (Evans et al. 1991; Evans and Black 1993), during summer months. These species may rely on nitrogen reallocated from older leaves when soil nitrogen is not available to support growth during summer. New growth in *Pinus* and *Juniperus* coincided with abscission of older leaves, and reproductive growth in *Artemisia* occurs after abscission of vegetative leaves (Evans and Black 1993). From 35 to 53% of the nitrogen in leaves of these species can be reabsorbed before abscission (Schlesinger et al. 1989). Reallocation of nitrogen can be accompanied by fractionation (Shearer et al. 1983; Gebauer and Schulze 1991), but no differences were observed for any species either between different aged leaves on a plant, or with leaf abscission.

The water-use pattern observed for *Chrysothamnus* is typical of many aridland perennials that shift to more stable water sources at depth during summer drought (Ehleringer et al. 1991). The increase in plant  $\delta^{15}\text{N}$  also indicates that *Chrysothamnus* is switching to a nitrogen source with a higher  $\delta^{15}\text{N}$  than found at the soil surface. Flanagan et al. (1992) demonstrated that *Chrysothamnus* relied on ground water during summer drought. This may also explain the seasonal increase in plant  $\delta^{15}\text{N}$ . We measured the  $\text{NO}_3^-$  concentration and isotopic composition of this water and found 1.4 mM  $\text{NO}_3^-$  with a  $\delta^{15}\text{N}$  of 5.9‰. This indicates that the expected trade-off between water and nitrogen use may not exist, because ground water is also a stable nitrogen source. This may have a significant impact on nitrogen cycling in arid regions, because it suggests a mechanism whereby plant species relying on groundwater can transfer nitrogen to the soil surface. This may be especially pronounced in disturbed areas because disturbance is often accompanied by an increase in woody perennial species such as *Chrysothamnus* (Daubenmire 1970).

The contrasting patterns of resource acquisition by co-occurring species may have important implications for community stability in aridlands. The primary source of nitrogen input in these communities is nitrogen fixation by the cryptobiotic crust. Disturbance of the crust by anthropogenic activity is currently widespread, and soil fertility may decrease because the primary source of input is eliminated, and gaseous nitrogen loss continues (Evans and Ehleringer 1993). Our results suggest species that rely on the episodic

availability of water and nitrogen at the soil surface may be most severely affected by disturbance. In contrast, woody perennials that switch to more stable water sources at depth during drought may not be as severely affected.

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## References

- Barnes CJ, Allison GB (1983) The distribution of deuterium and  $^{18}\text{O}$  in dry soils. 1. Theory. *J Hydrol (Amst)* 60: 141–156
- Barnes CJ, Allison GB (1988) Tracing of water movement in the unsaturated zone using stable isotopes of hydrogen and oxygen. *J Hydrol (Amst)* 100: 143–176
- Belnap J (1993) Recovery rates of cryptobiotic crusts: inoculant use and assessment methods. *Great Basin Nat* 53: 89–95
- Binkley D, Vitousek P (1989) Soil nutrient availability. In: Pearcy RW, Ehleringer JR, Mooney HA, Rundel PW (eds) *Plant physiological ecology. Field methods and instrumentation*. Chapman and Hall, New York, pp 75–96
- Burke IC (1989) Control of nitrogen mineralization in a Sagebrush Steppe landscape. *Ecology* 70: 1115–1126
- Chapin FS, Bloom AJ, Field C, Waring RH (1987) Plant responses to multiple environmental factors. *Bioscience* 37: 49–57
- Charley JL, West NE (1977) Micro-patterns of nitrogen mineralization activity in soils of some shrub-dominated semi-desert ecosystems of Utah. *Soil Biol Biochem* 9: 357–365
- Daubenmire R (1970) *Steppe vegetation of Washington*. Washington Agricultural Experiment Station Technical Bulletin 72, Pullman
- Dawson TE, Ehleringer JR (1991) Streamside trees that do not use stream water. *Nature* 350: 335–337
- DeLucia EH, Schlesinger WH (1991) Resource-use efficiency and drought tolerance in adjacent Great Basin and Sierran plants. *Ecology* 72: 51–58
- Doescher PS, Miller RF, Wang J, Rose J (1990) Effects of nitrogen availability on growth and photosynthesis of *Artemisia tridentata* ssp. *wyomingensis*. *Great Basin Nat* 50: 9–19
- Ehleringer JR, Dawson TE (1992) Water uptake by plants: perspectives from stable isotope composition. *Plant Cell Environ* 15: 1073–1082
- Ehleringer JR, Phillips SL, Schuster WSF, Sandquist DR (1991) Differential utilization of summer rains by desert plants. *Oecologia* 88: 430–434
- Ehleringer JR, Mooney HA, Rundel PW, Evans RD, Palma B, Delatorre J (1992) Lack of nitrogen cycling in the Atacama Desert. *Nature* 359: 316–318
- Ettershank G, Ettershank J, Bryant M, Whitford WG (1978) Effects of nitrogen fertilization on primary production in a Chihuahuan desert ecosystem. *J Arid Environ* 1: 135–139
- Evans RD, Black RA (1993) Growth, photosynthesis, and resource investment for vegetative and reproductive modules of *Artemisia tridentata*. *Ecology* 74: 1516–1528
- Evans RD, Ehleringer JR (1993) A break in the nitrogen cycle of aridlands: evidence from  $\delta^{15}\text{N}$  of soils. *Oecologia* 94: 314–317
- Evans RD, Black RA, Link SO (1991) Reproductive growth during drought in *Artemisia tridentata*. *Funct Ecol* 5: 676–683

- Field C, Mooney HA (1986) The photosynthesis-nitrogen relationship in wild plants. In: Givnish TJ (ed) *On the economy of plant form and function*. Cambridge University Press, Cambridge, pp 25–55
- Fisher FM, Zak JC, Cunningham GL, Whitford WG (1988) Water and nitrogen effects on growth and allocation patterns of creosotebush in the northern Chihuahuan Desert. *J Range Manage* 41: 387–391
- Flanagan LB, Ehleringer JR (1991) Stable isotope composition of stem and leaf water: applications to the study of plant water use. *Funct Ecol* 5: 270–277
- Flanagan LB, Ehleringer JR, Marshall JD (1992) Differential uptake of summer precipitation among co-occurring trees and shrubs in a pinyon-juniper woodland. *Plant Cell Environ* 15: 831–836
- Garten CT (1993) Variation in foliar  $^{15}\text{N}$  abundance and the availability of soil nitrogen on Walker Branch watershed. *Ecology* 74: 2098–2113
- Gebauer G, Schulze E-D (1991) Carbon and nitrogen isotope ratios in different compartments of a healthy and a declining *Picea abies* forest in the Fichtelgebirge, NE Bavaria. *Oecologia* 87: 198–207
- Handley LL, Raven JA (1992) The use of natural abundance of nitrogen isotopes in plant physiology and ecology. *Plant Cell Environ* 15: 965–985
- Harper KT, Marble JR (1988) A role for nonvascular plants in management of arid and semiarid regions. In: Tueller PT (ed) *Vegetation science applications for rangeland analysis and management*. Kluwer, Boston, pp 135–169
- Högberg P (1990)  $^{15}\text{N}$  natural abundance as a possible marker of the ectomycorrhizal habit of trees in mixed African woodlands. *New Phytol* 115: 483–486
- Keeney DR (1982) Nitrogen-availability indices. In: Page AL, Miller RH, Keeney DR (eds) *Methods of soil analysis. 2. Chemical and microbiological properties*, 2nd edn. American Society of Agronomy, Madison, pp 711–733
- Keeney DR, Nelson DW (1982) Nitrogen – inorganic forms. In: Page AL, Miller RH, Keeney DR (eds) *Methods of soil analysis. 2. Chemical and microbiological properties*, 2nd edn. American Society of Agronomy, Madison, pp 643–698
- Lajtha K, Barnes F (1991) Carbon gain and water use in pinyon pine-juniper woodlands of northern New Mexico: field versus phytotron chamber measurements. *Tree Physiol* 9: 59–67
- Mariotti A, Mariotti F, Champigny M-L, Amarger N, Moyse A (1982) Nitrogen isotope fractionation associated with nitrate reductase activity and uptake of  $\text{NO}_3^-$  by Pearl Millet. *Plant Physiol* 69: 880–884
- Miller RF, Doescher PS, Wang J (1991) Response of *Artemisia tridentata* ssp. *wyomingensis* and *Stipa thurberiana* to nitrogen amendments. *Am Midl Nat* 125: 104–113
- Nadelhoffer KJ, Fry B (1988) Controls on natural nitrogen-15 and carbon-13 abundances in forest soil organic matter. *Soil Sci Soc Am J* 52: 1633–1640
- Nadelhoffer KJ, Fry B (1994) Nitrogen isotope studies in forest ecosystems. In: Lajtha K, Michener R (eds) *Stable isotopes in ecology*. Blackwell, Oxford (in press)
- Neter J, Wasserman W, Kutner MH (1985) *Applied linear statistical models*, 2nd edn. Irwin, Homewood
- Nye PH, Tinker PB (1977) *Solute movement in the soil-root system*. University of California Press, Berkeley
- Schlesinger WH, DeLucia EH, Billings WD (1989) Nutrient-use efficiency of woody plants on contrasting soils in the western Great Basin, Nevada. *Ecology* 70: 105–113
- Schlesinger WH, Reynolds JF, Cunningham GL, Heunneke LF, Jarrell WH, Virginia RA, Whitford WG (1990) Biological feedbacks in global desertification. *Science* 247: 1043–1048
- Schulze E-D (1986) Whole-plant responses to drought. *Aust J Plant Physiol* 13: 127–141
- Sharifi MR, Meinzer FC, Nilsen ET, Rundel PW, Virginia RA, Jarrell WM, Herman DJ, Clark PC (1988) Effect of manipulation of water and nitrogen supplies on the quantitative phenology of *Larrea tridentata* (Creosote Bush) in the Sonoran Desert of California. *Am J Bot* 75: 1163–1174
- Shearer G, Kohl DH (1986)  $\text{N}_2$ -fixation in field settings: estimations based on natural  $^{15}\text{N}$  abundance. *Aust J Plant Physiol* 13: 699–756
- Shearer G, Kohl DH, Virginia RA, Bryan BA, Skeeters JL, Nilsen ET, Sharifi MR, Rundel PW (1983) Estimates of  $\text{N}_2$ -fixation from variation in the natural abundance of  $^{15}\text{N}$  in Sonoran Desert ecosystems. *Oecologia* 56: 365–373
- Turner NC (1986) Adaptation to water deficits: a changing perspective. *Aust J Plant Physiol* 13: 175–190
- Virginia RA, Delwiche CC (1982) Natural  $^{15}\text{N}$  abundance of presumed  $\text{N}_2$ -fixing and non- $\text{N}_2$ -fixing plants from selected ecosystems. *Oecologia* 54: 317–325
- White JWC, Cook ER, Lawrence JR, Broecker WS (1985) The D/H ratios of sap in trees: implications for water sources and tree ring D/H ratios. *Geochim Cosmochim Acta* 49: 237–246
- Yoneyama T, Kaneko A (1989) Variations in the natural abundance of  $^{15}\text{N}$  in nitrogenous fractions of komatsuna plants supplied with nitrate. *Plant Cell Physiol* 30: 957–962