Differential uptake of summer precipitation among co-occurring trees and shrubs in a pinyon-juniper woodland

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ABSTRACT

Measurements of the ratio of deuterium to hydrogen (D/H) in stem xylem water were used to determine the relative uptake of summer precipitation by four co-occurring plant species in southern Utah. The species compared included two trees, *Juniperus osteosperma* and *Pinus edulis*, and two shrubs, *Artemisia tridentata* and *Chrysothamnus nauseosus*. There were significant differences among species in the relative use of summer precipitation. *Chrysothamnus nauseosus* had stem water D/H ratios in May through August 1990 that were not significantly different from that of groundwater. In contrast, the other three species had stem water D/H ratios that were intermediate between the groundwater value and summer precipitation values, indicating that a mixture of both precipitation and groundwater was being used by these species. The two tree species generally had higher D/H values than did *A. tridentata* indicating a higher average uptake of summer precipitation, although the roots of *J. osteosperma* and *P. edulis* may not be as responsive to small precipitation events as *A. tridentata*. There was a strong negative correlation between stem water D/H ratios and predawn water potential, which suggests a relationship between plant rooting pattern and water source use. In addition, water-use efficiency during photosynthetic gas exchange, calculated from leaf carbon isotope composition, differed among species and was strongly correlated with differences in the relative uptake of summer precipitation.

Key-words: stable isotopes; D/H ratios; $^{13}C/^{12}C$ ratios; water-use efficiency; water potential; aridlands; pinyon-juniper woodland.

INTRODUCTION

Soil moisture available to plants in the semi-arid regions of the southwestern United States predominantly comes

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from melting snow, accumulated during the winter months, and winter-spring rains (Caldwell 1985; Dobrowolski, Caldwell & Richards 1990). Summer precipitation is low and highly unpredictable in semi-arid regions (Ehleringer & Mooney 1983), and in general, is only effective in wetting the surface layers of the soil, except in years of very high rainfall (Caldwell 1985).

The significance of summer precipitation for perennial plant growth in aridlands is unclear. Rain mostly occurs in amounts of 10mm or less, and these small amounts are often considered to be unimportant for perennial plants (Noy-Meir 1973; Sala & Lauenroth 1982). However, Sala & Lauenroth (1982) showed that a simulated 5 mm rain caused a significant change in leaf water potential and stomatal conductance in *Bouteloua gracilis* that lasted for up to 2d. In general, the importance of summer rain to plant growth would depend on the amount of summer precipitation, the relative ease that precipitation can penetrate or runoff the soil surface, and the distribution pattern of functional plant roots in the soil (Noy-Meir 1973; Dobrowolski *et al.* 1990). At present, there is little direct information about the use of summer precipitation by perennial plants in semi-arid ecosystems.

It is possible to determine the uptake of summer precipitation by measuring the stable isotopic composition of plant stem water (White *et al.* 1985; White 1988; Flanagan & Ehleringer 1991). Since no isotopic fractionation occurs during water uptake by plant roots (Dawson & Ehleringer 1991), the isotopic composition of water in roots and stems reflects that of the water taken up by roots. In temperate, continental locations the isotopic composition of summer precipitation differs from that of water in the saturated soil zone (groundwater; Dansgaard 1964; Gat 1980). Therefore, it is possible to trace the relative uptake of summer precipitation by measuring the stable isotopic composition of plant stem water (White *et al.* 1985; White 1988; Flanagan & Ehleringer 1991).

Here we report measurements of the stable hydrogen isotope ratio of plant stem water that indicate seasonal differences in the uptake of precipitation among major tree and shrub species in a pinyon-juniper woodland in southern Utah. We have also found that the efficiency of

water-use during photosynthetic gas exchange (estimated from measurements of leaf carbon isotopic composition; Farquhar, Ehleringer & Hubick 1989) varied among species and was strongly correlated with differences in the uptake of summer precipitation.

MATERIALS AND METHODS

Two tree (*Juniperus osteosperma, Pinus edulis*) and two shrub (*Artemisia tridentata, Chrysothamnus nauseosus*) species were examined from a site adjacent to Coral Pink Sand Dunes State Park, Utah (latitude 37°03', longitude 112°45', elevation 1855 m). The vegetation at the site occurs on sand deposits overlaying a perched groundwater table. The four study species represent the major tree and shrub species of this vegetation-type in southern Utah (West 1988). Average precipitation (1941–1988) at the nearest U.S. National Weather Service Station located at Kanab, Utah, approximately 20 Km from the study site, is 319 mm annually. The majority of this precipitation (67%) occurs in the months October through April. The amount of rain normally received during the main growth period (May through September) is approximately 84 mm.

Initial stem water samples, primarily from *J. osteosperma*, were collected during the summer of 1989. Based on the initial results, we planned a more detailed study comparing water use in different species which was conducted in 1990. In April 1990, four locations were chosen where all four study species were growing in close proximity (<5 m apart). At each location one individual from each species was tagged and stem samples were collected from each plant at intervals during the period from April to September 1990. Plant water potential was measured during the May, July and August 1990 collection trips (see Table 2 below for the exact sampling dates) with a pressure chamber (PMS Instrument Co., Corvallis, OR, USA). One small branch sample was cut at approximately the mid-canopy level for each of the four tagged individuals of all species. Water potential was measured before dawn and in the mid-afternoon (approximately 1300–1500 h local time).

Stem samples (approximately 7×60 mm) were cut from the plants in the field and immediately placed in a glass tube which was sealed with a rubber stopper and wrapped with Parafilm. One sample per tagged plant was collected at mid-day on each sampling date (see Table 1 below for the exact sampling dates). The plant samples were frozen until water was extracted from the tissue using a cryogenic vacuum distillation apparatus (see Dalton 1989 for a schematic diagram of an apparatus similar to the one used in our studies; Ehleringer & Osmond 1989).

Summer precipitation was collected in a standard rain gauge or in 100-cm³ beakers (or other similarly sized vessels). Samples of snow accumulated on the study plot were collected in early February in both 1989 and 1990.

Groundwater samples were obtained from a spring at the study site. Environmental water samples were stored in glass vials with a tightly sealing cap and frozen until they were analysed for hydrogen isotopic composition.

Water samples were prepared for measurements of the hydrogen isotopic composition by reacting approximately 5 mm³ of water with zinc (Coleman *et al.* 1982) in an evacuated tube at 500 °C. The zinc was obtained from the laboratory of J.M. Hayes, Departments of Chemistry and Geology, Indiana University. The resulting hydrogen gas was analysed for isotopic composition on either a Finnigan-Mat delta E or delta S gas isotope ratio mass spectrometer. Precision of the measurements of a laboratory standard was ±1·4‰ (see below for unit definition) for the delta E and ±1·0‰ for the delta S mass spectrometers (±SD).

Leaf samples were collected from all four study species for carbon isotopic analysis. Leaves were collected in late August 1990 so that the tissue carbon isotopic compositions would provide information about leaf gas exchange properties integrated over the growing season (Farquhar, Ehleringer & Hubick 1989). For the tree species, current season's needle samples were cut from two canopy heights (approximately one-third and two-thirds of total tree height) at each of the four cardinal compass directions, and combined for each individually tagged tree, dried and finely ground. Current season's leaf tissue was removed from several positions over the whole canopy for the two smaller shrub species, combined for a tagged individual, dried and finely ground. The carbon isotopic composition of purified CO_2, generated from leaf tissue in an in-vial combustion procedure using cupric oxide wire and silver foil as catalysts (Hachey *et al.* 1987; Ehleringer & Osmond 1989), was measured on the mass spectrometers described above.

Isotopic compositions are expressed using delta notation in parts per thousand (‰), $\delta = [R_{Sample}/R_{Standard} - 1] \times 10^3$‰, where R is the molar ratio of heavy to light isotope (D/H or $^{13}C/^{12}C$), the standard for water samples is standard mean ocean water (SMOW) and the standard for carbon samples is Pee Dee Belemnite (PDB) limestone (Ehleringer & Osmond 1989).

RESULTS

The hydrogen isotope composition of groundwater, obtained from a spring located at the study site, was constant throughout the year, with an average δD value of −96±1‰ (±SD, n =15, samples collected at intervals from September 1988 through October 1990). In contrast, the δD values for spring and summer precipitation were higher than the groundwater value and the δD values of winter precipitation were lower than groundwater (Fig. 1), which is typical for continental, temperate locations (Dansgaard 1964; Gat 1980). Since the isotopic composition of the two potential sources for plant water were different during spring and summer,
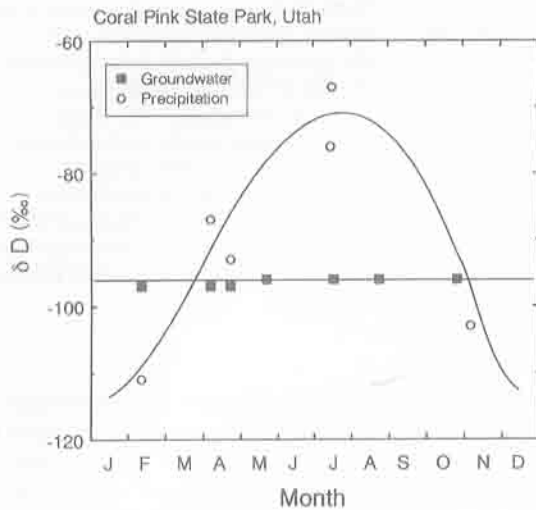
Figure 1. The hydrogen isotope composition (δD, ‰) of groundwater and precipitation at Coral Pink Sand Dunes State Park, Utah, during 1990.

the isotopic composition of plant stem water can be used to determine the relative uptake of summer precipitation.

The stem water samples were collected during the spring and summer months in 1989 and 1990. The majority of the stem water data were collected during 1990, a year which had precipitation amounts similar to the long-term average for the study area. The amount of rain during April–September 1990 was 99% of the long-term average for the area (U.S. National Weather Service Records). In contrast, 1989 was a very dry year. Precipitation during April–September 1989 was only 54% of the long-term average, with only trace amounts of rain in April and June (U.S. National Weather Service Records).

Our stem water D/H sampling during 1989 illustrated three patterns. Firstly, stem water in *A. tridentata* was enriched above that of groundwater, after a trace of

precipitation in early June, while the two tree species had stem water δD values similar to that of groundwater (Table 1). Comparison of stem water D/H ratios among the four study species in July indicated that, *C. nauseosus* and *J. osteosperma* showed no direct uptake of precipitation, while rain water was taken up by *A. tridentata* and *P. edulis* (Table 1). Finally, while *J. ostesperma* had stem water δD values similar to that of groundwater early in the summer of 1989, stem water D/H ratios during August were enriched above that of groundwater indicating that some precipitation was directly taken up by *J. oesteosperma* later in the summer (Table 1).

Different patterns for the relative use of precipitation among the species were observed during 1990. In early April 1990, there were no significant differences in stem water δD values among the species compared (Table 1). Stem water of all species had isotopic compositions enriched above groundwater, but similar to that of rain that fell the day previous to stem collection, indicating that on the April 1990 sampling date all species were using recent precipitation as their sole water source. However, on subsequent sampling dates during the 1990 growing season, there were significant differences among species for stem water δD values. *Chrysothamnus nauseosus* had stem water δD values in May through August that were not significantly different from that of groundwater. In contrast, the other three species had stem water δD values that were intermediate between the groundwater value and summer precipitation values, indicating that a mixture of both precipitation and groundwater was being used by these species. The two tree species generally had less negative δD values than did *A. tridentata*, indicating a higher average uptake of summer precipitation by the tree species (Table 1).

Significant differences among species were observed for both predrawn and midday water potential (Table 2). *Chrysothamnus nauseosus* had the highest predawn and midday water potentials, while the other three

Date	GW	PPT	Stem water			
			Pinus edulis	*Juniperus osteosperma*	*Artemisia tridentata*	*Chrysothamnus nauseosus*
1989						
10 June	−94	−67	−98±2	−94±3	−77±5	−
11 June	−	−	−97±2	−97±3	−83±7	−
21 July	−96	−	−	−97±5	−	−
23 July	−	−10	−76±4	−97*	−70*	−96*
28 August	−95	−	−	−58±3	−	−
1990						
9 April	−97	−87	−86±3ᵃ	−87±2ᵃ	−87±3ᵃ	−86±3ᵃ
24 May	−96	−	−75±4ᵃ	−82±3ᵃ	−89±1ᵇ	−94±5ᵇ
17 July	−96	−67	−75±2ᵃ	−77±2ᵃ,ᵇ	−81±1ᵇ	−95±5ᶜ
23 August	−96	−	−72±2ᵃ	−73±3ᵃ	−77±3ᵃ	−91±8ᵇ

Table 1. Comparison of the hydrogen isotopic composition (δD, ‰) of groundwater (GW), precipitation (PPT) and stem water in the two major tree and shrub species at Coral Pink State Park, Utah, during 1989 and 1990. The date listed indicates when stem samples were collected. Precipitation samples were collected the day before stem sample collection. Stem water values are the mean±standard deviation. In 1989, sample size varies from two to six, except*, where $n=1$. In 1990, $n=4$. Values within a horizontal row followed by different letters are significantly different ($P<0.05$) based on T-method multiple comparison tests after an analysis of variance (Sokal & Rohlf 1981)

Date	Pinus edulis	Juniperus osteosperma	Artemisia tridentata	Chrysothamnus nauseosus
Predawn				
25 May	-0.80 ± 0.27^a	$-0.74\pm0.19^{a,b}$	$-0.68\pm0.09^{a,b}$	-0.40 ± 0.07^b
18 July	-0.75 ± 0.04^a	-0.85 ± 0.08^a	-0.55 ± 0.09^b	-0.40 ± 0.04^c
23 August	$-0.74\pm0.09^{a,b}$	-0.83 ± 0.10^a	-0.74 ± 0.09^a	-0.56 ± 0.09^b
Midday				
25 May	-2.21 ± 0.20^a	-2.09 ± 0.26^a	-2.10 ± 0.18^a	-1.38 ± 0.09^b
18 July	-1.71 ± 0.23^b	-2.34 ± 0.17^a	-2.44 ± 0.24^a	-1.61 ± 0.13^b
23 August	-2.16 ± 0.11^b	-2.51 ± 0.17^a	-2.49 ± 0.13^a	-1.79 ± 0.13^c

Table 2. Comparison of the predawn and midday xylem water potential (MPa) in the two major tree and shrub species at the Coral Pink Sand Dunes site in southern Utah during 1990. Water potential values are the mean±standard deviation, $n=4$. Values within a horizontal row followed by different letters are significantly different ($P<0.05$) based on T-method multiple comparisons tests after an analysis of variance (Sokal & Rohlf 1981)

species were, in general, very similar. There was a strong negative correlation between stem water δD values and predawn water potential in July (Pearson correlation coefficient, $r=-0.828$, $n=16$, $P<0.01$, Fig. 2). Similar negative correlations between stem water δD and predawn water potential were also observed in May and August (May, $r=-0.597$, $n=16$, $P<0.01$; August, $r=-0.795$, $n=16$, $P<0.01$).

Leaf carbon isotope composition differed significantly among all species, with least negative leaf $\delta^{13}C$ values for *P. edulis* and those for *C. nauseosus* most negative (Fig. 2). Assuming that the leaf-air vapour pressure difference was equivalent for all species (3·0 kPa), there was a larger than two-fold difference in water-use efficiency among the species compared (Calculated water-use efficiency, CO_2 H_2O^{-1}, mmol mol^{-1}; *P. edulis*, 4.3 ± 0.3; *J. osteosperma*, 3.9 ± 0.3; *A. tridentata*, 2.7 ± 0.1; *C. nauseosus*, 2.0 ± 0.1. Values are the mean±standard deviation, $n=4$). Water-use efficiency was calculated from the leaf carbon isotopic composition (Fig. 2) using a $\delta^{13}C$ value of -7.9‰ for the source air following Farquhar *et al.* (1989). All means are significantly different ($P<0.05$) based on T-method multiple comparison tests after an analysis of variance (Sokal & Rohlf 1981). Differences in leaf carbon isotopic composition were associated with differences in the water uptake patterns among the species (Fig. 2). Calculated water-use efficiency was strongly correlated with the stem δD values for all species (May, $r=0.900$, $n=16$, $P<0.01$; July, $r=0.861$, $n=16$, $P<0.01$; August, $r=0.795$, $n=16$, $P<0.01$).

DISCUSSION

Our results indicated significant differences among species in the uptake of summer precipitation (Table 1). In addition, the stem water δD values were negatively correlated with predawn water potential (Fig. 2). We interpret these results to indicate that there were significant differences in rooting pattern among the species compared.

It was expected that species with different rooting patterns would have different predawn water potentials. Predawn water potential is a good indicator of the average soil water potential experienced by a plant

(Ritchie & Hinckley 1975). The soil water potential is low in the shallow soil layers and increases with depth in sandy soils (Richards & Caldwell 1987; Dobrowolski *et al.* 1990). Plants with a high proportion of active roots in the upper, dry soil horizons should have a lower predawn water potential than plants with roots predominantly in the deeper, moist soil horizons. Such a soil water potential gradient would of course be reversed for
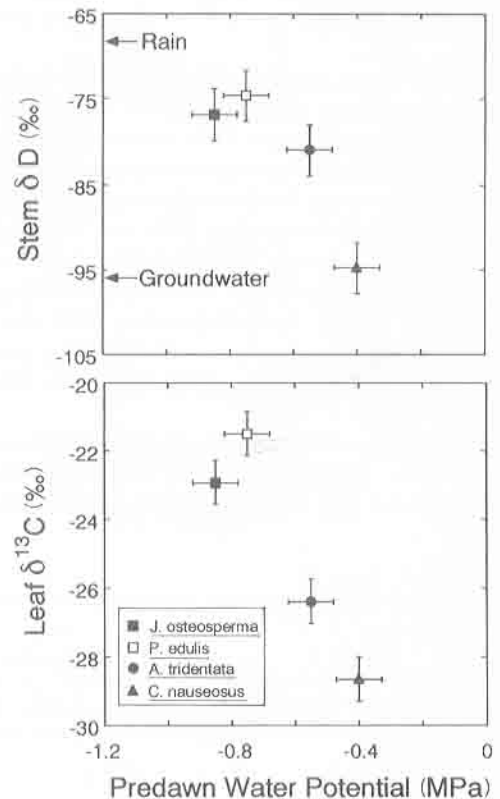

Figure 2. The relationship between plant water potential and stem water hydrogen isotope composition (δD, ‰) and leaf carbon isotope composition ($\delta^{13}C$, ‰). Stem water samples and water potential measurements were collected in July 1990. Leaf tissue samples were collected in August 1990. Values are means, $n=4$. The error bars represent 95% comparison intervals calculated by the T-method after an analysis of variance (Sokal & Rohlf 1981). Means whose intervals do not overlap are significantly different ($P<0.05$).

a short period of time after a substantial rainfall that wetted the shallow soil layers. In general, however, a lower soil water potential is expected in the shallow soil layers for two reasons (Dobrowolski *et al.* 1990). Firstly, the sandy soils allow rapid infiltration of water through the large soil pores. Secondly, the highest rooting density occurs in the uppermost soil layers so that water is preferentially absorbed from the shallow layers first (Dobrowolski *et al.* 1990).

The differences observed between *C. nauseosus* and *A. tridentata* for predawn water potential and stem δD values (Tables 1 & 2) are consistent with differences in root distribution pattern. Excavation studies indicate that *A. tridentata* has approximately the same maximum rooting depth as *C. nauseosus*, but a higher proportion of lateral roots particularly in the shallow soil horizons (Sturges 1977; Manning & Groeneveld 1989; Reynolds & Fraley 1989). Therefore, one would expect a higher uptake of precipitation in *A. tridentata* than in *C. nauseosus*.

The two tree species had lower average predawn water potentials than *A. tridentata*, suggesting that they may have a higher proportion of active roots in the shallow soil zones. The stem water δD values, on average, were higher in the tree species than in *A. tridentata*, which is consistent with this suggestion (Table 1). The absolute differences between the δD values for *A. tridentata* and the tree species in 1990 were small, however, so conclusions about differences in rooting pattern and precipitation uptake are preliminary and require confirmation from excavation studies and further D/H ratio sampling.

The high use of summer precipitation by *J. osteosperma* in 1990, indicated by the stem water δD values, contrasts with the low precipitation uptake measured in 1989 (Table 1), although summer rainfall in 1989 was only 54% of the long-term average at our study site in 1989 (U.S. National Weather Service Records). The particularly low rainfall in the spring and early summer of 1989 may have damaged existing roots and prevented new root growth in the shallow soil horizons, thus restricting uptake of small amounts of precipitation during 1989. Precipitation uptake returned in August 1989 after substantial rainfall occurred (Table 1), this was presumably associated with new root growth.

There were significant differences in leaf carbon isotopic compositon among all four of the species compared in this study (Fig. 2). Similar leaf δ¹³C values have been reported for the same or closely related species at different aridland sites in the southwestern United States (DeLucia, Schlesinger & Billings 1988; DeLucia & Schlesinger 1990; Lajtha & Barnes 1991). Since the carbon isotopic measurements were made on the current season's leaf tissue collected in late August, they should be representative of carbon fixed throughout the main growth season. In addition, all the species compared had small leaves so that leaf temperature should be similar to air temperature and the leaf-air

vapour pressure difference should be equivalent for the different species. Therefore, we suggest that leaf carbon isotopic compositions indicate significant differences among the four species for water-use efficiency integrated over the growing season (Farquhar *et al.* 1989).

It is interesting to note that the greater the utilization of summer precipitation, a relatively unstable water source in these environments (Ehleringer & Mooney 1983), the higher the water-use efficiency (the more conservative the water-use of a species; Table 1, (Fig. 2)). *Chrysothamnus nauseosus*, utilizing a stable groundwater source in late spring and summer, had the lowest water-use efficiency. The different pattern of root distribution and use of water sources observed between *C. nauseosus* and *A. tridentata* may in part explain the variation in leaf carbon isotope compositions and calculated water use efficiency for these species. However, there may also be significant differences in hydraulic architecture between the two shrub species that would influence water transport, stomatal conductance and water use efficiency (Tyree & Sperry 1989; Jones & Sutherland 1991). The differences in leaf gas exchange characteristics between the conifer and shrub species, implied by the δ¹³C values, are likely to be due to significant differences in xylem anatomy and hydraulic architecture (Tyree & Sperry 1989; Jones & Sutherland 1991).

In conclusion, the results indicate substantial uptake of summer precipitation by three of the perennial species studied, in a year with typical summer precipitation amounts. The ability of *C. nauseosus* to operate at low water-use efficiencies without making use of summer precipitation is likely to be related to the perched groundwater table at the study site. The high carbon gain, associated with a low water-use efficiency, may be required for *C. nauseosus* to effectively compete with *A. tridentata* and other species, despite a rooting pattern less well developed in the shallow, more nutrient rich soil layers (Manning & Groeneveld 1989; Dobrowolski *et al.* 1990). The low water use efficiency of *C. nauseosus* may be a compromise associated with a high nutrient use efficiency (DeLucia & Schlesinger 1990). The high use of summer precipitation by *P. edulis* is consistent with its distribution being restricted to relatively high elevations in semi-aridlands where summer precipitation is significant (West 1988). *Artemisia tridentata* is the most drought tolerant of the species compared here (West 1988; DeLucia & Schlesinger 1990). The greater drought tolerance of *A. tridentata* may in part be related to its ability to take up small amounts of summer precipitation, thus maximizing the use of a major limiting resource.

ACKNOWLEDGMENTS

REFERENCES

Caldwell M.M. (1985) Cold desert. In *Physiological Ecology of North American Plant Communities* (eds B.F. Chabot & H.A. Mooney), pp. 198–212. Chapman and Hall, London.

Coleman M.L., Shepard T.J., Durham J.J., Rouse J.E. & Moore G.R. (1982) Reduction of water with zinc for hydrogen isotope analysis. *Analytical Chemistry* **54**, 993–995.

Dansgaard W. (1964) Stable isotopes in precipitation. *Tellus* **16**, 436–468.

Dawson T.E. & Ehleringer J.R. (1991) Streamside trees that do not use stream water. *Nature* **350**, 335–337.

Dalton F.N. (1989) Plant root water extraction studies using stable isotopes. In *Structural and Functional Aspects of Transport in Roots* (ed. B.C. Loughman), pp. 151–155. Kluwer Academic Publishers, Hague.

DeLucia E.H., Schlesinger W.H. & Billings W.D. (1988) Water relations and the maintenance of Sierran conifers on hydrothermally altered rock. *Ecology* **69**, 303–311.

DeLucia E.H. & Schlesinger W.H. (1990) Ecophysiology of Great Basin and Sierra Nevada vegetation on contrasting soils. In *Plant Biology of the Basin and Range*, Ecological Studies 80 (eds C.B. Osmond, L.F. Pitelka & G.M. Hidy), pp. 143–178. Springer-Verlag, Berlin.

Dobrowoski J.P., Caldwell M.M. & Richards J.H. (1990) Basin hydrology and plant root systems. In *Plant Biology of the Basin and Range*, Ecological Studies 80 (eds C.B. Osmond, L.F. Pitelka & G.M. Hidy), pp. 243–292. Springer-Verlag, Berlin.

Ehleringer J.R. & Mooney H.A. (1983) Photosynthesis and productivity of desert and mediterranean-climate plants. In *Encyclopedia of Plant Physiology*, New Series, Vol. 12D (eds O.L. Lange, P.S. Nobel, C.B. Osmond & H. Ziegler) pp. 205–232. Springer-Verlag, Berlin.

Ehleringer J.R. & Osmond C.B. (1989) Stable isotopes. In *Plant Physiological Ecology. Field Methods and Instrumentation* (ed. R.W. Pearcy, J.R. Ehleringer, H.A. Mooney & P.W. Rundel), pp. 281–300. Chapman and Hall, London.

Farquhar G.D., Ehleringer J.R. & Hubick K.T. (1989) Carbon isotope discrimination and photosynthesis. *Annual Review of Plant Physiology and Plant Molecular Biology* **40**, 503–537.

Flanagan L.B. & Ehleringer J.R. (1991) Stable isotope composition of stem and leaf water: applications to the study of plant water use. *Functional Ecology* **5**, 270–277.

Gat J.R. (1980) The isotopes of hydrogen and oxygen in precipitation. In *Handbook of Environmental Isotope Geochemistry*, Vol. 1 (eds P. Fritz & J.-Ch. Fontes), pp. 24–48. Elsevier, Dordrecht.

Hachey D.L., Wong W.W., Boutton T.W. & Klein P.D. (1987) Isotope ratio measurements in nutrition and biomedical research. *Mass Spectrometry Reviews* **6**, 289–328.

Jones H.G. & Sutherland R.A. (1991) Stomatal control of xylem embolism. *Plant, Cell and Environment* **14**, 607–612.

Lajtha K. & Barnes F.J. (1991) Carbon gain and water use in pinyon pine-juniper woodlands of northern New Mexico: field versus phytotron chamber measurements. *Tree Physiology* **9**, 59–67.

Manning S.J. & Groeneveld D.P. (1989) Shrub rooting characteristics and water acquisition on xeric sites in the western great basin. In *Proceedings — Symposium on Cheatgrass Invasion, Shrub Dieoff, and Other Aspects of Shrub Biology and Management* (General Technical Report INT-276), pp. 238–244. U.S. Department of Agriculture, Ogden, UT.

Noy-Meir I. (1973) Desert ecosystems: environment and producers. *Annual Review of Ecology and Systematics* **4**, 25–52.

Reynolds T.D. & Fraley L. (1989) Root profiles of some native and exotic plant species in southeastern Idaho. *Environmental and Experimental Botany* **29**, 241–248.

Richards J.H. & Caldwell M.M. (1987) Hydraulic lift: substantial nocturnal water transport between soil layers by *Artemisia tridentata* roots. *Oecologia* **73**, 486–489.

Ritchie G.A. & Hinckley T.M. (1975) The pressure chamber as an instrument for ecological research. *Advances in Ecological Research* **9**, 165–254.

Sala O.E. & Laurenroth W.K. (1982) Small rainfall events: an ecological role in semiarid regions. *Oecologia* **53**, 301–304.

Sokal R.R. & Rohlf F.J. (1981) *Biometry*, 2nd edn. Freeman, New York, NY.

Sturges D.L. (1977) Soil water withdrawal and root characteristics of big sagebrush. *The American Midland Naturalist* **98**, 257–274.

Tyree M.T. & Sperry J.S. (1989) Vulnerability of xylem to cavitation and embolism. *Annual Review of Plant Physiology and Plant Molecular Biology* **40**, 19–38.

West N.E. (1988) Intermountain deserts, shrub steppes, and woodlands. In *North American Terrestrial Vegetation* (ed. M.G. Barbour & W.D. Billings), pp. 209–230. Cambridge University Press, Cambridge.

White J.W.C. (1988) Stable hydrogen isotope ratios in plants: a review of current theory and some potential applications. In *Stable Isotopes in Ecological Research* (eds P.W. Rundel, J.R. Ehleringer & K.A. Nagy), pp. 142–162. Springer-Verlag, Berlin.

White J.W.C., Cook E.R., Lawrence J.R. & Broecker W.S. (1985) The D/H ratios of sap in trees: implications for water sources and tree ring D/H ratios. *Geochimica et Cosmochomica Acta* **49**, 237–246.