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# Summer and winter drought in a cold desert ecosystem (Colorado Plateau) part II: effects on plant carbon assimilation and growth

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## Abstract

We investigated the effects of winter and summer drought on a shrub/grass community of the Colorado Plateau in western North America, a winter-cold, summer-hot desert that receives both winter and summer precipitation. Summer, winter and yearlong drought treatments were imposed for 2 consecutive years using rainout shelters. 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. Growth for all three species was far more sensitive to winter than to summer drought. The primary reason was that plants did not grow in summer and also did not appear to use summer-assimilated carbon to support growth in the following spring. We hypothesize that the relative scarcity and uncertainty of summer rain on the Colorado Plateau prevents most species from evolving adaptations that would improve their use of summer rain. Together with the results of the companion paper, which focused on plant water relations, we conclude that variation in fall to spring precipitation would have strong effects on primary productivity, and could cause reversible fluctuations in community composition, while increased variation in summer precipitation, through causing high rates of mortality among shallow-rooted species in dry years, has the potential to cause lasting and

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perhaps irreversible community change, especially if coinciding with the invasion of western landscapes by cheatgrass, tumble weed and other grazing tolerant exotics.

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## 1. Introduction

Desert plants are typically exposed to extreme fluctuations in soil water availability, driven chiefly by precipitation and high rates of evapo-transpiration. Desert plants are generally well adapted to such fluctuations through a variety of physiological, morphological and phenological adaptations and life history strategies. It is widely thought that this functional and morphological diversity, interacting with environmental variation, helps to maintain species diversity and governs the long-term balance of species in desert plant communities (Chesson et al., 2004).

The patterns of resource fluctuation are expected to change, however, with global warming and an intensification of the global hydrologic cycle (Dettinger et al., 1998; Groisman et al., 1999; Easterling et al., 2000). Since we do not fully understand how environmental fluctuations govern plant communities today, we are unable to anticipate how drastically altered temperature and precipitation patterns will change future communities. Sala et al. (2000) speculated that rapid climate change, interacting with land use changes and the spread of invasive species, could lead to the loss of species diversity and widespread disruption of ecosystem functions.

Studies attempting to address the potential effects of altered precipitation patterns have primarily focused on plant water relations, less so on growth and reproduction (but see Reynolds et al., 1999). While there is a well-developed theory on the interactions between soil water, plant water status and assimilation rates (e.g. Nobel, 1999), extrapolating from rates of carbon assimilation to plant growth is a much more difficult task. This link is governed by the long-term allocation strategies of plants, which are highly variable between and within species and not easily observable (Bazzaz, 1997). Yet, patterns of plant allocation hold the ultimate control over the long-term responses of communities and ecosystems to climate change (Chapin et al., 2000; Lavorel and Garnier, 2002).

In this study, we measured climate impacts on both soil and plant water relations, and on plant growth and aspects of reproduction. An extensive analysis of the water relations is described in the companion article (Schwinning et al., 2004). Here we focus on carbon assimilation and growth. In the experiment, we imposed summer, winter and yearlong drought conditions on dominant plants of a Colorado Plateau scrubland community. The three species selected for this study represented contrasting plant functional types. *Oryzopsis hymenoides* is a C<sub>3</sub> perennial grasses, *Gutierrezia sarothrae* is a relatively shallow-rooted herbaceous shrubs, and

*Ceratoides lanata* is a deep-rooted woody shrub.  $C_4$  grasses, while present at the experimental site, were not considered in this study, as previous experiments indicated that they represent a relatively minor component of the community (Schwinning et al., 2002).

The three species were much more similar in their water uptake patterns than we originally expected (Schwinning et al., 2004). For example, during an 80% wetter than average summer all three species, if exposed to summer rain, took up water from a soil layer at 0–30 cm. In the absence of water inputs, all species appeared to use the same deeper water sources for much of the time. All species had relatively minor physiological responses (predawn water potentials, leaf conductance) to the winter drought treatment, and major responses to the summer drought treatment. We attributed this to an ability to compensate for lack of winter water input by growing spring roots deeper in the soil profile where water left over from previous wet seasons was still available. Overall, the perennial grass *O. hymenoides* benefited slightly more from wet soil conditions (in terms of water status) than the two shrubs. However, the water status of the deepest-rooted shrub *C. lanata* was least negatively affected by severe drought conditions, presumably by having access to deeper soil water reserves than the other two species. Thus, there was evidence that the three species partitioned soil water through variation in availability either within a rainy season or between years. Below, we examine the consequences of winter and summer water availability for carbon assimilation and growth.

## 2. Methods

### 2.1. Site information and experimental design

The site description and details of the experimental design are given in the companion paper (Schwinning et al., 2004). Briefly, the study was conducted near Canyonlands National Park in southern Utah (N38.17548 W109.72018) on a site dominated about equally by low shrubs and perennial grasses. Besides the annual spring-active grass *Bromus tectorum*, *O. hymenoides*, *G. sarothrae* and *C. lanata* were the most common species at the site.

The experiment consisted of a complete factorial design with two factors (season and precipitation treatment) at two levels (summer or winter, and drought or ambient rainfall). Treatments were distributed over three blocks with two replicates per block. Drought conditions were imposed by 4 m × 4 m rainout shelters during the summer and winter intervals, either April–September or September–April. The shelters, made from corrugated, UV-filter coated, polycarbonate panels (Suntuff Inc., Livingston, NJ) were open on all sides. Shelter roofs reduced ambient light levels by about 13–20% and increased the soil and air temperature within 5 cm of the soil surface by 3–4 and 1–2 °C, respectively. However, air temperatures at leaf level were not significantly affected.

## 2.2. Leaf photosynthesis rates

Maximal photosynthesis rates were determined with a portable infrared gas analyser system (LiCor 6200, Licor Instruments, Lincoln, NE, USA). Rates were measured approximately between the 9:30 a.m. and 12:00 p.m. hours solar time, around the time of day when photosynthesis rates were expected to be maximal. After the measurements, leaves were collected, stored in wetted coin envelopes and kept cold until leaf area was determined with a Licor 3100 Area Meter (Licor Instruments).

## 2.3. Growth and flowering

At the beginning of the first growing season in April 1999, plants were tagged with plastic-coated wire to quantify growth through the elongation of terminal branches, or, in the case of *O. hymenoides*, through stem and leaf blade elongation. The procedures used for *G. sarothrae* and *C. lanata* were similar: On April 24, terminal shoots were tagged at the base of old stems from which new (present-year) stems originated. Therefore, the length of the tagged stems reflected mostly the length of actively growing shoots. Five such shoots were tagged per plot, in random locations throughout the plot area. In the grass, *O. hymenoides*, the bases of new shoots were tagged at ground level, with five tags per plot, randomly distributed. The lengths of tagged branches and of grass leaves were measured repeatedly, at the end of spring and the end of summer to distinguish spring growth from growth that may have been brought on by summer rain. At the beginning of the second spring in March 2000, new grass shoots were tagged, since the shoots of the previous year had senesced. We did not retag branches on the shrubs but continued to take stem length measurements on the same terminal branches that were used the year before.

The sizes of tagged shoots were quantified in a number of ways, including methods that separated old and new branches or represented stem growth relative to initial tagged stem length. In the end, the simplest measure proved most robust in statistical analysis. Vegetative growth is presented as the average change in total stem length (*C. lanata* and *G. sarothrae*) per tagged branch or total stem plus green leaf blade length per tagged tiller (*O. hymenoides*).

Flower production was quantified indirectly. For the two shrubs, we determined a “flowering branch percentage” by determining the percent of total stem length that bore flowers. Flower production in *O. hymenoides* was quantified through a visual score between 0 and 4, where 0 indicated no inflorescence, 1 a small inflorescence of about 5 cm diameter and 4 a large inflorescence with a diameter of about 20 cm.

## 2.4. Leaf C and N analysis

Leaf nitrogen correlates strongly with photosynthetic capacity (Field and Mooney, 1986). Plants are thought to balance leaf nitrogen content with actual photosynthetic rates, so that photosynthetic capacity does not far exceed actual photosynthetic rate (Farquhar et al., 2002). Thus, changes in leaf nitrogen content

indicate not only a change in photosynthetic capacity, but also a change in the leaf's overall carbon economy.

The carbon isotope discrimination value ( $\Delta$ ) of leaf carbon contains information on the water status experienced during the time of carbon assimilation (Farquhar et al., 1989). In particular, the leaf  $\Delta$ -value is positively correlated with ratio of intracellular to ambient CO<sub>2</sub> concentrations in C<sub>3</sub> species.  $\Delta$  is defined as the difference in the  $\delta^{13}\text{C}$  value of the atmospheric source of CO<sub>2</sub> (assumed to be constant at  $-8\text{‰}$ .) and a derived carbon pool (in this case, leaf carbon). The  $\delta^{13}\text{C}$  notation expresses carbon isotope ratios as

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

where  $R$  is the molar ratio of heavy and light isotopes and  $R_{\text{standard}}$  is based on Pee Dee Belemnite for carbon.

Both diffusion and CO<sub>2</sub> fixation discriminate against the heavier isotope of C, making the  $\delta^{13}\text{C}$  value of plant carbon more negative than  $-8\text{‰}$ , and the  $\Delta$ -value positive. The greater the diffusion limitation as a consequence of partial stomatal closure, the more negative the  $\delta^{13}\text{C}$  of assimilate, and the greater the  $\Delta$ -value. Even though water stress may have long ceased at the time of sampling, structural carbon in the leaf maintains this imprint of past water stress. We measured both leaf-N content and the carbon isotope composition of leaves to get a time-integrated measure of water stress impacts on the carbon economy of plants.

Leaves were collected on the same days that photosynthesis measurements were conducted. About 3–5 leaves were collected from different parts of the canopy and bulked. Samples were dried at 70 °C for 48 h and ground to a fine powder. Samples of 2 mg were combusted in a Carla Erba elemental analyser (CE Instruments, Milan, Italy) and immediately diverted to an isotope ratio mass spectrometer operating in continuous flow mode (Delta S. Finnigan MAT, San Jose, CA, USA).

## 2.5. Statistical methods

Within each of the 24 experimental plots, three species were monitored, thus the factor “species” was treated as a repeated variable in all analyses that included species comparisons, using the statistical package for Repeated Analysis of Variance by SPSS, Version 8.0 (SPSS, Inc.). Block effects were not significant, so block was discarded as a factor in all analyses. Variables were either not transformed or log-transformed to pass the Box Test. Transformed variables did not generally satisfy the sphericity assumption of repeated analysis of variance, so we 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  $0.1 > p > 0.05$  we refer to this as “marginal significance”.

Species comparisons were not performed for growth and flowering, since these measures could not be meaningfully compared. No data transformation could be identified to justify a parametric analysis of the flowering data. We therefore performed the Kruskal Wallance Test on ranked data.

### 3. Results

#### 3.1. Leaf photosynthesis

Leaf photosynthesis rates were generally at their highest point of the year in early spring, although spring photosynthesis in *C. lanata* and *G. sarothrae* were much lower in the second compared to the first spring (Fig. 1). The winter drought treatment had significant effects on the photosynthetic rates only of *O. hymenoides*, in June 1999 and April 2000, but these were small compared to the summer drought effects of 1999. Thus, what little impact the winter drought treatment had on plant water status in spring (Schwinning et al., 2004), did not generally translate into significant differences in carbon assimilation.

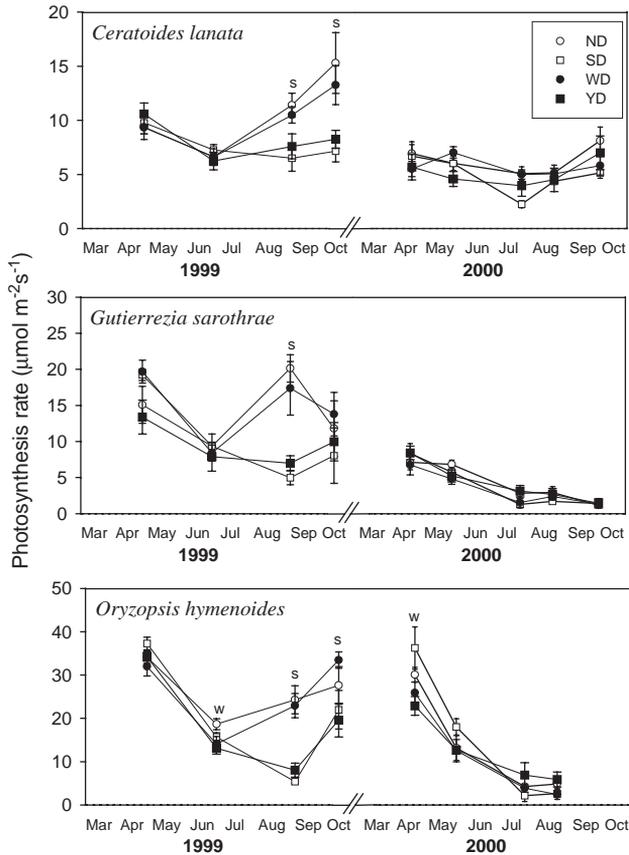


Fig. 1. Rates of photosynthesis at all measurement dates across all treatments. Error bars represent standard errors of the mean. "s" and "w" denote significant effects of summer and winter drought in a two-factor analysis of variance.

Table 1  
Differences in average temperature and humidity in the growing seasons of 1999 and 2000

	Average daily temperature (°C)		Average daily relative humidity (%)	
	1999	2000	1999	2000
March	9.7	6.5	33	55
April	9.1	15.0	45	27
May	17.0	20.6	17	24
June	23.4	24.6	26	23
July	26.4	28.4	40	21
August	23.7	27.3	49	32
September	18.9	23.1	40	27

The summer drought treatment significantly reduced photosynthesis in September 1999 in all three species. This was expected given the strong effect of the treatment on  $\Psi_{\text{predawn}}$  and leaf conductance (Schwinnig et al., 2004). Plants in open plots (ND/WD) experienced a 80% wetter than average summer with three rainfall events > 15 mm between July and September. In October, the photosynthesis rates of *C. lanata* and *O. hymenoides* in open plots were still significantly higher than in shelter-covered plots, but in *G. sarothrae* the effect of the summer drought treatment on photosynthesis had become insignificant.

Although SD and YD plots were shelter-covered from mid-April to mid-October, photosynthesis rates of *O. hymenoides* also increased between September and October in 1999. This increase was due to the growth of a second leaf cohort, which occurred across all treatments. In 2000, this second cohort did not appear and photosynthetic rates remained low. These differences in the grass leaf dynamics of 1999 and 2000 were apparently not directly related to precipitation inputs, since the presence of rainout shelters did not prevent leaf growth in late summer of 1999. Atmospheric conditions may therefore have been chiefly responsible for triggering leaf growth. There were indeed large differences in air temperature and humidity during the late summers of 1999 and 2000 (Table 1). For example, in August/September, average daily temperature was 3–4 °C higher in 2000 and relative humidity was 10–20% lower.

### 3.2. Leaf nitrogen content

Leaf-N declined between early spring and late summer in both years and independent of drought treatments (Fig. 2). Thus, despite of the exceptionally wet summer of 1999, and the strong positive responses in photosynthetic rates, plants in open plots (ND and WD) did not increase or even maintain the N-content of leaves between June and September. The one exception was *O. hymenoides* in 1999, which increased leaf-N between September and October, because of the increasing fraction of young leaves from the developing leaf cohort in the sample.

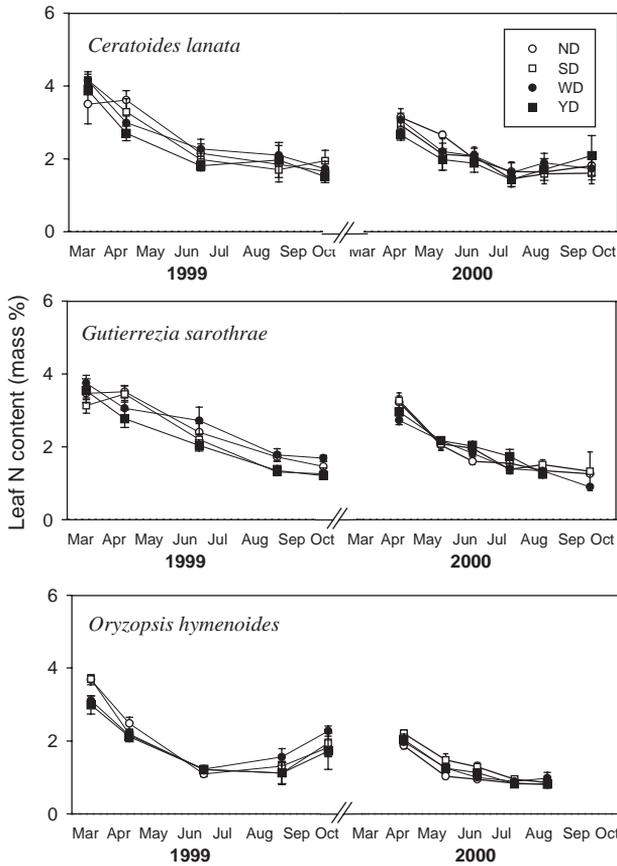


Fig. 2. Leaf N-content at all measurement dates across all treatments. Error bars represent standard errors of the mean. Summer and winter drought effects were not significant.

### 3.3. Growth and flowering

Spring growth of terminal branches measured from April to June was significantly reduced by the winter drought treatment in all three species (Fig. 3). In 1999, winter drought effects were highly significant across species, but in 2000 only *O. hymenoides* responded to the winter drought treatment. With the exception of *G. sarothrae*, spring growth was much lower in 2000 compared to 1999. In fact, growth from April to June in *C. lanata* was insignificantly different from zero. There was growth earlier in the season, however (data not shown), but this earlier growth was also not affected by the drought treatments.

Growth during summer (July–August) was not affected by any of the drought treatments (Fig. 4). In *C. lanata*, branch growth was close to or even below zero, indicating that there was no growth and that branches lost length due to senescence

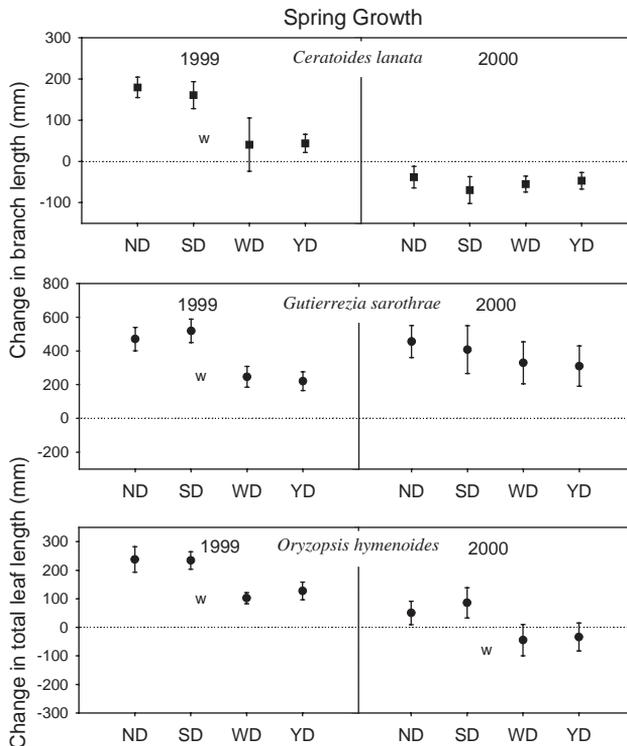


Fig. 3. Measures of spring growth from April through June. In the two shrubs (top two panels) growth was estimated through the increase in the stem length of terminal branches. In the grass (bottom panel) growth was estimated through the increase in total leaf length. Error bars represent standard errors of the mean. “w” denotes significant effects of winter drought. Summer drought effects were not significant.

and breakage. Negative growth rates in *O. hymenoides* in 1999 also indicated no growth and leaf senescence. In 2000, we were unable to report a summer growth value for *O. hymenoides*, because by the end of the interval all leaves had become senescent. There was clearly no growth, and instead complete loss of the spring leaf biomass. The slightly positive growth rate in *G. sarothrae* in 1999 was associated with branch elongation during flowering and did not indicate the growth of new vegetative branches. Thus, it is safe to conclude that none of the three species responded to summer rain, because none of the species grew during the mid-summer interval.

Flowering was significantly reduced by the winter drought treatment, but not by the summer drought treatment (Fig. 5). Winter drought significantly reduced flowering in *C. lanata* and *O. hymenoides* (in one instance, only marginally significantly) in both years. We detected no drought effects on flowering in *G. sarothrae*. In this species, almost all terminal branches set flowers during summer, apparently independent of soil moisture, or other environmental conditions.

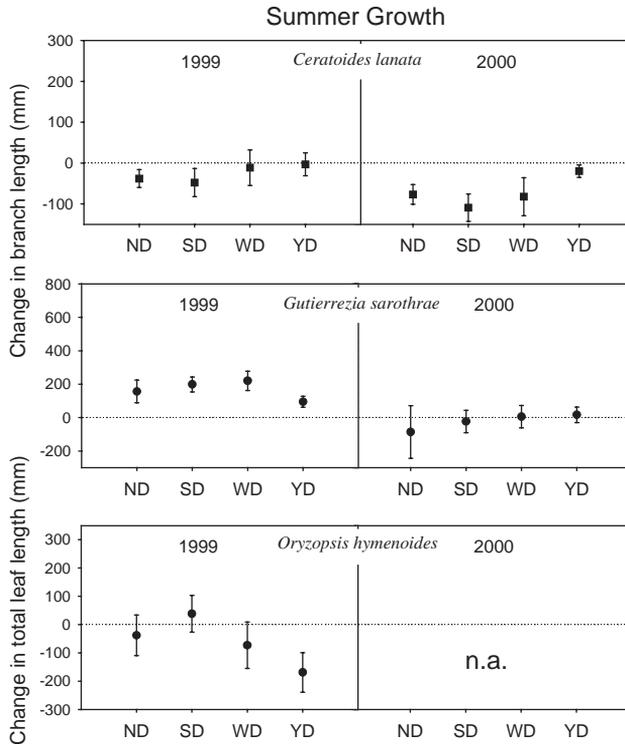


Fig. 4. Measures of summer growth from July through August. Growth was estimated as for Fig. 3. Error bars represent standard errors of the mean. Summer and winter drought effects were not significant.

### 3.4. Leaf carbon discrimination $\Delta$

The leaf  $\Delta$ -value of all three species was significantly reduced by the winter drought treatment in both years (Fig. 6), indicating that plants on plots with reduced winter recharge experienced greater water stress during the time that they assimilated carbon for leaf growth. Effects of the summer drought treatment on leaf  $\Delta$  were significant in *G. sarothrae* and *O. hymenoides* in 1999 and on one measurement date in 2000 in *O. hymenoides*.

There also were differences in the lag times between the drought treatment and its impact on leaf  $\Delta$ -values. In *C. lanata*, winter drought effects on leaf  $\Delta$  were not significant through most of the year but were becoming so by October 1999 and were highly significant on the first measurement date in 2000. In *G. sarothrae*, winter drought effects on leaf  $\Delta$  had become highly significant by mid-June 1999. By September 1999, summer drought effects had also become significant, but the effect was short-lived and did not carry over into 2000.

In *O. hymenoides*, significant treatment effects on leaf  $\Delta$  were recorded as early as April 1999. However, the effect was opposite, suggesting that the winter drought treatment had reduced stomatal limitation of photosynthesis rather than increased it.

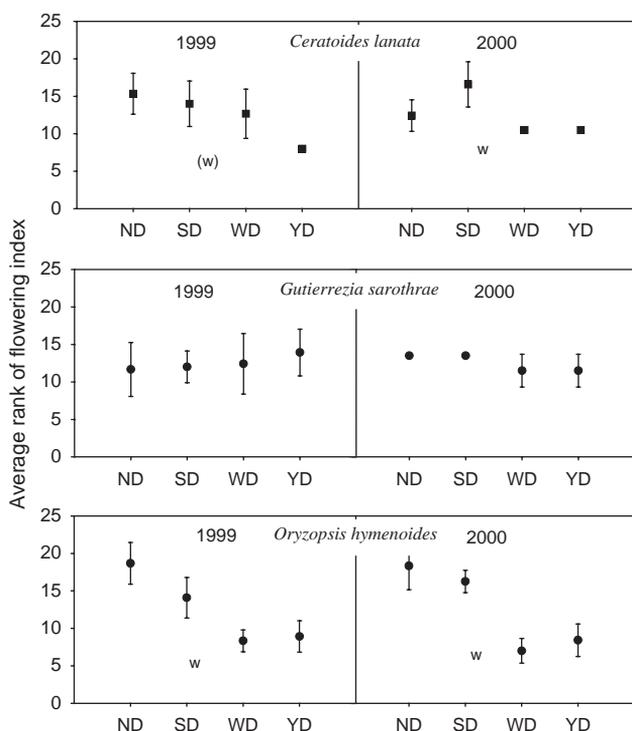


Fig. 5. Ranked flowering data. Error bars represent standard errors of the mean rank. “w” denotes significant effects of winter drought in a Kruskal-Wallis test.

Since it is unlikely that water shortage would have had this effect, temperature may have been the mediating factor (Ehleringer et al., 1992). Since the rainout shelters increased near-surface air and soil temperatures by a few °C, young grass leaves just emerging from the ground in early spring could have encountered more benign conditions for photosynthesis under shelter cover. Shrub species would not have been affected in this way, because their leaves were farther from the surface where air temperatures were not affected by the rainout shelters. By June, the treatment effect had reversed, indicating that the net effect rainout shelters on grass leaf growth was negative, as in the shrub species. The summer drought treatment significantly reduced leaf  $\Delta$  of *O. hymenoides* throughout the summer of 1999 and again in June of 2000.

#### 4. Discussion

The primary result of this experiment was that winter drought rather than summer drought significantly reduced plant growth in all the three study species (Figs. 3 and 4). Furthermore, winter drought reduced at least one component of reproductive

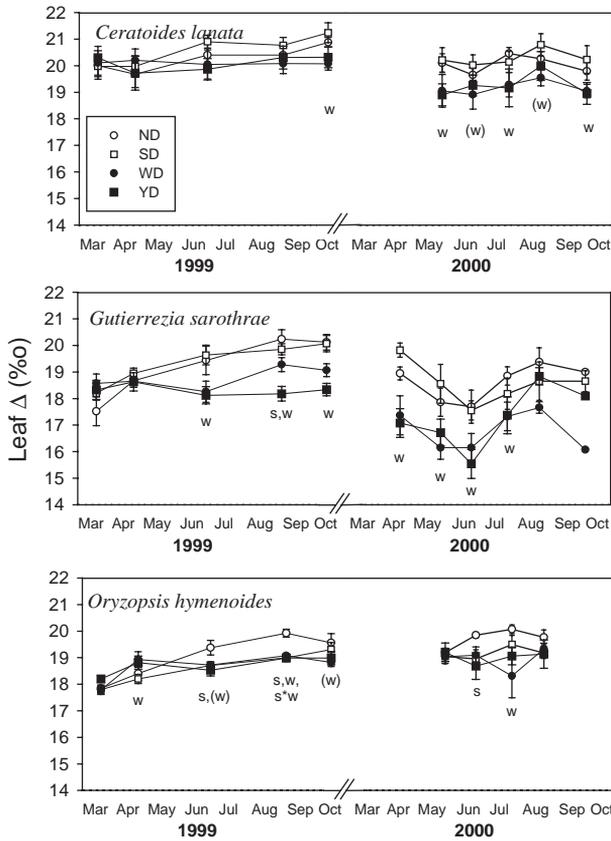


Fig. 6. Leaf  $\Delta$ -values at all measurement dates across all treatments. Error bars represent standard errors of the mean. “s” and “w” denote significant effects of summer and winter drought in a two-factor analysis of variance. Brackets denote marginal significance with  $(0.05 > p > 0.06)$ .

function (the length of flowering branches) in two species (*C. lanata* and *O. hymenoides*; Fig. 5). Both species flowered and set seed prior to the onset of the summer rainy season, so that it is unlikely that summer precipitation conditions could have affected other components of seed yield.

Failure to detect an effect of the winter drought treatment in *G. sarothrae* does not necessarily indicate that there was none, since we did not measure all components of reproductive function. Also, in this species we cannot categorically exclude that the summer drought treatment had no effect on reproduction in *G. sarothrae*, since this species flowers late (July/August), coinciding with the summer rainy season. However, in a 13-year study of the population dynamics of *G. sarothrae* on the Colorado Plateau, Ralphs and Sanders (2002) found no indication that summer precipitation influenced recruitment or population growth in any way.

It is well known that the Colorado Plateau cold desert has only one main growing season in spring (Caldwell et al., 1977; Caldwell, 1985; Comstock and Ehleringer,

1992), although, as we saw in this study, grasses can grow a second leaf cohort in late summer/early fall and the evergreen *C. lanata* may begin leaf growth as early as fall. However, it has not been fully appreciated until now how small the effect of even a large summer rainfall amount is on the growth of dominant C<sub>3</sub> species. Even shallow-rooted shrubs and grasses, which are capable of taking up large amounts of summer soil moisture, and clearly assimilate carbon at a higher rate after large rainfall events (Fig. 1), do not appear to use this added carbon for growth and reproduction to any appreciable degree. Gebauer et al. (2002), in a study assessing the degree of competition for summer rain, found that once-a-year additions of 25 mm water in summer over three years also had no positive effect on growth in the shrub species *Atriplex confertifolia* and *G. sarothrae*, although the treatment did significantly increase  $\Psi_{\text{predawn}}$  and leaf conductance. In another study, the addition of 50 mm water in summer had a small effect on the growth of the deep-rooted shrub *Coleogyne ramosissima* in summer, but primarily increased growth in the following spring (Ehleringer et al., 1999), most likely because irrigation water was carried over in the soil from summer into spring.

Some uncertainties concerning the effect of winter precipitation on growth remain, however. For example, in the two shrubs, winter drought effects were significant only in 1999, although the effect of rainout shelters on soil moisture was greater in 2000 (Schwinning et al., 2004). However, soil moisture recharge was not the only difference in the environmental conditions of the two years. In general, the warm season of 2000 was much hotter and drier than in 1999, starting as early as April (Table 1). In 1999, average air temperatures during the March/April growing season were comparatively mild at 9–10 °C, while in 2000, temperatures rose rapidly from 6.5 °C with 55% relative humidity in March to 15 °C and 27% relative humidity in April. It is possible that this sudden shift from relatively cold and moist to warm and dry conditions decreased the efficiency of soil water use by the plant community. Indeed, the photosynthesis rates of *C. lanata* and *G. sarothrae* in April of 2000 were similar to photosynthesis rates under summer drought conditions in the previous year and the photosynthesis rates also indicated no effect of the winter drought treatment (Fig. 1). Quite in contrast, April photosynthesis in *O. hymenoides* was high in winter-open plots, and significantly reduced by the winter drought treatment, as was spring growth. One plausible scenario is therefore that spring growth in the two shrubs was primarily constrained by atmospheric conditions in 2000, rather than by winter precipitation. If this interpretation is correct, it would suggest a rather more complex relationship between precipitation and primary productivity than commonly assumed.

#### 4.1. Species differences in the timing of precipitation use

One of the most intriguing results of this experiment was that species appeared to differ in the timing with which drought treatments left an imprint on the leaf  $\Delta$ -values. This could simply indicate that species began to experience water stress at different times. However, the water status data show that species responded to water stress in concert (Schwinning et al., 2004). A more likely explanation is that species

used different amounts of stored, pre-treatment carbon to construct leaves (Ehleringer et al., 1992). In the case of *C. lanata*, leaves in the spring of 1999 may have been constructed chiefly from carbon fixed in the previous fall, before shelter construction in November, since winter drought effects on leaf  $\Delta$ -values were not significant until October 1999. Similarly, the leaf  $\Delta$ -values of 2000 probably reflected the conditions for carbon assimilation in the fall of 1999.

In *G. sarothrae* and *O. hymenoides*, winter drought effects on leaf  $\Delta$  first appeared in mid-June 1999 (ignoring the possible temperature-mediated effect on *O. hymenoides* leaf  $\Delta$  in April 1999), indicating that a significant amount of leaf carbon originated from assimilation using spring precipitation.

By September 1999, the summer drought treatment had also impacted leaf  $\Delta$ -values in both *G. sarothrae* and *O. hymenoides*, suggesting that carbon assimilated in response to late spring and summer rainfall immediately exchanged with or added to leaf carbon. However, this effect of summer drought on leaf  $\Delta$ -values did not carry over into fall or the following spring, suggesting that summer-assimilated carbon did not contribute significantly to spring growth.

Thus, the two more shallow-rooted species appeared to build leaf biomass in spring primarily from carbon assimilated in exchange for winter/spring precipitation, while leaf growth in the deep-rooted shrub *C. lanata* appeared to be linked primarily to precipitation in the previous fall/winter period. All three species apparently lacked the capacity to use summer-assimilated carbon to construct new leaves in the following fall or spring, consistent with the lack of a summer drought treatment effects on growth. The fate of summer-assimilated carbon is unknown, but may have been simply lost by respiration and with the abscission of the previous year's leaf cohort.

#### 4.2. Summer rain use, life history strategies and species fitness

Williams and Ehleringer (2000) hypothesized that relative insensitivity to summer rain is expected in populations not regularly exposed to summer precipitation. Our study site on the Colorado Plateau is situated on the northern boundary of the Arizona monsoon system and experiences a low average number of significant monsoon events per year and high inter-annual variability (Bryson and Lowry, 1955; Mitchell, 1976; Ehleringer, 1994). While plants of this region have varying degrees of morphological and physiological competence to take up summer rainwater and increase rates of photosynthesis, their overall life history strategies appears rather mal-adapted to translate summer-assimilated carbon into significant fitness gains. By contrast, many plant species from regions with higher monsoonal activity can grow a second leaf cohort in summer, given a rain trigger (Comstock and Ehleringer, 1986), and set seed for a second time (Chew and Chew, 1965). Plants in this study were comparatively rigid phenologically: shrub canopies did not grow in response to the unusually large summer rain events in 1999, nor did they halt the seasonal decline of leaf nitrogen content (Fig. 2). Schwinning and Sala (2004) hypothesized that active responses to pulses of summer moisture, including, e.g., the growth of new leaves, requires an initial carbon layout cost that may not pay off on average in  $C_3$  plants in

regions where summer precipitation is relatively rare and uncertain, and would therefore result in long-term fitness losses rather than gains. Under these circumstances, natural selection would prevent the rise of phenotypically more plastic genotypes.

The absence of an effect of summer rain on growth does not imply however, that summer precipitation does not affect species' fitness. The companion paper (Schwinning et al., 2004) indicates that summer drought could have strong effects on adult survivorship. Furthermore, summer drought probably affects adult mortality in a species-specific manner, with the most shallow-rooted species running out of soil water first, and the most deep-rooted species having no difficulty surviving a 2-year drought, as simulated in this study.

#### 4.3. Potential effects of changing seasonal precipitation patterns on the Colorado Plateau

This and other studies illustrate that both summer and winter precipitation influence vegetation processes on the Colorado Plateau, although through very different kinds of mechanisms. Fall to spring precipitation is clearly the primary driver of primary productivity and without exception, Colorado Plateau plant species share this resource. One would expect that species partition cold season precipitation in some way. Unfortunately, very little is known about the partitioning rules, as most studies focused on the partitioning of winter- versus summer-derived water (e.g. Ehleringer et al., 1991; Flanagan et al., 1992; Donovan and Ehleringer, 1994; Lin et al., 1996).

In the companion paper, we argued that species of the Colorado Plateau are likely to partition water by time within a rainy season or between years. This suggests that within season variation in precipitation (and temperature) patterns or between-year variation in precipitation amount can influence the relative competitiveness of species in a given year. For example, a wet fall followed by a dry spring would presumably favour *C. lanata* at the expense of *G. sarothrae*, while the converse pattern may favour *G. sarothrae* more than *C. lanata*. This kind of variability would affect community composition through shifting the competitive balances of its species. Reversible shifts in community composition have probably occurred many times on the Colorado Plateau since the establishment of current climate patterns ca. 10,000 years ago (Betancourt et al., 1990, Cole et al., 1997). Our findings suggest that the native plant species are relatively well adapted to deal with varying levels and patterns of winter precipitation by adjusting spring root growth and the location of root deployment.

The effect of summer precipitation on the plant community is apparently quite different. Changing the competitive interactions between species does not appear to be the main issue (Gebauer et al., 2002). However, an extremely hot and dry summer can take shallow-rooted grasses and herbaceous shrubs to the limit of their stress tolerance. While community change via changes in competitive interactions is slow, and probably fully reversible, change due to the die-off of certain community members is rapid with potentially long recovery times that depend on recruitment

rates. An increase in mortality, e.g. through an increase of summer drought frequency, would also make the community more vulnerable to invasions. On the Colorado Plateau, the winter annual cheatgrass (*B. tectorum*) is of particular concern, as a cheatgrass invasion often prevents the return of the community to its previous state, as biogeochemical interactions are profoundly altered on invaded sites (Evans et al., 2001; Booth et al., 2003). Accelerated cycling between extremely dry and extremely wet summers could also provide ideal conditions for the invasion and explosive proliferation of annuals that germinate in winter/spring and use summer precipitation to enhance reproductive output. *Salsola hymenoclea* is such a species, already known as a particularly aggressive invader into disturbed ecosystems on the Colorado Plateau and elsewhere.

Winter and summer precipitation on the Colorado Plateau are associated with two distinct weather systems, which are both potentially affected by an amplification of the El Niño/Southern Oscillation phenomenon through global warming (Higgins et al., 1998; Harshburger et al., 2002). Changes in the average and/or the variability of winter precipitation should have strong but largely foreseeable effects on the primary productivity and community composition of Colorado Plateau vegetation. By contrast, changes in summer precipitation, particularly if associated with an increase in the frequency of summer droughts, could generate far more uncertainties and irreversible ecological changes.

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