

RESEARCH ARTICLE

Altered precipitation has asymmetric impacts on annual plant communities in warm and cool growing seasons

Marko J. Spasojevic^{1*}, Peter M. Homyak², G. Darrel Jenerette³, Mike L. Goulden⁴, Shane McFaul¹, Tesa Madsen-McQueen¹, Lisa Schauer¹, and Miguel Solis¹

While altered precipitation regimes can greatly impact biodiversity and ecosystem functioning, we lack a comprehensive view of how these impacts are mediated by changes to the seasonality of precipitation (i.e., whether it rains more/less in one season relative to another). Over 2 years, we examined how altered seasonal precipitation influenced annual plant biomass and species richness, Simpson's diversity, and community composition of annual plant communities in a dryland ecosystem that receives both winter and summer rainfall and has distinct annual plant communities in each season. Using a rainfall exclusion, collection, and distribution system, we excluded precipitation and added water during each season individually and compared responses to control plots which received ambient summer and winter precipitation. In control plots, we found five times greater annual plant biomass, twice as many species, and higher diversity in winter relative to summer. Adding water increased annual plant biomass in summer only, did not change richness or diversity in either summer or winter, and modestly shifted community composition. Excluding precipitation in either season reduced annual plant biomass, richness, and Simpson's diversity. However, in the second winter season, biomass was higher in the plots where precipitation was excluded in the previous summer seasons suggesting that reduced productivity in the summer may facilitate biomass in the winter. Our results suggest that increased precipitation in summer may have stronger short-term impacts on annual plant biodiversity and ecosystem function relative to increased winter precipitation. In contrast, decreasing precipitation may have ubiquitous negative effects on annual plants across both summer and winter but may lead to increased biomass in the following off-seasons. These patterns suggest that annual plant communities exhibit asymmetries in their community and ecosystem responses to altered seasonal precipitation and that considering the seasonality of precipitation is important for predicting the effects of altered precipitation regimes.

Keywords: Altered precipitation, Boyd-Deep Canyon Reserve, Climate change, Seasonal precipitation, Sonoran Desert

Introduction

Model projections and long-term measurements suggest anthropogenic climate change will change total precipitation amounts, increase precipitation variability, and increase the likelihood of extreme precipitation events (Cook and Seager, 2013; IPCC, 2014; Stocker et al., 2014; Stott, 2016; Luong et al., 2017; Pendergrass et al., 2017).

However, much of the research on the effects of altered precipitation on biodiversity and ecosystem functioning (e.g., biomass production, nitrogen cycling, decomposition) has instead focused on drought (e.g., Clark et al., 2016; Copeland et al., 2016; Smith et al., 2016; Schwalm et al., 2017). Although drought has large effects on biodiversity and ecosystem functioning, changes to precipitation regimes are much more spatially and temporally complex (Smith, 2011; Beier et al., 2012). For example, the effects of altered precipitation variability on species richness have been found to be context dependent, with some studies finding a negative relationship between precipitation variability and species richness (Knapp et al., 2002), some finding a positive relationship (Xia et al., 2010), and others finding no relationship (Hallett et al., 2013; Irl et al., 2015; Zhang et al. 2018). Similarly, studies on altered precipitation severity have also found context dependency (Smith, 2011; Frank et al., 2015), ranging

¹ Department of Evolution, Ecology, and Organismal Biology, University of California Riverside, Riverside, CA, USA

² Department of Environmental Sciences, University of California Riverside, Riverside, CA, USA

³ Department of Botany and Plant Sciences, University of California Riverside, Riverside, CA, USA

⁴ Department of Earth System Sciences, University of California Irvine, Irvine, CA, USA

* Corresponding author:
Email: markos@ucr.edu

from relatively small impacts on biodiversity and ecosystem function (Jentsch et al., 2011), to substantial effects over both short and long time scales (Breda et al., 2006; Hoover et al., 2014; De Boeck et al., 2016). Developing a better understanding of the sources of context dependency associated with the impacts of altered precipitation is necessary for forecasting community and ecosystem trajectories in response to climate change.

One key source of context dependency associated with the impacts of altered precipitation on biodiversity and ecosystem functioning is the seasonality of precipitation (i.e., whether it rains more or less in one season relative to another; Shen et al., 2008; Potts et al., 2019). For example, a byproduct of the Dust Bowl drought in the 1930s was a shift toward more precipitation in the cool relative to the warm season, and this change in the seasonality of precipitation provided a previously unidentified mechanism to explain the seemingly context-dependent shifts in plant community composition that were observed (Knapp et al., 2020). While the seasonality of precipitation has been identified as a key driver of biodiversity and ecosystem functioning (Tonkin et al., 2017), how alterations to the seasonality of precipitation affect biodiversity and ecosystem functioning have not been well studied outside of a few research sites (e.g., Huxman et al., 2004; English et al., 2005; Potts et al., 2006). First, many of the studies that experimentally alter precipitation are located in regions where precipitation occurs mainly during a single growing season, such as in Mediterranean grasslands (e.g., Harrison et al., 2018) and woodlands (e.g., Limousin et al., 2009), or desert grasslands (e.g., Báez et al., 2013). While informative for these ecosystems, most of the terrestrial landmass has seasonal precipitation that extends beyond 1 season (Konapala et al., 2020). Second, a large number of studies in systems where precipitation extends beyond 1 season are located in colder climates that receive growing-season precipitation as rain and non-growing-season precipitation as snow. While these studies typically find that altered growing-season (rain) or non-growing-season (snow) precipitation can each impact biodiversity and/or ecosystem functioning (e.g., Knapp et al., 2002; Farrer et al., 2015), few studies directly examine the impact of altered precipitation in both seasons (e.g., Ignace, 2006; de Dios et al., 2014). Finally, while many modeling studies have sought to address alterations to precipitation in more spatially and temporally complex ways (e.g., Xu et al., 2016; Trugman et al., 2018; Wu et al., 2018), a recent model-data intercomparison found that many models have a low capacity for reproducing the seasonal sensitivity of vegetation productivity to rainfall at a given site (Paschalis et al., 2020). Thus, despite the wealth of studies examining altered precipitation regimes, key gaps remain in our understanding of how alterations to the seasonality of precipitation directly impact biodiversity and ecosystem functioning.

Dry lands provide a unique opportunity to evaluate the effects of altered seasonal precipitation on biodiversity and ecosystem functioning, as many have biannual precipitation patterns (they receive both winter and summer precipitation, Loik et al., 2004; Shen et al., 2016) and have

two distinct growing seasons and distinct annual plant communities in each season (Mulroy and Rundel, 1977; Ludwig et al., 1988). Importantly, precipitation is well known to be a key driver of germination, growth, and productivity of annual plants in dryland systems (Beatley, 1974; Crimmins et al., 2013). Moreover, there is increasing evidence that summer and winter plant communities can respond differently to precipitation inputs (Paruelo et al., 1999; Guo et al., 2002; Yahdjian and Sala, 2006; Ignace et al., 2007; Scott et al., 2009; Jenerette et al., 2010). While some evidence suggests that ecosystem functioning is more sensitive to summer than winter moisture variability (Jenerette and Chatterjee, 2012; Shen et al., 2016), summer annual plant communities are generally understudied due to their ephemeral nature (e.g., English et al., 2005), and we lack a comprehensive picture of how altered seasonal precipitation will impact annual plant biodiversity and ecosystem functioning across seasons in dryland ecosystems (Bai et al., 2008; Gherardi and Sala, 2019).

Here, we asked how annual plant biodiversity (species richness, Simpson's diversity index, and community composition) and ecosystem function (annual plant biomass) respond to changes in the seasonality of precipitation. We address this question in a dryland ecosystem (annual plants in a Colorado Desert Pinyon-Juniper woodland) with a variable biannual precipitation regime featuring both summer and winter precipitation and distinct annual plant communities in each season (Ting et al., 1976). First, we compare variation in biomass and biodiversity among seasons (summer vs. winter) to provide the natural backdrop for our experimental treatments. Second, to assess how biodiversity and ecosystem function respond to altered seasonal precipitation, we constructed a rainfall manipulation experiment (starting in 2017) that either excluded (*Summer-* or *Winter-* treatments) or increased seasonal precipitation (*Summer+* or *Winter+* treatments). Our goal with the rainfall exclusion treatment (*Summer-* or *Winter-* treatments) was to isolate the effects of a precipitation in a single season (e.g., the *Summer-* treatment only has winter precipitation) as compared to control plots and minimize the potential for any antecedent effects from precipitation in the earlier season (Potts et al., 2006). We predict that the precipitation exclusions will reduce biomass and diversity in the season that the exclusions are applied, but the next season biomass may be higher due to an increased availability of nutrients accumulated when biomass/growth was low in the previous season (Jenerette et al., 2010; Shen et al., 2016). Our goal with the rainfall addition treatments is to assess the effect of additional seasonal precipitation on annual plant biomass and biodiversity as compared to control plots that received ambient precipitation. As precipitation is highly variable in this system (Ting et al., 1976), our rainfall manipulations are designed to: (1) fall within the natural annual variation in precipitation and (2) mimic seasonal precipitation in a wetter year. As this is a water-limited system, we predict adding water will increase biomass in both seasons (relative to control plots) but that the effects on biodiversity will be more nuanced. Water additions may increase richness and

diversity by ameliorating environmental stress (e.g., Beatley, 1974; Crimmins et al., 2013) or may reduce richness and diversity by increasing competitive interactions as biomass increases (e.g., Gremer et al., 2013; Huxman et al., 2013). Thus, our statistical and qualitative comparisons focus on comparing exclusion treatments (*Summer-* or *Winter-*) or addition treatments (*Summer+* or *Winter+*) with *Control* (ambient), and not all possible pairwise comparisons are explored or reported.

Methods

Study site

This study was conducted in annual plant communities at the Pinyon Flats research site—part of the Philip L. Boyd Deep Canyon Desert Reserve in California, United States (Lat. 33.610193, Long. -116.451682; elevation 1,293 m). Located at the western edge of the Colorado/Sonoran Desert biogeographic region, Pinyon Flats has two growing seasons, a cool/wet winter season that extends from November through May and a warm/dry summer season that extends from June through October (Ting et al., 1976). During the winter season, temperature ranges between an average low of 4.4°C in December and an average high of 21.4°C in April. During the summer season, temperature ranges between an average low of 18.7°C in June and an average high of 33.3°C in July. Pinyon Flats receives an average of 220 mm of precipitation per year (average from 1988 to 2019) and has a biannual precipitation regime with an average of 151 mm falling in the winter season (range 22 mm in 2006 to 404 mm in 1992) and an average of 71 mm falling in the summer (range 2 mm in 2002 to 183 mm in 2004). All climate data are available from the Pinyon Crest weather station (<https://deepcanyon.ucnrs.org/weather-data/>). The soils are gravelly fine sandy loams classified as Typic Xerorthents and mapped within the Omstott series. The landscape at Pinyon Flats was historically dominated by *Juniperus californica* (Cupressaceae) and *Pinus monophylla* (Pinaceae) with a diversity of annual plants growing in the open spaces between these dominant species. However, the site burned in 1994, and the dominant trees have not fully recovered.

Experimental design

To examine the effect of altered precipitation seasonality on species composition and biomass in annual plant communities, we established 24 plots (6 × 8.5 m; 51.85 m²) with the following precipitation treatments arranged from overall driest to overall wettest (**Figure 1A**): *Winter-* ($n = 4$) received ambient summer precipitation and had a roof during winter to exclude all direct winter rainfall; *Summer-* ($n = 4$) received ambient winter precipitation and had a roof during summer to exclude all direct summer rainfall; *Control* ($n = 8$) received both ambient summer and ambient winter precipitation; *Summer+* ($n = 4$) received ambient winter precipitation and had water added during the summer; *Winter+* ($n = 4$) received ambient summer precipitation and had water added during the winter. On the *Winter-* and *Summer-* plots, we erected metal frames

and covered them with polyethylene plastic (Tuff Lite IV 28' x 70' TES IR/AC manufactured by Berry Plastics, Evansville, IN). The frames were aligned with the prevailing wind direction to help with air flow under the roofs. *Summer-* roofs were placed in early summer (July 7, 2018, and July 23, 2019; no rain fell in June) and kept on until mid-Fall (November 8, 2018, and October 22, 2019; before any winter precipitation fell) when the roofs were moved to the *Winter-* treatments.

During each season, precipitation was collected from rainout shelters by way of a downslope PVC system where rain flows off of the plastic roofs into side gutters which connect to a 4-in. PVC pipe system that runs to four 1,500-gallon tanks. We then added the water that fell on the *Summer-* roofs to the *Summer+* plots and added the water that fell on the *Winter-* roofs to the *Winter+* plots; all water was added within a week of the rainfall event. The amount of water added after a given rainfall event was always less than the amount of precipitation that fell due to inefficiencies in our distribution system (i.e., water remained in pipes and tanks, leaks, etc.). We added water to each water addition plot by pumping water from the storage tanks up to the plots and distributing it evenly across the plot using 17 mm Netafim drip tubing with and ensured the same amount of water was added to each plot using water meters (model: 1 DAE AS250U). This same overall design has been used successfully in nearby coastal sage scrub communities to induce drought (Allison et al., 2013; Kimball et al., 2014a). The *Winter-* and *Summer-* roofs did not exclude any overland flow of water, rainfall blown in by heavy winds, or water moving into the plots via diffusion through the soil matrix.

To sample species composition and biomass of the annual plant community in each treatment, we established six 1-m² subplots in each plot (**Figure 1B**). Within the central 0.5 m² of each subplot (light blue square in **Figure 1B**), we measured community composition, in the same location every year, using a point-intercept approach with 50 points recording all hits at each point and noting the presence of any species not hit. In the area between where species composition was sampled and the outer edge of the subplot, we sampled aboveground biomass in an additional 0.25 m² area (green squares in **Figure 1B**). We rotated the location of biomass sampling to a different side each season to not resample the same location. For each harvest we clipped all aboveground biomass, dried it for 4 days at 60°C, and weighed it to the nearest 0.01 g. All subplots were placed at least 1 m from the edge of the plot to reduce the potential for edge effects from the rainfall manipulation shelters.

Over the last 30 years, precipitation was highly variable among years and seasons (**Figure 2A**), and the ratio of summer to winter rain also varied over time, with more recent years having more winter than summer rain (**Figure 2B**). The amount of water added to the *Summer+* and *Winter+* treatments varied among our sampling seasons and was dependent on the annual precipitation in that year and specific season. In 2018, the *Summer+* plots received the equivalent of 29 mm of additional precipitation; in 2019, the *Winter+* plots received the equivalent of 133

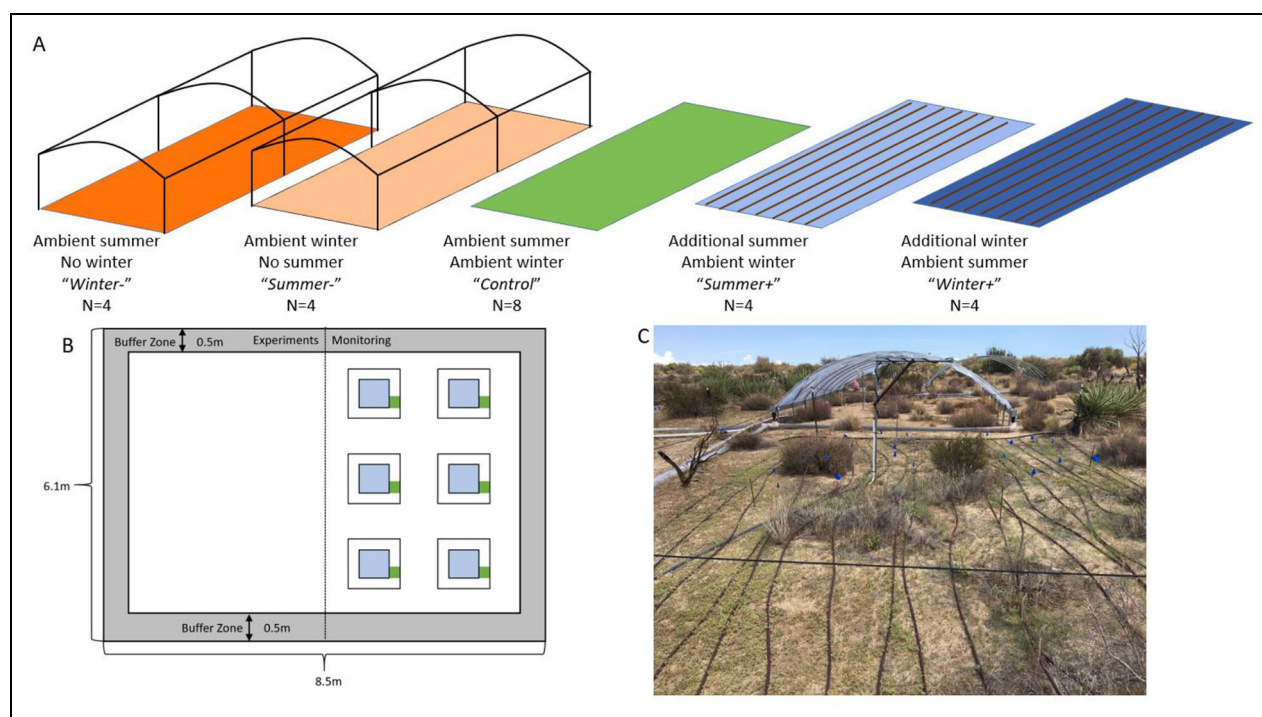


Figure 1. Experimental layout of the Pinyon Flats precipitation experiment. A) 24 (51.85 m²) plots were established with the following precipitation treatments arranged along an aridity gradient: *Winter-* received ambient summer precipitation and had a roof during winter to exclude all winter rainfall; *Summer-* received ambient winter precipitation and had a roof during summer to exclude all summer rainfall; *Control* received both ambient summer and ambient winter and had no manipulations; *Summer+* received ambient winter precipitation and had water added during the summer; *Winter+* received ambient summer precipitation and had water added during the winter. Treatment color codes are preserved throughout our figures. B) Each plot contained six 1 m² plots (black outlined squares) in which the center 0.5 m² was sampled for annual plant species composition (light blue squares) and a 25 cm² subplot was harvested for biomass (green squares). The location of the biomass sampling rotated each season. C) A photo of a water addition plot and a rainfall exclusion plot. DOI: <https://doi.org/10.1525/elementa.2021.00014.f1>

mm of additional precipitation; in 2019, the *Summer+* plots received the equivalent of 22 mm of additional precipitation; in 2020, the *Winter+* plots received the equivalent of 108 mm of additional precipitation (**Figure 2C**).

Statistical analysis

To test how annual plant biomass, species richness, Simpson's diversity index ($D = 1 - \sum_{i=1}^S p_i^2$), and composition differed among seasons (summer vs. winter), we averaged the biomass in subplots for only the control plots and compared values among control plots in each sampling period using a generalized linear mixed model with sampling period as a predictor variable, Plot ID as a random factor, and biomass (g/m²), richness, or Simpson's diversity index as our response variable and then compared individual sampling periods using Tukey post hoc comparisons. Biomass was log transformed prior to analyses, but raw biomass values are plotted and reported. We then used permutational analysis of variance (PERMANOVA: Anderson, 2001) in the Vegan package (Oksanen et al., 2013) in R to test for differences in community composition among seasons (including the effect of plot identity). PERMANOVA is very similar to an ANOVA but allows the analysis of differences in species composition rather than species numbers (Anderson, 2001). Next, we tested for

pairwise differences among treatments in community composition using the pairwise.adonis function (Martinez Arbizu, 2020). Finally, we used indicator species analysis (Dufrene and Legendre, 1997) to ask which species are driving significant differences in community composition for the above significant PERMANOVAs.

To test how biomass, species richness, and Simpson's diversity index differed among treatments within a season, we averaged our response variables among subplots for each plot and compared treatments using separate ANOVAs in each season with treatment as a categorical predictor and biomass (g/m²), richness, or Simpson's diversity index as our response variable. For all 3 variables, we then compared each treatment's values to *Control* using a Dunnett's test. Analyses were conducted in JMP version 13 (SAS Institute Inc., Cary, N.C.). We then used PERMANOVA to test for differences in community composition among treatments and sampling periods, tested for pairwise differences among treatments in community composition, and used indicator species analysis to ask which species are driving significant differences in community composition for the above significant PERMANOVAs (as described above).

Finally, to visualize differences in community composition among seasons, treatments, and sampling periods, we used a nonmetric multidimensional scaling (NMDS) based

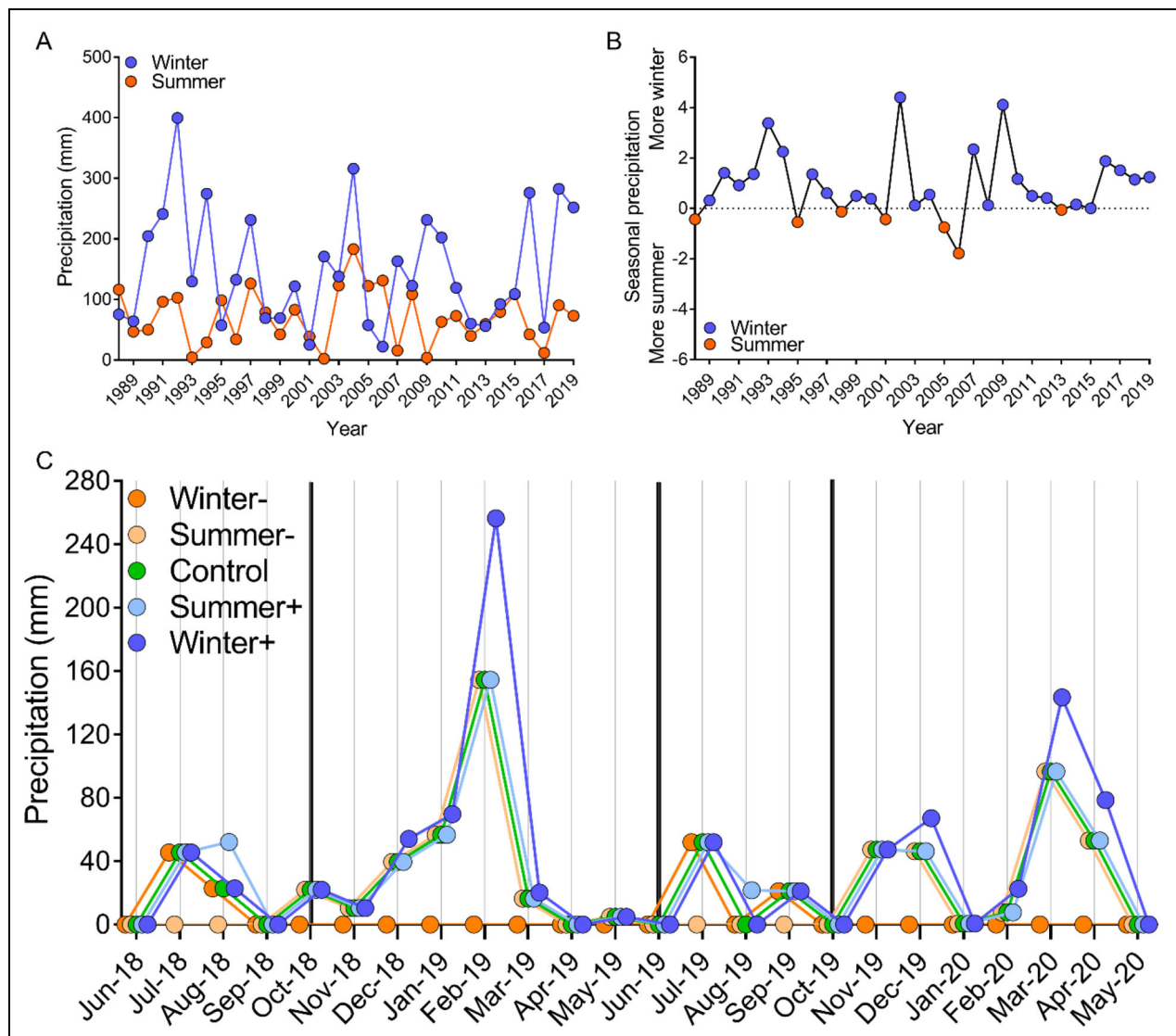


Figure 2. A) Total precipitation over the last 30 years at the site divided into winter (November through May) and summer (June through October) precipitation, where year indicates the year at the start of the season (i.e., June or November). B) Ratio of winter to summer precipitation where positive values indicate more winter precipitation and negative values indicate more summer precipitation. Over the first 15 years (1989 to 2004), 5 years had more summer than winter rain, while in the last 15 years (2005 to 2019) only 2 years had more summer rain. C) Precipitation (mm) received by each treatment over the 2 years of the experiment (see text for seasonal totals). Dark orange points *Winter-* received ambient summer precipitation and had winter precipitation excluded with a roof; light orange *Summer-* received ambient winter precipitation and had summer precipitation excluded with a roof; green *Control* received both ambient summer and ambient winter and had no manipulations; light blue *Summer+* received ambient winter precipitation and had water added during the summer; dark blue *Winter+* received ambient summer precipitation and had water added during the winter; points slightly offset to increase visibility. Black vertical lines differentiate seasons. DOI: <https://doi.org/10.1525/elementa.2021.00014.f2>

on Bray–Curtis dissimilarity among plots in R (R Core Team, 2019). Bray–Curtis dissimilarity is a semi-metric measure of dissimilarity used for continuous numerical data and does not group samples by shared zeros in the dataset (Beals, 1984).

Results

Differences among season (control plots only)

In general, we found that annual plant biomass and biodiversity differed among seasons (summer and winter)

with some variation among sampling years. Biomass significantly differed among seasons ($F_{3,21} = 45.29$, $P < 0.001$), and winter of 2019 biomass ($79.86 \text{ g/m}^2 \pm 9.89$) was significantly higher than all other seasons. Summer 2019 ($23.90 \text{ g/m}^2 \pm 2.54$) and winter 2020 ($29.96 \text{ g/m}^2 \pm 4.76$) did not significantly differ, but summer 2018 ($12.24 \text{ g/m}^2 \pm 2.84$) was significantly lower than winter 2020 (based on Tukey post hoc comparisons). Species richness significantly differed among seasons ($F_{3,21} = 33.96$, $P < 0.001$) and was consistently lower in

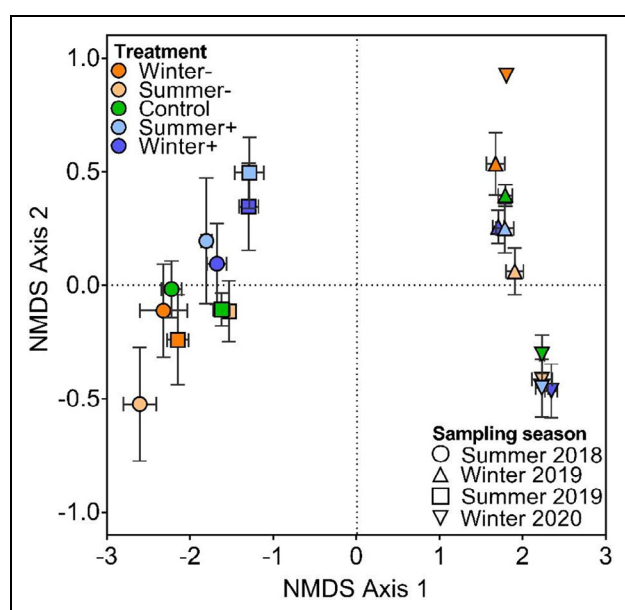


Figure 3. Nonmetric multidimensional scaling ordination plot visualizing composition differences of annual plant communities among treatments (colors) and sampling periods (shapes); stress = 0.06. Each symbol represents the mean NMDS scores (± 1 standard deviation) for plots classified within a group. Symbols closer to each other are more similar than those further apart. Dark orange points *Winter-* received ambient summer precipitation and had winter precipitation excluded with a roof; light orange points *Summer-* received ambient winter precipitation and had summer precipitation excluded with a roof; green points *Control* received both ambient summer and ambient winter and had no manipulations; light blue points *Summer+* received ambient winter precipitation and had water added during the summer; dark blue points *Winter+* received ambient summer precipitation and had water added during the winter. Circles represent summer 2018. Up-pointing triangles represent winter 2019. Squares represent summer 2019. Down-pointing triangles represent winter 2020. DOI: <https://doi.org/10.1525/elementa.2021.00014.f3>

summer than in winter (summer 2018: 4.7 ± 0.4 species per plot; summer 2019: 4.5 ± 0.4 ; winter 2018: 8.6 ± 0.5 ; winter 2019: 8.6 ± 0.4) but did not differ among either summer season or either winter season (based on Tukey post hoc comparisons). Simpson's diversity index varied among sampling seasons ($F_{3,21} = 13.67$, $P < 0.001$) with no difference between summer 2018 (0.45 ± 0.02) and summer 2019 (0.48 ± 0.03), no difference between summer 2019 and winter 2019 (0.54 ± 0.03), and winter 2020 (0.64 ± 0.03) having significantly greater Simpson's diversity than the other 3 sampling periods. Finally, we found that composition significantly differed among seasons ($F_{1,28} = 40.26$, $P = 0.001$, **Figure 3**); summer annual plant communities were dominated by *Portulaca oleracea* (Portulacaceae) and *Bouteloua aristoides* (Poaceae), and winter plant communities were dominated by *Erodium*

cicutarium (Geraniaceae) and *Bromus madritensis* (Poaceae). Across both seasons and both years, we found a total of 54 species of annual plants present, with 16 species unique to summer, 33 species unique to winter, and 5 species found in both seasons (Supplementary Table 1).

Main effects of altered seasonal precipitation on biomass and biodiversity within each sampling period

In general, we found that altered precipitation resulted in significant differences in annual plant biomass among treatments in each sampling period (summer 2018: $F_{4,19} = 24.16$, $P < 0.001$, **Figure 4A**; winter 2019: $F_{4,19} = 7.36$, $P < 0.001$, **Figure 4B**; summer 2019: $F_{4,19} = 16.40$, $P < 0.001$, **Figure 4C**; winter 2020: $F_{4,19} = 11.22$, $P < 0.001$, **Figure 4D**). Similarly, we generally found that annual plant biodiversity patterns significantly differed among treatments for summer 2018, winter 2019, and winter 2020 (but not summer 2019) for both species richness (summer 2018: $F_{4,19} = 12.58$, $P < 0.001$, **Figure 5A**; winter 2019: $F_{4,19} = 33.10$, $P < 0.001$, **Figure 5B**; summer 2019: $F_{4,19} = 1.19$, $P = 0.32$, **Figure 5C**; winter 2020: $F_{4,19} = 53.03$, $P < 0.001$, **Figure 5D**) and Simpson's diversity index (summer 2018: $F_{4,19} = 10.72$, $P < 0.001$, **Figure 5E**; winter 2019: $F_{4,19} = 32.70$, $P < 0.001$, **Figure 5F**; summer 2019: $F_{4,19} = 1.41$, $P = 0.27$, **Figure 5G**; winter 2020: $F_{4,19} = 51.42$, $P < 0.001$, **Figure 5H**). Finally, we found that community composition (**Figure 3**) significantly differed between treatments in all four sampling periods: summer 2018 ($F_{1,19} = 2.22$, $P = 0.04$), winter 2019 ($F_{1,19} = 2.46$, $P = 0.008$), summer 2019 ($F_{1,19} = 5.77$, $P = 0.01$), winter 2020 ($F_{1,16} = 3.25$, $P = 0.03$). Below we report contrasts between water exclusion plots (*Summer-* or *Winter-*) and *Control* plots and between water addition plots (*Summer+* or *Winter+*) and *Control* plots.

Effects of water exclusion treatments

We found that excluding water in both summer (*Summer-* treatments: 2018: $P = 0.038$; 2019: $P < 0.001$) and winter (*Winter-* treatments: 2019: $P < 0.001$; 2020: $P = 0.001$) resulted in lower biomass than in *Control* plots. Unexpectedly, in winter 2020, we found significantly more biomass in the *Summer-* treatment ($P = 0.045$) than in *Control* plots (**Figure 4D**). Moreover, we found that excluding water resulted in lower annual plant species richness in summer 2018 (*Summer-* treatment: $P < 0.001$) and both winter seasons (*Winter-* treatments: 2019: $P < 0.001$; 2020: $P < 0.001$), and lower Simpson's diversity in summer 2018 (*Summer-* treatments: 2018: $P < 0.001$) and both winter seasons (*Winter-* treatments: 2019: $P < 0.001$; 2020: $P < 0.001$) than in *Control* plots. Unexpectedly, in winter 2019, we found that the *Summer-* plots had significantly greater ($P = 0.01$) Simpson's diversity than the *Control* plots (0.70 vs. 0.55, respectively). Finally, we found that the *Summer-* treatment significantly differed from the *Control* ($F_{1,1} = 3.41$, $P = 0.02$) in summer 2018 and that difference was driven by *P. oleracea* (Portulacaceae) in the *Summer-* treatment. In winter 2019, the *Winter-* plots differed from both *Summer-* ($F_{1,1} = 7.12$, $P = 0.03$) and *Winter+* ($F_{1,1} = 3.33$, $P = 0.05$), but not *Control*, and those differences were driven by

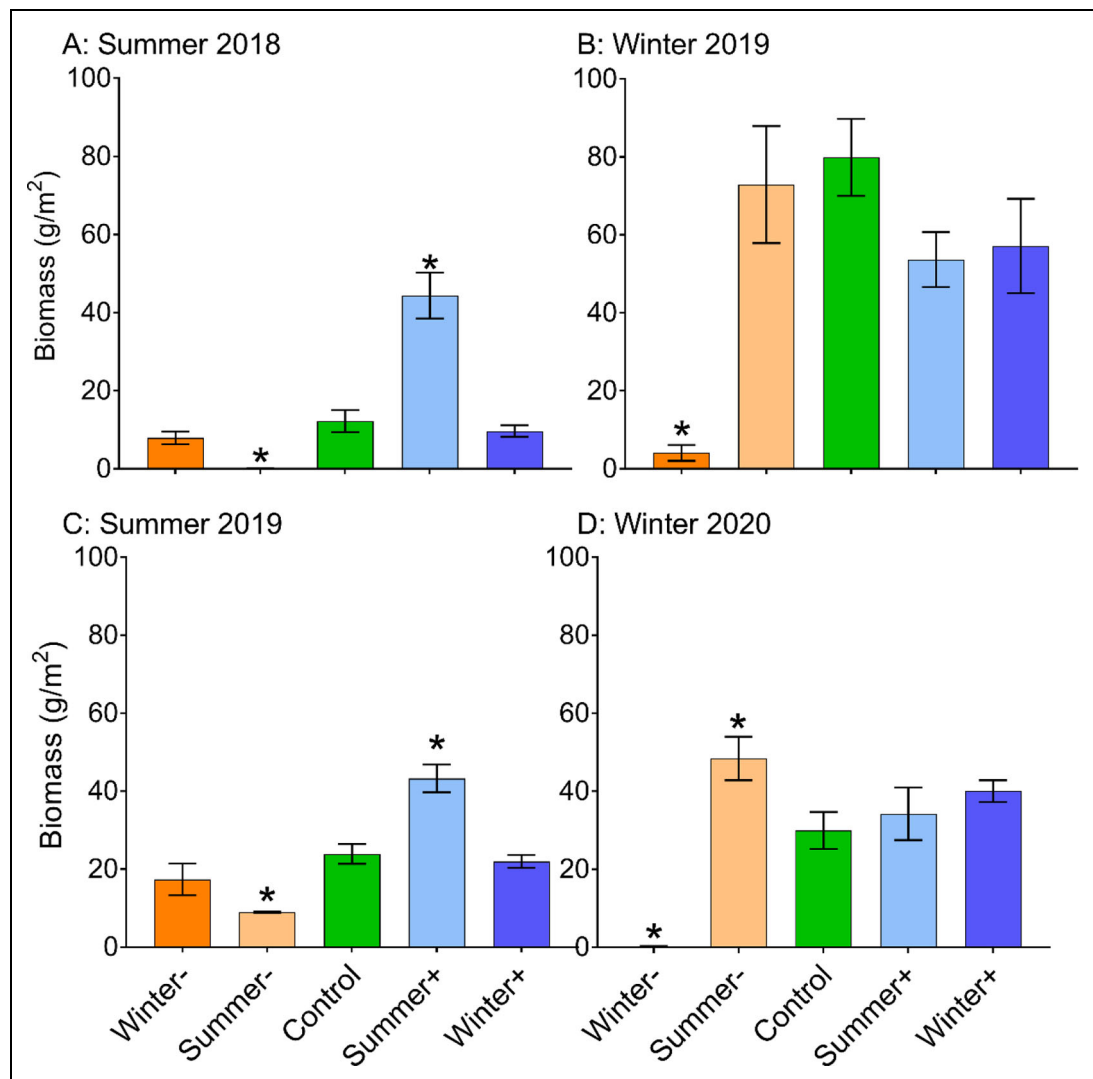


Figure 4. Annual plant biomass ($\pm$ S.E.) response to precipitation treatments by season. Dark orange bars *Winter-* received ambient summer precipitation and had winter precipitation excluded with a roof; light orange bars *Summer-* received ambient winter precipitation and had summer precipitation excluded with a roof; green bars *Control* received both ambient summer and ambient winter and had no manipulations; light blue bars *Summer+* received ambient winter precipitation and had water added during the summer; dark blue bars *Winter+* received ambient summer precipitation and had water added during the winter. Stars (*) indicate treatments that significantly differed from Control based on a Dunnett's test. DOI: <https://doi.org/10.1525/elementa.2021.00014.f4>

E. cicutarium (Geraniaceae) in the *Winter-* plots. Finally, in winter 2020, the differences in community composition were driven by *Euphorbia micromera* (Euphorbiaceae) and *Descurainia pinnata* (Brassicaceae) in the *Winter-* plots, but our low samples size did not allow us to detect a difference in the pairwise tests.

Effects of water addition treatments

Interestingly, the annual plant biomass response to water addition was asymmetric among seasons. In summer, we found that adding water (*Summer+* treatments) resulted in higher biomass than in *Control* plots (2018: $P < 0.001$; 2019: $P < 0.001$), but when adding water in winter (*Winter+* treatments) biomass did not differ from the *Control* (2019: $P = 0.12$; 2020: $P = 0.13$). However, adding water had no effect on richness or Simpson's diversity in any sampling period. Despite the lack of an effect on

taxonomic diversity metrics, the only case where we found a difference in composition in response to water addition was in summer 2019 where the *Summer+* plots differed from *Control* ($F_{1,1} = 7.43$, $P = 0.002$) and *Summer-* ($F_{1,1} = 6.51$, $P = 0.005$) plots and these differences in community composition were driven by *B. aristoides* (Poaceae) in the *Summer+* plots. All other pairwise comparisons of differences in species composition not related to our focal questions are found in Appendix 1.

Discussion

While changes in precipitation are known to affect biodiversity and ecosystem functioning (Smith, 2011; Beier et al., 2012), most studies primarily alter the total amount of precipitation (e.g., Clark et al., 2016; Copeland et al., 2016; Smith et al., 2016; Schwalm et al., 2017) and generally ignore the seasonality of precipitation (i.e., whether it

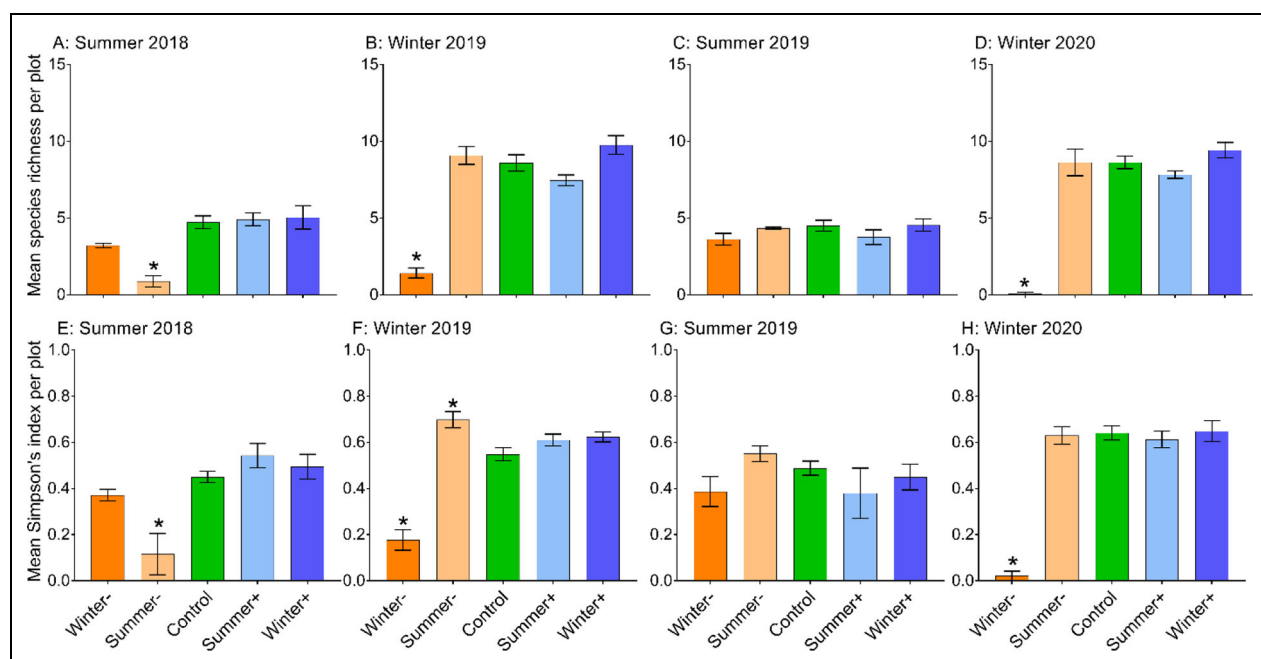


Figure 5. Response ($\pm$ S.E.) of species richness (A, B, C, D) and Simpson's diversity index (E, F, G, H) of the annual plant community to precipitation treatments by season. Dark orange bars *Winter-* received ambient summer precipitation and had winter precipitation excluded with a roof; light orange bars *Summer-* received ambient winter precipitation and had summer precipitation excluded with a roof; green bars *Control* received both ambient summer and ambient winter and had no manipulations; light blue bars *Summer+* received ambient winter precipitation and had water added during the summer; dark blue bars *Winter+* received ambient summer precipitation and had water added during the winter. Stars (*) indicate treatments that significantly differed from Control based on a Dunnett's test. DOI: <https://doi.org/10.1525/elementa.2021.00014.f5>

rains more or less in one season relative to another (see Knapp et al., 2002, 2020). Our study illustrates how precipitation seasonality may mediate the impacts of altered precipitation regimes on biodiversity and ecosystem functioning. Specifically, we found nuanced asymmetric seasonal responses. First, we found that excluding rainfall reduced biomass in both summer and winter but may have led to increased biomass in the following season. Second, we found that increased precipitation increased annual plant biomass in summer, but not winter, despite this being a water limited dryland ecosystem. Third, we found modest responses of biodiversity where increased precipitation did not affect annual plant richness or Simpson's diversity in either summer or winter but decreased precipitation reduced both richness and Simpson's diversity in both winter seasons but only in the first summer season. Finally, we found increased precipitation led to a shift in annual plant species composition in both summer seasons but not winter, while decreased precipitation shifted community composition in both winter seasons and in only 1 summer season. These results are consistent with the hypothesis that precipitation seasonality is a key driver of biodiversity and ecosystem functioning (Tonkin et al., 2017) but contrasts with a meta-analysis showing that annual net primary productivity was more sensitive to precipitation additions than reductions (Wilcox et al., 2017).

Biomass response to altered seasonal precipitation

In general, we found that annual plant biomass was greater in winter than in summer (Figure 4), likely reflecting the generally longer and wetter winter growing season (Dimmitt, 2000a). In all cases, excluding precipitation greatly reduced biomass, consistent with our understanding of dryland ecosystems (Mulroy and Rundel, 1977; Ludwig et al., 1988; Dimmitt et al., 2015). Despite excluding precipitation, we still measured biomass in many of the *Summer-* plots in summer and in the *Winter-* plots in winter, though it was significantly lower than in *Control* plots. Although we excluded precipitation, we believe that water still reached our plots via overland flow or as rain blown under the roofs by wind due to the presence of biomass (living plants) under the roofs that exclude all direct rainfall. Indeed, overland flow can be an important source of water for many plants (Schlesinger et al., 1989; Ludwig et al., 2005), and summer storms may produce relatively large volumes of water over short time periods (Wayne Higgins et al., 2003; Morin et al., 2006; Fiener and Auerswald, 2009), exceeding soil infiltration rates and causing water to move laterally across the landscape (Wayne Higgins et al., 2003; Bennett et al., 2020).

Interestingly, in winter 2020, biomass was higher in the *Summer-* plots than in *Control* plots (Figure 4D) even though the *Summer-* treatment did not receive direct summer rain the previous 2 summers and was exposed to the

same ambient rainfall in both winters as in the *Control* plots. Moreover, the *Summer*- plots did not differ in composition from the *Control* plots in winter 2020, suggesting that the differences in biomass were not a result of differences in the functional composition of the communities. Instead, this finding is consistent with previous studies in dryland ecosystems suggesting that reduced productivity in the previous season (i.e., the reduced biomass in the *Summer*- treatments during summer) may help facilitate increased ecosystem functioning the following season via increased availability of nutrients accumulated from the prior season when growth was low (Jenerette et al., 2010; Shen et al., 2016) and further highlights the importance of lag effects in annual plant community responses to precipitation (Dudney et al., 2017).

Finally, we found that increased precipitation increased biomass in summer (*Summer+* > *Control*) but had no effect in winter (*Winter+* = *Control*; **Figure 4**) suggesting that biomass was not water limited in either winter season highlighting the asymmetric response of additional precipitation among seasons. These results align with the general observation that the summer annual plant community is more water limited than the winter community (Dimmitt, 2000b; Dimmitt et al., 2015) and suggest that summer season ecosystem function may be more mediated by precipitation than winter ecosystem function. While beyond the scope of our measurements, the patterns we found have implications for carbon (C) assimilation. However, the Hierarchical Pulse-Dynamics Framework (Collins et al., 2014) suggests that short-term gains in production (as seen in the increased biomass in the *Summer+* treatment) may be balanced over multiyear time frames as reserves gained in 1 year may be respired in another (Anderson-Teixeira et al., 2011; Shen et al., 2016). Longer term monitoring of biomass in this experiment will help understand the multiyear dynamics of the summer annual community biomass and whether additional summer precipitation may have lasting effects on the C cycle or be counterbalanced by low rainfall summers.

Biodiversity and composition responses to altered seasonal precipitation

Excluding seasonal precipitation (the *Summer*- and *Winter*-treatments) generally decreased both species richness and Simpson's diversity and shifted composition. In general, this is a water-limited ecosystem (Mulroy and Rundel, 1977; Ludwig et al., 1988; Dimmitt et al., 2015), where water (and temperature) triggers germination (low temperatures and rain in winter and high temperatures and rain in summer; Beatley, 1974; Guo et al., 2002). Our rainfall exclusion in both seasons likely reduced precipitation enough that only some individuals of some species germinated and survived to adulthood. This was evident in the strong impact on composition in 3 of the 4 seasons when we excluded precipitation. In summer 2018, the difference in composition between the *Control* plots and the *Summer*- plots was driven by an increased abundance of *P. oleracea* (Portulacaceae) in the *Summer*- treatment. *P. oleracea* is a widely distributed weedy species that

originated in the Mediterranean and is considered invasive in dry lands of the Sonoran biogeographic region (Van Devender et al., 2006). In winter 2019, the difference in composition between the *Control* and the *Winter*- plots was due to an increased abundance of exotic *E. cicutarium* (Geraniaceae) in the *Winter*- plots. *E. cicutarium* is another invasive species (Van Devender et al., 2006) whose high water use efficiency (Kimball et al., 2014b) likely contributed to its success in this rainfall exclusion treatment and in winter 2020. Finally, in winter 2020, the difference in composition between the *Control* and the *Winter*- plots was driven by increased abundances of exotic *E. cicutarium* and the native *D. pinnata* (Brassicaceae). *D. pinnata* has been found to germinate under a wider range of conditions than some other dryland species (Forbis, 2010) which may contribute to its success here. Future work examining the functional diversity of these species may help explain the mechanisms underlying these changes in composition.

The one case where excluding precipitation did not have a strong effect was in summer 2019, where the annual plant communities in the *Summer*- treatment did not differ from *Control* in species richness, Simpson's diversity, nor community composition. While biomass in this treatment was significantly lower than the *Control*, biomass was 60 times higher in summer 2019 than in the previous summer (summer 2018: 0.15 ± 0.05 g/m², summer 2019: 9.0 ± 0.17 g/m²). This higher biomass suggests that more water may have entered these plots (wind-blown or via overland flow) and was likely enough to trigger germination of the same set of species in the *Summer*- treatment as in the *Control* plots.

In contrast, we found that water addition had no effect on either species richness nor on Simpson's diversity in either summer or winter, suggesting that water neither limited the establishment of any species during these 2 years (e.g., Beatley, 1974; Crimmins et al., 2013) nor substantially altered competitive interactions that may mediate diversity as is found in other dryland ecosystems (e.g., Gremer et al., 2013; Huxman et al., 2013). The only case where we found an effect of increased precipitation on biodiversity was in summer 2019, where the *Summer+* plots differed in composition from *Control* plots. This difference in composition was driven by an increased abundance of the native grass *B. aristidoides* (Poaceae) when water was added (approximately 30% relative abundance in *Control* vs. approximately 70% relative abundance in *Summer+*). Previous research in the Chihuahuan dry lands found that *B. aristidoides* did not respond to the addition of either 6 or 25 mm of additional precipitation and was only found in plots fertilized with nitrogen (N; Gutierrez et al., 1988). In summer 2019, we added 22 mm of precipitation, similar to the 25 mm of additional precipitation in the Gutierrez et al. (1988) study, and the differing responses may be the result of different locally adapted populations, however, future studies are needed.

Despite the changes in composition in 2019, our results largely suggest that the biodiversity of the summer plant communities is generally resistant to increases in the amount of precipitation, despite large changes in

biomass of the same plant communities. This pattern of relatively resistant biodiversity, but substantial changes in ecosystem function (biomass) in the summer, but not in winter, may be a result of two different factors. First, the overall higher biomass and greater precipitation in the winter suggests that the summer plant communities may simply have been more water limited than the winter community during the 2 years of our study. In this case, the winter annual community biomass was potentially limited by a second resource (e.g., N). Future research examining the seed bank at this site will give a better picture of the pool of species potentially able to contribute to diversity during each season and whether there are more species in the summer seed bank that did not germinate. Second, from an evolutionary perspective, the summer annual plant community may have a more plastic evolutionary strategy for coping with environmental change (Hoffmann and Sgro, 2011; Bortero et al., 2015) than the winter annual plant community. In this case, the summer annuals are potentially more able to rapidly respond to changing environmental conditions and capitalize on the “good times” (e.g., Bradshaw, 1965; Scheiner, 2013) than the winter annual plant community.

Conclusion

In summary, we found asymmetric seasonal responses to altered season precipitation in this dryland ecosystem. Specifically, our results suggest that increased summer precipitation may have stronger short-term impacts on annual plant biodiversity and ecosystem function than increased winter precipitation. In contrast, decreasing precipitation may have ubiquitous negative effects on annual plants across both summer and winter but may lead to increased biomass in the following off-seasons. Moreover, our results suggest that the biodiversity of both summer and winter plant communities is generally resistant (shows little change) to increases in the amount of precipitation, despite large changes in biomass. Taken together, our results suggest that a deeper consideration of the seasonality of altered precipitation has the potential to help resolve some of the context dependency observed in biodiversity and ecosystem response to altered precipitation regimes.

Data accessibility statement

All species composition and biomass data used in these analyses are publicly available on Dryad at <https://doi.org/10.6086/D1XT3V>.

Supplemental files

The supplemental files for this article can be found as follows:

Supplementary Table 1. List of annual plant species in each season and their relative abundance across all subplots and all time points within each season.

Appendix 1. All other pairwise comparisons of differences in species composition not related to our focal question.

Acknowledgments

We thank the Boyd-Deep Canyon NRS (<https://doi.org/10.21973/N3V66D>) for logistic support, Erin McCann, Alexander Krichels, Aral C. Greene, Holly Andrews, Stuart Schwab, Clarissa Rodriguez, Danielle Logan, Robert Johnson, and Jon Botthoff for help in the field. The authors would also like to respectfully acknowledge and recognize our responsibility to the original and current caretakers of the land, air, and water at Pinyon Flats: the ʔíviluqaletem (Cahuilla) people and all of their ancestors and descendants. We are grateful to have the opportunity to work on these homelands.

Funding

This work was partially supported by the National Science Foundation (DEB 1916622 and 1656062).

Competing interests

PMH is an associate editor at Elementa but had no role in the reviewing or handling of this manuscript.

Author contributions

Contributed to conception and design: MJS, PMH, GDJ, MLG.

Contributed to acquisition of data: SM, TM-M, LS, MS.

Contributed to analysis of data: MJS.

Drafted and/or revised this article: MJS, PMH, GDJ, TM-M.

Approved the submitted version for publication: MJS, PMH, GDJ.

References

- Allison, SD, Lu, Y, Weihe, C, Goulden, ML, Martiny, AC, Treseder, KK, Martiny, JB. 2013. Microbial abundance and composition influence litter decomposition response to environmental change. *Ecology* **94**: 714–725.
- Anderson, MJ. 2001. A new method for non-parametric multivariate analysis of variance. *Austral Ecology* **26**: 32–46.
- Anderson-Teixeira, KJ, Delong, JP, Fox, AM, Brese, DA, Litvak, ME. 2011. Differential responses of production and respiration to temperature and moisture drive the carbon balance across a climatic gradient in New Mexico. *Global Change Biology* **17**: 410–424.
- Báez, S, Collins, SL, Pockman, WT, Johnson, JE, Small, EE. 2013. Effects of experimental rainfall manipulations on Chihuahuan Desert grassland and shrubland plant communities. *Oecologia* **172**: 1117–1127.
- Bai, Y, Wu, J, Xing, Q, Pan, Q, Huang, J, Yang, D, Han, X. 2008. Primary production and rain use efficiency across a precipitation gradient on the Mongolia plateau. *Ecology* **89**: 2140–2153.
- Beals, EW. 1984. Bray-Curtis ordination - An effective strategy for analysis of multivariate ecological data. *Advances in Ecological Research* **14**: 1–55.
- Beatley, JC. 1974. Phenological events and their environmental triggers in Mojave-desert ecosystems. *Ecology* **55**: 856–863.
- Beier, C, Beierkuhnlein, C, Wohlgemuth, T, Penuelas, J, Emmett, B, Körner, C, de Boeck, H, Christensen,

- JH, Leuzinger, S, Janssens, IA. 2012. Precipitation manipulation experiments—challenges and recommendations for the future. *Ecology Letters* **15**: 899–911.
- Bennett, KE, Miller, G, Talsma, C, Jonko, A, Bruggeman, A, Atchley, A, Lavadie-Bulnes, A, Kwicklis, E, Middleton, R. 2020. Future water resource shifts in the high desert Southwest of Northern New Mexico, USA. *Journal of Hydrology: Regional Studies* **28**: 100678.
- Botero, CA, Weissing, FJ, Wright, J, Rubenstein, DR. 2015. Evolutionary tipping points in the capacity to adapt to environmental change. *Proceedings of the National Academy of Sciences of the United States of America* **112**: 184–189.
- Bradshaw, AD. 1965. Evolutionary significance of phenotypic plasticity in plants. *Advances in Genetics* **13**: 115–155.
- Bréda, N, Huc, R, Granier, A, Dreyer, E. 2006. Temperate forest trees and stands under severe drought: A review of ecophysiological responses, adaptation processes and long-term consequences. *Annals of Forest Science* **63**: 625–644.
- Clark, JS, Iverson, L, Woodall, CW, Allen, CD, Bell, DM, Bragg, DC, D'Amato, AW, Davis, FW, Hersh, MH, Ibanez, I. 2016. The impacts of increasing drought on forest dynamics, structure, and biodiversity in the United States. *Global Change Biology* **22**: 2329–2352.
- Collins, SL, Belnap, J, Grimm, NB, Rudgers, JA, Dahm, CN, D'odorico, P, Litvak, M, Natvig, DO, Peters, DC, Pockman, WT, Sinsabaugh, RL, Wolf, BO. 2014. A multiscale, hierarchical model of pulse dynamics in rid-land ecosystems. *Annual Review of Ecology, Evolution, and Systematics* **45**: 397–419.
- Cook, BI, Seager, R. 2013. The response of the North American Monsoon to increased greenhouse gas forcing. *Journal of Geophysical Research-Atmospheres* **118**: 1690–1699.
- Copeland, SM, Harrison, SP, Latimer, AM, Damschen, EI, Eskelinen, AM, Fernandez-Going, B, Spasojevic, MJ, Anacker, BL, Thorne, JH. 2016. Ecological effects of extreme drought on Californian herbaceous plant communities. *Ecological Monographs* **86**: 295–311.
- Crimmins, TM, Crimmins, MA, Bertelsen, CD. 2013. Spring and summer patterns in flowering onset, duration, and constancy across a water-limited gradient. *American Journal of Botany* **100**: 1137–1147.
- De Boeck, HJ, Bassin, S, Verlinden, M, Zeiter, M, Hiltbrunner, E. 2016. Simulated heat waves affected alpine grassland only in combination with drought. *New Phytologist* **209**: 531–541.
- de Dios, VR, Weltzin, JF, Sun, W, Huxman, TE, Williams, DG. 2014. Transitions from grassland to savanna under drought through passive facilitation by grasses. *Journal of Vegetation Science* **25**: 93–946.
- Dimmitt, MA. 2000a. Biomes and communities of the Sonoran Desert region, in Dimmitt, MA, Comus, PW, Phillips, SJ, Brewer, LM eds., *A natural history of the Sonoran Desert*. Oakland, CA: University of California Press: 3–18.
- Dimmitt, MA. 2000b. Plant ecology of the Sonoran Desert region, in Dimmitt, MA, Comus, PW, Phillips, SJ, Brewer, LM eds., *A natural history of the Sonoran Desert*. Oakland, CA: University of California Press.
- Dimmitt, MA, Comus, PW, Phillips, SJ, Brewer, LM. 2015. *A natural history of the Sonoran Desert*. Oakland, CA: University of California Press.
- Dudney, J, Hallett, LM, Larios, L, Farrer, EC, Spotswood, EN, Stein, C, Suding, KN. 2017. Lagging behind: Have we overlooked previous-year rainfall effects in annual grasslands? *Journal of Ecology* **105**: 484–495.
- Dufrene, M, Legendre, P. 1997. Species assemblages and indicator species: The need for a flexible asymmetrical approach. *Ecological Monographs* **67**(3): 345–366.
- English, NB, Weltzin, JF, Fravolini, A, Thomas, L, Williams, DG. 2005. The influence of soil texture and vegetation on soil moisture under rainout shelters in a semi-desert grassland. *Journal of Arid Environments* **63**: 324–343.
- Farrer, EC, Ashton, IW, Spasojevic, MJ, Fu, S, Gonzalez, DJ, Suding, KN. 2015. Indirect effects of global change accumulate to alter plant diversity but not ecosystem function in alpine tundra. *Journal of Ecology* **103**: 351–360.
- Fiener, P, Auerswald, K. 2009. Spatial variability of rainfall on a sub-kilometre scale. *Earth Surface Processes and Landforms* **34**: 848–859.
- Forbis, TA. 2010. Germination phenology of some Great Basin native annual forb species. *Plant Species Biology* **25**: 221–230.
- Frank, D, Reichstein, M, Bahn, M, Thonicke, K, Frank, D, Mahecha, MD, Smith, P, Van der Velde, M, Vicca, S, Babst, F, Beer, C, Buchmann, N, Canadell, JG, Ciais, P, Cramer, W, Ibrom, A, Miglietta, F, Poulter, B, Rammig, A, Seneviratne, SI, Walz, A, Wattenbach, M, Zavala, MA, Zscheischler, J. 2015. Effects of climate extremes on the terrestrial carbon cycle: Concepts, processes and potential future impacts. *Global Change Biology* **21**: 2861–2880.
- Gherardi, LA, Sala, OE. 2019. Effect of interannual precipitation variability on dryland productivity: A global synthesis. *Global Change Biology* **25**: 269–276.
- Gremer, JR, Kimball, S, Keck, KR, Huxman, TE, Angert, AL, Venable, DL. 2013. Water-use efficiency and relative growth rate mediate competitive interactions in Sonoran Desert winter annual plants. *American Journal of Botany* **100**: 2009–2015.
- Guo, QF, Brown, JH, Valone, TJ. 2002. Long-term dynamics of winter and summer annual communities in the Chihuahuan Desert. *Journal of Vegetation Science* **13**: 575–584.
- Gutierrez, JR, Da Silva, OA, Pagani, MI, Weems, D, Whitford, WG. 1988. Effects of different patterns of supplemental water and nitrogen fertilization on productivity and composition of Chihuahuan Desert annual plants. *American Midland Naturalist* **119**(2): 336–343.
- Hallett, LM, Hsu, JS, Cleland, EE, Collins, SL, Dickson, TL, Farrer, EC, Gherardi, LA, Gross, KL, Hobbs,

- RJ, Turnbull, L, Suding, KN. 2013. Biotic mechanisms of community stability shift along a precipitation gradient. *Ecology* **95**: 1693–1700.
- Harrison, SP, LaForgia, ML, Latimer, AM. 2018. Climate-driven diversity change in annual grasslands: Drought plus deluge does not equal normal. *Global Change Biology* **24**: 1782–1792.
- Hoffmann, AA, Sgro, CM. 2011. Climate change and evolutionary adaptation. *Nature* **470**: 479–485.
- Hoover, DL, Knapp, AK, Smith, MD. 2014. Resistance and resilience of a grassland ecosystem to climate extremes. *Ecology* **95**: 2646–2656.
- Huxman, TE, Kimball, S, Angert, AL, Gremer, JR, Barron-Gafford, GA, Venable, DL. 2013. Understanding past, contemporary, and future dynamics of plants, populations, and communities using Sonoran Desert winter annuals. *American Journal of Botany* **100**: 1369–1380.
- Huxman, TE, Snyder, KA, Tissue, D, Leffler, AJ, Ogle, K, Pockman, WT, Sandquist, DR, Potts, DL, Schwinning, S. 2004. Precipitation pulses and carbon fluxes in semiarid and arid ecosystems. *Oecologia* **141**: 254–268.
- Ignace, DD. 2006. *Functional responses of Sonoran Desert plant species to precipitation* [doctoral dissertation, The University of Arizona]. ProQuest Dissertations Publishing. Available at <https://repository.arizona.edu/handle/10150/196132>.
- Ignace, DD, Huxman, TE, Weltzin, JF, Williams, DG. 2007. Leaf gas exchange and water status responses of a native and non-native grass to precipitation across contrasting soil surfaces in the Sonoran Desert. *Oecologia* **152**: 401–413.
- IPCC. 2014. Climate change 2014: Impacts, adaptation, and vulnerability. Part A: Global and sectoral aspects, in Field, CB, Barros, VR, Dokken, DJ, Mach, KJ, Mastrandrea, MD, Bilir, TE, Chatterjee, M, Ebi, KL, Estrada, YO, Genova, RC, Girma, B, Kissel, ES, Levy, AN, MacCracken, S, Mastrandrea, PR, White, LL eds., *Contribution of working group II to the fifth assessment report of the Intergovernmental Panel on Climate Change*. Cambridge, UK: Cambridge University Press.
- Irl, SD, Harter, DE, Steinbauer, MJ, Gallego Puyol, D, Fernández-Palacios, JM, Jentsch, A, Beierkuhnlein, C. 2015. Climate vs. topography–spatial patterns of plant species diversity and endemism on a high-elevation island. *Journal of Ecology* **103**: 1621–1633.
- Jenerette, GD, Chatterjee, A. 2012. Soil metabolic pulses: Water, substrate, and biological regulation. *Ecology* **93**: 959–966.
- Jenerette, GD, Scott, RL, Huete, AR. 2010. Functional differences between summer and winter season rain assessed with MODIS-derived phenology in a semi-arid region. *Journal of Vegetation Science* **21**: 16–30.
- Jentsch, A, Kreyling, J, Elmer, M, Gellesch, E, Glaser, B, Grant, K, Hein, R, Lara, M, Mirzae, H, Nadler, SE. 2011. Climate extremes initiate ecosystem-regulating functions while maintaining productivity. *Journal of Ecology* **99**: 689–702.
- Kimball, S, Goulden, ML, Suding, KN, Parker, S. 2014a. Altered water and nitrogen input shifts succession in a southern California coastal sage community. *Ecological Applications* **24**: 1390–1404.
- Kimball, S, Gremer, JR, Barron-Gafford, GA, Angert, AL, Huxman, TE, Venable, DL. 2014b. High water-use efficiency and growth contribute to success of non-native *Erodium cicutarium* in a Sonoran Desert winter annual community. *Conservation Physiology* **2**: cou006.
- Knapp, AK, Chen, A, Griffin-Nolan, RJ, Baur, LE, Carroll, CJW, Gray, JE, Hoffman, AM, Li, X, Post, AK, Slette, IJ, Collins, SL, Luo, Y, Smith, MD. 2020. Resolving the dust bowl paradox of grassland responses to extreme drought. *Proceedings of the National Academy of Sciences* **117**(36): 22249–22255.
- Knapp, AK, Fay, PA, Blair, JM, Collins, SL, Smith, MD, Carlisle, JD, Harper, CW, Danner, BT, Lett, MS, McCarron, JK. 2002. Rainfall variability, carbon cycling, and plant species diversity in a mesic grassland. *Science* **298**: 2202–2205.
- Konapala, G, Mishra, AK, Wada, Y, Mann, ME. 2020. Climate change will affect global water availability through compounding changes in seasonal precipitation and evaporation. *Nature Communications* **11**: 1–10.
- Limousin, JM, Rambal, S, Ourcival, JM, Rocheteau, A, Joffre, R, Rodriguez-Cortina, R. 2009. Long-term transpiration change with rainfall decline in a Mediterranean *Quercus ilex* forest. *Global Change Biology* **15**: 2163–2175.
- Loik, ME, Breshears, DD, Lauenroth, WK, Belnap, J. 2004. A multi-scale perspective of water pulses in dryland ecosystems: Climatology and ecohydrology of the western USA. *Oecologia* **141**: 269–281.
- Ludwig, JA, Cunningham, G, Whitson, P. 1988. Distribution of annual plants in North American deserts. *Journal of Arid Environments* **15**: 221–227.
- Ludwig, JA, Wilcox, BP, Breshears, DD, Tongway, DJ, Imeson, AC. 2005. Vegetation patches and runoff–erosion as interacting ecohydrological processes in semiarid landscapes. *Ecology* **86**: 288–297.
- Luong, TM, Castro, CL, Chang, HI, Lahmers, T, Adams, DK, Ochoa-Moya, CA. 2017. The more extreme nature of North American monsoon precipitation in the southwestern United States as revealed by a historical climatology of simulated severe weather events. *Journal of Applied Meteorology and Climatology* **56**: 2509–2529.
- Martinez Arbizu, P. 2020. pairwiseAdonis: Pairwise multilevel comparison using adonis. R package version 0.0.2017;1. Available at <https://github.com/pmartinezarbizu/pairwiseAdonis>.
- Morin, E, Goodrich, DC, Maddox, RA, Gao, X, Gupta, HV, Sorooshian, S. 2006. Spatial patterns in thunderstorm rainfall events and their coupling with watershed hydrological response. *Advances in Water Resources* **29**: 843–860.
- Mulroy, TW, Rundel, PW. 1977. Annual plants - Adaptations to desert environments. *Bioscience* **27**: 109–114.
- Oksanen, J, Blanchet, FG, Kindt, R, Legendre, P, Minchin, PR, O'Hara, RB, Simpson, GL, Solymos, P, Henry, M,

- Stevens, MH, Wagner, H.** 2013. vegan: Community Ecology Package. R package version 2.0-9. Available at <https://cran.r-project.org/web/packages/vegan/index.html>.
- Paruelo, JM, Lauenroth, WK, Burke, IC, Sala, OE.** 1999. Grassland precipitation-use efficiency varies across a resource gradient. *Ecosystems* **2**: 64–68.
- Paschalis, A, Fatichi, S, Zscheischler, J, Ciais, P, Bahn, M, Boysen, L, Chang, J, De Kauwe, M, Estiarte, M, Goll, D, Hanson, PJ.** 2020. Rainfall manipulation experiments as simulated by terrestrial biosphere models: Where do we stand? *Global Change Biology* **26**(6): 3336–3355.
- Pendergrass, AG, Knutti, R, Lehner, F, Deser, C, Sanderson, BM.** 2017. Precipitation variability increases in a warmer climate. *Scientific Reports* **7**: 1–9.
- Potts, DL, Barron-Gafford, GA, Butterfield, BJ, Fay, PA, Hultine, KR.** 2019. Bloom and Bust: Ecological consequences of precipitation variability in aridlands. *Plant Ecology* **220**: 135–139.
- Potts, DL, Huxman, TE, Cable, JM, English, NB, Ignace, DD, Eilts, JA, Mason, MJ, Weltzin, JF, Williams, DG.** 2006. Antecedent moisture and seasonal precipitation influence the response of canopy-scale carbon and water exchange to rainfall pulses in a semi-arid grassland. *New Phytologist* **170**: 849–860.
- R Core Team.** 2019. *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
- Scheiner, SM.** 2013. The genetics of phenotypic plasticity. XII. Temporal and spatial heterogeneity. *Ecology and Evolution* **3**: 4596–4609.
- Schlesinger, WH, Fonteyn, PJ, Reiners, WA.** 1989. Effects of overland flow on plant water relations, erosion, and soil water percolation on a Mojave Desert landscape. *Soil Science Society of America Journal* **53**: 1567–1572.
- Schwalm, CR, Anderegg, WR, Michalak, AM, Fisher, JB, Biondi, F, Koch, G, Litvak, M, Ogle, K, Shaw, JD, Wolf, A.** 2017. Global patterns of drought recovery. *Nature* **548**: 202–205.
- Scott, RL, Jenerette, GD, Potts, DL, Huxman, TE.** 2009. Effects of seasonal drought on net carbon dioxide exchange from a woody-plant-encroached semiarid grassland. *Journal of Geophysical Research: Biogeosciences* **114**: G04004. Available at <https://agupubs.onlinelibrary.wiley.com/doi/full/10.1029/2008JG000900>.
- Shen, W, Jenerette, GD, Hui, D, Phillips, RP, Ren, H.** 2008. Effects of changing precipitation regimes on dryland soil respiration and C pool dynamics at rainfall event, seasonal and interannual scales. *Journal of Geophysical Research: Biogeosciences* **113**: G03024. Available at <https://agupubs.onlinelibrary.wiley.com/doi/epdf/10.1029/2008JG000685>.
- Shen, W, Jenerette, GD, Hui, D, Scott, RL.** 2016. Precipitation legacy effects on dryland ecosystem carbon fluxes: Direction, magnitude and biogeochemical carryovers. *Biogeosciences* **13**: 425–439.
- Smith, MD.** 2011. The ecological role of climate extremes: Current understanding and future prospects. *Journal of Ecology* **99**: 651–655.
- Smith, MD, Wilcox, K, Sala, O, Phillips, R, Luo, Y, Knapp, A, Lemoine, NP.** 2016. Drought-Net: A global network merging observations, experiments, and modeling to forecast terrestrial ecosystem sensitivity to drought. *AGUFM* **2016**: B11J–06.
- Stocker, TF, Qin, D, Plattner, G-K, Tignor, MM, Allen, SK, Boschung, J, Nauels, A, Xia, Y, Bex, V, Midgley, PM.** 2014. Climate change 2013: The physical science basis. Cambridge, UK: Cambridge University Press. Contribution of working group I to the fifth assessment report of the Intergovernmental Panel on Climate Change.
- Stott, P.** 2016. How climate change affects extreme weather events. *Science* **352**: 1517–1518.
- Ting, IP, Jennings, B, Adams, A.** 1976. *Deep Canyon, a desert wilderness for science*. Riverside, CA: Philip L. Boyd Deep Canyon Desert Research Center, University of California.
- Tonkin, JD, Bogan, MT, Bonada, N, Rios-Touma, B, Lytle, DA.** 2017. Seasonality and predictability shape temporal species diversity. *Ecology* **98**: 1201–1216.
- Trugman, AT, Medvigy, D, Mankin, JS, Anderegg, WR.** 2018. Soil moisture stress as a major driver of carbon cycle uncertainty. *Geophysical Research Letters* **45**: 6495–6503.
- Van Devender, TR, Felger, RS, Reina-G, AL, Sánchez-Escalante, JJ, Tellman, B.** 2006. Sonora: Non-native and invasive plants, in Van Devender, TR, Espinosa-García, FJ, Harper-Lore, BL, Hubbard, T eds., *Invasive plants on the move: Controlling them in North America*. Tuscon, AZ: Arizona-Sonora Desert Museum: 85–124.
- Wayne Higgins, R, Douglas, A, Hahmann, A, Berbery, EH, Gutzler, D, Shuttleworth, J, Stensrud, D, Amador, J, Carbone, R, Cortez, M.** 2003. Progress in Pan American CLIVAR research: The North American monsoon system. *Atmosfera* **16**: 29–65.
- Wilcox, KR, Shi, Z, Gherardi, LA, Lemoine, NP, Koerner, SE, Hoover, DL, Bork, E, Byrne, KM, Cahill Jr J, Collins, SL.** 2017. Asymmetric responses of primary productivity to precipitation extremes: A synthesis of grassland precipitation manipulation experiments. *Global Change Biology* **23**(10): 4376–4385.
- Wu, D, Ciais, P, Viovy, N, Knapp, AK, Wilcox, K, Bahn, M, Smith, MD, Vicca, S, Fatichi, S, Zscheischler, J.** 2018. Asymmetric responses of primary productivity to altered precipitation simulated by ecosystem models across three long-term grassland sites. *Biogeosciences* **15**: 3421–3437.
- Xia, Y, Moore, DI, Collins, SL, Muldavin, EH.** 2010. Aboveground production and species richness of annuals in Chihuahuan Desert grassland and shrubland plant communities. *Journal of Arid Environments* **74**: 378–385.

- Xu, X, Medvigy, D, Powers, JS, Becknell, JM, Guan, K.** 2016. Diversity in plant hydraulic traits explains seasonal and inter-annual variations of vegetation dynamics in seasonally dry tropical forests. *New Phytologist* **212**: 80–95.
- Yahdjian, L, Sala, OE.** 2006. Vegetation structure constrains primary production response to water availability in the Patagonian steppe. *Ecology* **87**: 952–962.
- Zhang, Y, Loreau, M, He, N, Wang, J, Pan, Q, Bai, Y, Han, X.** 2018. Climate variability decreases species richness and community stability in a temperate grassland. *Oecologia* **188**: 183–192.

How to cite this article: Spasojevic, MJ, Homyak, PM, Jenerette, GD, Goulden, ML, McFaul, S, Madsen-McQueen, T, Schauer, L, Solis, M. 2022. Altered precipitation has asymmetric impacts on annual plant communities in warm and cool growing seasons. *Elementa: Science of the Anthropocene* 10(1). DOI: <https://doi.org/10.1525/elementa.2021.00014>

Domain Editor-in-Chief: Steven Allison, University of California, Irvine, CA, USA

Associate Editor: Danielle Ignace, Smith College, Northampton, MA, USA

Knowledge Domain: Ecology and Earth Systems

Published: February 18, 2022 **Accepted:** January 13, 2022 **Submitted:** February 16, 2021

Copyright: © 2022 The Author(s). This is an open-access article distributed under the terms of the Creative Commons Attribution 4.0 International License (CC-BY 4.0), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited. See <http://creativecommons.org/licenses/by/4.0/>.



Elem Sci Anth is a peer-reviewed open access journal published by University of California Press.

OPEN ACCESS