



Water Stress and Use of Summer Precipitation in a Great Basin Shrub Community

L. A. Donovan, J. R. Ehleringer

Functional Ecology, Volume 8, Issue 3 (Jun., 1994), 289-297.

Your use of the JSTOR database indicates your acceptance of JSTOR's Terms and Conditions of Use. A copy of JSTOR's Terms and Conditions of Use is available at <http://www.jstor.org/about/terms.html>, by contacting JSTOR at jstor-info@umich.edu, or by calling JSTOR at (888)388-3574, (734)998-9101 or (FAX) (734)998-9113. No part of a JSTOR transmission may be copied, downloaded, stored, further transmitted, transferred, distributed, altered, or otherwise used, in any form or by any means, except: (1) one stored electronic and one paper copy of any article solely for your personal, non-commercial use, or (2) with prior written permission of JSTOR and the publisher of the article or other text.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

Functional Ecology is published by British Ecological Society. Please contact the publisher for further permissions regarding the use of this work. Publisher contact information may be obtained at <http://www.jstor.org/journals/briteco.html>.

Functional Ecology
©1994 British Ecological Society

JSTOR and the JSTOR logo are trademarks of JSTOR, and are Registered in the U.S. Patent and Trademark Office. For more information on JSTOR contact jstor-info@umich.edu.

©2001 JSTOR

Water stress and use of summer precipitation in a Great Basin shrub community

L. A. DONOVAN and J. R. EHLERINGER*

Department of Land, Air and Water Resources, University of California, Davis, California 95616, USA and

*Department of Biology and Stable Isotope Ratio Facility for Environmental Research, University of Utah, Salt Lake City, Utah 84112, USA

Summary

1. Seasonal patterns of water stress (determined from predawn xylem pressure potentials) and relative use of summer precipitation (determined from hydrogen isotope composition) varied intraspecifically and interspecifically in a Great Basin shrub community.

2. The development of water stress during the dry season from June to July was positively correlated with the use of summer precipitation in August. The smallest plants generally developed the greatest water stress and took up the most summer precipitation, presumably due to being more dependent on shallow roots.

3. Among mature shrubs examined, moisture from summer precipitation was taken up by *Chrysothamnus viscidiflorus* and *Artemisia tridentata*, but not by *C. nauseosus*, *Juniperus osteosperma* and *Tetradymia canescens*.

4. For shrub species that are deeply rooted at maturity, such as *C. nauseosus*, the quantity and timing of available soil moisture is different for small establishing plants as compared to large reproductively mature plants.

Key-words: Hydrogen isotopes, plant size, precipitation, shrubs, water potential

Functional Ecology (1994) **8**, 289–297

Introduction

In semiarid and arid habitats, resource acquisition is often a function of rooting depth and distribution (Cody 1986; Davis & Mooney 1986; Manning & Groenvelde 1989). The large investment in root biomass (70–90% of total biomass) and the dominance of the shrub life form in the semiarid Great Basin have been attributed to temperature and soil moisture patterns (Caldwell 1985; West 1988; Dobrowolski, Caldwell & Richards 1990). Soil moisture is recharged by winter and early spring precipitation, and is then lost from shallow soils at mid-summer due to high temperatures and evapotranspiration rates (Campbell & Harris 1977; Caldwell 1985; Romo & Haferkamp 1989; Dobrowolski *et al.* 1990). Great Basin shrubs generally complete shoot growth by early summer (Caldwell 1985; L.A. Donovan, unpublished observation), but maintenance of carbon gain through the mid-summer dry period may be necessary for reproduction in late summer and autumn (Comstock, Cooper & Ehleringer 1988; Manning & Groenvelde 1989). Although the perennial woody life form is often distinguished as a group for comparison to other life forms, there is a great deal of variation

within shrubs as to seasonal water stress and rooting depth and distribution (Branson, Miller & McQueen 1976; Klepper, Gano & Cadwell 1985; Cody 1986; Davis & Mooney 1986; Manning & Groenvelde 1989; Reynolds & Fraley 1989; Ehleringer *et al.* 1991).

Interspecific variation in water stress of shrubs has been attributed to differences in species-specific rooting depths and distributions and, hence, available soil moisture (Branson *et al.* 1976; Manning & Groenvelde 1989; Reynolds & Fraley 1989). In addition, there is intraspecific variation, with establishing and/or smaller plants being more water stressed (as indicated by more negative xylem pressure potentials) than larger reproductive plants (Frazer & Davis 1988; Brown & Archer 1990; DeLucia & Schlessinger 1990; Knapp & Fahnestock 1990; Cui & Smith 1991; Donovan & Ehleringer 1991). During the summer growing season in the Great Basin, plants can potentially use two distinct water resources: the deeper soil moisture remaining from winter recharge and the infrequent soil moisture in shallow layers from summer convective storms (Dobrowolski *et al.* 1990). While rooting distribution indicates the soil volume potentially available for plant use, actual uptake is dependent on

root activity in soil areas where the moisture is available. The differential use of shallow and deep water sources can be determined from the water status of plants and hydrogen isotopic composition of water in plant roots and stems (White 1988).

Hydrogen isotope ratios (δD) can be used to trace plant water sources as there is no isotope fractionation when water is taken up by roots (White *et al.* 1985; White 1988; Dawson & Ehleringer 1991). White *et al.* (1985) originally used the seasonality of precipitation δD to show that eastern white pine trees from different habitats vary in their relative use of summer precipitation and ground water. The δD value of precipitation varies seasonally at mid-latitudes predominately as a function of temperature; δD values of precipitation are more negative (lower in deuterium content) in winter and less negative (higher in deuterium content) in summer (Dansgaard 1964; White *et al.* 1985). In the Great Basin, where the soil moisture and ground water recharge are mainly from winter precipitation, perennials can differ in their capacity to use summer precipitation (Ehleringer *et al.* 1991; Gregg 1991; Flanagan & Ehleringer 1991; Flanagan, Ehleringer & Marshall 1992). Intraspecific variation in water source has also been observed in *Acer negundo* growing in a streamside habitat (Dawson & Ehleringer 1991). Mature trees used water from deeper strata, whereas small streamside trees used stream water and small non-streamside trees used moisture in upper soil layers from recent precipitation. Thus, water sources with different δD values provide a means of determining the relative use of these water sources by individuals in a community.

The objective of this study was to determine the seasonal patterns of water stress and water source use for members of a lower elevation Great Basin shrub community. We hypothesized that: (1) there would be interspecific and intraspecific variation in development of water stress (declines in xylem pressure potentials) and use of different water sources during the summer growing season; (2) the intraspecific variation would be related to size/ life-history classes; and (3) that summer water stress and use of summer precipitation would be a function of roots in shallow soil layers, and hence be positively correlated.

Materials and methods

The study was conducted at the Tintic Range Experimental Station, Tintic, Utah (39° 55' N, 122° 03' W, elevation 1775 m) in 1991. The species included in the study represent all of the major woody shrubs in the study area; *Artemisia tridentata* Nutt. ssp. *tridentata* (Asteraceae), *Chrysothamnus nauseosus* ssp. *hololeucus* (Asteraceae), *C. viscidiflorus* (Hook.) Nutt. (Asteraceae), *Gutierrezia sarothrae* (Pursh) Britt. & Rusby (Asteraceae), *Juniperus osteosperma* (Torr.) Little (Cupressaceae) and *Tetradymia canescens* (Aster-

aceae). Mature reproductive individuals (adults) of all of the species were sampled, as well as non-reproductive individuals of *C. nauseosus* and *A. tridentata* (Table 1). The non-reproductive plants of *C. nauseosus* were divided into three classes: juveniles (older than 2 years of age), 1-year-old recruits and seedlings. The non-reproductive *A. tridentata* plants, designated as juveniles, were greater than 2 years of age. Height (m) was measured for all plants at the initiation of the study.

Hydrogen isotopic composition is expressed as the hydrogen isotope ratio (δD), in units of ‰:

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

where R_{sample} and R_{standard} are the molar ratios of D/H for the sample and standard (Standard Mean Ocean Water), respectively. Water samples were prepared for analysis of hydrogen isotope composition by reduction to diatomic hydrogen using zinc (Coleman *et al.* 1982). The zinc alloy was supplied by J. Hayes (Indiana University). The deuterium content of hydrogen gas was then measured on a isotope ratio mass spectrometer (delta S, Finnagan MAT, San Jose, California, USA).

Monthly precipitation amounts for 1991 were recorded with a permanent weather station maintained by Utah State University, at the Tintic field station. The amount of precipitation for the 14–15 August rain event was measured with rain gauges at the study area. Tintic precipitation samples for δD analysis were collected in Erlenmeyer flasks with funnels attached. They were cumulative samples for 7–19-day periods, with the exception of the 14–15 August rain event. To minimize evaporation, the flasks were buried (except for the funnel) and contained 10 ml of mineral oil. Mineral oil does not have an effect on the δD of rain-water (J. R. Ehleringer, unpublished observation). Salt Lake City precipitation samples for hydrogen isotope analysis, collected at the University of Utah, represent individual rain events. Precipitation samples were sealed in vials and frozen until analysis of hydrogen isotope composition.

Tintic soils are sandy-loams (S. E. Jensen, personal communication), with an appearance of a caliche layer at approximately 70 cm depth. Soils cores were collected several times during the 1991 season and divided into 0–35 and 35–70 cm depths. In addition, soils from 0–5 cm were collected on 29 July and 17 August. Soil moisture (%) was determined gravimetrically. Separate soil cores were used for determination of soil moisture δD . These cores were frozen until water samples were cryogenically distilled and analysed for δD .

Plants from each of the species and size/life-history classes (Table 1) were sampled for predawn xylem pressure potentials (Ψ_{pd}) and/or δD of stem water on 16 May, 4 June, 29 July, and 17 August. The 29 July sample date represented a period of dry soil conditions when there had been no substantial precipitation for over 1 month. The 17 August sample date followed a large summer precipitation event, 21 mm, on 14–15

Table 1. Species, size/life-history class designations, size (mean \pm SD), and results of one-way analysis of variance procedures (ANOVA) comparing predawn xylem pressure potentials (Ψ_{pd}) and hydrogen isotope composition (δD) across sampling dates

Shrub species	Life-history/ size class	Size (m)	ANOVA Ψ_{pd}			ANOVA δD		
			Dates	Reps	F value	Dates	Reps	F value
<i>Chrysothamnus nauseosus</i>	Large adults	1.15 \pm 0.14	4	6	22.1***	3	5–6	2.4 ^{NS}
	Small adults	0.48 \pm 0.16	4	6	25.8***	3	4–5	5.9*
	Juveniles	0.15 \pm 0.07	4	7	17.7***	3	5–7	0.8 ^{NS}
	1-year-olds	0.05 \pm 0.01	3	3–4	9.4**	3	2–8	53.5***
	Seedlings	0.02 \pm 0.01	4	1–5	9.4**	3	1–4	25.0**
<i>Juniperus osteosperma</i>	Adults	3.4 \pm 1.65	3	3	6.9*	3	2–3	0.4 ^{NS}
<i>Artemisia tridentata</i>	Adults	1.07 \pm 0.25	3	3	28.6***	3	3	29.1***
	Juveniles	0.12 \pm 0.05	3	3	23.3**	3	3	60.1***
<i>Chrysothamnus viscidiflorus</i>	Adults	0.57 \pm 0.08	3	3	7.01*	3	2–3	9.6*
<i>Tetradymia canescens</i>	Adults	0.37 \pm 0.08	3	3	77.7***	3	3	2.1 ^{NS}
<i>Gutierrezia sarrothrae</i>	Adults	0.16 \pm 0.04	3	3	3.0 ^{NS}	3	3	3.4 ^{NS}

For the ANOVA: dates indicates number of dates compared, reps indicates number of replicates per date and results are presented as F value and significance (^{NS} $P > 0.05$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$).

August. Ψ_{pd} of randomly selected stems were measured with a pressure chamber (PMS Instruments, Corvallis, Oregon, USA). For *C. nauseosus* seedlings, water potential data were not available for May, because stems were brittle and snapped before completion of pressure chamber measurements. Samples were harvested at dawn for determination of δD of stem water. Woody stems were excised from large plants, and roots were excavated (0–10 cm depth) for *C. nauseosus* seedlings and 1-year-olds that had little or no woody tissue available. Stem and root samples were sealed in vials and frozen until water was extracted using cryogenic distillation. Samples were analysed for δD as previously described. For Ψ_{pd} and δD determinations, the same plants were generally sampled repeatedly on successive dates. The exceptions were individuals in size/life-history classes where sampling on one date used most of the available tissue and effectively killed the plants: juveniles of *A. tridentata*, and seedlings and 1-year-olds of *C. nauseosus*. For these classes, subsequent sampling dates used replacement individuals of the same size and in the same approximate locations as the initial plants.

For each of the 11 species and size/life-history classes, Ψ_{pd} and δD values were compared with a one-way analysis of variance (ANOVA) with date as the independent variable, and a Duncan–Waller *K*-ratio test (SAS software system for data analysis; SAS 1989). For each sampling date, an additional one-way ANOVA was used to compare Ψ_{pd} and δD values

(dependent variables) among the size/life-history classes of *C. nauseosus* (independent variable).

Results

The area receives an average of 374 mm precipitation annually (23-year mean), with 272 mm received from January to September (Owens 1987). The 1991 precipitation for January to September was 275 mm and the monthly patterns were similar to the 23-year mean (Fig. 1). The δD values for the integrated precipitation samples from Tintic are consistent with the more complete record of individual storm events from Salt Lake City (Fig. 1). δD values for precipitation were most negative in the winter and were least negative in July and August. Precipitation from the 21-mm storm event on 14 and 15 August had a δD value of -55% .

Soil moisture content at each depth was highest in May (spring) and lowest in July (mid-summer). The 14–15 August precipitation infiltrated the 0–5 cm soil layer, increasing the soil moisture content from 1.8 to 6.9%, and increasing the soil moisture δD value from -107.5 to -69% (Fig. 2). The soil moisture and soil water δD values for the 0–35 cm soil layer increased slightly after the August rain event indicating less of an effect of the precipitation when soil moisture values were integrated over the greater depth. At the 35–70 cm depth, the soil moisture content and the soil moisture δD did not change in response to the 14–15

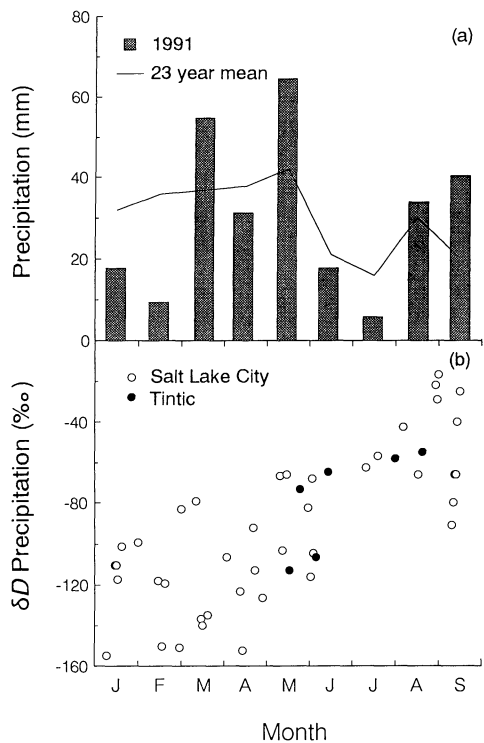


Fig. 1. (a) The monthly amount of precipitation for January to September 1991 and the 23-year average of monthly precipitation at Tintic, Utah and (b) the hydrogen isotopic composition of the 1991 precipitation (δD) for integrated events at Tintic and for individual rain events in Salt Lake City, Utah (160 km north-east of Tintic).

August rain event, indicating that precipitation from the storm did not penetrate to this soil layer.

Each size/life-history class of *C. nauseosus* had the least negative Ψ_{pd} value in June and responded differentially to the declining precipitation and soil moisture during the season (Fig. 3). The large adults *C. nauseosus* had Ψ_{pd} values that changed relatively little during the summer season. An ANOVA across sampling dates indicates that the values for July and August were significantly lower than those for May (Table 1, Fig. 3), but Ψ_{pd} values remained above -1.0 MPa for the season. For both small adults and juveniles, July and August Ψ_{pd} values fell to -1.5 MPa, significantly lower than May and June values, but the slight increases in Ψ_{pd} values from July to August were not significant (Table 1, Fig. 3). July and August Ψ_{pd} values were also significantly lower than earlier season values for the 1-year-olds and seedling classes, with Ψ_{pd} values reaching minimums of -2.3 and -3.7 MPa, respectively (Table 1, Fig. 3). Additional one-way ANOVA, comparing the five classes of *C. nauseosus* on each sampling date (class is the independent variable), indicated a progression in Ψ_{pd} values on both the July and August sampling dates: large adults > small adults = juveniles > 1-year-olds > seedlings (July, $F = 21.2$, $df = 4$, $P < 0.001$; August, $F = 21.7$, $df = 4$, $P < 0.001$).

May δD values for the size/life-history classes of *C.*

nauseosus, ranging from -109 to -114 ‰, were similar to the δD values of the precipitation presumed to recharge soil moisture (Figs 1 and 3). The δD value of large adults did not change significantly throughout the season, whereas the small adults showed a small but significant increase in August (Table 1, Fig. 3). The 1-year-old and seedling classes showed the greatest seasonal change in δD values, with July and August values being significantly greater than those for May (Table 1, Fig. 3). For these classes, the August δD values of the plants approached the δD value for the August rain event. The July δD value of -70.8 ‰ for the seedlings appears to be an anomaly as the integrated δD values for soil moisture at all depths on this date were less than -100 ‰.

The Ψ_{pd} and δD responses of the size/life-history classes of *C. nauseosus* can be compared to the other species and size/life-history classes examined in the community, arranged in order of descending height: adults of *J. osteosperma*, *A. tridentata*, *C. viscidiflorus*, *T. canescens* and *G. sarothrae*, and juveniles of *A. tridentata* (Table 1). The range of June Ψ_{pd} values (-0.63 to -0.92 MPa) for this group was similar to that for the *C. nauseosus* classes (Figs 3 and 4). For all of these classes, except *G. sarothrae*, the Ψ_{pd} values for July and August were significantly lower than those for June (Table 1, Fig. 4). *Gutierrezia sarothrae* had a high variance in Ψ_{pd} values within each date so that the ANOVA comparing among dates was not significant, even though the pattern was consistent with that of similar-sized members of the community. Only the juveniles of *A. tridentata* responded to the August precipitation with a significant increase in Ψ_{pd} (Table 1, Fig. 4).

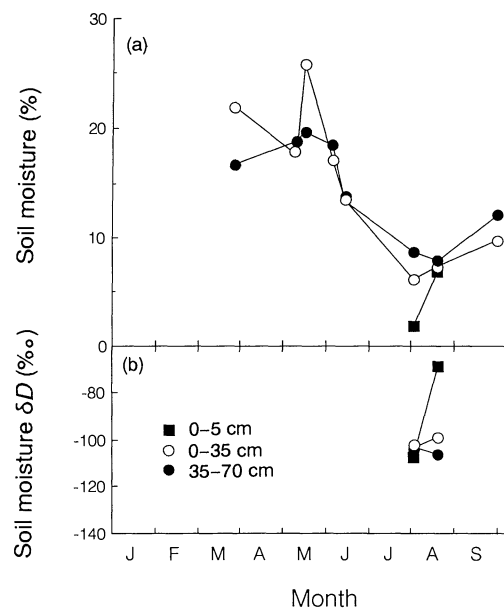


Fig. 2. (a) Soil moisture (%) and (b) hydrogen isotopic composition of soil moisture (δD) for 0–5, 0–35 and 35–70 cm depths for January to September 1991 at Tintic, Utah.

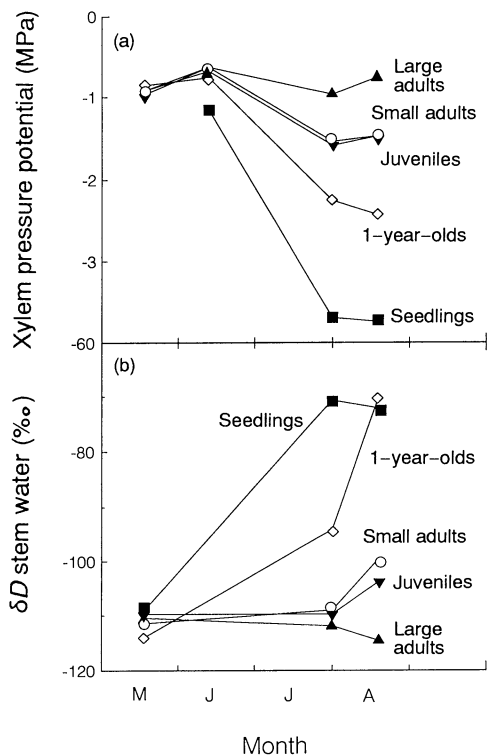


Fig. 3. (a) Predawn xylem pressure potentials (Ψ_{pd}) and (b) hydrogen isotopic composition of stem water (δD) plotted by date for *Chrysothamnus nauseosus* size/life-history classes at Tintic, Utah, for May to August 1991: large adults, small adults, juveniles, 1-year-olds, seedlings.

In May, the δD values for community group were similar to those of *C. nauseosus* and to those of winter and early spring precipitation (Figs 1, 3 and 4). For *J. osteosperma* and *T. canescens* the δD values were not significantly different at any time during the season (Table 1, Fig. 4). For *A. tridentata* adults and juveniles, and *C. viscidiflorus*, the May δD values were not significantly different than those for July, but the August values were significantly greater than those for May and July (Table 1, Fig. 4). *Gutierrezia sarothrae* again had high variance within each date so that even though the pattern of means was similar to that of the similar-sized *A. tridentata* juveniles, the August δD values were not significantly greater than those for the other dates (Table 1, Fig. 4). The ranges of Ψ_{pd} and δD values for the community group were less than the range observed for the size/life-history classes of *C. nauseosus* (Figs 3 and 4).

The relationship between water stress as represented by Ψ_{pd} values and water source as represented by δD values was examined by using two composite variables. An estimate of the seasonal water stress was calculated as the difference between Ψ_{pd} values in June when the plants were least water stressed and in July when the plants were most water stressed. An estimate of the seasonal shift in water source was calculated as the

difference between δD values in May and those in August. When all of the species and size/life-history classes are included, there was a positive linear relationship between seasonal water stress and seasonal shift in water source ($r=0.80$, $n=11$, $P<0.01$, Fig. 5).

The composite variables of seasonal water stress and shift in water source were plotted as a function of plant size for the classes of *C. nauseosus* and for other species in the study. There was a significant log-linear relationship between plant height and seasonal shift in water source within the classes of *C. nauseosus* ($r=0.88$, $P<0.05$, $n=5$, Fig. 6) and for all the classes examined in the study ($r=0.76$, $P<0.01$, $n=11$, data not shown). The log-linear relationship between plant height and seasonal water stress was also significant within *C. nauseosus* ($r=0.93$, $n=5$, $P<0.01$, Fig. 6), but not for all of the classes in the study ($r=0.54$, $n=11$, $P=0.1$, data not shown).

Discussion

There was interspecific and intraspecific variation in the patterns of seasonal water stress and of water source use in this shrub community. The precipitation, soil and plant data as a whole indicated that the increased plant δD values in August could generally

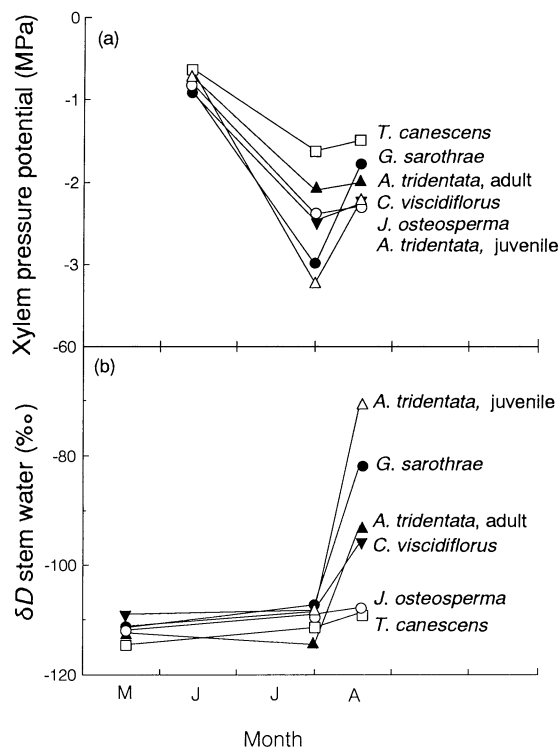


Fig. 4. (a) Predawn xylem pressure potentials (Ψ_{pd}) and (b) hydrogen isotopic composition of stem water (δD) plotted by date for woody shrubs at Tintic, Utah, for May to August 1991: *Artemisia tridentata* adults and juveniles, *Chrysothamnus viscidiflorus*, *Gutierrezia sarothrae*, *Juniperus osteosperma* and *Tetradymia canescens*.

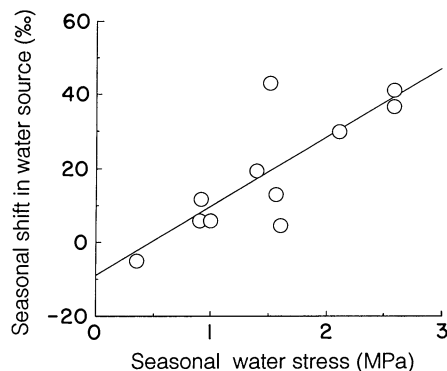


Fig. 5. Seasonal shift in hydrogen isotopic composition of water source (May to August stem water δD) as a function of seasonal water stress (June to July predawn xylem pressure potentials) for *Artemisia tridentata* adults and juveniles, *Chrysothamnus viscidiflorus*, *Gutierrezia sarothrae*, *Juniperus osteosperma*, *Tetradymia canescens*, and the five size/life-history classes of *Chrysothamnus nauseosus*. $y = -9.1 + 18.7x$, $r = 0.80$, $n = 11$, $P < 0.01$.

be interpreted as uptake of moisture from the early August rain event. The variation in seasonal Ψ_{pd} and δD responses to the rain event appeared to be related to plant root depth and distribution.

The lack of use of summer rain by *C. nauseosus* (large adults), *J. osteosperma* and *T. canescens* suggests that they lacked active roots in the shallow soil layers at that time. Previous reports have also indicated that *C. nauseosus* does not take up summer rain (Ehleringer *et al.* 1991; Flanagan & Ehleringer 1991; Flanagan *et al.* 1992). The responses of *J. osteosperma* to summer rain have been variable and appear to depend on characteristics of the habitats and the precipitation event (Flanagan & Ehleringer 1991; Gregg 1991; Flanagan *et al.* 1992). Of these three species that did not use summer rain, *C. nauseosus* showed the least seasonal change in Ψ_{pd} . This is consistent with previous reports of *C. nauseosus* as one of the most deeply rooted and least water-stressed shrubs in the community (Branson *et al.* 1976; Klepper *et al.* 1985). *Juniperus osteosperma* and *T. canescens* did show seasonal declines in water potentials. If plant Ψ_{pd} values are interpreted as the plant being in equilibration with the soil Ψ_{pd} in the area of uptake (Ritchie & Hinckley 1975; Davis & Mooney 1985), then the Ψ_{pd} responses indicate that mature *C. nauseosus* may be rooted in deeper, moister areas than *J. osteosperma* and *T. canescens* at this site.

Uptake of summer rain by *C. viscidiflorus*, *A. tridentata* and *G. sarothrae* was indicated by seasonal δD shifts. The percentage of summer precipitation in the plant was estimated with a two-end member mixing model (White *et al.* 1985), using a deep soil moisture δD value of -111.3‰ (average May stem value) and an August rain event δD value -55‰ . The stem

samples from adults of *C. viscidiflorus*, *A. tridentata* and *G. sarothrae* contained 28%, 34%, and 54% summer precipitation, respectively, 48 h after the storm. However, the actual percentages were probably event and sampling time specific, and the more important point was that these plants had active roots in the upper soil zones at a time of year when soils were generally dry. *Chrysothamnus viscidiflorus* and *A. tridentata* adults both showed seasonal declines in Ψ_{pd} , as has previously been found (Branson *et al.* 1976; Campbell & Harris 1977; Sturges 1977; Miller 1988; Romo & Haferkamp 1989). *Gutierrezia sarothrae* appeared to show the greatest seasonal development of water stress of the adults of species sampled, although the seasonal differences were not statistically significant due to high variance and low replication at each date. Root profiles for *C. viscidiflorus* and *A. tridentata* have been reported to be similar in depth, with some roots near the surface, but with *A. tridentata* having more lateral spread in shallow soil layers (Tablet 1964; Sturges 1977; Klepper *et al.* 1985; Richards & Caldwell 1987; Reynolds & Fraley 1989). For *A. tridentata*, the maintenance of active roots in shallow soil layers is probably assisted by the process of hydraulic lift, where water is transported through roots from deep soil layers to shallower layers and is later used to maintain transpiration (Richards & Cald-

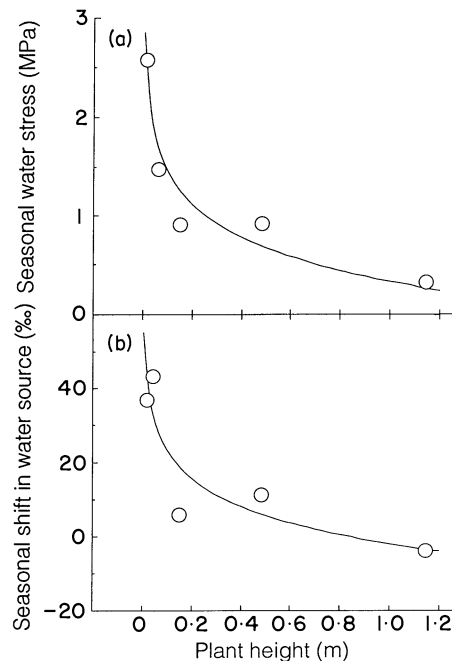


Fig. 6. The relationship between plant height and (a) seasonal shift in hydrogen isotopic composition of stem water (May to August stem water δD), $y = -2.07 - [25.5 \log(x)]$, $r = 0.88$, and (b) seasonal development of water stress (June to July xylem pressure potential) $y = 0.33 - [1.12 \log(x)]$, $r = 0.93$, for the five size/life-history classes of *Chrysothamnus nauseosus*.

well 1987; Caldwell & Richards 1989; Dobrowolski *et al.* 1990). Given the similarity in rooting characteristics and Ψ_{pd} and δD responses, *C. viscidiflorus* may also have been using hydraulic lift to increase water available for transpiration. As hydraulic lift results in deep soil water being transported to shallow soil layers, it probably affects the distribution of both the quantity and the δD value of soil moisture. However, the use of δD values to distinguish winter recharge and summer precipitation sources remains valid as long as there is no fractionation associated with the flux of water in and out of the roots in the shallow soil layers.

Intraspecific differences in seasonal Ψ_{pd} and δD responses indicate differential use of water sources among the life-history classes of *A. tridentata* and *C. nauseosus*. For *A. tridentata*, juveniles stems contained more than twice as much summer precipitation (75%), and developed greater seasonal water stress compared to adults. For *C. nauseosus*, the intraspecific variation for seasonal development of water stress and for use of summer precipitation was greater than the interspecific variation among adults of species in the community. The seedlings and 1-year-olds were the most water-stressed plants sampled during July, and appeared to contain up to 75% water from the August rain event. The seasonal development of stress and uptake of summer precipitation decreased with increasing size, age and rooting depth, with *C. nauseosus* juveniles and small adult stems containing less than 20% water from the rain event, and large adults containing no summer precipitation. Thus, the progressively larger developmental or life-history classes of a shrub species may be exposed to a predictable change of environmental conditions as they grow and become established. In the Great Basin, the high rates of seedling mortality associated with water stress (Young & Evans 1974; Owens 1987; Donovan, Mousberg & Ehleringer 1993) could select for specialized seedling drought tolerance or avoidance mechanisms (Cook 1979). The shift in water availability and selective pressures as a function of size could further select for developmental shifts in characters, maximizing the fitness of each life-history/size class to the environment to which it is likely to be exposed (Donovan & Ehleringer 1992).

Rooting depth and distribution obviously affect nutrient uptake as well as water uptake. Maintenance of active shallow roots may be important for uptake of nitrogen concentrated near the soil surface (Drew 1979; Dobrowolski *et al.* 1990). However, *C. nauseosus* adults have few shallow roots and yet have greater leaf nitrogen concentrations than shallow-rooted juveniles (Donovan & Ehleringer 1992). Adults may have taken up adequate nitrogen from the pulse associated with spring soil moisture recharge, or have exploited a greater soil volume due to higher transpiration rates. Nitrogen availability is probably an important cofactor in determining the below-ground structure in this

community, and more needs to be known about the seasonal and spatial variation in nitrogen use.

There is an apparent lack of agreement in July δD values for the precipitation, soil moisture and the seedlings of *C. nauseosus*. As the summer precipitation events were all around -60‰ , and the seedling root water was at -60‰ , we would expect the soil moisture to have been in the same range, particularly in the 0–5 cm layer. However, none of the rain events in July infiltrated more than a few millimetres and the soil layers have δD values less than -100‰ in July. This discrepancy is probably associated with the extremely low soil moisture content in July. In unsaturated soils, isotopic fractionation does occur during evapotranspiration and enrichment results in a maximum (less negative) δD for soil moisture in the region of evaporation (Zimmermann, Ehhalt & Munnich 1967; Barnes & Allison 1988). In addition, the soil layer above the enrichment zone may show a strong decline in δD values due to diffusion of water vapour to the soil surface region from the region of evaporation (Barnes & Allison 1988). The depth of this variation in the profile varies with substrate, but often occurs within 1–10 cm of the surface. In our study, the integration of the soil moisture for 0–5 cm and for 0–35 cm may have been on too gross a scale to pick up the variation in the profile, and in effect may have integrated the maximums and minimums to give no apparent difference. Seedlings of *C. nauseosus* may have been taking up either moisture from small rain events that did not substantially alter the δD values in the soil profile, or moisture with an enriched δD value at the zone of evaporative enrichment. Alternatively, the water in the seedling roots may have become enriched due to evaporative loss of moisture to the dry soil zone. Tracing of water sources in very dry soils and in very water-stressed plants may require the use of oxygen isotopes in addition to hydrogen isotopes in order to identify modification involving evaporative enrichment (Zimmermann *et al.* 1967; Allison, Barnes & Hughes 1983; Barnes & Allison 1988).

Acknowledgements

Research was funded by a National Science Foundation Dissertation Improvement Grant no. BSR-8914534. L.A.D. was supported, in part, by an American Fellowship from the American Association of University Women. We would like to thank C. Call and D. Vogel for assistance at the Utah State University Tintic, Utah facility. C. Cook and C.F. Kitty provided assistance with the isotope analyses.

References

- Allison, G.B., Barnes, C.J. & Hughes, M.W. (1983) The distribution of deuterium and ^{18}O in dry soils 2. Experimental. *Journal of Hydrology*, **64**, 377–397.

- Barnes, C.J. & Allison, G.B. (1988) Tracing of water movement in the unsaturated zone using stable isotopes of hydrogen and oxygen. *Journal of Hydrology*, **100**, 143–176.
- Branson, F.A., Miller, R.F. & McQueen, I.S. (1976) Moisture relationships in twelve northern desert shrub communities near Grand Junction, Colorado. *Ecology*, **57**, 1104–1124.
- Brown, J.R. & Archer, S. (1990) Water relations of a perennial grass and seedling vs adult woody plants in a subtropical savanna, Texas. *Oikos*, **57**, 366–374.
- Caldwell, M.M. (1985) Cold desert. *Physiological Ecology of North American Plant Communities* (eds B. F. Chabot & H. A. Mooney), pp. 198–212. Chapman & Hall, New York.
- Caldwell, M.M. & Richards, J.H. (1989) Hydraulic lift: water efflux from upper roots improves effectiveness of water uptake by deep roots. *Oecologia*, **79**, 1–5.
- Campbell, G.S. & Harris, G.A. (1977) Water relations and water use patterns for *Artemisia tridentata* Nutt. in wet and dry years. *Ecology*, **58**, 652–659.
- Cody, M.L. (1986) Structural niches in plant communities. *Community Ecology* (eds J. Diamond & T. Case), pp. 381–405. Harper & Row, San Francisco.
- Coleman, M.L., Shepherd, 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.
- Comstock, J.P., Cooper, T.A. & Ehleringer, J.R. (1988) Seasonal patterns of canopy development and carbon gain in nineteen warm desert shrub species. *Oecologia*, **75**, 327–335.
- Cook, R.E. (1979) Patterns of juvenile mortality and recruitment in plants. *Topics in Plant Population Biology* (eds O. T. Solbrig, S. Jain, G. B. Johnson & P. H. Raven), pp. 207–231. Columbia University Press, New York.
- Cui, M. & Smith, W.K. (1991) Photosynthesis, water relations and mortality in *Abies lasiocarpa* seedlings during natural establishment. *Tree Physiology*, **8**, 37–46.
- Dansgaard, W. (1964) Stable isotopes in precipitation. *Tellus*, **16**, 436–468.
- Davis, S.D. & Mooney, H.A. (1985) Comparative water relations of adjacent California shrub and grassland communities. *Oecologia*, **66**, 522–529.
- Davis, S.D. & Mooney, H.A. (1986) Water use patterns of four co-occurring chaparral shrubs. *Oecologia*, **70**, 172–177.
- Dawson, T.E. & Ehleringer, J.R. (1991) Streamside trees that do not use stream water. *Nature*, **350**, 335–337.
- DeLucia, E.H. & Schlessinger, W.H. (1990) Ecophysiology of Great Basin and Sierra Nevada vegetation on contrasting soils. *Plant Biology of the Basin and Range* (eds C. B. Osmond, L. F. Pitelka & G. M. Hidy), pp. 143–178. Springer-Verlag, New York.
- Dobrowolski, J.P., Caldwell, M.M. & Richards, J.H. (1990) Basin hydrology and plant root systems. *Plant Biology of the Basin and Range* (eds C. B. Osmond, L. F. Pitelka & G. M. Hidy), pp. 243–292. Springer-Verlag, New York.
- Donovan L.A. & Ehleringer, J.R. (1991) Ecophysiological differences among juvenile and reproductive plants of several woody species. *Oecologia*, **86**, 594–597.
- Donovan, L.A. & Ehleringer, J.R. (1992) Contrasting water-use patterns among size and life-history classes of a semi-arid shrub. *Functional Ecology*, **6**, 482–488.
- Donovan, L.A., Mausberg, J. & Ehleringer, J.R. (1993) Seedling size and survival for *Chrysothamnus nauseosus*. *Great Basin Naturalist*, **53**, 237–245.
- Drew, M.C. (1979) Root development and activities. *Aridland Ecosystems: Structure, Functioning and Management*, vol. 1 (eds D. W. Goodall & R. A. Perry), pp. 573–606. Cambridge University Press, Cambridge.
- Ehleringer, J.R., Phillips, S.L., Schuster, W.S.F. & Sandquist, D.R. (1991) Differential utilization of summer rains by desert plants. *Oecologia*, **88**, 430–434.
- 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.
- Flanagan, L.B., Ehleringer, J.R. & Marshall, J.D. (1992) Differential uptake of summer precipitation among co-occurring trees and shrubs in a pinyon–juniper woodland. *Plant Cell and Environment*, **15**, 831–836.
- Frazer, J.M. & Davis, S.D. (1988) Differential survival of chaparral seedlings during the first summer drought after wildfire. *Oecologia*, **76**, 215–221.
- Gregg, J. (1991) *The differential occurrence of the mistletoe, Phoradendron juniperinum, on its host, Juniperus osteosperma, in the Western United States*. MSc thesis, University of Utah, Salt Lake City, Utah, USA.
- Klepper, E.L., Gano, K.A. & Cadwell, L.L. (1985) *Rooting depth and distributions of deep-rooted plants in the 200 Area Control Zone of the Hanford Site*. Pacific Northwest Laboratory Report no. 5247. National Technical Information Service, Springfield.
- Knapp, A.K. & Fahnestock, J.T. (1990) Influence of plant size on the carbon and water relations of *Cucurbita foetidissima* HBK. *Functional Ecology*, **4**, 789–797.
- Manning, S.J. & Groenewald, D.P. (1989) Shrub rooting characteristics and water acquisition on xeric sites in the western Great Basin. *Symposium on Cheatgrass Invasion, Shrub Dieback, and Other Aspects of Shrub Biology and Management*, pp. 238–244. General Technical Report INT-276, Intermountain Research Station, U.S. Department of Agriculture, Forest Service.
- Miller, R.F. (1988) Comparison of water use by *Artemisia tridentata* spp. *wyomingensis* and *Chrysothamnus viscidiflorus* spp. *viscidiflorus*. *Journal of Range Management*, **41**, 58–62.
- Owens, M.K. (1987) *Recruitment of big sagebrush (Artemisia tridentata Nutt. spp. tridentata) into a seeded foothill rangeland in Utah*. PhD dissertation, Utah State University, Logan, Utah, USA.
- Reynolds, T.D. & Fraley, L., Jr. (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.
- Romo, J.T. & Haferkamp M.R. (1989) Water relations of *Artemisia tridentata* ssp. *wyomingensis* and *Sarcobatus vermiculatus* in the steppe of Southeastern Oregon. *American Midland Naturalist*, **121**, 155–164.
- SAS Institute Inc. (1989) *SAS/STAT User's Guide*, Version 6, edn 4, vol. 2. SAS Institute, Inc., Cary, North Carolina.
- Sturges, D.L. (1977) Soil water withdrawal and root characteristics of big sagebrush. *American Midland Naturalist*, **98**, 257–274.
- Tabler, R.D. (1964) The root system of *Artemisia tridentata* at 9,500 feet in Wyoming. *Ecology*, **45**, 633–636.
- West, N.E. (1988) Intermountain deserts, shrub steppes, and woodlands. *North American Terrestrial Vegetation* (eds M. G. Barbour & W. D. Billings), pp. 210–230. Cambridge University Press, New York.
- White, J.W.C. (1988) Stable hydrogen isotope ratios in plants: a review of current theory and some potential applications. *Stable Isotopes in Ecological Research* (eds P. W. Rundel, J. R. Ehleringer & K. A. Nagy), pp. 142–162. Springer-Verlag, New York.
- White, J.W.C., Cook, E.R., Lawrence, J.R. & Broecker,

- W.S. (1985) The D/H ratio of sap in trees: implications for water sources and tree ring D/H ratios. *Geochimica et Cosmochimica Acta*, **49**, 237–246.
- Young, J.A. & Evans, R.A. (1974) Population dynamics of green rabbitbrush in disturbed big sagebrush communities. *Journal of Range Management*, **27**, 127–132.
- Zimmermann, U., Ehhalt, D. & Munnich, K.O. (1967) Soil-

water movement and evapotranspiration: changes in the isotopic composition of the water. *Proceedings Symposium Isotopes in Hydrology, Vienna, 1966*, pp. 567–584. International Atomic Energy Agency, Vienna.

Received 25 August 1992; revised 6 April 1993; accepted 24 June 1993