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Testing the apparent resistance of three dominant plants to chronic drought on the Colorado Plateau

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Summary

1. Many drylands, including the south-western United States, are projected to become more water-limited as these regions become warmer and drier with climate change. Such chronic drought may push individual species or plant functional types beyond key thresholds leading to reduced growth or even mortality. Indeed, recent observational and experimental evidence from the Colorado Plateau suggests that C_3 grasses are the most vulnerable to chronic drought, while C_4 grasses and C_3 shrubs appear to have greater resistance.

2. The effects of chronic, or press-drought are predicted to begin at the physiological level and translate up to higher hierarchical levels. To date, the drought resistance of C_4 grasses and C_3 shrubs in this region has been only evaluated at the community level and thus we lack information on whether there are sensitivities to drought at lower hierarchical levels. In this study, we tested the apparent drought resistance of three dominant species (*Pleuraphis jamesii*, a C_4 rhizomatous grass; *Coleogyne ramosissima*, a C_3 drought-deciduous shrub; and *Ephedra viridis*, a C_3 evergreen shrub) to an ongoing experimental press-drought (-35% precipitation) by comparing individual-level responses (ecophysiology and growth dynamics) to community-level responses (plant cover).

3. For all three species, we observed consistent responses across all hierarchical levels: *P. jamesii* was sensitive to drought across all measured variables, while the shrubs *C. ramosissima* and *E. viridis* had little to no responses to the experimental press-drought at any given level.

4. *Synthesis.* Our findings suggest that the apparent drought resistance at higher hierarchical levels, such as cover, may serve as good proxies for lower-level responses. Furthermore, it appears the shrubs are avoiding drought, possibly by utilizing moisture at deeper soil layers, while the grasses are limited to shallower layers and must endure the drought conditions. Give this differential sensitivity to drought, a future with less precipitation and higher temperatures may increase the dominance of shrubs on the Colorado Plateau, as grasses succumb to chronic water stress.

Key-words: cold desert, dryland, ecophysiology, Hierarchical Response Framework, normalized difference vegetation index, photosynthesis, plant functional types, press, soil moisture dynamics

Introduction

Drylands are characterized by low annual rainfall, warm temperatures and high interannual variability in precipitation (Noy-Meir 1973; Davidowitz 2002; Millennium Ecosystem Assessment 2005; Knapp *et al.* 2015). Plants survive in these harsh, water-limited ecosystems through a range of ecophysiological, morphological and phenological adaptations (Ward 2009). Global climate models predict many drylands will experience even greater water stress as these regions become warmer and drier (IPCC 2013), including the south-western United States (Cook, Ault & Smerdon 2015). Given that dryland plant community productivity and composition is primarily limited by water availability (Noy-Meir 1973), chronic changes in aridity may have large impacts on ecosystem structure and function, particularly if dominant plants and/or plant functional types (PFTs) are differentially impacted.

The Hierarchical Response Framework (HRF; Smith, Knapp & Collins 2009) describes how distinct ecological processes, from the individual level to the ecosystem level, may change through time in response to chronic changes in resources (i.e. presses). A press may be an increase in a resource, such as nitrogen deposition, or a decrease in resource, such as soil moisture. Our focus here is on the latter type of press, more specifically a press-drought, driven by chronic reductions in rainfall and/or higher temperatures (Hoover, Duniway & Belnap 2015). The HRF explains that the initial responses to such a press condition are at the individual physiological level, causing stress (e.g. water stress) that leads to reduced growth, productivity and/or reproductive output. Therefore, the initial

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responses to a press may be subtle, which contrasts with the rapid and potentially dramatic ecological responses from an extreme climatic event (Smith 2011). However, as the press continues, the HRF predicts that the thresholds of individual species or plant functional types may be exceeded, leading to mortality and reordering of species in the community and eventual immigration of new species (Smith, Knapp & Collins 2009). Such shifts in community composition may result in large changes in ecosystem function.

Over the past few decades, the Colorado Plateau has experienced increased aridity due to warming temperatures and high interannual variability in precipitation (Hereford, Webb & Graham 2002; Munson *et al.* 2011). During this climate press, there has been a decrease in the canopy cover of C_3 perennial grasses, an increase in both C_3 and C_4 shrubs, and no change in the cover of C_4 perennial grasses (Munson *et al.* 2011). These observations mirror the results of an ongoing press-drought experiment (35% precipitation reduction), which spans a large geographic area of the Colorado Plateau (Hoover, Duniway & Belnap 2015). After 4 years of press-drought, there were clear differential sensitivities to drought among the dominant PFTs: C_3 grasses had high mortality and canopy cover changes with drought, C_4 grasses and shrubs had reduced cover but no mortality, and C_3 shrubs had no cover changes or mortality (Hoover, Duniway & Belnap 2015). Thus, there is strong experimental and observational evidence that the C_3 grasses are living at or near their thresholds in this region, given that moderate changes in climate can lead to such rapid and dramatic loss of this important PFT.

What is less certain and perhaps more intriguing is the apparent resistance to drought of the other PFTs, particularly the C_4 grasses and C_3 shrubs. The HRF predicts that individual-level responses will translate up to higher hierarchical levels. To date, only community-level responses have been examined, using long-term observations and experimental approaches (Munson *et al.* 2011; Hoover, Duniway & Belnap 2015); thus, it is not certain whether the observed lack of major responses are due to high resistance to drought or that these individual-level responses have not yet translated to detectable community-level responses. Here, we examined individual-level ecophysiology and seasonal growth patterns of three dominant species representing different taxonomic groups: *Ephedra viridis*, an evergreen C_3 shrub (Gnetales); *Coleogyne ramosissima*, a drought-deciduous C_3 shrub (dicot); and *Pleuraphis jamesii*, a perennial, rhizomatous C_4 grass (monocot). These species differ in many plant functional traits (e.g. physiology, anatomy and life history), which may affect their drought resistance and lead to divergent responses.

We first examined key environmental drivers – precipitation inputs and soil moisture – to examine how the precipitation treatments were affecting soil moisture dynamics. On the Colorado Plateau, grasses derive about 85% of their moisture from the near-surface soil depths, while shrubs obtain only approximately 54% of their water from these depths (Ehleringer 2001). Soil water in these shallow depths is fairly dynamic, with wetting and drying occurring in response to precipitation events, 71% of which are <5 mm (Bowling, Grote & Belnap 2011). In contrast, larger events are rare and thus wetting of soils at deeper depths is far less frequent and, when it does occur, dry down is slow and prolonged (Schwinning & Ehleringer 2001; Duniway, Herrick & Curtis Monger 2010; Bowling, Grote & Belnap 2011). Therefore, to examine the effect of drought on grasses and shrubs, it is important to consider how drought differentially impacts soil moisture at different depths in the soil profile (Schwinning, Starr & Ehleringer 2005). We hypothesized that the drought treatment would have greater impacts on near-surface soil moisture than deeper soil moisture as seen in a similar rainfall manipulation study by Schwinning, Starr & Ehleringer (2005).

Next, we examined the ecophysiological responses of select plant species to drought, which should be one of the most sensitive and important individual-level biological processes to water limitations. Photosynthesis is one of the primary functions for plant growth and water stress can lead to stomatal closure which will limit photosynthesis and carbon uptake. Therefore, during the spring of 2014, we examined leaf water potential and net photosynthesis for signs of an ecophysiological response to the drought treatments. If the press-drought caused plant water stress, we expected both lower leaf water potential and photosynthetic rates in the drought plots relative to the control plots.

Given that ecophysiological measurements were conducted intermittently (monthly), a lack of treatment effects could be attributed to the timing of the measurements, and thus continuous or time-integrated measurements may reveal drought sensitivities in the absence of significant ecophysiological differences. Therefore, in addition to photosynthesis and leaf water potential, we measured carbon isotope ratios ($\delta^{13}C$) and normalized difference vegetation index (NDVI) at the individual plant level. The $\delta^{13}C$ measure provides an integrated measurement of the intrinsic water use efficiency (WUE) of a plant during the time when the carbon in the tissues of a given leaf was assimilated (Farquhar, O'Leary & Berry 1982; Farquhar 1983). If the drought treatments were causing water stress, we expected to see lower $\delta^{13}C$ values under the drought treatment. In addition, we measured differences in plant greenness across the growing season using individual plant-level NDVI measurements, which are correlated with longer-term changes in leaf area index, photosynthesis and biomass (Prince, Goward & Dye 1991; Gamon, Field & Goulden 1995; Paruelo *et al.* 1997). We hypothesized that drought sensitivities would manifest in two ways in the greenness data: first, seasonal greenness (i.e. growing season length and time-integrated greenness) would be reduced particularly in response to wet periods and second, growing season length would be shorter.

Materials and methods

STUDY SITE AND EXPERIMENTAL DESIGN

This study took place on the Colorado Plateau, a physiographic province spanning a 210 000 km^2 region of Utah, Arizona, New Mexico and Colorado (see inset Fig. 1; Hereford, Webb & Graham 2002). The climate in the region is characterized as a cold semi-arid dryland

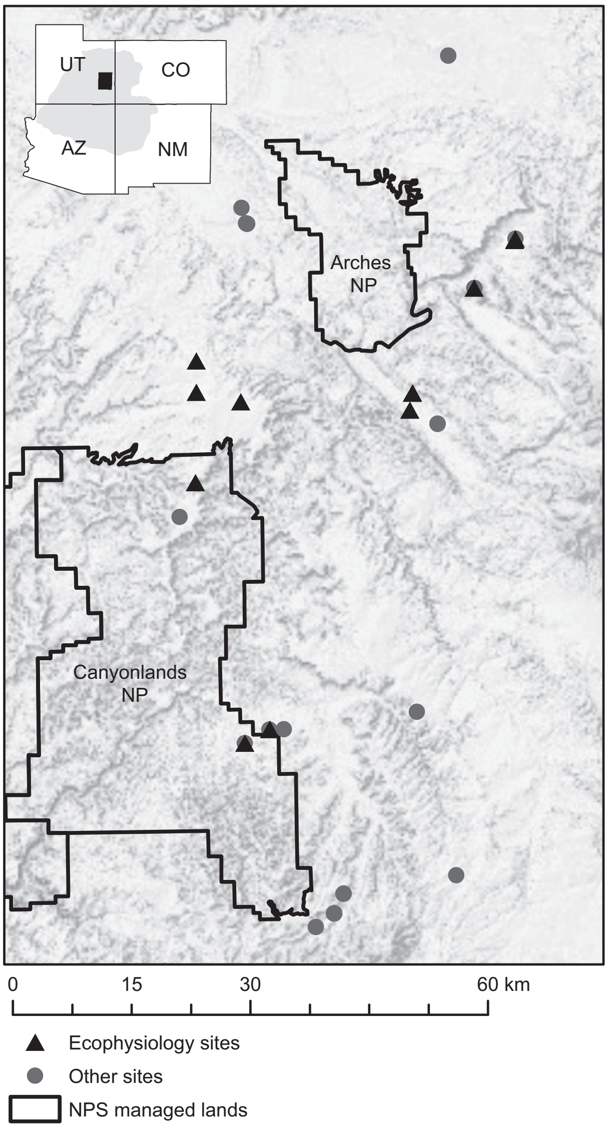

Fig. 1. Map of study sites. Within the Colorado Plateau (grey area on inset map), 40 study sites were selected to represent a wide range of plant communities common to this region. Each site consisted of paired plots receiving either control (ambient precipitation) or drought (35% reduction) treatments. For this study, ecophysiological measurements were conducted at a subset of the sites (12) where the three target species were present (*n* = 5 sites/species).

with bimodal precipitation; cool season moisture is derived from frontal systems originating in the eastern Pacific Ocean, while warm season moisture is derived from convective storms associated with the Mexican monsoon (Hereford, Webb & Graham 2002). The maximum recharge for both deep and shallow soil moisture generally occurs during the cool season due to cool temperatures, consistent precipitation (as rain and snow) and low potential evapotranspiration. As a result, peak biomass typically occurs in mid- to late spring in response to high soil water availability and warming temperatures. However, heavy monsoon years can trigger a second ‘greening up’ period during the summer for certain species, especially grasses.

Our drought experiment consisted of forty sites established in 2010 across a 4500 km^2 region of the Colorado Plateau in south-eastern Utah, spanning a range of plant community types common to the region (Fig. 1). Each site consisted of two 150 × 200 cm plots, which were randomly assigned to either control (ambient precipitation) or drought (35% precipitation reduction) treatments. Precipitation was reduced year-round in the drought treatments from 2011 to 2014 using 230 × 310 cm wide shelters with slanted roofs (~1 m tall) composed of V-shaped plexiglass strips that intercepted 35% of precipitation and removed it from the plot using a series of gutters. Plots were hydrologically isolated using vinyl flashing (buried to a depth of 30 cm) around the plot.

Each of the forty sites was established over one or two target species (14 species total) consisting of four PFTs (C_3 grasses, C_4 grasses, C_3 shrubs and C_4 shrubs; see Hoover, Duniway & Belnap 2015 for more details). In this study, we used a subset of sites in this drought network that were located on sandy soils (12 sites total), and focused on three dominant species (*n* = 5 sites per species): an evergreen C_3 shrub (*Ephedra viridis*), a C_3 drought-deciduous shrub (*Coleogyne ramosissima*) and a perennial C_4 rhizomatous grass (*Pleuraphis jamesii*),

ENVIRONMENTAL DATA

Precipitation data were obtained from the Global Historical Climatology Network (1900–2014; http://www.ncdc.noaa.gov/oa/climate/ghcn-daily/) using a station centrally located within our rainfall shelter network (Station USC00425733). During ecophysiology campaigns, meteorological conditions (precipitation, temperature, relative humidity, and wind speed) were measured hourly at a centrally located study site. Soil moisture was measured using 30 cm water content reflectometer probes (CS650, Campbell Scientific, Logan UT, USA) inserted horizontally at three depths: shallow (10 cm), intermediate (20 cm) and deep (40 cm, unless bedrock was encountered in which the deep probes were placed between 20 and 40 cm; *n* = 3–5 per treatment/depth). Soil apparent permittivity was calculated based on equations provided by manufacturer and converted to soil volumetric water content using the Topp, Davis & Annan (1980) equation. Volumetric water content was recorded at 30-min intervals, which were averaged to obtain the daily values used for analysis.

BIOTIC DATA

Each year, plants, litter and ground cover were visually estimated in each plot using four 75 × 100 cm frames. For each vascular plant species, canopy cover was recorded only for parts of the plants that were alive and green (e.g. dead branches and senesced leaves were excluded; see Hoover, Duniway & Belnap 2015 for more information).

Ecophysiology (net photosynthesis and leaf water potential) was measured on the three target species before, during and after the peak of the spring growing season (April–June) in 2014. Sampling ecophysiology across such a vast network of sites was challenging, as each sampling campaign required almost 600 km of driving. Measurements were collected midday (between 1000–1500 MDT), so multiple days were needed to measure all sites. We sampled during days that had no precipitation and minimal variability in meteorological conditions (temperature, humidity, photosynthetically active radiation and wind; see Table 1). Within each plot, two morphologically similar individuals were measured for both net photosynthesis (A_{net}) and leaf water potential (ψ_{mid}), with a total of twenty individuals per species per sample campaign. A_{net} and ψ_{mid} were collected on adjacent leaves or branches with southern exposure (to ensure full sunlight) that were representative of the whole plant status (e.g. we did not pick an unhealthy leaf on a healthy plant or vice versa). Given the unique plant structure of each species, we standardized the measurement location for placing the gas exchange cuvette or making the cut for ψ_{mid}: between the fourth and fifth node on branches of *E. viridis*; 15 cm from the tip of a straight

Table 1. Meteorological conditions during ecophysiology sampling campaigns

Campaign	April			May			June		
Date	4/18	4/20	4/21	5/27	5/28	5/30	6/30	7/1	7/2
Temperature (°C)	22.7	22.3	23.7	28.4	31.0	28.4	35.2	31.9	33.9
RH (%)	20.5	32.3	26.7	30.4	20.6	24.7	10.3	8.7	8.5
PAR (μmol m^{-2} s^{-1})	1247	1566	1581	1787	1580	1781	1805	1809	1786
Rain (mm)	0	0	0	0	0	0	0	0	0
Wind (m s^{-1})	1.82	1.31	1.41	1.42	1.96	1.72	2.48	2.67	1.46

Hourly temperature, relative humidity (RH), photosynthetically active radiation (PAR), rain and wind were measured at a weather station centrally located in our rainfall shelter network. Because of the distance among sites, monthly sampling campaigns were taken over 3 days. Here we show the averages of key weather parameters during sampling time (1000–1500 CD) during those days for each of the three sampling campaigns.

branch of *C. ramosissima*; and on the middle of the leaf of the youngest yet fully emerged leaf of *P. jamesii*. A_{net} was measured at 5-s intervals for 2–6 min (depending on stability) using a LI-6400 (LiCOR, Inc., Lincoln, NE, USA) with the following settings: light intensity was maintained at 2000 μmol m^{-2} s^{-1}, CO_2 concentration was at 400 μmol mol^{-1}, and relative humidity was at ambient levels. Leaf area was manually entered prior to measurement for *E. viridis* (based on stem diameter) and *P. jamesii* (based on leaf width), while *C. ramosissima* leaves were collected after measurements, scanned and measured area using an image processing program (IMAGEJ 1.48v, National Institutes of Health, Bethesda, MD, USA) and recalculated on the LI-6400 machine. A_{net} was calculated for each leaf by using an objective selection algorithm to choose a 1-min period where variability and slope were minimized (MATLAB R2015a, The MathWorks, Inc., Natick, MA, USA). ψ_{mid} was measured on a single branch (shrubs) or leaf (grass) per individual using a Scholander-type pressure chamber (PMS Instruments, Inc., Corvallis, OR, USA).

During the last ecophysiology campaign (June), we collected two leaves/branches per individual for $\delta^{13}C$ analysis. Plants were dried at 60 °C for 24 h and then shipped to Cornell University for analysis. At the laboratory, plants were ground and analysed on a Thermo Delta V isotope ratio mass spectrometer interfaced to a NC2500 elemental analyser (CE Instruments Ltd., Hindley Green, Wigan, UK). Leaf carbon isotopes were measured against a primary reference scale Vienna Pee Dee Belemnite. The error across samples was 0.38‰, and the overall standard deviation for internal BCBG standard (plant material) was 0.04‰.

We measured the normalized difference vegetation index (NDVI) at the individual plant level from March through November using spectral reflectance sensors (Decagon Devices Inc. Pullman, WA, USA) and used these measurements to estimate greenness. The sensors were two-band radiometers, measuring the 650- and 810-nm central wavelengths with 10 nm full width and half maximum band width. Two sensor types were used. Up-facing radiometers were placed at 1.5 m above ground in a clear area (one per site) and measured the incoming radiation (SRS-Ni, hemispherical with 180° field of view). Down-facing radiometers were placed above individual target plants ($n = 2$ per plot) and measured the reflected radiation off the canopy (SRS-Nr, field stop with 36° field of view). The down-facing radiometers were set at species-specific field of views (*E. viridis* and *C. ramosissima* = 14.8 cm and *P. jamesii* = 12.0 cm). Sensors were placed above the most densely vegetated section of the plant, which was typically near the centre. Ecophysiology measurements were taken just outside this area. We were concerned that the shelters would create an experimental artefact for the NDVI sensors due to shading from the infrastructure. To address this, we took measurements every 10 min between 1030 and 1430 MDT for each sensor. As the field of view for the NDVI measurements was smaller than the gaps between the slats (~17.5 cm), we selected the maximum NDVI measurement for each sensor during a given day to avoid the effects of shelter artefacts and clouds. Greenness was calculated using the following equation based on Royo & Villegas (2011):

$$\text{Greenness (NDVI)} = \frac{\rho\text{NIR} - \rho\text{red}}{\rho\text{NIR} + \rho\text{red}} \qquad \text{eqn 1}$$

where ρNIR is the percentage reflectance of the near infrared (the ratio of the reflected NIR from the vegetation to the incident NIR) and ρred is percentage reflectance of the red (the ratio of reflected red of the vegetation to the incident red). Daily greenness data were smoothed across the whole time period using local regression (PROC LOESS, span = 0.1; SAS v9.3, SAS Institute, Raleigh, NC, USA), which is a nonparametric method that estimates local regression surfaces (Cleveland & Loader 1996). We calculated three phenological metrics based on Ma *et al.* (2013): the start, end and length of the growing season. The start of the growing season was defined as the minimum greenness value at the start of the growing season plus 10% of the seasonal maximum. The end of the growing season was when greenness reached the same value defining the start of the growing season following the seasonal maximum. Finally, the growing season length was defined as the difference in days between the start and the end of the growing season. Time-integrated greenness was the sum of greenness over a selected period of time.

STATISTICAL ANALYSES

Soil moisture data were analysed by the period preceding each ecophysiological measurement (~3 weeks). For each probe, mean volumetric water content was calculated for a given period, and then data were analysed using a mixed-model analysis of variance (PROC MIXED, SAS 9.3) with treatment and depth as a fixed factor and site as the random effect. Canopy cover and ecophysiology were analysed using a repeated-measures mixed-model analysis of variance (PROC MIXED, SAS 9.3) with treatment as fixed factors, date as repeated measures and site as the random effect. Growing season length, greenness and $\delta^{13}C$ were analysed using a mixed-model analysis of variance (PROC MIXED, SAS 9.3) with treatment as a fixed factor and site as the random effect. For all analyses, any non-normal data were transformed prior to analyses.

Results

PRECIPITATION AND SOIL MOISTURE

The monthly precipitation was quite variable during the spring of 2014 (April–June) relative to historical records:

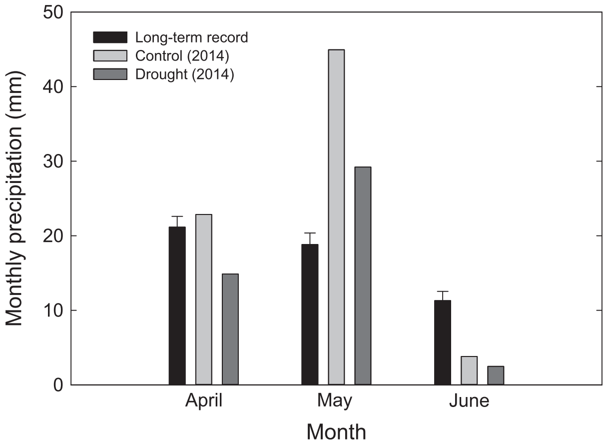

Fig. 2. Monthly precipitation. Monthly long-term record (1900–2014) from a weather station centrally located within the rainfall shelter network, versus the 2014 precipitation amounts received in control and drought treatments (error bars for the long-term record are 1 ± SE).

April was normal, May was wet, and June was dry (Fig. 2). Over the course of the 2014 spring period, control plots received 71.6 mm, which is wetter than the historical average for this period (51.3 mm), while the drought treatments resulted in conditions that were slightly drier than normal (46.6 mm). Although we observed treatment effects on soil moisture, treatment effects did not vary with soil depth (no treatment x depth interaction). During April and May, soil moisture was significantly lower in the drought plots relative to the controls, but in June there were no treatment differences (Fig. 3).

CANOPY COVER

Canopy cover was evaluated across all 4 years since treatments were imposed (2011–2014). Differential responses to drought were apparent among the three species investigated. *P. jamesii* was the only species to exhibit significantly reduced cover due to the treatments (Table 2). All species had significant ($P < 0.05$) or marginally significant ($P < 0.10$) effects of year, but there were no treatment-by-year interaction effects (Table 2).

ECOPHYSIOLOGY

During the three measurement periods in the spring of 2014, we observed no treatment effects for A_{net} and ψ_{mid} for *E. viridis* or *C. ramosissima* (Fig. 4). However, there were strong effects of month sampled on ψ_{mid} for both species ($P < 0.001$), with June being significantly lower than the other two months. For A_{net}, month had a significant effect on *C. ramosissima* ($P < 0.001$), but not for *E. viridis* ($P = 0.865$). *P. jamesii*, on the other hand, had strong treatment effects for both A_{net} and ψ_{mid}, with significant reductions in both ecophysiological measurements during all 3 months (Fig. 4).

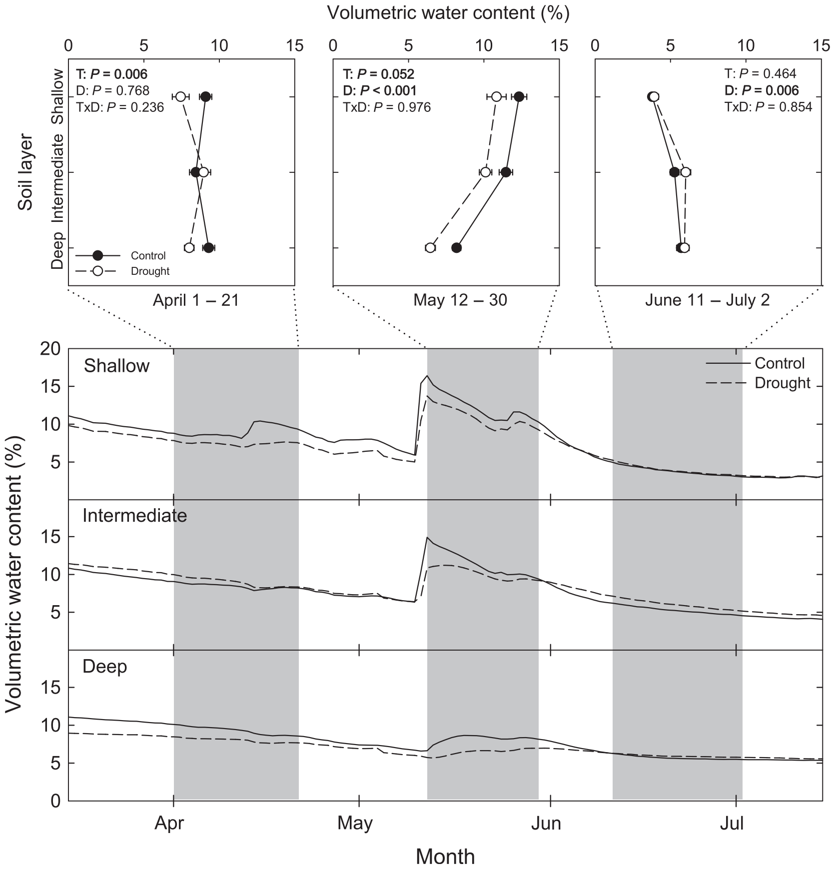

Fig. 3. Soil moisture. (Bottom) Mean volumetric water content at shallow (10 cm), intermediate (20 cm) and deep (~40 cm) soil layers for control and drought treatments during the spring and early summer of 2014 (*n* = 3–5 per treatment). Shaded area indicates the approximate 3-week period preceding ecophysiological measurements. (Top) These 3-week period were analysed to examine the effect of drought treatment (T), depth (D) and their interaction (TxD). For each period, the *P*-values from mixed model are shown with bold indicating significant points ($P \leq 0.05$). Points represent means ± 1 SE.

Table 2. Repeated-measures mixed-model ANOVA of plant cover

Effect	*Pleuraphis jamesii*			*Coleogyne ramosissima*			*Ephedra viridis*		
	d.f.	*F*	*P*-value	d.f.	*F*	*P*-value	d.f.	*F*	*P*-value
Treatment	1, 84	6.7	**0.011**	1, 42	0.7	0.401	1, 35	0.8	0.387
Year	3, 84	30.6	**<0.001**	3, 42	2.6	0.065	3, 35	4.4	**0.010**
Treatment × Year	3, 84	0.1	0.979	3, 42	0.5	0.692	3, 35	0.4	0.784

Responses of three dominant species during the press-drought treatment years (2011–2014). The data were log-transformed prior to analysis. Bold values indicate significant effects (*P*-value < 0.05).

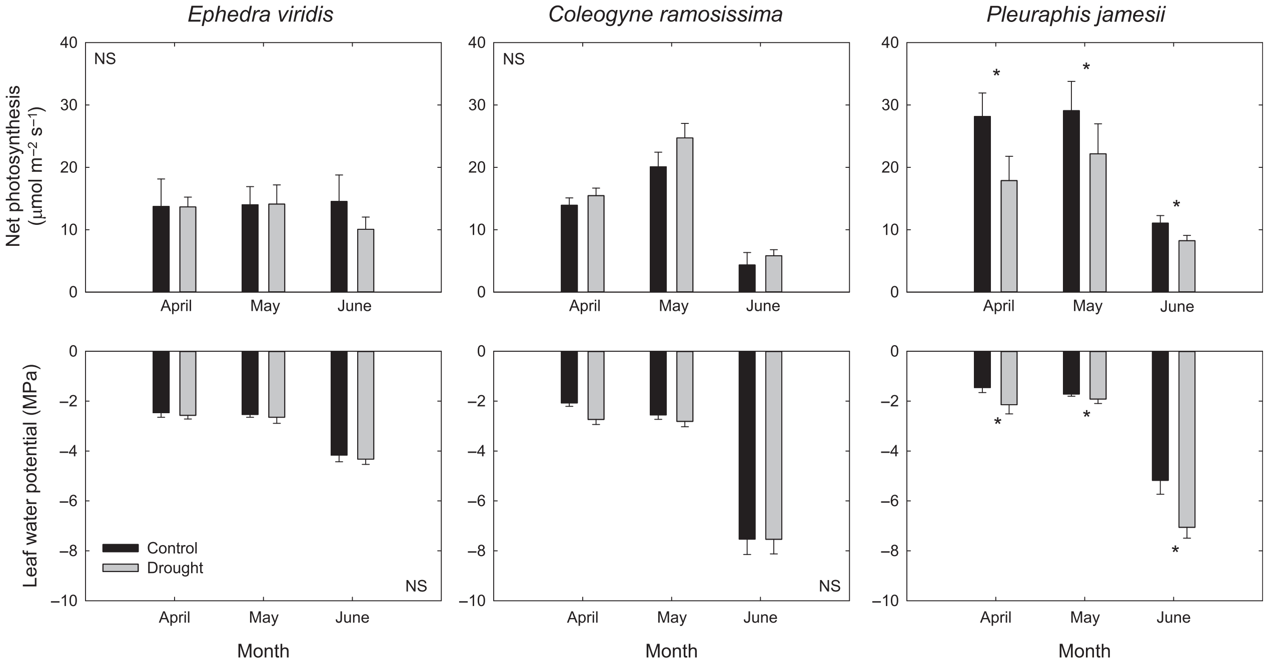

Fig. 4. Ecophysiological responses. Responses of net photosynthesis (A_{net}) and midday leaf water potential (ψ_{mid}) to the precipitation treatments during the spring of 2014. Measurements dates correspond to Table 2. Bars represent means (n = 5), asterisks indicate significant treatment differences (P < 0.05), and n.s. indicates non-significant differences.

CARBON ISOTOPES

Much like the ecophysiology, there were no significant treatment effects in δ^{13}C for either *E. viridis* (P = 0.536; Fig. 5) or *C. ramosissima* (P = 0.630; Fig. 5). In contrast, *P. jamesii* had significantly lower δ^{13}C values under the drought treatment (P = 0.034; Fig. 5).

GREENNESS

Unlike the other biotic data, we saw some evidence for lower greenness under the drought treatment, relative to the control for all three species, although the effects were not consistent across time (Fig. 6). Based on the seasonal trends, there were minimal differences in the spring for *E. viridis*, but as the season progressed, the treatments diverged (Fig. 6). Treatment differences were already apparent in *C. ramosissima* at the start of the measurement period, with maximum differences appearing in May (Fig. 6). Finally, in *P. jamesii*, the treatment differences were most pronounced in two periods, the peak of the spring

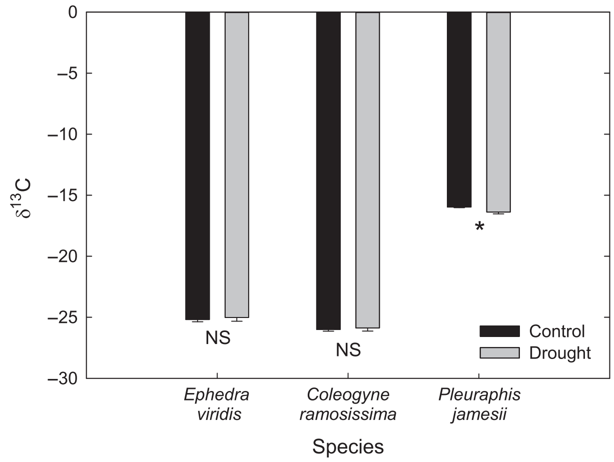

Fig. 5. Carbon isotope discrimination. δ^{13}C values from tissue samples obtained during the last ecophysiology sampling campaign (June). Bars represent means (n = 5), asterisks indicate significant treatment differences (P < 0.05), and n.s. indicates non-significant differences.

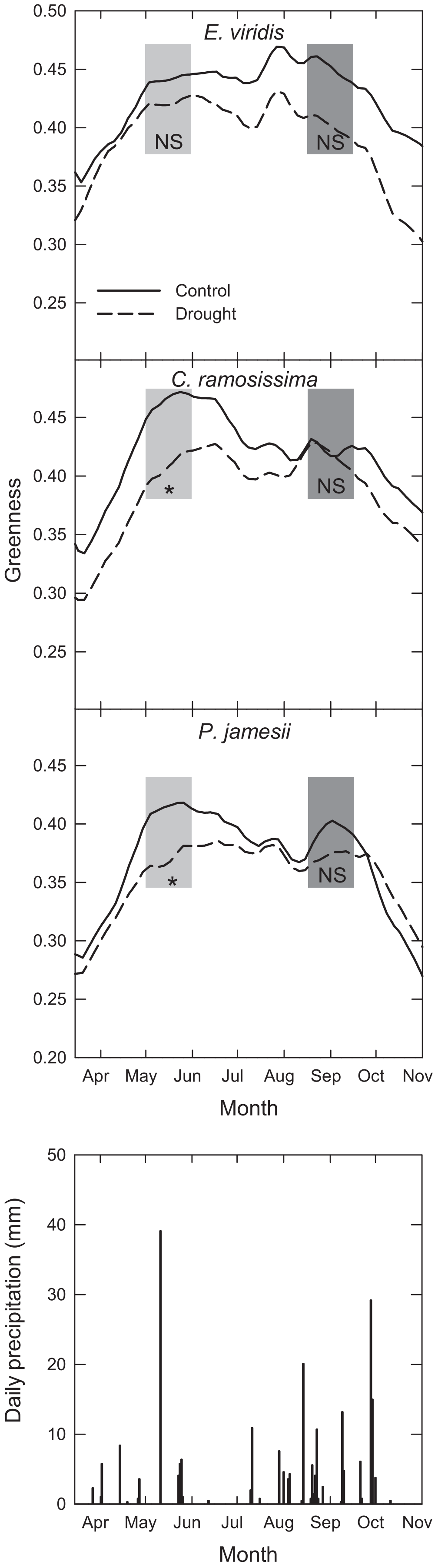

Fig. 6. Greenness and precipitation. (Top) Daily greenness values for control (solid lines) and drought (dashed lines) treatments in 2014. Lines are smoothed averages of 10 individual plants per treatment. Shaded bars indicate timing of seasonal analyses – spring (May 1–31; light grey) and monsoon (August 15–September 15; dark grey). Asterisks indicate significant treatment effects ($P < 0.05$), n.s. = non-significant. (Bottom) Daily precipitation from a weather station centrally located within the precipitation network.

growing season in May and in response to an above average monsoon in late August which triggered a second green-up (Fig. 6). When we analysed these data across the whole growing season using the time-integrated greenness measurements, there were no significant treatment effects for any species (*E. viridis*: $F = 2.13$, $P = 0.172$; *C. ramosissima*: $F = 0.36$, $P = 0.562$; *P. jamesii*: $F = 0.23$ $P = 0.636$). In addition to patterns of greenness, we examined the time-integrated greenness measures during two critical moisture periods: the wettest month (May) and the peak of the Monsoon (August 15–September 15). During May, we saw lower greenness in the drought treatment for *C. ramosissima* ($F = 6.73$, $P = 0.027$) and *P. jamesii* ($F = 8.94$, $P = 0.011$), but not *E. viridis* ($F = 0.58$, $P = 0.464$). No species exhibited any significant treatment effects during the wet monsoon period (*E. viridis*: $F = 1.10$, $P = 0.319$; *C. ramosissima*: $F = 0.17$, $P = 0.691$; *P. jamesii*: $F = 3.16$, $P = 0.103$). Finally, we found no evidence that the drought treatment decreased the growing season length for any species (*E. viridis*: $F = 4.00$, $P = 0.139$; *C. ramosissima*: $F = 0.08$, $P = 0.795$; *P. jamesii*: $F = 0.08$, $P = 0.904$; Fig. 7).

Discussion

PRECIPITATION AND SOIL MOISTURE DYNAMICS

The drought treatment significantly impacted soil moisture availability, although these effects varied temporally but not with depth. Given that the precipitation manipulations reduced event size, we expected the largest differences in soil moisture between treatments to occur during wet periods. Indeed,

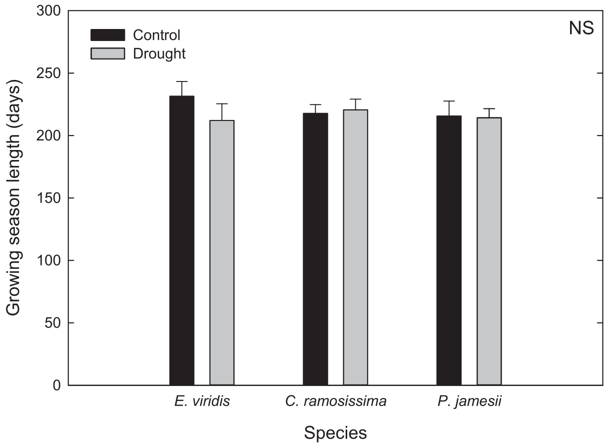

Fig. 7. Growing season length. Mean growing season length based on greenness values for the precipitation treatments ($n = 5$). Bars represent means ($n = 5$) and n.s. indicates non-significant differences ($P > 0.05$).

the above average precipitation that occurred during spring of 2014 reduced soil moisture in the drought treatments relative to the control during the wettest months (April and May; Fig. 3). However, during dry periods, the differences between treatments should have attenuated as evapotranspiration losses brought soil moisture towards the wilting point in both treatments, as evident during the dry month of June (Fig. 3). These soil moisture dynamics suggest that the treatment effects of rainfall shelters can be transient and drought legacies on soil moisture can be 'erased' when inherent soil moisture limits are encountered by both treatments (dry soil conditions observed here during the June period).

Soil moisture measured at a given depth is determined by the physical properties of the soil at the measurement depth and depths above, as well as legacies of past water inputs (precipitation) and water losses (evaporation, transpiration and bypass flows) from the previous hours, days and months (Monger *et al.* 2015). Based on a similar drought study by Schwinning, Starr & Ehleringer (2005), we expected the year-round drought treatment would create a monotonically vertical moisture gradient with soil moisture increasing with depth, with treatment effects more pronounced at shallower than deeper depths. However, we observed no interaction between precipitation treatment and soil depth for any period (Fig. 3). Overall, these results suggest that the effects of the drought were not limited to the shallow-rooted grass species as expected and that deeper-rooted species, such as the shrubs, may have experienced water limitations during the wettest months of the growing season as well.

ECOPHYSIOLOGICAL RESPONSES

Despite significantly drier soil profiles in the drought plots, the droughted shrubs showed no signs of greater water stress at the ecophysiological level, although the dominant grass *P. jamesii* was negatively affected (Fig. 4&5). These results were consistent with the canopy cover patterns (Table 2). During each of the sample periods, *P. jamesii* had lower A_{net} and ψ_{mid} in the drought treatment compared to the control, while no treatment differences were apparent in *E. viridis* or *C. ramosissima* (Fig. 4). For *P. jamesii*, the link between the press-drought and the ecological response was clear – lower soil moisture was decreasing ψ_{mid}, which, in turn, reduced carbon gain through photosynthesis and decreased cover. However, there was no such link between soil moisture and the ecophysiological responses of the two shrubs. One possible explanation is that our discrete ecophysiological measurements somehow missed key moments during the spring when treatment differences occurred. Yet we saw no evidence for this based on the time-integrated $\delta^{13}C$ measurement, as neither *E. viridis* nor *C. ramosissima* had significant treatment effects (Fig. 5), suggesting there were no changes in the WUE of either species.

GREENNESS

We hypothesized that the drought treatment would impact the plants by delaying green-up, shortening growing season length and reducing greenness during the growing season. The results supported the latter but not the former two. First, there was no evidence suggesting the start or end of the growing season changed in response to drought (Fig. 6), nor was there any evidence that the growing season length changed (Fig. 7). Combined, this suggests that drought is not impacting the window that carbon may be assimilated at the seasonal scale. Secondly, during the wet month of May, the greenness for *C. ramosissima* and *P. jamesii* was reduced relative to the control, but these differences were not significant in response to the monsoon moisture. NDVI, as an index for plant greenness, is correlated with many factors such as photosynthesis, leaf area index and productivity (Gamon, Field & Goulden 1995; Mänd *et al.* 2010). Thus, it is difficult to assign a single mechanism for the muted response to the spring moisture we observed in the drought treatments.

TESTING THE APPARENT RESISTANCE TO CHRONIC DROUGHT

The plant species investigated in this study have shown resistance to 4 years of chronic precipitation reductions. Although the C_4 grasses, including *P. jamesii*, had reductions in plant cover (Table 2), they did not suffer widespread mortality, as seen with the C_3 grasses, thus demonstrating a higher drought resistance among the grasses (Hoover, Duniway & Belnap 2015). Meanwhile, *C. ramosissima*, *E. viridis* and the other C_3 shrubs in this study exhibited no change in plant cover in response to the drought treatments (Table 2; Hoover, Duniway & Belnap 2015). The question we asked here was whether the resistance to drought was a result of enduring water-limiting conditions or avoiding them.

The response of *P. jamesii* to reduced soil moisture was consistent across several hierarchical levels as observed in reductions in function from the leaf to the whole plant level. The roots of *P. jamesii* are confined to the upper soil profile, with few roots deeper than 50 cm (West 1972) and the main region of water uptake is reported to be in the top 10 cm (Schwinning, Starr & Ehleringer 2003). Therefore, *P. jamesii* individuals in the drought treatment were forced to endure rather than avoid drought, with the dry soil conditions negatively impacting a wide range of plant functions. However, previous studies have shown that *P. jamesii* has the ability to rapidly assimilate carbon in response to pulse of precipitation by quickly restoring the photosynthetic apparatus and having a high WUE (Schwinning *et al.* 2002). In a direct comparison with the dominant C_3 grass in this experiment, *Achnatherum hymenoides*, Schwinning, Starr & Ehleringer (2003) found that *P. jamesii* had twice the WUE in response to a summer precipitation pulse, despite having similar rooting patterns. The precipitation manipulation imposed drought by reducing event size and limiting soil moisture availability over time, which would favour plants such as *P. jamesii* that can rapidly and efficiently respond to transient moisture resources. Therefore, although this species experiences drought stress and reduced carbon gain, it avoids mortality by enduring drought. Eventually, *P. jamesii* may not be able to sustain such prolonged reductions in carbon uptake and will suffer mortality like the C_3 grasses (Hoover, Duniway & Belnap 2015).

The patterns of drought tolerance in the shrubs were also relatively consistent across the various individual-level plant functions we examined, as there were no drought effects at the ecophysiological or whole plant level, with the exception of spring greenness for *C. ramosissima* (Fig. 6). The soil moisture data showed surprisingly that the drought treatments were affecting deeper soil depths (40 cm depth; Fig. 3), but this consistent difference in measured water availability did not affect the deeper-rooted shrubs. While we assumed the shrubs were obtaining their moisture from the measured soil layers, it is possible that they were instead using even deeper soil depths for moisture. There is little information on the rooting morphology of *E. viridis*, but a nearby relative, *E. nevadensis*, has root network with few roots at the surface (0–20 cm) a maximum fine root density in the 20- to 30-cm layer and deep roots that penetrate to 2 m (Wallace & Romney 1972; Wallace, Romney & Cha 1980). Therefore, while most of the roots are confined to shallower soil layers (where moisture is most abundant seasonally), they may have the capacity to access deeper layers not impacted by drought and avoid drought in space. Similarly, *C. ramosissima* has the highest root biomass from 10 to 30 cm with large taproots can penetrate to deeper layers (U.S. Forest Service 2015). However, some evidence suggests that *C. ramosissima* is unable to access or utilize deeper soil moisture (Lin, Phillips & Ehleringer 1996; Gebauer & Ehleringer 2000), although this may vary with soil depths and characteristics. In addition to depth, the root systems of shrubs much further laterally than grasses and thus have a greater volume of soil to forage for water (Schenk & Jackson 2002). Therefore, it is possible that the extensive root systems of shrubs maintain plant water above stressful levels by accessing a greater volume of soil laterally and with depth.

Hydraulic redistribution, which passively transports water through roots from deep, moist to dry, shallow soil layers, may also increase drought resistance in these shrubs (Caldwell, Dawson & Richards 1998; Neumann & Cardon 2012). This movement of water can enhance water balance during dry periods by delaying soil moisture depletion at the surface, and reducing shallow root embolism and loss of maximum root conductivity (Prieto, Ryel & Tognetti 2014). Although hydraulic redistribution is not documented in either of the focal shrub species, it occurs in many dryland species including a species within the genus *Ephedra* (*Ephedra nevadensis*; Yoder & Nowak 1999) and several other shrubs common on the Colorado Plateau (Caldwell, Dawson & Richards 1998; Neumann & Cardon 2012).

In addition to root morphological traits, other plant functional traits, such as photosynthetic pathway, cavitation resistance and life history, may influence drought resistance across the three focal species of this study. Although photosynthetic pathway is often an important trait correlated with drought resistance, in this study the plant with C_4 photosynthesis had the lowest drought resistance, suggesting that this trait alone was not sufficient to predict drought tolerance. However, among the grasses within this study, C_3 grasses were much more vulnerable to drought than the C_4 grasses (Hoover, Duniway & Belnap 2015). Cavitation resistance is another important trait influencing drought resistance; xylem structural features determine the susceptibility of the vascular system to embolisms, in which small air bubbles enter the transpiration stream and expand to fill conduits with air, thereby disrupting the transport of water from the roots to the leaves (Meinzer *et al.* 2010; Gleason *et al.* 2016). The distribution of woody plants has been correlated with the ability to maintain hydraulic function under drought conditions globally (Nardini & Luglio 2014; Gleason *et al.* 2016) and in drylands of the south-western United States (Hacke, Sperry & Pittermann 2000; Pockman & Sperry 2000). In contrast, there has been no correlation observed between vulnerability of leaf hydraulic conductance and drought mortality in grasses, suggesting hydraulic traits were decoupled from other plant functions (Ocheltree, Nippert & Prasad 2016). Finally, these three species also differ in their life history as both shrubs are slow-growing and can live for hundreds of years in this region (Bowers, Webb & Rondeau 1995). Such a life-history strategy requires adaptations that can allow these plants to persist in an environment with low and highly variable water availability.

SUMMARY

As predicted by the HRF (Smith, Knapp & Collins 2009), effects of a press begin at the physiological level and can translate up to higher hierarchical levels. In our study, we found a clear link between patterns of soil moisture, ecophysiology and the community-level responses of plant cover for the three species. These results are consistent with the HRF and suggest that higher-level responses (e.g. cover) may be sufficient to predict lower-level response (e.g. ecophysiology). However, drought resistance is likely to vary in time and space due to the interaction between the characteristics of drought (e.g. magnitude and pattern) and the landscape (e.g. soil depth, soil texture, parent material and community type). Therefore, additional work is needed to understand the relationship between leaf-level responses and observations at higher spatial scales, such as remote sensing, in order to identify possible deviations from these predictions.

Climate change may alter resource availability in novel ways that may exceed the adaptations of some or many dominant plant species on the Colorado Plateau, leading to large changes in community structure and ecosystem function. Currently, much of the region is dominated by mixed communities of evergreen or deciduous shrubs and perennial grasses (Schwinning & Belnap 2008). Both observations and experimental evidence strongly suggest that decreased water availability in the future will have greater negative impacts on grasses relative to shrubs in this region (Munson *et al.* 2011; Hoover, Duniway & Belnap 2015). Like many other dryland ecosystems, climate change may transform this region into a shrub-dominated ecosystem as grasses succumb to drought.

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Data accessibility

Data are available upon request (DLHoover@usgs.gov) or can be found at www.data.gov.

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