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Summer and winter drought in a cold desert ecosystem (Colorado Plateau) part I: effects on soil water and plant water uptake

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Abstract

We investigated the effects of winter and summer drought on plants of the Colorado Plateau in western North America. This winter-cold, summer-hot desert region receives both winter and summer precipitation. Droughts were imposed for two consecutive years using rainout shelters. Here, we examine drought effects on the hydrologic interactions between plants and soil. We chose three perennial species for this study, representing different rooting patterns and responsiveness to precipitation pulses: *Oryzopsis hymenoides*, a perennial bunch grass with shallow roots; *Gutierrezia sarothrae*, a subshrub with dimorphic roots; and *Ceratoides lanata*, a predominantly deep-rooted woody shrub. Drought effects on plant water status were qualitatively similar among species, despite morphological differences. Summer drought affected the water status of all species more negatively than winter drought. Isotopic analysis of stem water revealed that all three species took up deeper soil water under drought conditions and shallow soil water after a large rainfall event in summer. Thus all three species appeared to use the same water sources most of the time. However, after a particularly dry summer, only the deepest-rooted species continued to take up soil water, while the more shallow-rooted species were either dead or dormant. Our study suggests therefore that

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increased occurrence of summer drought could favor the most deep-rooted species in ecosystem.

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1. Introduction

Global climate change is expected to impact ecosystem processes worldwide (Vitousek, 1994). In addition to increases in temperature and atmospheric [CO₂], climate models also predict profound changes in precipitation patterns over large regions of the world (IPCC, 2001). Although specific precipitation predictions differ between models, all models agree on two general issues: (1) changes in rainfall averages will be season-specific, so that trends in winter precipitation may not be of the same direction or magnitude as trends in summer precipitation and (2) inter-annual variation in rainfall amount will likely increase (Dettinger et al., 1998; Easterling et al., 2000; Groisman et al., 1999). Arid/semiarid systems may be among the most sensitive to precipitation changes, because of the central role that soil moisture plays in governing almost all ecosystem processes (Noy-Meir, 1973; Le Houérou, 1984; Weltzin et al., 2003), including plant functional diversity (Walter, 1971; Cowling et al., 1994; Neilson, 1995; Paruelo and Lauenroth, 1996; Paruelo et al., 1998; Schwinning and Ehleringer, 2001; Knapp et al., 2002).

Increased precipitation variability is tantamount to an increase in the frequency of both drought events and rainfall extremes. While several recent studies have focused on the effects of large rainfall events in arid ecosystems (e.g. Golluscio et al., 1998; Schwinning et al., 2002; Gebauer et al., 2003), fewer studies have examined the effects of prolonged drought periods (but see Reynolds et al., 1999). In this study, we explored the drought responses of species representing dominant plant life forms on the Colorado Plateau of western North America. For two consecutive years, we imposed drought either in winter, in summer or yearlong, and compared the effects of these treatments to a control under ambient precipitation conditions.

Our primary goal was to determine whether plant life forms with contrasting root distributions responded differently to summer and winter drought. Previous studies found only minor differences between species in winter-derived soil moisture use in spring, but large differences in summer rainwater use (Ehleringer et al., 1991; Lin et al., 1996; Ehleringer et al., 1998). This suggests that winter drought would also exert similar effects on most species and not cause major shifts in community composition, while summer drought could potentially affect species differently. Against this hypothesis stand observations from other ecosystems, where changes in winter precipitation had profound effects on plant diversity (Brown et al., 1997; Polis et al., 1997; Shepherd et al., 2002).

Precipitation effects on plants are mediated primarily by the distribution and dynamics of soil water interacting with species' root distributions (Cohen, 1970;

Walter, 1971; Noy-Meir, 1973). According to Walter's (1971) simple but elegant two-layer model, moderate amounts of summer precipitation recharge only shallow soil layers, where water is readily taken up by shallow-rooted grasses, while winter precipitation or very large summer rainfall events that recharge deeper soil layers make water available also to deeper-rooted woody plants. Applying this model to the Colorado Plateau ecosystem, we expected that (1) winter drought should reduce water availability in spring across shallow and deeper soil layers and reduce the spring plant water status of grasses and shrubs. (2) Summer drought should reduce the water availability primarily of shallow soil layers and impose more negative effects on the water status of grasses than on shrubs. (3) Yearlong drought should establish a monotonically decreasing vertical soil moisture gradient, such that the most deep-rooted shrubs would have the most water available and the least negatively impacted water status.

2. Methods

2.1. Study species

Three species were selected to represent dominant plant life forms on the Colorado Plateau. Indian ricegrass (*Oryzopsis hymenoides*) is a C₃ perennial bunch grass with predominantly shallow roots; broom snakeweed (*Gutierrezia sarothrae*) is a sub-shrub with a dimorphic root system (Wan et al., 1994) consisting of a moderately deep (ca. 1 m) vertical tap root and an extensive shallow root system. Winterfat (*Ceratoides lanata*) is a predominantly deep-rooted (> 1 m), woody shrub. Previous experiments established that, on a leaf-area basis, *O. hymenoides* takes up 2–3x more summer rainwater than *G. sarothrae*, and *G. sarothrae* 1.5–2x more than *C. lanata* (Schwinning et al., 2003).

2.2. Site description, plot selection and preparation

The research site was Bureau of Land Management property located near the Needles District of Canyonlands National Park in southern Utah, USA (N38.17548 W109.72018). Vegetation cover was composed of mixed grasses and shrubs. The grass community was dominated by the spring-active annual grass *Bromus tectorum* (75%) and two native perennial grasses *O. hymenoides* (10%) and *H. jamesii* (6%). Shrub cover was primarily composed of *G. sarothrae* (63%) and *C. lanata* (31%). The soil had sparse biological crust cover and was uniformly sandy with depth. There were caliche carbonate deposits at approximately 30 cm, but not at a density to prevent water infiltration past this layer. The research area had been spring grazed by cattle until January 1999, when fences were erected. In Moab, the nearest weather station to the research site with a long-term record, mean monthly temperature is –1 °C during the coldest month of the year (January) and 27 °C during the hottest month (July) with daytime maximum temperatures averaging 37 °C. The mean annual precipitation at our site is 215 mm, with a near-even precipitation distribution

across months, except for the month of June, which is much drier than average. Precipitation data during the time of the experiment were provided by a nearby Park Service weather station, approximately 3 km from the field site (CLIM-MET Site #3).

2.3. Experimental design and analysis

Within the fenced area, three sites were identified that contained well-mixed stands of the three study species and assigned block status. Within each block, eight 3.5×3.5 m plots were installed by burying aluminum flashing 20 cm deep along the plot borders to constrain the lateral expansion of shallow root systems. Drought treatments were randomly assigned with two replicates per block.

The experiment was a complete factorial design with two factors at two levels and six replications per treatment. The factors were seasonal timing of treatment (winter/summer) and rainfall treatment (drought/ambient). The four resulting treatment combinations were winter drought (WD), summer drought (SD), yearlong drought (YD) and no drought (ND). Within each plot, we measured the physiological status of the three species, thus the factor “species” was a “repeated variable” in the analysis of variance (SPSS, Version 8.0, SPSS Inc.). Block effects were generally not significant, we therefore do not report on them here. Where necessary, variables were log- or square-root transformed to pass the Box Test for equality of the variance–covariance matrix. The variance–covariance matrix commonly did not conform to the sphericity assumption of repeated analysis of variance. To compensate, we routinely used the lower-bound epsilon, i.e. the most conservative method, to adjust the degrees of freedom in the significance test (SPSS Inc., 1999). Significance testing was done at the $P = 0.05$ level. When $P < 0.01$, we called effects “highly significant” and “marginally significant” when $0.1 < P < 0.05$.

Drought treatments were imposed through rainout shelters. They were first erected on November 18, 1998 on plots marked for winter and yearlong drought. The winter drought treatment ended when the summer drought treatment started on April 28, 1999 and shelters were exchanged between plots accordingly. Shelters were moved two more times, on October 23, 1999 (transitioning from summer to winter drought) and on April 25, 2000 (winter to summer drought). In November 2000, all shelters were removed.

2.4. Rainout shelter design and microclimate effects

Shelter roofs were made of clear corrugated polycarbonate panels (Suntuff Inc, Livingston, NJ), coated with a UV filter described by the manufacturer as 90% transparent to visible light. PAR levels under shelters were reduced by 13–20% at the time of photosynthetic measurement, but the reduced levels still exceeded saturating levels for C_3 plants on cloudless days ($> 1000 \mu\text{Em}^{-2} \text{s}^{-1}$).

Roofs measured $4 \times 4 \text{ m}^2$ and were held up at 1.5 m above ground by 9 fence posts. A slight slant routed intercepted rainwater into side-mounted gutters. From there water drained into ground gutters and spilled at least 10 m away from any plot. In winter, snow was brushed off the shelter roofs.

Besides keeping precipitation off the experimental plots, the shelters also increased temperatures near the soil surface. Temperature increases at 5 cm soil depth and 5 cm above the ground were in the range of 3–4 °C and 1–2 °C, respectively. However, air temperature at leaf height (determined during photosynthetic measurements) was not significantly affected (results of ANOVA not shown). The temperature effect likely accelerated rates of soil evaporation and drying of the soil surface. It may also have accelerated the onset of spring growth in the grasses. Informal observations indicated that *O. hymenoides* began to grow one week earlier under winter-sheltered plots. However, when plant sizes were assessed in April, no significant size differences were found between treatments.

2.5. Soil water content and hydrogen isotope composition

Hydrogen isotope ratios vary within soils in space and time, because of variation in the isotopic composition of precipitation (the δD of winter precipitation is more negative than that of summer precipitation), and because of evaporative enrichment near the soil surface (Dawson et al., 1998). Plant roots do not discriminate between water molecules with different isotope composition, thus water transported through plant xylem is a linear mix of all soil water sources used by the plant. The isotopic composition of xylem water can therefore be used to trace the origin of water in the transpiration stream, provided there are only a few distinct sources of known isotopic composition. Isotope analysis of stem water has been used to trace plant water uptake either to specific soil layers (e.g. Drake and Franks, 2003) or directly to the seasonal precipitation (e.g. Ehleringer et al., 1991). In the latter case, it is assumed that plant water uptake from evaporation-enriched, dry soil layers near the soil surface is negligible. In this study we also used isotope analysis to trace the infiltration depth of summer and winter water in the soil profile.

Until April 1999, soil moisture was monitored in one plot per treatment in 15 cm intervals using segmented TDR probes (MoisturePoint type F, Environmental Sensors, Inc., Victoria, British Columbia Canada). To add replication and increase the accuracy of the measurements, we later began to take soil cores in every plot and determined soil moisture content gravimetrically. Soil cores were taken in random locations, but not inside plant canopies and at least 20 cm away from the plot borders. Soil cores were taken in 10 cm intervals, usually to a depth of 60 cm. However, extremely dry conditions sometimes made it impossible to collect soil from below 50 cm, because the dry sand spilled from the augur before it could be collected at the surface. In the second year we added a sample at 1 m depth, expecting that one full year of drought treatments could have significantly affected soil moisture below 60 cm depths. Soil samples were well-mixed and sub-sampled for hydrogen isotope analysis. The rest was weighed, dried at 90 °C for 24 h, and weighed again to determine gravimetric water content. Sub-samples were stored in screw capped glass vials, sealed with parafilm and frozen until extraction. Soil water was extracted through cold trapping under vacuum (Ehleringer et al., 2000). From the extracts, 2 μ l 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 $\pm 1\%$ precision. Hydrogen isotope ratios are expressed in the δ notation in parts per thousand (‰):

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

2.6. Plant water relations

We inferred the water status of plants from predawn water potentials (Ψ_{predawn}) and leaf conductance. Ψ_{predawn} is generally regarded as the root-system integrated measure of plant-available soil water, while leaf conductance represents the stomatal response to soil water availability, among other factors.

Predawn water potentials between 0 and -6.5 MPa were measured on foliated terminal branches of the two shrubs and green leaf blades of the grass between 3 am and dawn using Scholander pressure bombs. Stem samples for determining the isotopic composition of stem water were taken shortly after sunrise. We collected lower, fully suberized stem sections of branches that had green leaves at the top to ensure that stem xylem was filled with recent transpiration water and to minimize the possibility of evaporative enrichment within the stem section. For sampling *O. hymenoides*, we collected sheath-covered stems just above the soil surface. The storage, extraction and analysis procedure followed that of the soil samples.

Leaf conductance values were calculated from leaf gas exchange rates, determined with a portable infrared gas analyzer system (LiCor 6200, Licor Instruments, Lincoln, NE, USA) between the hours of 9:30 a.m.–12:00 pm solar time, at the time of day when photosynthetic rates were expected to be maximal. Afterwards, measured leaves were collected, stored in wetted coin envelopes and kept cold until leaf area was determined with a LiCor 3100 Area Meter (Licor Instruments).

3. Results

3.1. Drought treatment effects on total soil water

In rainout shelter experiments, treatment contrasts depend on the occurrence of natural precipitation. In this experiment, the effect of the winter drought treatment on soil water was greater in the second year of the experiment, because of substantial snowfall in December/January, while the effect of the summer drought treatment was greater in the first year, when summer rainfall was 80% above average.

There was little precipitation between the dates that rainout shelters were first erected in mid-November and when they were removed in April (Fig. 1). By March of the first year, the differences in the soil water content of the top 60 cm of sheltered and open plots amounted to only 20 mm. In the second year the difference was 50 mm.

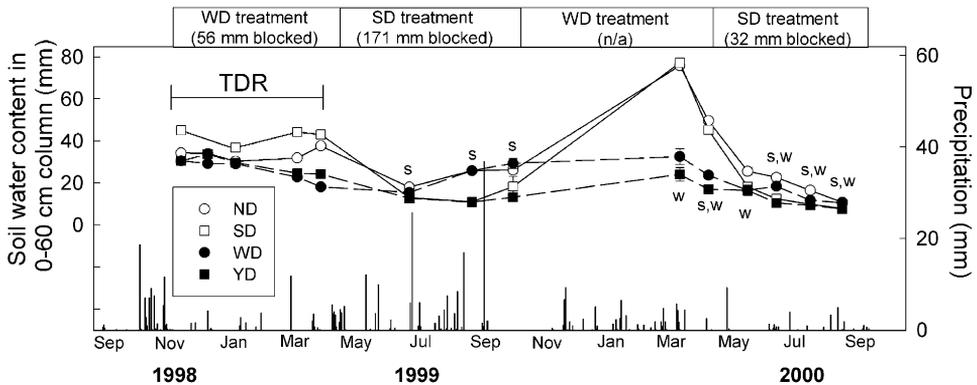


Fig. 1. Precipitation record (bars) from the CLIM-MET Site #3, about 3 km from the field site, and soil water content in the top 60 cm across the four drought treatments. On the top of the graph, the time periods are indicated over which winter drought (WD) and summer drought (SD) were imposed through rainout shelters, along with estimates of the cumulative precipitation water withheld. Precipitation data for the second winter are not available, because substantial snowfall in December/January was not recorded correctly by the tipping bucket rain gauge. For the period marked TDR, data were collected using Time Domain Reflectometry without replication. Thereafter, water content was determined gravimetrically across all plots. “s” and “w” denote significant effects of the summer and winter drought treatments at the $P = 0.05$ level in a two-factor ANOVA. Error bars represent standard errors.

In the first summer, soil moisture in open plots increased between July and September, while it continued to decline in shelter-covered plots. By contrast, the second summer was 70% drier-than-average. Although effects of the summer drought treatment on soil moisture were significant in the second year, they may have been due to the effect of the previous summer drought treatment rather than the current, because they were already significant in April, when that year’s summer drought treatment had only just begun. Winter and summer drought treatment effects continued to be significant until late summer. The lowest soil moisture content over the two-year experiment was recorded at the end of August 2000.

3.2. Soil moisture profiles

We hypothesized that winter and summer drought should have different effects on vertical soil moisture distribution. We assessed this by measuring soil moisture distributions at two critical times during the growing season (Fig. 2). At the end of winter in both years, soil moisture tended to increase with depth, indicating that soil had begun to dry out from the top. Winter drought decreased water contents along the entire measured profile. After the first winter, differences due to the presence of rainout shelters in winter were most pronounced in the top 15 cm of the soil (Fig. 2A), because of a recent small rainfall event. At the end of the second winter, water profile differences between winter-covered and winter-open plots were much greater, highly significant and extended to at least 1 m depth (Fig. 2C). In addition, the previous summer drought still had a significant effect on soil moisture.

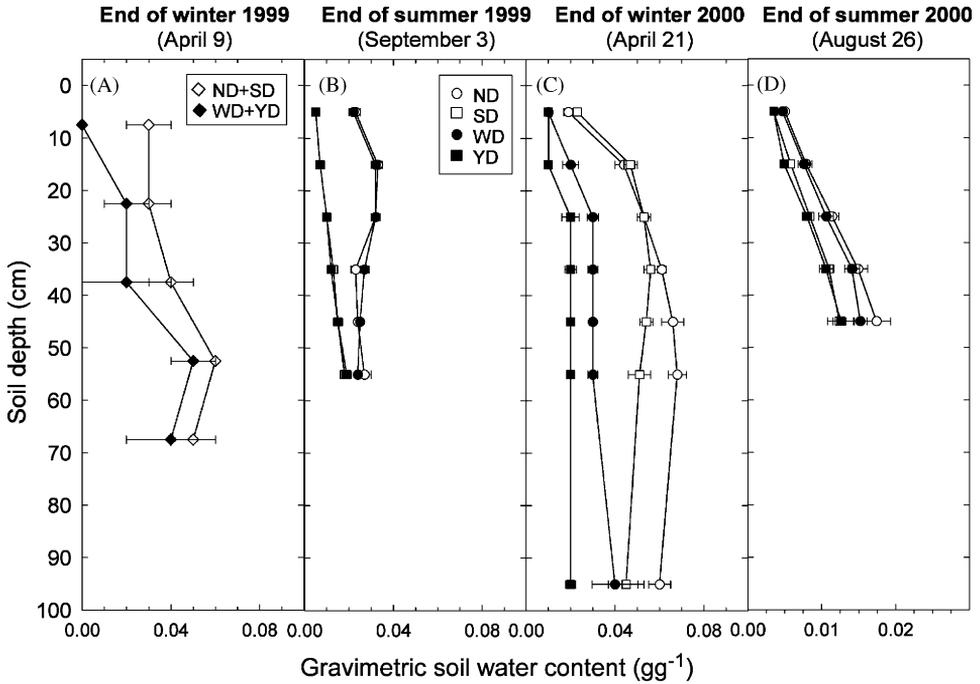


Fig. 2. Profiles of gravimetric soil water content on several dates during the experimental period. Error bars represent standard errors. In April 1999, soil moisture was measured by TDR in 15 cm intervals to 75 cm depth. At all other times, soil water was measured gravimetrically, usually to 60 cm, except in April 2000, when a sample at 1 m was added, and in August 2000, when the soil was too dry to extract soil samples below 50 cm on most plots. To highlight treatment differences the x-axis scale in panel D was magnified.

At the end of the first (wet) summer, summer-covered plots (SD, YD) were drier throughout the measured profile compared to summer-open plots (ND, WD) (Fig. 2B). The largest differences occurred between 0 and 30 cm were probably due to a 17 mm rainfall event that had occurred one week earlier. By contrast, at the end of the second (dry) summer, soil water across all treatments was extremely low (Fig. 2D, note the scale change on the x-axis), though summer drought effects still remained significant.

Analysis of the hydrogen isotope ratio (δD), performed once per summer after rainfall events (Fig. 3), provided additional information on soil water dynamics by depth. The bulge of moist soil at 0–30 cm seen in the first summer (Fig. 2B) had a distinctly less negative δD than deeper soil water, consistent with the expected δD of summer precipitation (Fig. 3A). δD increased with depth between 0 and 30 cm, probably because rainwater mixed with increasing amounts of residual winter water that had a lower δD . Soil water below 30 cm, and in the entire profile in YD plots, had a δD of -65 to -75 ‰, suggesting that soil water below 30 cm originated

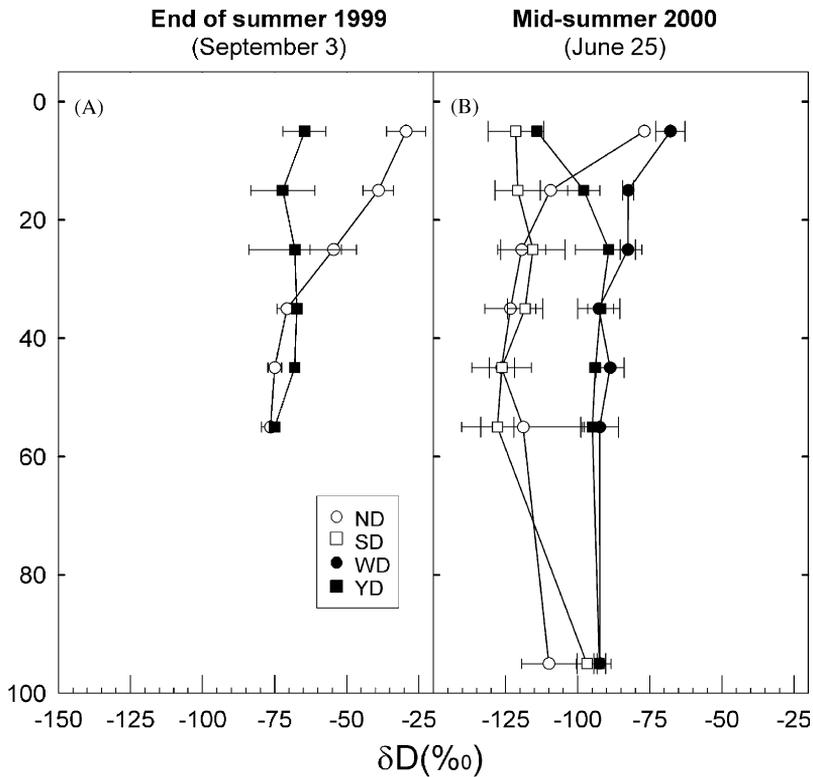


Fig. 3. Profiles of soil water hydrogen isotope ratio (δD) on two dates in summer of both years. Error bars represent standard errors. In 1999, we only included the most extreme treatments (ND and YD) in the analysis, expecting no large differences between the δD of ND and WD plots, and between SD and YD plots. In 2000, we measured all samples and added a data point at 1 m depth.

entirely in cool season precipitation. Nevertheless, summer drought significantly reduced soil water content below 30 cm (Fig. 2B). Thus, stored winter water was depleted at an accelerated rate in the summer drought treatment.

The δD profile collected in June of the second summer showed that winter-open plots had received highly depleted winter precipitation (ca. -120‰), consistent with snowmelt as the main source of water (Fig. 3B). The soil water δD of plots that were winter-covered was also somewhat lower than in the previous year, suggesting that some snowmelt water had entered sheltered plots. At 1 m depth there were still significant differences in the δD of ND and winter-covered (WD, YD) plots, thus winter recharge went at least this deep. The δD at 1 m in SD plots, however, which also received winter precipitation, were indistinguishable from that of winter-covered plots, indicating that the previous summer drought treatment must have shortened the infiltration depth of winter precipitation to less than 1 m, most likely by increasing the storage capacity of the intermediate soil layers.

3.3. Plant water status

Ψ_{predawn} was significantly different between species on all measurement dates, and whenever there were significant drought effects, there also were significant species*drought interactions.

Across species, the winter drought treatment had significant effects on Ψ_{predawn} on 6 out of 11 measurement dates, chiefly between March and May (data not shown). Winter drought effects on Ψ_{predawn} at the end of winter were also significant for all species individually, except for *O. hymenoides* at the end of the first winter (Fig. 4). By contrast, significant effects of the summer drought treatment were seen only once, in September of the first (wet) summer. Summer drought effects increased in the order of increasingly shallow root distributions (*C. lanata* < *G. sarothrae* < *O. hymenoides*) and were much greater than the effects of the winter drought treatments (note the scale change in Fig. 4).

At the end of the second winter, Ψ_{predawn} of plants in YD plots were somewhat lower than in the previous year, but not nearly as low as in the previous summer, suggesting that these plants recovered somehow from water stress, despite of YD plots receiving no or minimal water inputs in the intervening period. Spring growth would have allowed plants to grow new roots in wetter portions of the soil, either deeper in the soil profile or outside of the sheltered plot area. Isotopic evidence (shown below) points to the first alternative.

Winter drought effects on leaf conductance were significant only at the end of the second winter (Fig. 5) when species*winter drought interactions were also significant. *O. hymenoides* was most sensitive to the winter drought treatment.

Summer drought effects on leaf conductance were significant only in the first (wet) year, but species*drought interactions were insignificant. By the end of the second summer, all measured conductance values were near the detection limit and insignificantly different between drought treatments and species.

3.4. Plant water sources

Species differences in Ψ_{predawn} and leaf conductance indicate that species may have used different water sources. To test this possibility, we analyzed the δD of stem water. There were no differences in stem water δD at the end of the first winter; all δD values clustered around -70% (data not shown). This value is consistent with the soil water δD over much of the profile in all treatments (Fig. 3A). Thus, conclusions about specific soil water sources could not be drawn.

At the end of the first (wet) summer, plants that had received summer rain had more enriched stem water than plants that were shelter-covered in summer, consistent with the uptake of summer rainwater (Fig. 6). Since there were neither species differences in leaf conductance nor in stem water δD values, all three species must have extracted water from the same soil source and transpired it at similar rates. The transpiration water originated almost surely from the layer of wet soil at 0–30 cm (Fig. 2B), which had a δD value of between -30 and -50% (Fig. 3A), identical to the range of stem water δD (Fig. 6). Plants that had not received summer

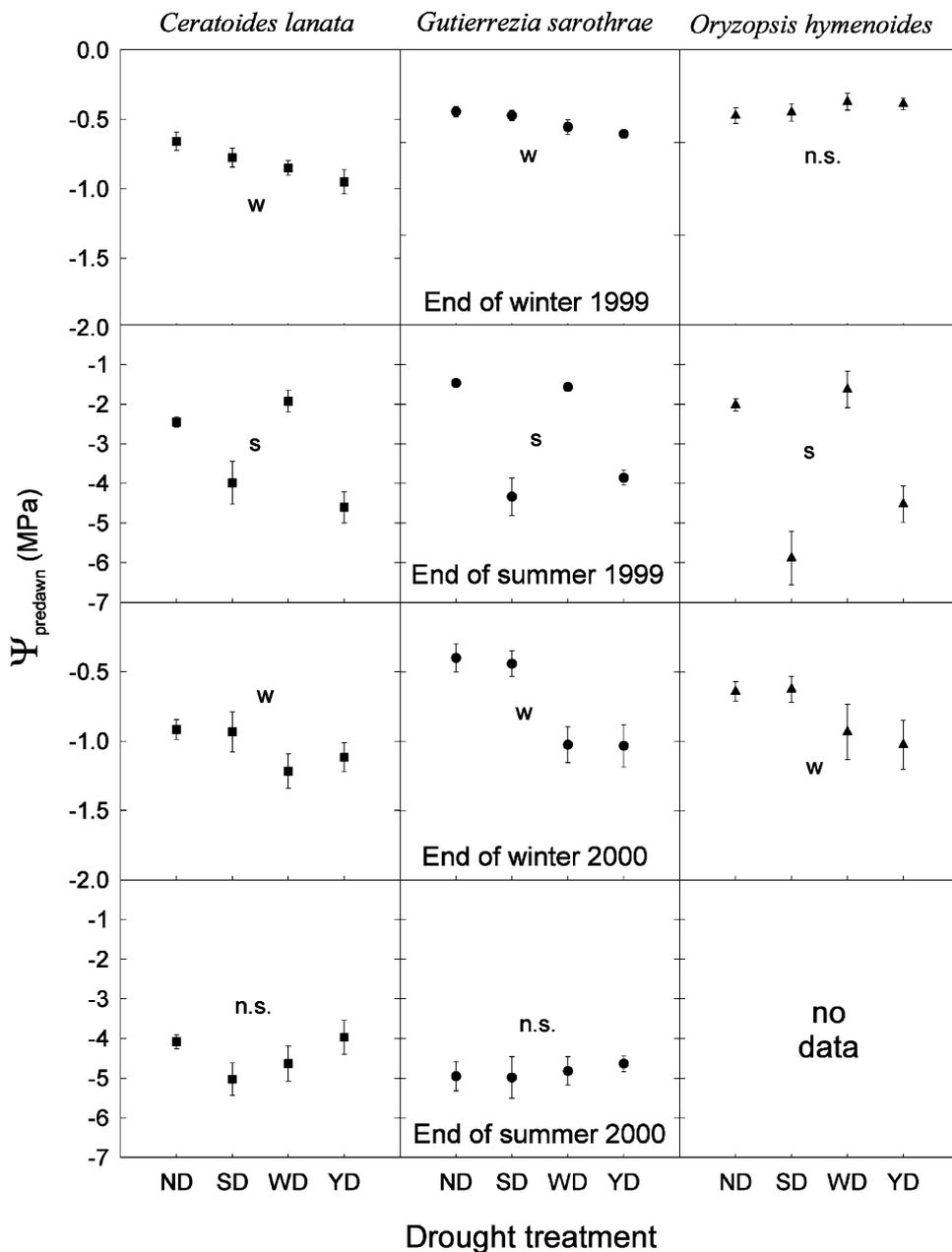


Fig. 4. Drought effects on predawn water potentials (Ψ_{predawn}) at the ends of winter and summer in both experimental years. “s” and “w” denote significant effects of the summer and winter drought treatments in a two-factor ANOVA. “n.s.” signifies non-significant effects of drought treatments. Note the scale change between end of winter and end of summer data. At the end of summer in 2000, all *O. hymenoides* leaves were senescent and we were unable to collect water potential data.

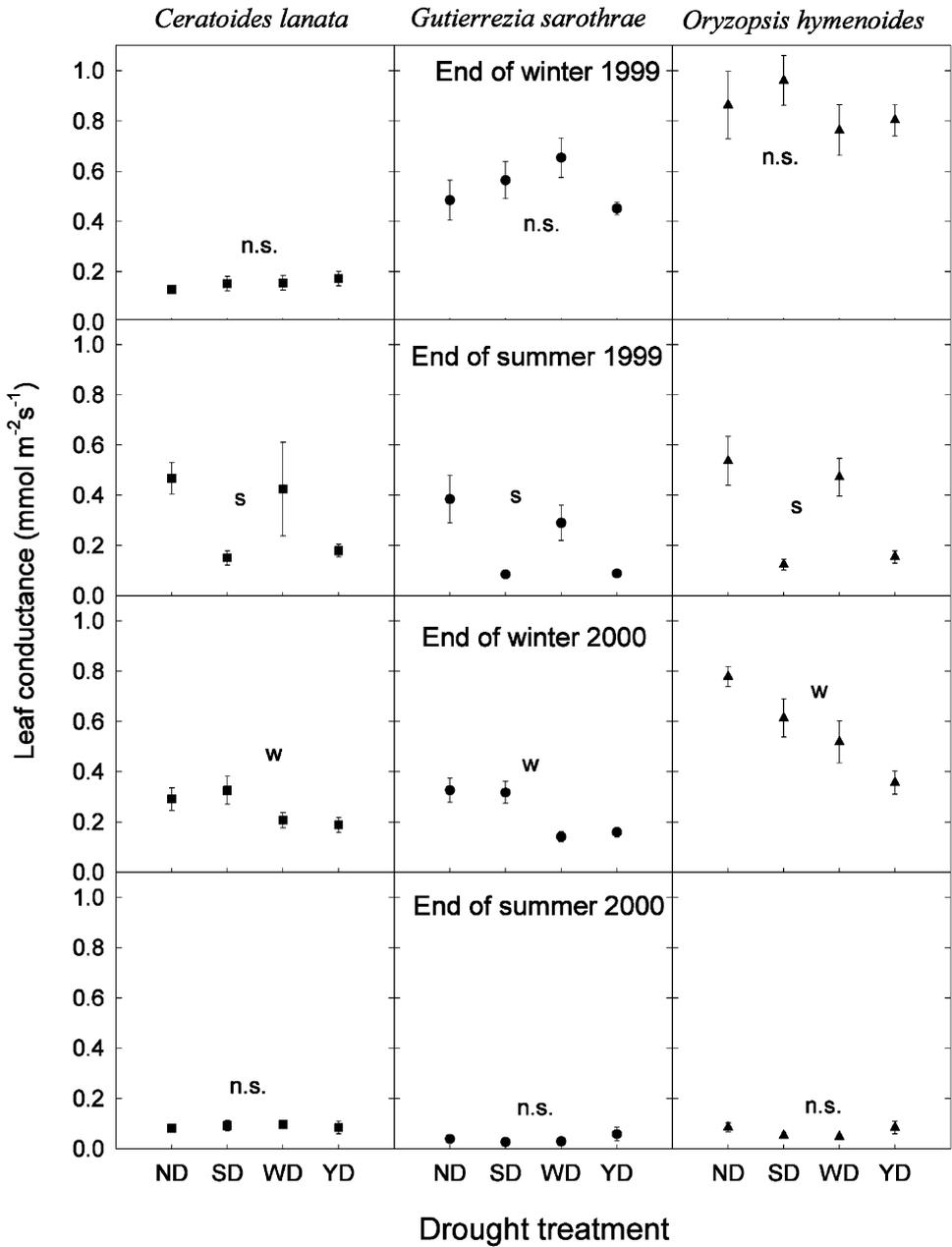


Fig. 5. Drought effects on leaf conductance at the ends of winter and summer in both experimental years. Labels as in Fig. 4.

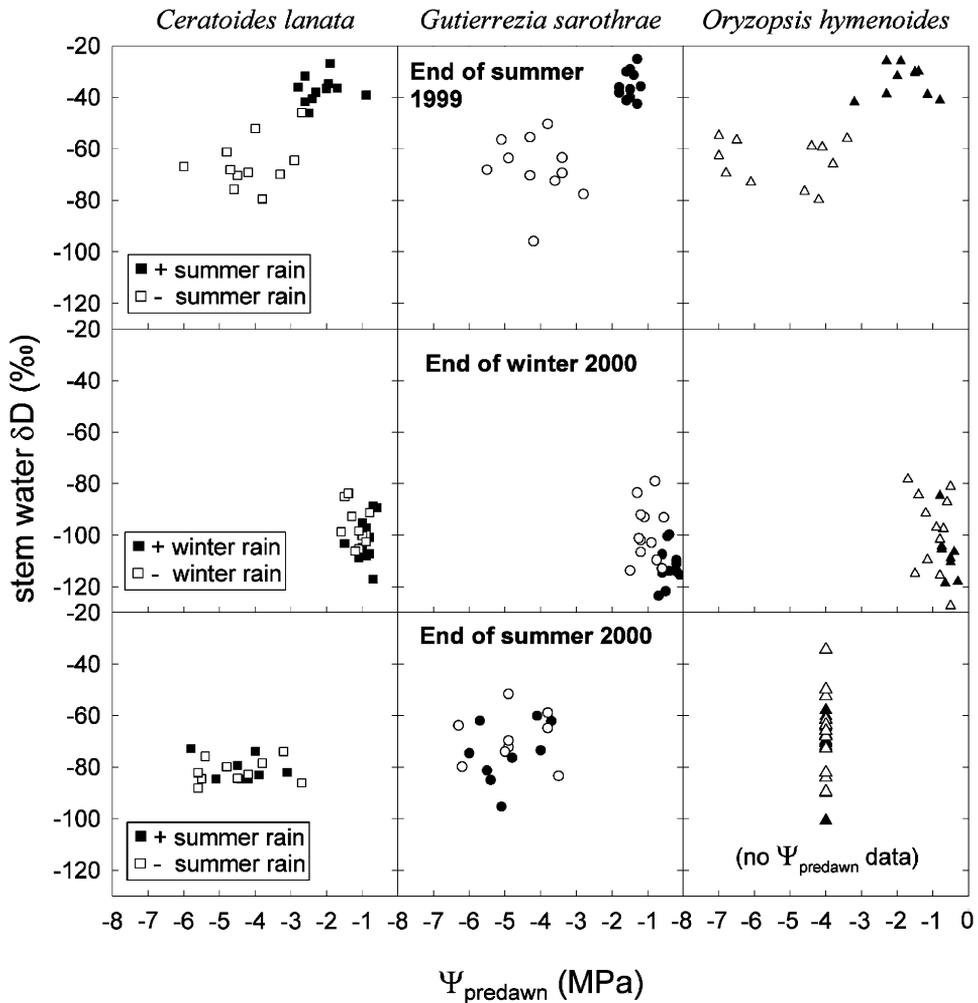


Fig. 6. Stem water δD vs. predawn water potentials (Ψ_{predawn}) on the ends of both summers and the end of the second winter.

rain (in SD and YD plots) had a stem water δD of around -65% , a close match to the δD of soil water anywhere in the profile from 0 to 60 cm, although stem water could have also originated from below 60 cm.

At the end of the second winter, there were again no differences among species in stem water δD . Across species, the δD of plants exposed to winter rain was significantly lower by about 11% compared to plants that had not been exposed, indicating a greater use of more depleted winter water. However, the stem water δD values were not quite as low as that of snowmelt measured in deeper soil layers (Fig. 3B). Thus, plants most likely used, at least in part, less depleted, more shallow

soil water from a March rainfall event. The fact that the stem water δD of shelter-covered plants was significantly different from that of plants in open plots indicates that they used a different water source, all but ruling out the possibility that shelter-covered plants had access to shallow soil water outside of the plot area.

The stem water δD of the shelter-covered plants overlapped quite well with range measured for deeper soil water in the same treatments (Fig. 3), however, at least in YD plots the water content down to 1 m depth would have been too low to produce Ψ_{predawn} values of -1 Mpa (based on a measured moisture release curve, data not shown). This suggests that plants, after one year of continuous drought, deployed new roots below 1 m soil depths, tapping into water reserves that were older than one year.

At the end of summer in 2000, drought treatments had no effects on stem water δD and again there were no significant species differences. There was noticeably more scatter in the stem water δD values of *G. sarothrae* and *O. hymenoides* compared to *C. lanata*. This scatter could indicate that plants had not conducted water in some time and that stem water reflected the δD of soil water when plants last transpired, confounded with a slow evaporative enrichment of stored stem water. This interpretation is strengthened by the extremely low water status of the two species at the time (in fact, the xylem potential of *O. hymenoides* was below the measurement limit of the Scholander pressure bomb). By contrast, there was very little scatter in the stem water δD values of *C. lanata*, indicating that this species still transported water, albeit at a very low rate, and took it from an isotopically quite uniform water source in the soil. The δD value of about -80% suggested a source below 1 m depth (Fig. 3B).

4. Discussion

4.1. Summer drought effects

We hypothesized that summer drought should primarily affect the availability of shallow soil water during summer and have the most negative effect on the most shallow-rooted species, *O. hymenoides*, and very little effect on the deepest-rooted shrub, *C. lanata*. This prediction was not supported by the data. Summer drought affected the water status of all three species similarly (Figs. 4 and 5), except that summer drought was slightly less stressful for *C. lanata* and summer rain slightly more beneficial for *O. hymenoides* (Fig. 4). In addition, we underestimated the capacity of the deepest-rooted species in this study, *C. lanata*, to shift water uptake to relatively shallow soil regions, when most soil water was concentrated there (Fig. 6).

Contrary to our initial hypothesis, summer drought decreased soil moisture not just in the shallow but also in deeper soil layers (Fig. 2b). The isotopic evidence pointed to an accelerated depletion of winter water stored below 30 cm in the soil profile (Figs. 2B and 3A). Many desert perennials, particularly those with dimorphic root systems, are capable of using soil water flexibly according to

availability (Pelaez et al., 1994; Montaña et al., 1995; Smith et al., 1995; Lin et al., 1996; BassiriRad et al., 1999). These plants compensate for reduced water availability in the shallow soil with increased uptake from deeper layers (Schwinning et al., 2002). At our field site the root-dimorphic species *G. sarothrae* was common, thus may have been primarily responsible for accelerating the depletion of deeper water under summer drought conditions. As a consequence, summer drought also affected *C. lanata*, the deepest-rooted species in our study.

Summer drought affected deeper soil moisture in another way, by reducing the infiltration depth of winter precipitation. Consequently, the summer drought of 1999 had carry-over effects on soil moisture at almost all depths throughout the summer of 2000.

4.2. Winter drought effects

We predicted that winter drought should reduce the availability of shallow and deeper soil water in spring and thereby affect the water status of all community members. This was supported by the data. In both years, winter drought had slight, but significant effects on Ψ_{predawn} (Fig. 4), with the exception of *O. hymenoides* in 1999. The moderate winter drought treatment in 1998/99 did not cause sufficient water stress to lower leaf conductance in the following spring, but did in the second year of the experiment (Fig. 4). *O. hymenoides* was markedly more sensitive to winter drought than the other two species, while *C. lanata* was least sensitive. This pattern was similar to the one observed in response to summer drought, suggesting that the grass achieved the greatest flux rates in response to recent precipitation inputs, but was also least tolerant of drought at any time of year.

Plant water status was far less impacted by lack of precipitation inputs in winter/spring than in summer. The absence of a winter drought effect on spring leaf conductance could be explained by the less arid atmospheric conditions in spring compared to summer. But this does not explain the difference in the sensitivity of Ψ_{predawn} to winter and summer drought, since Ψ_{predawn} is independent of atmospheric conditions and indicative only of soil moisture availability in the root zone. We suspect that in spring plants adjusted their patterns of root growth to match patterns of soil moisture availability, thereby buffering against variation in winter recharge.

Fernandez and Caldwell (1975) reported that cold desert shrubs shifted root growth activities downward between April and October, presumably following receding soil water reserves and Wan et al. (2002) showed that the patterns of root deployment in *G. sarothrae* adjusted to variation in the timing of irrigation. Apparently, the timing and location of root deployment in spring is highly plastic, allowing plants to optimize water status during times of rapid growth. As conditions get hotter and drier in summer they seem to lose this capacity for buffering against low water potentials (Comstock and Ehleringer, 1992; Bilbrough and Caldwell, 1997). Perhaps plants avoid the carbon investment required for growing even deeper roots, when the potential carbon returns for such a strategy are likely to be small (Schwinning and Sala, 2004).

4.3. Yearlong drought effects

As expected, yearlong drought conditions established a monotonic gradient in water availability (Fig. 2). We further hypothesized that this condition would be least detrimental to the deepest-rooted species and this was also confirmed. During the driest period of the experiment, the summer of 2000, only *C. lanata* was apparently still able to transport water. Its stem water δD of around -80‰ (Fig. 6) suggested a rather deep origin, perhaps lower than the 1 m depth that we probed in June of 2000, which had a δD of -90‰ . Assuming a linear soil moisture gradient, we estimated that water should become extractable (at a soil water potential of ~ 4 MPa) between 2.0 and 2.5 m depth, a depth unlikely to be reached by *G. sarothrae* or *O. hymenoides* roots, but quite possibly within the reach of the *C. lanata* root system.

4.4. How do plant functional types partition soil water?

Since Walter's (1971) two-layer hypotheses for the water relations and coexistence of plants in arid and semi-arid environments, researchers have set out to demonstrate that plants in water-limited regions use different water sources (e.g. Sala and Lauenroth, 1985; Sala et al., 1989; Ehleringer et al., 1991; Pelaez et al., 1994; Montaña et al., 1995; Smith et al., 1995; Weltzin and McPherson, 1997; Dodd et al., 1998; Golluscio et al., 1998; Yoder and Nowak, 1999). Results have been mixed, some supporting the hypotheses of water partitioning, while others did not unequivocally do so. Reynolds et al. (2000) suggested that water partitioning should be more common in semi-arid regions with annual rainfall > 300 mm, where deep infiltration occurs more commonly, but that below this precipitation level, "plants are drinking from the same cup", despite of differences in root distributions. The results of this study are consistent with Reynolds et al. (2000), and the most direct evidence of this was seen in the stem water δD data (Fig. 6), which did not reveal any differences in the water sources of three morphologically very different species under a wide range of soil moisture conditions. With an annual average precipitation of 215 mm, this study area on the Colorado Plateau is well under the 300 mm threshold envisioned by Reynolds et al. (2000).

Reynolds argued that, in the Chihuahua ecosystem, species are more likely to partition water in time than in space through differences in plant phenology, for example, through differences in the peak activities of evergreens and drought-deciduous shrubs (Reynolds et al., 1999). However, in a winter-cold desert such as the Colorado Plateau, the growing season is shortened by temperature constraints. With only a few exceptions (notably C_4 grasses; Schwinning et al., 2002), all species are more active in spring than in summer. This should give species much less opportunity to partition water through differences in phenology (Fernandez and Caldwell, 1975).

If plants of the Colorado Plateau do not partition soil water by depth in the soil profile, nor in time through phenological differences, is there any other way? This study suggests a third possibility of partitioning by time within a season or across years, through variation in transpiration rates. This mechanism has also been

described by McAuliffe (2003) and Chesson et al. (2004). In this study, the shallow-rooted *O. hymenoides* had the highest leaf conductance whenever soil water was most abundant, independent of season, but also was most sensitive to drought conditions. This pattern is readily explained by the shallow, dense fine root systems of grasses in general, which allow plants to extract water rapidly after recent precipitation, but are also the first to run out of extractable water, as soils dry out. Thus grasses on the Colorado Plateau may have the water uptake advantage early during a pulse event or during a rainy season (spring or summer), but the advantage is likely to turn over to deeper-rooted species during dry intervals.

With continuing drought conditions, as the plant-extractable water recedes down in the soil profile, species should disconnect from the remaining soil water, one by one, in the order of their rooting depths. In this study, only *C. lanata* was still able to transport water during the most extreme drought condition of this experiment, at the end of the second summer. Once plants are separated from soil water, unless there is new water input, death is only a matter of time, either because plant water potentials decrease until lethal levels are reached, or because plants run out of enough carbon reserves to fuel resprouting from surviving meristems.

It is difficult to fully anticipate how rare and extreme conditions contribute to the long-term stability of desert communities. Based on this study, we would predict that an increase in drought frequency, particularly the frequency of summer drought, should favor the survivorship of deep-rooted woody plants over more shallow-rooted shrubs and grasses. Unless the shallow-rooted species can compensate with an enhanced recruitment response to wet years, ecosystems such as the Colorado Plateau may shift towards greater woody cover. While Walter's model (1971) and subsequent observations (Brown et al., 1997) suggested that increases average winter precipitation could result in woody encroachment into grasslands, this study suggests that increases in precipitation variability alone, particularly in summer, could also have such effects.

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