









ARTICLE

Seasonal drought treatments impact plant and microbial uptake of nitrogen in a mixed shrub grassland on the Colorado Plateau

Rebecca Finger-Higgins¹  | David L. Hoover²  | Anna C. Knight¹  |
 Savannah L. Wilson¹  | Tara B. B. Bishop^{1,3}  | Robin Reibold¹  |
 Sasha C. Reed¹  | Michael C. Duniway¹ 

¹US Geological Survey, Southwest Biological Science Center, Moab, Utah, USA

²USDA-ARS Rangeland Resource and Systems Research Unit, Crops Research Laboratory, Fort Collins, Colorado, USA

³Department of Earth Science, Utah Valley University, Orem, Utah, USA

Correspondence

Rebecca Finger-Higgins
 Email: rfinger-higgins@usgs.gov

Present address

Savannah L. Wilson, Center for Ecosystem Science and Society, Northern Arizona University, Flagstaff, Arizona, USA.

Funding information

US Geological Survey, Grant/Award Number: EMA-Land Change Science Program BASIS# EN05U4U_Tas

Handling Editor: Joseph B. Yavitt

Abstract

For many drylands, both long- and short-term drought conditions can accentuate landscape heterogeneity at both temporal (e.g., role of seasonal patterns) and spatial (e.g., patchy plant cover) scales. Furthermore, short-term drought conditions occurring over one season can exacerbate long-term, multidecadal droughts or aridification, by limiting soil water recharge, decreasing plant growth, and altering biogeochemical cycles. Here, we examine how experimentally altered seasonal precipitation regimes in a mixed shrub grassland on the Colorado Plateau impact soil moisture, vegetation, and carbon and nitrogen cycling. The experiment was conducted from 2015 to 2019, during a regional multidecadal drought event, and consisted of three precipitation treatments, which were implemented with removable drought shelters intercepting ~66% of incoming precipitation including: control (ambient precipitation conditions, no shelter), warm season drought (sheltered April–October), and cool season drought (sheltered November–March). To track changes in vegetation, we measured biomass of the dominant shrub, *Ephedra viridis*, and estimated perennial plant and ground cover in the spring and the fall. Soil moisture dynamics suggested that warm season experimental drought had longer and more consistent drought legacy effects (occurring two out of the four drought cycles) than either cool season drought or ambient conditions, even during the driest years. We also found that *E. viridis* biomass remained consistent across treatments, while bunchgrass cover declined by 25% by 2019 across all treatments, with the earliest declines noticeable in the warm season drought plots. Extractable dissolved inorganic nitrogen and microbial biomass nitrogen concentrations appeared sensitive to seasonal drought conditions, with dissolved inorganic nitrogen increasing and microbial biomass nitrogen decreasing with reduced soil volumetric water content. Carbon stocks were not sensitive to drought but were greater under *E. viridis* patches.

This is an open access article under the terms of the [Creative Commons Attribution](https://creativecommons.org/licenses/by/4.0/) License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

Published 2024. This article is a U.S. Government work and is in the public domain in the USA. *Ecology* published by Wiley Periodicals LLC on behalf of The Ecological Society of America.

Additionally, we found that under *E. viridis*, there was a negative relationship between dissolved inorganic nitrogen and microbial biomass nitrogen, suggesting that drought-induced increases in dissolved inorganic nitrogen may be due to declines in nitrogen uptake from microbes and plants alike. This work suggests that perennial grass plant–soil feedbacks are more vulnerable to both short-term (seasonal) and long-term (multiyear) drought events than shrubs, which can impact the future trajectory of dryland mixed shrub grassland ecosystems as drought frequency and intensity will likely continue to increase with ongoing climate change.

KEYWORDS

drought, drylands, *Ephedra viridis*, fertile islands, grasslands

INTRODUCTION

Dryland ecosystems are highly sensitive to changes in precipitation patterns, as soil water availability is a key limiting resource governing arid and semiarid terrestrial ecosystem processes (drylands hereafter) (Bradford et al., 2020; Noy-Meir, 1973; Schwinning et al., 2005). Owing to climate change, many drylands are being confronted with an increase in the frequency and duration of ecological droughts (Williams et al., 2020), defined as episodic deficits in water availability that drive ecosystems beyond thresholds of vulnerability to abrupt change (Berdugo et al., 2020; Crausbay et al., 2017). These ecosystem thresholds can be governed by both the nature of a drought event (intensity, duration, and timing) and the resistance (capacity to withstand change) and resiliency (capacity for recovery of function) of a given system (Bestelmeyer, 2006; Holling, 1992; Hoover et al., 2021; Tilman & Downing, 1994). The potential for abrupt shifts in ecological function, due to episodic but increasingly frequent and intense ecological droughts in drylands, will have global impacts, given that drylands cover over 40% of terrestrial land surface and house over 2.5 billion people (Environmental Management Group, 2011; Právník, 2016; Reynolds et al., 2007). Accordingly, understanding the response of drylands to ecological drought is fundamental for human well-being and the functioning of Earth's ecosystems.

Ecological drought has been implicated in the shifts of dryland grasslands from a relatively homogenous distribution of nutrients and water resources to patchy, shrubbier, landscapes characterized by microsites of nutrient-rich soils supporting dryland perennial plants, often called “fertile islands” (Ridolfi et al., 2008; Schlesinger et al., 1990; Tiedemann & Klemmedson, 1973). Within these fertile islands, the soils contain higher concentrations of carbon (C) and nitrogen (N) than adjacent interspace soils, due

to a positive feedback between both abiotic and biotic processes (de Graaff et al., 2014; Ding & Eldridge, 2021; Schlesinger et al., 1990). Additionally, the magnitude of the fertile island effect (i.e., the difference in C and/or N and in the islands under plants vs. the surrounding interspace) will likely vary by perennial plant functional types (grasses or shrubs) (Ochoa-Hueso et al., 2018). Larger, woody shrubs, with wider canopies and deeper roots, are often better at withstanding drought while also retaining and accumulating soil and nutrients than perennial grasses, due to efficiencies in trapping soil sediments, recycling plant litter, tolerance of burial (e.g., coppice dunes), and acquiring resources (Archer et al., 2017; Li, Ravi, et al., 2022). Prevailing hypotheses about fertile islands predict that the strength of fertile islands will increase with both canopy size and aridity (Ding & Eldridge, 2021), but these patterns are yet to be extensively tested with seasonal drought dynamics.

The intensity, duration, and timing of ecological drought conditions are typically measured by temporal and spatial deficits in soil moisture, which directly impacts vegetation through controls on photosynthesis, biomass production, plant mortality, and linkages to soil biogeochemical cycles (Berdugo et al., 2022; Gremer et al., 2015). Both pulse (short-term) and press (long-term) deviations from historical climatic precipitation patterns can impact soil moisture temporally (e.g., soil recharge timing) and spatially (e.g., the vertical distribution within soil profile) (Bradford et al., 2020; Hoover et al., 2015, 2021; Li, Qian, et al., 2022; Reynolds et al., 1999). Severe, pulse drought conditions commonly occur during extreme hot-dry conditions, when atmosphere demands for moisture are high due to increased evapotranspiration rates and vapor pressure deficit (Bradford et al., 2020). Such warm conditions can lead to plant stress and mortality (Breshears et al., 2005, 2021; Winkler et al., 2019). However, in some drylands, drought conditions can be caused by a decrease

in cool, nongrowing season precipitation. Cool season precipitation can be vital for soil water recharge which can support the succeeding growing season, as atmospheric evaporation and transpiration losses are low allowing water to accumulate belowground (Bowling et al., 2010; Comstock & Ehleringer, 1992; Gremer et al., 2015). The balance and timing of precipitation and drought events are also likely to differentially impact components of the plant community due to differences in plant phenology, drought tolerance, and rooting patterns. For example, a cool season drought may have a greater impact on early active herbaceous species and deep-rooted shrubs due to reduced soil recharge from winter precipitation, while a warm season drought may more greatly impact warm season perennial grasses and other species able to respond to short pulses of increased warm season soil moisture (Gremer et al., 2018). Multiyear, press-type droughts can also alter grass-shrub cover patterns and landscape heterogeneity (Finger-Higgins et al., 2023; Gremer et al., 2018; Munson, Belnap, Schelz, et al., 2011; Reynolds et al., 1999). For perennial grasses and other shallow-rooted species, warming and drying trends can lead to increases in dormancy and even mortality (Gremer et al., 2015; Hoover et al., 2017; Winkler et al., 2019). Conversely, woody plants like shrubs, often show more resistance and resiliency to drought due to deeper rooting strategies and positive feedbacks with the soil system (e.g., higher nutrients due to leaf litter inputs, root exudates) (Archer et al., 2017; Schlesinger et al., 1990). Therefore, some drylands will likely see a shift in dominant plant community types, resulting in a greater presence of woody, shrubby species.

These drought-induced shifts in vegetation composition and structure can be reinforced by shifts in biogeochemical cycles (Delgado-Baquerizo et al., 2013; Hooper & Johnson, 1999), potentially decoupled from vegetation primary production as a result of rapidly increasing aridity (Finger-Higgins et al., 2023; Homyak et al., 2016, 2017; Yahdjian et al., 2006). For instance, a meta-analysis of precipitation reduction and removal experiments found that extractable NH_4^+ -N (a common and readily biologically available form of N) increased by 25% overall with precipitation reductions, which was attributed to decreases in plant production and N immobilization (Homyak et al., 2017). Another meta-analysis of drought studies from forest, shrublands and grasslands found that across ecosystem types, dissolved organic C (DOC) concentrations increased, likely due to inhibited decomposition and mineralization (Deng et al., 2021). The decoupling of biogeochemical cycles is proposed as an important indicator of aridity ecosystem thresholds (Berdugo et al., 2021), where soil microbial resilience to drought could result in a loss of soil nutrients due to declining inputs from vegetation (Allison, 2023).

Here, we examine seasonal drought impacts in a mixed shrub grassland on the Colorado Plateau. The Colorado Plateau is a model system to assess changes in seasonal precipitation drought patterns, as soil water availability in the region is driven by the balance between cool- and warm-season precipitation patterns and evaporative demand (Bowling et al., 2010; Comstock & Ehleringer, 1992; Gremer et al., 2018; Hoover et al., 2021). In addition, the region has experienced numerous press drought events, including an ongoing regional megadrought (20+ year drought) starting in the early 2000s (Williams et al., 2022; Zhang et al., 2021). The megadrought has been connected to changes in plant cover and shifts in biogeochemistry (Finger-Higgins et al., 2023); however, questions remain regarding how short-term, seasonal drought events might further impact ecosystems as multiple global change drivers interact.

This study investigates how cool versus warm seasonal drought treatments impact vegetation cover, soil C and N cycling, and microbial biomass after 4 years of experimentation in a mixed shrub grassland. Focal plant species for this study are a dominant perennial bunchgrass, Indian ricegrass (*Achnatherum hymenoides* Roem & Shult.) and the dominant shrub, Mormon tea (*Ephedra viridis* Coville). These species were selected for their commonness on the Colorado Plateau and their known physiological difference, with *A. hymenoides* predicted to show greater sensitivity to changes in water availability than *E. viridis* (Hoover et al., 2015, 2017, 2021; Munson, Belnap, Schelz, et al., 2011). We hypothesized that seasonal drought conditions would lead to decreases in grass cover and concurrent increases in available N in the soil due to reductions in plant and microbial N uptake. We expected grass cover to decline especially for the cool season drought treatments, because of reduced water availability prior to spring green-up (Bowling et al., 2010). Additionally, we predicted that the shrub *E. viridis* would be less sensitive to either seasonal drought treatment due to physiological advantages associated with being a long-living, evergreen shrub. In regard to C and N concentrations, we predicted that the impacts of both the cool season and warm season drought would result in increase in soil available N and DOC. We also predicted that drought effects on biogeochemical cycles would be more pronounced in soils underneath vegetation than in interspace areas. We anticipated the largest response of biogeochemical cycling to drought to occur under bunchgrasses, as *A. hymenoides* is likely to be highly sensitive to water reductions by decreasing N uptake and limiting photosynthesis (Hoover et al., 2017, 2021). Finally, we predicted that the strength of the fertile island would be highest during seasonal drought periods, with a greater difference between

E. viridis and the interspace than *A. hymenoides* and the interspace (Ding & Eldridge, 2021).

METHODS

Site description

Our study was conducted in a mixed shrub grassland ecosystem on the Colorado Plateau in southeastern Utah, USA (38.19° N, 109.75° W; 1505 m elevation). The dominant shrub is *E. viridis* interspersed with several perennial grass species (Hoover et al., 2019), with a history of light winter cattle grazing prior to the establishment of this study. The site resides in a semiarid (mean annual precipitation = 221 mm), continental climate with cool winters (mean low temperature = -6.5°C) and warm summers (mean high temperature = 32.7°C) (Hoover et al., 2021). Monthly precipitation amount is fairly consistent throughout the year on average due to the Colorado Plateau's location intersecting two moisture trajectories coming from opposite directions (winter storm fronts from the Gulf of Alaska and summer convection storms from the Gulf of California [monsoon]; Hereford & Webb, 1992; Schwinning et al., 2008). However, despite relatively consistent incoming precipitation levels across the year, soil water availability varies greatly due to seasonal differences in temperature and evaporative demand (Chenoweth et al., 2023; Gremer et al., 2015). Soil water recharge often occurs during the cool season (November–April), due to low evapotranspiration demand which often help initiate and support springtime plant growth (Comstock & Ehleringer, 1992). Summertime precipitation (July–September) can facilitate a second green-up as convective, monsoonal rains can provide an additional surge of soil moisture (Comstock & Ehleringer, 1992).

Seasonal drought treatments

Seasonal drought treatments have previously been described in Hoover et al. (2021). Briefly, plots were randomly assigned to two community types based on the presence or absence of the shrub *E. viridis* in one half of each plot (“G + G” = grass-only community and “G + E” = grass with *E. viridis* community). Dominant perennial grass species comprised four bunchgrasses (two C_3 and two C_4 photosynthetic pathway) and one rhizomatous grass (C_4 photosynthetic pathway) (Hoover et al., 2019). The two C_3 (cool season) grasses included *A. hymenoides* and *Hesperostipa comata*, while C_4 (warm season) grasses included *Aristida purpurea*, *Pleuraphis*

jamesii, and *Sporobolus* spp. Once community types were designated, each 4×4 m plots was hydrologically isolated from the surrounding area. Drought treatments were then assigned using a stratified random approach with six blocks. Therefore, each block contained one replicate of each drought treatment and community combination ($n = 36$; Hoover et al., 2021).

From May 2015 to April 2019, we applied three precipitation manipulation treatments within a fenced 3.2-ha study area: control (ambient precipitation), cool season drought (66% ambient precipitation excluded from early November to the end of April), and warm season drought (66% ambient precipitation excluded from early May to the end of October) (Hoover et al., 2021). Drought treatments were applied with passive precipitation shelters which, expanded past the survey plots thus droughting all plants and ground cover types, as described in Hoover et al., 2021. Shelters were transferred 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). All shelters were finally removed in April 2019 for a total of 4 cycles of both drought treatments.

To quantify the impacts of our drought manipulations, precipitation was measured on site using an hourly tipping rain gauge (TE25MM, Texas Electronics, Dallas, TX). Additionally, within each plot, soil moisture was calculated every 30 min at shallow (5–25 cm) and deep (30–50 cm) depths (CS650 sensors, Campbell Scientific, Logan, UT) in the center of each plot (Grote et al., 2023; Hoover et al., 2021).

Vegetation cover and *E. viridis* biomass estimates

Aboveground vegetation and ground cover were measured via ocular estimates in the spring (April–May) and fall (September), from May 2015 and through September 2019. During field data collection, lofted scaffolding was used to prevent disturbance when sampling plots. This was particularly important during the collection of *E. viridis* biomass estimates as it allowed us to measure the entire plant ($n = 18$) without damaging evergreen and woody plant tissue. Ocular cover estimates were observed at subplot level, where four permanent 1 m^2 subplots were estimated within each plot. Percent cover of plant foliar cover and ground cover categories was estimated to the nearest 1%. For extreme values (cover $<5\%$ or $>95\%$), estimates were to the nearest 0.1% (Hatton et al., 1986). Where multiple cover types overlapped, only the top-most cover type was measured such that percent cover estimates for all cover types in each subplot summed to 100%. Live foliar cover,

defined as green tissue or woody tissue supporting green tissue, was estimated for each plant species rooted within or with canopy overhanging into a subplot. Dead or senescent plant material was not included in overall plant percent cover, but instead classified as either standing dead (rooted) or ground litter (detached). Additional ground cover categories included developed biological soil crust (lichen, moss, or dark cyanobacteria), rocks with a diameter greater than 5 mm, and bare ground (soil surface not covered by live or dead plant material, litter, biological soil crust, or rocks). Ground cover classes, including bare ground, biological soil crust, rocks, and litter, were later grouped during analysis as an estimate of the cover of plant interspaces (portions of the plot without any rooted foliar cover; interspace cover hereafter). For perennial grass analysis, only the half (two subplots) that consistently did not contain *E. viridis* were included. Perennial grass cover was later combined into one functional group to evaluate variations in grass cover through time and by treatment. Other plant species observed were also divided into plant functional types including forbs, shrubs (most sub-shrubs less than 0.5 m in height), and annual grasses (which only included one species, *Vulpia octoflora*).

E. viridis biomass was quantified using an allometric equation to estimate biomass from plant volume to allow for non-destructive repeated sampling. The volume of each *E. viridis* individual within the experimental plots was estimated by measuring plant height to the nearest 5 cm in each cell of a 25 × 25 cm grid spanning the plant's footprint. In spring 2015, the volumes of an additional 10 individuals outside of the experimental plots were measured for calibration. All aboveground biomass of the off-plot individuals was harvested, dried for 48 h at 60°C, and then weighed to the nearest 0.1 g. The volumes and weights of the off-plot individuals were used to build a linear model predicting aboveground biomass as a function of volume ($R^2 = 0.916$). This allometric model was then used to estimate within-plot *E. viridis* biomass from volume measurements.

Soil sampling and analysis

Following the end of the drought treatments, soil samples were collected to explore trends in key biogeochemical cycles, including C, N, and phosphorus (P). Soils were collected after the final summer drought period on 2 November 2018, and following the final winter drought period on 28 April 2019.

Soil samples were collected at all plots and underneath focal species, *E. viridis* (shrub; $n = 18$) and *A. hymenoides* (grass; $n = 36$), and within the interspace ($n = 36$). *A. hymenoides* was selected as a representative

dominant grass species for soil collection as it is a non-rhizomatous bunchgrass, so samples could easily be collected from underneath separate individuals. At each sample point, two 0–10 cm deep, 2.5 cm diameter soil cores were collected underneath either a target species or the plant interspace, and then homogenized. Upon returning to the lab, soils were sieved at 2 mm and unincorporated organic matter was removed. Subsamples of homogenized soil from fall 2018 and spring 2019 were then used for the analyses described below. Dissolved inorganic N (DIN), considered to be the sum of the nitrate (NO_3^-) and ammonium (NH_4^+) pools, was determined by shaking 8 g of the sample with 30 mL of 2 M potassium chloride for 1 h (Robertson et al., 1999). Orthophosphate (PO_4^{3-}) was extracted by shaking 8 g of sample with 30 mL of 0.5 M sodium bicarbonate (adjusted to pH 8.5) for 16 h (Olsen, 1954). Nitrate, ammonium, and orthophosphate were analyzed using a Westco Smartchem 200 discrete autoanalyzer (KPM analytics, Milford, MA). DOC and total dissolved N (TDN) were extracted by shaking 8 g of sample with 30 mL of 0.5 M potassium sulfate for 1 h. Microbial biomass C and N (MB-C and MB-N, respectively) were measured using chloroform fumigation-extraction with a 0.5 M potassium sulfate solution (Brookes et al., 1985). MB-C and MB-N were defined as the difference between the fumigated value and the unfumigated value (DOC and TDN) (Brookes et al., 1985). DOC, TDN, MB-C, and MB-N extracts were analyzed using a Shimadzu TOC-Vcpn and TNM-1 analyzer (Kyoto, Japan). All extracts were filtered using Whatman #1 filter papers (Cytiva, Marlborough, MA).

The spring 2019 soil samples were also analyzed for total soil C (TC) and N (TN), as we assumed that these pools would be less dynamic, and therefore, less likely to change between fall and spring sampling events. TC and TN were measured by analyzing soils dried at 60°C with a varioMicro Cube elemental analyzer (Elementar Americas, Mt. Laurel, NJ). Additionally, we analyzed soils for total soil inorganic C (IC), which was measured with a modified pressure calcimetry assay (Sherrod et al., 2002) and total organic C (OC) was calculated as the difference between TC and IC.

Statistical analysis

To model the effects of the seasonal drought treatments on soil volumetric moisture and biogeochemistry, we used linear mixed effects models. Models for soil volumetric water content (VWC) were constructed with drought treatment and day of experiment as fixed effects, with community types (G + G or G + E) nested in block as a random effect. When exploring relationships

between soil moisture and biological metrics in the regression models, we used deep (30–50 cm) soil VWC as this metric of soil moisture was more representative of long-term plot level water (Bowling et al., 2010). Potential differences between experimentally droughted plots and ambient plots were assessed using the 95% CI between treatments. For biogeochemistry variables, block with nested community type (G + G or G + E) was initially used as a random effect to account for potential spatial autocorrelation and the impacts of shrub and grass competition which was beyond the scope of this study. However, for some models, community type (as a random effect) did not enhance model performance (and sometime inhibited model convergence) so block alone was used as a random effect.

To track variations in vegetation biomass and percent cover of plant species and interspace percent cover, we constructed generalized additive models (GAMs) across the different drought treatment plots. GAMs are flexible regression functions which can be used to estimate smooth functional relationships between predictor variables and response for non-linear data (Pedersen et al., 2019). Here, we choose to use GAMs, as plant cover was not expected to have a linear relationship with treatment variables as there would likely be a season impact on cover values. Interspace was calculated as the combined cover classes of ground litter, dead standing litter, bare soil, rocks, and developed biological soil crusts. GAMs were constructed using a smoothing function for sampling period (spring or fall and year) by drought treatment (ambient, cool season drought, warm season drought) and estimated using restricted maximum likelihood.

Statistical analyses were conducted in R version 4.23. For linear mixed effects we used the “lmer” function in the R package “lme4” (Bates et al., 2015) and the “lme” function in the R package “nlme” (Pinheiro et al., 2022). GAMs as were constructed with the “mgcv” package in R (Pedersen et al., 2019). Models were checked for assumptions (i.e., normal distribution of residuals, the residuals have constant variance) using the “performance” package (Lüdecke et al., 2021) and summary statistics were reported using the “sjPlot” package (Lüdecke, 2022). Data were log transformed when required to adhere to model requirements. All data generated for this study are available from the USGS ScienceBase Catalog (Finger-Higgins et al., 2024).

RESULTS

Precipitation and soil moisture

Over the duration of the experimental drought treatments (29 April 2015–31 October 2019), annual precipitation was

above the long-term average of 210 mm for first and fourth years (265.2 mm, 29 April 2015–26 April 2016, and 240.4 mm, 28 April 2018–16 April 2019) 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; Figure 1), driven in part by regional megadrought conditions. Concurrent drought treatment effects on shallow (5–25 cm) soil moisture were negative (less than ambient) during all the drought treatments (warm and cool drought 1–4, Figure 1), but only significant for deep (30–50 cm) soil moisture for parts of warm droughts 1, 3, and 4, and briefly cool droughts 1 and 4 (Figure 1). Additionally, we observed both positive and negative legacy effects on soil moisture in both drought treatments, with legacy effects (defined as treatment effects continuing after season experiment drought period had ended; sensu Hoover et al., 2021) slightly more common in the warm drought plots than cool drought plots (Figure 1). Negative legacy drought conditions occurred in the warm drought plots during cool season droughts 1, 2, and 4, in shallow soils, and cool season droughts 1 and 4 in deep soils, with cool season drought legacies only occurring following the removal of all drought shelters in April 2019. Conversely, we did see short periods of positive soil moisture legacies for both warm and cool droughts, often occurring several months after the drought shelters had been removed (Figure 1).

Additionally, during soil collection in fall 2018, soil conditions were significantly drier in the warm drought plots, resulting from the effects of the drought shelters during warm season 4 (Figure 1). However, for the spring 2019 soil collection there were only subtle and not statistically significant differences between the treatments even following the full cool season 4 drought season (Figure 1).

Variations in vegetation and interspace cover

As the drought experiment treatments progressed, we observed notable treatment differences between perennial grass versus interspace cover, but not for *E. viridis* biomass (Figure 2, Table 1). For perennial grass cover, warm season drought plots had the lowest average cover, followed by cool season drought plots, and finally ambient plots cover (Figure 2, Table 1). Perennial grass species cover was dominated by *A. hymenoides* (C₃, cool season grass), and *A. purpurea*, *P. jamesii*, and *Sporobolus* sp. (C₄ warm season grasses) (Appendix S1: Figure S1), with notable declines in all grass species across all drought treatment plots. Declines of *A. hymenoides* were most noticeable in the cool season drought plots, with a shift in

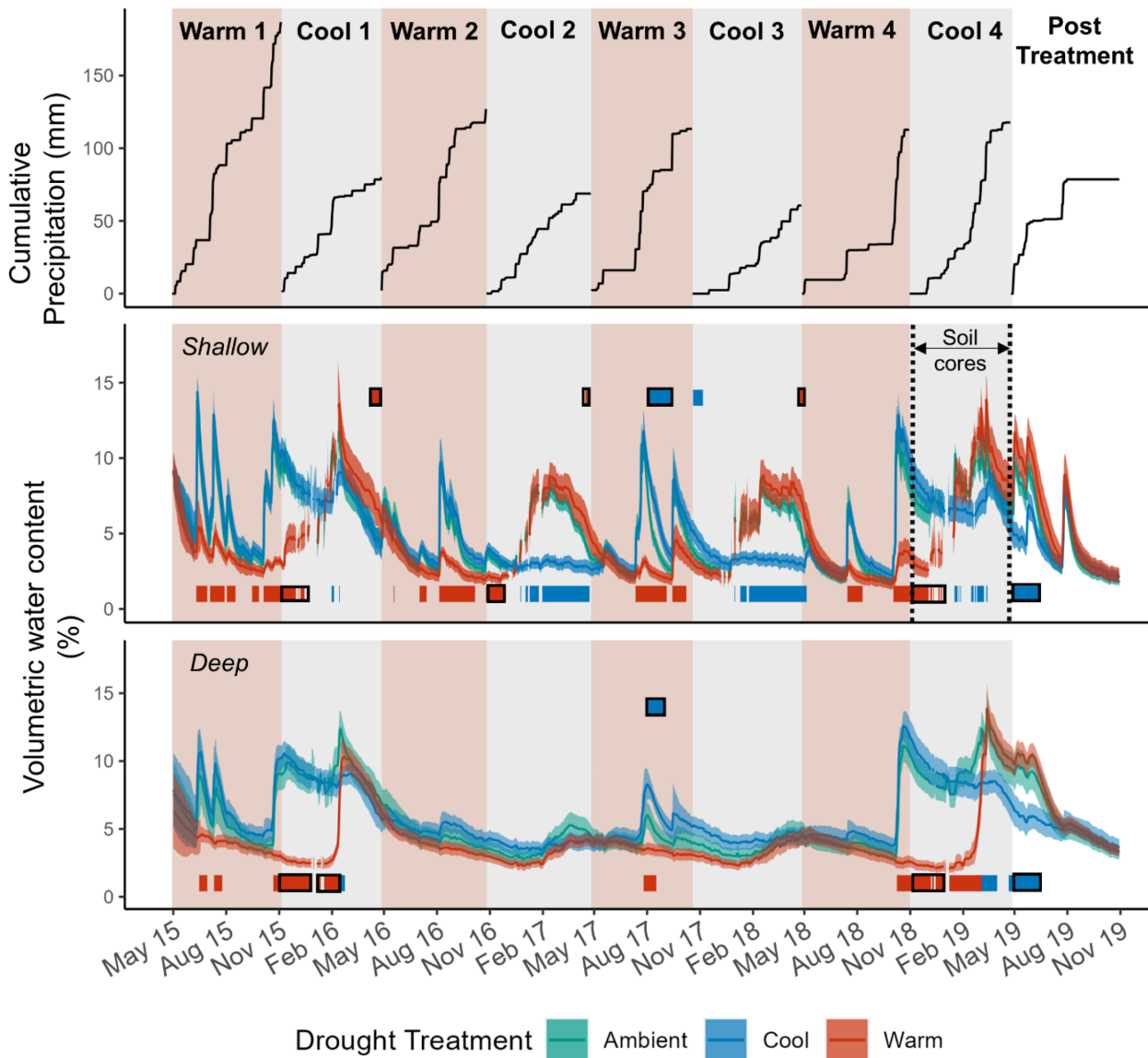


FIGURE 1 Precipitation and soil moisture (volumetric water content %) at shallow (5–25 cm) and deep (30–50 cm) depths. Precipitation is shown as the cumulative precipitation (in millimeters) that fell on the ambient plots during each drought period (top). Volumetric water recorded from 5 to 25 cm, recorded with soil probes located at plots experiencing different experimental drought treatments including: Ambient, cool season drought, and warm season drought (middle and bottom). Dark red and blue bars above and below soil moisture indicate treatments are greater than ambient (positive effect), while bars below indicate that they are less than ambient (negative effects). Bars without black borders are current treatments, while those with black boxes are due to drought legacies. Data were removed when soil temperatures were at or below freezing. Dotted vertical lines indicate the date and soil conditions when soil cores were collected for biogeochemical analysis. Figure modified from Hoover et al. (2021).

the grass community towards a greater proportion of the C_4 grasses, *P. jamesii* and *Sporobolus* sp. (Appendix S1: Figure S1). Conversely, in the warm season drought plots, more cover declines occurred in the C_4 grasses (Appendix S1: Figure S1). Declines in grass cover also translated into decreases in total cover, with both small shrubs and forbs also decreasing in cover during the experiment (Appendix S1: Figure S2). Along with

reduced grass cover, we observed increases in cover of interspaces, with the greatest interspace cover occurring in the warm drought plots, followed by cool season drought plot, and then ambient plots (Figure 2, Table 1). Most of the interspace cover comprised either bare ground or litter, with biological soil crusts often only covering between 1% and 2% of the plot. Cover classes also varied by year, with grass cover likely

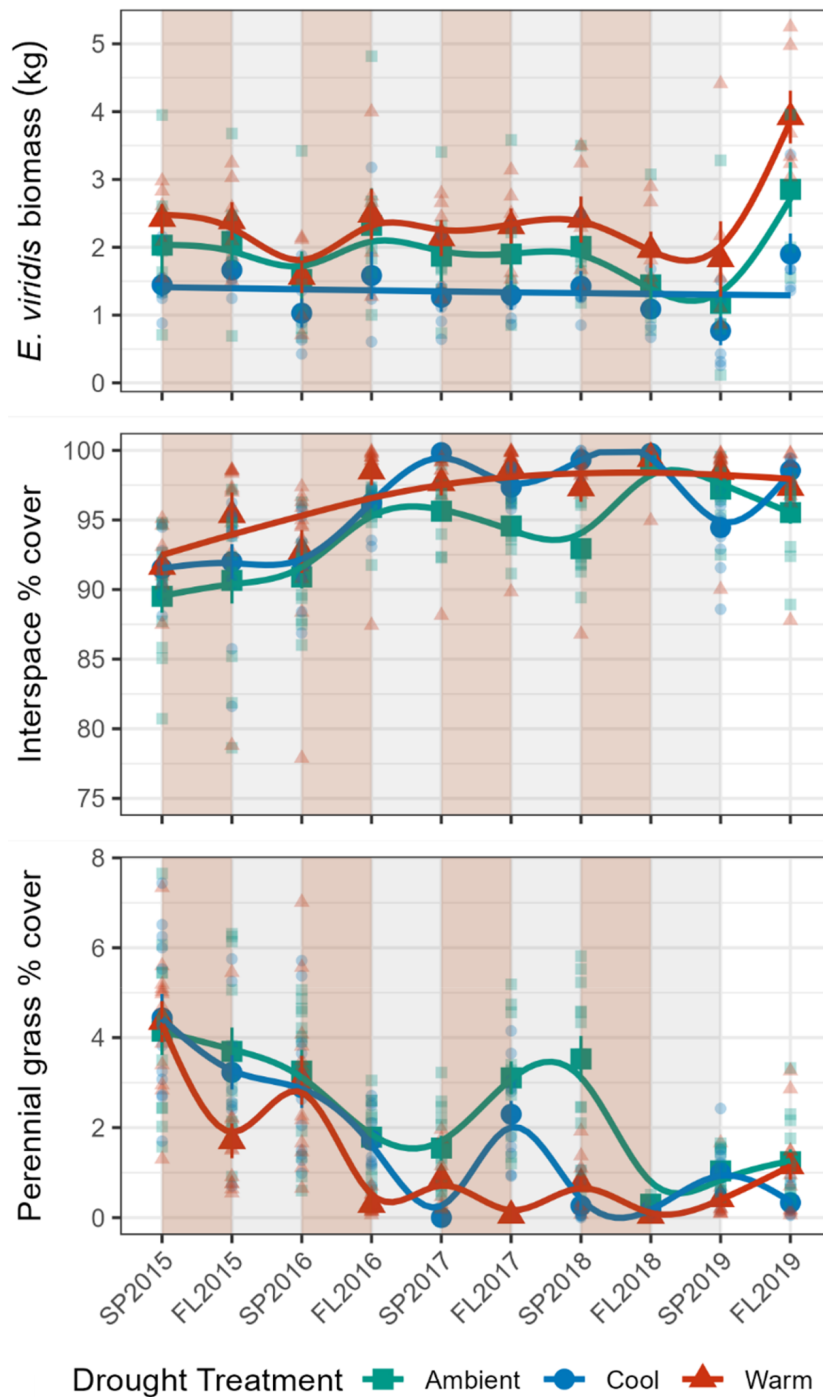


FIGURE 2 Generalized additive models and biomass estimates for *Ephedra viridis* biomass (in grams per square meter) (top), percent cover of interspace (middle), and percent cover of dominant perennial grasses (bottom) within plots in the three drought treatments of no drought control (ambient), cool season drought (cool), and warm season drought (warm) within the two grass cover subplots within each plot. Shading indicates applied season drought treatment with light red indicating warm drought, gray indicating cool drought, and no shading indicating the end of experimental drought treatments. Larger points indicate mean values at sampling dates with error bars ± 1 SE, while smaller shaded points represent individual data points. Summary statistics presented in Table 1.

responding to both experimental drought seasonality and ambient drought conditions. *E. viridis* biomass also experienced slight declines over the course of the study but was able to recover by fall 2019 (Figure 2).

Biogeochemical concentrations and fluxes

Following the 4 years of warm and cool season drought treatments, we found no significant effect of drought

TABLE 1 Summary statistics for generalized additive models of variations in individual *Ephedra viridis* biomass (in kilograms) (top), the percent cover of interspace (middle), and percent cover of dominant perennial grasses (bottom) within plots in the three drought treatments of no-drought control (ambient), cool season drought (cool), and warm season drought (warm).

Cover type	Parametric coefficient			Smoothing terms			Adjusted R^2
	Drought treatment	Estimate (SEM)	Posthoc	Smoothing	EDF	p-value	
<i>E. viridis</i> individual biomass (kg)	Ambient	2.86 (0.13)	B	s(Date: Ambient)	6.65	0.009	0.533
	Cool	2.31 (0.12)	C	s(Date:Cool)	1.12	0.751	
	Warm	3.33 (0.12)	A	s(Date:Warm)	7.16	<0.001	
Interspace cover (%)	Ambient	90.70 (0.51)	A	s(Date: Ambient)	6.69	<0.001	0.504
	Cool	91.96 (0.46)	B	s(Date:Cool)	7.71	<0.001	
	Warm	92.84 (0.46)	C	s(Date:Warm)	8.26	<0.001	
Perennial grass cover (%)	Ambient	2.61 (0.14)	A	s(Date: Ambient)	8.3	<0.001	0.648
	Cool	2.08 (0.13)	B	s(Date:Cool)	2.29	<0.001	
	Warm	1.63 (0.13)	C	s(Date:Warm)	2.72	<0.001	

Note: Letters with parametric coefficients indicate post hoc pairwise tests (Tukey’s honestly significant difference) with letters indicating statistically differences between cover types ($n = 360$). Effective degrees of freedom (EDF) indicate the amount of curvature in the generalized additive model, with 1 equivalent to a linear relationship.

TABLE 2 ANOVA tables of liner mixed effects models of variations total nitrogen (TN, in micrograms per gram), total carbon (TC, in micrograms per gram), total organic carbon (OC, in micrograms per gram), and total inorganic C (IC, in micrograms per gram) by sample collection date (Year), drought treatment (Drought), and cover type (Type).

Response	Predictors	χ^2	df	p-value
TN ($\mu\text{g g}^{-1}$)	Drought	0.64	2, 71	0.727
	Type	129.31	2, 73	<0.001
	Drought \times Type	1.6	4, 71	0.809
TC ($\mu\text{g g}^{-1}$)	Drought	0.411	2, 71	0.814
	Type	19.09	2, 73	<0.001
	Drought \times Type	3.03	4, 71	0.552
OC ($\mu\text{g g}^{-1}$)	Drought	0.282	2, 71	0.869
	Type	44.58	2, 73	<0.001
	Drought \times Type	3.93	4, 71	0.416
IC ($\mu\text{g g}^{-1}$)	Drought	3.76	2, 71	0.152
	Type	2.13	2, 73	0.345
	Drought \times Type	0.77	4, 71	0.942

Note: Block and community type were used as random effects ($n = 90$). Values in bold indicate significance where p -value < 0.05.

treatment on total soil N and C concentrations including: total N, total C, organic C, and inorganic C (Appendix S1: Figure S3; Table 2). However, we did observe a noticeable

effect of cover type on total N, total C, and organic C (Table 2). For total N, we observed highest amounts of total N underneath *E. viridis* plants, followed by *A. hymenoides*, and then interspace (Appendix S1: Figure S3). Total C and organic C also had highest amounts underneath the *E. viridis* shrubs, yet there was not a significant difference between the interspace and *A. hymenoides* (Appendix S1: Figure S3). Inorganic C amounts were not statistically different under different cover type or in response to the drought treatments. Additionally, we found that extractable DOC concentrations, microbial biomass C, and extractable PO_4^{3-} were all best predicted by cover type and did not show significant response to the experimental drought treatments, regardless of year or season of collection (Figure 3, Table 3; Appendix S1: Figure S4 and Table S1).

In contrast to the relative stability of total C and DOC pools, drought treatment, cover type, and year of soil collection were all significant predictors for concentrations of dissolved inorganic N and microbial biomass N (Figure 3, Table 3). DIN concentrations were highest in all warm season drought plot in fall 2018 (Figure 3; Appendix S1: Table S1), with high concentration of DIN remaining for the warm droughted *E. viridis* plots into spring 2019 soil collection. Interspace soils, both in the ambient and cool season drought, consistently had the lowest concentration of DIN in both fall 2018 and spring 2019

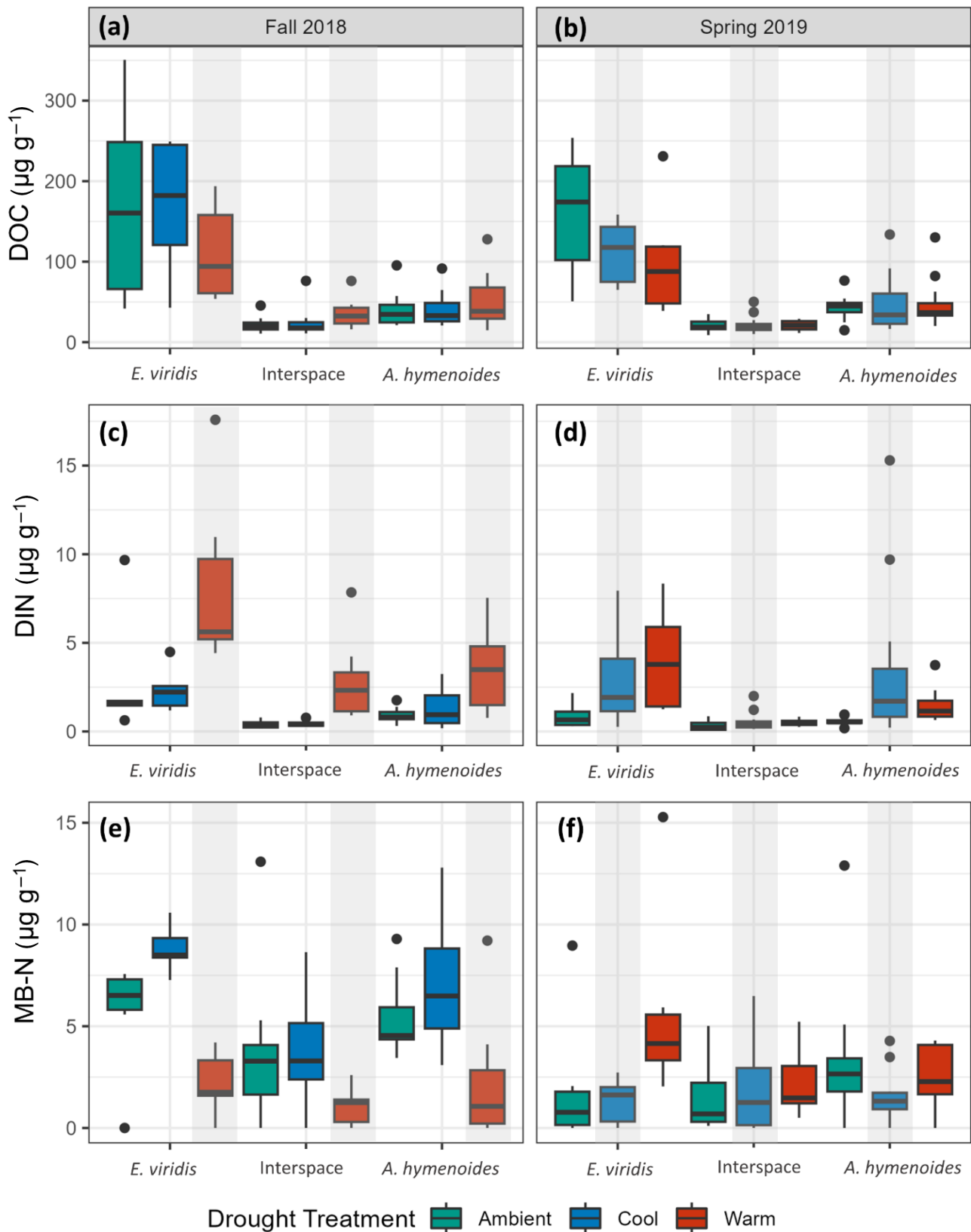


FIGURE 3 Variations in dissolved organic carbon (DOC, in micrograms per gram) (a, b), extractable dissolved inorganic nitrogen (DIN, in micrograms per gram) (c, d), and microbial biomass nitrogen (MB-N, in micrograms per gram) (e, f) by sample collection date (fall 2018 [left column] and spring 2019 [right column]) drought treatments (ambient, cool, warm), and cover types (*Ephedra viridis*, interspace, and *Achnatherum hymenoides*). Gray bars in each panel indicate the plots that were most recently droughted. Associated statistics are in Table 3.

TABLE 3 ANOVA tables of liner mixed effects models of variations in dissolved organic carbon (DOC, in micrograms per gram), extractable dissolved inorganic nitrogen (DIN, in micrograms per gram), and microbial biomass nitrogen (MB-N, in micrograms per gram) by sample collection date (Year), drought treatment (Drought), and cover type (Type).

Response	Predictors	χ^2	sd	p-value
log(DOC [$\mu\text{g g}^{-1}$])	Year	0.90	1, 160	0.34
	Drought	0.40	2, 160	0.82
	Cover type	257.75	2, 160	<0.001
	Year: Drought	1.87	2, 160	0.39
	Year: Type	2.18	2, 160	0.34
	Drought: Type	7.56	4, 160	0.11
	Year: Drought: Type	2.32	4, 160	0.68
log(DIN [$\mu\text{g g}^{-1}$])	Year	12.20	1, 160	<0.001
	Drought	48.87	2, 160	<0.001
	Cover type	57.22	2, 160	<0.001
	Year: Drought	17.01	2, 160	<0.001
	Year: Type	1.48	2, 160	0.48
	Drought: Type	5.63	4, 160	0.23
	Year: Drought: Type	1.85	4, 160	0.76
MB-N ($\mu\text{g g}^{-1}$)	Year	25.29	1, 160	<0.001
	Drought	14.08	2, 160	<0.001
	Cover type	20.28	2, 160	<0.001
	Year: Drought	45.18	2, 160	<0.001
	Year: Type	4.35	2, 160	0.11
	Drought: Type	3.83	4, 160	0.43
	Year: Drought: Type	14.17	4, 160	0.01

Note: Block and community type were used as random effects ($n = 180$). Values in bold indicate where p -value < 0.05 .

(Figure 3; Appendix S1: Table S1). Trends in MB-N were much more variable, with some of the highest concentrations found in fall 2018 in the cool season drought and ambient plots underneath both *E. viridis* and *A. hymenoides* (Appendix S1: Table S1). Most of the other plots did not significantly diverge, especially in 2019 (Figure 3; Appendix S1: Table S1).

Because there was not a significant difference in soil moisture between treatments in spring 2019 (Figure 1), we focused on soils collected in fall 2018 to explore potential mechanisms for drought treatment differences with DIN and MB-N fluxes. Using linear mixed effects models, we found that DIN was negatively correlated with deep volumetric soil moisture for all focal cover types (*E. viridis*, interspace, and *A. hymenoides*) (Figure 4; Appendix S1: Table S2). Conversely, we observed a positive relationship between MB-N and VWC moisture for all focal cover types (*E. viridis*, interspace, and *A. hymenoides*) (Figure 4; Appendix S1: Table S2). We also found that DIN was predicted by MB-N (Figure 4; Appendix S1: Table S2).

DISCUSSION

Vegetation response to pulse and press drought conditions

While this experiment was designed to test the impacts of seasonal precipitation reductions (pulse droughts), some of our results were confounded by a regional megadrought that occurred in concert with this experiment (press drought) (Finger-Higgins et al., 2023; Williams et al., 2020, 2022). First, the effects of the seasonal drought treatments were mostly confined to the shallow soils (5–25 cm), with only two recharge events of deeper soils (30–50 cm; even in ambient), leading to limited treatment effects on deep soil moisture (Figure 1). This lack of deep recharge is partially reflective of the episodic nature of deep soil wetting in drylands (Duniway et al., 2018) and ambient regional drought conditions drying the soil profile. Second, we observed a steady decline in grass cover with a corresponding increase in interspace cover regardless of drought treatments, again suggesting that we

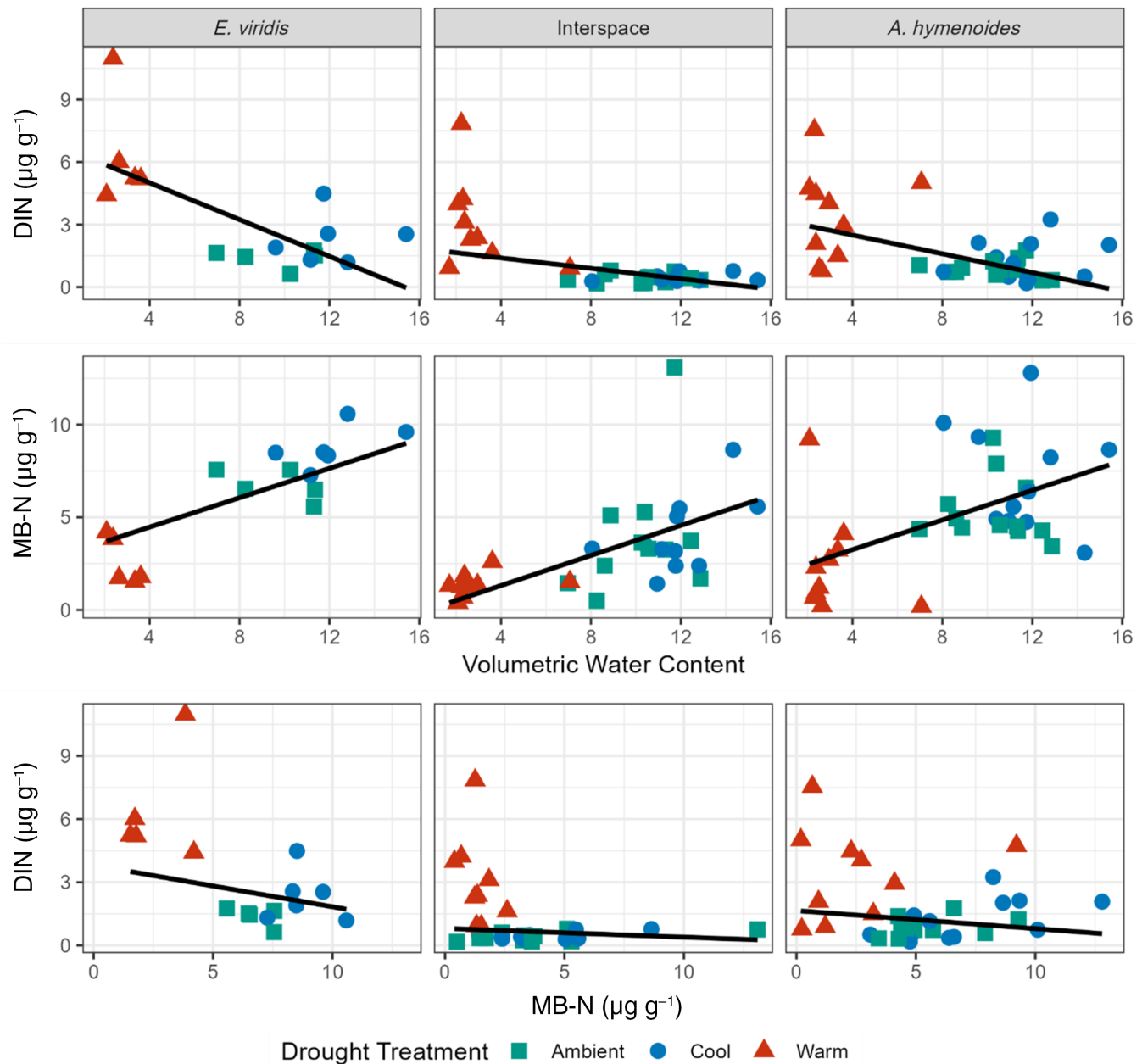


FIGURE 4 Linear mixed model regression of dissolved inorganic nitrogen (DIN, in micrograms per gram), volumetric water content from deep soils (30–50 cm), and microbial biomass nitrogen (MB-N, in micrograms per gram) by cover types (*Ephedra viridis*, interspace, and *Achnatherum hymenoides*) from soil cores that were collected in 2018. Colors indicate differences in drought treatments with ambient (teal squares), cool season drought (blue circle), and warm season drought (red triangle). Regression lines indicate significant relationship ($p < 0.05$). Data and regression model including DIN have been back transformed for figure presentation. Associated statistics in Appendix S1: Table S2.

were observing larger, more landscape level responses to the regional megadrought (Duniway et al., 2023; Finger-Higgins et al., 2023; Gremer et al., 2018). Reductions in grass cover from both the press and pulse droughts was likely driven both by a reduction in the size of individuals and by an increase in mortality (Winkler et al., 2019), which could limit grass recovery if and when drought conditions abate. Therefore, observed declines in

ambient treatment of grass cover were likely caused by megadrought conditions which then compounded the impacts of the imposed experimental seasonal droughts.

Moreover, the seasonal drought experiment provided clues to the specific mechanisms leading to grass cover declines. The first 2 years of pronounced declines in grass cover in both experimental drought treatments were likely driven by plant mortality (Dannenberg et al., 2022;

Winkler et al., 2019). Extreme hot and dry conditions that occur in the summer may be particularly deadly to perennial grass species regardless of photosynthetic pathway (C_3 vs. C_4) (Dannenbergh et al., 2022; Schwinning et al., 2005; Witwicki et al., 2016). Many grass species in the warm season drought plots, including dominant warm season C_4 grasses, demonstrated little to no resiliency to drought, even following winter precipitation recharge of shallow soils (Appendix S1: Figure S1). Experimental winter drought conditions also impeded grass growth, with the lowest cover of perennial grasses in the spring sampling events of 2017 and 2018 (Figure 2), which could be related to delayed phenology due to reductions in cool season soil moisture storage (Hoover et al., 2021). Additionally, the lack of deep soil recharge over much of the duration of this study might have also contributed to an increase in competition for water with neighboring vegetation in shallower soils (Hoover et al., 2021; Reynolds et al., 2004; Schwinning et al., 2005). The constriction of ecological niche partitioning within the soil profile most likely favors woody species like *E. viridis*, which has extensive root structures, photosynthetic evergreen tissues, and high cavitation resistance (Hoover et al., 2017; Munson, Belnap, Schelz, et al., 2011; Winkler et al., 2019). The competitive advantages of *E. viridis* can also be observed by steady estimated biomass across the study, suggesting that this plant is resistant to long-term drought conditions. Such competitive advantages of *E. viridis* also supports prevailing theory that increases in aridity will favor shrubbier and more patchy dryland landscapes in a warmer and drier climate (Archer et al., 2017; Li, Ravi, et al., 2022; Schlesinger et al., 1990).

Controls of drought and vegetation on biogeochemistry

Even with 4 years of seasonal droughts, we found that C, N, and P cycling were better predicted by vegetation cover type (shrub vs. grass vs. interspace) than seasonal soil moisture dynamics (Figure 4; Appendix S1: Figure S2). Such strong microsite control over soil biogeochemistry even in the face of strong experimental drought treatments highlights the importance of fine-scale dryland heterogeneity and its interactions with global change drivers. Additionally, we cannot rule out that the experimental seasonal drought treatments failed to affect certain components of soil biogeochemistry, as the regional ambient drought conditions might have had a stronger effect across study plots. *E. viridis* soils consistently had the highest concentrations of TN, TC, OC, DOC, and PO_4^{3-} , indicating that these shrub patches remain nutrient-rich hotspots across a wide range of

conditions (Ding & Eldridge, 2021; D'Odorico et al., 2010; Ochoa-Hueso et al., 2018; Ridolfi et al., 2008; Schlesinger et al., 1990). To a slightly lesser extent, *A. hymenoides* soils had higher mean concentrations of TN, OC, and DOC than interspace soils, suggesting that even these smaller perennials grass patches can develop fertile microsites that persist across drought conditions (Ding & Eldridge, 2021). The greater fertility islands underneath *E. viridis* and other similar shrubs relative to grasses and interspaces could strongly contribute to shrub resilience by providing a level of protection against drought mortality (e.g., more resources to draw upon when needed; Grossiord et al., 2018), which might contribute to shrub persistence across the greater region (Gremer et al., 2018). It should also be noted that this study site has a history of seasonal grazing, which likely reduced biological soil crust development and soil fertility, especially in the interspaces (Belnap et al., 2006; Neff et al., 2005), and which could have positive feedbacks to greater shrub patch fertility (Archer et al., 2017). If site history and increased aridity leads to grass loss and greater and patchier shrub cover across the Colorado Plateau (Duniway et al., 2022; Munson, Belnap, Schelz, et al., 2011), we expect ecosystem C storage to become similarly more patchy. Thus, soil C storage will be more isolated to more sparsely microsites underneath persisting woody vegetation, as has been seen in other ecosystems globally (Barger et al., 2011; Tiedemann & Klemmedson, 1973).

Unlike C dynamics, we found that dynamic N pools, including DIN availability and MB-N, were responsive to seasonal drought conditions (Figure 3, Table 3). Increases in DIN availability in response to experimental drought conditions are increasingly well documented through previous research and meta-analysis (Deng et al., 2021; Finger-Higgins et al., 2023; Homyak et al., 2017). Drought-induced increases in DIN are often attributed to reductions in plant and microbial uptake, yet these hypothesized mechanisms are infrequently directly measured. Here, we provide further support for this hypothesis through the observed negative relationship between MB-N and DIN availability underneath *E. viridis* (Figure 4). These patterns suggest that DIN concentrations accumulate during periods of drought as microbial pools and the uptake is slow due to water limitations. Additionally, the largest mean concentrations of DIN were underneath *E. viridis* (followed by *A. hymenoides*), especially in the two seasonally droughted plots, thus our data suggest that patch size and type remain critical in regulating biogeochemical cycling and fertile island dynamics. The clear trade-offs between MB-N and DIN underneath *E. viridis* are also likely related to a more stable above- and belowground biological community that is more resilient to large variations in soil moisture,

while both *A. hymenoides* and interspace plant–soil systems are more susceptible to quick changes in community composition (e.g., mortality, annual plant growth, fungal stability) following ecological drought (Gremer et al., 2015; Munson, Belnap, Schelz, et al., 2011; Ochoa-Hueso et al., 2018; Winkler et al., 2019).

Increases in DIN availability underneath vegetation during drought may also play an important role in drought recovery for shrubs. Because N is considered to be a key limiting resource in dryland communities, often second only to water availability (Hooper & Johnson, 1999), N accumulation during drought could help prime both plant and microbial biological activity once precipitation arrives (Choi et al., 2022). Such drought “fertilization” effects may be responsible for the increase in *E. viridis* biomass across treatments following the cessation of the drought experiment; however it is unclear if and how long such trends would continue. Because rewetting events following dry periods are understood to drive biogeochemical cycling in drylands (Choi et al., 2022; Reynolds et al., 2004), further investigation is needed to explore how pulse recharges of water can impact dryland systems experiencing long-term and seasonal drought conditions, and how microsite variability could further control larger system responses. Ultimately, long-lasting and particularly harsh drought conditions may diminish the amount of N that can accumulate underneath perennial vegetation (Finger-Higgins et al., 2023), which can be symptomatic of a threshold resulting in the decline of even the most resilient vegetation types (Berdugo et al., 2021). As anthropogenic climate change continues to make precipitation patterns more erratic and harder to predict (both frequency and intensity), understanding how and if vegetation and plant–soil connections can resist and respond to both press and pulse drought conditions will be vital to anticipating the future trajectory of dryland ecosystems.

CONCLUSION

Given that ecological drought conditions are predicted to become more prevalent throughout the 21st century, studies like this one are critical for considering the effects of both short-term, pulse drought conditions, and long-term, press drought conditions on vegetation stability on the Colorado Plateau. Further, drought commonly comes in different seasons and an improved understanding of the seasonal variability in drought effects on dryland ecosystems is greatly needed. Our findings support previous work in the region that suggests that perennial grasses are particularly sensitive to declines in soil moisture, both at intra- and interannual scales. Shrubs, however, appear resilient to prolonged periods of limited moisture

(Gremer et al., 2018; Hoover et al., 2017; Munson, Belnap, Schelz, et al., 2011; Winkler et al., 2019). The stability of dryland shrubs coupled with declines in perennial grasslands could also alter biogeochemical cycling, as C and N fluxes and pools become concentrated underneath surviving shrubs (Delgado-Baquerizo et al., 2018), with larger interspace areas more susceptible to nutrient loss via erosion pathways (Munson, Belnap, & Okin, 2011). Dryland ecosystems represent a temporal and spatial patchwork of resource availability and controls, and understanding potential increases in spatial and temporal heterogeneity can inform how these landscapes can best be managed to provide for plant and ecosystem resiliency.

AUTHOR CONTRIBUTIONS

David L. Hoover, Michael C. Duniway, and Sasha C. Reed conceived and designed the experiment and methodology. David L. Hoover, Michael C. Duniway, Anna C. Knight, Robin Reibold, and Savannah L. Wilson collected the data. Rebecca Finger-Higgins, David L. Hoover, Tara B. B. Bishop, Anna C. Knight, and Michael C. Duniway analyzed the data. Rebecca Finger-Higgins wrote the first draft of the manuscript with contributions from David L. Hoover, Anna C. Knight, Robin Reibold, and Savannah L. Wilson. All authors contributed to editing and approved the final version of the submitted manuscript.

ACKNOWLEDGMENTS

The US Geological Survey Land Change Science Program and the Ecosystem Mission Area supported this work. The authors are in gratitude to the past and current USGS technicians for helping with project establishment, maintenance, data collection, and shelter moving, including Alix Pfennigwerth, Jessica Mikenas, Rose Egelhoff, and Sean Hoy-Skubik. Additionally, we would like to thank USGS Southwest Biological Research Station staff, including Erika Geiger and Ed Grote, for logistical and technical support. Any use of trade names is for descriptive purposes only and does not imply endorsement by the US Government.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Finger-Higgins et al., 2024) are available in the USGS ScienceBase Catalog at <https://doi.org/10.5066/P98UFIG6>.

ORCID

Rebecca Finger-Higgins  <https://orcid.org/0000-0002-7645-504X>

David L. Hoover  <https://orcid.org/0000-0002-9326-9791>

Anna C. Knight  <https://orcid.org/0000-0002-9455-2855>
 Savannah L. Wilson  <https://orcid.org/0000-0003-4229-4089>
 Tara B. B. Bishop  <https://orcid.org/0000-0001-7828-1541>
 Robin Reibold  <https://orcid.org/0000-0002-3323-487X>
 Sasha C. Reed  <https://orcid.org/0000-0002-8597-8619>
 Michael C. Duniway  <https://orcid.org/0000-0002-9643-2785>

REFERENCES

- Allison, S. D. 2023. "Microbial Drought Resistance May Destabilize Soil Carbon." *Trends in Microbiology* 31: 780–87.
- Archer, S. R., E. M. Andersen, K. I. Predick, S. Schwinning, R. J. Steidl, and S. R. Woods. 2017. "Woody Plant Encroachment: Causes and Consequences." In *Rangeland Systems*, edited by D. D. Briske, 25–84. Cham: Springer International Publishing.
- Barger, N. N., S. R. Archer, J. L. Campbell, C. Huang, J. A. Morton, and A. K. Knapp. 2011. "Woody Plant Proliferation in North American Drylands: A Synthesis of Impacts on Ecosystem Carbon Balance." *Journal of Geophysical Research* 116: G00K07.
- Bates, D., M. Machler, B. Bolker, and S. Walker. 2015. "Fitting Linear Mixed-Effects Models Using lme4." *Journal of Statistical Software* 67: 1–48.
- Belnap, J., S. L. Phillips, and T. Troxler. 2006. "Soil Lichen and Moss Cover and Species Richness Can be Highly Dynamic: The Effects of Invasion by the Annual Exotic Grass *Bromus tectorum*, Precipitation, and Temperature on Biological Soil Crusts in SE Utah." *Applied Soil Ecology* 32: 63–76.
- Berdugo, M., M. Delgado-Baquerizo, S. Soliveres, R. Hernández-Clemente, Y. Zhao, J. J. Gaitán, N. Gross, et al. 2020. "Global Ecosystem Thresholds Driven by Aridity." *Science* 367: 787–790.
- Berdugo, M., J. J. Gaitán, M. Delgado-Baquerizo, T. W. Crowther, and V. Dakos. 2022. "Prevalence and Drivers of Abrupt Vegetation Shifts in Global Drylands." *Proceedings of the National Academy of Sciences of the United States of America* 119: e2123393119.
- Berdugo, M., B. Vidiella, R. V. Solé, and F. T. Maestre. 2021. "Ecological Mechanisms Underlying Aridity Thresholds in Global Drylands." *Functional Ecology* 36: 4–23. <https://doi.org/10.1111/1365-2435.13962>.
- Bestelmeyer, B. T. 2006. "Threshold Concepts and Their Use in Rangeland Management and Restoration: The Good, the Bad, and the Insidious." *Restoration Ecology* 14: 325–29.
- Bowling, D. R., S. Bethers-Marchetti, C. K. Lunch, E. E. Grote, and J. Belnap. 2010. "Carbon, Water, and Energy Fluxes in a Semiarid Cold Desert Grassland during and Following Multiyear Drought." *Journal of Geophysical Research* 115: G04026.
- Bradford, J. B., D. R. Schlaepfer, W. K. Lauenroth, and K. A. Palmquist. 2020. "Robust Ecological Drought Projections for Drylands in the 21st Century." *Global Change Biology* 26: 3906–19.
- Breshears, D. D., N. S. Cobb, P. M. Rich, K. P. Price, C. D. Allen, R. G. Balice, W. H. Romme, et al. 2005. "Regional Vegetation Die-Off in Response to Global-Change-Type Drought." *Proceedings of the National Academy of Sciences of the United States of America* 102: 15144–48.
- Breshears, D. D., J. B. Fontaine, K. X. Ruthrof, J. P. Field, X. Feng, J. R. Burger, D. J. Law, J. Kala, G. E. St, and J. Hardy. 2021. "Underappreciated Plant Vulnerabilities to Heat Waves." *New Phytologist* 231: 32–39.
- Brookes, P. C., A. Landman, G. Pruden, and D. S. Jenkinson. 1985. "Chloroform Fumigation and the Release of Soil Nitrogen: A Rapid Direct Extraction Method to Measure Microbial Biomass Nitrogen in Soil." *Soil Biology and Biochemistry* 17: 837–842.
- Chenoweth, D. A., D. R. Schlaepfer, J. C. Chambers, J. L. Brown, A. K. Urza, B. Hanberry, D. Board, M. Crist, and J. B. Bradford. 2023. "Ecologically Relevant Moisture and Temperature Metrics for Assessing Dryland Ecosystem Dynamics." *Ecohydrology* 16: e2509.
- Choi, R. T., S. C. Reed, and C. L. Tucker. 2022. "Multiple Resource Limitation of Dryland Soil Microbial Carbon Cycling on the Colorado Plateau." *Ecology* 103: e3671.
- Comstock, J. P., and J. R. Ehleringer. 1992. "Plant Adaptation in the Great Basin and Colorado Plateau." *Great Basin Naturalist* 52: 195215.
- Crausbay, S. D., A. R. Ramirez, S. L. Carter, M. S. Cross, K. R. Hall, D. J. Bathke, J. L. Betancourt, et al. 2017. "Defining Ecological Drought for the Twenty-First Century." *Bulletin of the American Meteorological Society* 98: 2543–50.
- Dannenber, M. P., D. Yan, M. L. Barnes, W. K. Smith, M. R. Johnston, R. L. Scott, J. A. Biederman, et al. 2022. "Exceptional Heat and Atmospheric Dryness Amplified Losses of Primary Production during the 2020 U.S. Southwest Hot Drought." *Global Change Biology* 28(16): 4794–4806.
- de Graaff, M.-A., H. L. Throop, P. S. J. Verburg, J. A. Arnone, and X. Campos. 2014. "A Synthesis of Climate and Vegetation Cover Effects on Biogeochemical Cycling in Shrub-Dominated Drylands." *Ecosystems* 17: 931–945.
- Delgado-Baquerizo, M., D. J. Eldridge, F. T. Maestre, V. Ochoa, B. Gozalo, P. B. Reich, and B. K. Singh. 2018. "Aridity Decouples C:N:P Stoichiometry across Multiple Trophic Levels in Terrestrial Ecosystems." *Ecosystems* 21: 459–468.
- Delgado-Baquerizo, M., F. T. Maestre, A. Gallardo, M. A. Bowker, M. D. Wallenstein, J. L. Quero, V. Ochoa, et al. 2013. "Decoupling of Soil Nutrient Cycles as a Function of Aridity in Global Drylands." *Nature* 502: 672–76.
- Deng, L., C. Peng, D.-G. Kim, J. Li, Y. Liu, X. Hai, Q. Liu, C. Huang, Z. Shangguan, and Y. Kuzyakov. 2021. "Drought Effects on Soil Carbon and Nitrogen Dynamics in Global Natural Ecosystems." *Earth-Science Reviews* 214: 103501.
- Ding, J., and D. J. Eldridge. 2021. "The Fertile Island Effect Varies with Aridity and Plant Patch Type across an Extensive Continental Gradient." *Plant and Soil* 459: 173–183.
- D'Odorico, P., J. D. Fuentes, W. T. Pockman, S. L. Collins, Y. He, J. S. Medeiros, S. DeWekker, and M. E. Litvak. 2010. "Positive Feedback between Microclimate and Shrub Encroachment in the Northern Chihuahuan Desert." *Ecosphere* 1: 1–11.
- Duniway, M. C., C. Benson, T. W. Nauman, A. Knight, J. B. Bradford, S. M. Munson, D. Witwicki, et al. 2022. "Geologic, Geomorphic, and Edaphic Underpinnings of Dryland Ecosystems: Colorado Plateau Landscapes in a Changing World." *Ecosphere* 13: e4273.

- Duniway, M. C., R. Finger-Higgins, E. L. Geiger, D. L. Hoover, A. A. Pfennigwerth, A. C. Knight, M. Van Scoyoc, M. Miller, and J. Belnap. 2023. "Ecosystem Resilience to Invasion and Drought: Insights after 24 Years in a Rare Never-Grazed Grassland." *Global Change Biology* 29: 5866–80.
- Duniway, M. C., M. D. Petrie, D. P. C. Peters, J. P. Anderson, K. Crossland, and J. E. Herrick. 2018. "Soil Water Dynamics at 15 Locations Distributed across a Desert Landscape: Insights from a 27-Yr Dataset." *Ecosphere* 9: e02335.
- Environmental Management Group. 2011. *Global Drylands: A UN System-Wide Response*. Geneva: United Nations.
- Finger-Higgins, R., T. B. B. Bishop, J. Belnap, E. L. Geiger, E. E. Grote, D. L. Hoover, S. C. Reed, and M. C. Duniway. 2023. "Droughting a Megadrought: Ecological Consequences of a Decade of Experimental Drought atop Aridification on the Colorado Plateau." *Global Change Biology* 29: 3364–77.
- Finger-Higgins, R., A. C. Knight, D. Hoover, E. E. Grote, and M. C. Duniway. 2024. "Plant Composition, Shrub Biomass, and Soil Biogeochemistry from an Experimental Drought Treatment on the Colorado Plateau: U.S. Geological Survey Data Release." USGS ScienceBase. <https://doi.org/10.5066/P98UFIG6>.
- Gremer, J. R., C. Andrews, J. R. Norris, L. P. Thomas, S. M. Munson, M. C. Duniway, and J. B. Bradford. 2018. "Increasing Temperature Seasonality May Overwhelm Shifts in Soil Moisture to Favor Shrub over Grass Dominance in Colorado Plateau Drylands." *Oecologia* 188: 1195–1207.
- Gremer, J. R., J. B. Bradford, S. M. Munson, and M. C. Duniway. 2015. "Desert Grassland Responses to Climate and Soil Moisture Suggest Divergent Vulnerabilities across the Southwestern United States." *Global Change Biology* 21: 4049–62.
- Grossiord, C., A. Gessler, S. C. Reed, I. Borrego, A. D. Collins, L. T. Dickman, M. Ryan, et al. 2018. "Reductions in Tree Performance during Hotter Droughts Are Mitigated by Shifts in Nitrogen Cycling." *Plant, Cell & Environment* 41: 2627–37.
- Grote, E. E., M. C. Duniway, S. C. Reed, D. L. Hoover, E. L. Geiger, and J. Belnap. 2023. "Meteorological Measurements from Five Weather Stations in Grand and San Juan Counties in Southeastern Utah." USGS ScienceBase. <https://doi.org/10.5066/P9B4SUIY>.
- Hatton, T. J., N. E. West, and P. S. Johnson. 1986. "Relationships of the Error Associated with Ocular Estimation and Actual Total Cover." *Journal of Range Management* 39: 91.
- Hereford, R., and R. H. Webb. 1992. "Historic Variation of Warm-Season Rainfall, Southern Colorado Plateau, Southwestern U.S.A." *Climatic Change* 22: 239–256.
- Holling, C. S. 1992. "Resilience and Stability of Ecological Systems." *Ecology* 73: 1445–61.
- Homyak, P. M., S. D. Allison, T. E. Huxman, M. L. Goulden, and K. K. Treseder. 2017. "Effects of Drought Manipulation on Soil Nitrogen Cycling: A Meta-Analysis." *Journal of Geophysical Research: Biogeosciences* 122: 3260–72.
- Homyak, P. M., J. C. Blankinship, K. Marchus, D. M. Lucero, J. O. Sickman, and J. P. Schimel. 2016. "Aridity and Plant Uptake Interact to Make Dryland Soils Hotspots for Nitric Oxide (NO) Emissions." *Proceedings of the National Academy of Sciences of the United States of America* 113(19): E2608–E2616.
- Hooper, D. U., and L. Johnson. 1999. "Nitrogen Limitation in Dryland Ecosystems: Responses to Geographical and Temporal Variation in Precipitation." *Biogeochemistry* 46: 247–293.
- Hoover, D. L., M. C. Duniway, and J. Belnap. 2015. "Pulse-Drought atop Press-Drought: Unexpected Plant Responses and Implications for Dryland Ecosystems." *Oecologia* 179: 1211–21.
- Hoover, D. L., M. C. Duniway, and J. Belnap. 2017. "Testing the Apparent Resistance of Three Dominant Plants to Chronic Drought on the Colorado Plateau." *Journal of Ecology* 105: 152–162.
- Hoover, D. L., K. Koriakin, J. Albrigtsen, and T. Ocheltree. 2019. "Comparing Water-Related Plant Functional Traits among Dominant Grasses of the Colorado Plateau: Implications for Drought Resistance." *Plant and Soil* 441: 207–218.
- Hoover, D. L., A. A. Pfennigwerth, and M. C. Duniway. 2021. "Drought Resistance and Resilience: The Role of Soil Moisture-Plant Interactions and Legacies in a Dryland Ecosystem." *Journal of Ecology* 109: 3280–94. <https://doi.org/10.1111/1365-2745.13681>.
- Li, J., S. Ravi, G. Wang, R. S. Van Pelt, T. E. Gill, and J. B. Sankey. 2022. "Woody Plant Encroachment of Grassland and the Reversibility of Shrub Dominance: Erosion, Fire, and Feedback Processes." *Ecosphere* 13: e3949.
- Li, L., R. Qian, W. Liu, W. Wang, J. A. Biederman, B. Zhang, X. Kang, et al. 2022. "Drought Timing Influences the Sensitivity of a Semiarid Grassland to Drought." *Geoderma* 412: 115714.
- Lüdecke, D. 2022. "sjPlot: Data Visualization for Statistics in Social Science." R Package 2.8.11.
- Lüdecke, D., M. Ben-Shachar, I. Patil, P. Waggoner, and D. Makowski. 2021. "performance: An R Package for Assessment, Comparison and Testing of Statistical Models." *Journal of Open Source Software* 6: 3139.
- Munson, S. M., J. Belnap, and G. S. Okin. 2011. "Responses of Wind Erosion to Climate-Induced Vegetation Changes on the Colorado Plateau." *Proceedings of the National Academy of Sciences of the United States of America* 108: 3854–59.
- Munson, S. M., J. Belnap, C. D. Schelz, M. Moran, and T. W. Carolin. 2011. "On the Brink of Change: Plant Responses to Climate on the Colorado Plateau." *Ecosphere* 2: art68.
- Neff, J. C., R. L. Reynolds, J. Belnap, and P. Lamothe. 2005. "Multi-Decadal Impacts of Grazing on Soil Physical and Biogeochemical Properties in Southeast Utah." *Ecological Applications* 15: 87–95.
- Noy-Meir, I. 1973. "Desert Ecosystems: Environment and Producers." *Annual Review of Ecology and Systematics* 4: 25–51.
- Ochoa-Hueso, R., D. J. Eldridge, M. Delgado-Baquerizo, S. Soliveres, M. A. Bowker, N. Gross, Y. L. Bagousse-Pinguet, et al. 2018. "Soil Fungal Abundance and Plant Functional Traits Drive Fertile Island Formation in Global Drylands." *Journal of Ecology* 106: 242–253.
- Olsen, S. R. 1954. *Estimation of Available Phosphorus in Soils by Extraction with Sodium Bicarbonate*. Washington, DC: US Department of Agriculture.
- Pedersen, E. J., D. L. Miller, G. L. Simpson, and N. Ross. 2019. "Hierarchical Generalized Additive Models in Ecology: An Introduction with Mgc." *PeerJ* 7: e6876.
- Pinheiro, J., D. Bates, and R Core Team. 2022. "nlme: Linear and Nonlinear Mixed Effects Models." R Package Version 3.1-160.
- Právělie, R. 2016. "Drylands Extent and Environmental Issues. A Global Approach." *Earth-Science Reviews* 161: 259–278.

- Reynolds, J. F., P. R. Kemp, K. Ogle, and R. J. Fernández. 2004. "Modifying the 'Pulse-Reserve' Paradigm for Deserts of North America: Precipitation Pulses, Soil Water, and Plant Responses." *Oecologia* 141: 194–210.
- Reynolds, J. F., F. T. Maestre, P. R. Kemp, D. M. Stafford-Smith, and E. Lambin. 2007. "Natural and Human Dimensions of Land Degradation in Drylands: Causes and Consequences." In *Terrestrial Ecosystems in a Changing World* 247–257. Berlin and Heidelberg: Springer.
- Reynolds, J. F., R. A. Virginia, P. R. Kemp, A. G. de Soyza, and D. C. Tremmel. 1999. "Impact of Drought on Desert Shrubs: Effects of Seasonality and Degree of Resource Island Development." *Ecological Monographs* 69: 69–106.
- Ridolfi, L., F. Laio, and P. D'Odorico. 2008. "Fertility Island Formation and Evolution in Dryland Ecosystems." *Ecology and Society* 13: art5.
- Robertson, G. P., D. Wedin, P. M. Groffman, and J. M. Blair. 1999. "Soil Carbon and Nitrogen Availability: Nitrogen Mineralization and Soil Respiration Potentials." In *Standard Methods of Long-Term Ecological Research*, edited by G. P. Robertson, D. C. Coleman, C. S. Bledsoe, and P. Sollins, 258–271. New York: Oxford University Press.
- Schlesinger, W. H., J. F. Reynolds, G. L. Cunningham, L. F. Huenneke, W. M. Jarrell, R. A. Virginia, and W. G. Whitford. 1990. "Biological Feedbacks in Global Desertification." *Science* 247: 1043–48.
- Schwinning, S., J. Belnap, D. R. Bowling, and J. R. Ehleringer. 2008. "Sensitivity of the Colorado Plateau to Change: Climate, Ecosystems, and Society." *Ecology and Society* 13: art28.
- Schwinning, S., B. I. Starr, and J. R. Ehleringer. 2005. "Summer and Winter Drought in a Cold Desert Ecosystem (Colorado Plateau) Part I: Effects on Soil Water and Plant Water Uptake." *Journal of Arid Environments* 60: 547–566.
- Sherrod, L. A., G. Dunn, G. A. Peterson, and R. L. Kolberg. 2002. "Inorganic Carbon Analysis by Modified Pressure-Calcimeter Method." *Soil Science Society of America Journal* 66: 299–305.
- Tiedemann, A. R., and J. O. Klemmedson. 1973. "Nutrient Availability in Desert Grassland Soils under Mesquite (*Prosopis juliflora*) Trees and Adjacent Open Areas." *Soil Science Society of America Journal* 37: 107–111.
- Tilman, D., and J. A. Downing. 1994. "Biodiversity and Stability in Grasslands." *Nature* 367: 363–65.
- Williams, A. P., B. I. Cook, and J. E. Smerdon. 2022. "Rapid Intensification of the Emerging Southwestern North American Megadrought in 2020–2021." *Nature Climate Change* 12: 232–34.
- Williams, A. P., E. R. Cook, J. E. Smerdon, B. I. Cook, J. T. Abatzoglou, K. Bolles, S. H. Baek, A. M. Badger, and B. Livneh. 2020. "Large Contribution from Anthropogenic Warming to an Emerging North American Megadrought." *Science* 368: 314–18.
- Winkler, D. E., J. Belnap, D. Hoover, S. C. Reed, and M. C. Duniway. 2019. "Shrub Persistence and Increased Grass Mortality in Response to Drought in Dryland Systems." *Global Change Biology* 25: 3121–35.
- Witwicki, D. L., S. M. Munson, and D. P. Thoma. 2016. "Effects of Climate and Water Balance across Grasslands of Varying C₃ and C₄ Grass Cover." *Ecosphere* 7: e01577.
- Yahdjian, L., O. E. Sala, and A. T. Austin. 2006. "Differential Controls of Water Input on Litter Decomposition and Nitrogen Dynamics in the Patagonian Steppe." *Ecosystems* 9: 128–141.
- Zhang, F., J. A. Biederman, M. P. Dannenberg, D. Yan, S. C. Reed, and W. K. Smith. 2021. "Five Decades of Observed Daily Precipitation Reveal Longer and More Variable Drought Events across Much of the Western United States." *Geophysical Research Letters* 48: e2020GL092293.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Finger-Higgins, Rebecca, David L. Hoover, Anna C. Knight, Savannah L. Wilson, Tara B. B. Bishop, Robin Reibold, Sasha C. Reed, and Michael C. Duniway. 2024. "Seasonal Drought Treatments Impact Plant and Microbial Uptake of Nitrogen in a Mixed Shrub Grassland on the Colorado Plateau." *Ecology* e4393. <https://doi.org/10.1002/ecy.4393>