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ECOLOGICAL SYSTEMS, SPECIES AND SUBDISCIPLINES

Research Article

Drought resistance and resilience: The role of soil moisture–plant interactions and legacies in a dryland ecosystem

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Abstract

1. In many regions of the world, climate change is projected to reduce water availability through changes in the hydrological cycle, including more frequent and intense droughts, as well as seasonal shifts in precipitation. In water-limited ecosystems, such as drylands, lower soil water availability may exceed the adaptive capacity of many organisms, leading to cascading ecological effects during (concurrent effects) and after drought (legacy effects). The magnitude and duration of concurrent and legacy effects depends on drought intensity, duration and timing as well as the resistance and resilience of the ecosystem.
2. Here, we investigated the effects of drought seasonality and plant community composition on two dominant perennial grasses, *Achnatherum hymenoides* (C₃ photosynthesis) and *Pleuraphis jamesii* (C₄ photosynthesis), in a dryland ecosystem. The experiment consisted of three precipitation treatments: control (ambient precipitation), cool-season drought (–66% ambient precipitation November–April) and warm-season drought (–66% ambient precipitation May–October), applied in two plant communities (perennial grasses with or without a large shrub, *Ephedra viridis*) over a 3-year period. We examined the concurrent and legacy effects of seasonal drought on soil moisture, phenology and biomass.
3. Drought treatments had strong concurrent and legacy effects on soil moisture, which impacted the phenology and biomass of the two grasses. Drought reduced growing season length by delaying green-up (cool-season drought) or advancing senescence (warm-season drought) and reduced biomass for both species. Biomass and phenology legacy effects from drought emerged in the second and third years of the experiment. While we observed differential sensitivity to drought legacies between the two grasses, we found limited evidence that shrub presence had interactive effects with the drought treatment.
4. *Synthesis.* The results from this study highlight how abiotic and biotic legacies can develop and influence a community's resistance and resilience to subsequent droughts. When the frequency of repeated extreme events, such as recurring seasonal droughts, exceeds the capacity of organisms or ecosystems to recover (i.e. resilience), persistent drought legacies can reduce the resistance to subsequent

drought events. Overall, these results highlight how drought legacies are a product of ecological resistance and resilience to past drought and can influence ecosystem vulnerability to future droughts.

KEYWORDS

biomass, Colorado Plateau, phenology, resilience, resistance, seasonal drought, soil moisture

1 | INTRODUCTION

Ecosystem patterns and processes are shaped by current environmental conditions as well as the legacies of past events (Johnstone et al., 2016; Monger et al., 2015; Ogle et al., 2015; Sala et al., 2012). While organisms are often well-adapted to historical climate variability and disturbance regimes, increases in extreme events with climate change may exceed this adaptive capacity, with potential immediate and prolonged impacts on ecosystem structure and function (IPCC, 2013; Smith, 2011). The magnitude, duration and direction of these responses will be governed by the resistance (capacity to withstand change) and resilience (capacity for recovery of function) of the given ecosystem (Pimm, 1984; Tilman & Downing, 1994). However, intertwined with this are legacies, which both affect the resistance to current environmental conditions and are influenced by the resistance and resilience to past events. Thus, identifying how legacies develop and influence ecosystem vulnerability to future events is critical to understanding how ecosystems will function in a more extreme world.

Global climate models predict that droughts will increase in intensity, duration and frequency, due to rising temperatures and altered precipitation patterns with climate change (IPCC, 2013; Trenberth et al., 2014). The ecological impacts of drought during the event or 'concurrent effects' and those that persist after the climate anomaly subsides or 'legacy effects' are driven by ecosystem resistance and resilience. The magnitude of such ecological impacts can be quantified in relation to a pre-disturbance baseline, or as a comparison between drought and control treatments in factorial experiments (Ingrish & Bahn, 2018). The concurrent effects of drought are determined by the resistance of an ecosystem and can be quantified by measuring abiotic (e.g. soil moisture) and biotic (e.g. phenology, productivity) impacts. When these impacts persist after the climatic anomaly subsides, legacies can develop, with effects on organisms and ecosystems (De Boeck et al., 2018; Monger et al., 2015; Petrie et al., 2018; Sala et al., 2012). Drought legacies are often negative (relative to the baseline) in grasslands and forests (Anderegg et al. 2015; Sala et al., 2012), although positive legacies have been observed (Griffin-Nolan et al., 2018). Drought legacies can be abiotic, driven by carryover effects of soil moisture (Bisigato et al., 2013; Sherry et al., 2008, 2012), or biotic, driven by changes in individual plants (e.g. changes in tillers, stolons or axillary bud production; Reichmann & Sala, 2014) and/or shifts in the plant community (e.g. mortality, community reordering; Hoover et al., 2014; Smith, 2011). The resilience of a given ecosystem determines the

magnitude and duration of such legacies, and often quantified by recovery rate or return time to baseline conditions (Ingrish & Bahn, 2018). If recovery is not complete before a subsequent drought, then drought legacies can impact the resistance to the next event by altering the pre-event baseline. Thus, legacies can affect the resistance to current environmental conditions and are a product of resistance and resilience to past events.

Experiments and observations suggest that grass-dominated drylands tend to have both low resistance and resilience to drought and thus have a higher likelihood of developing drought legacies as well as being affected by legacies of past droughts (Sala et al., 2012; Stuart-Haëntjens et al., 2018). In drylands, plant phenology and growth are often driven by periodic moisture availability, with plants adapted to maximize growth when water is available (Collins et al., 2008, 2014; Noy-Meir, 1973; Reynolds et al., 2004; Schwinning & Kelly, 2013). The seasonal timing of drought may affect soil moisture both temporally (e.g. during the growing season) and spatially (e.g. the vertical distribution within soil profile), leading to novel ecohydrological regimes and potential mismatches between plant life cycles and phenology (Knapp et al., 2020). These effects will largely depend on local plant adaptations to historical seasonal patterns of water availability (Schwinning & Ehleringer, 2001; Siepielski et al., 2017; Williams et al., 2017). Therefore, the seasonal timing of drought can have a large effect on concurrent ecological responses and the development of legacies in dryland ecosystems.

Given that water is the most limiting factor in drylands, competition for this resource should be high within plant communities. However, variation in plant functional traits can allow for the stable coexistence of species within a plant community by facilitating spatial and temporal niche partitioning (Reich, 2014; Reynolds et al., 2007; Schwinning & Ehleringer, 2001; Silvertown et al., 2015). The ecohydrological niche of dryland ecosystems may be governed by differences in rooting depths (spatial partitioning) or phenological timing (temporal partitioning), allowing plants to avoid direct competition for water resources (Lauenroth et al., 2014; Nobel, 1997; Reynolds et al., 2004; Schwinning & Kelly, 2013; Silvertown et al., 2015). For example, interactions between shrubs and grasses can be neutral through vertical partitioning in the soil profile, wherein grasses utilize shallow soil moisture and shrubs access deeper soil moisture (e.g. Walter's two-layer model; Walter, 1973). However, without ecohydrological niche partitioning, shrubs and grasses may compete for water resources, particularly during drought years (e.g. Pierce et al., 2018) when the plant community is 'drinking from the same cup' (sensu Hunter, 1989; Reynolds et al., 2004). Thus, a given

species' success during and following drought may be determined by its spatial and temporal ecohydrological niche, and its ability to compete for water with the neighbouring plant community.

In the Colorado Plateau, situated in the southwestern United States, seasonal soil moisture availability is driven by the balance of cool- and warm-season precipitation patterns and evaporative demand (Comstock & Ehleringer, 1992; Gremer et al., 2015). The ecohydrology of the region supports a wide range of perennial grasses, forbs, shrubs, cacti and annual plant species that exhibit differential responses to changes in water availability (Gremer et al., 2015; Hoover et al., 2015, 2017; Munson et al., 2011; Thoma et al., 2018; Winkler et al., 2019; Witwicki et al., 2016). In this region, cool-season (C_3 photosynthesis) and warm-season (C_4 photosynthesis) grasses overlap phenologically for much of the year, despite differences in photosynthetic pathways and optimal temperatures. Spring is the ideal growing times for cool-season grasses due to low temperatures and high soil moisture, yet C_4 grasses can complete all phenological stages during this period as well (Comstock & Ehleringer, 1992). On the other hand, during the summer, both grasses can be active if monsoon rains deliver sufficient moisture, despite hotter conditions often favouring warm-season grasses (Comstock & Ehleringer, 1992; Schwinning et al., 2008). Such phenological difference may be due to physiological trait variation, as warm-season grasses are able to maintain higher photosynthetic rates and water use efficiencies than cool-season grasses as temperatures increase seasonally (Winkler et al., 2020). This study focuses on two dominant perennial grasses species, Indian ricegrass (*Achnatherum hymenoides* Roem. & Schult.), a C_3 perennial bunchgrass, and James' galleta (*Pleuraphis jamesii* Torr.), a C_4 perennial rhizomatous grass and their interaction with Mormon tea (*Ephedra viridis* Coville), a common C_3 shrub. These three species vary in their responses to water availability, with *A. hymenoides* the most sensitive, *E. viridis* the least and *P. jamesii* intermediate (Hoover et al., 2015, 2017, 2019; Munson et al., 2011; Winkler et al., 2019). Additionally, long-term observations suggest that populations of *E. viridis* are expanding in the region, while *P. jamesii* populations are stable, and *A. hymenoides* populations are contracting (Munson et al., 2011). While the mechanisms driving these plant community changes have yet to be resolved, differences in photosynthetic pathway, rooting structure and phenology have been proposed as potential factors (Hoover et al., 2015, 2017, 2019; Munson et al., 2011; Winkler et al., 2019, 2020).

In this study, we investigated the resistance and resilience of a native mixed grass-shrubland of the Colorado Plateau to repeated seasonal droughts with a focus on concurrent and legacy effects of drought. The experiment consisted of three precipitation treatments (ambient precipitation, warm-season drought and cool-season drought), applied in two plant communities (grasses with or without neighbouring *E. viridis*; Figure 1). We focused on phenology and above-ground biomass responses of *A. hymenoides* and *P. jamesii* to understand species-level resistance and resilience to differences in seasonal timing of drought and the interactive effects of plant community with drought. Following the framework of Ingrisch and Bahn (2018), we quantified resistance and resilience as a comparison

between control and drought treatments in our experiment. Drought resistance was assessed by quantifying the difference between control and drought treatments during the seasonal drought treatment period (concurrent effects), whereas drought resilience was assessed by quantifying the differences (i.e. magnitude and duration) between control and drought treatments when seasonal drought treatments were not imposed (legacy effects).

Our study tested four hypotheses. First, we expected both seasonal drought treatments to have negative concurrent and legacy effects on soil moisture (abiotic response), where soil moisture in drought treatments is reduced relative to ambient conditions. The duration and magnitude of the concurrent and legacy drought effects on soil moisture should be driven by the timing and amount of ambient precipitation. As a drought treatment begins or ends, precipitation will cause divergence (at drought treatment beginning) or convergence (after drought treatment ends) with the ambient precipitation treatment. Second, we predicted that such reductions in soil moisture would impact the phenology and above-ground biomass (biotic responses) for both grass species but that drought treatments would have differential effects on the grasses. Specifically, we expected the cool-season grass, *A. hymenoides*, to be more sensitive to cool-season drought and the warm-season grass, *P. jamesii*, to be more sensitive to the warm-season drought. Third, we expected that due to these sensitivities, biotic legacies (e.g. prolonged effects on phenology or biomass) would develop and increase in magnitude over time with repeated droughts. Fourth, we predicted that there would be an interaction between plant community and drought treatment, with stronger (more negative) drought effects on phenology and biomass in plots with *E. viridis*, relative to those without. Walter's two-layer model (Walter, 1973), suggests that below-ground niche partitioning will lead to reduced competition between grasses and shrubs. However, while rooting information on *E. viridis* is limited, *E. nevadensis* (a nearby relative) has most of its fine roots in the 20–30 cm depth (in addition to deep >2 m roots), where perennial grasses are also primarily rooted (Hoover et al., 2019). Thus, we expect there will be an increased competition for water between *E. viridis* and the grasses in shallow layers, where water is most abundant seasonally, due to limited below-ground vertical niche partitioning (Hoover et al., 2017; Pierce et al., 2018).

2 | MATERIALS AND METHODS

2.1 | Site description

This study was conducted in a native grass-shrubland community in the Colorado Plateau in southeastern Utah, USA (38.19°N, 109.75°W; 1505 m elevation), near Canyonlands National Park (Figure 1a). In 2015, we established a 3.2-ha study enclosure in a site with a history of light winter cattle grazing prior to fencing. Soils at the site are deep (>1.5 m) with loamy fine sand texture and little variability in soil texture across space and depth. The plant community is dominated by native shrubs, forbs and perennial grasses. In the study plots prior

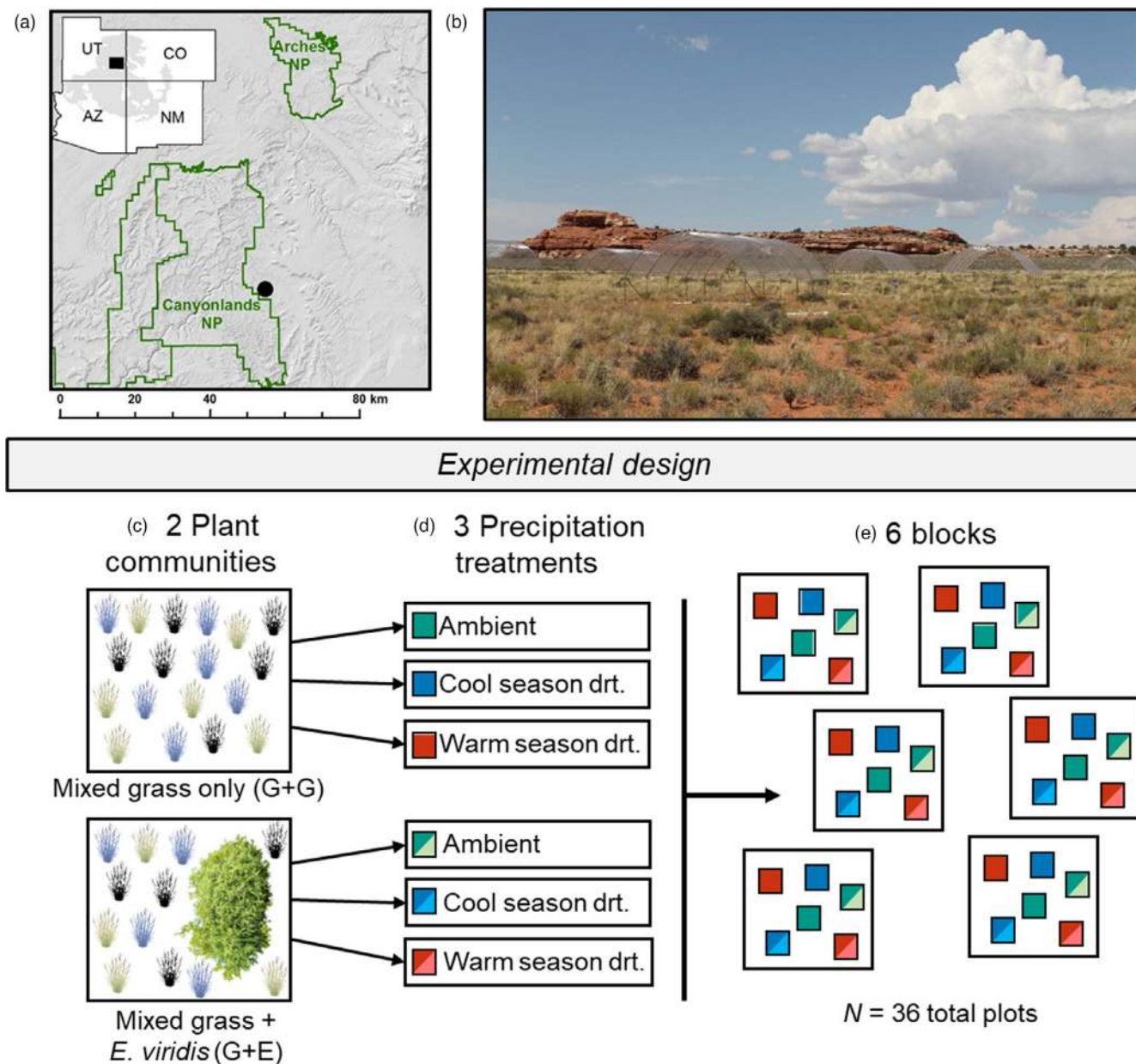


FIGURE 1 Site location and experimental design. (a) Map of study site. The study site (black dot) is situated on the Colorado Plateau (grey-shaded area on inset map) just outside the Needles District of Canyonlands National Park (NP) in southeastern Utah, USA. (b) Photograph of study site. Thirty-six 4 × 4 m plots were situated in a random stratified design in an enclosed 3.2-ha native grassland. (c) Five individuals each of *Achnatherum hymenoides* (dominant C_3 or cool-season grass species) and *Pleuraphis jamesii* (dominant C_4 or warm-season grass species) were tagged on one half of each plot containing a mixed grass only (G + G), or mixed grass and *Ephedra viridis* (dominant shrub) community (G + E). Biomass and phenological timing of the tagged grass individuals were monitored throughout the duration of the experiment. (d) Each plot was subjected to one of the three experimental drought treatments: ambient control (ambient precipitation year-round), warm-season drought (66% ambient precipitation excluded from May to October), cool-season drought (66% ambient precipitation exclusion from November to April). (e) Total sample size. $N = 2$ communities × 3 drought treatments × 6 blocks = 36 total plots

to treatments (spring 2015), *A. hymenoides* and *P. jamesii* were 63% of the grass relative cover, while *E. viridis* was the most dominant plant (33% of the relative cover of all plants). The climate in this region is characterized as continental, with cool winters (mean low temperature = -6.5°C), warm summers (mean high temperature = 32.7°C) and low precipitation (mean annual precipitation = 221 mm; Gremer et al., 2015). While average monthly precipitation is fairly consistent

throughout the year, water availability is not, due to differences in temperature and evaporative demand (Comstock & Ehleringer, 1992; Gremer et al., 2015). Low potential evapotranspiration in the cool season (November through April) allows for soil moisture recharge in the spring, when plants initiate growth and can complete all phenological stages (Comstock & Ehleringer, 1992). A second green-up can occur in summer during the monsoon season (July through

September), though the monsoon intensity has high inter-annual variability (Comstock & Ehleringer, 1992).

2.2 | Experimental design

The ecohydrology of this region allowed us to design a unique precipitation manipulation experiment examining the effects of seasonal timing of drought on this ecosystem in two community types. We applied three precipitation manipulation treatments: control (ambient precipitation year-round), cool-season drought (66% ambient precipitation excluded from November to April) and warm-season drought (66% ambient precipitation excluded from May to October; Figure 1). We randomly assigned precipitation treatments to two community types based on the presence or absence of the shrub *Ephedra viridis* in one half of each plot ('G + G' = grass only community and 'G + E' = grass with *E. viridis* community; Figure 1c).

Within the fenced study area, we used a stratified random approach to select 4 × 4 m plots. First, to identify candidate G + E plots, we mapped and measured the volume of each *E. viridis* individual (or patch if more than one individual was intertwined) within the fenced area ($N = 83$; volume estimated using length, width and height measurements) and recorded the abundance of perennial species cover in the adjoining 4 × 2 m area. To identify candidate G + G plots, we randomly select 48 points >10 m from any *E. viridis* individual and conducted abundance surveys of perennial species cover in the 4 × 4 m area surrounding each point. We then selected 18 G + E plots that were (a) most similar in terms of *E. viridis* volume and adjoining perennial grass composition and (b) >10 m apart from other plots to accommodate drought infrastructure. Next, we selected 18 G + G plots with a perennial grass composition most similar to those in the G + E plots. We organized the plots into six experimental blocks, each containing one replicate of each drought and community treatment combination, with drought treatments randomly assigned ($n = 36$ total plots; Figure 1).

We applied precipitation treatments with passive precipitation reduction shelters that excluded precipitation by 66% (Figure 1b; Yahdjian & Sala, 2002). To buffer the experiment against high inter-annual variability in precipitation, we selected a 66% precipitation reduction magnitude because it would result in an extreme drought (<5th percentile) in all but very wet years (Hoover et al., 2018). Each shelter consisted of a 20' × 30' cold frame greenhouse structure (Stuppy, Kansas City, Missouri, USA), partially covered (75%) with strips of clear polycarbonate plastic (Dynaglas Plus, PALRAM Industries, Kutztown, Pennsylvania, USA) that removes approximately 66% of ambient precipitation away from the plot (Hoover et al., 2015). Over a 3-year period, shelters were moved between cool- and warm-season plots, ending one seasonal drought and starting the other in late October (start of cool-drought treatment) or April (start of warm-drought treatment). To hydrologically isolate all plots (including ambient), aluminium flashing was installed 10 cm above-ground and plots were trenched to a depth of 1 m and wrapped in two layers of 6-mil polyethylene sheeting.

2.3 | Precipitation and soil moisture

Precipitation was measured on site using an hourly tipping rain gauge (TE25MM, Texas Electronics, Dallas, TX). Within each plot, soil moisture was recorded at 30-min intervals, at shallow (5–25 cm) and deep (30–50 cm) depths using 30-cm soil moisture and temperature sensors (CS650, Campbell Scientific, Logan, UT, USA), inserted diagonally (45°) in the centre of each plot ($N = 2$ sensors × 36 plots = 72 sensors). To calculate soil apparent permittivity, we applied manufacturer-provided equations and converted values to soil volumetric water content using the Topp et al. (1980) equation, then averaged these values to obtain daily means used for analysis.

2.4 | Phenology and biomass

We measured above-ground biomass in the spring (April) and fall (September), and plant phenology biweekly on five individuals of each of the two target grass species (*A. hymenoides* and *P. jamesii*) per plot ($N = 5$ individuals × 36 plots = 180 tagged individuals per species). All monitored individuals were tagged and assigned unique identifiers to enable biweekly greenness estimates (%) during 2016 and 2017. During biweekly phenology sampling, each tagged individual was assessed for greenness. For a given individual, plant greenness was visually estimated as the cover of green tissue (0%–100%). We then calculated the following phenological metrics for each individual and year: (a) start of season, defined as the earliest day of the year on which the individual was not dormant (greenness >0%); (b) end of season, defined as the last day of the year on which the individual was not dormant; (c) growing season length, defined as the number of days between the start and end of the growing season for each individual. If individuals never presented green tissue, values of '0' were assigned to growing season length, but no values were assigned to the start or end of the growing season.

To estimate the above-ground biomass of each tagged individual, we used a combination of non-destructive morphological measurements within plots and morphological measurements with destructive harvest along nearby transects. For both grass species, we measured plant height, length, width and basal circumference, as well as the number of live culms, green leaves and green inflorescences of all 'clumps' pertaining to a tagged individual during peak greenness each spring and fall throughout the experiment. For *A. hymenoides*, we considered any intraspecific clumps <3 cm from a central tagged clump part of the same individual; for *P. jamesii*, we used the same criteria but, due to its rhizomatous nature, constrained each individual to a 20-cm circular area. We sampled the same morphological measurements and clipped the above-ground green biomass from eight individuals per species along an east-west 12-m transect within the block but outside plot boundaries. Biomass samples were transported to the laboratory, dried for 48 hr at 60°C and weighed to the nearest 0.01 g ($N = 8$ individuals × 6 blocks = 48 biomass samples per species per

sampling period). We then used data from the transects outside the plots to develop linear allometric models estimating biomass within the plots. Specifically, we built multiple linear regression models ('lm' function in *stats* package, R v3.5.1) for each species (*A. hymenoides* or *P. jamesii*) and biomass sampling season (spring or fall) to predict green biomass for individuals within a plot-based plant volume (calculated using a truncated cone model based on basal circumference and plant height, length and width measurements), number of green culms, number of green leaves and number of green inflorescences (Table S1). All model explained >75% of biomass variance (adjusted $R^2 = 0.80, 0.80, 0.76$ and 0.91 for spring *A. hymenoides*, spring *P. jamesii*, fall *A. hymenoides* and fall *P. jamesii* models respectively).

2.5 | Statistical analysis

To assess the effects of precipitation treatment, day and plant community type on daily volumetric water content, we analysed soil moisture with linear mixed effects models using the 'lmer' function in the R package *LME4* (Bates et al., 2015). Models for shallow and deep soil moisture were run independently, with precipitation treatments, community and day of the experiment (e.g. first day of experiment = day 1) as fixed effects, and plot nested within block as random effect. To assess when warm- and cool-drought treatments diverged from ambient, we used differences in the 95% confidence interval between treatments. Concurrent precipitation effects occurred when drought treatments were different from ambient during the treatment (e.g. soil moisture in warm-drought treatment different from ambient during the warm drought). In this study, we define a drought legacy when a drought treatment diverged from ambient when the treatment was not imposed (e.g. soil moisture in warm-drought treatment different from ambient during the cool-drought period). Furthermore, we quantified concurrent and legacy effects of soil moisture as negative if the volumetric water content was lower in the treatment relative to ambient and positive if greater than ambient.

We built linear mixed effects models using the 'lmer' function in R to predict variation in above-ground biomass and three phenological metrics (start of season, end of season and growing season length). Initial saturated models indicated strong differences in responses among seasons (spring and fall) and target species (*A. hymenoides* and *P. jamesii*); therefore, all models presented here have been subset by season and species. Models included precipitation treatment, community and year as fixed effects, and individual nested within plot and block as random effects. To assess significant differences among groups, we calculated post hoc Tukey's pairwise differences. For all analyses, response variables were transformed as needed to increase conformance to normality. All analyses were performed in R v. 3.3.2 (R Foundation for Statistical Computing, Vienna, Austria). The datasets described are available through the USGS ScienceBase-Catalog (Geiger et al., in prep).

3 | RESULTS

3.1 | Precipitation and soil moisture

During the first experimental year (29 April 2015–26 April 2016), precipitation was above the long-term average of 210 mm (265.2 mm), while the second (27 April 2016–25 April 2017) and third years (26 April 2017–27 April 2018) were both below average (194.0 and 171.6 mm respectively; Table S2 and Figure 2a). Historically, precipitation is almost evenly split between warm and cool seasons, with 54% occurring during the warm season (May–October) and 46% occurring in the cool season (November–April). However, during the 3 years of this study, precipitation shifted more towards the warm season, which received 67% of the annual rainfall (422.7 mm total), while 33% occurred during the cool season (208.1 mm total). Therefore, despite having the same precipitation reduction (66%) over the same length of time (three, 6-month periods), the warm-season treatments received more total precipitation than the cool-season treatments (493.5 versus 351.8 mm respectively) during this experiment (Table S2).

Concurrent drought treatment effects on soil moisture were negative (less than ambient), with the largest effects in the shallow depths (Table 1 and Table S3; Figure 2). The negative effects on shallow soil moisture occurred in both treatments, with the warm-season drought less than ambient 48% of the time, and the cool-season drought less than ambient 49% of the time (Table S3; Figure 2). Concurrent drought effects on deep soil moisture rarely occurred (warm season, 4%; cool season, 0%; Table S3; Figure 2). During first drought periods, shallow soil moisture was lower than ambient for 106 days in warm-season drought, but only 7 days in cool-season drought. During the second and third experimental years, concurrent effects of drought on shallow soil moisture were pronounced for both warm- and cool-season drought treatments (43%–68% of the time), with only minor impacts at deep soil moisture (Table S3; Figure 2).

Both positive and negative legacy effects on soil moisture occurred in both drought treatments. When the first warm-season drought treatments ended (shelters moved to cool-season drought in October), a negative soil moisture legacy persisted at shallow depths for 48 days, and deep depths for 102 days (Table S3; Figure 2). Following the second warm-season drought, there was a 36-day negative soil moisture legacy at shallow depths (Table S3; Figure 2). During the six treatment periods, there were no negative legacies of the cool-season treatment at either depth (Table S3; Figure 2). However, we observed positive soil moisture legacies for both warm- and cool-season droughts, where soil moisture was higher in formerly droughted plots than ambient, often long after drought shelters were removed (Table S3; Figure 2). For example, despite the treatments ending in the fall, shallow soil moisture in the warm-season drought treatment was higher than ambient every spring for 5–17 days when plant green-up was occurring (Table S3; Figure 2). The positive legacy of the cool-season drought was also apparent in the third warm period when soil moisture increased at both shallow (44 days) and deep (31 days) soil depths (Table S3; Figure 2). These

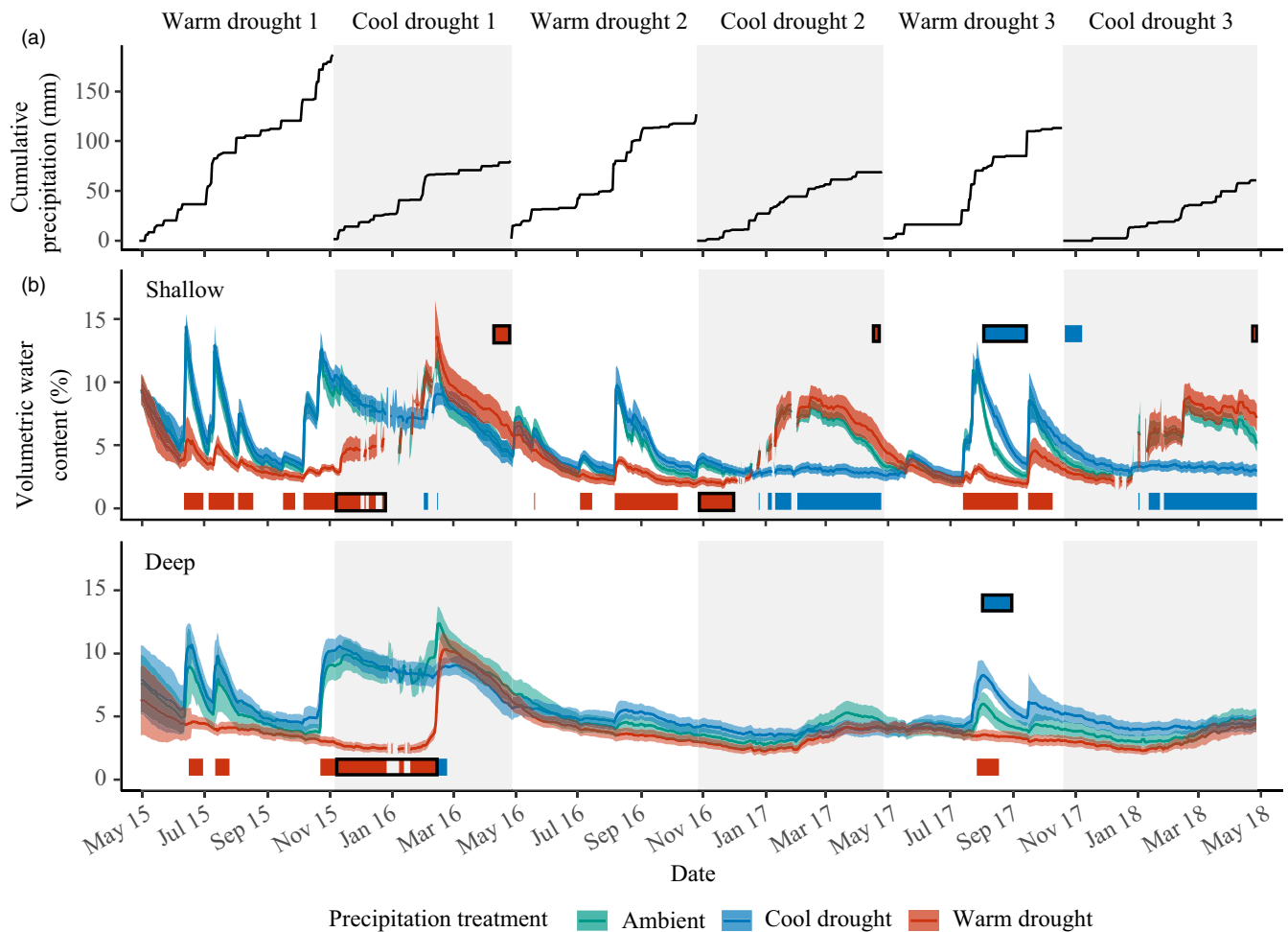


FIGURE 2 Precipitation and soil moisture. Hydrological dynamics through six experimental drought periods (light red shading: warm-season drought periods; light blue shading: cool-season drought periods). (a) Cumulative daily precipitation for each drought period (see Table S2 for more details). (b) Volumetric water content at shallow (5–25 cm) and deep (30–50 cm) soil depths. Lines indicate treatment means ($n = 12$ plots) and shading around each line indicates 95% confidence interval. Dark red and blue bars above and below soil moisture lines indicate warm-season or cool-season drought treatment differences from ambient respectively. Bars above soil moisture lines indicate treatments are greater than ambient (positive effect), while bars below indicate they are less than ambient (negative effect). Bars without black borders are current treatment effects, while those with black borders are drought legacies. Data were removed when soil temperatures were at or below freezing

increases in soil moisture primarily occurred in response to a monsoon rain pulse in the late summer of 2017 (Figure 2).

3.2 | Phenological responses

Both seasonal drought treatments had strong impacts on phenology, with the effects of drought, year and drought \times year significant for both *A. hymenoides* and *P. jamesii* (Table 2). The warm-season drought treatments in 2016 reduced growing season length by 34 days for *A. hymenoides* and 29 days for *P. jamesii*, due to an earlier end of the growing season (i.e. advanced senescence; Figure 3). In 2017, both warm- and cool-season drought treatments reduced the growing season length of both species, but through different mechanisms. Specifically, individuals experiencing cool-season drought had a shorter growing season due to a delayed start to the growing season

(i.e. later green-up), whereas individuals experiencing warm-season drought senesced earlier (Figure 3). Seasonal drought treatments also affected the growing seasons of the two species differently. Cool-season drought had a larger effect on *A. hymenoides*, reducing the growing season by 153 days, while warm-season drought only reduced it by 82 days (Figure 3). However, we found no significant differences in *P. jamesii* growing season length between warm- or cool-season drought treatments (Figure 3). The timing and magnitude of the effect of cool-season drought relative to ambient on plant greenness also differed among the two species in 2017. Specifically, *P. jamesii* greenness in the cool-season treatment converged with ambient at day of year (DOY) 208, corresponding with a large increase in soil moisture in cool-season drought treatment plots (Figures 2 and 3). On the other hand, *A. hymenoides* greenness in the cool-season drought treatment did not converge with ambient levels until DOY 304, corresponding with a second pulse in soil moisture later in the growing season (Figures 2 and 3).

TABLE 1 Soil moisture ANOVA. Repeated-measures mixed-model ANOVA of soil moisture at shallow (5–25 cm) and deep (30–50 cm) depths. Bold indicates significant effects ($p < 0.05$)

Soil moisture depth	Effect	Chi.sq	df	p
Shallow	Drought	6.7	2	0.035
	Day	2,280.4	1	<0.001
	Community	1.7	1	0.189
	Drought:Day	2,001.1	2	<0.001
	Drought:Community	2.2	2	0.332
	Day:Community	0.6	1	0.442
	Drought:Day:Community	22.7	2	<0.001
Deep	Drought	7.1	2	0.029
	Day	11,857.8	1	<0.001
	Community	0.1	1	0.816
	Drought:Day	1,084.7	2	<0.001
	Drought:Community	4.1	2	0.127
	Day:Community	258.0	1	<0.001
	Drought:Day:Community	0.1	2	0.951

TABLE 2 Phenology ANOVA. Repeated-measures mixed-model ANOVA of phenological metric for the two focal grasses. Bold values indicate significant effects ($p < 0.05$)

Phenology metric	Effect	<i>A. hymenoides</i> (C ₃)			<i>P. jamesii</i> (C ₄)		
		Chi.sq	df	p	Chi.sq	df	p
Growing season start	Drought	378.5	2	<0.001	348.0	2	<0.001
	Community	0.5	1	0.479	0.5	1	0.474
	Year	135.8	1	<0.001	399.6	1	<0.001
	Drought:Community	4.3	2	0.114	2.9	2	0.240
	Drought:Year	546.5	2	<0.001	622.6	2	<0.001
	Community:Year	0.5	1	0.487	0.0	1	0.945
	Drought:Community:Year	2.9	2	0.232	7.4	2	0.025
Growing season length	Drought	69.5	2	<0.001	38.1	2	<0.001
	Community	0.9	1	0.335	0.4	1	0.550
	Year	108.5	1	<0.001	82.8	1	<0.001
	Drought:Community	5.5	2	0.065	0.8	2	0.679
	Drought:Year	200.6	2	<0.001	80.3	2	<0.001
	Community:Year	4.8	1	0.028	0.0	1	0.933
	Drought:Community:Year	5.1	2	0.076	1.9	2	0.389
Growing season end	Drought	52.4	2	<0.001	142.4	2	<0.001
	Community	0.3	1	0.570	0.8	1	0.360
	Year	6.7	1	0.010	3.3	1	0.069
	Drought:Community	1.3	2	0.517	2.2	2	0.326
	Drought:Year	8.4	2	0.015	33.7	2	<0.001
	Community:Year	2.1	1	0.149	0.3	1	0.567
	Drought:Community:Year	2.8	2	0.248	4.1	2	0.128

Despite our hypothesis that *E. viridis* would have negative, interactive effects with drought, the effects of community type on phenology were minor (Table 2). For both *A. hymenoides* and *P. jamesii*, we found no significant main effects of community type or drought

× community interaction on any phenological metrics (Table 2). For *A. hymenoides*, there was a significant interaction between year and community for growing season length, with the growing season 18 days shorter for individuals growing in G + E plots relative to those in G + G

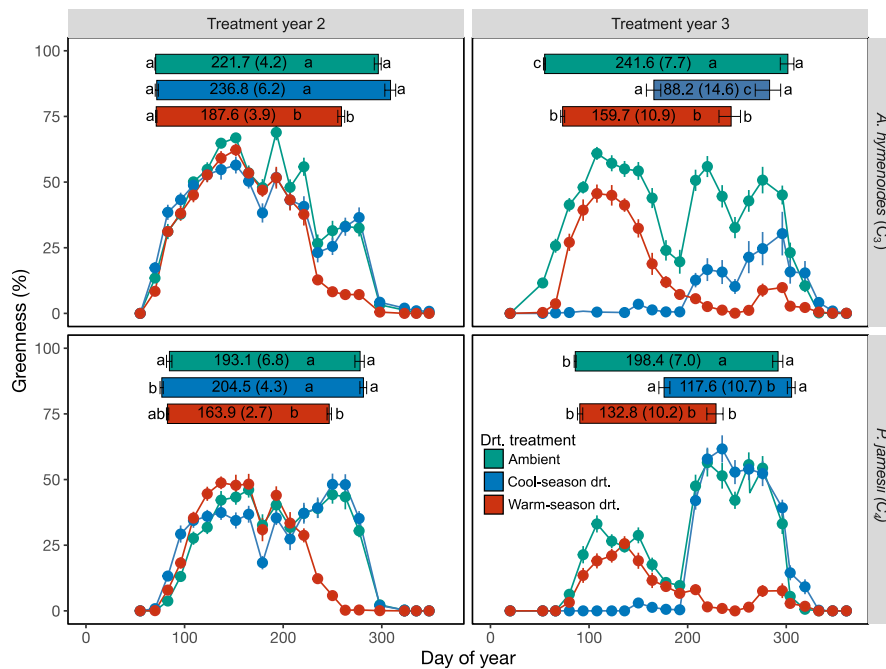


FIGURE 3 Phenology. Plant greenness over time for the two dominant grasses. In the bottom portion of each panel, lines connect biweekly phenological means (points) and error bars (± 1 SE) for each precipitation treatment. In the upper portion of each panel, bars indicate phenological metrics, with the left side indicating mean start of growing season and right side indicating mean end of growing season, and error bars (± 1 SE) for each precipitation treatment. The width of the bars = length of growing seasons, with the mean value, and error (± 1 SE) in parentheses, listed inside each bar. Letters denote significant treatment differences for each species, year and phenology metric. Drt. = drought

Effect	Fall			Spring		
	Chi.sq	df	p	Chi.sq	df	p
<i>A. hymenoides</i>						
Drought	40.553	2	<0.001	73.852	2	<0.001
Year	411.656	2	<0.001	340.178	2	<0.001
Community	5.185	1	0.023	3.997	1	0.046
Drought:Year	105.999	4	<0.001	123.992	4	<0.001
Drought:Community	1.426	2	0.490	2.479	2	0.290
Year:Community	5.81	2	0.055	3.053	2	0.217
Drought:Year:Community	9.966	4	0.041	2.732	4	0.604
<i>P. jamesii</i>						
Drought	111.385	2	<0.001	69.482	2	<0.001
Year	73.962	2	<0.001	368.293	2	<0.001
Community	1.683	1	0.195	0.264	1	0.607
Drought:Year	106.073	4	<0.001	220.961	4	<0.001
Drought:Community	2.881	2	0.237	4.6	2	0.100
Year:Community	1.625	2	0.444	1.862	2	0.394
Drought:Year:Community	5.942	4	0.204	30.293	4	<0.001

TABLE 3 Biomass ANOVA. Repeated-measures mixed-model ANOVA of above-ground biomass for the two focal grasses. Bold values indicate significant effects ($p < 0.05$)

plots. Additionally, there was a significant drought \times community \times year interaction for growing season start in *P. jamesii* (Table 2), but Tukey-adjusted pairwise comparisons failed to find a significant difference between community types within a precipitation treatment and year.

3.3 | Biomass

We observed strong effects of drought, year and drought \times year on individual biomass for both species in both seasons (Table 3).

Overall, drought effects were minor in the first year, with larger effects emerging in the second and third experimental years. During the first experimental year, we found no significant effects of the drought treatments for *A. hymenoides* in either season (Figure 4). Conversely, *P. jamesii* fall biomass was 37% lower in the warm-season drought treatment than ambient or the cool-season drought treatment in the first year (Figure 4). In year 2, fall biomass of both species had decreased significantly under the warm-season drought treatment (*A. hymenoides*, 60.7% decrease; *P. jamesii*, 90.2% decrease relative to ambient; Figure 4). During the spring of year 2, there were

no legacy effects of the previous year's warm-drought treatment, as biomass for both species recovered to ambient levels (Figure 4). The cool-season drought had large effects on spring biomass in year 2, resulting in almost no growth for *A. hymenoides* and *P. jamesii* (98.4 and 100% decreases from ambient biomass respectively; Figure 4).

During the third experimental year, legacy effects from prior seasons' drought treatment were evident for *A. hymenoides* biomass, whereas *P. jamesii* biomass continued to respond only to the concurrent effects of the drought treatment. In the fall of year 3, both species produced significantly lower biomass in the warm-season drought treatment (relative to the ambient control), indicating concurrent responses to the treatments, and *A. hymenoides* still produced less biomass under cool-season drought, indicating a legacy effect. Similarly, in the spring of the third experimental year, both species produced significantly less biomass under cool-season drought, whereas only *A. hymenoides* produced significantly less biomass under warm-season drought relative to ambient (Figure 4). The divergent impacts of drought legacies on the two grasses were also apparent when examining the main effects of drought treatment on biomass. For *P. jamesii*, the effects of drought were only significant immediately following the period of drought (i.e. warm-season drought affecting the following fall biomass and cool-season drought affecting the following spring biomass), whereas for *A. hymenoides*, there were significant effects of both drought treatments in both seasons (Figure 4).

Plant community did not have strong interactive effects with drought on above-ground biomass (Table 3). We found a main effect of community on *A. hymenoides* biomass, with significantly lower biomass in G + E plots, although this difference was observed in pre-treatment biomass (spring 2015 biomass was 22% lower in G + E; $\chi^2 = 5.78$, $df = 1$, $p = 0.016$), suggesting a pre-existing community-level difference unrelated to the experimental

treatments. Biomass of both species was affected by a significant three-way interaction of drought \times year \times community (*A. hymenoides* in the fall and *P. jamesii* in the spring; Table 3). However, Tukey post hoc comparisons of this interaction show differences among the drought treatments within a given community and year, but no differences between communities within a drought treatment and year. This suggests that the presence of *E. viridis* did not alter the effects of drought for either species.

4 | DISCUSSION

In this study, we investigated the effects of drought seasonality and plant community on the resistance and resilience of two dominant perennial grasses in a dryland ecosystem. We observed both the concurrent and legacy effects of seasonal droughts on soil moisture, plant phenology and biomass. Drought treatments had strong concurrent effects on soil moisture, particularly in the shallow soil layers. Legacy effects on soil moisture manifested as either negative soil moisture legacies persisting once seasonal drought treatments ended, or as positive soil moisture legacies emerging months after treatment cessation. These changes in soil moisture with drought affected the phenology and above-ground biomass of both grasses. Drought treatments reduced growing season length due to shifts in green-up and senescence, while reductions in above-ground biomass occurred and grew larger through time. Biotic legacies emerged in year 2 of the treatments and were most pronounced in year 3. While we observed differential sensitivity to drought seasonality between the two grasses, we found limited evidence of plant community (shrub presence or not) interactive effect with the drought treatments. The results from this study highlight how resistance and resilience of an ecosystem

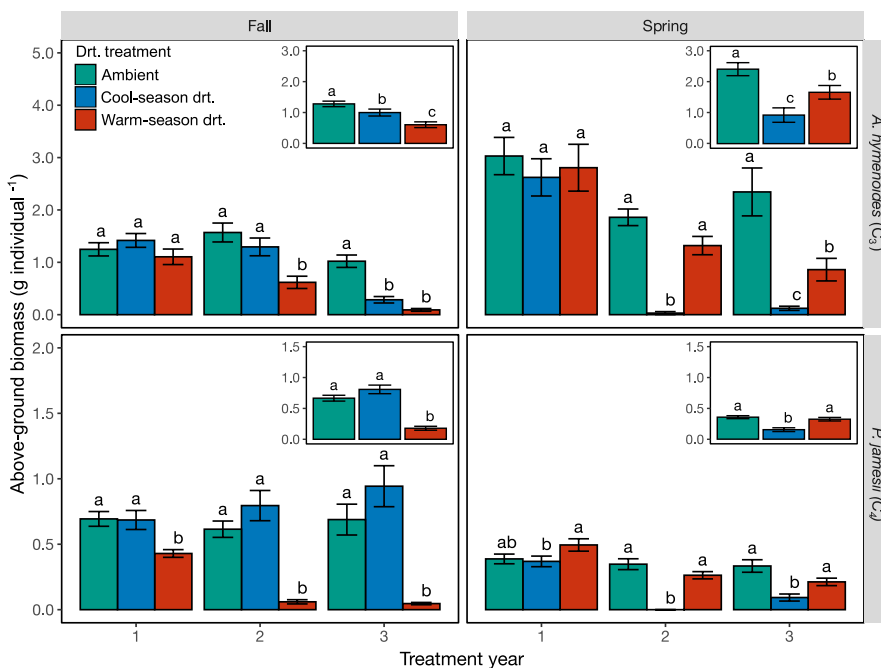


FIGURE 4 Above-ground biomass. Above-ground biomass for each species, precipitation treatment and season. Precipitation treatments began in May 2015, so drought treatment years are as follows: 1 = Fall 2015, Spring 2016; 2 = Fall 2016, Spring 2017; 3 = Fall 2017, Spring 2018. Bars represent mean individual above-ground biomass (± 1 SE), with inset graphs showing the means averaged across years. Letters denote significant differences. Drt. = drought

to drought is influenced by abiotic and biotic interactions and the emergence of legacies.

4.1 | Concurrent and legacy effects of drought—Abiotic responses

Consistent with our first hypothesis, we observed both the concurrent and legacy effects of seasonal drought on soil moisture. Both drought treatments effectively reduced soil moisture at shallow and deep depths, despite greater overall precipitation amounts during the warm-season drought periods of the experiment. These concurrent effects were much stronger in shallow than deep soil moisture depths (Table S3; Figure 2), a result similar to the study by Schwinning et al. (2005). At shallow depths, soil moisture was reduced in every drought period for almost half of the time (Table S3), except the first cool-season drought. This latter exception was due to prolonged storage of soil moisture from a large October storm event occurring immediately before the start of the first cool-season drought treatment (Figure 2). We also observed no effects of this first cool-season drought on phenology or biomass (Figures 3 and 4), suggesting that such large precipitation events in the fall can store soil moisture and serve as a short-term abiotic ecosystem buffer against cool-season precipitation deficits. The importance of fall precipitation on plant growth has been observed in other dryland ecosystems (Li et al., 2015).

Negative soil moisture legacies were evident under both drought treatments, with moisture deficits lasting up to several months after the shelters were removed, suggesting that abiotic effects of drought can persist even once normal climatic conditions return (Table S3; Figure 2). Similar soil moisture legacy effects have been observed in other global change experiments, with legacy effects lasting up to 10 months (Sherry et al., 2008, 2012). In other experiments, high potential evapotranspiration rates can 'erase' soil moisture legacies as both control and drought treatments converge at very low soil moisture due to evaporative losses (Reichmann et al., 2013). As we observed in the first year of our cool-season drought treatment, very wet conditions can erase soil moisture drought legacies as well. This suggests that soil moisture legacies from experimental drought are contingent on soil moisture conditions both preceding and following the drought, with impacts on ecosystem resistance and resilience to drought.

Although we predicted negative soil moisture legacies, we also observed unexpected positive soil moisture legacies, wherein soil moisture in drought treatments was higher than ambient for several months after drought treatments ended (Figure 2). These results suggest a positive vegetation feedback on soil moisture, leading to higher water availability in drought treatments than the ambient control (Figure 2). Though subtle, this effect is most pronounced in the third year of the treatments and coincided with negative phenology and biomass legacies for *A. hymenoides* (Figures 3 and 4). While plant growth is limited by soil moisture availability, soil moisture is modified by vegetation through water use, thus there is a strong coupling between precipitation, soil moisture and vegetation in drylands (Noy-Meir, 1973).

We hypothesize that as *A. hymenoides* (and potentially other species with low drought resistance) reduced growth or died with drought, community-level water demand decreased. As a result, soil moisture remained high in formerly droughted plots relative to ambient plots. Thus, plant-mediated increases in soil moisture during recovery from drought could increase the availability of this critical dryland resource for surviving individuals of the extant plant community or open niche space for species immigration (Smith et al., 2009).

4.2 | Concurrent effects of drought—Biotic responses

Our results supported the hypothesis that both warm- and cool-season drought negatively affect growth and phenology of dominant warm- and cool-season grass species, but we found little evidence for species-specific responses to the concurrent effects of drought. Previous research suggests that cool-season C_3 grasses in this dryland ecosystem are more sensitive to reduced water availability than warm-season C_4 grasses (Gremer et al., 2015; Hoover et al., 2015, 2017; Munson et al., 2011; Thoma et al., 2018; Winkler et al., 2019; Witwicki et al., 2016). Expanding on this work, we hypothesized that each grass species would be more sensitive to drought during their respective optimal growing season. As previously noted, cool- and warm-season grasses can overlap phenologically during two distinct growth periods during the year: the cool, wet spring and the hot, summer monsoon (Comstock & Ehleringer, 1992). In drylands limited so severely by water, each species can evidently capitalize on soil moisture as it becomes available, even when temperatures are not optimal for their respective photosynthetic pathway (Comstock & Ehleringer, 1992; Schwinning et al., 2008).

Both warm- and cool-season drought treatments reduced the growing season of both species, and each type of drought seasonality affected a different critical phenological period for the grasses. Plants in the cool-season drought treatments greened-up later in the season and delayed the start of the growing season. In contrast, plants senesced earlier in the warm-season drought treatments, ending the growing season early (Figure 3). Such delays in growing season onset or advances in growing season ending with drought have been observed in other ecosystems (e.g. Cui et al., 2017; Kang et al., 2018). The only evidence we found for species-specific seasonal effects was during the first warm-season drought, which significantly reduced biomass in *P. jamesii* but not in *A. hymenoides* (Figure 4). *P. jamesii* can respond rapidly (via growth) to monsoon pulses in soil moisture (Schwinning et al., 2002), and two large precipitation events occurred during the first year of the warm-season drought. Therefore, it is likely that the significant increases in *P. jamesii* biomass that year may have been driven by pulses in growth for the ambient and cool-season drought treatments. During the second and third year of the drought treatments, both species responded with large decreases in biomass and reductions in growing season length (Figures 3 and 4).

4.3 | Legacy effects of drought—Biotic responses

In addition to concurrent treatment effects, we found strong evidence for biotic legacies with drought, as predicted. In the third experimental year, legacy effects emerged for both species (Figures 3 and 4). In the spring of 2017, green-up was delayed by 82 days in *A. hymenoides* and 81 days for *P. jamesii* in the warm-season drought treatment, even though this precipitation treatment concluded the previous October (Figures 3 and 4). We also observed a legacy effect on *A. hymenoides* biomass in the cool-season drought treatment, which was significantly reduced in the fall of 2016, but not for *P. jamesii* biomass (Figure 4). This suggests a differential response to drought legacies between the two species; the cool-season grass, *A. hymenoides*, had shifted phenology and reduced biomass, while *P. jamesii* only had shifted phenology. The C_4 photosynthetic pathway allows *P. jamesii* to more effectively utilize summer water pulses than *A. hymenoides*; this likely explains the fall 2017 phenological greenness 'recovery' of *P. jamesii* but not *A. hymenoides* to ambient levels in cool-season drought treatments (Figure 3).

The resistance and resilience of an ecosystem to drought is influenced by abiotic and biotic interactions and the emergence of legacies. In our study, soil moisture legacies from the prior seasonal drought treatment generally persisted until precipitation increased soil moisture in formerly droughted treatment to ambient levels, erasing the abiotic legacy. In some seasons, the length of the drought legacy was relatively short (days to weeks), but in others, it persisted for several months. This had direct effects on biotic responses, specifically by delaying spring green-up (Figure 3). However, in some cases when soil moisture legacies were erased by precipitation, we continued to observe biotic legacy effects. This suggests that when biotic legacy effects are uncoupled from abiotic legacies, there are likely physiological or morphological changes in plants (i.e. changes in carbon storage, rooting depth or allocation), which may have lasting effects on future growth, reproduction and/or survival. We observed the strongest biotic legacies in *A. hymenoides*, the cool-season grass with well-documented low drought resistance (e.g. Hoover et al., 2019; Munson et al., 2011; Winkler et al., 2019). Strong biotic legacies from drought may impede recovery and thereby reduce drought resilience. On the other hand, *P. jamesii* has a suite of traits that may allow for better drought resistance than *A. hymenoides*, including more conservative saturated hydraulic conductivity, lower root:shoot ratio and deeper maximum rooting depth (Hoover et al., 2019). Higher drought resistance can allow for quicker recovery post-drought (i.e. higher resilience) if the impacts during drought (relative baseline conditions) are reduced.

4.4 | Interaction between seasonal drought and the plant community

Although we predicted interactions between drought seasonality and plant community, there were no significant differences between G + E and G + G communities within a given drought treatment.

It is possible that this plant community follows Walter's two-layer model, wherein shrubs and grasses do not directly compete for soil moisture because of niche partitioning; rather, shrubs access deep water, while grasses utilize shallow water (Walter, 1973). However, we observed some evidence that the shrubs may be impacting soil moisture availability for the grasses. First, we observed a three-way interaction between drought treatment, plant community and day for shallow soil moisture (Table 1), with soil moisture slightly higher in G + G than G + E plots in both warm- and cool-season droughts, but these differences were transient and marginal. Second, there were main effects of community type on *A. hymenoides* biomass (Table 3), with biomass lower in G + E versus G + G plots. However, this effect was present pre-treatment, suggesting that such effects exist irrespective of drought. Combined, these results suggest that shrub-grass competition for water may occur in shallow depths but is not necessarily exacerbated by drought at the biotic level. Extensive surface and subsurface roots, photosynthetic evergreen stems and cavitation resistance are several traits of *E. viridis* that provide high drought resistance (Hoover et al., 2017; Winkler et al., 2019; Yoder & Nowak, 1999). Additionally, *E. viridis* can grow vegetatively from established individuals and has been expanding in the region (Munson et al., 2011). Thus, a combination of high drought resistance and resilience (e.g. post-drought vegetative growth) may provide *E. viridis* with the ability to survive and thrive in an increasingly drought-prone environment.

5 | IMPLICATIONS

These results have significant implications for the ecosystems and communities of the Colorado Plateau. Water availability is projected to decrease over the next century due to reduced precipitation and increased temperatures (Seager et al., 2007). Extreme droughts are projected to increase in frequency, duration and severity in the southwestern United States, with droughts potentially more likely in the cool season (Cook et al., 2014; Seager et al., 2007; USGCRP, 2017). On the other hand, other modelling projections for the drylands of North America suggest that soil water availability may be highest in the cool season and lowest in the warm season (Bradford et al., 2020). Results from this study suggest that the seasonal timing of drought can have large impacts on the phenology and biomass of two of the region's dominant grass species, which are key sources of forage for both native herbivores and livestock (Schwinning et al., 2008; Witwicki et al., 2016). While we did not observe the effects of drought on the grasses exacerbated by the shrub *E. viridis*, drought-induced grass mortality may open potential niche space for the vegetative expansion of *E. viridis* (Munson et al., 2011) or the immigration of non-native species (Smith et al., 2009).

This study also revealed how the interaction between soil moisture (abiotic), plants (biotic) and legacies affect individual species' resistance and resilience to drought. The concurrent effects of drought have been well-documented: precipitation deficits reduce soil moisture, which leads to a biotic water stress threshold which reduces

plant growth or eventually leads to plant mortality (Smith, 2011). By experimentally simulating both cool- and warm-season drought over a 3-year period, this study illuminated novel biotic and abiotic interactions and legacies with drought. Soil moisture legacies persisted for weeks to months after the drought treatments were removed, reducing plant growth until large precipitation events erased soil moisture deficits. We also observed a potential biotic–abiotic feedback where reduced growth or loss of individual plants with drought may have caused positive soil moisture legacies due to lower water demand from plants. In contrast to soil moisture legacies, biotic legacies took longer to emerge but were more prolonged and may result in lasting effects on ecosystem structure and function if resilience is low. Low rates of recovery from past droughts may reduce the resistance to future droughts, as reduced growth or mortality of individuals impact the starting baseline of the new event. The results from this study highlight how abiotic–biotic interactions and drought legacies can influence a community's resistance and resilience to drought.

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AUTHORS' CONTRIBUTIONS

D.L.H. and M.C.D. conceived and designed the experiment; D.L.H., M.C.D. and A.A.P. designed the methodology, analysed the data, wrote the manuscript and gave final approval for publication; D.L.H. and A.A.P. collected the data.

PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/1365-2745.13681>.

DATA AVAILABILITY STATEMENT

Data generated during this study are available from the USGS ScienceBase-Catalog <https://doi.org/10.5066/P9I9FXH9> (Hoover & Duniway, 2021).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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