

## Differential utilization of summer rains by desert plants

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Abstract. The differential utilization of summer rains by desert plants was investigated using stable isotope ratios of carbon and oxygen. The study was conducted in a semi-arid region of the southwestern United States where summer rains are the primary source of water for most plants. The results show that different plant species utilize summer rains differently, with some species showing a strong preference for summer rains and others showing a more generalized water use strategy. This differential utilization is likely due to differences in plant morphology, root depth, and water-use efficiency.

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**Summary.** Seasonal changes in the hydrogen isotope ratios of xylem waters were measured to determine water sources used for growth in desert plants of southern Utah. While all species used winter-spring recharge precipitation for spring growth, utilization of summer rains was life-form dependent. Annuals and succulent perennials exhibited a complete dependence on summer precipitation. Herbaceous and woody perennial species simultaneously utilized both summer precipitation and remaining winter-spring precipitation, with herbaceous species much more reliant on the summer precipitation component. Several of the woody perennials exhibited no response to summer precipitation. Currently, precipitation in southern Utah is evenly partitioned between winter and summer time periods; however, global circulation models predict that summer precipitation will increase in response to anticipated climate change. Our data indicate that components within the community will differentially respond to the change in precipitation patterns. These results are discussed in relation to impact on competition and possible changes in community structure.

**Key words:** Hydrogen isotope ratio – Desert ecology – Water source – Climate change

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Water is the limiting factor for plant growth in desert environments and primary productivity is often linearly dependent on precipitation input (Whittaker and Niering 1975; Hadley and Szarek 1981; Ehleringer and Mooney 1983). The survival of perennial species through extended drought periods is a product of both the ability of roots to acquire remaining soil moisture and the ability of shoots to tolerate water stress (MacMahon and Schimpf 1981; Ehleringer 1985; Smith and Nowak 1990). Plant species within desert ecosystems are sensitive to episodic events (1–10 years) such as prolonged droughts or unusual wet periods, which can result in marked physiologi-

cal changes and dramatic shifts in community composition (Stockton and Meko 1975; MacMahon and Schimpf 1981; Turner 1990). Analyses of how desert plant communities respond to gradual changes over extended periods of time (> 50 years) are more difficult to obtain. Yet, these are the critical data needed in order to predict how desert ecosystems might respond to the anticipated climate changes associated with a doubling of atmospheric CO<sub>2</sub> (e.g., changes in precipitation patterns) as predicted by global circulation models (Schlesinger and Mitchell 1987).

To begin to address this critical issue, we measured the stable isotopic composition of xylem sap and water stress levels of the dominant species in a desert scrub community in southern Utah. This was done to determine the patterns and sources of water in relation to current precipitation and environmental conditions. The study region was chosen because the deserts throughout this part of North America currently receive approximately equal amounts of precipitation from winter (Pacific fronts) and summer (monsoon) storms (Markham 1970; Sellers and Hill 1974). Global circulation models of anticipated climate change in response to a doubling of atmospheric CO<sub>2</sub> concentration predict that the amount of winter-spring precipitation in this region should remain constant, but that the amounts of summer precipitation should increase (Schlesinger and Mitchell 1987). Long-term analysis of precipitation records over the past 100 years for this part of North America indicate that summer precipitation has been gradually increasing while winter precipitation has remained constant (McDonald 1958; von Eschen 1958; Williams 1979).

During the annual hydrologic cycle of these deserts, soils are recharged by winter-spring precipitation; the gentle rains associated with winter storm systems allow for greater penetration of the precipitation into the soil and cool temperatures reduce evaporative and transpirational water losses (Caldwell 1985). Precipitation from these frontal storms has an average hydrogen isotope ratio ( $\delta D$ ) of approximately  $-90\text{‰}$  at interior desert sites (Winograd 1985; Ingraham and Taylor 1991; Fla-

nagan and Ehleringer 1991); well waters sampled at these desert sites are characterized by similar values (Winograd 1985, Flanagan and Ehleringer 1991), confirming that frontal storms in winter and spring are largely responsible for recharging of the soil moisture profile. Plant growth resumes with warmer temperatures in spring, utilizing soil moisture accumulated during winter and spring months. During water uptake by individual roots of a plant, there is no isotopic fractionation against lighter or heavier isotopic forms of hydrogen (White et al. 1985; Dawson and Ehleringer 1991), thus measurements of the  $\delta D$  in stem xylem sap should reflect the isotope signal of winter-spring storms.

Early summer drought is eventually relieved by summer precipitation with a stable isotopic composition of approximately  $-25\text{‰}$  (Milne, Benson and McKinley 1987; Benson and Klieforth 1989; Flanagan and Ehleringer 1991). This summer rain provides a very different isotopic signature and can be used for directly evaluating the extent to which plants can and do utilize summer rain. Summer precipitation is associated with convective thunderstorms, which, while recharging the upper soil layers, are thought not to be effective in recharging the entire soil profile because of much greater runoff and higher evaporation rates (Simpson et al. 1987). Previous excavation studies of desert plants had shown that roots of perennials occurred in all of the soil zones likely to be recharged on an annual basis, that a few actually penetrated to perched water tables, and that roots of annuals were limited to the upper soil layers (Cannon 1911; Forseth et al. 1984; Manning and Barbour 1988; Manning and Groenvelde 1989). Therefore, in response to anticipated changes in precipitation patterns due to global warming, we would expect that annuals would be better able to utilize the summer rains than perennials, but that there should be no differences among perennial species.

## Materials and methods

Plants were sampled in the desert scrub vegetation immediately north of Stud Horse Point, Glen Canyon National Recreation Area, Utah (lat.  $37^{\circ} 01' N$ , long.  $111^{\circ} 36' W$ , 1,200 m elev.) during 1989 and 1990. The species sampled were distinguished on the basis of life form. The annuals included *Ambrosia acanthicarpa*, *Dicoria brandegei*, *Helianthus anomolus*, *Kallstroemia californica*, and *Sal-*

*sola iberica*. The herbaceous perennials included *Astragalus mollissimus*, *Cordylanthus wrightii*, *Croton californicus*, *Cryptantha confertifolia*, *Sphaeralcea grossularifolia*, *Sphaeralcea parvifolia*, and *Sporobolus flexuosus*. The woody perennials included *Artemisia filifolia*, *Atriplex canescens*, *Coleogyne ramosissima*, *Chrysothamnus nauseosus*, *Chrysothamnus pulchellus*, *Cowania mexicana*, *Ephedra cutleri*, *Eriogonum corymbosum*, *Fraxinus anomala*, *Gutierrezia sarothrae*, *Oenothera pallida*, *Quercus undulata*, and *Vanclevea stylosa*. The succulent perennial was *Yucca angustissima*.

Xylem sap was cryogenically distilled from suberized stems (Ehleringer and Osmond, 1989). Hydrogen isotope composition of water was then determined of a Finnigan MAT delta S isotope ratio mass spectrometer after hydrogen had been reduced to its diatomic form (Coleman et al. 1982). The Coleman et al. (1982) procedure was modified using zinc from J. Hayes (Indiana University) and incubating the reaction at 500 C. Overall precision of the measurement was  $\pm 1.0\text{‰}$ .

Precipitation samples were collected by National Park Service personnel at Wahweap, Utah, 10 km from the study site. Hydrogen isotope ratios were measured on individual storm events; these values were then weighted for daily precipitation amounts.

Hydrogen isotope ratio ( $\delta D$ ) is expressed in  $\delta$  notation with units of  $\text{‰}$  as

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

where R refers to the D/H ratio of sample and standard, respectively. The standard used for  $\delta D$  was SMOW.

Carbon isotope discrimination ( $\Delta$ ) was measured on samples collected in August, 1989. Leaves from three plants were bulked and ground to pass through a 40 mesh screen. Leaf tissue was then combusted to produce  $\text{CO}_2$  and the carbon isotope ratio was measured on a Finnigan MAT delta S isotope ratio mass spectrometer. The  $\Delta$  values were calculated from  $\delta^{13}\text{C}$  values using an atmospheric value of  $-8\text{‰}$ .

Midday values of plant water potential were measured with a Scholander-type pressure chamber.

## Results and discussion

Following winter precipitation,  $\delta D$  values of xylem sap did not differ among perennial life forms during the spring (ANOVA,  $F = 1.754$ ,  $df = 2$ ,  $p = 0.212$ , annuals were absent until very late spring). Although there was some storm-to-storm variation in  $\delta D$  (absolute range of  $-62$  to  $-107\text{‰}$ ), the average winter precipitation value was  $-88.3\text{‰}$ , which was very similar to the  $\delta D$  values of many of the species in spring. This indicated that all perennial species were utilizing waters that had fallen during the winter (Table 1). As the  $\delta D$  of precipitation

**Table 1.** Hydrogen isotope ratios ( $\delta D$ ,  $\text{‰}$ ) in xylem sap of common species representing different life forms in the community at Stud Horse Point, Utah. Data are mean and standard deviation for all species within a life form per sample period. Sample size per species was 2–3 per sample period. Spring samples were collected on April

23, 1990, summer samples on August 6, 1989, early summer samples on July 9, 1990, and autumn samples on September 18, 1989. The second set of summer samples referred to in the text were collected on August 14, 1990

| Life form            | Number of species | Rain Periods    |                 | Drought Periods |                 |
|----------------------|-------------------|-----------------|-----------------|-----------------|-----------------|
|                      |                   | Spring          | Summer          | Early Summer    | Autumn          |
| annual               | 5                 | –               | $-26.0 \pm 3.3$ | $-48.3 \pm 5.7$ | $-31.8 \pm 4.5$ |
| herbaceous perennial | 7                 | $-82.5 \pm 4.3$ | $-31.9 \pm 4.6$ | $-70.7 \pm 5.6$ | $-70.8 \pm 4.1$ |
| woody perennial      | 13                | $-91.8 \pm 2.4$ | $-53.5 \pm 3.4$ | $-79.4 \pm 2.8$ | $-76.7 \pm 2.8$ |
| succulent perennial  | 1                 | $-84.0 \pm 3.0$ | $-22.0 \pm 3.0$ | $-54.0 \pm 1.0$ | $-25.5 \pm 1.5$ |
| well water           |                   | $-91$           | $-90$           | $-92$           | $-92$           |

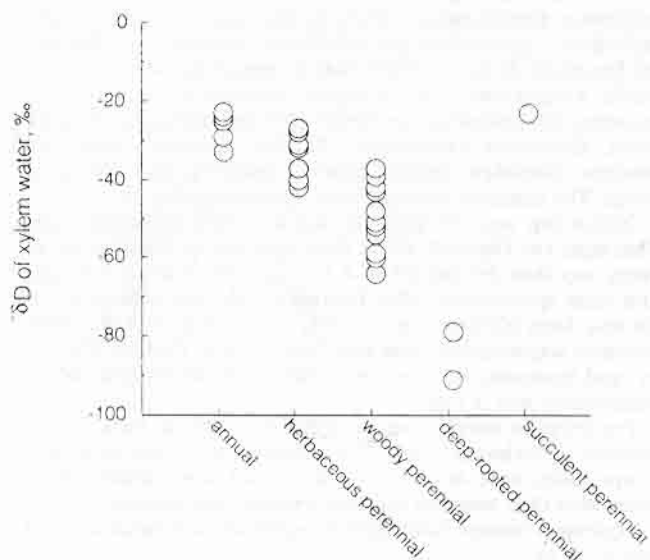


Fig. 1. Hydrogen isotope ratios of xylem sap from common plant species during the summer at Stud Horse Point, Utah

is positively related to temperature at the time of rainfall (Dansgaard 1964; Ingraham and Taylor 1991), the small difference in the  $\delta D$  values between herbaceous and woody perennials could be interpreted as indicating that herbaceous species were utilizing more of the moisture from late winter storms. We can not rule out the possibility that one or more of the deeply-rooted woody species were also utilizing groundwaters, since the  $\delta D$  of well water had a similar isotopic signature (Table 1).

Summer rains are isotopically heavier because of the warmer temperatures, and this is reflected in the  $\delta D$  values of stem waters. In contrast to the pattern of spring soil moisture usage,  $\delta D$  values of xylem sap differed significantly among life forms during the summer (ANOVA,  $F = 35.37$ ,  $df = 3$ ,  $p < 0.001$ ) (Table 1). Annuals and the one succulent perennial in the community utilized only the summer rains, whereas herbaceous and woody perennials used different mixtures of winter and summer water sources (Table 1; Fig. 1). Two deeply-rooted perennials utilized little of the summer precipitation and appeared instead to be accessing ground water or remaining winter soil moisture, since the  $\delta D$  values of stem waters were similar to that of well water. The difference in  $\delta D$  values of herbaceous versus all woody perennials was significant (Student's *t*-test,  $t = 3.46$ ,  $df = 18$ ,  $p = 0.003$ ). Using a two-end-member linear mixing model, we calculated that, on average, 91% of the waters in herbaceous perennials and 57% of the waters in woody species were from summer rains.

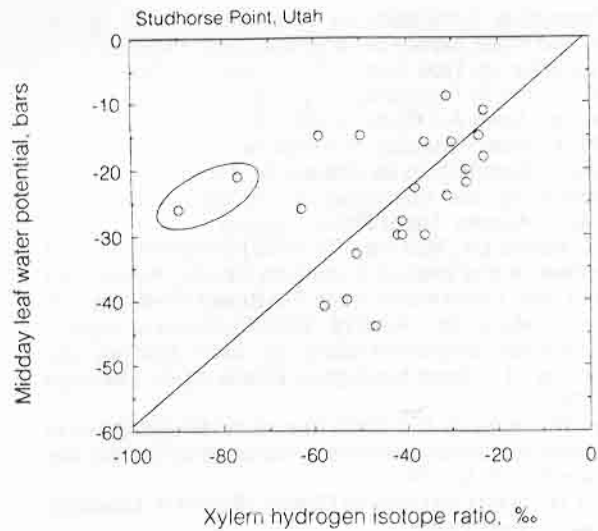
By fall, when the moisture from the summer rains was essentially depleted (as measured by plant water stress),  $\delta D$  values of xylem sap were still significantly different among life forms (ANOVA,  $F = 24.18$ ,  $df = 3$ ,  $p < 0.001$ ). However, this analysis really only indicated that roots of annuals and the succulent perennial were restricted to upper surface layers, whereas both herbaceous and woody perennials, also having deeper roots, had shifted between possible water sources. With the upper soil lay-

ers depleted, perennials species switched back to exploit the remaining moisture in deeper soil layers (Table 1) and there was no difference in the  $\delta D$  values of stem waters among perennial types at that time (Student's *t*-test,  $t = 1.13$ ,  $df = 17$ ,  $p = 0.273$ ). Consequently during this drought period, woody and herbaceous perennials all competed for limiting moisture from the same depths. A similar pattern was seen when perennial plants were sampled in the drought period in early July before the onset of summer rains (Table 1). During that early summer drought period,  $\delta D$  values of herbaceous and woody perennial stem waters were again not different from each other (Student's *t*-test,  $t = 1.37$ ,  $df = 13$ ,  $p = 0.192$ ). Thus, in the drought periods of early summer and again in fall, as well as in the wet periods following winter rains, herbaceous and woody perennials utilized the same water source, soil moisture at greater depths. During drought periods plants may compete for soil moisture, and the effects of limited moisture would impact growth, reproduction, and survival (Fonteyn and Mahall 1978; Robberecht et al. 1983; Ehleringer 1984). In contrast, it is only during the rainy summer months that herbaceous perennials have greater access to soil moisture (from summer rains) than do woody perennials, and thus should be able to gain a competitive advantage by utilizing this critical resource which is not as available to woody perennials.

A similar comparative pattern in  $\delta D$  sap values was repeated in the summer of 1990, where again herbaceous perennials exhibited a greater utilization of summer rains than did woody perennials (Student's *t*-test,  $t = 3.07$ ,  $df = 19$ ,  $p = 0.006$ ). In fact, the strong positive correlation ( $r = 0.546$ ,  $n = 22$ ,  $p = 0.009$ ) between  $\delta D$  values of different species in the summer of 1989 versus 1990 indicated little change in the fraction of summer precipitation used by the different species. In other words, individual species appeared to have relatively fixed patterns of root activity for water uptake during summer months.

The  $\delta D$  values for xylem sap of all species during the summer were marginally correlated with water stress levels as measured by midday water potentials, indicating that species with access to summer rains were less water stressed (1989:  $r = 0.396$ ,  $n = 24$ ,  $p = 0.055$ ; 1990:  $r = 0.373$ ,  $n = 26$ ,  $p = 0.061$ ). This pattern, however, was obscured by including in the analysis the two deeply-rooted woody perennials that appeared to be accessing ground water (Fig. 2). When these two species were eliminated from the analysis, water source and water stress were very significantly correlated (1989:  $r = 0.608$ ,  $n = 22$ ,  $p = 0.003$ ; 1990:  $r = 0.449$ ,  $n = 24$ ,  $p = 0.028$ ).

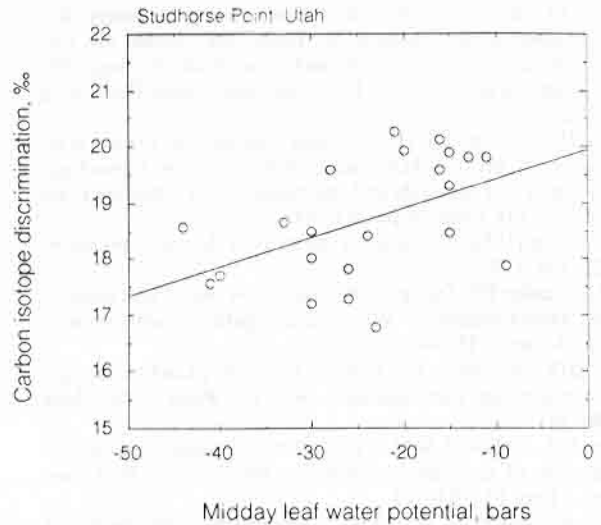
The negative relationship between plant access to summer precipitation and water stress was also reflected in the efficiency with which that water was used (again excluding the two species with direct access to ground water). Integrated long-term water-use efficiency, the ratio of photosynthesis to transpiration, can be estimated from carbon isotopic composition of leaf tissues (Farquhar et al. 1989). When water stress was regressed against carbon isotope composition, there was a significant positive relationship (Fig. 3) ( $r = 0.481$ ,  $n = 22$ ,  $p = 0.023$ ). Greater access to and utilization of summer rains was



**Fig. 2.** The correlation of xylem hydrogen isotope ratio and midday leaf water potential for different species at Studhorse Point, Utah following summer rains. Circled data are two species thought to be primarily utilizing groundwater

associated with decreased plant water-use efficiency in different species. The lack of uptake of appreciable amounts of summer precipitation by most woody perennials resulted in significantly lower water potentials in these species and presumably corresponding reductions in growth rate. Community-level productivity studies have in the past indicated that growth of most woody desert perennials was limited to the spring, and that little growth occurred in most perennials in response to summer rains (Beatley 1974; Fernandez and Caldwell 1975; Hodgkinson et al. 1978; Everett et al. 1980; Turner and Randall 1987). Why several of these perennial species seem incapable of responding to summer rains is unclear. In contrast to these summer-stress patterns, there were no significant relationships between  $\delta D$  values and plant water potential for any other period of the year.

It is well documented that competition for water in deserts influences species interactions and community dynamics (Fowler 1986). Plants with higher growth rates access more of the limiting soil moisture resource. Our results indicate that perennial species utilized the same water source during spring growth and were dependent on the same limiting water source for survival through drought periods. The differential ability of herbaceous perennial species to utilize summer precipitation more than woody perennials implies that this life form should compete more successfully as summer precipitation becomes an increasing component of the total water input in these desert ecosystems. Based on the anticipated changes in summer precipitation from global circulation models (Schlesinger and Mitchell 1987), we predict that competition will favor an increase in frequency of herbaceous and succulent perennials over time, while woody perennials should decrease in frequency. Deeply-rooted woody perennials (phreatophytic) accessing ground water should not be negatively impacted by the change in summer rains as these plants appear to utilize this



**Fig. 3.** The correlation of carbon isotope discrimination (inversely related to water-use efficiency) and midday leaf water potential for different species at Studhorse Point, Utah following summer rains

consistent alternative water source during summer months.

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