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## **Monsoonal precipitation responses of shrubs in a cold desert community on the Colorado Plateau**

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**Abstract** South-eastern Utah forms a northern border for the region currently influenced by the Arizona monsoonal system, which feeds moisture and summer precipitation into western North America. One major consequence predicted by global climate change scenarios is an intensification of monsoonal (summer) precipitation in the aridland areas of the western United States. We examined the capacity of dominant perennial shrubs in a Colorado Plateau cold desert ecosystem of southern Utah, United States, to use summer moisture inputs. We simulated increases of 25 and 50 mm summer rain events on *Atriplex canescens*, *Artemisia filifolia*, *Chrysothamnus nauseosus*, *Coleogyne ramosissima*, and *Vancleavea stylosa*, in July and September with an isotopically enriched water (enriched in deuterium but not  $^{18}\text{O}$ ). The uptake of this artificial water source was estimated by analyzing hydrogen and oxygen isotope ratios of stem water. The predawn and midday xylem water potentials and foliar carbon isotope discrimination were measured to estimate changes in water status and water-use efficiency. *At. canescens* and *Ch. nauseosus* showed little if any uptake of summer rains in either July or September. The predawn and midday xylem water potentials for control and treatment plants of these two species were not significantly different from each other. For *A. filifolia* and *V. stylosa*, up to 50% of xylem water was from the simulated summer rain, but the predawn and midday xylem water potentials were not significantly affected by the additional summer moisture input. In contrast, *C. ramosissima* showed significant uptake of the simulated summer rain (>50% of xylem water was from the artificial summer rain) and an increase in both predawn and

midday water potentials. The percent uptake of simulated summer rain was greater when those rains were applied in September than in July, implying that high soil temperature in midsummer may in some way inhibit water uptake. Foliar carbon isotope discrimination increased significantly in the three shrubs taking up simulated summer rain, but pre-treatment differences in the absolute discrimination values were maintained among species. The ecological implications of our results are discussed in terms of the dynamics of this desert community in response to changes in the frequency and dependability of summer rains that might be associated with a northward shift in the Arizona monsoon boundary.

**Key words** Climate change · Desert shrubs · Colorado plateau · Stable isotope ratio · Summer precipitation

## Introduction

Precipitation input into the arid regions of western North America is derived from winter storms out of the Pacific, summer moisture out of the Gulf of Mexico and south-eastern Pacific generated by the Arizona monsoon system, or both. The interior deserts of Arizona, Nevada, and Utah represent the driest regions of western North America, resulting from a combination of rainshadow effects and either the southern limits of winter moisture input or the northern limits of summer moisture input or both (Houghton 1979; Comstock and Ehleringer 1992). Shifts in strengths of storm-generating conditions in the Pacific and in the Gulf influence both the magnitude and seasonality of soil moisture availability (Bryson and Lowry 1955; Mitchell 1976) and therefore constrain periods of primary productivity activity in these aridland ecosystems (Caldwell 1985; Caldwell and Richards 1989; Dobrowolski et al. 1990). One major consequence predicted by global climate change scenarios is a global intensification of monsoonal (summer) precipitation (Schlesinger and Mitchell 1987; Mitchell et al. 1990), which will likely have an impact in the aridland areas of the western United States.

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South-eastern Utah (north-western portions of the Colorado Plateau) forms a broad northern border for the region influenced by the Arizona monsoonal system (Bryson and Lowry 1955; Mitchell 1976). The effect of the Colorado Plateau is to create a plateau monsoon analogous to that observed in Tibet (Tang and Reiter 1984). Annual precipitation in these aridland Colorado Plateau ecosystems is 100–250 mm, depending on orographic factors and elevation (Houghton 1979). While on average approximately half the annual moisture is from summer events, the year-to-year variability in this precipitation input is high and depends on the intensity of the Arizona monsoon system that develops in a particular year (Houghton 1979; Adang and Gall 1989; Moore et al. 1989). Variations in the intensities and predictability of summer rain should have significant impacts, since water is the single most important factor influencing primary productivity in these aridland ecosystems (Ehleringer and Mooney 1983; Hadley and Szarek 1981; Smith and Nowak 1990). The paleoecological records indicate that these interior aridland regions have changed significantly over the millennia and in recent times in response to changes in climatic conditions (Van Devender and Spaulding 1979; Van Devender et al. 1987; Betancourt et al. 1990; Cole 1990; Stine 1994).

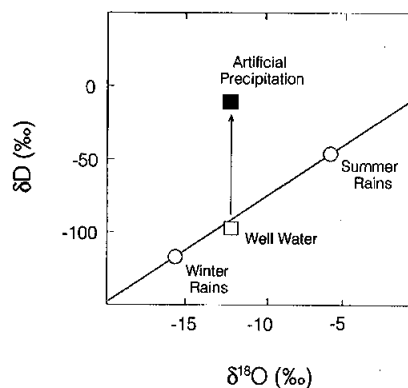
There is increasing evidence of niche differentiation among plants with respect to soil moisture use in Utah aridland and semi-arid woodland ecosystems. While it might be predicted that, when precipitation is the limiting factor to productivity, all perennial species would respond to and use summer moisture inputs, this appears not to be the case. Ehleringer et al. (1991) showed that following summer rains several of the woods perennial shrubs species in a desert shrub of southern Utah were not using that moisture input. Other woody perennials in this ecosystem derived 30–60% of their transpiration water from the upper soil layers wetted by summer rains. It was only the crassulacean acid metabolism (CAM), annual, and herbaceous perennial components of the ecosystem that fully used moisture derived from summer rains. In a nearby pinyon-juniper woodland, Flanagan et al. (1992) and Evans and Ehleringer (1994) demonstrated equivalent water-source partitioning, with tree species most dependent on summer surface layers and also having the highest water-use efficiencies. Gregg (1991) showed that the use of summer moisture by junipers was dependent on the predictability of those summer rains: trees from sites with infrequent monsoon rains relied on moisture from deep layers even following monsoon events. Donovan and Ehleringer (1994) showed that a differential moisture utilization pattern occurred among aridland shrubs in central Utah; in that study they showed that while some adult plants might not fully utilize moisture from surface layers, juveniles were more dependent on this summer-derived moisture source. In a nearby oak-maple woodland, Phillips and Ehleringer (1995) observed that neither oaks nor maples used surface moisture, but instead relied on the moisture from deeper soil layers derived from winter precipitation events.

If monsoonal systems are expected to intensify under elevated atmospheric  $\text{CO}_2$  conditions, as predicted by general circulation models (GCMs; Schlesinger and Mitchell 1987; Mitchell et al. 1990), then it is particularly important to know if the dominant species located on the monsoonal boundaries will be sensitive to a change in the amount of summer moisture input. Based on field observations, Ehleringer et al. (1991) suggested a differential sensitivity among vegetation components, implying possible long-term instability in current species composition with a shift in precipitation input patterns. To further characterize a differential ability for perennial species in cold desert ecosystems of Utah to use summer rains, we conducted a field irrigation experiment to quantify timing and ability to take up moisture from summer rain events. We simulated a 25–50 mm increase in summer rains during July and September on five dominant perennials in an aridland ecosystem on the Utah-Arizona border. We hypothesized that uptake of summer rain would be significantly different among these five species, with some species utilizing that moisture while other species would not, but that the monthly timing of moisture input would not have a significant effect on summer rain use. To conduct this experiment, we took advantage of the fact that the stable isotope ratios of precipitation at our study site differed between winter and summer precipitation events (Fig. 1). By isotopically enriching the hydrogen isotope ratio of our artificial rain events, we could triangulate and distinguish among deep soil (winter-recharge water source), shallow soil (recent summer rain events), our treatment, or combinations thereof as the water source being used by a plant.

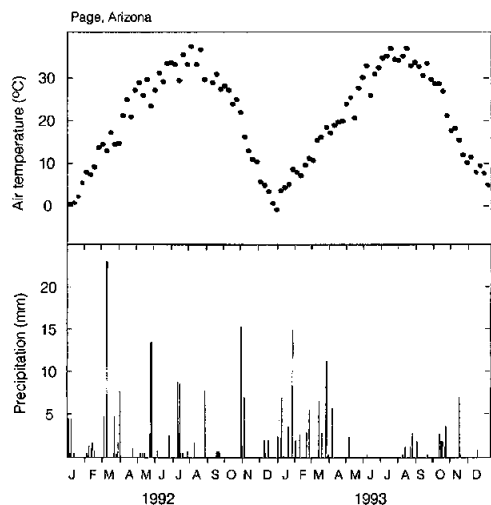
## Materials and methods

### Study site

The study site was located at Stud Horse Point, Utah in the Glen Canyon National Recreation Area (37°0'N, 110°36'W, 1200 m elevation). The plant community at the study site was a cold desert



**Fig. 1**  $\delta\text{D}$  and  $\delta^{18}\text{O}$  values for winter-spring precipitation, summer precipitation, well water and the artificial precipitation water used in this study. The solid line represents the local meteoric water line (MWL) for the precipitation collected during 1989–1993 ( $\delta\text{D}=7.1$   $\delta^{18}\text{O}-7.9\text{‰}$ )



**Fig. 2** Weekly mean maximum air temperature and daily precipitation in 1992 and 1993 for Page, Arizona, about 16 km east of Stud Horse Point, Utah

shrub vegetation, dominated by perennial species including *Artemisia filifolia*, *Atriplex canescens*, *Coleogyne ramosissima*, *Chrysothamnus nauseosus*, *Ephedra cutleri*, *Gutierrezia sarothrae*, *Oenothera pallida*, *Sphaeralcea* sp., and *Vancelevia stylosa* (Ehleringer et al. 1991). Precipitation records from nearby Page, Arizona indicate a mean annual precipitation of 119 mm, with about 40% of this precipitation occurring during the summer (July–September). In 1993, the total precipitation at the study site was comparable to the long-term average, but summer rain represented only 7% of the total precipitation (Fig. 2), making the year suitable for a study on the impact of supplemental summer rain. The monthly maximum air temperature averaged 35.3°C in July and 5.8°C in January of 1993 (Fig. 2).

#### Summer rain irrigation experiment

Within an experimental plot of 50 m × 70 m at the study site, 15 mature plants were selected and tagged in August 1992 for each of the five most common woody perennials: *A. filifolia*, *At. canescens*, *C. ramosissima*, *Ch. nauseosus*, and *V. stylosa*. Each of the 15 plants within a species was randomly divided into one of three groups: a control receiving no supplemental precipitation, a treatment receiving 25 mm supplemental precipitation, and a treatment receiving 50 mm supplemental precipitation. Supplemental precipitation events occurred on 8 July and 12 September 1993; these plants had received a single additional precipitation event in August 1992. The artificial summer rain was prepared by combining heavy water (DHO) with local well water into a 2500-l tank. The isotopically labeled precipitation water was applied to treatment plants through an overhead sprinkler system located above each plant. The simulated precipitation was distributed over a ~7-m<sup>2</sup> area surrounding the main stem of each plant at a rate slow enough to prevent run off (~30–60 min per treatment). Soils were saturated to a depth of 20–25 cm deep for the 25-mm treatment and 40–45 cm deep for the 50-mm treatment.

#### Water source and water potential sampling

Samples of the well water, labelled precipitation water, and soil water from different depths were collected for hydrogen and oxygen isotopic analyses; samples were sealed in glass vials with screw caps and wrapped secure with parafilm. For determination of plant water source, a fully suberized stem sample was collected from each plant once monthly between May and October; samples

were immediately sealed in glass vials as described above and kept frozen until the water could be extracted. In July and September, the stem samples were collected one day before precipitation treatment and then again three days following the treatment. In preliminary experiments, we had determined that three days was sufficient for detection of watering treatment. To assess the possible impact in artificial summer rain events on plant water source, we calculated the difference between the after and before  $\delta D$  xylem sap values as a quantification of the response to summer rains, and then applied this to a two-end-member mixing model (Dawson 1993).

To monitor the response of plant water relations to a simulated summer rain event, we measured plant predawn and midday xylem water potentials with a pressure chamber (PMS Instruments, Corvallis, Oregon, USA) on the same days that water source samples were collected.

#### Stable isotope analyses

Water and plant tissue isotope composition are expressed as stable isotope ratios using delta notation in parts per thousand (‰) as

$$\delta = [R_{\text{sample}}/R_{\text{standard}} - 1] \cdot 1000\text{‰},$$

where  $R$  is the molar ratio of heavy to light isotopes ( $D/H$ ,  $^{18}O/^{16}O$ ,  $^{13}C/^{12}C$ ) and the standard is SMOW for hydrogen and oxygen and PDB for carbon.

Stem and soil waters were cryogenically distilled from the original samples (Ehleringer and Osmond 1989) and the water was stored in a sealed glass tube. Subsamples of the extracted water and source waters were prepared for hydrogen isotope ratio analyses by reacting ~3  $\mu$ l of water with zinc (provided by the laboratory of J.M. Hayes, Department of Chemistry and Geology, Indiana University, USA) in an evacuated pyrex tube at 500°C (modified from Coleman et al. 1982). The resulting hydrogen gas was introduced in an isotope ratio mass spectrometer.

Oxygen isotope ratios of water samples were measured with the  $CO_2$ - $H_2O$  equilibrium method at 25°C as originally described by Epstein and Mayeda (1953) and as modified by Socki et al. (1992).

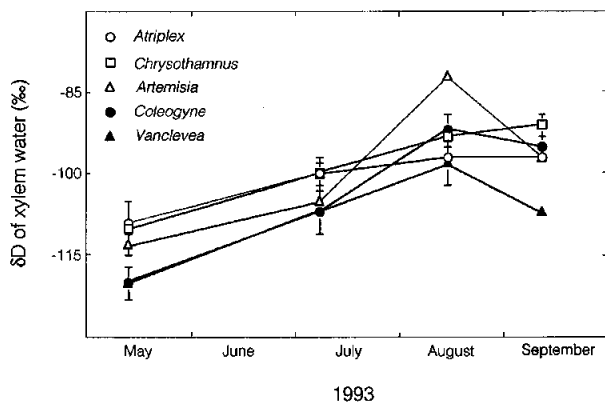
For carbon isotope ratio analyses, five to ten mature leaves were collected in early October and bulked to form a single sample. Leaf samples were dried at 75°C for 48 h and then ground in a mortar and pestle to a fine powder. Carbon isotope ratios of leaf samples were measured by flash combustion of 2-mg samples on an elemental analyzer coupled to the mass spectrometer. Carbon isotope discrimination ( $\Delta$ ) was calculated from leaf carbon isotope ratios using a carbon isotope ratio value of -8‰ for atmospheric carbon dioxide (Ehleringer et al. 1991).

All isotope measurements were made on an isotope ratio mass spectrometer (delta S, Finnigan MAT, San Jose, California, USA). The overall measurement precision based on repeated measurements of two secondary standards was  $\pm 1.1\text{‰}$  for  $\delta D$ ,  $\pm 0.4\text{‰}$  for  $\delta^{18}O$ , and  $\pm 0.11$  for  $\delta^{13}C$ .

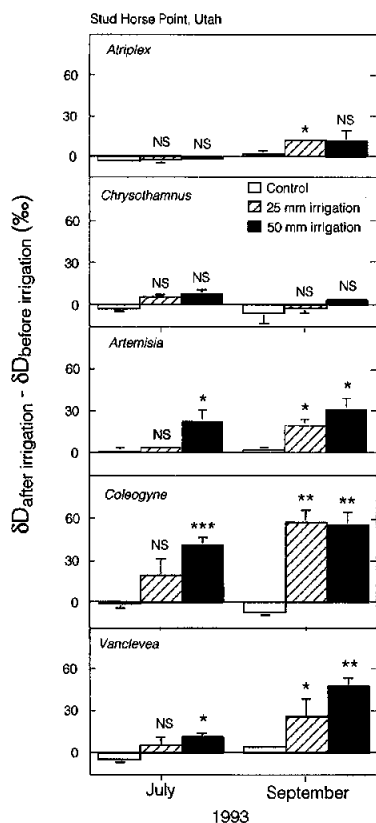
## Results

#### Isotopic composition of stem water

Hydrogen isotope ratios ( $\delta D$ ) of the enriched precipitation water averaged  $-10 \pm 2\text{‰}$  ( $n=5$ ), significantly higher than that of the well water ( $-92 \pm 0.1\text{‰}$ ,  $n=4$ ) or natural summer rain events at Stud Horse Point ( $-48 \pm 9\text{‰}$ ,  $n=7$ ) (Fig. 1). As expected, oxygen isotope ratio ( $\delta^{18}O$ ) of the applied precipitation ( $-11.1 \pm 0.1$ ,  $n=5$ ) was not significantly different from that of the well water ( $-11.2 \pm 0.1\text{‰}$ ,  $n=3$ ). Natural summer rain events at Stud Horse Point had significantly higher  $\delta^{18}O$  value ( $-6.1 \pm 1.3\text{‰}$ ,



**Fig. 3** Seasonal changes in  $\delta D$  values of stem xylem sap of control plants at Stud Horse Point, Utah for 1993. Each point represents the mean and standard error of the measurements on five plants



**Fig. 4** Changes in  $\delta D$  values ( $\delta D_{\text{after irrigation}} - \delta D_{\text{before irrigation}}$ ) of stem xylem sap from five dominant perennial species of a cold desert community at Stud Horse Point, Utah after receiving simulated summer rain having a  $\delta D$  value of  $-10\text{‰}$  in July and September. Each bar represents the mean and standard error of the measurements on five plants, and the significance level is for the comparison of the mean between the control plants and the plants receiving either 25 mm or 50 mm summer rain treatments ( $n=5$ ): NS, not significant,  $P>0.05$ , \*  $P<0.05$ , \*\*  $P<0.01$ , \*\*\*  $P<0.001$  ( $t$ -test)

$n=7$ ) than the enriched artificial precipitation water (Fig. 1).

Control plants of all five species showed a slight trend toward increasing  $\delta D$  xylem sap values through the summer (Fig. 3). Although there was effectively no precipita-

tion input during this time, the slightly enriched water source values (from  $-115\text{‰}$  in May to  $-100\text{‰}$  in September) may have reflected the result of an evaporative soil-water enrichment occurring throughout the soil profile. The increase in *A. filifolia* and *C. ramosissima* xylem sap  $\delta D$  values in August likely reflected a response to a natural rain event that had occurred several days prior to the sampling.

In both *At. canescens* and *Ch. nauseosus*, there was no statistically significant water-source response following a simulated rainfall event or either 25 mm or 50 mm in July (Fig. 4). Hydrogen isotope ratios of xylem sap in both species did not change in response to an artificial rain event that was  $\sim 90\text{‰}$  more enriched than the background water source. Although both species were in leaf and active in July, neither species appeared to use this moisture which had saturated the upper 40–45 cm of the soil profile. When summer precipitation was applied again in September, there was still no response to this moisture in the upper soil layers by *Ch. nauseosus*. However, *At. canescens* did exhibit a slight response to the September precipitation event, although only the 25 mm treatment was statistically significant.

There were no significant differences in  $\delta^{18}\text{O}$  values of xylem water among the controls and treatments in these two species, or, in fact, for any of the species in this study (Table 1). Additionally, the  $\delta^{18}\text{O}$  values of xylem sap before and after the artificial precipitation treatment were not significantly different from each other (Table 1). Thus, we could use the  $\delta D$  values of xylem sap and the linear mixing model outlined in Dawson (1993) to estimate the percentage of the simulated summer rain water taken up by the plant. Using the end members of  $-100\text{‰}$  for average deep-soil water (Fig. 3) and  $-10\text{‰}$  for the irrigation water (Fig. 1), we estimated the percent uptake of summer rain by *At. canescens* and *Ch. nauseosus* (Table 2). Consistent with the lack of a statistical change in xylem sap  $\delta D$  values, *At. canescens* had only 1–2% of its xylem water derived from the summer rains applied in July and 13% in September (Table 2). In *Ch. nauseosus*, 5–7% of stem water came from the summer rain treatment in July and 2–3% in September (Table 2).

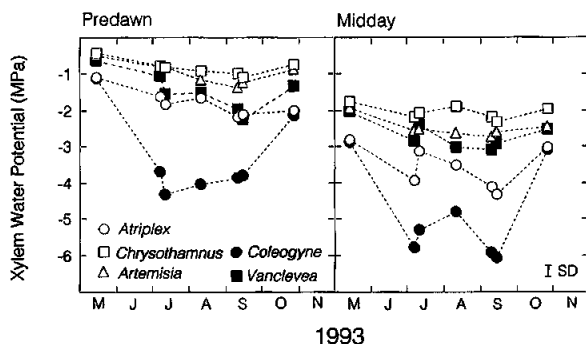
In contrast, *A. filifolia*, *C. ramosissima*, and *V. stylosa* responded to a July summer rain event of 50 mm, but not to a rain event of 25 mm (Fig. 4). All three species were active and in leaf at this time. However, by September, the response to the simulated summer rain event was much greater in these three species (Fig. 4). In the late summer treatment, all three species responded significantly to both 25-mm and 50-mm treatments. When these  $\delta D$  values were used to calculate the percent of water taken up that was derived from summer rain under different treatments, the percentages for these three species were much greater than for *Atriplex* and *Chrysothamnus*. In response to summer rain events in July, *Artemisia* derived 5–25% of its xylem water from that summer rain event; the percentages increased to 20–35% when the precipitation was applied in September (Table

**Table 1** The average  $\delta^{18}\text{O}$  values (‰, mean $\pm$ SE,  $n=5$ ) for stem xylem sap from plants before and after receiving different summer rain treatments in July for the five dominant perennial species of a cold desert community at Stud Horse Point, Utah. No significant difference in the mean was observed between three summer rain treatments or between before and after the irrigation within each treatment (all  $P>0.05$ ,  $t$ -test,  $n=5$ )

Species	Sampling time	Summer rain treatment		
		0 mm	25 mm	50 mm
<i>Atriplex canescens</i>	before irrigation	-10.3 $\pm$ 0.3	-10.0 $\pm$ 0.3	-10.1 $\pm$ 0.1
	after irrigation	-10.5 $\pm$ 0.2	-10.7 $\pm$ 0.2	-10.5 $\pm$ 0.2
<i>Chrysothamnus nauseosus</i>	before irrigation	-11.3 $\pm$ 0.4	-12.9 $\pm$ 1.0	-12.3 $\pm$ 0.8
	after irrigation	-11.6 $\pm$ 0.4	-11.3 $\pm$ 0.9	-12.2 $\pm$ 0.8
<i>Artemisia filifolia</i>	before irrigation	-11.5 $\pm$ 0.2	-11.3 $\pm$ 0.2	-10.8 $\pm$ 0.5
	after irrigation	-11.0 $\pm$ 0.6	-11.2 $\pm$ 0.5	-10.3 $\pm$ 0.8
<i>Coleogyne ramosissima</i>	before irrigation	-12.4 $\pm$ 0.4	-12.2 $\pm$ 0.2	11.9 $\pm$ 0.4
	after irrigation	-11.5 $\pm$ 0.3	-11.5 $\pm$ 0.5	-11.4 $\pm$ 0.2
<i>Vancleavea stylosa</i>	before irrigation	-11.4 $\pm$ 0.1	-10.7 $\pm$ 0.3	-11.0 $\pm$ 0.4
	after irrigation	-10.9 $\pm$ 0.3	-11.1 $\pm$ 0.2	-11.5 $\pm$ 0.2

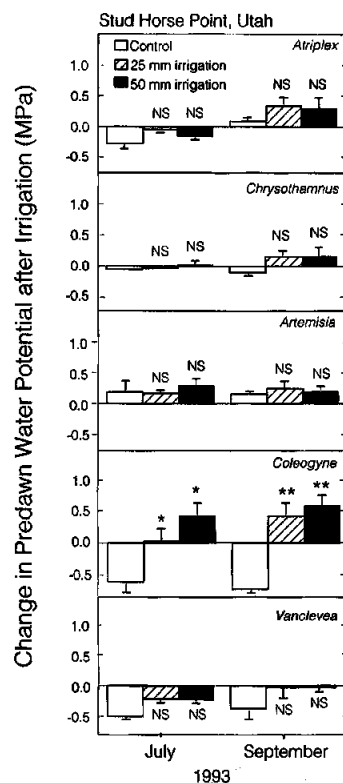
**Table 2** Estimated percentage of the simulated summer rain utilized by the five dominant perennial species of a cold desert community at Stud Horse Point, Utah. The fraction of the simulated summer rain used was expressed in the percentage of stem water derived from the artificial rain, basing on the hydrogen isotope ratios of stem water after irrigation and the two end members of -100‰ for deep soil water and -10‰ for the irrigation water, respectively

Species	Treatment	Summer rain used (%)	
		July	September
<i>Atriplex canescens</i>	25 mm rain	1	13
	50 mm rain	2	13
<i>Chrysothamnus nauseosus</i>	25 mm rain	5	2
	50 mm rain	7	3
<i>Artemisia filifolia</i>	25 mm rain	5	20
	50 mm rain	25	35
<i>Coleogyne ramosissima</i>	25 mm rain	20	55
	50 mm rain	42	58
<i>Vancleavea stylosa</i>	25 mm rain	12	27
	50 mm rain	16	52



**Fig. 5** Seasonal changes in predawn and midday xylem water potentials of the five dominant perennial species of a cold desert community at Stud Horse Point, Utah. Each point represents the mean and standard error of the measurements on five plants

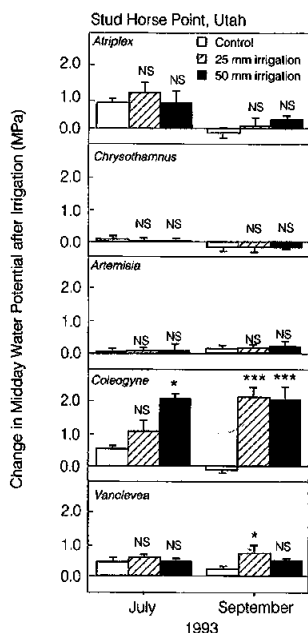
2). A similar pattern was observed in *Vancleavea*, where 12–16% of the xylem water in July and 27–52% of the xylem water in September was derived from the summer precipitation event. The response was even greater in *Coleogyne*, where 20–42% of the xylem water in July and 55–58% of the xylem water in September was derived from summer precipitation events.



**Fig. 6** Changes in predawn xylem water potentials of the five dominant perennial species after irrigation of 0, 25 and 50 mm simulated summer rain in July and September of 1993 in a cold desert community at Stud Horse Point, Utah. Each bar represents the mean and standard error of the measurements on five plants, and the significance level is for the comparison of the mean between the control plants and the plants receiving either 25 mm or 50 mm summer rain treatments ( $n=5$ ): NS, not significant,  $P>0.05$ , \*  $P<0.05$ , \*\*  $P<0.01$ , \*\*\*  $P<0.001$  ( $t$ -test)

#### Predawn and midday xylem water potentials

Neither *Artemisia* ( $F=0.819$ ,  $P=0.566$ , ANOVA) nor *Chrysothamnus* ( $F=1.24$ ,  $P=0.305$ , ANOVA) showed any significant seasonal changes in predawn or midday xylem water potentials (Fig. 5). These two species maintained the highest predawn and midday xylem water potentials throughout the year, with the average predawn water potentials of -0.94 and -0.83 MPa and midday potentials of



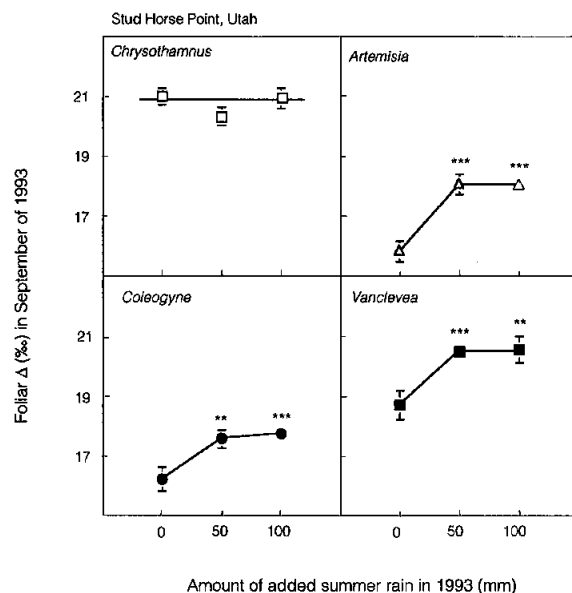
**Fig. 7** Changes in midday xylem water potentials of the five dominant perennial species after receiving 25 and 50 mm summer rain in July and September. Each bar represents the mean and standard error of the measurements on five plants, and the significance level is for the comparison of the mean between the control plants and the plants receiving either 25 mm or 50 mm summer rain treatments ( $n=5$ ): NS, not significant,  $P>0.05$ ; \*  $P<0.05$ , \*\*  $P<0.01$ , \*\*\*  $P<0.001$  ( $t$ -test)

–3.34 and –2.06 MPa for *Artemisia* and *Chrysothamnus*, respectively. Predawn and midday xylem water potentials of *Atriplex* and *Vancleavea* decreased 1.0–1.2 MPa between May and September, before returning to early season values by late October (Fig. 5). Predawn and midday xylem water potentials *Coleogyne* exhibited the sharpest changes, decreasing to predawn values of less than –4 MPa in summer (~3.0 MPa decrease), but then also returned to early season values by late October.

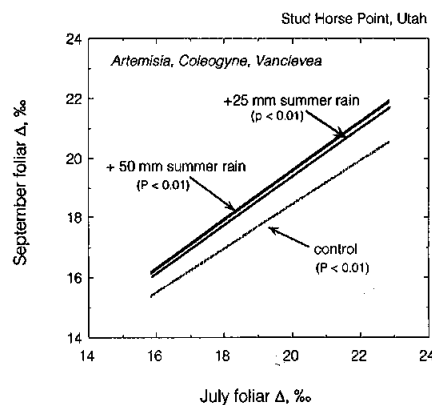
Even though a 25-mm or 50-mm summer rain treatment was applied in July and September, *Atriplex*, *Artemisia*, *Chrysothamnus* and *Vancleavea* did not show significant improvements in predawn xylem water potentials (Fig. 6). Essentially the same patterns were observed for midday water potentials (Fig. 7). The only species to show a predawn water potential change following the precipitation treatment was *Coleogyne* (Fig. 6). Midday water potentials of *Coleogyne* also increased significantly after receiving 25 or 50 mm artificial summer rain, except for the plants receiving 25 mm summer rain in July (Fig. 7).

### Foliar carbon isotope discrimination

In *Chrysothamnus*, there was no significant change in foliar carbon isotope discrimination ( $\Delta$ ) in response to the simulated summer rain increase (Fig. 8). However, in the other three  $C_3$  species (*Artemisia*, *Coleogyne* and *Vancleavea*), foliar  $\Delta$  values increased significantly in response to additional summer rains (Fig. 8). The average foliar  $\Delta$



**Fig. 8** Effects of summer rain increase in July 1993 on foliar carbon isotope discrimination of four  $C_3$  species measured in September at Stud Horse Point, Utah. Each point represents the mean and standard error of the measurements on five plants, and the significance level is for the comparison of the mean between the control plants and the plants receiving either 25 mm or 50 mm summer rain treatment ( $n=5$ ): NS, not significant,  $P>0.05$ ; \*  $P<0.05$ , \*\*  $P<0.01$ , \*\*\*  $P<0.001$  ( $t$ -test)



**Fig. 9** The relationship between leaf carbon isotope discrimination of samples collected in July before irrigation and in September following irrigation for individual plants of *Artemisia filifolia*, *Coleogyne ramosissima*, and *Vancleavea stylosa*

value for the plants receiving additional summer rain was 2.0–2.5‰ higher than the control plants, and the two precipitation treatments had a similar effect on foliar  $\Delta$  (Fig. 8). Although  $\Delta$  values acclimated to the higher levels of soil water availability, differences between species were maintained (Fig. 8, 9). Thus, the  $\Delta$  rankings among species remained the same even though environmental conditions had changed.

The  $C_4$  species *At. canescens* exhibited no significant changes in foliar carbon isotope discrimination with values of  $7.6\pm 0.2\text{‰}$ ,  $7.4\pm 0.2\text{‰}$ ,  $7.5\pm 0.2\text{‰}$  for control plants, 25-mm treatment plants, and 50-mm treatment plants (data not shown in Fig. 8).

## Discussion

### Utilization of summer rain by desert shrubs

Previous studies have applied hydrogen isotope ratio analyses of stem water to estimate the utilization of summer rain (reviewed in Ehleringer and Dawson 1992). In many ecosystems such as in southern Utah, this approach is feasible because winter-spring and summer rain events have distinct hydrogen isotope ratios (Benson and Klieforth 1989; Ingraham et al. 1991; Friedman et al. 1992). However, the soil moisture available for plant uptake in aridlands may be undergoing evaporative enrichment (Craig et al. 1963; Zimmermann et al. 1967; Barnes and Allison 1983). We observed that  $\delta D$  values of xylem sap from all five perennial species increased by an average of 15‰ during the summer growing season, even though there was no significant rains during this period. Thus, calculations of surface versus deep soil moisture uptake involving only  $\delta D$  values of xylem sap might overestimate the utilization of a summer rain input moisture, since evaporative enrichment tends to increase the  $\delta D$  values in the upper soil layers. In the present study, it is likely just a coincidence that the  $\delta^{18}O$  values of the enriched winter-precipitation signal remaining in the soil were the same as those of the well water applied in the artificial precipitation experiments.

Our results indicated that the five dominant perennial species in this cold desert ecosystem had differential capacities to use summer rain. Changes in  $\delta D$  values of xylem sap following an artificial rain event showed significant differences among species, with the greatest response occurring in *C. ramosissima* and the smallest response in *Ch. nauseosus*. In those species that responded, the larger the summer rain event, the greater the fractional increase in summer rain use. Within 3 days, the rain water added to the soil had not undergone significant evaporation, since there were no significant differences in  $\delta^{18}O$  values of stem xylem sap before and after the precipitation event. Thus, the increase in  $\delta D$  values of xylem sap in these three shrub species must result from the uptake of the simulated summer rain. The relative uptake of summer rain, expressed in the maximum percentage of stem water derived from the simulated summer rain, varied from 1 to 58% among these five perennial species. Overall this pattern is consistent with what Ehleringer et al. (1991) had observed for woody perennials at Stud Horse Point, Utah. However, these values are substantially lower than the summer rain usage values by herbaceous summer perennials at this site.

### Effects of temperature on summer rain uptake by desert shrubs

We find it quite interesting that these woody perennials would differ in their capacities to take up summer moisture at different times during the summer. For all species, the capacity to take up moisture from the surface layers

was greater in September, a cooler month, than it was in July. The suggestion that soil temperature may play a role in water uptake has received limited attention in the literature. However, it is worth noting that Ehleringer et al. (1991) observed that woody and nonwoody perennials had the same capacity to take up moisture during the winter-spring months; it is only during the summer months that we see this life-form distinction. One possible explanation is that many of these woody perennials do not maintain surface roots for water uptake during the summer. Root excavation studies, however, showed that all of these species had some live roots in the upper soil layers (S.L. Phillips and J.R. Ehleringer, unpublished work). Since water limitations usually limit productivity in these ecosystems, it is surprising that the surface roots did not take up this available resource (summer rain) (Ehleringer et al. 1991). Ehleringer and Dawson (1992) hypothesize that woody perennials in these ecosystems may be allocating carbon belowground to those portions of the possible rooting zones most likely to have moisture on a long-term basis. If the probability of summer moisture in the upper soil layers is sufficiently low, the amount of water taken up through time per carbon invested in roots may be greater to the plant if available carbon was allocated to roots in deeper soil layers.

A second possible explanation for the apparent lack of summer rain uptake by some species is that high soil temperatures during the summer, combined with late spring drought before the monsoon rains arrived, had inactivated the shallow-depth roots and prevented root regrowth in these upper soil layers. Caldwell and colleagues have shown a seasonal progression of fine root production into deeper soil layers for shrub and grass species in nearby sagebrush steppe ecosystems (Fernandez and Caldwell 1975; Caldwell 1985; Caldwell and Richards 1986) where summer rains are uncommon. Perhaps when summer moisture was applied in our experiments, the soils were then too warm to reactivate the fine surface roots in some species. This would provide a simple mechanism for why some species responded to rain in spring (Ehleringer et al. 1991) and in late summer, but not during midsummer. There is evidence to suggest that this may be the case. In a study of fine root mortality in sugar maples, Hendrick and Pregitzer (1993) observed that higher root mortality in the upper soil layers was associated with warmer soil temperatures. However, several of the species in our study also commonly occur in more southerly habitats with a greater fraction of the annual rains from summer monsoons. It may be that there is substantial population-level variability in the response to summer rains. Ehleringer and Dawson (1992) cite data showing a latitudinal gradient in the response of juniper to summer rains. D. Williams and J.R. Ehleringer (unpublished work) have also shown similar population-level differences in the response to summer rains for *Pinus edulis* and *Quercus gambelii*.

In our study, we found that the changes in  $\delta D$  values of stem water after the irrigation were much greater in September than in July in four of the five shrub species



studied (Fig. 4, Table 2). In *Atriplex*, *Artemisia*, *Coleogyne* and *Vancleavea*, the percentage differences in uptake of surface moisture between July and September was 1% vs 13%, 5% vs 20%, 20% vs 55%, and 12 vs 27%, respectively, if 25 mm rain was applied; these percentages changed to 2% vs 13%, 25% vs 35%, 42% vs 58%, and 16% vs 52%, respectively, if 50 mm rain was applied (Table 2). We hypothesized that the temperature differences may be the major factor responsible for such difference in uptake of summer rain by desert shrubs between July and September. Air temperatures during 1993 were very similar to the long-term average and so it is unlikely that the decreased moisture uptake in summer was due to unusually warm soil temperatures. Flanagan et al. (1992) had investigated summer moisture uptake in a nearby pinyon-juniper woodland over 2 years. Consistent with our observations, they observed less summer moisture uptake by *Juniperus osteosperma* in 1989 (a warm summer) than in 1990 (a cooler summer).

#### Constant relative changes in carbon isotope discrimination

While it appears that *Artemisia* and *Vancleavea* did not use summer moisture inputs, that moisture may have remained in the soil for later use by these plants. Since the leaf carbon isotope discrimination ( $\Delta$ ) of these two species as well as of *Coleogyne* became more positive with additional summer rains (Fig. 8), it is apparent that this moisture resulted in increased intercellular  $\text{CO}_2$  levels (Farquhar et al. 1989). Ehleringer (1993a, b) suggested that  $\Delta$  values were a measure of a metabolic "set point" for gas exchange metabolism and that species-level differences in  $\Delta$  values should remain nearly constant as environmental resource levels fluctuated. Consistent with this model, the rankings of species differences before and after the additional moisture treatments remained constant. In fact, genotypic rankings of all species remained constant; that is, there was a constant shift in  $\Delta$  values, but the slope of the  $\Delta$  values before and after the treatment effects remained on the one-to-one line.

#### Responses of plant water relations to summer rain increase in desert shrubs

Among the five dominant perennial species studied, there were three different responses in plant water relations to the simulated summer rain increase. *Atriplex* and *Chrysothamnus* showed no response in predawn or midday water potential to the simulated summer rain increase, and likewise neither species used summer surface moisture input. Yet *Chrysothamnus* maintained relatively high predawn and midday water potentials, indicating that this species had access to a stable water source throughout the summer growing season (probably the water in deep soil layers recharged by winter-spring precipitation), whereas *Atriplex* experienced much more

negative predawn and midday water potentials. Previous studies showed that *Chrysothamnus* used little surface soil moisture during summer growing season (Ehleringer et al. 1991; Flanagan et al. 1992; Donovan and Ehleringer 1992, 1994). In contrast, *Atriplex* showed a significant decrease in xylem water potentials that was not relieved by summer rain. *Atriplex* has  $\text{C}_4$  photosynthesis, which may play some role in allowing these plants to remain photosynthetically active with a greater water-use efficiency, despite not having access to deep water nor using summer surface moisture inputs.

As a second pattern, *Artemisia* and *Vancleavea* exhibited no significant increases in xylem water potentials, although both species showed a significant uptake of the simulated summer rain. We hypothesize that these species are capable of switching between near-surface and deeper-soil moisture sources depending on water availability and modulating transpiration rates so that water potential gradients remain essentially constant. During dry periods in the summer, these species utilize moisture from deeper depths as a water source, but can switch and use soil moisture in the upper layer when summer rains come. Throughout the summer, control plants of these two species also maintained relatively high xylem water potentials. This feature is less common among woody perennials at our cold desert site in southern Utah (Ehleringer et al. 1991), but is instead similar to the pattern observed in herbaceous perennials. If water is the most limiting factor for plant growth in the summer, then these species capable of switching between surface and non-surface moisture sources should have a significant competitive advantage over species such as *Atriplex* during periods when summer moisture inputs increase.

The third pattern, exhibited by *Coleogyne*, is indicative of a perennial plant with limited access to deeper soil layers, because there was a significant improvement in plant water potentials in response to summer moisture input. *Coleogyne* exhibited the greatest decrease in xylem water potentials during the summer growing season, and also the greatest improvements in leaf water potentials, suggesting that these plants may have experienced the most serious water stress during drought. *Coleogyne* has a distributional range in arid zones between California and Utah where winter temperatures are cold enough to prevent much growth activity during winter (Bowns and West 1976). Its distribution is also a transitional band between monsoon and non-monsoon desert ecosystems. It is likely that growth in such a species might be very responsive to increased nonsoonal inputs, but there is very little information yet about how much growth will occur in response to these summer rain events relative to spring growth.

#### Monsoon boundary fluctuation and vegetation change in aridlands of the Colorado Plateau

Water is commonly accepted as the factor most limiting primary productivity in aridland ecosystems (Ha-

dley and Szarek 1981; Evanari et al. 1986; Smith and Nowak 1990). Cold winter temperatures prevent much plant growth during the winter months on the Colorado Plateau (Comstock and Ehleringer 1992) and thus the growth of most woody perennials in these cold desert ecosystems is greatest in the spring as temperatures warm and while soil moisture levels is highest (Everett et al. 1980; Caldwell 1985; Turner and Randal 1987). Any increase in soil moisture available for plant utilization during water limited periods may have significant effects on plant growth, plant competition and thus the potential to alter community composition (Fowler 1986). Therefore, species capable of utilizing summer rain should be at a competitive advantage over those that cannot utilize summer rain as the Arizona monsoon boundary periodically shifts across the Colorado Plateau. Ehleringer et al. (1991) observed that herbaceous perennials in the Colorado Plateau desert utilized summer moisture inputs much more extensively than did woody perennials. A similar niche differentiation pattern has been described by Sala et al. (1989) for aridland plants in Patagonia. The outcome from both sets of ecophysiological studies is the prediction that as summer monsoonal rains increase, the herbaceous perennials should be at a competitive advantage over most of the woody perennials in accessing that resource. Based on the results of this study, woody components, such as *Atriplex* may be most impacted by this competition. On the other hand, *Artemisia*, *Coleogyne*, and *Vanclevea* may compete favorably with herbaceous dicots and grasses, with the competitive outcome influenced by additional factors such as disturbance and herbivore relationships.

Taylor and Rose (1992) used tree-ring chronologies to reconstruct long-term climatic conditions and observed short-term drought cycles of 20–80 years on the Colorado Plateau over the past 2 millennia. These drought cycles could be associated with migrations in the northern boundary of the Arizona monsoonal system and are of long enough duration to influence aridland vegetation composition, especially the dynamics of herbaceous perennial vegetation components, which tend to be shorter-lived. Packrat midden data (Betancourt et al. 1990) provide a longer-term record showing a general southward movement in the amount of rainfall in some parts of the Great Basin and Colorado Plateau since the Holocene, but these midden data may not provide us with a means of distinguishing winter from summer precipitation if there is interpopulation-level variation in the ability to use summer rains as suggested by Ehleringer and Dawson (1992).

As a consequence of increased atmospheric CO<sub>2</sub>, both soil temperature (Rind et al. 1990) and summer rain (Schlesinger and Mitchell 1987; Mitchell et al. 1990) are likely to increase in some portions of the western United States. Our results suggest that the species composition of many cold desert communities may be sensitive to these changes. The five dominant perennial species in the studied cold desert community have significantly different capability of utilizing summer rain, contrasting

with patterns previously shown for herbaceous species (Ehleringer et al. 1991). These woody perennials also differed in summer water uptake in a way that is consistent with the hypothesis that soil temperature may play a direct role in the capacity to take surface moisture. Consistent with this is the recent observation by Harte and Shaw (1995) that altered soil temperature plays a direct role in shifting life-form dominance within a community.

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