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## RESEARCH ARTICLE

# Primary production responses to extreme changes in North American Monsoon precipitation vary by elevation and plant functional composition through time

Seth M. Munson<sup>1</sup>  | John B. Bradford<sup>1</sup>  | Bradley J. Butterfield<sup>2</sup>  |  
Jennifer R. Gremer<sup>3</sup> 

<sup>1</sup>U.S. Geological Survey, Southwest Biological Science Center, Flagstaff, Arizona, USA

<sup>2</sup>Department of Biological Sciences, Northern Arizona University, Flagstaff, Arizona, USA

<sup>3</sup>Department of Evolution and Ecology and Center for Population Biology, University of California, Davis, California, USA

## Correspondence

Seth M. Munson

Email: [smunson@usgs.gov](mailto:smunson@usgs.gov)

## Funding information

U.S. Geological Survey

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## Abstract

1. Primary production in dryland ecosystems is limited by water availability and projected to be strongly affected by future shifts in seasonal precipitation. Warm-season precipitation derived from the North American Monsoon contributes 40% of annual precipitation to dryland ecosystems in the southwestern United States and is projected to become more variable. However, there is large uncertainty on whether this variability will be expressed as either extreme wet or dry years and how primary production of different plant functional types will respond across widespread elevation gradients in this region.
2. We experimentally imposed extreme drought and water addition treatments from 2016 to 2020, during which ambient warm-season precipitation declined to reach historic lows, to understand production sensitivity of dominant plant functional types along a 1000 m elevation gradient.
3. We found that the production responses of plant functional types to monsoon precipitation extremes were dependent on the number of treatment years that occurred across sites along the elevation gradient. C<sub>4</sub> perennial grasses were most responsive to precipitation manipulation treatments, followed by C<sub>3</sub> perennial grasses and annuals, while perennial forbs and shrubs had weak or no responses. C<sub>4</sub> perennial grass reductions due to extreme drought were generally stronger or occurred earlier at low elevation sites, while multi-year extreme drought extended negative effects to C<sub>3</sub> perennial grasses at high elevation, and all sites showed delayed responses to multi-year water addition. We found that the sensitivity of C<sub>3</sub> perennial grass production differed for extreme drought and water addition compared to ambient precipitation at one site, but other sites and plant functional types had similar sensitivities to the different treatment types.
4. *Synthesis.* The upward advance of primary production responsiveness from single- to multi-year extreme changes in warm-season precipitation suggests more immediate shifts in functional composition and carbon cycling at low elevation,

while high elevation ecosystems may become less resistant as the effects of extreme precipitation compound through time.

#### KEYWORDS

C<sub>3</sub> and C<sub>4</sub> perennial grasses, dryland ecosystem, extreme precipitation, global climate change, grassland, plant functional type and composition, southwestern United States

## 1 | INTRODUCTION

Primary productivity in dryland ecosystems is highly sensitive to changes in water availability (Huxman et al., 2004; Knapp & Smith, 2001; Maurer et al., 2020; Ukkola et al., 2021). Changes in productivity across space and through time drive carbon storage, nutrient cycling and land–atmosphere interactions (IPCC, 2014). Shifts from carbon sinks to carbon sources in drylands are mainly driven by water availability (Scott et al., 2015), and because drylands cover nearly half of the global land area and store one-third of the global carbon stock (Hanan et al., 2021), this variation can impact the global carbon cycle (Lal, 2004). Assessing differences in the sensitivity of production across highly responsive dryland ecosystems can inform their vulnerability to climate change and uncover the underlying mechanisms necessary to improve regional predictions of future ecosystem function.

Primary productivity and its sensitivity to water availability may be fundamentally altered if both the magnitude and duration of precipitation are pushed to extremes under climate change. Warming is intensifying the hydrological cycle (Huntington, 2006), creating severe and protracted drought (Cook et al., 2015) as well as deluges of intense or persistent rainfall events (Fischer & Knutti, 2016). These changes in precipitation are considered extreme when they fall at the maximum or minimum ends of the historical range of variability and have the capacity to induce concomitant extreme changes in productivity (Smith, 2011). Short-term extreme water shortages or periods of heavy rainfall may be initially met with modest changes in productivity, but the effects will likely be magnified as extreme conditions persist over multiple years, such that stress and nonlinear threshold responses are increasingly likely over time. Understanding whether the sensitivity of production differs under extreme dry versus wet periods (Wilcox et al., 2017), and if production–precipitation relationships change over the short to long term (Munson et al., 2021) requires further examination.

Dryland ecosystems in the southwestern United States are forecasted to experience up to 5°C increases in temperature and decreases in annual precipitation by 2100 (Garfin et al., 2013). However, future declines in annual precipitation are expected to be largely attributable to less cool-season moisture (Seager & Vecchi, 2010). There is much larger uncertainty in forecasts of warm-season precipitation driven by the North American Monsoon, which, on average, contributes approximately 40% of annual precipitation in the southwestern United States (Higgins et al., 1999). While some models show a weakening of warm-season precipitation (Pascale et al., 2017),

others have forecasted no change and mixed responses (Colorado-Ruiz et al., 2018; Cook & Seager, 2013; Seth et al., 2011), or increases in North American Monsoon moisture (Luong et al., 2017). Regional forecasts that are better able to incorporate topography than many general circulation models generally show high elevation sites will likely have future increases, and low elevation sites may experience decreases in monsoon precipitation (Pascale et al., 2019). Regardless of the direction of changes in precipitation, the net effect, especially at low elevation, may be reductions in soil moisture due to increasing temperatures and potential evapotranspiration (Ault et al., 2016; Cook et al., 2015; Seager et al., 2007; Weiss et al., 2009).

Elevation and associated changes in climate and plant functional composition strongly influence primary production, but we know little about how different functional types may respond to future warm-season precipitation extremes along elevation gradients over the short and long term. Determining relative plant functional type sensitivities can help generalize plant species responses (Chapin III, 1993) and reveal the potential for plant community turnover and shifts in ecosystem function under climate change (Munson et al., 2021; Smith, 2011). Understanding how these sensitivities vary across elevation gradients is much needed to scale-up inferences of productivity changes across topographically diverse regions (Sundqvist et al., 2013). Arid and semi-arid ecosystems at low elevation typically contain a large proportion of plant functional types with drought resistance traits that span unique hydrological niches in space and time (Fischer & Turner, 1978; Noy-Meir, 1973; Reynolds et al., 2004). Shrubs and deeply rooted perennial forbs can avoid warm-season drought by accessing deep soil moisture (Walter, 1971), but many grow slowly in response to increases in monsoon precipitation due to structural and physiological limitations that allow them to resist drought (Munson et al., 2013; Orians & Solbrig, 1977) and because monsoon precipitation typically only wets soil surface layers (Ehleringer et al., 1991). C<sub>3</sub> perennial grasses may avoid warm-season drought by growing early in the spring but may not be as responsive to above average summer rainfall as C<sub>4</sub> perennial grasses and annuals that have rapid warm-season growth (Ogle & Reynolds, 2004; Witwicki et al., 2016). Although plant functional types at low elevation express multiple drought resistance strategies, many are at their physiological limits due to chronically low soil moisture and productivity may become constrained under prolonged water shortages (Fischer & Turner, 1978; Orians & Solbrig, 1977).

More mesic ecosystems at high elevation may be limited by temperature, growing season, light and nutrients (Burke et al., 1998), such that the production of multiple plant functional types is less

sensitive to changes in water availability. Alternatively, snowmelt and spring precipitation may have a greater influence on growth than warm-season precipitation and favour a high contribution of production from deeply rooted woody plants and forbs, as well as  $C_3$  perennial grasses with a cool-season phenology (Herrmann et al., 2016; Witwicki et al., 2016). Prolonged drought in relatively mesic ecosystems can interrupt consistently high soil moisture throughout the growing season and induce water stress and reductions in primary productivity of perennial grasses (Heisler-White et al., 2009), responses which may become more pronounced over time. Production changes at relatively mesic sites may be accentuated because they have more productivity to lose in a dry year and greater capacity to increase productivity when water is abundant due to higher plant cover and meristem densities than arid and semi-arid sites (Dalglish & Hartnett, 2006).

We conducted a standardized experimental precipitation manipulation study across an elevation gradient to help understand production sensitivity of different plant functional types to the large range of future warm-season precipitation uncertainty associated with the North American Monsoon in the southwestern United States. Extreme drought and water addition were imposed over 5 years, which broke the tight coupling of precipitation and temperature associated with elevation gradients, to test how future novel climate change could influence productivity. Our objectives were to: (1) determine how primary production responds to warm-season precipitation extremes over time; (2) compare production sensitivities to warm-season precipitation (slopes of production–precipitation relationships) across an elevation gradient; (3) evaluate whether the sensitivity of production differed under extreme drought and water addition compared to ambient precipitation. As we expected plant life-form, longevity and photosynthetic pathway to vary across sites and influence the degree to which production responded, we evaluated these objectives in herbaceous plant communities composed of the functional types:  $C_4$  perennial grasses,  $C_3$  perennial grasses, perennial forbs, shrubs and annuals (annual grasses and forbs).

## 2 | MATERIALS AND METHODS

We selected five study sites along an elevation gradient on and adjacent to the San Francisco Mountains near Flagstaff, Arizona, which is centred in the southwestern United States. These sites transition from: (1) desert scrub (1566 m a.s.l.) and (2) desert grassland (1636 m), to (3) juniper savanna (1930 m), to (4) ponderosa pine meadow (2179 m) and (5) mixed conifer meadow (2591 m) that all have no woody overstorey. The amount of mean annual precipitation and mean warm-season (May–September) precipitation from the North American Monsoon increases from low to high elevation sites, although the per cent of mean warm-season precipitation relative to mean annual precipitation at each site slightly decreases (Table 1). Mean annual and mean warm-season temperatures decrease from low to high elevation sites. All sites had fencing to exclude large herbivores, including deer, elk and domestic livestock.

In 2016, we imposed precipitation manipulation treatments, which consisted of ambient precipitation, extreme drought and water addition in 2 m × 3 m plots at each of the five sites. Each of the three treatments was randomly assigned to four replicate plots at each site. Metal flashing was vertically buried 30 cm beneath the soil surface around the perimeter of all the plots to hydrologically isolate them. The precipitation manipulation infrastructure was previously described in Munson et al. (2019). Drought plots were covered by a rain-out shelter consisting of a metal frame that supported a roof with bands of ultraviolet transmitting acrylic (Solacryl SUVT; 11 × 200 cm, bent into a V shape at 60°) placed at 20° angles that covered a total of half of the plot. We temporarily installed a network of 54 rain gauges inside and 14 gauges outside a drought plot and found that over the course of three 20–35 mm events, the shelter excluded  $53 \pm 3\%$  of ambient precipitation. The lowest side of the shelters (60 cm) faced towards the southwest prevailing wind direction to minimize precipitation blown into the plot.

Water excluded from the shelters on drought plots was redistributed to water addition plots. Specifically, excluded water was channelled into a gutter on the lowest side of the shelter and into closed catchment barrels. Water was redistributed after rainfall events above 10 mm, or when barrels were about half full, using four sprinklers at the corners of the water addition plots. When water addition was implemented, we connected hosing and a battery-powered pump from the catchment barrels to the PVC fittings below the sprinkler heads and ran the pump until water was drained from the barrels. We recorded the volume of water in the barrels and the time watering was implemented, from which we determined that  $32 \pm 3\%$  of ambient precipitation was added on to the water addition plots (~20% of ambient precipitation excluded from rainout plots was lost through inefficiencies of our pumping and storage equipment) on top of the ambient precipitation they received. As we were interested in how warm-season precipitation influenced primary production, shelters and sprinklers were in place at all sites from the beginning of May through the end of September.

Climate data were collected on site for the study period using weather stations and supplemented with historical data from PRISM (<http://www.prism.oregonstate.edu>). We installed weather stations at the desert grassland and mixed conifer meadow sites to measure air temperature with a Meter ATMOS14 sensor and precipitation with a Meter ECRN-100 tipping-bucket rain gauge. We used existing weather stations at the remaining three sites, which measured air temperature from a Visala HMP155 probe and precipitation with a Geonor Rain Can T200B gauge. All weather stations were operating on or before summer 2015. PRISM monthly precipitation data were extracted to determine the historical (1980–2014) distribution of precipitation and to relate to precipitation recorded from weather stations during the study period (2015–2020). We also installed Decagon (5TM, 10HS and GS1) soil moisture sensors at 0–10 cm (shallow) and 20–30 cm (deep) soil depths in three of the four replicate plots for each treatment at each site. The sensors recorded soil volumetric water content to a EM50 data logger every hour beginning in summer 2015.

**TABLE 1** Location, elevation, mean annual precipitation (MAP), mean warm-season precipitation (MWP), per cent of mean warm-season relative to mean annual precipitation, mean annual temperature (MAT), mean warm-season temperature (MWT) and dominant species at the five study sites in Arizona. Precipitation and temperature were extracted from 1980 to 2020 PRISM data (<http://www.prism.oregonstate.edu>)

Site	Location (decimal degrees)	Elevation (m)	MAP (mm)	MWP (mm)	MWP/MAP (%)	MAT (°C)	MWT (°C)	Dominant species
Desert Scrub	35.685, -111.479	1566	196	100	51	13.8	22.4	<i>Bouteloua eriopoda</i> , <i>Achnatherum hymenoides</i> , <i>Atriplex confertifolia</i>
Desert Grassland	35.584, -111.513	1636	244	121	50	13.0	21.6	<i>Bouteloua eriopoda</i> , <i>Pleuraphis jamesii</i>
Juniper Savanna	35.588, -111.972	1930	486	208	43	9.9	17.6	<i>Bouteloua gracilis</i> , <i>Hesperostipa comata</i> , <i>Ericameria nauseosa</i>
Ponderosa Meadow	35.162, -111.733	2179	579	241	42	7.3	14.4	<i>Festuca arizonica</i> , <i>Muhlenbergia montana</i> , <i>Elymus elymoides</i> , <i>Potentilla hippiana</i>
Mixed Conifer Meadow	35.329, -111.730	2591	658	269	41	6.9	14.2	<i>Festuca arizonica</i> , <i>Bromus porteri</i> , <i>Poa pratensis</i> , <i>Muhlenbergia montana</i> , <i>Geum triflorum</i>

We harvested above-ground net primary production (ANPP) at peak production at the end of the growing season in September using a non-destructive two-step method (Munson et al., 2019). We measured ANPP in 2015 to capture conditions before rainfall manipulation treatments were implemented, and then in 2016–2020 after treatment implementation. Each year we first made visual estimates of canopy cover and measured height of each live green or recently senesced (alive earlier in the growing season) vegetative unit by species that fell inside two 1 m<sup>2</sup> quadrats located at the north and south corners of the plots. Second, we used 1 m<sup>2</sup> quadrats to harvest plants by species outside, but adjacent to, the experimental plots. Harvests consisted of clipping above-ground plant biomass of plants outside the plots, but of the same cover and height of plants inside the plots, above the root crown to avoid destructively sampling inside plots intended for long-term study. Clipped live and recently senesced plant tissues (growth from current year) were separated from dead plant material and biomass from growth in previous years, put in a drying oven at 50°C for 4 days, and weighed. We were not able to account for herbivory from small herbivores, root exudates and volatile emissions that are components of ANPP (Chapin & Eviner, 2014), and therefore our measurements are an underestimate. We used linear regressions with intercepts through the origin to relate dry biomass weight clipped outside the plots to plant cover and height measured inside the plots (Munson et al., 2019). The regressions revealed a high amount of variance in biomass explained by cover and height ( $R^2 > 0.90$ ,  $p < 0.05$ ). We derived the dry biomass weight from the regressions, averaged between the two quadrats in each plot. We summed ANPP according to plant functional types: C<sub>4</sub> perennial grasses, C<sub>3</sub> perennial grasses, perennial forbs (herbaceous dicots), low-growing shrubs (woody plants <2 m height) and annual species.

Warm-season (May–September) precipitation from PRISM data was strongly correlated to weather station records from 2015 to 2020 at each site ( $r = 0.93$ – $0.99$ ). We used the slopes of these relationships to correct over- or under-estimates of the historical PRISM warm-season precipitation (1980–2014) record at each site. We then determined the historical percentile of warm-season precipitation

for each study year (2015–2020) by calculating the percentage of accumulated warm-season precipitation from the weather station record at each site relative to its corrected historical warm-season precipitation distribution. Warm-season precipitation was correlated with warm-season shallow ( $r = 0.66$ – $0.90$ ) and deep ( $r = 0.74$ – $0.88$ ) soil moisture from 2015 to 2020 at each site.

To determine how primary production responded to warm-season precipitation treatments over time across sites, we first performed a four-way repeated-measures ANOVA on total ANPP (all plant functional types combined) with site, plant functional type, treatment (control, drought, water addition) and year as main effects. We modelled the repeated measures of plot as a within-subject measure of year by specifying error as 'plot/year' using the *aov* function in R (all analyses were conducted using R Version 4.1.0, R Core Team, 2021). We then conducted three-way repeated-measures ANOVA for each plant functional type with site, treatment and year as main effects on the repeated measure of plot. We performed planned pairwise comparisons between drought or water addition and control treatments in each year for plant functional type at each site. To determine which climate and soil moisture variables explained production responses across all treatments, we built linear and nonlinear regression models of primary production and warm-season (May–September), cool-season (previous October–April) and annual (previous October–September) precipitation, temperature and shallow and deep soil moisture in the same periods. We found that warm-season precipitation and linear models consistently explained high variation for total, C<sub>3</sub> and C<sub>4</sub> perennial grass ANPP, while other precipitation and soil moisture periods inconsistently explained ANPP of other plant functional types. To compare production sensitivities to warm-season precipitation across an elevation gradient, we compared the slopes of ANPP with respect to warm-season precipitation of the same plant functional type across sites. To evaluate whether the sensitivity of production differed under extreme drought and water addition compared to ambient precipitation, we compared the ANPP-precipitation slopes of the same plant functional type across treatment types. We tested whether slopes varied by site and treatment type using

ANCOVA models in which warm-season precipitation was a continuous independent variable and site or treatment were categorical independent variables. If there were significant interactions between warm-season precipitation and site, or warm-season precipitation and treatment, we performed planned pairwise comparisons among sites or treatments with pairwise contrasts using the `EMMEANS` R package (Lenth, 2021). We used regression to test whether the proportion of ANPP in extreme drought or water addition treatments relative to the control ( $\text{ANPP}_{\text{treatment}}/\text{ANPP}_{\text{control}}$ ) changed through time. Data did not meet normality or homogeneity of variance assumptions based on Shapiro–Wilk and Levene's tests, respectively, and were therefore transformed using optimal Box–Cox transformations to meet assumptions. We present back-transformed values with raw (a priori) standard errors for ease of interpretation.

### 3 | RESULTS

Ambient warm-season precipitation in 2015 (pre-treatment) and 2016 (post-treatment) was average to very wet with sites receiving 55%–99% of historical (1980–2014) May–September precipitation (Figure 1). Ambient precipitation declined during the study to reach historically dry extremes (<5th or 1st historical percentiles) in 2019–2020. Drought treatments amplified this drying such that extreme drought plots in the desert scrub and juniper savanna reached <1% of historical warm-season precipitation beginning in 2017 and in the ponderosa pine meadow beginning in 2018. Water addition treatments increased warm-season precipitation to >99% at all sites in 2016 and to >95% at the ponderosa pine meadow in 2017 and desert grassland and mixed conifer meadow in 2018, but largely maintained average precipitation or kept precipitation from reaching extreme lows from 2018 to 2019 at many of the sites. This is because water was experimentally added relative to ambient precipitation amounts. A lack of ambient precipitation in 2020 led to all plots receiving water addition treatments to fall to <1% of historical precipitation in 2020 across all sites.

#### 3.1 | All plant functional types

Total ANPP (all plant functional types combined) in 2015 (pre-treatment) generally increased with increasing elevation, although the juniper savanna had the lowest total ANPP (Figure S1).  $C_4$  perennial grasses and shrubs contributed a high amount of ANPP at the three low elevation sites,  $C_3$  perennial grasses and perennial forbs contributed a high amount of ANPP at the two highest elevation sites, and annuals contributed a low amount of ANPP at all the sites. Total ANPP responses to extreme drought and water addition depended on the site and year (Table 2). Total ANPP was reduced by extreme drought treatments at the desert grassland (Figure 2b) and juniper savanna (Figure 2c) in 2016 and 2018, while decreases at the ponderosa pine meadow occurred later from 2018 to 2020 (Figure 2d), and at the mixed conifer meadow in 2020 (Figure 2e). Total ANPP only increased

with water addition at the mixed conifer meadow in 2020 (Figure 2e). The proportion of total ANPP reduced by extreme drought relative to control plots increased at the mixed conifer meadow through time (Figure 2j). The proportion of total ANPP increased by water addition relative to control plots increased at the desert scrub (Figure 2f) and ponderosa pine meadow (Figure 2i) through time.

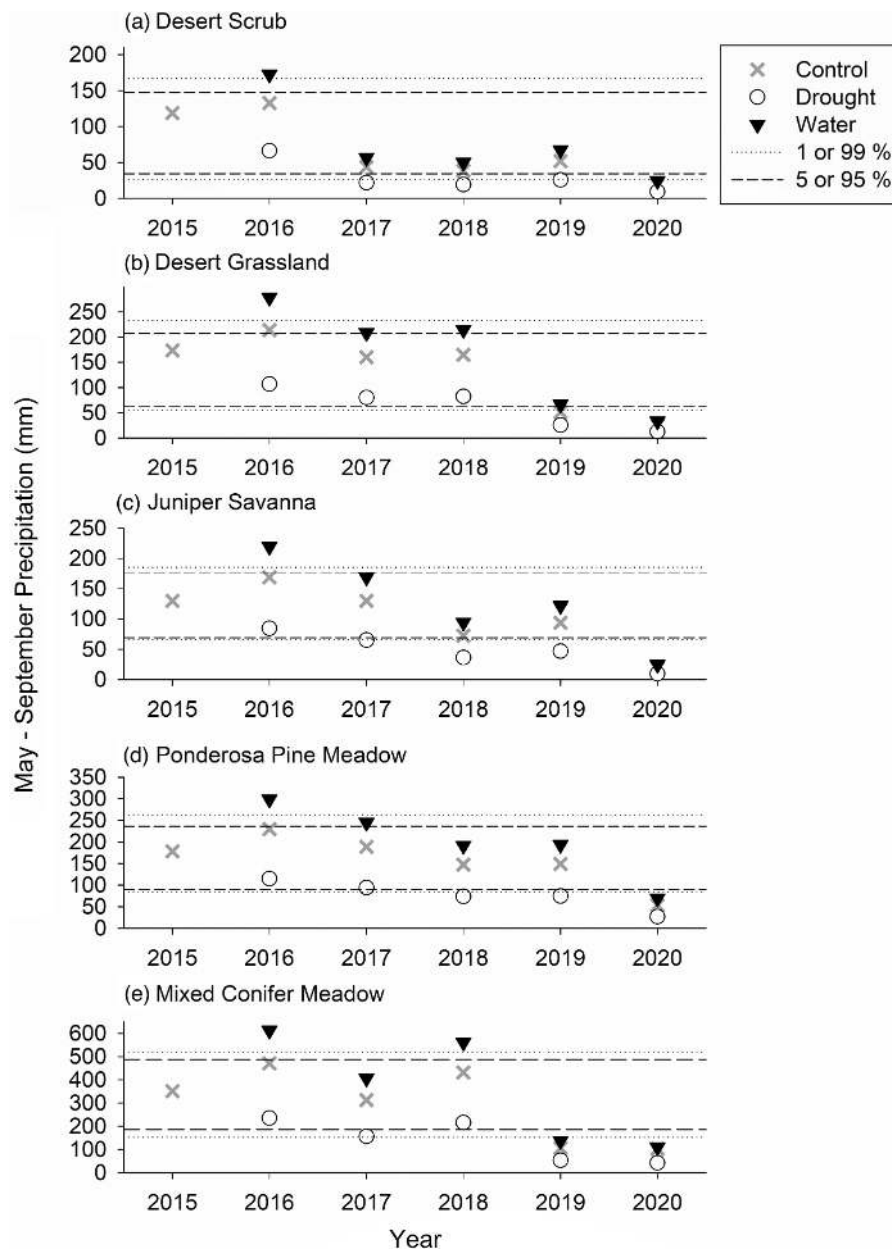
#### 3.2 | $C_4$ perennial grasses

$C_4$  perennial grass ANPP was reduced by extreme drought treatments in 2016 and most subsequent years at the desert grassland (Figure 3b) and juniper savanna (Figure 3c), while decreases occurred later in 2018 and in subsequent years at the desert scrub (Figure 3a) and high elevation meadows (Figure 3d,e). The proportion of  $C_4$  perennial grass ANPP reduced by extreme drought relative to control plots increased at all the sites through time (all  $p < 0.05$ ; Figures 3f–j).  $C_4$  perennial grass ANPP increased with water addition at the three low elevation sites in certain years from 2017 to 2020 (Figures 3a–c), but either did not respond at the ponderosa pine meadow (Figure 3d) or decreased in 2018 at the mixed conifer meadow (Figure 3e). The proportion of  $C_4$  perennial grass ANPP increased by water addition relative to control plots increased at the desert grassland (Figure 3g) and juniper savanna (Figure 3h) through time ( $p < 0.05$ ), but not the other sites. When the effects of all treatments were combined,  $C_4$  perennial grass ANPP had higher warm-season precipitation sensitivity at the three low elevation sites (ANPP–precipitation slopes =  $0.25\text{--}0.33\text{ g mm}^{-1}$ ) compared to the ponderosa pine meadow ( $0.13\text{ g mm}^{-1}$ ) ( $t = 2.10$ ,  $p < 0.05$ ), and was not related to warm-season precipitation at the mixed conifer meadow (Figure 4a). There were no differences in the sensitivity of  $C_4$  perennial grass ANPP to extreme drought or water addition relative to ambient precipitation.

#### 3.3 | $C_3$ perennial grasses

$C_3$  perennial grass ANPP was reduced by extreme drought treatments in 2018 and 2020 at the ponderosa pine (Figure 5c) and in 2020 in the mixed conifer meadow (Figure 5d), but the two low elevation sites composed of  $C_3$  perennial grasses were unresponsive (Figure 5a,b). The desert grassland site did not have  $C_3$  perennial grasses. The proportion of  $C_3$  perennial grass ANPP reduced by extreme drought relative to control plots increased through time at the desert scrub (Figure 5e), ponderosa pine (Figure 5g) and mixed conifer meadows (Figure 5h) (all  $p < 0.05$ ). Water addition increased  $C_3$  perennial grass ANPP at the juniper savanna in 2017 (Figure 5b) and at the mixed conifer meadow in 2016, 2018 and 2020 (Figure 5d), but the proportion of ANPP that increased by water addition did not increase through time (Figure 5e–h). When all treatments were combined,  $C_3$  perennial grass ANPP had sensitivity to changes in warm-season precipitation at the desert scrub (ANPP–precipitation slope =  $0.13\text{ g mm}^{-1}$ ) and ponderosa pine meadow ( $0.22\text{ g mm}^{-1}$ ), but there were no relationships at the juniper savanna and mixed conifer meadow (Figure 4b). Sustained extreme warm-season drought





**FIGURE 1** May–September precipitation in control, drought and water addition treatments from 2015 to 2020 at (a) desert scrub, (b) desert grassland, (c) juniper savanna, (d) ponderosa pine meadow and (e) mixed conifer meadow. The 1st and 99th percentiles of historical (1980–2014) precipitation at each site are shown by dotted lines, and the 5th and 95th percentiles are shown by short dashed lines.

at the ponderosa pine meadow induced a relatively large decline of  $C_3$  perennial grasses ( $0.80\text{gmm}^{-1}$ ) compared to moderate enhancements with increasing ambient precipitation (control) ( $0.39\text{gmm}^{-1}$ ), and effects saturating under water addition.

### 3.4 | Annuals

ANPP of annuals increased in extreme drought treatments in 2017 and 2019 at the juniper savanna, and then in 2020 in the extreme drought treatment across the desert grassland (Figure 6b), juniper savanna (Figure 6c) and ponderosa pine meadow (Figure 6d). In contrast, water addition had no effect on ANPP of annuals. When all treatments were combined, ANPP of annuals was not sensitive to warm-season precipitation or climate and soil moisture variables in other periods.

### 3.5 | Perennial forbs and shrubs

Perennial forb (Figure S2) and shrub (Figure S3) ANPP did not respond to any treatments in any years (treatment effect  $p > 0.10$  in each year for each site); although there was an overall significant effect of treatment on shrub ANPP (Table 2) with higher ANPP in extreme drought compared to water addition treatments ( $t = 2.3$ ,  $p = 0.02$ ). Perennial forbs and shrubs were not related to warm-season precipitation at any site when all treatment types were combined. Perennial forbs were sensitive to warm-season shallow soil moisture at the ponderosa pine meadow ( $r^2 = 0.38$ ,  $p < 0.01$ ) and shrubs were sensitive to warm-season deep soil moisture at the desert scrub ( $r^2 = 0.67$ ,  $p < 0.0001$ ) but other sites did not show sensitivity to climate and soil moisture in other periods.

**TABLE 2** Four-way repeated-measures ANOVA results for total of all plant functional types combined and three-way repeated-measures ANOVA results for each plant functional type with site, plant functional type (four-way ANOVA only), treatment (control, drought, water addition), and year as main effects, and their interactions

	df	SS	MS	F	p
Total (all plant functional types)					
Site	4	5.67	1.42	28.35	<0.0001
PFT	4	62.79	15.70	313.94	<0.0001
Treatment	2	0.20	0.10	2.02	0.13
Year	5	1.76	0.35	7.06	<0.0001
Site × PFT	14	10.39	0.74	14.84	<0.0001
Site × Treatment	8	0.41	0.05	1.02	0.42
PFT × Treatment	8	3.09	0.39	7.74	<0.0001
Site × Year	20	5.57	0.28	5.57	<0.0001
PFT × Year	20	8.99	0.45	8.99	<0.0001
Treatment × Year	10	0.39	0.04	0.79	0.64
Site × PFT × Treatment	26	1.71	0.07	1.37	0.11
Site × PFT × Year	66	9.28	0.14	2.77	<0.0001
Site × Treatment × Year	40	0.88	0.02	0.44	0.99
PFT × Treatment × Year	40	2.51	0.06	1.25	0.13
Site × PFT × Treatment × Year	94	1.72	0.02	0.37	1.00
Residuals	2878	143.96	0.05		
<b>C<sub>4</sub> Perennial Grasses</b>					
Site	4	101.47	25.34	140.19	<0.0001
Treatment	2	60.37	30.19	166.83	<0.0001
Year	5	32.19	6.44	35.580	<0.0001
Site × Treatment	8	4.22	0.53	2.92	<0.01
Site × Year	20	68.41	3.42	18.91	<0.0001
Treatment × Year	10	15.26	1.53	8.43	<0.0001
Site × Treatment × Year	40	7.90	0.20	1.09	0.34
Residuals	264	47.77	0.18		
<b>C<sub>3</sub> Perennial Grasses</b>					
Site	3	322.00	107.32	349.904	<0.0001
Treatment	2	16.30	8.16	26.615	<0.0001
Year	5	11.60	2.32	7.563	<0.0001
Site × Treatment	6	11.40	1.91	6.212	<0.0001
Site × Year	15	42.30	2.82	9.188	<0.0001
Treatment × Year	10	7.10	0.71	2.307	0.01

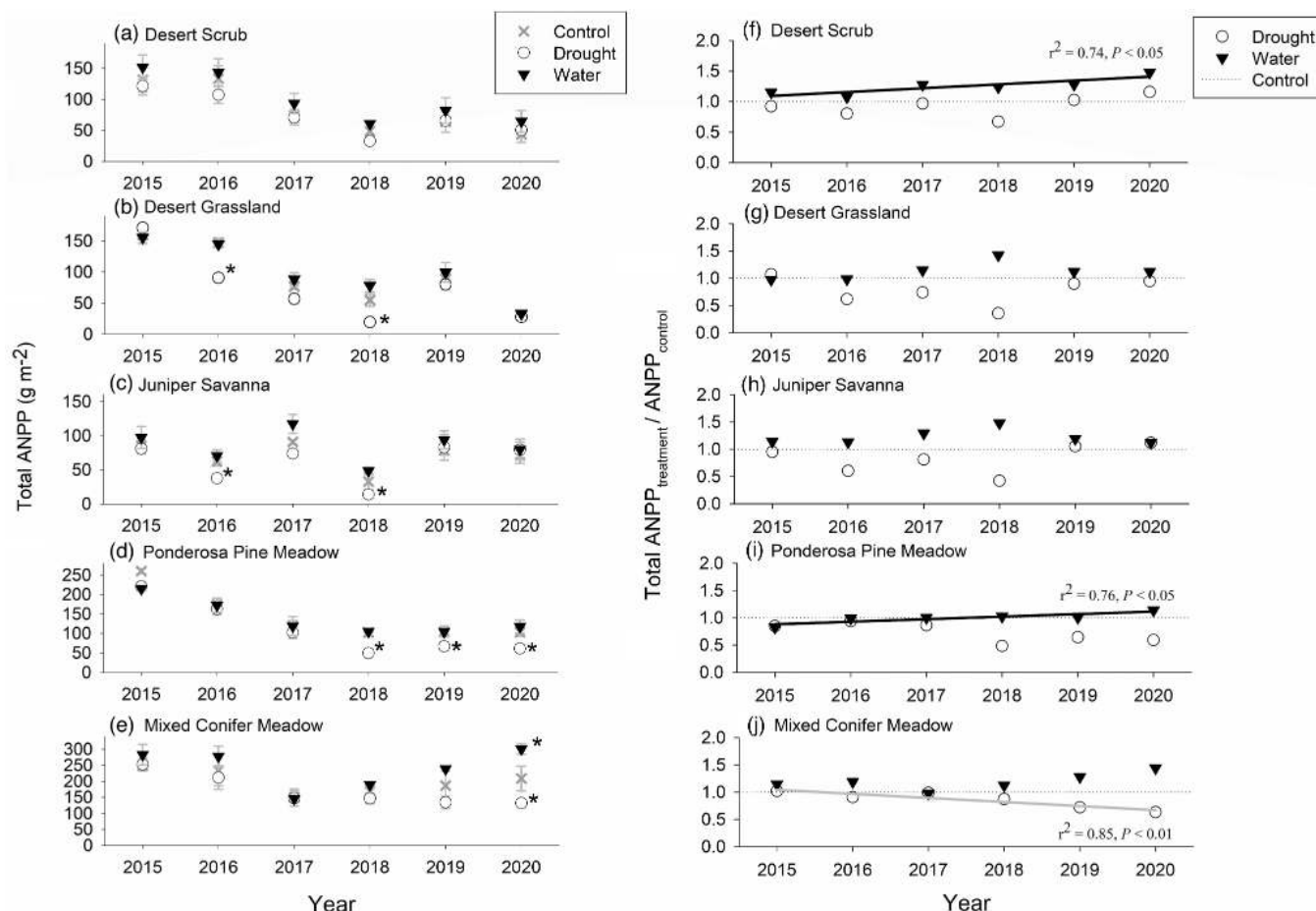
**TABLE 2** (Continued)

	df	SS	MS	F	p
Site × Treatment × Year	30	5.80	0.19	0.626	0.94
Residuals	210	64.40	0.31		
<b>Annuals</b>					
Site	4	4.832	1.2081	25.697	<0.0001
Treatment	2	1.207	0.6033	12.833	<0.0001
Year	5	3.212	0.6424	13.664	<0.0001
Site × Treatment	8	1.461	0.1826	3.885	<0.001
Site × Year	20	19.406	0.9703	20.639	<0.0001
Treatment × Year	10	3.394	0.3394	7.219	<0.0001
Site × Treatment × Year	40	5.395	0.1349	2.869	<0.0001
Residuals	264	12.412	0.047		
<b>Perennial Forbs</b>					
Site	4	2.2695	0.5674	55.139	<0.0001
Treatment	2	0.0107	0.0053	0.518	0.60
Year	5	0.0994	0.0199	1.932	0.09
Site × Treatment	8	0.2935	0.0367	3.565	<0.001
Site × Year	20	0.4275	0.0214	2.077	<0.01
Treatment × Year	10	0.1178	0.0118	1.145	0.33
Site × Treatment × Year	40	0.7218	0.018	1.754	<0.01
Residuals	264	2.7165	0.0103		
<b>Shrubs</b>					
Site	1	25.45	25.451	21.694	<0.0001
Treatment	2	8.03	4.013	3.421	0.04
Year	5	2.67	0.535	0.456	0.81
Site × Treatment	2	1.78	0.89	0.758	0.47
Site × Year	5	12.55	2.51	2.14	0.07
Treatment × Year	10	3.42	0.342	0.291	0.98
Site × Treatment × Year	10	2.54	0.254	0.216	0.99
Residuals	102	119.66	1.173		

## 4 | DISCUSSION

The effect of extreme warm-season drought on total above-ground net primary productivity occurred after a single year at low elevation and took multiple years at high elevation. Total production responses to warm-season water addition were only realized at the highest elevation site. Production responses to extreme warm-season precipitation varied by plant functional type, with C<sub>4</sub> perennial grasses the most responsive, followed by C<sub>3</sub> perennial grasses and annuals, and perennial forbs and shrubs had no responses. Production sensitivity to warm-season precipitation differed under extreme drought and water addition compared





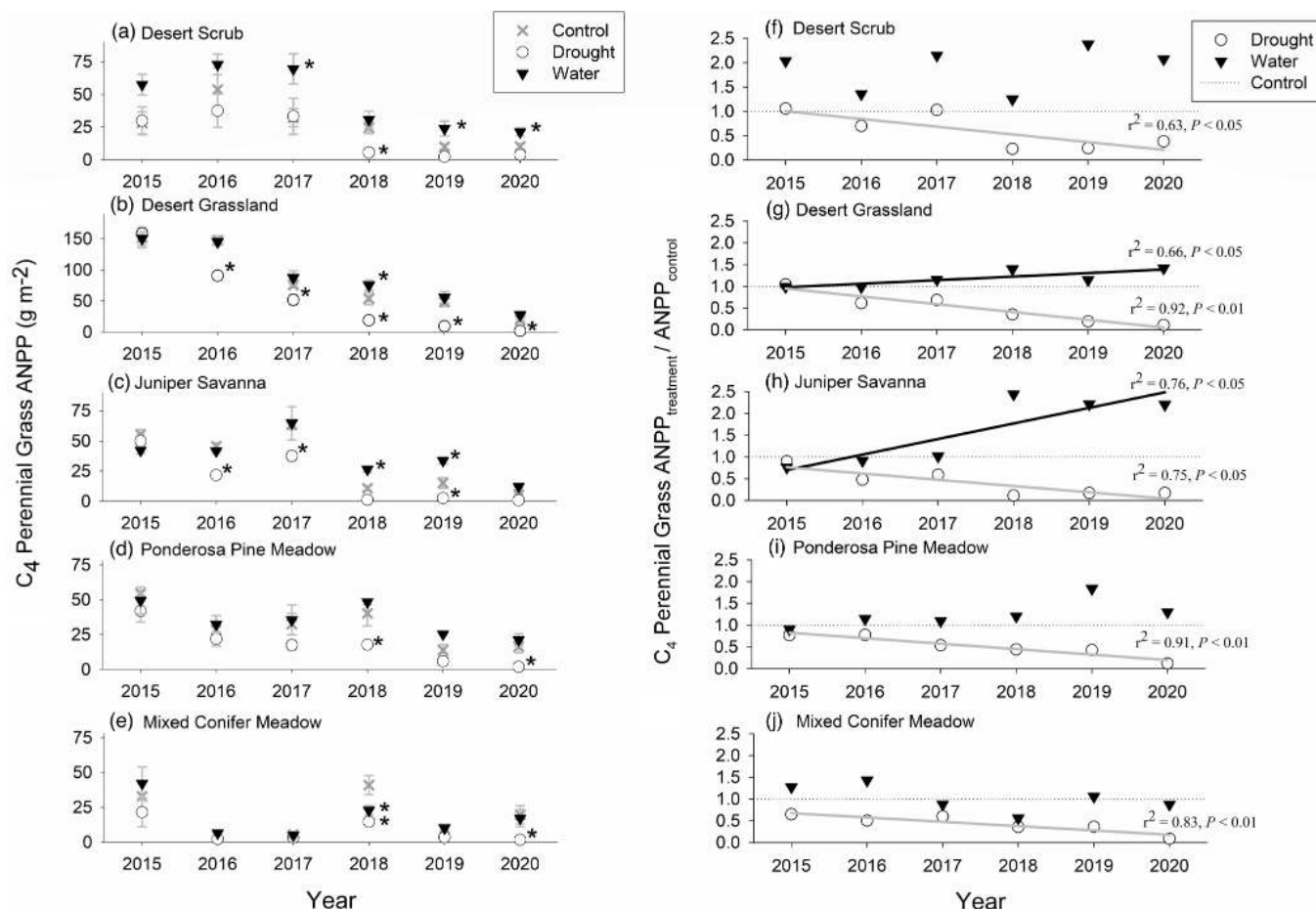
**FIGURE 2** Above-ground net primary production (ANPP) of all plant functional types (total) in control, drought and water addition treatments (a–e), and the ratio of all plant functional types (total) ANPP in treatments (drought or water addition) relative to control (f–j), from 2015 to 2020 at desert scrub (a, f), desert grassland (b, g), juniper savanna (c, h), ponderosa pine meadow (d, i) and mixed conifer meadow (e, j). Asterisks (\*) for (a)–(e) indicate significant differences between either drought or water addition treatments and the control. Solid lines for (f)–(i) indicate significant relationships for water addition (black) and drought (grey).

to ambient precipitation for *C*<sub>3</sub> perennial grasses at the ponderosa pine meadow, but other sites, where *C*<sub>3</sub> and *C*<sub>4</sub> perennial grasses were responsive, had similar sensitivities among different precipitation treatments.

The large responses of *C*<sub>4</sub> perennial grasses to extreme changes in warm-season precipitation can be explained by their primary growth occurring in May–September when treatments were implemented (Jameson, 1965; Witwicki et al., 2016). *Bouteloua eriopoda* and *B. gracilis*, which were dominant at the low elevation desert scrub and grassland, and juniper savanna, respectively, are known to have strong growth and recruitment responses to summer precipitation in the southwestern United States (Muldavin et al., 2008; Peters et al., 2010). Although containing drought-tolerant species, extreme warm-season drought pushed precipitation to <1% of the historical distribution at the juniper savanna for four of the study years, which suppressed *C*<sub>4</sub> perennial grass growth and led to reduced production by the end of the growing season. Extreme drought treatments in the desert grassland did not cause this same extreme until 2019, although reductions in ANPP at low elevation sites due to water deficit confirms previous results of arid sites having high sensitivity relative to more mesic sites (Huxman et al., 2004; Knapp

& Smith, 2001; Maurer et al., 2020). Decreases in *C*<sub>4</sub> perennial grass ANPP due to experimentally imposed extreme drought were amplified through time relative to control plots while there were natural reductions in ambient warm-season rainfall during our experiment, such that *C*<sub>4</sub> perennial grass production fell to <10 g m<sup>-2</sup> (48%–91% ANPP reduction relative to control) at all the sites in the last 2 years of the study. This reduction is similar to the results of Hoover et al. (2015), who found intensification of grass decline when short-term extreme drought was experimentally induced on top of a long dry period and suggests accelerated loss and mortality of perennial grass species.

In contrast, a lack of initial *C*<sub>4</sub> perennial grass ANPP responses to extreme drought treatments at the high elevation meadows may be due to soils at cooler sites retaining sufficient moisture to maintain growth through the summer. Indeed, the mixed conifer meadow had above average ambient warm-season precipitation in 2016 and 2018 and both high elevation meadows maintained higher warm-season soil volumetric water content from 2016 to 2019 across treatment types than the three low elevation sites ( $p < 0.05$ ). Although a previous study projected an expansion of North American grassland production into the spring and fall under future summer drought



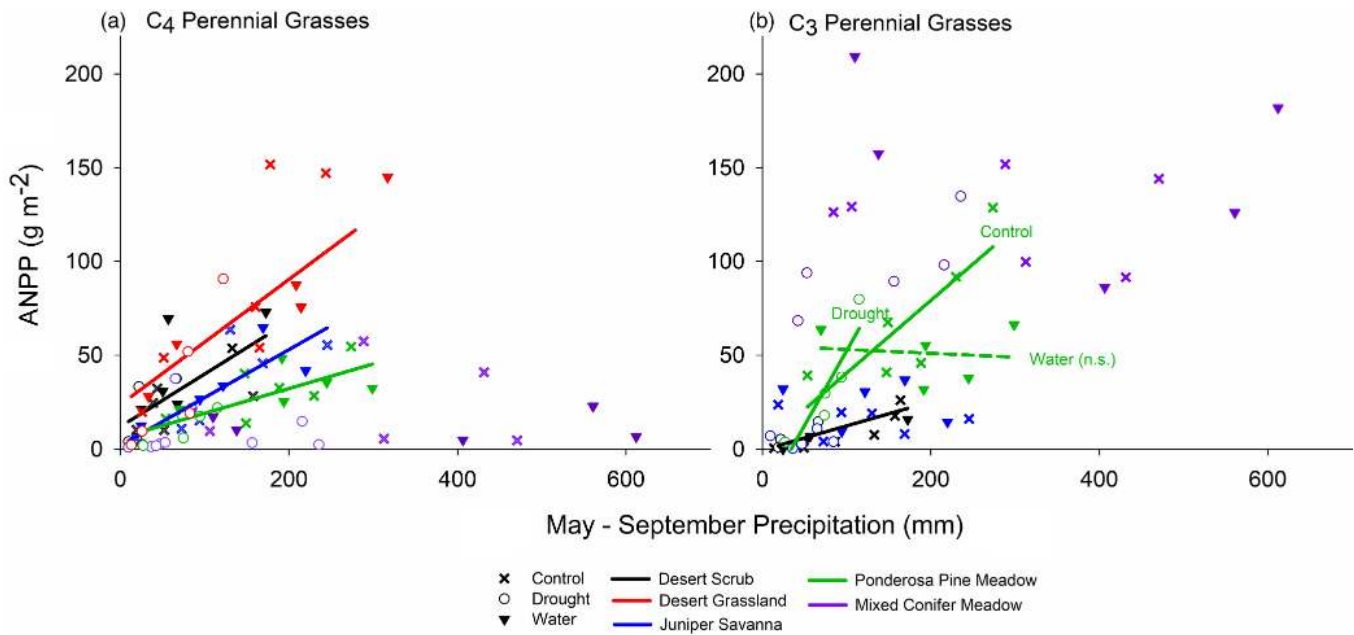
**FIGURE 3** Above-ground net primary production (ANPP) of  $C_4$  perennial grasses in control, drought, and water addition treatments (a–e), and the ratio of  $C_4$  perennial grass ANPP in treatments (drought or water addition) relative to control (f–j), from 2015 to 2020 at desert scrub (a, f), desert grassland (b, g), juniper savanna (c, h), ponderosa pine meadow (d, i) and mixed conifer meadow (e, j). Asterisks (\*) for (a)–(e) indicate significant differences between either drought or water addition treatments and the control. Solid lines for (f)–(i) indicate significant relationships for water addition (black) and drought (grey).

(Hufkens et al., 2016), our results suggest that the capacity to maintain production for many  $C_4$  grasses in the southwestern United States may be limited to wet and high elevation areas, and only under short-term summer drought. Long-term sustained decreases in summer rainfall, especially when coupled with warmer summer temperatures, are likely to lead to reduction and eventual loss of  $C_4$  perennial grass production, similar to losses in the Great Plains during the Dust Bowl (Knapp et al., 2020). Our results indicate that  $C_4$  perennial grass declines and losses in the southwestern United States will likely first occur at low elevation and progress up in elevation over time in multi-year summer drought scenarios.

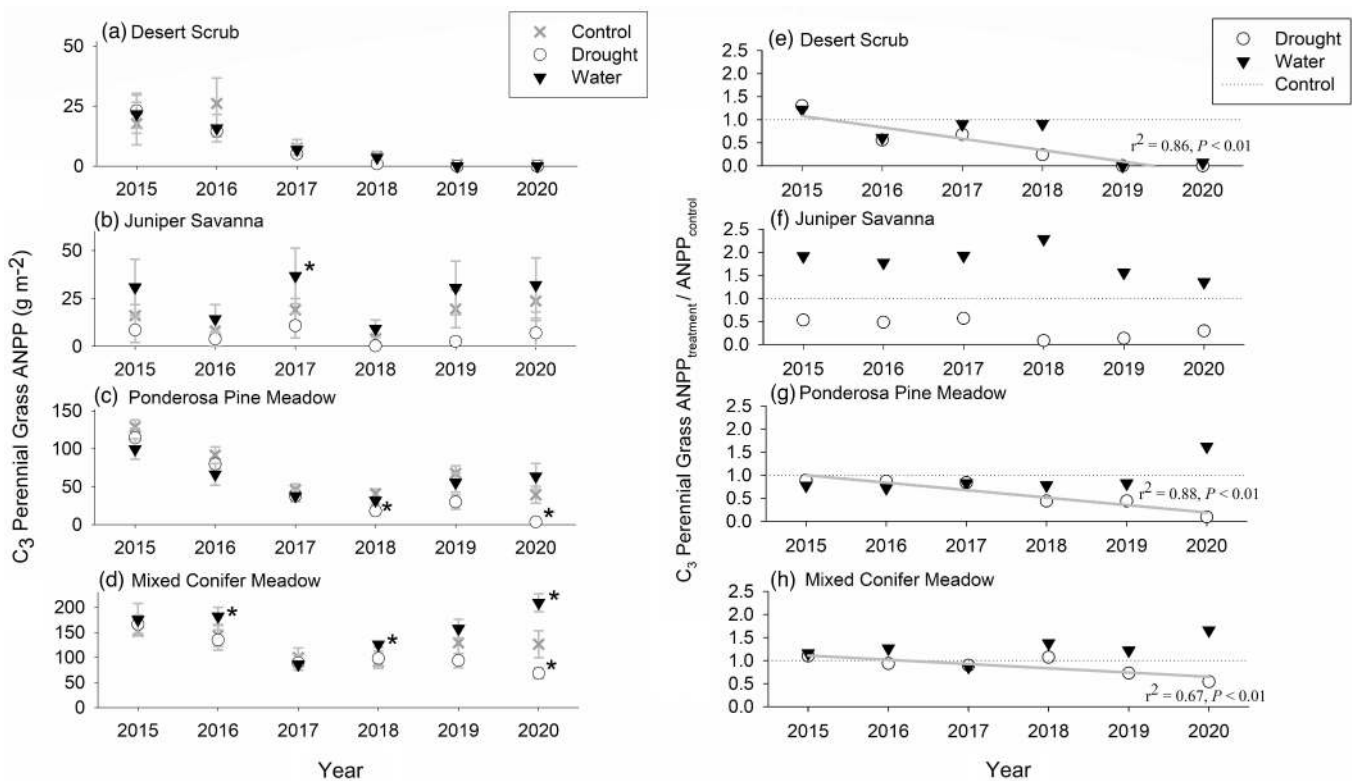
A delayed response of  $C_4$  perennial grass production to water addition at low elevation may be attributable to limited basal cover and meristem density at these arid and semiarid sites (Dalglish & Hartnett, 2006). The three low elevation sites had one-third of total plant density ( $32.5 \pm 3.7$  plants  $m^{-2}$ ) as the two high elevation sites ( $112.8 \pm 11.6$  plants  $m^{-2}$ ) at the beginning of the study ( $t = 9.8, p < 0.0001$ ). Arid grasslands dominated by *B. eriopoda* can take several years to respond to above-average rainfall (Peters et al., 2012), which is likely due to tiller and stolon densities in previous years affecting growth responses in the current

year (Reichmann et al., 2013). In contrast, high elevation sites had no  $C_4$  ANPP responses to water addition except at the mixed conifer meadow in 2018, which had decreases in production. These losses were likely attributable to competition from increased  $C_3$  perennial grass production in the same year and point out the importance of potential interactions among functional types (Ode et al., 1980).

The decrease in ambient warm-season precipitation over the course of our study meant that water addition treatments only initially created above average historical precipitation. As our study progressed, ANPP decreased in both the extreme drought and control plots (although disproportionately more in the drought plots), and water addition buffered ANPP declines, rather than enhancing ANPP, relative to the previous year. Large pulses of moisture that punctuate a drought have been previously shown to elevate grass productivity in a semi-arid grassland (Heisler-White et al., 2009) and increase  $C_4$  perennial grass growth in our study area (Jameson, 1965), but our results suggest that multi-year drought may minimize this capacity, especially as precipitation pulses fall below a threshold amount. Our results suggest that future climate change scenarios that increase warm-season monsoon moisture will likely affect  $C_4$

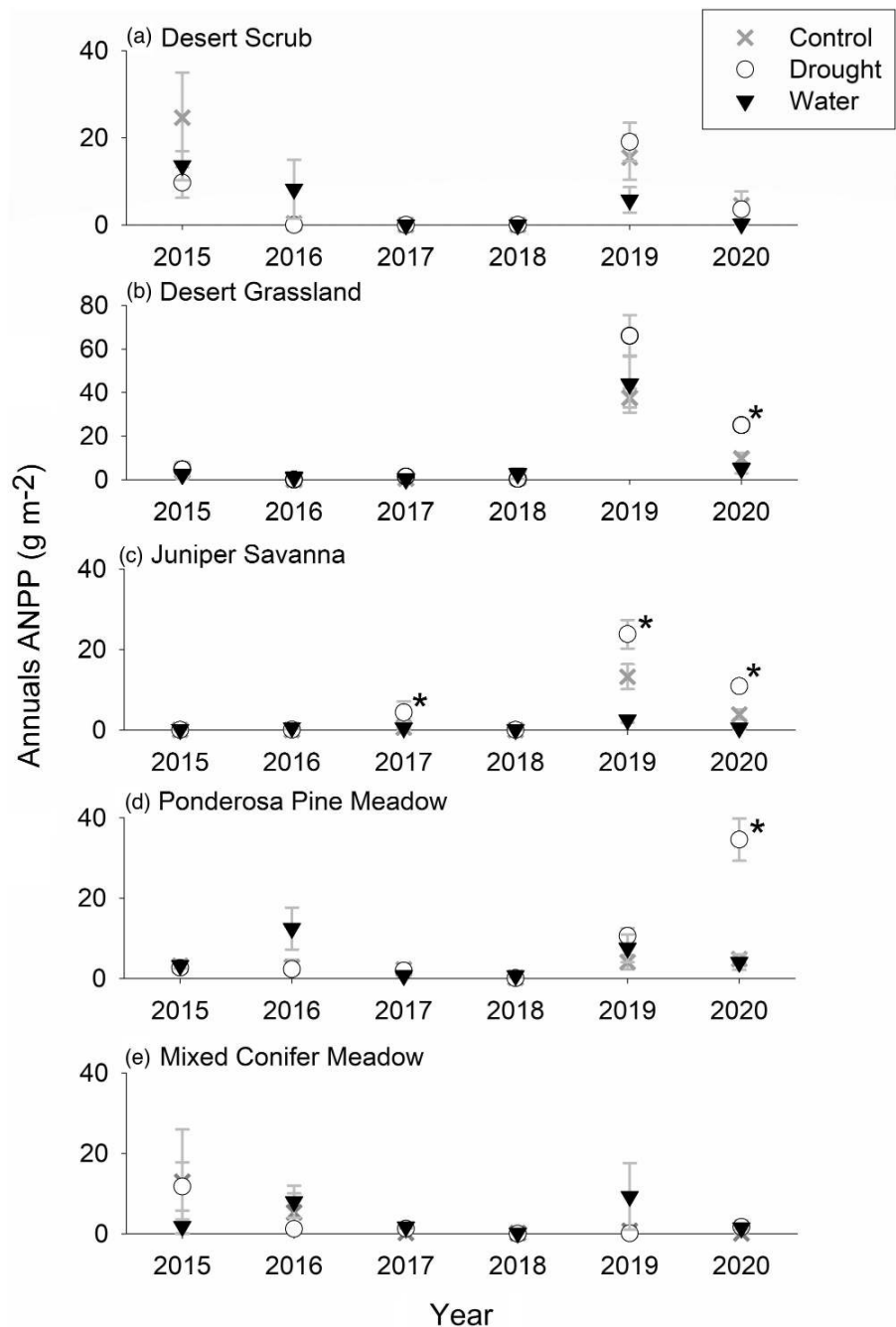


**FIGURE 4** Above-ground net primary production (ANPP) of (a) C<sub>4</sub> perennial grasses and (b) C<sub>3</sub> perennial grasses in relation to May-September (warm-season) precipitation at each site across control, drought and water addition treatments. Solid lines indicate significant, and short dashed lines indicate non-significant, relationships. C<sub>4</sub> perennial grasses in desert scrub: Slope = 0.28,  $R^2 = 0.43$ ,  $p < 0.01$ ; desert grassland: Slope = 0.33,  $R^2 = 0.33$ ,  $p = 0.02$ ; juniper savanna: Slope = 0.25,  $R^2 = 0.68$ ,  $p < 0.0001$ ; ponderosa pine meadow: Slope = 0.13,  $R^2 = 0.58$ ,  $p < 0.001$ . C<sub>3</sub> perennial grasses in desert scrub: Slope = 0.13,  $R^2 = 0.71$ ,  $p < 0.001$ ; ponderosa pine meadow (drought): Slope = 0.80,  $R^2 = 0.82$ ,  $p = 0.04$ , ponderosa pine meadow (control): Slope = 0.39,  $R^2 = 0.69$ ,  $p = 0.04$ , ponderosa pine meadow (water addition): Not significant (n.s.)



**FIGURE 5** Above-ground net primary production (ANPP) of C<sub>3</sub> perennial grasses in control, drought and water addition treatments (a–d), and the ratio of C<sub>3</sub> perennial grass ANPP in treatments (drought or water addition) relative to control (e–h), from 2015 to 2020 at desert scrub (a, e), juniper savanna (b, f), ponderosa pine meadow (c, g) and mixed conifer meadow (d, h). The desert grassland did not have C<sub>3</sub> perennial grasses. Asterisks (\*) for (a)–(d) indicate significant differences between either drought or water addition treatments and the control. Solid lines for (e)–(h) indicate significant relationships for water addition (black) and drought (grey).

**FIGURE 6** Above-ground net primary production (ANPP) of annuals in control, drought and water addition treatments from 2015 to 2020 at (a) desert scrub, (b) desert grassland, (c) juniper savanna, (d) ponderosa pine meadow and (e) mixed conifer meadow. Asterisks (\*) indicate significant differences between either drought or water addition treatments and the control.



perennial grass productivity if elevated rainfall is maintained for multiple years at low, but not high, elevation in the southwestern United States. However, expected warming trends in low elevations of the Southwest (Garfin et al., 2013) may limit this potential.

Similar to  $C_4$  perennial grass ANPP,  $C_3$  perennial grass ANPP was initially unaffected by warm-season extreme drought treatments and then declined after 3–5 years of extreme drought treatments at the high elevation meadows. Resistance to 1–2 years of warm-season extreme drought treatment was likely partially attributable to early growth of  $C_3$  perennial grasses that can be supported by spring snowmelt and precipitation (Jameson, 1965), which we did not exclude in our study. However, we found little evidence that cool-season precipitation or soil moisture influenced  $C_3$  perennial grass ANPP at our study sites. In contrast to differences in photosynthetic

pathway and phenology,  $C_3$  and  $C_4$  perennial grasses in northern Arizona share conservative leaf traits (low specific leaf area and high leaf dry matter content) that may explain similar initial resistance at high elevation sites (Laughlin et al., 2010). Our results indicate that even if spring moisture is maintained in the future, multi-year shortfalls in warm-season precipitation can eventually affect  $C_3$  perennial grasses. However, future warming will accelerate snowmelt at high elevation sites, and an earlier and more rapid dry-down of spring soil moisture can compound reductions in  $C_3$  perennial grass productivity (Gremer et al., 2018; Munson et al., 2011). Although a steep ANPP-precipitation slope for  $C_3$  perennial grasses under extreme drought compared to other treatments at the ponderosa pine meadow points to an increasing likelihood of abrupt thresholds under long-term drought conditions (Munson et al., 2021), this was



the only evidence of treatments changing production sensitivity across our study elevation gradient.  $C_3$  perennial grass ANPP likely had minimal response to warm-season extreme drought treatments at low elevation sites because production was initially low and variable, although the desert grassland showed sensitivity to warm-season precipitation when all treatments were combined.

Water addition increased  $C_3$  perennial grass ANPP at the juniper savanna and mixed conifer meadow. Although we expected increased soil moisture in the warm season to benefit  $C_4$  more than  $C_3$  perennial grasses, as has been previously documented for high elevation sites in our study area (Pearson et al., 1971), there was more initial  $C_3$  perennial grass biomass at the mixed conifer meadow, which along with very high ambient warm-season precipitation in 2016 and 2018, created a large capacity to respond. Hoover et al. (2019) found that many of the same  $C_3$  perennial grass species in our study have high above-ground biomass allocation optimized for fast growth rates. Additional warm-season precipitation can prolong or reinstate the growth of  $C_3$  perennial grasses, which normally senesce in the early summer (Comstock & Ehleringer, 1992; Jameson, 1965). Many  $C_3$  species in our study occur in the warmest limits of their congeners, including *Festuca arizonica* (Weaver, 1979), and can be sensitive to monsoon precipitation (Pearson, 1942). Results from our study suggest that shifts in future monsoon activity have the potential to affect production of  $C_3$  perennial grass species more than expected, particularly for species growing in areas that already receive a high proportion of warm-season precipitation in the southwestern United States.

While perennial grasses responded to warm-season precipitation treatments, perennial forbs and shrubs did not. Moore et al. (2006) found a 4–5 years lag before perennial forbs responded to tree thinning treatments at nearby study sites, indicating their long response times. However, we found some evidence that they were sensitive to shallow soil moisture at the ponderosa pine meadow. Shrubs are deeply rooted and generally more sensitive to cool-season compared to warm-season precipitation in our study area (Ehleringer et al., 1991). Indeed, shrubs at the desert scrub site in our study responded to deep warm-season soil moisture and there was some evidence that they increased in extreme drought compared to water addition treatments. Shrub resistance to drought suggests that they may survive under enhanced aridity forecasted for the southwestern United States. Previous studies have found that warming temperature and shifting soil moisture availability expected under climate change is likely to lead to greater shrub dominance across the Colorado Plateau (Gremer et al., 2018; Munson et al., 2011). However, further experiments are needed to understand the capacity of shrubs to withstand hot droughts. Increases in shrub productivity are not likely to occur over the short term in response to enhancements of warm-season precipitation alone, as there were no responses to water addition in our study.

Perennial grasses and their utilization of shallow soil moisture likely limited the abundance of annuals at the beginning of our study. As extreme drought reduced perennial grass ANPP through time over the course of our experiment, annuals likely faced less competition for soil moisture and could increase opportunistically to pulses of

ambient rainfall due to their rapid growth, especially in the last year of our study. Responsive annuals were largely cool-season species, although we did not find any evidence that they were sensitive to cool-season moisture at any of the sites. Many of the annuals that responded at the desert grassland and juniper savanna sites were non-native species, although native annuals dominated the response at the ponderosa pine meadow. Increases in annual non-native species have occurred in northern Arizona in response to disturbances that reduce the abundance of perennial vegetation (Fulé et al., 2005). Importantly, our results demonstrate that reductions in perennial vegetation induced by prolonged warm-season drought can allow annuals, and potentially those of non-native origin, to increase in dominance.

## 5 | CONCLUSIONS

Our findings indicate that future decreases in warm-season precipitation from the North American Monsoon in the southwestern United States will likely immediately suppress  $C_4$  perennial grass productivity at low elevation, with this negative effect growing as the duration of time with warm-season water shortages increases. Multi-year warm-season drought will extend to affect both  $C_4$  and  $C_3$  perennial grass productivity at all elevations, with less sensitivity in perennial forb and shrub productivity. Reductions in perennial grass production can allow annuals, including those with non-native origin, to increase in abundance. In the context of future warming, increases in monsoon precipitation would likely only affect ANPP if wetter soil moisture conditions are sustained, or reach higher extremes than we were able to achieve in our study; in which case, elevated moisture in the warm-season can enhance  $C_4$  perennial grass ANPP at low elevation and  $C_3$  perennial grass productivity at high elevation. We found limited support for extreme drought inducing disproportionately large responses for  $C_3$  perennial grasses at one site, suggesting that most production losses or gains of plant functional types will be in proportion to future warm-season precipitation changes. The changes in productivity we found in our study can portend shifts in functional composition and carbon cycling, which can collectively transform ecosystem function in the southwestern United States.

## AUTHORS' CONTRIBUTIONS

S.M.M., J.B.B., B.J.B. and J.R.G. designed the experiment; S.M.M. collected the data, developed and conducted analyses and wrote the paper; J.B.B., B.J.B. and J.R.G. assisted with writing and editing.

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## PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/1365-2745.13947>.

## DATA AVAILABILITY STATEMENT

Data for this paper are available from ScienceBase (Munson, 2022) <https://doi.org/10.5066/P9TGGMOE>.

## ORCID

Seth M. Munson  <https://orcid.org/0000-0002-2736-6374>

John B. Bradford  <https://orcid.org/0000-0001-9257-6303>

Bradley J. Butterfield  <https://orcid.org/0000-0003-0974-9811>

Jennifer R. Gremer  <https://orcid.org/0000-0001-8983-5482>

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## SUPPORTING INFORMATION

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

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