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Deuterium enriched irrigation indicates different forms of rain use in shrub/grass species of the Colorado Plateau

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Abstract We contrasted the seasonal use of simulated large rain events (24 mm) by three native species of the arid Colorado Plateau: the perennial grass *Hilaria jamesii* and two shrubs *Artemesia filifolia* and *Coleogyne ramosissima*. Deuterium-enriched water was used to distinguish shallow “pulse” water from water in deeper soil layers that were unaffected by the water input. We also measured the leaf gas exchange rates of watered and unwatered control plants for 5 days after the rain event. *H. jamesii* had twice the pulse water proportion in its xylem than the two shrubs in spring (approx. 70% vs 35%). In summer, the pulse water proportions of all species were around 70%. The increase in the relative pulse water uptake of the two shrubs was caused primarily by a reduction in the rate of water uptake from deeper sources, consistent with the decrease in the availability of stored winter water. Rain increased the rates of gas exchange in *C. ramosissima* in both seasons, in *H. jamesii* only in summer and had no significant effect on *A. filifolia*. In *H. jamesii*, summer rain also increased water use efficiency. This suggests three principle mechanisms for rainwater use: (1) immediate increase in gas exchange via stomatal opening (*C. ramosissima*), (2) immediate increase in water use efficiency through restoration of the photosynthetic apparatus (*H. jamesii*) and (3) conservation of deeper soil water, potentially extending photosynthetic activity into later drought periods (*A. filifolia*). On a ground-area basis, *A. filifolia* was by far the largest consumer of spring and summer rain, due to its greater ground cover, while rain use by *H. jamesii* was negligible. We hypothesize that a population’s fraction of the total community Leaf Area Index, more than species identity, determines which species takes up most of the spring and summer precipitation and we discuss this idea in the context of Walter and Stadelmann’s (1974, In:

Brown JW Jr (ed) Desert biology. Academic Press, New York, pp 213–310) water partitioning hypothesis.

Keywords Arid ecosystems · Plant functional types · Precipitation pulse use · Stable isotope label · Water partitioning

Introduction

Arid and semiarid regions are considered among the most sensitive to shifting climatic conditions (Schlesinger et al. 1990; Houghten et al. 1996), particularly to those, which impact the intensity, frequency and seasonal distribution of rainfall events (Ehleringer et al. 1999). There is broad consensus that certain seasonal and year-to-year precipitation patterns can affect the distribution of functional types (sensu Gitay and Nobel 1997, e.g. annuals, grasses, shrubs, trees) of arid lands (Ehleringer et al. 1991; Burgess 1995; Brown et al. 1997; Sala et al. 1997), but the mechanisms responsible for mediating such effects have not been identified with certainty (Schulze et al. 1996). One hypothesis is that different plant functional types extract water from different depths in the soil horizon, realizing in this way a resource niche separation (Walter 1979). Different layers are typically recharged at different times by different annual precipitation components. For example, summer rains do not usually recharge deeper soil layers, because the soil moisture they introduce is lost to evaporation before it can infiltrate deeply (Ehleringer et al. 1998; Ingraham et al. 1998). Rain generated by monsoon-type convection storms rarely infiltrates below 20 cm in the soil profile (Fernandez and Caldwell 1975; Sala and Lauenroth 1982). Thus, as a generalization for arid and semi-arid lands, soil moisture near the soil surface is recharged by recent rain events, while soil moisture deeper down is recharged predominantly by winter precipitation. The hypothesis of niche separation could explain, not only why different functional types can coexist under one climatic condition (Walter and Stadelmann 1974; Cody 1986; Smith and Nobel

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1986), it also could set the stage for predicting community responses when changing seasonal precipitation patterns alter the magnitude of water recharge into different soil layers (Sala et al. 1997; Ehleringer et al. 1998; Schwinnig and Ehleringer 2001).

White et al. (1985) pioneered a method for determining water sources used by tree species of Eastern forests in the USA by analyzing the stable isotope composition of sap water and comparing it to the isotope composition of summer rain, winter precipitation and ground water. Later, Ehleringer et al. (1991) applied this method to an arid ecosystem in the southern USA. This and many consecutive experiments since then suggest that there are consistent differences in the water use patterns between broad life form categories. Herbaceous plants, grasses and cacti use primarily shallow soil water from recent rain-showers, riparian trees and deep-rooted shrubs use primarily deeper soil water or ground water, while shrubs and some trees often use a mixture of water sources (Dawson and Ehleringer 1991; Flanagan et al. 1992; Lin et al. 1996; Dodd et al. 1998; Jackson et al. 1999; Williams and Ehleringer 2000). Similar differences were recently reported to exist between tree species of a tropical forest during the dry season (Meintzer et al. 1999; Stratton et al. 2000).

Apart from these broad differences between major plant life forms, there is also evidence for substantial overlap in the water use of the dominant vegetation components. For one, the water sources of immature plants may be more similar than those of adult plants (Donovan and Ehleringer 1992). Weltzin and McPherson (1997) showed that the water sources of grasses and tree seedlings in a temperate savanna overlap for up to 2 years, when both take water from 20–35 cm in the soil profile (see also Davis et al. 1998). Secondly, within major life forms, the water requirements for different species can be quite similar. Minimal differences were observed, for example, in the water use between drought-deciduous and evergreen shrubs in the summer-rain dominated Chihuahuan Desert (Reynolds et al. 1999; Yoder and Nowak 1999). In a cold desert shrub community, the rainwater proportion in the sap water of six dominant shrubs was between 20% and 80% during the driest time of the year, suggesting that all six shrubs were quite capable of using summer rain and differed only in the proportional use of the different water sources (see also Lin et al. 1996). Similarly, along an aridity gradient in Patagonia, Schulze et al. (1996) found that all dominant plant species used water from recent rainfall events, rather than from saturated water supply at greater depth.

The available data suggest that plant species in water-limited environments, do not generally divide up soil water resources equally, but that species differences in the water use tend to be gradual rather than categorical. This makes it far more difficult to evaluate the hypothesis of niche separation and to predict the likely effect of precipitation change on community composition. Isotope tracer methods alone cannot resolve this question, since they only determine the proportional water uptake from

different sources. To determine the potential degree of competition between individuals or populations, one must ultimately estimate the absolute consumption rates for shared water sources.

As an alternative to isotope tracer studies, community-wide rates of water uptake have been estimated in experiments where one functional type or species was removed and the effects on the soil water balance were examined (e.g. Robberecht et al. 1983; Sala et al. 1989; Montaña et al. 1995; Briones et al. 1998; Dodd et al. 1998). The drawback here is that the effects of removing biomass per se cannot be clearly distinguished from the effect of removing a particular functional type. In addition, species may change their patterns of water uptake after disturbance.

It seems that a combination of methods, capable of identifying both the proportional and absolute use of different soil water sources by plants, and conducted across a range of soil moisture conditions, will provide the most reliable assessment of the potential for niche separation (Dodd et al. 1998). This is what we have done in the present experiment. We focused on the uses of spring and summer rain events, which in many arid and semiarid ecosystems, including the Colorado Plateau where this experiment was conducted, make up at least half of the annual precipitation input. We quantified the rates of water uptake in three co-dominant plant species following a large simulated rainfall event (24 mm), once in spring, when the water content of deeper soil layers was still high from winter recharge, and once again in summer, when stored water had been partially depleted. Events of this size occur on average only once a year in the study region, thus our experiments simulated rare events, but with potentially large impact on annual primary productivity. We used hydrogen-enriched water in the rain simulation to determine precisely the mixture of recent “rain-water” and other soil water in the transpiration stream of plants. In addition, we measured the leaf transpiration and photosynthesis rates of watered plants, to determine the absolute leaf-based flux rate of recent “rain” and “other” water through the plant. We also measured transpiration and photosynthesis rates of non-watered control plants to determine the increase of gas exchange rates due to rain. Finally, we simulated a second, earlier rain of unlabelled water to one-half of the experimental population to see whether the possible formation of “rain roots” (Nobel 1988) enabled plants to take up more water from a second rainfall. The three species chosen for this study (one grass, two shrubs) were among the dominant species in the region and we expected them, based on prior experimental data, to be distinctly different in their relative use of pulse water.

Materials and methods

Experimental design

The study area was located just outside the Canyonlands National Park boundary in the Needles district, Utah. The soil is sandy with

no horizon development and carbonate deposits at ca. 30 cm. Mean monthly temperatures range from -2.3°C in January to 25.6°C in July. Precipitation averages 215 mm per year with even distribution between seasons and high inter-annual variation. In the year of the experiment (1998), both winter and summer precipitation had been average. The area is spring-grazed by cattle. Two sites were selected based on their high densities in the three study species. One was a sand dune dominated by *Artemisia filifolia* (site 1). The other was located at the foot of a rocky outcrop, dominated by *Coleogyne ramosissima* and also containing a relatively high density of *Hilaria jamesii* (site 2). The two sites were ca. 200 m apart.

The study species were selected for their differences in water use. *H. jamesii* (galleta) is a rhizomatous perennial C_4 grass with predominantly shallow roots, although a small portion of the root system can extend below 1 m (West et al. 1972). Like other perennial grasses, *H. jamesii* was expected to respond strongly to spring and summer rain (Sala et al. 1989). *C. ramosissima* (blackbrush) is an evergreen woody shrub with xeromorphic leaves. It has been shown to take up a nearly 1:1 mixture of recent rainwater and water stored in deeper soil layers (Ehleringer and Cook 1991; Donovan and Ehleringer 1994; Lin et al. 1996). *A. filifolia* (sand sagebrush) is an evergreen woody shrub with high flux potential, and is considered an indicator of sandy soil. Previous experiments indicated that *A. filifolia* also takes up summer rain, but considerably less than *C. ramosissima* (Flanagan et al. 1992; Lin et al. 1996; Gebauer and Ehleringer 2000).

The experimental plots were circular with a radius 1.5 m centered on either a *C. ramosissima* or an *A. filifolia* plant. Plots centered on *C. ramosissima* also contained *H. jamesii* target plants. Plots were selected to contain target plants of similarly large sizes and at distances of at least 1 m from the next nearest plot. All treatments were assigned randomly. No plants were chosen twice as target plants (i.e. in spring and summer).

The spring experiment included two watering events. On May 20, five plots in each site were watered with 24 mm well water. Water was applied to the entire plot area (7.07 m^2) with a handheld sprinkler as uniformly as possible. The application rate was 1–2 mm per minute to minimize runoff. On May 27, deuterium-enriched well water ($\delta\text{D}=310\text{‰}$) was applied in the same way to three previously watered plots and three other plots at each site. Altogether the experiment included 10 target plots at each site: 3 plots were watered on both occasions (WW in Fig. 1), 2 plots were watered only on May 20 (WD), 3 plots only on May 27 (DW), and 2 control plots were not watered at all (DD). The spring treatment was affected by a natural precipitation event only once, during the night following the first water application. The 5 days following the second irrigation were uniformly sunny with temperatures between 28 and 43°C at the times of measurement.

The summer experiment followed the design of the spring experiment, but sample sizes were increased. On July 13, 6 plots were watered at each site. On July 20, 3 of these were watered again along with 6 other plots. Altogether, there were 18 experimental plots at each site, 3 watered on both occasions (WW), 3 watered on the first occasion only (WD), 6 watered on the second occasion only (DW), and 6 non-watered control plots (DD). Several natural rain events interfered with the summer experiment, most notably two events on July 22 (at night) and July 24 (during the day), each infiltrating the soil to ca. 4 cm. Scattered clouds and temperatures between 28 and 47°C characterized the 5 days following the second rain event at the times of measurements.

Sampling and measurement

Soil samples were taken in the evenings following the two simulated rain events and 6 or 7 days after the second event in both seasons. Samples were taken from 0–20 cm and 20–40 cm, well-mixed and divided for isotope and soil moisture analysis. Samples for isotope analysis were transferred into glass vials, sealed with screw caps and Para film wraps, and stored at -20°C until the time of extraction. Samples for soil moisture analysis were oven-dried

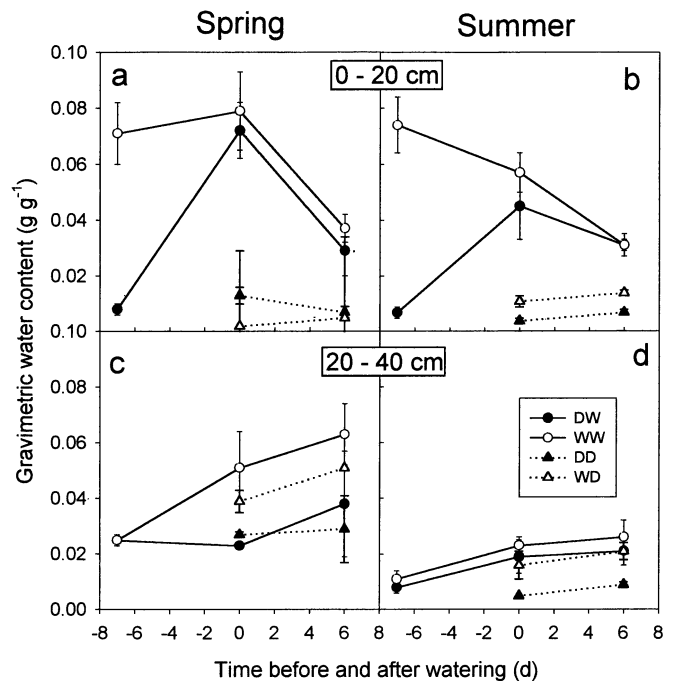


Fig. 1 Soil moisture during the experimental periods. DW dry-wet (irrigated on the second occasion only), WW wet-wet (irrigated on both occasions), DD, dry-dry (not irrigated), WD wet-dry (irrigated on the first occasion only)

for 24 h at 90°C . In each site, three samples were taken per treatment in random locations.

Plant samples for water source determination were taken in the early morning, in the two shrub species, from fully suberized portions of the stem. In the grass, portions of the stem above and below ground (rhizomes) were collected, removing any lateral roots. Stem samples were placed in glass vials and stored in the same way as the soil samples.

The hydrogen isotope ratio of soil and plant water samples were determined on a Finnigan-Mat delta S gas isotope ratio mass spectrometer. Prior to analysis, water was extracted quantitatively through cold trapping. Then, $5 \mu\text{l}$ sub-samples were reduced to H_2 using a zinc catalyst at 500°C (modified after Coleman et al. 1982).

Leaf gas exchange rates were determined with a portable infrared gas analyzer system (LiCor 6200, Licor Instruments, Lincoln, Neb., USA) on days 1, 2, 3 and 5 after the second watering events. Five measurements per day were obtained for sunlit leaves at approximately 730–830, 930–1030, 1130–1230, 1330–1430 and 1530–1630 hours, Mountain Standard Time. For the two shrub species, the same leaves were measured throughout the day, collected in the evenings and stored in wetted coin envelopes. In *H. jamesii*, a different leaf was measured and collected each time. Green-leaf areas were determined a few days later using a LiCor 3100 Area Meter (Licor Instruments). These measurements included only plants that were watered once during the second watering event of each season and non-watered control plants.

Leaf area indices of the three species in the two sites were estimated as the product of plant density and the average leaf area per plant. The densities of the three species were estimated using the Point-Centered-Quadrant method (Bonham 1989) with 30 points in each of the two sites. For shrubs identified as nearest to the random point, the longest and perpendicular-to-the-longest diameters and their heights were also measured. The leaf areas of these plants were estimated from empirical regressions between plant canopy dimensions and total leaf area per plant (for *A. filifolia*: $R^2=0.87$, *C. ramosissima*: $R^2=0.96$). These empirical relationships were determined separately by sampling 5–10 whole canopies of

Table 1 Hydrogen isotope ratios of various water sources considered in the calculation of relative pulse water use. The irrigation water amount added to the soil was estimated as the difference of the soil water content of DD and WD, or DW and WW, at 0–20 cm on the day that the labeled water was applied. Soil water δD values for control plants (DD and WD) represent the average of two plots over 5 days. δD s labeled * are deduced from the amount of water and the δD s of the two sources (irrigation water

and DD or WD). For example, the δD of the DW plot at 0–20 cm was determined by solving $[4.0 \times (-73) + 18.0 \times 310] / 22.0$. The δD s of the DD and WD control plants represent averages over three replicates and 5 days. Pulse percentages in plant xylem were calculated as in this example: $\delta D = x\%$ in *H. jamesii* (DW) in summer: $\% \text{ pulse} = (-50\% - x) / (-50\% - 284\%) \times 100$. Note that δD s can be manipulated as though they were concentrations, because the deuterium fraction in total hydrogen is extremely small

Source	Spring		Summer	
	Water content (mm)	δD (‰)	Water content (mm)	δD (‰)
Without previous pulse				
Soil, 0–20 cm (DD)	4.0	-73	1.2	-62
Irrigation water	18.0	+310	15.9	+310
Soil, 0–20 cm (DW)	22.0	+240*	17.1	+284*
<i>A. filifolia</i> (DD)		-78		-83
<i>C. ramosissima</i> (DD)		-64		-69
<i>H. jamesii</i> (DD)		-62		-50
With previous pulse				
Soil, 0–20 cm (WD)	10.5	-78	3.5	-55
Irrigation water	13.7	+310	14.1	+310
Soil, 0–20 cm (WW)	24.2	+142*	17.6	+238*
<i>A. filifolia</i> (WD)		-82		-78
<i>C. ramosissima</i> (WD)		-83		-72
<i>H. jamesii</i> (WD)		-62		-42

varying sizes, determining their leaf dry mass, and estimating the total leaf area on the basis of previously established specific leaf weights. For *H. jamesii*, the average leaf area per plant was estimated directly, by randomly harvesting 25 shoots and determining their average green leaf area. LAIs were determined only once in late May, between the spring and summer experiments. Minor variation between the LAIs in spring and summer may have occurred, but these would have been dwarfed by the much larger species differences in LAI.

Numerical analysis

Percent pulse water in plant xylem was calculated slightly differently than in previous studies that involved the application of isotopically enriched irrigation water (e.g. Lin et al. 1996; Gebauer and Ehleringer 2000). In these studies, pure irrigation water was taken as the 100% reference for irrigation-pulse water use. The so calculated pulse water percentage in xylem is governed by two dilution processes: first the dilution of labeled irrigation water with the native soil water present in the wetting zone prior to irrigation, and second the dilution of isotopically-enriched shallow soil water with non-enriched deeper soil water in the plant xylem. This method estimates the proportional use of irrigation water versus any other water that was in the soil previous to irrigation, irrespective of location.

In this study, we were interested in determining the location of water uptake, which requires a different approach for calculating proportional water use (see also Moreira et al. 2000). Specifically, we wanted to distinguish water taken up from the wetting zone and from elsewhere in the soil profile, to determine whether or not shallow soil water uptake was enhanced through a previous irrigation event. Thus, we took the isotopic enrichment of soil water in the wetting zone, after water had been applied, as the 100% reference point for the calculation of pulse water percentage in the xylem.

The isotope ratio of the 0–20 cm layer, which corresponded roughly to the depth of the soil wetted after irrigation, was estimated numerically, assuming linear mixing between applied water

and resident soil water and taking into account the amount and the isotope ratios of these two water sources (Table 1). To verify these estimates, we also took some spot measurements of the isotope ratios of water in the top 20 cm of soil immediately following the irrigation. These were quite variable. However, our estimated isotope ratios fell within the range of the spot measurements.

To calculate the pulse water percentage in the xylem of plants, we also needed to determine the isotope ratio of any water source below 20 cm that the plants were using. Differences in the hydrogen isotope values of control plants indicated that these sources were slightly different for different species (Table 1). Thus, we adjusted the 0% reference point to the isotope ratio measured in the xylem of either DD or WD control plants, individually for each species and season. A sample calculation is shown in the legend to Table 1.

Further spot measurements of soil water indicated that the hydrogen isotope ratio in the 20–40 cm soil layer was initially unaffected by the application of labeled water to the surface, suggesting that there was no significant path for fast downward transport of water, such as along cracks or root channels. But the hydrogen isotope ratio of water at 20–40 cm was elevated after 7 days, consistent with a slow diffusion-driven transfer of water. This agrees with the independent observation of an increase in soil moisture below 20 cm, 7 days after water application.

Absolute rates of pulse water uptake were estimated by multiplying the pulse fraction in xylem water with the leaf transpiration rates. These multiplications were performed between the treatment averages calculated for each day. On day 4 after pulse, gas exchange rates were not collected, so the average rates between days 3 and 5 were taken as a substitute. For Fig. 4, these daily estimates were again averaged.

Treatment effects on percent rainwater uptake into plant xylem were determined using the untransformed variable with percent pulse water measured on consecutive days as a repeated measure. A full factorial model was used to determine the effects of species and water application a week prior. The replication number was three for all groups.

Treatment effects on the gravimetric soil water content were determined in separate analyses of variance for each depth and season combination. Site proved to have no significant effect on

Table 2 Community-wide comparisons. All fluxes are expressed on a ground-area basis. Photosynthesis and transpiration “added by rain” is the difference in the gas exchange rates between watered and control plants. “Transpiration of rainwater” is the portion of the transpiration flux of watered plants that comes from the

shallow soil (0–20 cm). All fluxes represent the daily rates averaged over the first 5 days after the rain simulation. Daily photosynthesis and transpiration rates are integrated only over the 9 daytime hours, during which gas exchange rates were measured

Species	Leaf Area Index (m m ⁻²)	Spring			Summer		
		Photo-synthesis added by rain (mmol m ⁻² day ⁻¹)	Transpiration added by rain (mol m ⁻² day ⁻¹)	Transpiration of rainwater (mol m ⁻² day ⁻¹)	Photo-synthesis added by rain (mmol m ⁻² day ⁻¹)	Transpiration added by rain (mol m ⁻² day ⁻¹)	Transpiration of rainwater (mol m ⁻² day ⁻¹)
<i>H. jamesii</i>	0.0002	n.s.	n.s.	0.07	0.05	0.02	0.02
<i>C. ramosissima</i>	0.0226	0.75	4.61	3.67	1.16	1.50	2.88
<i>A. filifolia</i>	0.0601	n.s.	n.s.	11.51	n.s.	n.s.	8.63

water content, so that the replication number of three was raised to six across sites.

Treatment effects on photosynthesis and transpiration rates were determined only for the once-irrigated treatment (DW), evaluated against the never-irrigated control (DD), using untransformed data. Due to time-demands of the gas exchange measurements, we were not able to include a test for the effect of the earlier watering events. Within each species-treatment combination, the five daily measurements were individually averaged across days 1, 2, 3 and 5 after watering. These averages were submitted to repeated measures ANOVA. Replication number was three in spring and six in summer.

The daily average rates of gas exchange were transformed in Table 2 into the unit mol m⁻² day⁻¹. “One day”, in this estimate, was taken to be the period between 730 and 1630 hours, when gas exchange measurements were taken. Since the measurements were quite evenly distributed within these 9 h periods, the instantaneous gas exchange rates were simply averaged to calculate the daily averages.

Results

Soil moisture

The first rain simulation (day 7) had a large initial effect on the top 20 cm soil that was similar in spring and in summer (Fig. 1). The second rain simulation left the top 20 cm soil somewhat drier in summer than in spring, in part because less water was added to the soil during the summer irrigation event than during the spring event, and in part because the residual soil moisture prior to the “day 0” irrigation event was lower in summer than in spring. Nevertheless, both the spring and summer events on “day 0” removed significant differences between previously watered and non-watered plots at 0–20 cm (Fig. 1a, b). At 20–40 cm, the gravimetric water content was on average ca. twice as high in spring than in summer during the entire experimental period (Fig. 1c, d). Watering did not have an immediate effect on soil moisture at this depth, but 6 or 7 days after each watering event, the water content of watered plots was slightly but significantly greater than the water content of non-watered plots. This suggests that over the course of several days after the pulse application, a fraction of the water applied to the 0–20 cm soil layer moved downward.

Rainwater uptake and use

We estimated the pulse water uptake of plants by assuming mixing of two homogeneous water sources. This must be considered an approximation, because neither the isotope ratio of the wetting zone, nor that of deeper soil layers was likely to be constant with depth. We accounted for the uncertainty in the isotope ratio of deeper soil water sources available to plants by taking the observed isotope ratio in the xylem of control plants as a reference. But there could have been a much larger variation in the isotope ratio within wetted top 20 cm of the soil, at least initially, with more enriched water near the top and less enriched water at the wetting front. This requires some caution in data interpretation: Hypothetically, if plant roots had been restricted to only a thin layer within the top 20 cm layer, there would have been uncertainty whether a certain isotope ratio in the xylem of plants corresponded to a small rate of water uptake from a more enriched region near the soil surface or to a larger rate of uptake from a less enriched region near the wetting front. If, on the other hand, plant roots had been randomly distributed over the 20 cm layer, taking an unbiased sample of the bulk water, the uncertainty in the calculation of pulse water fraction would be minimal.

The fact that three species did not change their xylem isotope ratios very much over the course of 5 days (Fig. 2), supports the second scenario more than the first, suggesting that our calculation of relative water uptake from is reliable. If plant roots had been restricted to only a fraction of the entire layer, we should have observed a drift in the isotope ratios of xylem water, with the redistribution of deuterium concentrations within the wetted horizon by diffusion. There may have been a brief signal of such a redistribution on day 1 of the summer experiment, when the pulse water percentage calculated for *H. jamesii* was above that of all following days, and conversely for the two shrubs. However, on day 2 both pulse percentages merged toward an intermediate value, indicating that by this time the isotope ratios in the top 20 cm of the soil had equilibrated. In spring, equilibration may have been faster, due to a greater soil water

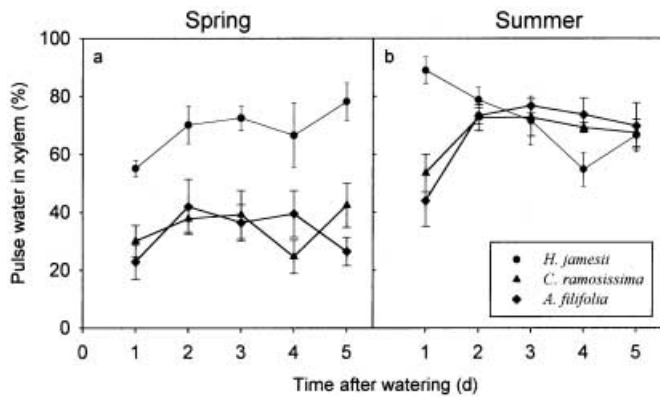


Fig. 2 The estimated percentages of pulse water (i.e. water from the 0–20 cm soil layer) in plant stems

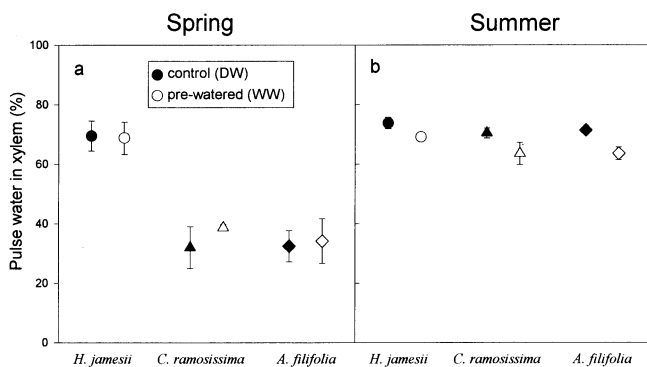


Fig. 3 The estimated percentages of pulse water in plant stems. Data are averages across the first 5 days after pulse application. The error bars represent standard errors for the mean across days

content and smaller diffusion resistance for water. Thus, we will assume that systematic errors introduced through uneven distribution of the deuterium label in the wetted horizon are minimal in comparison to differences among plants in relative water uptake from deeper, unlabelled soil water sources.

The pulse percentage calculated for *H. jamesii*'s in spring was ca. twice that of the other two species (Fig. 2a). Differences between *C. ramosissima* and *A. filifolia* were not significant. In all species, the proportion of pulse water in stem was independent of whether plants that had been watered a week prior (Fig. 3a).

In summer, species differences in relative pulse water use were not apparent in a repeated measures analysis including all 5 days (Fig. 3b), although, as discussed earlier, on day one, *H. jamesii* had a significantly greater apparent rainwater uptake than the other two species. There is another apparent drop in the calculated shallow water percentage in *H. jamesii* (though not significant) on day 4. This was probably due to a dilution of the hydrogen isotope label near the soil surface caused by rain on day 2. The apparent rainwater uptake of the two shrub species was not affected indicating once again that the roots

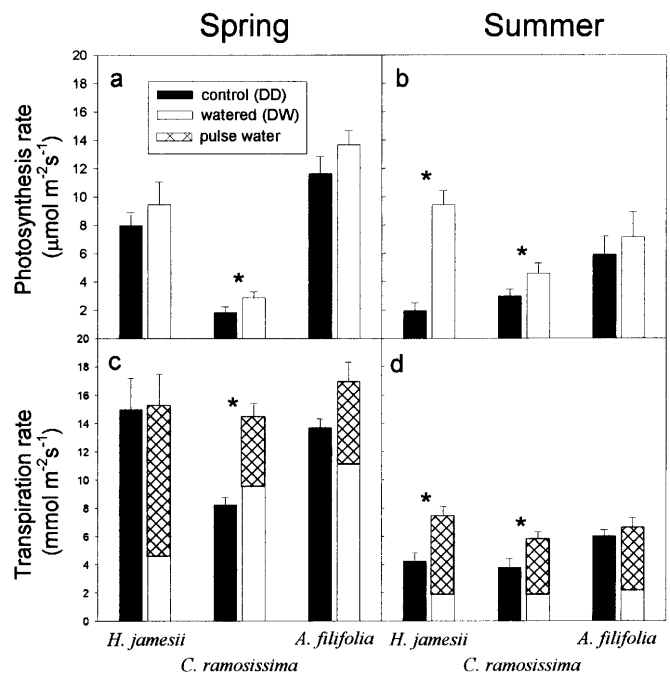


Fig. 4 Photosynthesis and transpiration rates of watered and control plants. Data are averages across the first 5 days after pulse application. The error bars represent standard errors for the mean across days. The hatched portions of the bars indicate the portion of the transpiration rate that was fed by pulse water. * significant differences between watered and control plants

of *H. jamesii* were more skewed toward the top than those of the two shrubs.

The relative rainwater uptake of the three species was more similar in summer than in spring (Fig. 2b), chiefly because *C. ramosissima* and *A. filifolia* doubled their relative pulse water uptake compared to spring, while the relative uptake of *H. jamesii* remained similar. In contrast to spring, pre-watering did make a difference to rainwater uptake in summer (Fig. 3b). Plants that had been watered a week prior took up significantly less rainwater from the more recent event than plants that had not been watered before ($P < 0.002$). The difference was small, however (–10%, on average).

The spring event had a significant effect on photosynthesis and transpiration rates only in *C. ramosissima* (Fig. 4a, c), where the photosynthesis rate increased by 55% and the transpiration rate by 76% over the rates of control plants. *C. ramosissima* added rainwater (hatched portion of bar) to the transpiration stream, while the rate of uptake from other soil water sources stayed the same. In contrast, *H. jamesii* did not increase its transpiration rate, but substituted water uptake from deeper in the soil profile with rainwater. The rainwater use of *A. filifolia* was more similar to that of *C. ramosissima*, i.e. adding to the transpiration rate, but differences in the transpiration rates were too small to be significant.

Overall, the gas exchange rates of control and watered plants in summer were lower than in spring (Fig. 4b, d). The summer rain event significantly in-

creased the gas exchange rates of *H. jamesii* and *C. ramosissima* over that of the control plants, but again not of *A. filifolia*. In *C. ramosissima*, the increase in photosynthesis due to summer rain was moderate and similar to spring. In *H. jamesii* summer rain increased the rate of photosynthesis almost 4-fold and was associated with a 2.7-fold increase in water use efficiency, suggesting a substantial recovery of photosynthetic capacity in this species. This was associated also with a visible greening of *H. jamesii*'s leaves. In *C. ramosissima* and *H. jamesii*, rainwater partly added to and partly substituted for other soil water sources. *A. filifolia* took up about as much rainwater as the other two species, but without significant effect on the transpiration rate.

Community-wide comparisons

To compare the water use of the three species on a land area, rather than a leaf area basis, photosynthesis and transpiration rates in Fig. 3 were multiplied with the estimated leaf area indices of the three species within the two experimental sites (Table 2). Simulated rain increased the photosynthetic rate the most in the *C. ramosissima* population and more so in summer than in spring. Although on an individual basis, rain increased the photosynthetic rate of *H. jamesii* far more than of the two shrub species, this added very little photosynthesis community-wide, because of *H. jamesii*'s low LAI.

Simulated rain increased the transpiration rates the most in *C. ramosissima* populations. However, the *A. filifolia* population extracted the most rainwater per unit ground area in both seasons. Thus paradoxically, the species that did not significantly increase its rates of transpiration and photosynthesis in response to spring or summer rain, consistently absorbed the greatest amount of rainwater from a unit ground area.

Discussion

In this study, we asked whether three dominant species of the Colorado Plateau were capable of partitioning soil water sources, in particular, pulses of water in the shallow soil created by large spring and summer rainfall events, and stored winter water in deeper soil layers. The grass had a significantly greater pulse water uptake only in spring. In summer, both the relative and the absolute rates of shallow water uptake of the three species were indistinguishable. In general, the similarities in the seasonal water use of these three species were greater than we originally expected. As a consequence LAI, more so than species identity, determined how rainwater was distributed amongst these three community members (Table 2).

We did find large differences, however, in the ways in which rainwater was used for carbon gain. In this respect, each species appeared to have a unique strategy. A species can:

1. Increase rates of gas exchange instantaneously without increasing water use efficiency (*C. ramosissima*, *H. jamesii* in spring);
2. Increase rates of gas exchange instantaneously and increase water use efficiency (*H. jamesii* in summer); or
3. Conserve the use of deeper soil water during pulse events, presumably extending photosynthetic activity into later drought periods (*A. filifolia*).

While there is direct evidence for the first two uses of rain water, the third is purely hypothetical. But it is very likely that deeper soil water conserved during a pulse event will be of some use later on, if only to maintain a certain rate of photosynthesis, as the stored water pool is depleted over the course of summer. The amount of deep water conserved may not be fully retrievable, as *A. filifolia* may be one among several other plant species that could use a higher availability of stored water.

A soil moisture pulse can have another type of delayed effect, when one pulse stimulates the growth of rain roots that enhance water uptake from a closely following rain event. Although we cannot exclude the possibility that in this experiment rain-induced roots aided the uptake of shallow soil water following the second rain event, we do know that this did not result in an increased relative rainwater uptake within the first 5 days (Fig. 3). On the contrary, in summer, the proportional uptake of shallow soil water was smaller following the second rain event, presumably because water from the previous event had percolated into deeper soil layers and allowed a greater rate of water uptake from there. Other studies have found rain roots to be important for the rapid absorption of rainwater by desert succulents (Nobel 1988), but a similar functionality has not been identified for other plant types.

The effects of soil water distribution on water partitioning

Rain events in the desert induce, for a short time, a steep water potential gradient. The gradient is particularly steep in summer, as deeper soil water sources tend to be more depleted. Since all water uptake is gradient driven, this must have strong effects on the rainwater use of plants.

In this study, the soil at 20–40 cm had become quite dry by July (–5.5 MPa according to a moisture release curve determined for the soil at the site), while the soil at 0–20 cm following the simulated rain event remained much closer to saturation (>–1.4 MPa) for the first 5 days after rain. During this time, all three species maintained similar hydrogen isotope ratios in their stems (equivalent to ca. 70% pulse water). In spring, when the soil water potential gradient was less steep (ca. –0.5 MPa at 0–20 cm and –1.5 MPa at 20–40 cm), the two shrubs extracted 35% of the transpiration steam from rainwater, only half of what the grass extracted. This pattern echoes

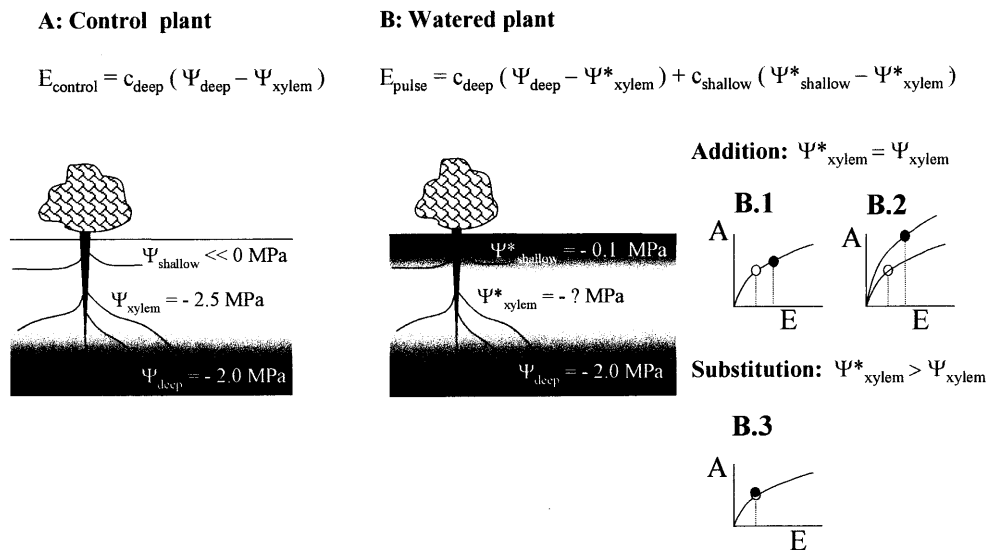


Fig. 5 The hydraulics of water uptake for control (A) and watered plants (B). **A** The transpiration rate E_{control} is proportional to the water potential gradient between deeper soil layers (Ψ_{deep}) and plant xylem (Ψ_{xylem}), and deeper soil-root conductance c_{deep} . The shallow soil is too dry for significant water exchange across the root-soil interface. **B** Moisture in the shallow soil adds a second water source and a second term to the transpiration rate E_{pulse} . **Addition**, if the additional water source has no effect on the xylem water potential of a watered plant (Ψ_{xylem}^*), the first transpiration term remains unchanged. **Substitution**, if the additional water source increases the xylem water potential of a watered plant, the first transpiration term decreases in magnitude. **B.1–B.3** hypothetical A:E curves with *open circles* marking the point of operation for control plants and *closed circles* for watered plants. **B.1** water use efficiency is not affected by watering, **B.2** water use efficiency is increased by watering. **B.3** water saved from the deeper soil can be used later with the same efficiency as before pulse

Substitution versus addition

In *H. jamesii* in spring and *A. filifolia* in summer, rainwater apparently substituted for other water sources without increasing total transpiration rate (Fig. 4). By contrast, *C. ramosissima* in spring added rainwater to the transpiration stream without changing the rate of water uptake from other water sources. Theoretically, the two cases are distinguished by the manner of stomatal control over transpiration (Fig. 5). In the case of addition, the stomata of watered plants are wider open than those of unwatered control plants, such that the daytime water potential of watered and control plants are the same. This manner of control tends to maintain the water potential gradient between soil and roots in deeper soil layers and therefore, the rate of water extraction. In the case of substitution – and this may be the more common case – the increase in transpiration due to stomatal opening in watered plants does not fully compensate for the enhanced water uptake capacity and as a result, the plant water potential of watered plants increases over that of control plants. This then decreases the soil-root water potential gradient in the deeper soil and the rate of water uptake from there.

We can superimpose on these water uptake patterns, the three forms of photosynthetic use of spring and summer rainwater suggested above. If rain increases the total transpiration rate, but not the water use efficiency (Fig. 5B.1), the carbon gains associated with pulse use can be predicted from the A:E curve (Cowan 1982). If water use efficiency also increases (Fig. 5B.2), carbon gain is likely to be higher (but so may be the costs of increasing water use efficiency). If plants instead do not increase total transpiration rates, but slow the use of deeper soil water (Fig. 5B.3), some of it may be used later, probably with a similar water use efficiency as in control plants. Since the A:E relationship is concave downward, and provided that the water losses associated with deferring water use are relatively small, we might expect that the carbon return for pulse water uptake un-

earlier observations of relatively greater pulse water use in summer, in herbaceous and woody perennials of the Colorado Plateau (Ehleringer et al. 1991; Gebauer and Ehleringer 2000). Convergent water use between the evergreen *Larrea tridentata* and the winter deciduous *Prosopis glandulosa* was also found by Reynolds et al. (1999), during a time when there was water near the surface, but very little below 30 cm. Similarly, Schulze et al. (1996) concluded that all plants along an aridity gradient in Patagonia use water from recent rain events in the topsoil.

These observations suggest that desert plants are able to realize water source partitioning only when water is relatively uniformly distributed throughout the rooting zone, such that vertical root distribution can exert a maximal effect on the vertical pattern of water uptake. At other times, water partitioning may not be possible, because soil water potentials, more than root distributions, dominate the patterns of water extraction by plants (Sala et al. 1981; Schwinning and Ehleringer 2001).

Table 3 Instantaneous and estimated delayed effects of pulse on carbon gain (summer only). Carbon gains are expressed on a ground-area basis. The instantaneous added carbon gain is calculated as the difference in the photosynthesis rate between watered and control plants integrated over the first 5 days after rainfall simulation, taking into account only 9 h per day, as in Table 2. Delayed added carbon gain is estimated by assuming that the water savings achieved in the deeper soil during pulse can be used some-

time later to maintain gas exchange at control rates. For example, in *A. filifolia* a saving of 37 mol m⁻² in deeper soil water, when used with the water use efficiency of control plants (0.987 mmol mol⁻¹) would add a carbon gain of 37.05×0.987=36.52 mmol m⁻² after termination of the pulse event. This is equivalent to 3.2 days of photosynthesis at the control rate. The numbers in parentheses indicate the percent delayed added carbon gain in total (instantaneous + delayed) added carbon gain

Species	Instantaneous added carbon gain for first 5 days (mmol m ⁻²)	Estimated delayed added carbon gain for first 5 days (mmol m ⁻²)	Total added carbon gain for first 5 days (mmol m ⁻²)
<i>H. jamesii</i>	0.24	0.03 (12%)	0.28
<i>C. ramosissima</i>	5.80	5.46 (49%)	11.26
<i>A. filifolia</i>	11.73 (n.s.)	36.52 (76%)	48.26

der strategy B.3 is potentially better than under B.1, but avoiding the costs that strategy B.2 is likely to carry.

The question of substitution versus addition is also potentially important for the prediction of evapotranspiration in arid and semi-arid ecosystems. For example, in the functional types model of Kemp et al. (1997), functional types differ in their capacity to extract water from the different soil layers, but the rates of extraction from each layer are independent. Thus, the use of a subsurface moisture pulse predicted by this model is necessarily additive. Walker and Langridge (1996) initially made a similar assumption in their model, but later added a “compensation effect” as a variable parameter, which allows for an increase in water uptake from deeper soil layers when the topsoil is dry compared to when it is wet. In essence, this parameter varies the degree of substitution between “1” (a strictly additive effect of a soil moisture pulse) and some maximum multiplier, which was given a default value of 1.5, equivalent to a 33% reduction of water uptake from deeper soil during the pulse. For comparison, the species in this study reduced the rate of water uptake from the deeper soil during pulse by between 0 and 70%. According to Walker and Langridge (1996) this compensation effect is necessary to correctly predict rates of water extraction by plants. We suggest that it may also be important for predicting how desert plants partition soil water resources. The propensity of a plant species to use different water sources in substitution or addition may be one of the defining characteristic of a plant functional type.

Assessing immediate and delayed effects of rainwater on primary productivity

If it is true that some effects of a rain event on plant photosynthesis take hold not in the immediate aftermath of the event, but at some undefined later time, then the spring and summer “rain use efficiency” (Le Houérou 1984) of ecosystems, if measured for single events, could easily be underestimated. For our system, we can estimate how large this error could potentially be. Although we have no direct way of measuring the carbon

gains achieved by utilizing water that was saved during a pulse event, a quick estimate may serve to illustrate the potential magnitude of such gains (Table 3). To calculate the values in Table 3, we assumed that water saved during the pulse event is stored without loss, extracted after the pulse event, and used with the water use efficiency of non-watered control plants. On this basis, we see that the carbon gains potentially achieved by *A. filifolia* through the use of rainwater may be larger than suggested by Table 2 and exceeding that of *C. ramosissima* 5-fold, instead of 3-fold when delayed effects are not considered. On the other hand, for the grass *H. jamesii* there is little gain in deferring water uptake, because of the low water use efficiency of control plants. To put these numbers into perspective, the annual primary productivity (ANPP) of the Great Basin Desert at an annual precipitation input of 215 mm is estimated at between 100–150 g m⁻² year⁻¹ (Le Houérou 1984) or 8–13 mol m⁻² year⁻¹. According to our calculations, an *A. filifolia* population would contribute only ca. 0.1% of the ANPP in the first 5 days following a large summer rainfall event, and 0.4% at some later time. These values are likely to underestimate the true contribution of a summer rainfall event to ANPP, for one, because the 24 mm rain event will not have been used entirely within the first 5 days after rain, and second, because we only considered a day length of 9 h when the actual day length was between 13 and 14 h. Nevertheless, the comparison suggests that summer rain, in a cold desert with winter rain, may only contribute a small percentage of the ANPP, but that this small percentage could still be grossly underestimated in certain vegetation types, if delayed effects of rain on photosynthesis are not considered.

Soil water partitioning and climate-community interactions

In this experiment, the relative and absolute (on a leaf area basis) rates of rainwater uptake were amazingly similar between one perennial grass species and two woody shrubs, particularly in summer. This is an ideal situation for asking what other factors could differentiate the abili-

ty of species to use various components of the annual precipitation input. One factor we did not consider is the size of a rainfall event. Sala and Lauenroth (1982) hypothesized that grasses should be better able than shrubs to exploit small rainfall events. Supporting this hypothesis, we observed that only *H. jamesii* responded to fluctuation of the hydrogen isotope ratio near the soil surface and this makes it likely that only *H. jamesii* would have been able to exploit smaller rainfall events that would have wetted only the first few centimeters of the soil profile.

We also saw substantial differentiation in the three species' abilities to convert water uptake into carbon gain. The water use efficiencies of plants extracting recent rainwater, for example in summer, ranked *H. jamesii* (1.26) > *A. filifolia* (1.07) > *C. ramosissima* (0.78), and for control plants that had access only to deeper soil water the ranking was *A. filifolia* (0.99) > *C. ramosissima* (0.79) > *H. jamesii* (0.47). This rank reversal for the efficiency with which different water sources were utilized creates another form of niche separation, capable of generating competitive tradeoffs in communities, even if water sources were shared proportionally (see also Sala and Lauenroth 1982). These differences in water use efficiencies are linked to whole-plant allocation patterns and the manner of control over plant water status, in addition to root distributions (Schwinning and Ehleringer 2001). Differentiation in the capacities of plants to capitalize on moisture pulses of various intensity, duration and location, while tolerating the moisture conditions in between, may be more central to understanding the dynamics of arid communities than the partitioning of plant water sources per se.

In our view, the present results challenge some of the simpler notions on niche separation between desert plants. We saw for example, that population LAI, more so than the relative uptake capacity for shallow soil water determines which vegetation component is the largest consumer of spring and summer rain. This begs the question of what determines population LAI. In a cold desert, the amount of stored water from winter precipitation may be primarily responsible for maintaining the LAI of shrub populations throughout the year. This means that among the positive effects of a wet winter on shrub populations is an enhanced ability to subsequently use summer precipitation. Even though the summer-rain derived carbon gain of a shallow-rooted summer-rain specialist, such as *H. jamesii*, is much greater than that of a shrub, *relative to its fraction of community LAI*, the absolute carbon gain of the shrub population can still be much greater, as seen in Table 3. This may suggest that the winter climate more so than summer climate determines the community composition of arid and semi-arid ecosystems, particularly, but perhaps not exclusively (see Turner 1990; Brown et al. 1997), in winter-cold regions with biseasonal rainfall distribution.

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