Oecologia (2015) 179:1211–1221
DOI 10.1007/s00442-015-3414-3

GLOBAL CHANGE ECOLOGY - ORIGINAL RESEARCH

Pulse-drought atop press-drought: unexpected plant responses and implications for dryland ecosystems

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Received: 13 December 2014 / Accepted: 24 July 2015 / Published online: 8 August 2015

Abstract In drylands, climate change is predicted to cause chronic reductions in water availability (press-droughts) through reduced precipitation and increased temperatures as well as increase the frequency and intensity of short-term extreme droughts (pulse-droughts). These changes in precipitation patterns may have profound ecosystem effects, depending on the sensitivities of the dominant plant functional types (PFTs). Here we present the responses of four Colorado Plateau PFTs to an experimentally imposed, 4-year, press-drought during which a natural pulse-drought occurred. Our objectives were to (1) identify the drought sensitivities of the PFTs, (2) assess the additive effects of the press- and pulse-drought, and (3) examine the interactive effects of soils and drought. Our results revealed that the C_3 grasses were the most sensitive PFT to drought, the C_3 shrubs were the most resistant, and the C_4 grasses and shrubs had intermediate drought sensitivities. Although we expected the C_3 grasses would have the greatest response to drought, the higher resistance of C_3 shrubs relative to the C_4 shrubs was contrary to our predictions based on the higher water use efficiency of C_4 photosynthesis. Also, the additive effects of press- and pulse-droughts caused high morality in C_3 grasses, which has large ecological and economic ramifications for this region. Furthermore, despite predictions based on the inverse texture hypothesis, we observed no interactive effects of soils with the drought treatment on cover or mortality. These results suggest that plant responses to droughts in drylands may differ from expectations and have large ecological effects if press- and pulse-droughts push species beyond physiological and mortality thresholds.

Keywords Plant functional types · Extreme drought · Ecosystem · Community · Thresholds

Introduction

Drylands cover 41 % of the terrestrial land surface and are one of the most vulnerable regions to climate change (Millennium Ecosystem Assessment 2005; IPCC 2014). These arid and semiarid ecosystems are extremely resource limited, most notably for water, and thus small changes in water availability can lead to large ecological changes (Sala and Lauenroth 1982; Schlesinger et al. 1990). This is particularly salient given that climate change is projected to reduce water availability through decreases in precipitation and increases in temperature (IPCC 2014). Such changes may threaten plant species and plant functional types (PFTs) already living at or near their physiological and mortality thresholds. Hence, there is growing concern about whether these ecosystems can keep pace with future climate change (Loarie et al. 2009; Maestre et al. 2012).

Like many drylands, the southwestern USA is predicted to experience warming and changes in precipitation. This past decade (2001–2010) was the warmest in the instrumental record (Garfin et al. 2013), and models predict continued warming for this region (Gutzler and Robbins 2010). While periods of drought are a climatic feature of the southwest, they are predicted to intensify because the extra heat from global warming will increase drying, creating "hot droughts" (Dai 2011; Overpeck 2013; Cook et al.

Communicated by Susanne Schwinning.

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2014). As a result, droughts will start faster, last longer, and be more intense than in the past (IPCC 2014). Furthermore, winter precipitation is predicted to decline (Cook and Seager 2013), which may have a large impact on regions with significant cool-season precipitation, including the Mojave, Great Basin, and Colorado Plateau deserts. Combined, these changes in climate will lead to chronic reductions in water availability (press-droughts) as well as an increase the frequency and intensity of short-term extreme droughts (pulse-droughts).

Press-droughts are continuous and typically subtle, while pulse-droughts are discrete and often extreme. Both have the potential to alter ecosystem structure and function by pushing species and PFTs beyond key thresholds (Smith et al. 2009; Smith 2011). For example, the Hierarchical Response Framework (Smith et al. 2009) suggests that initial responses to presses are physiological, resulting in reduced performance (e.g., less productivity, tissue dieback). As the press continues, physiological thresholds are eventually exceeded, approaching and then crossing mortality thresholds. Similarly, extreme pulse-droughts may cause reduced performance or mortality of plant individuals and PFTs, depending on the magnitude and duration of the event and the ecosystem resistance (Smith 2011; Reyer et al. 2013). Regardless of the individual type of drought, the sensitivities of dominant species or PFTs will govern ecosystem stability, as determined by their life history and physiological traits.

Precipitation manipulations are a common experimental approach used to examine the ecological effects of both press- and pulse-droughts. Most experiments impose water limitations by passively removing a proportion of ambient rainfall to simulate the direct effects of precipitation deficits and/or indirect effects of warming-induced soil drying (Beier et al. 2012). We define experimental press-droughts as modest precipitation reductions (<40 %) over longer time scales (4+ years; e.g. Johnson et al. 2008; Evans et al. 2011), while we consider experimental pulse-droughts are large precipitation reductions (>60 %) over shorter time scales (1–2 years; e.g. Reichmann et al. 2013; Hoover et al. 2014). The majority of experimentally imposed droughts are pulse-droughts as compared to press-droughts, with very little focus on the co-occurrence of these two drought types (Beier et al. 2012). Given that future extreme pulse-droughts in the southwestern USA will likely occur in the context of a chronic press-drought, assessing the additive effects of these two drought types on dominant PFTs is critical.

At local scales, soil and landscape attributes have been shown to mediate the influence of climate on dryland ecosystem composition and productivity (Noy-Meir 1973; Walter 1973; McAuliffe 1994; Reynolds et al. 2004). Soil surface texture in particular has been implicated as a key soil variable affecting dryland response to precipitation due to its influence on near-surface hydrologic processes (Noy-Meir 1973; Sala et al. 1988). For example, the inverse texture hypothesis (Noy-Meir 1973) suggests that drylands with a mean annual precipitation of <370 mm will have higher productivity in coarse soils than fine soils (Sala et al. 1988). Such interactions between soils and precipitation may be amplified under drought conditions; however, the majority of precipitation manipulation experiments are conducted at a single site and thus lack a range in soil types to test such hypotheses. In order to better forecast ecological resilience of dryland ecosystems to climate change, more information is needed regarding how sensitivity to drought varies across landscapes and how soils mediate those vegetation responses.

Here we present results from a 4-year experimentally imposed press-drought, during which a natural pulse-drought occurred, providing a unique opportunity to examine the interaction between the two types of drought. This rainfall manipulation study was novel in its geographic extent; 40 study sites spanned an approximately 4500-km^2 region of the Colorado Plateau in southeastern Utah, covering a wide range of PFTs, geologic substrates, and soil textures. We used the drought responses of the four dominant perennial native PFTs of this region C_3 grasses, C_4 grasses, C_3 shrubs, and C_4 shrubs; Table 1) to test three key hypotheses. First, we hypothesized that sensitivity to drought would be predictable based on life form (grasses vs. shrubs) and photosynthetic pathway C_3 vs. C_4). Grasses would be more sensitive to drought than shrubs due to differences in rooting depth and life history strategy (Schwinning and Ehleringer 2001), and within a given life form,

Table 1 Plant functional types, species, and parent materials

Plant functional type	Species	Parent material
C_3 Grasses	*Hesperostipa comata*	Sandstone
	Hesperostipa hypmenoides	Sandstone, shale
C_4 Grasses	*Bouteloua gracilis*	Sandstone
	Pleuraphis jamesii	Sandstone, shale
C_3 Shrubs	*Artemisia filifolia*	Sandstone
	Artemisia tridentata	Sandstone
	Certoides lanata	Sandstone, shale
	Chrysothammnus sp.	Sandstone
	Coleogyne ramosissima	Sandstone
	Ephedra sp.	Sandstone
	Gutierrezia sarothrae	Sandstone
	Yucca brevifolia	Sandstone
C_4 Shrubs	*Atriplex confertifolia*	Sandstone
	Atriplex corrugata	Shale

Study species were grouped into four common plant function types along with the parent material on which they occur on in this study

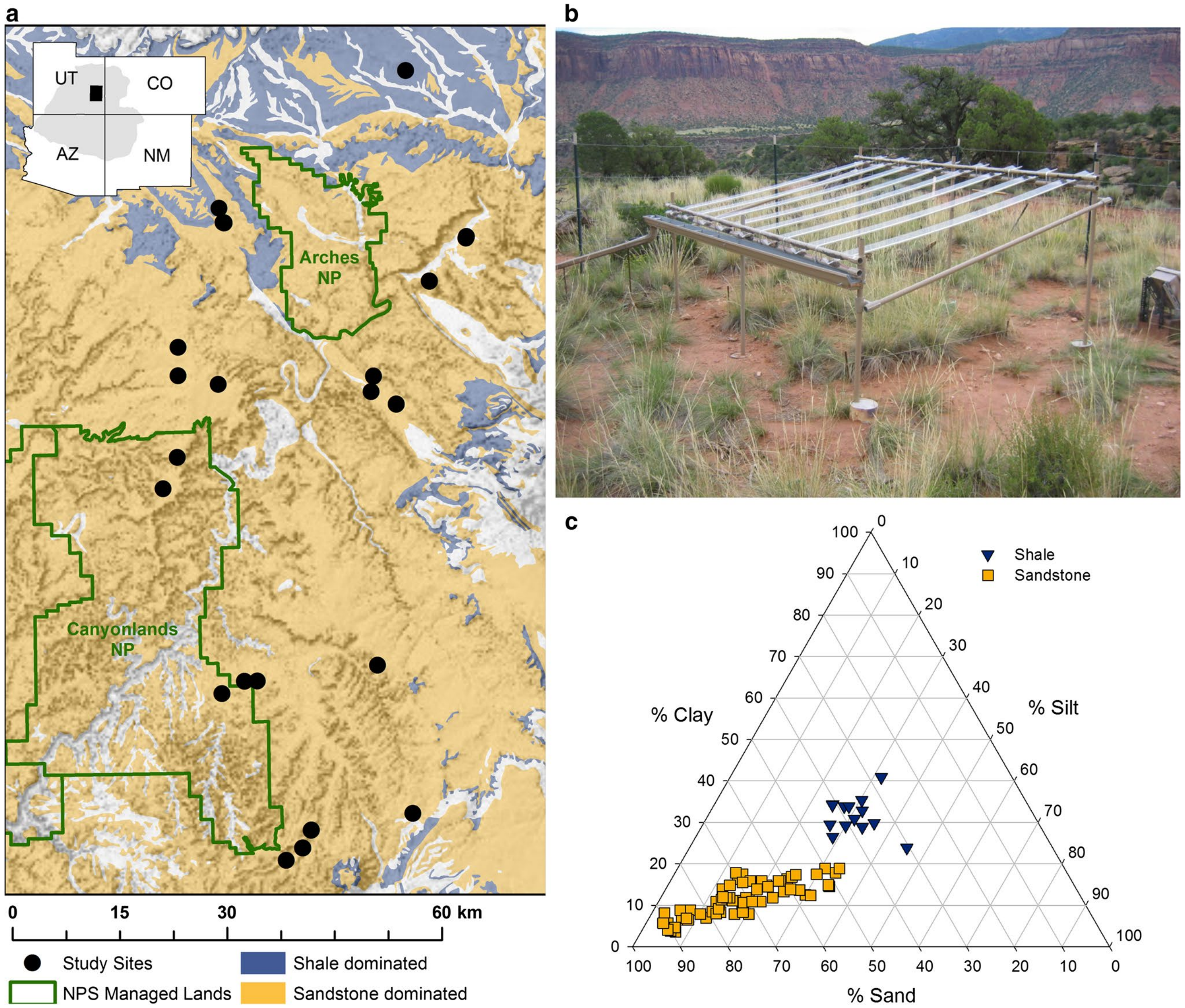

Fig. 1 Experimental design. **a** Map of study sites. Within the Colorado Plateau (*gray-shaded area* on *inset* map), sites were selected to represent a wide range of plant community types, parent materials, and soil textures. Each *black dot* represents one to four sites. *NPS* National Park Service. **b** Photo of a study site. Each site consisted of two paired plots receiving either drought (35 % precipitation reduction, shown here) or control (ambient precipitation, not shown) treatments. Plots were established in 2010, and year-round treatments were imposed between 2011 and 2014. **c** Soil texture sampled from each plot ($n = 80$) is overlaid on a textural triangle (*colors* indicate parent material)

plants with C_3 photosynthesis would be more sensitive than plants with C_4 photosynthesis because of differences in water use efficiency (Gebauer et al. 2002). Thus, our expected continuum of drought sensitivity (ranked from most to least drought sensitive) was C_3 grasses > C_4 grasses > C_3 shrubs > C_4 shrubs. Second, we predicted that the additive effects of the press- and pulse-droughts would be greater than the effect of the pulse-drought alone and push the more sensitive PFTs beyond critical thresholds. Third, as the experiment spanned a range of parent materials (sandstone and shale) and textures (fine to coarse), we hypothesized that the precipitation treatments would have stronger effects on fine soils/shale than on coarser soils/sandstone, as suggested by the inverse texture hypothesis (Noy-Meir 1973; Sala et al. 1988).

Methods

Experimental design

In 2010 (pretreatment year), we established 40 sites (blocks) across the Colorado Plateau in southeastern Utah, ranging in plant communities, parent materials, and soil textures common to the region (Table 1; Fig. 1a). Two 150 × 200-cm plots were established within each site, containing native target species, and then the plots were randomly assigned to either control or drought treatments. From 2011 to 2014, control plots received ambient rainfall while drought plots received 35 % rainfall reductions year-round using passive rainfall removal shelters (Fig. 1b). These shelters were 230 × 310 cm and sufficiently wide to provide a large buffer around the plots; the slanted roofs (10° slope, approx. 1 m high at the short end) was composed of V-shaped plexiglass strips that served as troughs to intercept rainfall. These strips were connected to a gutter system that directed water away from plot. To hydrologically isolate the plots, we installed vinyl flashing vertically around the plot (20 cm distant from outer edge of plot, but beneath the shelter), to a depth of 30 cm (to prevent belowground flow into plots), with 10 cm remaining aboveground (to prevent overland flow into plots). At each individual plot, two randomly selected surface soil horizon (soil depth 0–10 cm) samples were collected using a 1.6-cm diameter corer and homogenized; one subsample was analyzed for soil texture (percentage sand, silt and clay) by the hydrometer method (Gee and Or 2002). Since percentage sand (%sand) showed the greatest variation of the three texture types (Fig. 1c) it was used to test texture-related hypotheses in subsequent models.

Precipitation data

Long-term daily 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). Cool season precipitation (December through to May), a biologically critical moisture period for Colorado Plateau plant communities, was calculated for each year. Years were dropped from the analysis if >5 % of days were missing. The estimated probability density function was calculated using a lognormal function and compared with treatment precipitation.

Biotic data

In each plot, plants, ground cover, and litter were each visually estimated using four 75 × 100-cm frames. These measurements occurred annually near peak biomass, although the timing of this peak varies (between April and August) and is largely determined by the pattern and amount of rainfall for a given year. Ground cover included bare ground, rocks, and biological crusts, while litter included both standing litter (e.g. dead shrub branches or previous years' senesced leaves on grasses) and ground litter on the soil surface. For each species of green vascular plants, cover was recorded only for those parts of the plants that were alive and green. For example, branches of shrubs that were standing but had no green tissue were recorded as "standing litter" and did not count towards plant cover. In order to standardize cover estimates across all plots, years, and observers, the cover of each species was calculated using the following equation: % Cover species A = (raw cover species A/total plot cover) × 100, where the total plot cover was the summed values of all cover types (plants + litter + ground cover) in a given plot. Four PFTs were the focus of this analysis, which consisted of the summed cover of all species belonging to a given PFT per plot (Table 1). For each target species, a subset of individuals present in the plot were permanently tagged ($n = 2$–4 per plot) at the start of the experiment (2010) and tracked for various annual measurements, including mortality. To assess mortality, we recorded tagged individuals as dead if there were no green leaves or the current year's senesced leaves present.

Statistical analysis

Due to non-normality in the data, cover values were log-transformed prior to statistical analysis. To test the hypotheses related to changes in cover, we used a repeated measures mixed model analysis of variance (Proc Mixed, SAS 9.3; SAS Institute, Raleigh, NC) with treatment and year as fixed factors, year as a repeated measure, and site (block) as the random effect. Four models, consisting of different combinations of soil texture (continues variable, %sand) and parent material (categorical variable, sandstone, or shale), were compared using Akaike information criterion (AIC) values. The three-way model with treatment, year, and parent material had the lowest AIC for all four PFTs and was used for the analysis (Table 2). The experiment was designed to maximize the variability among sites, but minimize initial differences within a site; consequently, experiment-wide treatment means had large variances and thus were not the best way to show treatment effects. Instead, for each site, we calculated the difference between treatments in cover for each PFT present, and then calculated overall means and 95th percent confidence interval (CI) to examine the treatment effects over time.

Plant mortality was assessed in 2014, representing total mortality over the course of the study (2010–2014). The data were recorded as binary data (dead or alive), and analyzed using Proc Glimmix (SAS 9.3; SAS Institute) with a binary distribution and logistical function, treatment as a fixed effect, and site as a random effect. The model tested for significant differences between treatments, as well as whether a given treatment was associated with mortality that was significantly different from zero. We originally included soil texture and parent material, but neither of

Table 2 Mixed model comparisons

Overall AIC rank	Model	AIC values			
		C_3 Grasses	C_3 Shrubs	C_4 Grasses	C_4 Shrubs
1	Cover = Treatment|Year|PM	385.5	389.7	417.7	108.5
2	Cover = Treatment|Year	401.8	406.9	431.3	118.9
3	Cover = Treatment|Year|PM | %Sand	434.0	437.4	462.6	164.2
4	Cover = Treatment|Year| %Sand	443.2	446.3	482.2	165.0

The Akaike information criterion (AIC) values for several repeated mixed model analyses of variance for cover of four key plant functional types. Each model contains all possible interactions among variables. AIC ranks were determined by ranking models within each plant functional type (lower is better) and then taking the average for each model

PM Parent material

these factors had significant main effects or interactions and were therefore dropped from the model. Annual mortality was also assessed for C_3 grasses, both as a cumulative value and as a percentage of total mortality for the observed period (2010–2014). Total C_3 grass mortality was also compared with change in C_3 grass cover (2011–2014) using simple linear regression. We selected 2011 cover over the pretreatment year (2010) because it had similar precipitation amounts to 2014 (see Fig. 1), and thus cover changes was less influenced by interannual variability in ambient precipitation.

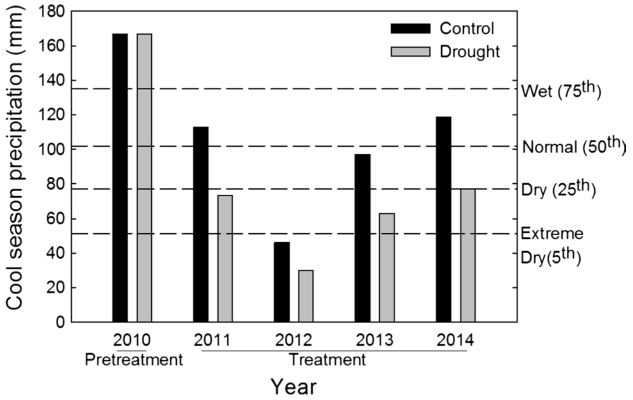

Fig. 2 Precipitation. Cool season precipitation (December through to May) for control (*black bars*) and drought (*gray bars*) plots during the pretreatment (2010) and treatment (2011–2014) years. *Horizontal broken lines* indicate the probability distribution function of long-term precipitation (1901–2014) for Moab, UT

Results

During 3 of the 4 years of the study (2011, 2013, 2014), control plots received near normal rainfall (approx. 50th percentile) while the drought plots experienced press-drought conditions (approx. 25th percentile; Fig. 2). In 2012, this study site, as well as most of the USA, experienced one of the worst droughts since the 1930s Dust Bowl (National Centers for Environmental Information, formerly National Climate Data Center, National Oceanic and Atmospheric Administration, Washington, DC). Based on long-term records, in 2012 the control and drought plots received precipitation near the 5th and 1st percentile, respectively (Fig. 2). Therefore, the additive effects of the press- and pulse-drought created roughly a 100-year drought (in the drought treatment) instead of a 20-year drought in the pulse-drought only (in the control treatment). However, the absolute difference in precipitation between the treatments in this extreme year was small (16.2 mm) relative to average cool season precipitation (102.0 mm). In contrast, in press-drought-only years, the absolute differences in precipitation between the control and drought treatments were larger (mean difference 38.3 mm).

Our results show that the experimental press-drought negatively impacted cover of C_3 grasses, C_4 grasses, and C_4 shrubs, but not C_3 shrubs (main effects of the drought treatment are given in Table 3; differences from zero are given in Fig. 3). However, the analysis of yearly treatment effects (control vs. treatment; Fig. 3) reveals important differences in temporal dynamics among all PFTs. Press-drought affected both grass PFTs starting in 2011, whereas the extreme pulse-drought (2012) had a noticeable greater negative impact on C_3 grasses than on C_4 grasses (Fig. 3). In 2013, the year following the pulse-drought, neither grass PFT showed strong treatment effects, but in 2014, C_3 grasses again were negatively affected by the press-drought treatments (Fig. 3). The two shrub PFTs responded very differently to the treatment: the C_3 shrubs were not detectably impacted by either drought type, while C_4 shrubs had a strong response to the 2012 pulse-drought, and this response persisted for the remainder of the experiment (Fig. 3). When we examined total mortality (2010–2014), C_3 grasses were the only PFT with significant main effects of the drought ($F = 6.41$; $p = 0.013$), with losses in control and drought treatments (33 and 53 % mortality, respectively), as well as differences between treatments (Fig. 4).

Table 3 Repeated measures mixed model analysis of variance

Functional type	Effect	Numerator *df*	Denominator *df*	*F* value	Pr > *F*
C_3 Grasses	Treatment	1	103	10.1	0.002*
	Year	3	103	9.8	<0.001*
	Treatment × Year	3	103	1.1	0.336
	PM	1	103	2.9	0.095
	Treatment × PM	1	103	0.6	0.439
	Year × PM	3	103	0.5	0.653
	Treatment × Year × PM	3	103	1.4	0.250
C_4 Grasses	Treatment	1	128	4.5	0.036*
	Year	3	128	27.2	<0.001*
	Treatment × Year	3	128	1.3	0.282
	PM	1	128	3.5	0.065
	Treatment × PM	1	128	0.1	0.723
	Year × PM	3	128	2.4	0.076
	Treatment × Year × PM	3	128	1.5	0.218
C_3 Shrubs	Treatment	1	140	1.9	0.170
	Year	3	140	5.4	0.002*
	Treatment × Year	3	140	1.7	0.167
	PM	1	140	6.0	0.016*
	Treatment × PM	1	140	3.8	0.053
	Year × PM	3	140	0.4	0.784
	Treatment × Year × PM	3	140	1.7	0.173
C_4 Shrubs	Treatment	1	44	16.0	<0.001*
	Year	3	44	3.0	0.042*
	Treatment × Year	3	44	1.5	0.235
	PM	1	44	4.2	0.046*
	Treatment × PM	1	44	0.1	0.732
	Year × PM	3	44	2.1	0.116
	Treatment × Year × PM	3	44	0.8	0.484

Response of plant cover of key plant functional types during the years drought treatments were imposed (2011–2014). The data were log-transformed prior to analysis

* Significant effects at $p < 0.05$

Given that the pulse-drought was a natural event affecting all treatments, we were unable to explicitly test the effects of press- and pulse-drought separately (e.g., press-drought was the only experimentally applied treatment). However, we were able to compare the effects of pulse-drought with and without a press-drought. Previously we had found that the C_3 grasses responded to both the press-drought (Table 3; Fig. 3) and the pulse-drought (Fig. 4; mortality in control plots is greater than zero), and therefore we focused on this PFT to examine possible additive effects of the two types of drought. When we examined annual mortality for the C_3 grasses in both treatments, there was little mortality before (2011) and during the pulse drought (2012), but there was a large increase in mortality immediately following the pulse drought (2013; Fig. 5a). This change became clear when we plotted each year's mortality as a percentage of the total mortality that occurred during the experiment (Fig. 5b). For the control treatment, the majority of the total mortality occurred between the 2012 and 2013 measurement dates (54 %), as 2011, 2012 and 2014 all had similar mortality rates (12–19 %; Fig. 5b). In contrast, the C_3 grasses in the drought treatment suffered high mortality in both 2013 (40 %) and 2014 (33 %; Fig. 5b). When we examined the link between experiment-long mortality and cover change together (2011–2014), there was a strong negative relationship between C_3 grass mortality and the observed drop in cover (Fig. 5c).

We found little evidence that the effect of the precipitation treatments varied with surface soil texture or geologic parent material (sandstone vs. shale). Based on AIC values, the best model included a parent material factor but not surface sand content. Plant cover was generally lower on the shale substrates, as reflected in some significant parent material main effects (Table 3). No PFT had a significant interaction between treatment and parent material although

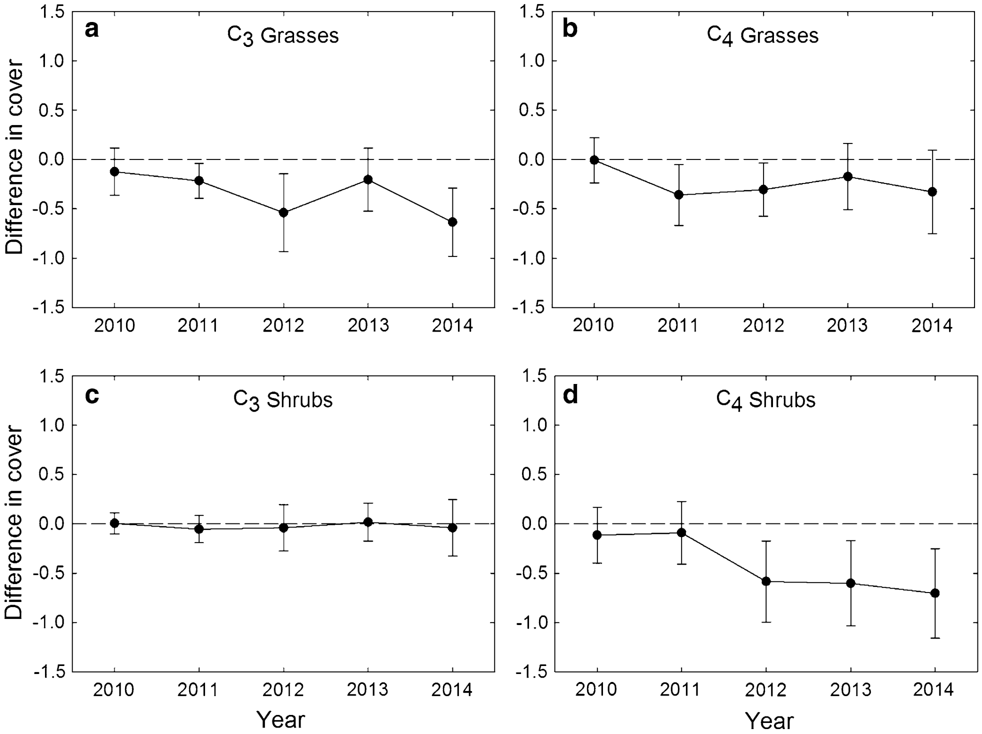

Fig. 3 Cover changes. Difference in cover between control and drought treatments for the plant functional types C_3 grasses (**a**), C_4 grasses (**b**), C_3 shrubs (**c**), and C_4 shrubs (**d**), during the pretreatment (2010) and treatment years (2011–2014) for control and drought treatments. Difference in cover was calculated for each plot using: $\ln(\text{cover}_{\text{drought}}/\text{cover}_{\text{control}})$. *Filled circles* Means, *error bars* 95th percent confidence interval (CI), *dashed line at zero* reference point for no difference in cover between treatments

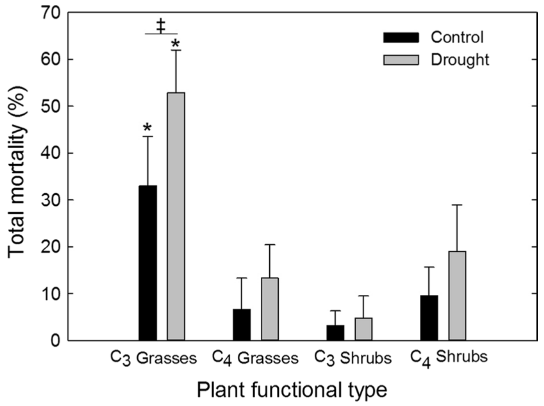

Fig. 4 Mortality. Total mortality of the four dominant plant functional types between 2010 and 2014 for the control and drought treatments. *Bars* Means, error bars +1 standard error (SE). *Symbols* denote significance at $p < 0.05$: *asterisk* mortality of a treatment is different than zero, *double dagger* significant difference between treatments of a given plant functional type

this interaction was marginally significant for C_3 shrubs ($p = 0.053$); however, this interaction did not show significant treatment effects on either parent material. Parent material had significant main effects on cover for C_3 shrubs ($p = 0.016$) and C_4 shrubs ($p = 0.046$) and marginally significant effects on C_3 grasses ($p = 0.095$) and C_4 grasses ($p = 0.065$). There were no main or interactive effects of parent material or soil texture on mortality.

Discussion

Climate change is projected to alter precipitation and increase temperatures, which will in turn reduce water availability for native plants in the southwestern USA (Garfin et al. 2013). Given that the drought sensitivities of dominant species or PFTs will govern ecosystem stability, in this study we focused on the responses of four key PFTs of the Colorado Plateau to an experimentally imposed 4-year press-drought during which a natural pulse-drought occurred. Overall we found that (1) the continuum of drought sensitivity (ranked from most to least drought sensitive) was C_3 grasses > C_4 grasses and C_4 shrubs > C_3 shrubs, (2) the additive effects of the press- and pulse-droughts were greater than the individual effects of the pulse drought on the C_3 grasses, and (3) there was no evidence that the press-drought treatment effects varied among soil types.

Differential drought sensitivities among plant functional types

There were three general responses to drought in this experiment that reflect differential PFT drought sensitivities: (1) decline in cover with mortality (C_3 grasses), (2) decline in cover without mortality (C_4 grasses and C_4 shrubs), or (3) no change in cover or mortality (C_3 shrubs). The results confirmed our hypothesis that C_3 grasses were the most

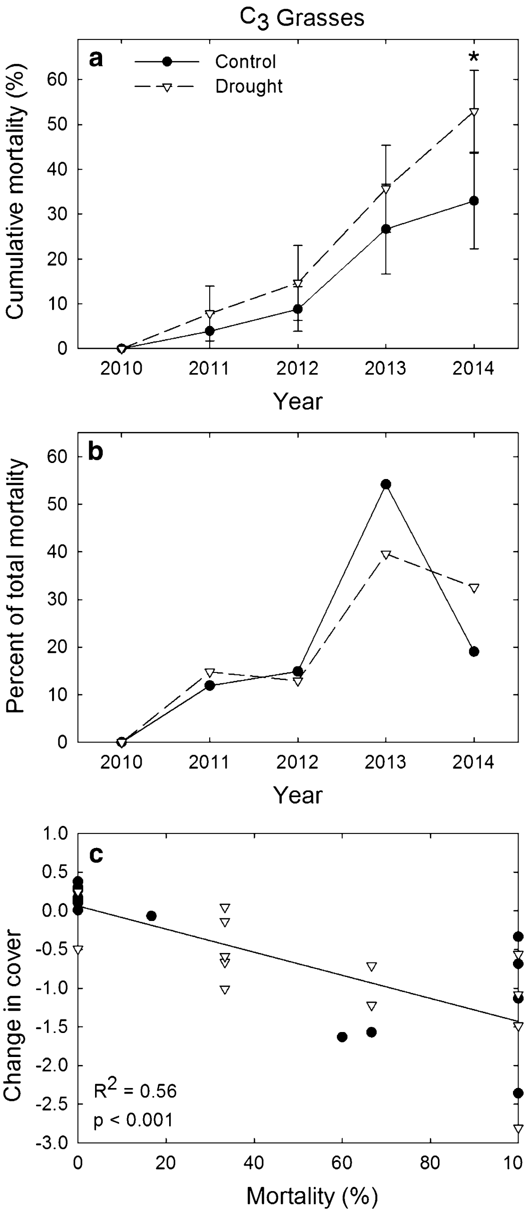

Fig. 5 C_3 Grass mortality and cover change. **a** Cumulative mortality of the C_3 grasses during the pretreatment (2010) and treatment years (2011–2014) for control and drought treatments. *Symbols* Means, *error bars* ±1 SE, *asterisks* denote significant differences at $p < 0.05$ between treatments for each year. **b** Annual percentage of total mortality for the C_3 grasses (2010–2014) for control and drought treatments. **c** Change in cover of the C_3 grasses and between pretreatment (2010) and final treatment year (2014) vs. total mortality. Difference in cover was calculated for each plot using the formula: $\ln(\text{cover}_{2014}/\text{cover}_{2010})$. *Line* Linear regression and statistics

sensitive PFT to drought, as this PFT crossed both physiological and mortality thresholds during the 2012 extreme drought. Within the grasses, photosynthetic pathway was a good predictor of drought tolerance, as the C_4 grasses were more resistant to drought stress than the C_3 grasses; this resistance was likely driven by the higher water use efficiency of the C_4 grasses in this region (Schwinning et al. 2003; Munson et al. 2011b). However, within the shrubs, the C_3 shrubs were more resistant to drought than the C_4 shrubs, which showed reductions in cover, reflecting a decline in physiological performance (resulting in senescence and/or dieback). These impacts were unexpected, as C_4 plants are considered to be highly drought-resistant, and the C_4 shrubs in this study are reported to have deep roots and high water use efficiency (Hodgkinson et al. 1978; Evans et al. 2012). While the C_4 shrubs do not yet show widespread mortality, the data indicate that additional years of press-drought may push them beyond mortality thresholds, with a substantial impact to the ecosystem (McAuliffe and Hamerlynck 2010).

The differential drought sensitivities of the PFTs documented here have significant ecological and economic implications for drylands at the local and regional levels. First, grasses are the primary source of forage for most native herbivores and domestic livestock in this system. The high drought sensitivity of these PFTs may disrupt multi-tropic interactions of native populations (McCluney et al. 2012), as well as have severe economic consequences for agricultural production (Schwinning et al. 2008). Secondly, mortality-driven cover change (e.g., C_3 grasses) will likely have greater ecological impacts than physiologically-driven cover change alone (e.g., C_4 grasses and shrubs). This is because mortality requires vegetation replacement through recruitment to maintain stability (Lloret and Escudero 2012), and recruitment events in dryland regions are infrequent, as they often depend on consecutive years of above-average precipitation (Beatley 1974). Mortality may also have prolonged effects on community structure and ecosystem function if the loss of individuals leads to shifts in community composition and/or increased exotic invasion (Smith et al. 2009). Finally, the inherently low perennial vegetative cover in drylands (<40 %) leaves these ecosystems susceptible to soil erosion, even when the native vegetation is intact. Further reductions in cover through losses of C_3 grasses will exponentially increase wind erosion and dust transport around the region (Munson et al. 2011a).

Additive effects of press- and pulse-droughts

Although these two drought types are often studied in isolation, pulse-droughts occurring with a background of press-droughts are likely to be the “new normal” with predicted climate change (e.g., “hot droughts”; Overpeck 2013). The additive effects of these two drought types may create novel climate scenarios that may alter ecosystem structure and function and thus impact critical ecosystem services. The C_3 grasses were most sensitive to drought, particularly the combination of press- and pulse-droughts (Fig. 5). Also, whereas mortality occurred in the pulse-drought only,

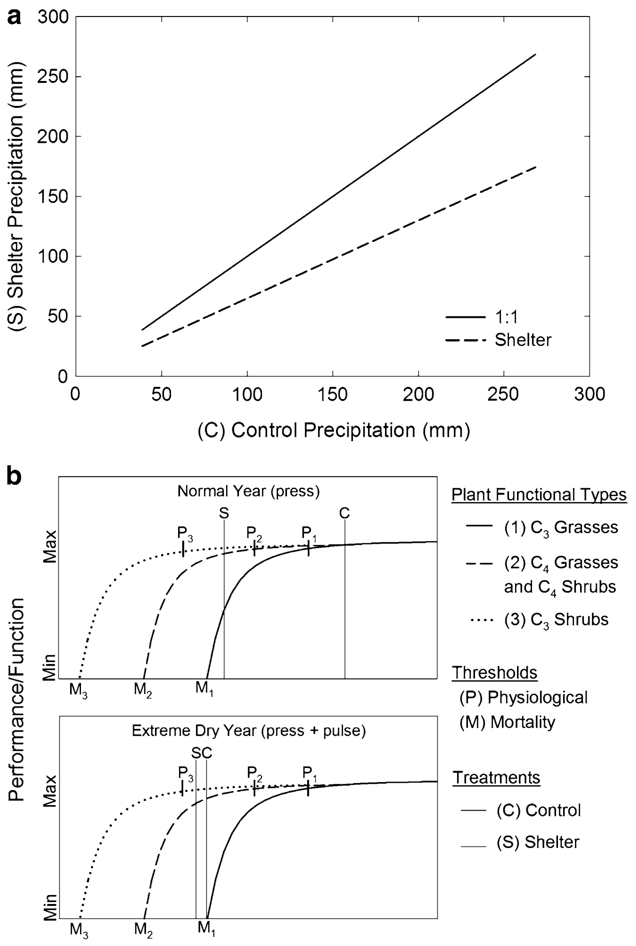

Fig. 6 Conceptual representation of experimental responses. **a** Control (*C*; ambient) vs. shelter (*S*; 35 % reduction) precipitation for the field study (range 1st–99th percentiles for control precipitation), showing that the absolute difference between the treatments decreases with lower control amounts. **b** There were three general responses to the treatments over the 4-year experiment: (1) reduced cover and mortality (C_3 grasses); (2) reduced cover but no mortality (C_4 grasses and shrubs); (3) no change in cover or mortality (C_3 shrubs). These figures illustrates how the precipitation treatments (*C* and *S*) and natural variability (*Normal Year* and *Extreme Dry Year*) interact with plant functional type (PFT) thresholds (*P* physiological threshold, *M* mortality threshold). During the normal year (*press*), there are cover reductions for all PFTs besides the C_3 shrubs as the two treatments straddle physiological thresholds; however C_3 grasses have the greatest reduction. Then during the extreme dry year (*press + pulse*), both treatments result in mortality for C_3 grasses and greater reductions in cover for C_4 grasses and shrubs. C_3 shrubs remain resistant to the extreme drought year. This conceptual framework is applicable for understanding responses of different PFTs, dominant plants, or other plant groupings to drought in any ecosystem

it was 60 % higher in the press- and pulse-drought. The perennial growth form of these plants makes it challenging to observe mortality in real time because within-season senescence cannot be assumed as death, and therefore it is often a lack of green-up the following year that is noted as mortality. So while there was not a marked increase in mortality in 2012, the pulse-drought year, mortality peaked in 2013 for both treatments (Fig. 5a, b) and remained high during the 2 years following drought for the press-drought treatment, while it decreased in the control (Fig. 5a, b). Furthermore, it appears that for the C_3 grasses, mortality was an important mechanism behind cover change (Fig. 5c). These results suggest that for the most drought-sensitive PFT, the additive effects of the press- and pulse-drought were greater than the effects of the pulse-drought alone.

Interannual variability in ambient precipitation (control) during the study period interacted with experimental treatments and imposed two different scenarios—normal (press-drought) and extreme dry (press- and pulse-drought) years. We highlight these dynamics in a conceptual model in Fig. 6. Whereas the percentage of rainfall removed by the drought shelters was fixed, the absolute treatment difference in rainfall decreased with lower total precipitation (Fig. 6a). These precipitation inputs impacted the performance of local species or PFTs, based on their individual responses to decreasing precipitation (Fig. 6b). Due to the non-linear nature of these responses, the small absolute reductions in rainfall actually had large effects during dry years (cover change and mortality), whereas large reductions in rainfall in wet years had smaller effects (cover change only; Fig. 6b). Hence, the large effect of the drought treatment occurred in 2012, despite a small reduction in precipitation relative to the control, which is indicative of a water availability threshold being crossed.

Interactions between precipitation treatment and soils/parent material

This experiment was novel with respect to other passive rainfall manipulation experiments conducted to date because it spanned a wide range of soil textures and parent materials; however, neither of these factors had the strong interaction with the press-drought treatments we predicted. Soil texture was eliminated from the plant cover mixed model (based on AIC) in favor of parent materials (Table 2). It should be noted that even in the model with soil texture (cover = treatment, year, %sand; with all interactions), there were no significant texture × drought treatment interactions for any PFT. Our study site spanned two parent materials—sandstone, dominated by coarse sandy soils, and shale, dominated by fine clayey soils (Fig. 1a, c). However, contrary to our hypothesis, there were no interactions between the parent materials and the treatments for cover (Table 3). In addition, when we examined the PFT with high mortality (C_3 grasses), parent material and %sand also lacked significant interactions with the treatment (PM $F = 0.28$, $p = 0.600$; %sand $F = 2.44$, $p = 0.122$). These results are inconsistent with the inverse texture hypothesis which portends that plant response to precipitation is mediated by surface soil properties (represented by treatment × parent material interaction in this study; Noy- Meir 1973; Sala et al. 1988).

This begs the question of why there were no interactions between the soils and the press-drought treatments evaluated here. There are three possible explanations for this result, which are not mutually exclusive. First, the experimental reductions in precipitation may have been too subtle (only reducing precipitation by 16.2 mm in pulse-drought and 38.3 mm in press-drought years), and soil interactions with treatments were masked by the strong effect of the pulse-drought on both treatments. While we observed main effects of the treatments from the experimental reductions, it is possible that larger treatment reductions or study periods with less interannual variability in precipitation are needed for observable interactions with soils. Second, the lack of an interaction may have been due to the high importance of winter precipitation in this ecosystem relative to the Central Plains region evaluated by Sala et al. (1988). The inverse texture hypothesis suggests that in drylands, coarse soils have a greater productivity response to precipitation than fine soils, in part because higher infiltration rates reduce run-off and evaporative losses (Sala et al. 1988). Winter precipitation on the Colorado Plateau is delivered by frontal storms characterized by relatively low-intensity precipitation (falling as rain or snow) and cool temperatures. Under these conditions, the effects of soil texture on near-surface hydrology (infiltration depth, run-off, and evaporation) may be minimized, relative to convective events common to warm-season rainfall of the Great Plains. One final possibility is that plants may be adapted to the hydrological regimes they currently inhabit, obfuscating the anticipated interactions. Of the 14 native perennial species we examined, ten occurred exclusively on sandstone, one was on shale only, and three "generalists" were found on both parent materials (Table 1). Thus, the lack of an interaction may have been driven by species occurring on only one parent material. To evaluate this alternative hypothesis, we examined the three "generalist" species independently, but neither *Pleuraphis jamesii* ($F = 0.11$, $p = 0.737$), *Hesperostipa hypmenoides* ($F = 0.52$, $p = 0.475$), or *Certoides lanata* ($F = 0.00$, $p = 0.965$) showed significant interactions between parent material and drought treatment.

Summary

Given that press- and pulse-droughts will be the "new normal" with predicted climate change, a greater understanding of PFT-specific thresholds to future climate patterns is needed to forecast responses in ecosystem structure and function. The results of our study demonstrate that current PFTs, as defined by life form (grass, shrub) and photosynthetic pathway (C_3, C_4), may not sufficiently predict drought sensitivity, but that alternative categorizations, based on other plant characteristics, may be required. Furthermore, these results highlight the importance of the additive effects of press- and pulse-droughts, particularly when species are at or near their tolerance thresholds: at that point, small precipitation reductions may result in disproportionate and unforeseen ecosystem responses.

Acknowledgments We would like to thank the many people who helped in establishing this experiment, especially Sue Phillips, Ed Grote, Matt van Soyoc, and Phil Adams. We would also like to thank Erika Geiger and Kristina Young for their help supervising the experiment and all of the field technicians for collecting the data. Any use of trade names is for descriptive purposes only and does not imply endorsement by the U.S. Government. We thank the USGS Climate and Land Use and Ecosystems programs for funding this effort.

Author contribution statements DLH, MCD, and JB wrote the manuscript; DLH collected field data in 2014, compiled data for analysis, and completed the statistical analysis with input from MCD and JB; JB acquired financial support and established and supervised the field project.

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