

Susanne Schwinning · Benjamin I. Starr ·
James R. Ehleringer

Dominant cold desert plants do not partition warm season precipitation by event size

Received: 19 November 2001 / Accepted: 6 March 2003 / Published online: 15 April 2003
© Springer-Verlag 2003

Abstract We conducted experiments to examine the quantitative relationships between rainfall event size and rainwater uptake and use by four common native plant species of the Colorado Plateau, including two perennial grasses, *Hilaria jamesii* (C₄) and *Oryzopsis hymenoides* (C₃), and two shrubs, *Ceratoides lanata* (C₃), and *Gutierrezia sarothrae* (C₃). Specifically, we tested the hypothesis that grasses use small rainfall events more efficiently than shrubs and lose this advantage when events are large. Rainfall events between 2 and 20 mm were simulated in spring and summer by applying pulses of deuterium-labeled irrigation water. Afterwards, pulse water fractions in stems and the rates of leaf gas exchange were monitored for 9 days. Cumulative pulse water uptake over this interval (estimated by integrating the product of pulse fraction in stem water and daytime transpiration rate over time) was approximately linearly related to the amount of pulse water added to the ground in all four species. Across species, consistently more pulse water was taken up in summer than in spring. Relative to their leaf areas, the two grass species took up more pulse water than the two shrub species, across all event sizes and in both seasons, thus refuting the initial hypothesis. In spring, pulse water uptake did not significantly increase photosynthetic rates and in summer, pulse water uptake had similar, but relatively small effects on the photosynthetic rates of the three C₃ plants, and a larger effect on the C₄ plant *H. jamesii*. Based on these data, we introduce an alternative hypothesis for the responses of plant functional types to rainfall events of

different sizes, building on cost-benefit considerations for active physiological responses to sudden, unpredictable changes in water availability.

Keywords Deuterium-labeled irrigation · Niche separation · Precipitation change · Rain use efficiency

Introduction

There is an emerging view that precipitation variability, more so than precipitation averages, dominates plant diversity in arid regions. Variability in the supply of the main limiting resources and of other environmental variables is thought to promote diversity by alternating competitive advantages over time, if plants are also capable of using advantages gained in favorable times for persisting through unfavorable times (Chesson and Huntly 1989). Understanding the role of variability is a prerequisite for anticipating the effects of climate change on communities and ecosystems, as climate change involves not just shifts in the central tendencies of climate variables, but also, and perhaps more so, climate pattern change (Groisman et al. 1999; Easterling et al. 2000).

Precipitation patterns are expressed at various time scales, and depending on the scale, can have different effects on communities. For example, patterns at the inter-annual to decadal scales may interact strongly with demographic phenomena, as weather patterns significantly longer than 1 year may often be necessary to remove adults from populations and establish new recruits (Turner 1990; Brown et al. 1997; Pierson and Turner 1998; Swetnam and Betancourt 1998). Intra-annual precipitation patterns, particularly the seasonal distribution of precipitation, are widely recognized as governing functional and species diversity, as plant species have been shown to diversify in their uses of winter-derived and summer-derived soil moisture (e.g. Cody 1989; Ehleringer et al. 1991; Cowling et al. 1994; Dodd et al. 1998). Whether or not precipitation patterns on even smaller time scales, such as could be generated by rainfall

S. Schwinning (✉) · B. I. Starr · J. R. Ehleringer
Biosphere 2 Center,
University of Utah,
P.O. Box 689, Oracle, AZ 85623, USA
e-mail: schwinn@mail.research.bio2.edu
Tel.: +1-520-8966462
Fax: +1-520-8966359

B. I. Starr · J. R. Ehleringer
Department of Biology,
University of Utah,
Salt Lake City, UT 84112, USA

size variation, can generate additional opportunities for resource partitioning is unclear. Sala and Lauenroth (1982) suggested this possibility, after observing that the perennial C₄ grass *Bouteloua gracilis* was able to increase gas exchange rates less than 24 h after rainfall events of 5 mm or less. They hypothesized that small rainfall events may selectively favor populations of predominantly shallow-rooted plant species, because deeper-rooted plants may require more time, or soil moisture at greater depth, to increase carbon gain. Conversely, deeper-rooted plants would be favored by large rainfall events, as their root systems would give them better access to more deeply infiltrated water.

To this date, there has been no formal evaluation of Sala and Lauenroth's (1982) hypothesis. While there are now many studies evaluating plant use of single rainfall events in arid to semi-arid ecosystems (e.g. Lin et al. 1996; Cui and Caldwell 1997; Golluscio et al. 1998; BassiriRad et al. 1999; Gebauer and Ehleringer 2000; Schwinning et al. 2002), very few have evaluated the effect of rainfall size (but see Lauenroth et al. 1987; Dougherty et al. 1996). Furthermore, most studies focusing on the effects of single events have involved relatively large applications of water (>20 mm), which are rare and atypical for arid ecosystems.

Here, we tested the hypothesis that plants belonging to different functional groupings have distinct non-linear responses to rainfall size, which would allow them to partition summer rain through event size. We imposed a range of rainfall sizes between 2 and 20 mm on four dominant members of a Colorado Plateau grass-shrub community. Rain was simulated using deuterium-labeled water to track the rates of rainwater uptake through time. The four species chosen for this study included two perennial grasses, *Hilaria jamesii* (C₄) and *Oryzopsis hymenoides* (C₃) to represent shallow-rooted rain-responsive plant types. The herbaceous shrub *Gutierrezia sarothrae* (C₃) was picked to represent a plant with an extensive lateral and deeper root system, equally capable of using both shallow and deeper soil water sources (Wan et al. 1993). *Ceratoides lanata* (C₃), a predominantly deeper-rooted woody shrub was chosen to represent the relatively rain-unresponsive type (Caldwell et al. 1977). Based on Sala and Lauenroth's (1982) hypothesis, we expected that the two grasses would achieve a distinctly greater cumulative water uptake than the two shrub species following smaller events. We also expected that *G. sarothrae* would achieve a cumulative pulse water uptake more similar to that of the two grasses following the largest events, and that *C. lanata* would perhaps not be able to take up significant amounts of pulse water from any rainfall event.

Materials and methods

Site selection and preparation

Sites were located on public land (under the jurisdiction of the Bureau of Land Management) near the Needles District entrance of Canyonland National Park in southern Utah, USA (N38.17548 W109.72018). The site had mixed grass and shrub cover. The grass community was dominated by the spring-active annual grass *Bromus tectorum* (75%) and the two native perennial grasses *O. hymenoides* (10%) and *H. jamesii* (6%). *G. sarothrae* and *C. lanata* together made up 95% of the total shrub cover and *G. sarothrae* covered about twice as much ground as *C. lanata*. The soil was sandy with no horizon development, sparse biological crust cover and caliche carbonate deposits at approximately 30 cm. Mean monthly temperatures in this region vary from -1°C in January to 27°C in July (Moab, Utah, Station 425733). Precipitation averages 215 mm per year with even distribution between seasons. The area was spring-grazed by cattle, but in January 1999 fences were erected to exclude cattle from an area of about 2 ha. For this study we selected two locations within the enclosure, one containing a relatively high density of *C. lanata* and *O. hymenoides*, the other of *G. sarothrae* and *H. jamesii*. The two sites were about 50 m apart.

One week prior to each of the four watering events, ten 4×4 m² plots were selected within each site, containing both shrub and grass species in sufficient quantity to allow repeated sampling of stem and leaf biomass. These plots were then covered by rainout shelters to prevent exposure to natural rainfall before and after watering. Shelter roofs were made of clear corrugated polycarbonate panels (Suntuf, Livingston, N.J.) that were coated with a UV-filter but were 90% transparent to visible light. The shelters were open on all sides and held up by fence posts approximately 1.5 m off the ground with a slant to allow rainwater to run off. These shelters stayed on the plots until the end of the 9-day observation period. The shelters raised the surface-soil and surface-air temperatures by about 3–4°C and 1–2°C, respectively. Thus, applied water probably evaporated faster than under ambient conditions, but since this effect of the rainout shelters was imposed equally on all experimental plots, it did not interfere with our ability to test the primary hypothesis, regarding species differences in pulse water use.

Watering

Plots were watered on 14 May and 28 June 1999, and on 20 May and 1 July 2000 with deuterium-enriched well water with a δD of 310‰. This was 320–400‰ more enriched than natural precipitation (winter or summer) in this region. In 1999, we targeted the water applications at 6 and 12 mm, and in 2000 at 12 and 24 mm. Event sizes were randomly assigned to plots. The 4×4 m² areas underneath the shelters were watered in quarter segments by hand-held hoses that were swept over the plots in regular motion to distribute water evenly. We estimated the volume of applied water by the time spent watering the plots, based on a known flow rate that was determined at the beginning of the day and checked from time to time throughout the day. The flow rate was adjusted to ca. 20 l per minute (equivalent to 1.25 mm per minute within a plot) to minimize runoff. For the 24 mm application, plots were watered in two installments to allow the first 12 mm to infiltrate before the second 12 mm was applied.

Soil moisture

Soil cores were taken in 10 cm intervals to a depth of 50 cm on the day before watering, in the evening of the watering day and 3, 6 and 9 days thereafter. At each of the two sites, three cores were taken per treatment from randomly chosen plots. Soil moisture was insignificantly different across sites so that the six samples per treatment were pooled for analysis. The gravimetric water content of well-mixed subsamples was determined by weighing before and

Table 1 Hydrogen isotope ratios of stem water before watering. The standard error of the mean is in parentheses. The hydrogen isotope of applied water was 310‰ throughout

Species	Spring 1999 (‰)	Spring 2000 (‰)	Summer 1999 (‰)	Summer 2000 (‰)
<i>Ceratoides lanata</i>	-88 (4)	-110 (3)	-71 (5)	-84 (7)
<i>Oryzopsis hymenoides</i>	-87 (6)	-111 (4)	-67 (3)	-78 (11)
<i>Gutierrezia sarothrae</i>	-95 (4)	-103 (4)	-78 (6)	-85 (2)
<i>Hilaria jamesii</i>	-97 (6)	-101 (6)	-76 (6)	-86 (5)

after drying at 90°C for 24 h. The actual amount of water added to the soil was estimated by adding any gains in the soil water content between the day before watering and just after watering. This measure was scaled to a unit ground area by multiplying with the bulk density (determined to be vertically homogeneous at 1,600 kg m⁻³) and the layer height (0.1 m).

Plant water status

Predawn water potentials were measured between 3 a.m. and dawn on the day prior to watering and on days 1 and 9 thereafter, using Scholander pressure bombs. We used foliated terminal branches of shrubs and leaf blades of grasses to determine the xylem water potentials.

Isotopic composition of stem water

Plant samples were taken early in the morning, in advance of the gas exchange measurements, one day before watering and on days 1, 2, 3, 5, 7, and 9 thereafter. We collected fully suberized stems of the two shrubs from low in the canopies. For *O. hymenoides*, we collected stems from near the soil surface and for *H. jamesii* we collected stems from above and below ground (rhizomes), removing any lateral roots. Stem samples were placed in glass vials, closed with screw caps, wrapped with Parafilm, and frozen until extraction. Stem water was extracted quantitatively through cold trapping under vacuum (Ehleringer et al. 2000). From the extracts, 5 µl sub-samples were reduced to H₂ using a zinc catalyst at 500°C (modified after Coleman et al. 1982). The hydrogen isotope ratios of the H₂ samples were determined on a Finnigan-Mat delta S gas isotope ratio mass spectrometer with ±1‰ precision.

Gas exchange

Leaf gas exchange rates were determined with a portable infrared gas analyzer system (LiCor 6200, Licor Instruments, Lincoln, Neb., USA) on the days before watering and on days 1, 2, 3, 5, 7 and 9 thereafter. Gas exchange rates were measured three times per day, approximately between 0830 and 1000, 1100 and 1230 and 1330 and 1500 hours, Mountain Standard Time. Branches or leaves of all species except *H. jamesii* were labeled with paper tags in the morning, measured repeatedly throughout the day and collected following the afternoon measurement for leaf area determination. For practical reasons, a different leaf of *H. jamesii* was measured and collected each time. The leaf samples were stored in wetted coin envelopes and kept cold until leaf area determination several days later, using a LiCor 3100 Area Meter (Licor Instruments).

Data reduction and analysis

The gas exchange data were reduced in two steps, first collapsing the three daytime measurements into one daytime average and second collapsing the six daytime averages into one cumulative measure. Data for individual plots were kept separate throughout. For estimating average daytime photosynthesis and transpiration rates, we integrated cumulative water losses and carbon gains over the course of the entire daytime, based on the assumptions that rates

at sunrise and sunset are zero and that rates change linearly between sampling points.

The daytime-integrated transpiration rates were multiplied with the pulse water fractions determined for the same days to estimate the daytime-integrated pulse transpiration rates, i.e. that portion of the total transpiration stream that was supplied by pulse water. To determine pulse water fractions in stems, we took the stem water isotope composition determined for the day before watering as the zero level (Table 1) and the isotopic composition of the irrigation water ($\delta D = 310\text{‰}$) as the 100% level and assumed linear mixing of irrigation water with stem water from other sources. Using this method, it is possible to calculate pulse water fractions of less than 0%. This happens if during the observation interval, plants take up no or very little pulse water and instead shift water uptake to deeper soil layers, where water usually has a more negative hydrogen isotope ratio. We calculated negative values between 0 and -10% on 84 occasions (out of a total of 1,085 data), mostly for *C. lanata*. To avoid the systematic underestimation of average pulse use through this artifact, we reset all negative pulse use percentages to zero.

In the second step of data reduction, to calculate interval-integrated measures of pulse use, we weighted the first three measurements (days 1, 2, 3) by a factor of one and the second three measurements (days 5, 7, 9) by a factor of two to account for differences in the time intervals between measurements.

To test for differences in water potentials before and after watering, we performed one-sample *t*-tests of their within-plot differences. The regression analysis underlying Fig. 4 were done following Sokal and Rohlf (1995) for the case of multiple values of *y* for one value of *x*.

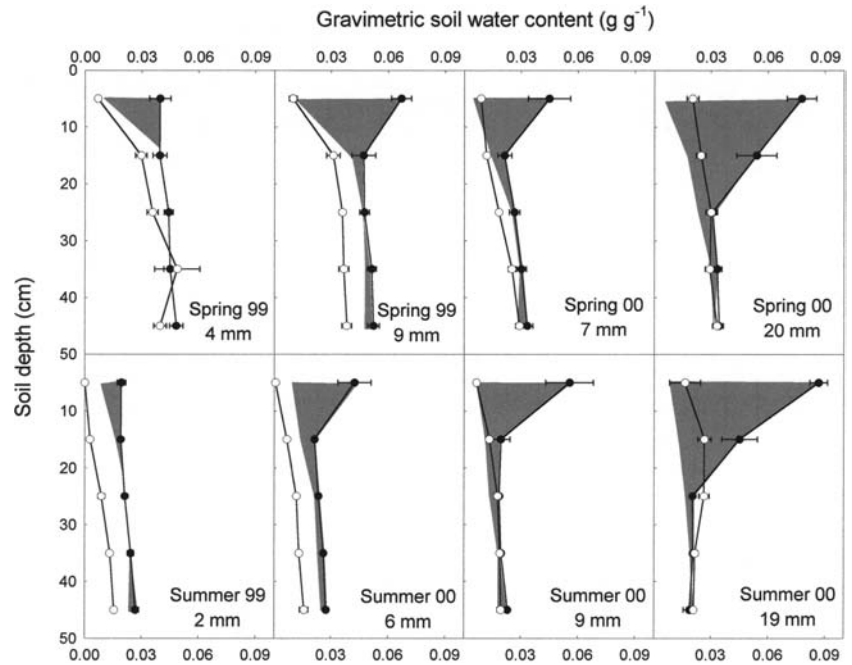
Results

Soil moisture pulse dynamics

Most watering events wetted primarily the first 10 cm below the soil surface (Fig. 1, shaded areas). The only significant increase in the water content at 10–20 cm was observed for three of the largest events (summer 2000: 9 mm and 19 mm, spring 2000: 20 mm; results of the ANOVA not shown). There were no immediate effects of watering below 20 cm, but following the 19 and 20 mm events, soil moisture at 20–30 cm was slightly but significantly higher 6 days after watering than before watering, suggesting that there was a slow downward diffusion of shallow soil water.

For all event sizes between 2 and 9 mm, as much or more water had disappeared from the top 50 cm of the soil in 9 days than had been added at the beginning of the interval (Fig. 1). In the summer of 2000, the 9 mm event added almost exactly the amount of water that was dissipated in the 9 days following, suggesting an average evapotranspiration rate from this layer of 1 mm per day, during the interval. Following the two largest events (19

Fig. 1 Gravimetric soil water content between 0 and 50 cm depth. *Filled circles*, water content immediately after watering; *open circles*, water content after 9 days. The *dark shaded areas* indicate the amount of water that was added to the soil during the watering events. *Error bars* indicate standard errors of the means



and 20 mm), about 30% of the applied water remained in the soil 9 days after watering.

Soil layers below 20 cm were wetter in spring than in summer and that difference was larger in 1999 than 2000. At the beginning of the spring experiment in 1999, there was an average of 16 mm more water available in the top 50 cm of soil than in the spring of 2000. By summer the difference between years had decreased to 3 mm, suggesting that the vegetation compensated for the initial difference in water availability by increasing water uptake from deeper soil layers.

Pulse effects on plant water status

We evaluated the effects of watering on plant water status by comparing the predawn water potentials 1 day before and 1 day after watering (Fig. 2). Spring events did not generally increase predawn water potentials, except in *H. jamesii*. In this case, predawn water potentials were significantly increased following the two smaller events but not the two larger events, suggesting that the effect of spring watering on the predawn water potentials of *H. jamesii* were either spurious, or that watering had some other physiological effect not directly related to increased water availability.

The largest summer event (19 mm) increased the predawn water potentials of all species except *C. lanata*, although in *O. hymenoides* the increase was only marginally significant because of large variability between plots. The 9 mm summer event significantly increased the predawn water potentials of the two grasses but not of the two shrubs. Summer events smaller than 9 mm had no significant effect on the water potentials of any of the four species.

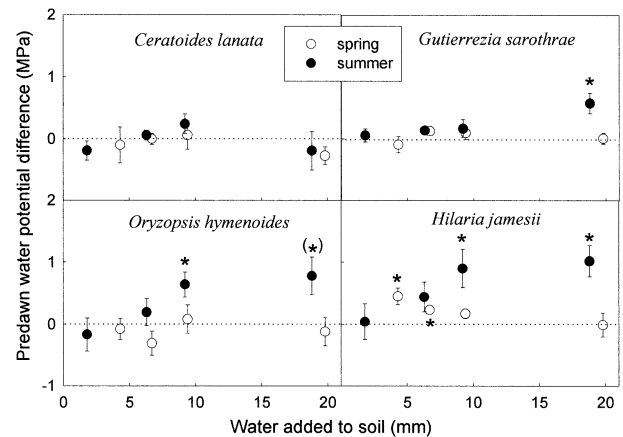


Fig. 2 Differences in the predawn water potentials measured on the days just before and after watering. Positive values indicate that the water potentials increased after watering. * indicates significant differences from zero at the 0.05 level. (*) is a marginally significant difference at $P=0.06$. *Error bars* indicate standard errors of the means

Pulse water uptake

All species had taken up deuterium-labeled pulse water less than 24 h after application. Thus, even the deepest-rooted plant, *C. lanata*, demonstrated some capacity to take up shallow soil water, although its proportion in the xylem was minute for 6 and 7 mm events (Fig. 3). Pulse water uptake was notably higher following the 19 and 20 mm events and nearly constant throughout the 9 day observation interval, suggesting that the bulk of the pulse water taken up by *C. lanata* originated from a region of the soil where soil water was not rapidly depleted, possibly near the 20 cm initial infiltration depth (Fig. 1).

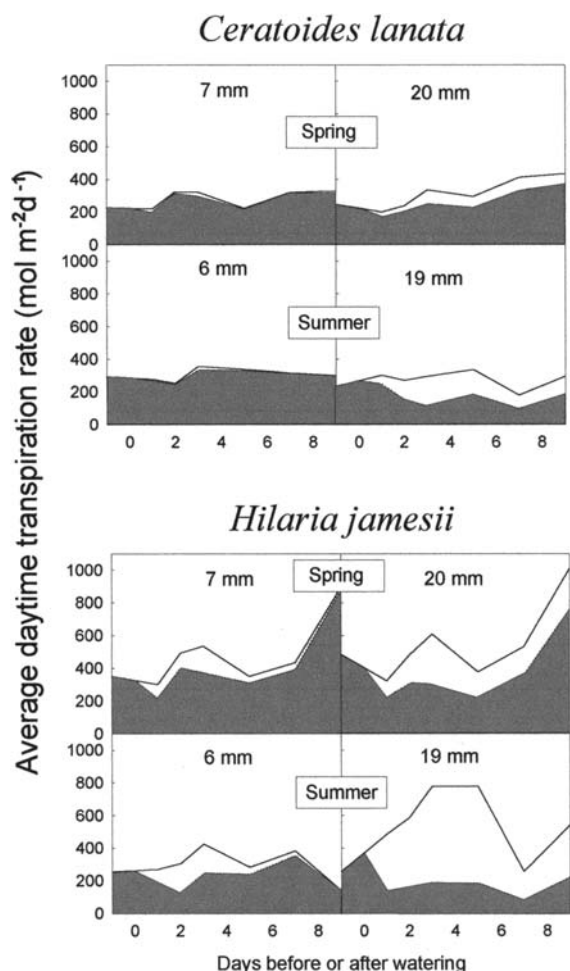


Fig. 3 Time course of transpiration rates in the deepest-and most shallow-rooted species, *Ceratoides lanata* and *Hilaria jamesii*. The white areas under the top curves are proportional to the amount of pulse water in the transpiration stream, shaded areas to the amount of water from other sources in the soil

By contrast, pulse water uptake by *H. jamesii* dropped sharply 3–5 days after watering, suggesting that its main region of uptake was, at least initially, at 0–10 cm, where water content declined more rapidly. Nevertheless, even after 9 days *H. jamesii* took up multiple times more pulse water than *C. lanata*.

Table 2 Regression analysis for pulse water transpiration on the amount of water added to the soil. Regression analysis corresponds to Fig. 4. The *F* and *P* statistics refer to tests of slope equality for the spring and summer regression lines. Pooled regression results are shown only when the test indicated non-significant differences.

Species	<i>F</i> _{1,4}	<i>P</i>	Spring			Summer			Pooled		
			Slope	y-intercept	<i>r</i> ²	Slope	y-intercept	<i>r</i> ²	Slope	y-intercept	<i>r</i> ²
<i>C. lanata</i>	4.78	0.094	0.6* (0.1)	–3 (2)	0.81	1.1* (0.2)	–4(2)	0.83	0.9* (0.2)	–3 (3)	0.70
<i>O. hymenoides</i>	1.78	0.232	3.0* (0.5)	–8 (6)	0.84	4.0* (0.5)	–7 (6)	0.88	3.5* (0.6)	–7 (7)	0.80
<i>G. sarothrae</i>	22.32	0.009	0.9* (0.1)	–1 (1)	0.64	2.1* (0.2)	–5 (2)	0.89			
<i>H. jamesii</i>	20.52	0.011	1.4* (0.1)	1 (1)	0.59	3.7* (0.5)	–5 (5)	0.93			

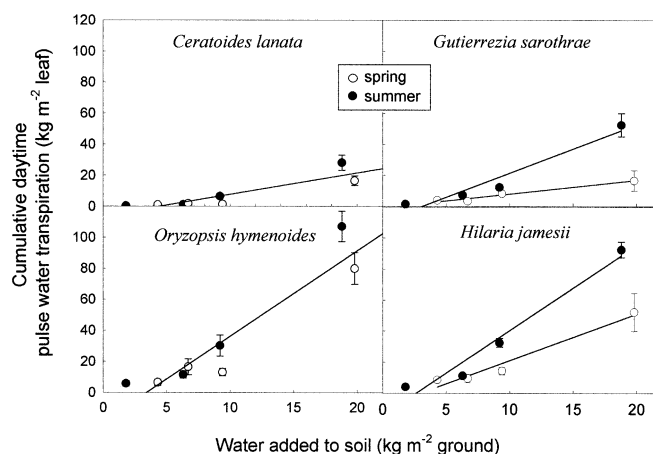


Fig. 4 Cumulative daytime pulse water transpiration over the first 9 days as a function of water added to the soil. Regression statistics are shown in Table 2. Error bars indicate standard errors of the means

Over the 9-day observation interval, cumulative pulse water transpiration was approximately linearly related to the amount of water added to the soil (Fig. 4, regression results in Table 2). The y-intercepts of all regression lines were statistically indistinguishable from zero, suggesting that there was no clear-cut threshold for the uptake of pulse water from the soil in any of the four species. All four species tended to transpire less pulse water in spring than in summer, but this seasonal effect was significant only in *G. sarothrae* and *H. jamesii*. The two shrubs transpired the least pulse water. In *C. lanata* this was less than 1 kg water per m² leaf area for every kilogram of water added per m² of ground area. *G. sarothrae* transpired as little pulse water in spring but twice as much in summer. The two grasses transpired around 3.5 kg m^{–2} leaf area per kg m^{–2} ground area in summer, but in *H. jamesii* the transpiration of pulse water was less than half as high in spring.

Pulse effects on photosynthesis

Pulse water uptake did not always increase the total transpiration rate, and therefore should not have always

* indicates significant differences from zero in the regression parameters. Standard errors of the parameter estimates are shown in brackets. The unit of slope is kg m^{–2} leaf area (kg m^{–2} ground area)^{–1}. The unit of the intercept is kg m^{–2} leaf area

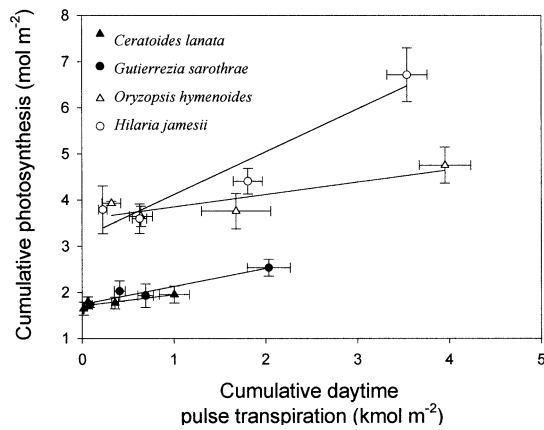


Fig. 5 Cumulative photosynthesis as a function of cumulative daytime pulse water transpiration, both over the first 9 days. Error bars indicate standard errors of the means

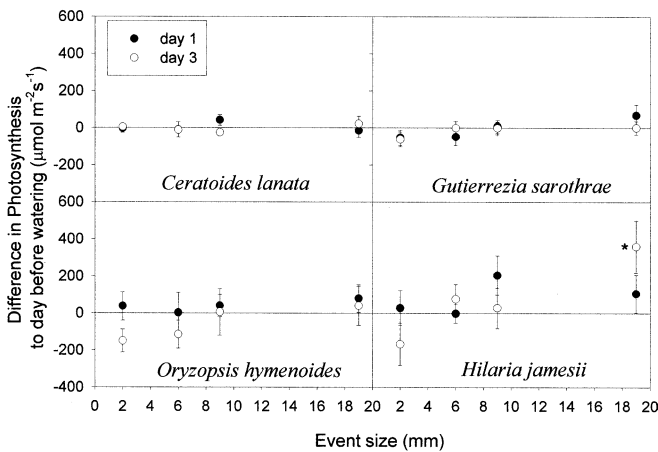


Fig. 6 Differences in the photosynthetic rates measured on the days just before and 1 or 3 days after watering. Positive values indicate that photosynthesis increased after watering. * indicates significant differences from zero at the 0.05 level. Error bars indicate standard errors of the means

increased photosynthesis. Pulse water uptake did in fact not increase photosynthesis rates in spring (data not shown). In summer, cumulative pulse water uptake over 9 days was significantly correlated with cumulative photosynthesis over the same interval, but the increase in photosynthesis due to pulse water uptake was quite small in all C₃ species (Fig. 5). On average, for every 100 mol of pulse water transpired, only 3 more mol of carbon were assimilated in the C₃ species. In *H. jamesii*, the only C₄ species in this study, photosynthesis increased by about 9 mol carbon for every 100 mol pulse water transpired.

To evaluate the time course of the photosynthetic response, we show the differences in the photosynthetic rates between the day before watering and either day 1 or 3 after watering in Fig. 6. With the exception of one (*H. jamesii*, 3 days after watering with 19 mm), differences were not significantly different from zero, suggesting no

large change in the rates of photosynthesis due to watering, consistent with the shallow slope in Fig. 5 for the C₃ plants. In the C₃ plants, photosynthetic rates were almost always lower 3 days after watering than one day after watering, indicating that if there was an effect of watering at all, it was quite ephemeral. The exception to these patterns was seen in *H. jamesii*, which did not show a significant increase in photosynthesis 1 day after watering with 19 mm, but did so 3 days after watering. This delayed response to watering suggests that *H. jamesii* undertook some active physiological adjustments that increased its rate of water transport (Fig. 3) and photosynthesis.

Discussion

Among the precipitation changes predicted for a large part of the world are changes in the intensity and sizes of rainfall events, with heavy rainfall events becoming more common and the time between events becoming longer (Fowler and Hennessy 1995; IPCC 1996; Easterling et al. 2000). If it were true that plant species diversified in their abilities to use rainfall events of different magnitudes, one would predict that changes in the “packaging” of precipitation alone (i.e. whether there were many small or few large events) could shift the balance between grasses and shrubs in a community. In fact, we found in this cold desert mixed grass/shrub community that species had approximately linear functional responses to rainfall event size. Well-known plant functional type differences in the capacity to use warm-season precipitation (Ehleringer et al. 1991; Golluscio et al. 1998; Schwinning et al. 2002) were maintained across a wide range of event sizes between 2 and 20 mm, which currently accounts for approximately 98% of all events and 88% of all precipitation in the warm season. Thus, the hypothesis that rainfall size represents a significant niche dimension for desert plants stands rejected.

In the four-species comparison, the C₄ grass *H. jamesii* clearly stands out as the species most capable of using soil moisture pulses in summer (Figs. 5, 6). Its average event use efficiency (as carbon assimilation added per water applied) was about twice that of *O. hymenoides*. Although *H. jamesii* extracted somewhat less pulse water (Fig. 4), it assimilated more than twice the carbon per water transpired, due to its C₄ mode of photosynthesis. The difference in the pulse use between *H. jamesii* and *C. lanata* was tenfold: in addition to the difference in water use efficiency, *H. jamesii* extracted on average five times more pulse water. Among the C₃ species, differences in event use were driven chiefly by differences in pulse water uptake, as the water use efficiencies were very similar. Spring events had no effect on photosynthesis, a phenomenon we observed before and attributed to larger availability of stored winter water at that time of year (Schwinning et al. 2002).

We did not compare the rain use of C₃ and C₄ shrubs in this experiment; however, it is doubtful that C₄ shrubs

have a significant advantage over C_3 shrubs with similar root distributions. Gebauer et al. (2002) consistently detected no photosynthetic response in the C_4 shrub *Atriplex confertifolia* to simulated 25 mm rain events, suggesting that a predominantly shallow root system is a prerequisite, though perhaps not sufficient, for effective summer rain use.

Species/event-size interactions on physiological responses to rain

This experiment illustrated that the magnitude of the physiological responses to summer rain depended on an interaction between event size and species. Small summer events (2 and 6 mm) had no significant effects on water status or photosynthesis in any species (Figs. 2, 6). Event sizes of 9 mm and larger significantly increased the water status of the two grasses (Fig. 2), but had a larger effect on the photosynthesis rate of *H. jamesii* (Figs. 5, 6). Only the largest summer event (19 mm) induced an increase in the water status of *G. sarothrae*, concurrent with a short-term increase in conductance (data not shown), and a non-significant, but positive effect on photosynthesis one day after watering (Fig. 6). Finally, neither water status, nor photosynthesis was significantly affected in *C. lanata* by any event size between 2 and 20 mm.

One way to interpret these data is that there are species-specific thresholds for event sizes below which plants do not respond or respond only passively to increased water availability (requiring no carbon investment, for example by opening stomata) and above which plants respond actively (requiring carbon investment, for example for the growth of new roots or photosynthetic enzymes). In the present study, response thresholds decreased in the order *C. lanata* > *G. sarothrae* > *O. hymenoides* > *H. jamesii*. Below we elaborate on this hypothesis in the context of a cost-benefit analysis for the use of pulsed resource.

An alternative model for the significance of event size for desert plants

The problem with intermittent and largely unpredictable resource supply is that organisms are often not in an optimal state to take advantage of the increased resource level when it becomes available. Thus, with the shallow soil being hot and dry most of summer, plants may not maintain many intact uptake roots near the soil surface and leaves may be few and with reduced photosynthetic capacity to lower maintenance costs during times of low carbon gain (Wong et al. 1979; Schulze and Hall 1982; Ehleringer 1983; Heckathorn et al. 1997). Then after rain, plants can respond in principally two ways: continue "business as usual" or invest to overcome some of the limitations on current water use (Comstock and Ehleringer 1986). The first choice is metabolically cheap but may result in only marginal benefits for the plant. The

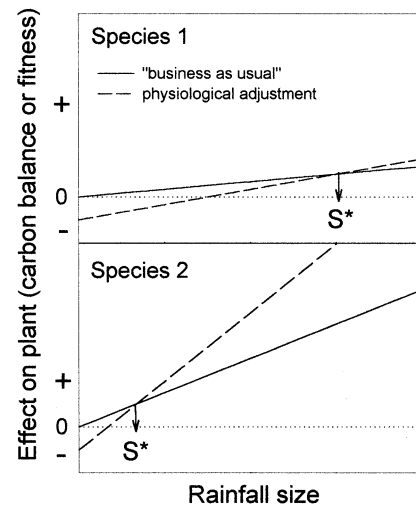


Fig. 7 The threshold-response hypothesis. The x -axis is a measure of rainfall size (e.g. mm), the y -axis indicates the net effect of rainwater use on the plant (carbon balance or fitness). *Solid lines*, hypothetical rainfall use of plants without active physiological responses; *broken lines*, hypothetical rainfall use of plants with active responses. Beyond the crossover point S^* physiological adjustments to increased water availability pay off, therefore species 2 should respond to lower event sizes than species 1. For details, see text

second choice is risky, it requires an initial carbon investment that may or may not pay for itself in subsequent carbon assimilation.

We illustrate a cost-benefit analysis for this scenario in Fig. 7. In this hypothetical example, two species differ in their current ("business as usual") capacities to increase carbon gain after rain, illustrated by the solid lines. Capacities might differ for different reasons, for example, because of differences in morphology (shallow vs deep-rooted) or because of differences in physiology (high vs low A/E). We further assume that some active adjustment, for example, the growth of rain roots or the synthesis of photosynthetic enzyme, potentially doubles either the uptake of rainwater or its exchange rate for carbon in each species, but also costs a certain fixed amount of carbon. The expected net carbon balance with the adjustment is illustrated by the broken lines. The intersections of the solid and broken lines mark the points beyond which physiological adjustments result in increased carbon gain for plants. This simple example suggests that plants with intrinsically greater rain use capacity should have a lower threshold for initiating physiological adjustments. Conversely, plants with intrinsically low rain use capacity should almost never initiate physiological adjustments, unless the rain event is exceptionally large.

In this simple illustration of the general principle we assumed that the carbon costs for doubling rain use are the same for both species (the broken lines have the same y -intercepts). However, this would rarely be the case. Differences in the carbon costs for physiological adjustments would shift the broken line up or down along the y -axis, changing the location of S^* , the rainfall threshold.

Specifically, if a doubling of rain use were more costly for the more responsive species 2, rainfall thresholds for the two species would be more similar, and vice versa. What the tendency would be among contrasting plant life forms is difficult to predict a priori, especially since different species could employ different strategies for increasing rain use in the short term. Thus, while a deep-rooted species might grow more shallow roots to overcome transport limitations, a shallow-rooted species might synthesize more photosynthetic enzymes to overcome biochemical limitations.

The present study ultimately does not address the new hypothesis on rainfall size; this would require direct observations of root growth and leaf biochemistry before and after rain. Nevertheless, it is interesting to interpret the present data in the light of it. In this experiment, all C₃ plants proved to be fairly non-responsive (apart from transient stomatal responses) to summer rain events, implying rainfall threshold sizes above 20 mm. This was somewhat surprising, especially in the case of the C₃ grass *O. hymenoides*, which extracted more rainwater than any other species. This relative unresponsiveness of the C₃ species may be related to the small contribution of summer rain compared to winter precipitation to the productivity of this ecosystem. Growth and reproduction in most shrubs and grasses of the Colorado Plateau are highly tuned to winter precipitation (Caldwell et al. 1977), with summer precipitation, although on average of the same magnitude as winter precipitation, possibly contributing little to overall fitness. For example, *O. hymenoides* completes seed production in June, before the onset of the summer rainy season, so carbon gain in summer can only result in additional leaf growth and possibly carbon storage to marginally increase winter survival and future reproduction. Thus, the incentives for *O. hymenoides* and other C₃ plants to risk carbon for improved summer rain use may be relatively small. By contrast, in desert systems where summer precipitation is a more dominant source of water, C₃ shrubs such as *Larrea tridentata* respond actively to sufficiently large summer rainfall events by initiating new leaf and root growth (Reynolds et al. 1999). As several other perennials of hot deserts with two rainy seasons, *L. tridentata* can flower and set seed twice per year, in spring and in summer, giving a potentially greater fitness payoff to active physiological responses to summer rain. This suggests that the cost-benefit analysis outlined in Fig. 7 depends not only on the life form characteristics of species, but also on the resource renewal patterns of the environment and the way these patterns shape the life history strategies of resident species. Thus, the y-axis in Fig. 7 should ultimately reflect rain effects on overall species fitness, while measures of carbon gain may be inexact proxies.

In contrast to all C₃ species in this study, *H. jamesii* showed signs of active physiological adjustment, expressed through a photosynthetic increase between days 1 and 3 after watering with 19 mm (Fig. 6). It suggests a rainfall threshold somewhere between 9 and 20 mm. This

is consistent with the results of a greenhouse experiment on another C₄ perennial grass of the Great Plains, *Bouteloua gracilis*, where, after severe drought conditions, new root growth was triggered by event sizes between 5 and 15 mm (Lauenroth et al. 1987). New root growth may have been the reason for the exceptionally high rain use in *H. jamesii* in this experiment as well. However, in another experiment on the same site (Schwinning et al. 2002), a 25 mm rain event that followed an intense drought condition doubled the A/E of *H. jamesii*, while there was no obvious enhancement of water transport capacity.

The response-threshold hypothesis hinges on the ability of plants to gauge the size of an event soon after it occurs (because any sensory delay time would subtract substantially from total expected carbon gain). It is possibly that simply the magnitude of the effect on plant water potential (Fig. 2) provides enough information about the pulse event. A water-potential signal would automatically integrate information on event size in relation to the distribution of functioning uptake roots. This also implies that maintaining uptake roots in dry soil is critical for summer rain users, as without such roots plants would be “blind” to changes in moisture availability and miss opportunities for carbon gain.

Implications for the effects of a shift to larger rainfall sizes

Sala and Lauenroth's (1982) hypothesis predicts that a shift to larger event sizes should favor shrubs over grasses in arid ecosystems. Our hypothesis predicts that summer events of almost any size and distribution should favor shallow-rooted species, particularly C₄ grasses such as *H. jamesii* and *B. gracilis* more than shrubs. Even though larger events may infiltrate beyond the bulk of the grass root system, which could potentially lower the rain use efficiency of these species, it appears that especially the C₄ grasses are capable of compensating for this effect, by enhancing water extraction rates or increasing water use efficiencies through active physiological adjustments. Thus, a shift towards larger rainfall sizes, without change in total precipitation in a given year, may not have significant effects on species interactions and plant community composition.

However, this scenario of holding total summer precipitation constant while increasing the number of large events is a somewhat artificial scenario. Statistical analyses of rainfall patterns show that wet and dry summers are distinguished primarily by the number of larger events (e.g. >15 mm), rather than the total number of rainfall events. Thus, a shift to larger event sizes implies either that summers would become wetter on average (this would clearly favor summer-rain users such as *H. jamesii*), or if this were not the case, that the disparity between the wettest and the driest summers would become more extreme, as both observational data and climate models predict (Easterling et al. 2000). The

potential consequences of increased inter-annual rainfall variation in plant communities are difficult to assess, especially in short-term experiments, as they could involve a large number of life history traits that go far beyond root distributions and the efficiency of water use, and may critically involve dormancy and reproductive strategies.

Acknowledgements This work was supported by the National Science Foundation (IBN 9814510). We would like to thank Danielle Pierce and Kim Davis for their important contributions to field and laboratory work and two anonymous reviewers who greatly helped us find our focus in the presentation of this study.

References

- BassiriRad H, Tremmel DC, Virginia RA, Reynolds JF, de Soyza AG, Brunell MH (1999) Short-term patterns in water and nitrogen acquisition by two desert shrubs following a simulated summer rain. *Plant Ecol* 145:27–36
- Brown JH, Valone TJ, Curtin CG (1997) Reorganization of an arid ecosystem in response to recent climate change. *Proc Natl Acad Sci USA* 94:9729–9733
- Caldwell MM, White RS, Moore RT, Camp LB (1977) Carbon balance, productivity; water use of cold-winter desert shrub communities dominated by C₃ and C₄ species. *Oecologia* 29:275–300
- Chesson P, Huntly N (1989) Short-term instabilities and long-term community dynamics. *Trends Ecol Evol* 4:293–298
- Cody ML (1989) Growth-form diversity and community structure in desert plants. *J Arid Environ* 17:199–210
- Coleman ML, Shepard TJ, Durham JJ, Rouse JE, Moore GR (1982) Reduction of water with zinc for hydrogen isotope analysis. *Ann Chem* 54:993–995
- Comstock J, Ehleringer JR (1986) Canopy dynamics and carbon gain in response to soil water availability in *Encelia frutescens* Gray, a drought-deciduous shrub. *Oecologia* 68:271–278
- Cowling RM, Esler KJ, Midgley GF, Honig MA (1994) Plant functional diversity, species diversity and climate in arid and semi-arid southern Africa. *J Arid Environ* 27:141–158
- Cui M, Caldwell MM (1997) A large ephemeral release of nitrogen upon wetting of dry soil and corresponding root responses in the field. *Plant Soil* 191: 291–299
- Dodd MB, Lauenroth WK, Welker JM (1998) Differential water resource use by herbaceous and woody plant life forms in a shortgrass steppe community. *Oecologia* 117:504–512
- Dougherty RL, Lauenroth WK, Singh JS (1996) Response of a grassland cactus to frequency and size of rainfall events in a North American shortgrass steppe. *J Ecol* 84:177–183
- Easterling DR, Meehl GA, Parmesan C, Changnon SA, Karl TR, Mearns LO (2000) Climate extremes: observations, modeling, and impacts. *Science* 289:2068–2074
- Ehleringer JR (1983) Ecophysiology of *Ameranthus palmeri*, a Sonoran Desert summer ephemeral. *Oecologia* 57:107–112
- Ehleringer JR, Phillips SL, Schuster WSF, Sandquist DR (1991) Differential utilization of summer rains by desert plants, implications for competition and climate change. *Oecologia* 88:430–434
- Ehleringer JR, Roden J, Dawson TE (2000) Assessing Ecosystem-level water relations through stable isotope ratio analysis. In: Sala OE, Jackson RB, Mooney HA, Howarth RW (eds) *Methods in ecosystem science*. Springer, Berlin Heidelberg New York, pp 181–214
- Fowler AM, Hennessy KJ (1995) Potential impacts of global warming on the frequency and magnitude of heavy precipitation. *Nat Hazards* 11:283–303
- Gebauer RLE, Ehleringer JR (2000) Water and nitrogen uptake patterns following moisture pulses in a cold desert community. *Ecology* 81:1415–1424
- Gebauer RLE, Schwinning S, Ehleringer JR (2002) Interspecific competition and resource pulse utilization in a cold desert community. *Ecology* 83:2602–2616
- Golluscio RA, Sala OE, Lauenroth WK (1998) Differential use of large summer rainfall events by shrubs and grasses: a manipulative experiment in the Patagonian steppe. *Oecologia* 115:17–25
- Groisman PY, Karl TR, Easterling DR, Knight RW, Jamason PF, Hennessy KJ, Suppiah R, Page CM, Wibig J, Fortuniak K, Razuvaev VN, Douglas A, Forland E, Zhai P-M (1999) Changes in the probability of heavy precipitation: important indicators of climatic change. *Climatic Change* 42:243–283
- Heckathorn SA, DeLucia EH, Zielinski RE (1997) The contribution of drought-related decreases in foliar nitrogen concentration to decreases in photosynthetic capacity during and after drought in prairie grasses. *Physiol Plant* 101:173–182
- IPCC (1996) *Climate change 1995. Contribution of working group I to the second assessment report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge
- Lauenroth WK, Sala OE, Milchunas DG, Lathrop, RW (1987) Root dynamics of *Bouteloua gracilis* during short-term recovery from drought. *Funct Ecol* 1:117–124
- Lin G, Phillips SL, Ehleringer JR (1996) Monsoonal precipitation responses of shrubs in a cold desert community on the Colorado Plateau. *Oecologia* 106:8–17
- Pierson EA, Turner RM (1998) An 85-year study of saguaro (*Carnegiea gigantea*) demography. *Ecology* 79:2676–2693
- Reynolds JF, Virginia RA, Kemp PR, de Soyza AG, Tremmel DC (1999) Impact of drought on desert shrubs: effects of seasonality and degree of resource island development. *Ecol Monogr* 69:69–106
- Sala OE, Lauenroth WK (1982) Small rainfall events: an ecological role in semiarid regions. *Ecology* 53:301–304
- Schulze E-D, Hall AE (1982) Stomatal responses, water loss and CO₂ assimilation rates of plants in contrasting environments. In: Lange O, Nobel PS, Osmond CB, Ziegler H (eds) *Water relations and carbon assimilation. Encyclopedia of plant physiology* 12B. New series. Springer, Berlin Heidelberg New York, pp 181–230
- Schwinning S, Davis K, Richardson L, Ehleringer JR (2002) Deuterium enriched irrigation indicates different forms of rain use in shrub/grass species of the Colorado Plateau. *Oecologia* 130:345–355
- Sokal RR, Rohlf FJ (1995) *Biometry. The principles and practice of statistics in biological research*, 3rd edn. Freeman, New York
- Swetnam TW, Betancourt JL (1998) Mesoscale disturbance and ecological response to decadal climate variability in the American Southwest. *J Climate* 11:3128–3147
- Turner RM (1990) Long-term vegetation change at a fully protected Sonoran (Mexico) desert site. *Ecology* 71:464–477
- Wan C, Sosebee RE, McMichael BL (1993) Growth, photosynthesis, and stomatal conductance in *Gutierrezia sarothrae* associated with hydraulic conductance and soil water extraction by deep roots. *Int J Plant Sci* 154:144–151
- Wong SC, Cowan IR, Farquhar GD (1979) Stomatal conductance correlates with photosynthetic capacity. *Nature* 282:424–426