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Regional grassland productivity responses to precipitation during multiyear above- and below-average rainfall periods

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Abstract

There is considerable uncertainty in the magnitude and direction of changes in precipitation associated with climate change, and ecosystem responses are also uncertain. Multiyear periods of above- and below-average rainfall may foretell consequences of changes in rainfall regime. We compiled long-term aboveground net primary productivity (ANPP) and precipitation (PPT) data for eight North American grasslands, and quantified relationships between ANPP and PPT at each site, and in 1–3 year periods of above- and below-average rainfall for mesic, semiarid cool, and semiarid warm grassland types. Our objective was to improve understanding of ANPP dynamics associated with changing climatic conditions by contrasting PPT–ANPP relationships in above- and below-average PPT years to those that occurred during sequences of multiple above- and below-average years. We found differences in PPT–ANPP relationships in above- and below-average years compared to long-term site averages, and variation in ANPP not explained by PPT totals that likely are attributed to legacy effects. The correlation between ANPP and current- and prior-year conditions changed from year to year throughout multiyear periods, with some legacy effects declining, and new responses emerging. Thus, ANPP in a given year was influenced by sequences of conditions that varied across grassland types and climates. Most importantly, the influence of prior-year ANPP often increased with the length of multiyear periods, whereas the influence of the amount of current-year PPT declined. Although the mechanisms by which a directional change in the frequency of above- and below-average years imposes a persistent change in grassland ANPP require further investigation, our results emphasize the importance of legacy effects on productivity for sequences of above- vs. below-average years, and illustrate the utility of long-term data to examine these patterns.

KEYWORDS
climate change, grassland dynamics, grassland productivity, legacy effects, precipitation

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1 | INTRODUCTION

Increasing temperatures and changing rainfall regimes are expected to have consequences for ecosystem dynamics across a range of scales, from fine-scale biogeochemical cycling to large-scale transitions between ecosystem states (Briggs et al., 2005; Fierer & Schimel, 2002; Peters, Yao, & Gosz, 2006). Although increasing temperatures will likely lengthen the growing season and promote higher productivity in temperate grasslands in spring and possibly reduce productivity in summer (Angert et al., 2005; Hufkens et al., 2016; Petrie, Brunsell, & Nippert, 2012), the complexities of how changes in precipitation affect productivity over multiple years are not well-understood (Mueller et al., 2016; Sala, Gherardi, Reichmann, Jobbagy, & Peters, 2012), and the magnitudes and even the directions of predicted changes in precipitation [PPT: mm] amount, seasonality, and intensity are uncertain (Greene & Seager, 2016; Gutzler & Robbins, 2011). Temperate grasslands experience high precipitation variability (annual amounts across grassland regions may range from 150 to 1,000 mm/year), and even small changes in the rainfall regime can have a strong effect on spatiotemporal grassland aboveground net primary productivity [ANPP: g m^{-2} $year^{-1}$] (Buis et al., 2009; Knapp, Ciais, & Smith, 2016). Although the importance of inter- and intra-annual variability in precipitation has been examined for multiple grassland types (e.g., Knapp, Briggs, & Koelliker, 2001; Sala et al., 2012), and drought has long been recognized as an important driver of grassland dynamics (e.g., Weaver & Albertson, 1936), the potential responses to a directional change in the multiyear pattern of precipitation have rarely been investigated (e.g., Hoover & Rogers, 2016; Reichmann & Sala, 2014), especially with respect to sequences of years with above-average precipitation (Peters, Havstad, Archer, & Sala, 2015; Peters, Yao, Sala, & Anderson, 2012). The future of these grasslands may include directional changes in the frequency of one or both of multiyear above- and below-average periods, and also an associated change in the transition between them; thus it is important to ascertain how changes in the pattern of these sequences of years may affect future grassland productivity.

The central grasslands region of North America includes a number of distinct grassland types that differ in functional group and species composition, as well as in seasonal and annual precipitation and temperature patterns, all of which are expected to influence productivity responses to changes in rainfall (Lauenroth, Burke, & Gutmann, 1999). Production in these grasslands, which range across an aridity gradient from arid and semiarid to mesic, exhibits both similar and differing responses to seasonal and annual precipitation (Lauenroth et al., 1999). For example, in arid and semiarid southwestern US grasslands, the majority of ANPP occurs during the summer to fall growing season and is associated with episodic monsoon rainfall events (Collins et al., 2010; Mendez-Barroso, Vivoni, Watts, & Rodriguez, 2009; Petrie et al., 2016). In contrast, ANPP is driven by large, relatively frequent rain events over the entire growing season in mesic grasslands in the eastern central grasslands region (Knapp et al., 2001; Nippert, Knapp, & Briggs, 2006), and may be strongly influenced by nongrowing season soil moisture recharge in the north (Flanagan & Adkinson, 2011; Wever, Flanagan, & Carlson, 2002). As a result, mesic grasslands are more sensitive to seasonal and annual patterns of total precipitation, whereas semiarid and desert grasslands are more sensitive to precipitation at shorter timescales (Collins et al., 2014; Petrie et al., 2016). These grasslands all experience multiyear above- and below-average rainfall periods (www.ecotrends.info), although most studies have focused on the effects of multiyear drought at individual sites [see Weaver and Albertson (1936) for multisite comparisons of multiyear drought effects, and Reichmann and Sala (2014) for both multiyear wet and dry effects]. Comparisons of the responses of ANPP to above- and below-average precipitation over multiple years have not been conducted for multiple grassland types in this region.

Although years with below- or above-average precipitation may decrease and increase productivity, respectively, these effects are not predictable across multiple grassland types or between multiple years (Nippert et al., 2006; Vermeire, Heitschmidt, & Rinella, 2009; Wilcox, Blair, Smith, & Knapp, 2016). Thus, it is difficult to ascribe changes in ANPP to changes in specific precipitation patterns. There is growing evidence that the legacy of prior-year conditions including plant available nutrients, meristem density, herbaceous biomass, temperature, and soil moisture can influence current-year ANPP (see Hermance, Sulieman, & Mustafa, 2016), although these legacies are difficult to disentangle from each other and may accumulate over a sequence of years (Gherardi & Sala, 2015; Mueller et al., 2016; Peters, Yao, Browning, & Rango, 2014; Reichmann, Sala, & Peters, 2013a). Furthermore, emergent responses, which occur subsequent to the first year of a multiyear rainfall period, have received little attention, in part because extended above- or below-average rainfall periods are expected to occur infrequently and are therefore impossible to observe a priori. Recent observations suggest that grassland responses to external forcings can change over multiple years as a result of legacies (Jones, Collins, Blair, Smith, & Knapp, 2016; Ratajczak et al., 2017), and comparing legacy and emergent components of ANPP in different grassland types can provide a more comprehensive understanding of how these processes influence ecosystem responses over periods of multiple years.

The majority of climate impact studies in grasslands have used short-term (1–3 year) manipulative experiments to examine effects of increases or decreases in precipitation on ecosystem processes (Heisler-White, Blair, Kelly, Harmoney, & Knapp, 2009; Reichmann, Sala, & Peters, 2013b; Yahdjian & Sala, 2010), or have used remote sensing to examine ecological responses to weather and climate variability (Zhang, Wylie, Ji, Gilmanov, & Tieszen, 2010; Zhang et al., 2011). There are studies that reported data for time periods longer than 50 years such as Lauenroth and Sala (1992), but they are relatively rare [see Sala et al. (2012) for a list of long time period ANPP studies]. Statistical or simulation models based on results of short-term studies are often used to predict longer term ecological responses to scenarios of predicted climate change (e.g., Gang et al., 2015; Hufkens et al., 2016; Liang et al., 2017). Although experiments and remote sensing are expanding in scope and scale, short-term observations and their model-based extensions have limited ability to predict events and processes that require long-term observations, such as plant population dynamics during or subsequent to a period of above- or below-average rainfall years (e.g., Peters et al., 2014). Long-term manipulative experiments of multiyear above- or below-average rainfall periods are beginning to investigate these processes, yet they are challenging and are not commonly conducted (see Gherardi & Sala, 2015; Zhu, Chiariello, Tobeck, Fukami, & Field, 2016; for exceptions). Remotely sensed data are only beginning to comprise enough years to examine ecosystem responses through time, and to inform regional modeling efforts (Gang et al., 2015; Hufkens et al., 2016; Liang et al., 2017). Alternatively, existing monitoring data of ecosystem responses under natural conditions over sufficient time periods to comprise extended above- or below-average periods can provide novel information on ecological patterns not captured by other techniques. These long-term data are increasingly available for other types of extreme, infrequent events, such as drought and wildfire (Anderson, Ellis, von Dohlen, & Romme, 2004; Easterling et al., 2000). We were especially interested in the ability of long-term data to capture legacy and emergent sensitivities of ANPP to precipitation over multiyear above- or below-average rainfall periods. Legacy effects have been quantified as the difference between the observed and the expected production based on long-term relationship between production and precipitation (Reichmann, Sala, & Peters, 2013b; Sala et al., 2012). Here, our definition of legacies is constrained to significant effects of prior-year PPT or ANPP on current-year ANPP. These legacies may occur in any year. We define emergent responses as current- and prior-year effects that do not occur normally, and instead occur subsequent to the first year of a multiyear rainfall period.

We hypothesized that the influence of legacies would differ between mesic and semiarid grassland types [Sala et al. (2012) found increasing legacy effects with mean annual precipitation], that their influence may increase during extended above- or below-average periods, and that new emergent responses may occur during these periods. Additionally, we hypothesized that ANPP in mesic grasslands would be proportionally less sensitive to small changes in year to year precipitation variability than in semiarid grasslands due to higher nutrient status and living biomass, which decreases their sensitivity to precipitation (Knapp et al., 2015; McCulley, Burke, & Lauenroth, 2009). Conversely, we expected ANPP in semiarid grasslands to be less sensitive to below-average years and drought because perennial grasses in these ecosystems are more drought tolerant than those in mesic ecosystems (Knapp et al., 2015). Recent studies in semiarid warm (arid) grasslands show that multiple sequential above-average years are needed for perennial grasses to respond through the production of seeds, germination and establishment of seedlings, and survival of young adult plants (Peters et al., 2014), whereas this sequence may be shorter in mesic grasslands because seed storage in the soil is more persistent, nutrients are more available, and loss of grass cover and meristem density is less frequent (Reichmann & Sala, 2014; Seastedt & Knapp, 1993). Thus, we expect mesic grasslands to be more sensitive to high precipitation than semiarid grasslands in the first above-average year following a below-average year or multiyear period.

We used a unique set of long-term (≥10 years) observations of ANPP and precipitation beginning in 1928 from eight grassland sites in the Great Plains and southwestern United States. Our goals were to examine relationships between these variables during multiyear above- or below-average periods throughout the central grasslands region, and to investigate variability in productivity responses to above- and below-average precipitation for mesic, semiarid cool, and semiarid warm grassland types. By evaluating relationships of precipitation with productivity (PPT–ANPP) over relatively longer intervals, we determined how single to multiyear above- or below-average periods shape ANPP through the legacy effects of prior conditions or through novel emergent responses that occur following one or more above- or below-average years, and we identified focal points for future investigation of legacy effects in grasslands. Our objectives were to: (i) improve our understanding of PPT–ANPP relationships in above- or below-average rainfall years for different North American grasslands, (ii) characterize single above- or below-average years and multiple year periods in these grasslands in the context of interannual precipitation variability, and (iii) contrast the importance of current conditions, prior-year legacies, and emergent responses to ANPP over sequences of 1–3 above- or below-average years, the longest periods sufficiently captured by these data for statistical analysis.

2 | MATERIALS AND METHODS

2.1 | Site characteristics

The central grasslands region of North America encompasses a large percentage of the total land area (12.5%) and consists of five major grassland types distinguished by the ecophysiology of the dominant species (C_3-cool season, C_4-warm season) and growth form of the plant community (short, mid, tall; Lauenroth et al., 1999). Grassland types occur along an aridity gradient from arid and semiarid in the west to mesic in the east, and a mean annual temperature gradient from 3°C in the north to 22°C in the south (Lauenroth et al., 1999; Peters et al., 2008). Productivity in these grasslands is driven primarily by warm-season PPT, although cool-season PPT and soil moisture recharge are important in cooler subregions (Flanagan & Adkinson, 2011; Zhang et al., 2010).

We focused on eight grassland sites with long-term ANPP and PPT data (Figures 1a and 2). Two sites are part of the US Department of Agriculture Long Term Agroecosystems Research (LTAR) Network (https://ltar.nal.usda.gov/), two sites are part of the National Science Foundation Long Term Ecological Research (LTER) Network (https://lternet.edu/), three sites are part of both networks, and one site is independent (Table 1). We classified sites into three grassland types based on Lauenroth et al. (1999) and then grouped by climate for analysis: (i) mesic grasslands including two tallgrass prairie grasslands in KS and OK (KNZ and GRL) and one southern mixedgrass site in KS (HYS), (ii) semiarid cool grasslands including one shortgrass steppe grassland in CO (SGS) and two northern mixed grasslands in ND and WY (HPG and NGP), and (iii) semiarid warm grasslands including two Chihuahuan Desert mixed grasslands in central (SEV) and southern (JRN) NM (Figure 1a, Table 1). These grasslands experience differing precipitation [PPT: mm] totals, mean annual air temperature [MAT: °C], and have differing productivity (Table 1; Figure 1b).

2.2 | Data sources

Our selection of sites was determined by availability of long-term field measurements (≥10 years) of ANPP and PPT that included at least one sequence of 3+ consecutive above- or below-average rainfall years (sensu; Peters et al., 2012). Years with missing ANPP data were excluded from the analysis and are not included in our total of 336 analysis years, although we retained PPT data to count multiple wet and dry years when corresponding ANPP data were not available. We used ungrazed grassland locations on representative soils for analysis. ANPP data collection and postprocessing methodology differed between sites, and although we only report values for total herbaceous vegetation, changes in species or lifeform composition may be an additional source of uncertainty.

When possible, we obtained monthly total PPT data from meteorological stations colocated at ANPP measurement sites. When local PPT data were not available, we obtained data from the nearest National Oceanic and Atmospheric Administration National Climatic Data Center (NCDC)/NOAA National Centers for Environmental Information (NCEI; https://www.ncdc.noaa.gov/) meteorological station (Table 1). These data provide the best characterization of PPT received at each ANPP measurement site, and the multiyear time periods we analyzed resulted in average annual PPT values within 10% of regional mean values for all sites. We defined an above-average water year or growing season as those with a positive (>0) precipitation anomaly [Pa: $(\mathrm{PPT} - \overline{\mathrm{PPT}})/\sigma^2_{\mathrm{PPT}}$] of site data compared to the regional, long-term PPT average and standard deviation from NCDC data, and defined a below-average water year similarly ($\mathrm{Pa} < 0$). To calculate long-term average and standard deviation of PPT for each site, we obtained monthly PPT data from 1910 to 2014 for the nearest 1–3 US Historical Climatology Network meteorological stations with similar site characteristics for all sites except for CPR and HPG (Williams et al., 2013). CPR and HPG are located in a region that experiences very high regional rainfall variability and a high degree of heterogeneity in grassland responses to PPT, and we therefore only used local long-term data to calculate long-term average and standard deviation of PPT for these sites. By comparing local data to long-term regional averages, we were able to somewhat ameliorate uncertainties in site PPT measurements by focusing on Pa.

2.3 | Data analysis

We evaluated PPT–ANPP relationships over four PPT time periods: calendar year, water year (October–September), growing season (May–September), and nongrowing season (October–April). Water year PPT was a slightly better predictor of ANPP on average for the mesic and semiarid cool grassland sites of our study, and for all grasslands on average, whereas growing season PPT was a slightly better predictor only for semiarid warm grasslands (not shown). Thus, we selected water year comparison among sites. To compare the sensitivity of ANPP to PPT in single above- and below-average years (Obj. 1), we regressed PPT–ANPP in groupings of above-average water years, below-average water years, and all water years combined for each grassland site. To better characterize above- and below-average years and multiyear periods (Obj. 2), we evaluated the pattern and frequency of single and multiyear periods for these grassland sites, contrasted the seasonal distribution of PPT between above- and below-average water years, and explored the relationship between growing season PPT and water year PPT at these sites.

To contrast the importance of current conditions, prior-year legacies, and emergent responses to ANPP (Obj. 3), we first correlated ANPP and ecosystem water-use efficiency (WUE: $\mathrm{g\ m^{-2}\ mm^{-1}}$) to current-year and prior-year ($n-1$) conditions (legacies) for all above- and below-average water years and growing seasons, which identified broad relationships in mesic, semiarid cool, and semiarid warm grassland types. To identify patterns in legacy and emergent responses from year-to-year during multiyear above- and below-average periods, we focused on the pattern of significant relationships for differing time windows of analysis. Within periods of consecutive above- and below-average growing season and water year rainfall, we correlated ANPP to explanatory variables (ANPP, PPT) in the current and preceding water year or growing season (i.e., all 2nd years compared to the 2nd and 1st). By focusing on the proportion of significant relationships over different windows of analysis and their average slope, we characterized how legacy effects changed and emergent responses developed over multiple years of above- or below-average rainfall without knowing exactly what windows of analysis contained the most information. We identified six windows of analysis for mesic,

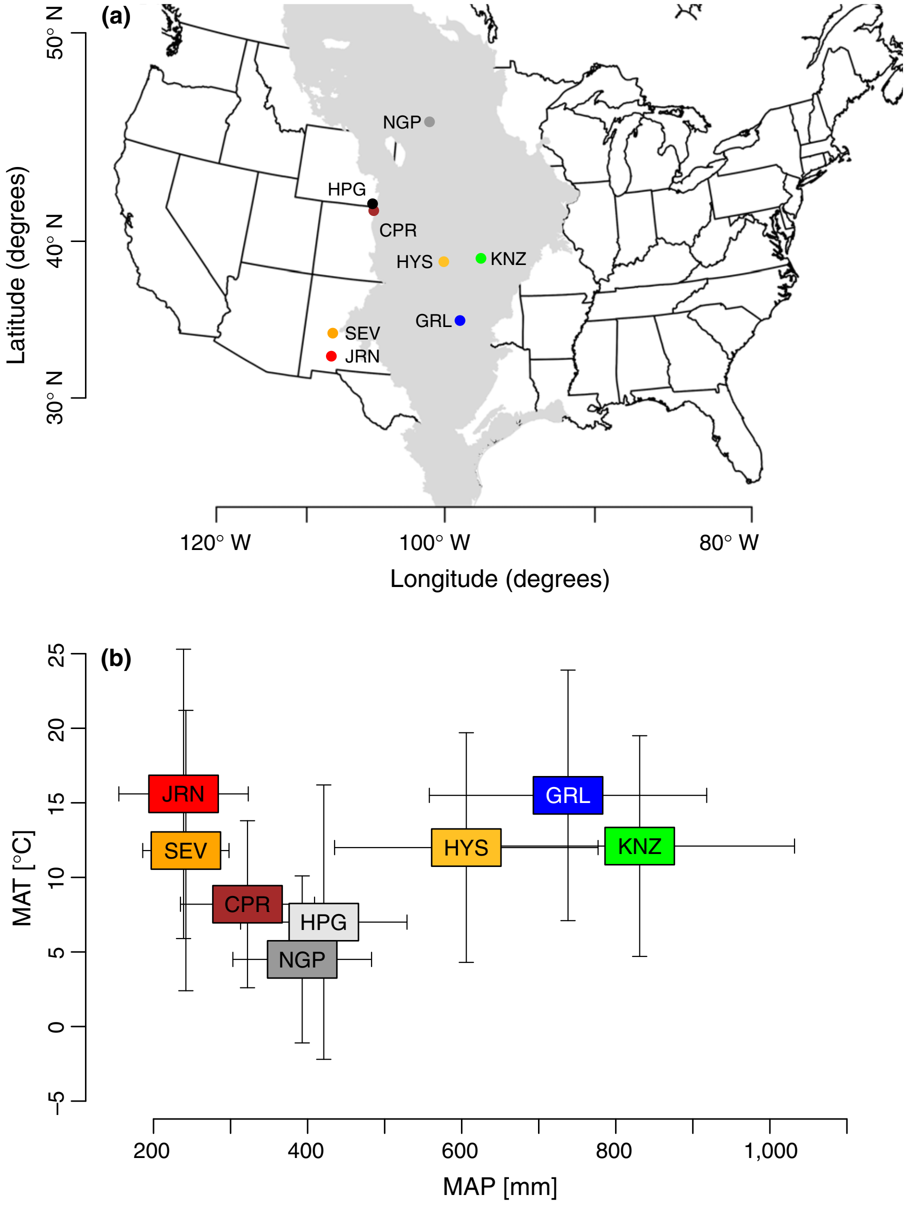

FIGURE 1 Map of grassland sites, with the United States EPA Great Plains ecoregion in gray (Panel a). Scatterplot of observed mean annual precipitation [MAP: mm] and mean annual air temperature [MAT: °C] for each grassland site (Panel b). Error bars show the standard deviation in annual MAP and monthly MAT [Colour figure can be viewed at wileyonlinelibrary.com]

semiarid cool, and semiarid warm grassland groupings: all years and growing seasons in all above- or below-average periods (two windows; high degrees of freedom), water years and growing seasons in a 2-year above- or below-average period (two windows; moderate degrees of freedom), and water years and growing seasons in a 3-year above- or below-average period (two windows; low degrees of freedom). We identified legacies and emergent responses by grassland type (mesic, semiarid cool and semiarid warm) because individual sites often did not include sufficient observations of multiyear periods. All analyses were conducted using R-project statistical computing software (R Development Core Team, 2016), and significance was determined at $p < .05$.

3 | RESULTS

3.1 | Obj. 1: Current-year and legacy effects in PPT–ANPP relationships in single above- and below-average rainfall years

Aboveground net primary productivity was positively correlated to water year PPT at all grassland sites, and in above- and below-average water years at all sites with sufficient observations (Figure 3). Generally, the slope of PPT–ANPP was highest in semiarid warm grasslands (JRN, SEV), and was lowest in semiarid cool grasslands (CPR, HPG, and NGP). The slope of PPT–ANPP differed among

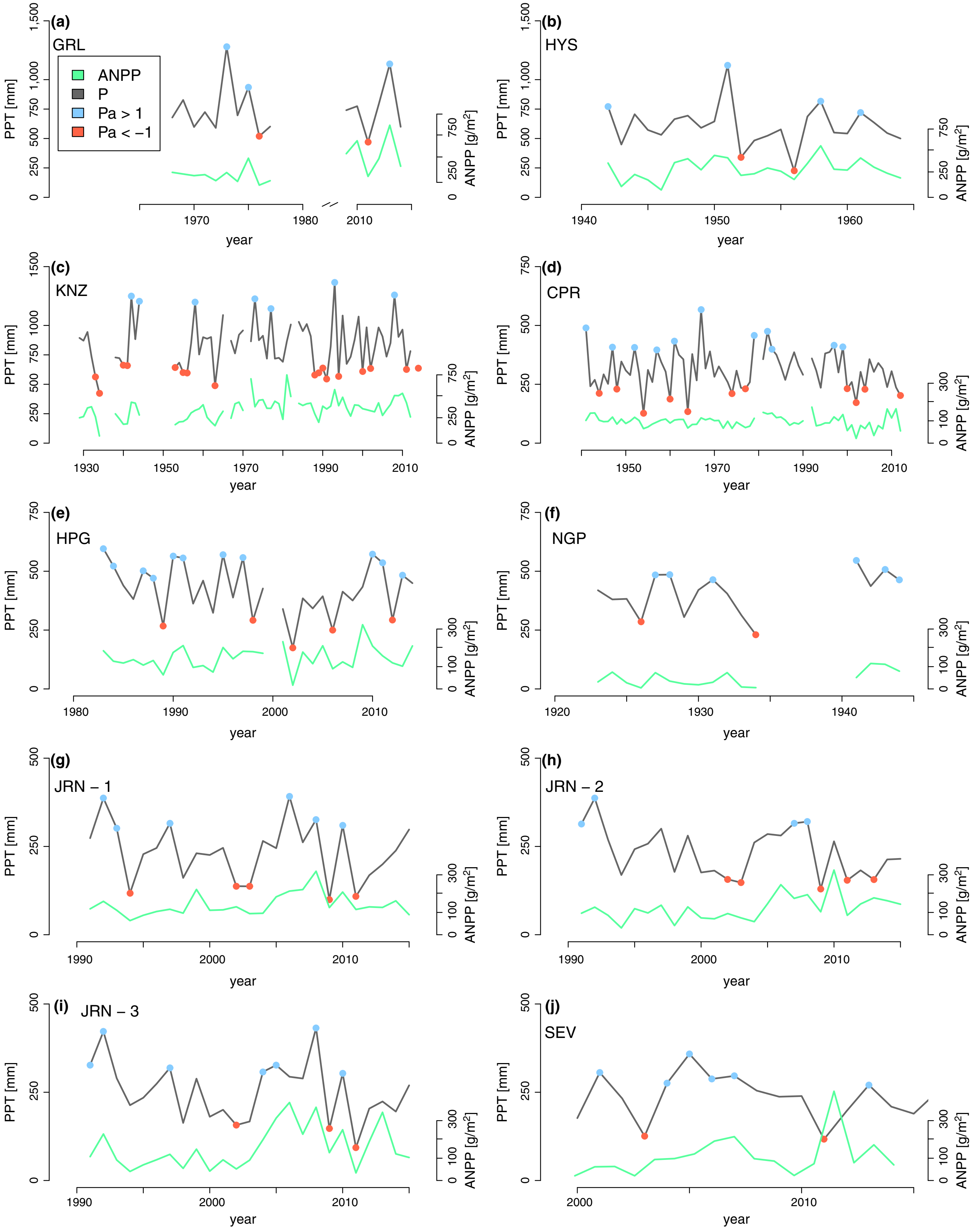

FIGURE 2 Timeseries of water year precipitation [PPT: mm] and aboveground net primary production [ANPP: g/m²] for each grassland site. Water year PPT anomaly [Pa: $(\mathrm{PPT}-\overline{\mathrm{PPT}})/\sigma^2_{\mathrm{PPT}}$]>1.0 is indicated by blue dots, and water year Pa < −1.0 is indicated by red dots. JRN data included three grassland sites [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 1 Site names, affiliations (Long Term Agroecosystem Research (LTAR) and Ecological Research (LTER) Networks) and characteristics

Site Name, Affiliation	ID	Grassland type	Latitude [°N]	Longitude [°W]	Elevation [m]	Regional MAP [mm]	Study MAP [mm]	MAT [°C]	ANPP [g/m^2]	# years	Data range	Data source
Grazing lands Research Laboratory (LTAR)	GRL	MG	35.55	98.04	420	741 ± 187	744 ± 180	15.5	216 ± 79	18	1966–1977 2009–2014	PPT: GRL LTAR ANPP: R5-R8 watersheds 1966–1977 exclosure experiment 2009–2015
Hays Mixed Prairie	HYS	MG	38.86	99.33	600	559 ± 150	606 ± 171	12.0	291 ± 118	24	1941–1964	PPT: Hays, NOAA NCDC ANPP: Hulett and Tomanek (1969)
Konza Prairie (LTER)	KNZ	MG	39.09	96.58	380	826 ± 198	833 ± 201	12.1	354 ± 135	79	1928–2016	PPT: NOAA NCDC 1928–1967 HQ1MET station 1988–2016, KNZ LTER ANPP: FHK sites 1–5 1928–1967 01b site 1984–2016, KNZ LTER
Central Plains Experimental Range (LTAR/LTER)	CPR	SC	40.82	104.75	1,600	312 ± 87	312 ± 87	8.2	96 ± 28	71	1939–2012	PPT: ARS Headquarters 1939–1990 ESA 11 & 12 1983–2012, CPR LTAR ANPP: GI site 1939–1990 ESA site 1983–2012, CPR LTAR
High Plains Grassland (LTAR)	HPG	SC	41.20	104.89	2,100	385 ± 84	421 ± 108	6.0	146 ± 60	32	1982–2014	PPT: HPG LTAR ANPP: CL, CM, CH, HPG LTAR
Northern Great Plains Research Laboratory (LTAR)	NGP	SC	46.77	100.92	590	405 ± 100	393 ± 90	5.5	44 ± 36	17	1920–1944	PPT: Mandan, NOAA NCDC ANPP: NGP LTAR
Jornada Experimental Range (LTAR/LTER)	JRN	SW	32.62	106.74	1,310	232 ± 79	242 ± 84	15.6	137 ± 81	78	1990–2015	PPT: BASN, IBPE, SUMM, JRN LTER ANPP: BASN, IBPE, SUMM, JRN LTER
Sevilleta National Wildlife Refuge (LTER)	SEV	SW	34.35	106.88	1,610	266 ± 106	236 ± 56	11.8	75 ± 43	17	1999–2015	PPT: 5 points, SEV LTER ANPP: 5 points, SEV LTER

Regional mean annual precipitation [MAP: mm] and mean annual temperature [MAT: °C] are values from 1910 to 2014 from the nearest 2–3 United States Historical Climatology Network sites or from local long-term data for CPR and HPG, whereas Study MAP and ANPP are values from each site's study period. A small percentage of years at CPR, KNZ, HPG and NGP do not have available data. Grassland types are mesic (MG), semiarid cool (SC), and semiarid warm (SW).

above-average water years, below-average water years, and all years combined at most grassland sites, yet there was no pattern in these slopes across sites or within grassland types (Figure 3). Comparisons of below-average (Pa < 0) and slightly above-average (Pa $= 0.0$–1.0) water years at individual sites showed that ANPP is significantly lower in water years with even slightly below-average PPT (Pa ~ -0.05 to -1.0) compared to years with average precipitation ($p < .05$).

3.2 | Obj. 2: PPT in above- and below-average years compared to multiyear periods

The majority of water year PPT occurs from March through October in mesic and semiarid cool grasslands (86% and 87%, respectively), and from July through October in semiarid warm grasslands (61%), when the largest increase or decrease in monthly rainfall also occurred (Figure 4). This highlights the importance of both water year PPT and growing season PPT on total ANPP. Generally, growing season and water year PPT exhibit similar anomalies, with the average Pearson's $r = 0.72 \pm 0.28$, with notably lower r values only at SEV, which had data spanning a relatively low number of years (Figure 5). Across all grassland sites, water years that were out of phase with growing season rainfall (one above-average, one below) occurred in only 20% of years, and had a low average Pa of ±0.35. Thus, for these grassland sites, it can be expected that an above-average growing season is of similar relative magnitude to its coinciding water year because it is uncommon for them to be out of phase, and out-of-phase conditions are usually small in magnitude and occur during years with near-average PPT, such that Pa is small (Figure 5). As a result, months with the largest average rainfall magnitude drive differences between above- and below-average growing seasons and water years in nearly every year on record. The proportion of above- and below-average water years was similar over the time periods of our study (55% above the regional average, 45% below-average; Table S1). Both above- and below-average multiyear periods occur frequently in these grasslands; 51% of water years on record were year 2+ of a multiyear above- and below-average period, and 27% of years were year 3+ (Table S1).

3.3 | Obj. 3: Legacy effects and emergent responses on ANPP during above and below-average multiyear periods

Although ANPP was positively correlated to PPT at all grassland sites (Figure 3), we observed variation in ANPP that was higher or lower than water year and growing season PPT would suggest (Figure 5). We hypothesized that these variations in ANPP were due to the legacy effect of prior years, which would— in the context of PPT variability— support higher ANPP as a multiyear above-average period progressed, and would inhibit ANPP in a similar below-average period (see Figure 6b for an example). Yet, we also observed high variation in ANPP within multiyear periods in mesic, semiarid cool, and semiarid warm grassland groupings that was difficult to attribute to any single or group of predictor variables (illustrated for semiarid warm grasslands in Figure 6a). Thus, our hypothesis that ANPP would be lower in later below-average years compared to earlier below-average years with similar Pa (e.g., year 3 ANPP lower than year 2), and would be higher in later above-average years compared to earlier above-average years with similar Pa was refuted, although some multiyear periods did show these patterns.

For all above- and below-average water years and in all above- and below-average growing seasons (Table 2), we found that significant PPT–ANPP and ANPP_{n-1}–ANPP ($n-1$ is prior year) relationships occurred in the highest frequency across grassland groupings. Mesic grasslands had the most frequent significant relationships in both above- and below-average years and seasons, whereas semiarid cool and semiarid warm grasslands had fewer significant relationships, but with steeper slopes (Table 2). Increasing PPT was correlated with a decline in grassland water-use efficiency [WUE: $\text{g m}^{-2}\ \text{mm}^{-1}$]. The results of this initial analysis suggest a diverse set of potential influences on ANPP, especially current-year PPT and prior-year ANPP.

During multiyear below-average periods in mesic grasslands, the frequency of significant PPT–ANPP relationships declined from year 1 to year 3, the legacy effect of prior-year PPT declined from year 1 to year 2, the frequency and slope of significant ANPP_{n-1}–ANPP relationships increased from year 1 to year 2 (Table 3). The frequency and slope of ANPP_{n-1}–ANPP increased from year 1 to year 2 in semiarid cool grasslands, and we only found a single significant relationship for semiarid warm grasslands in below-average year 2 (Table 3). During above-average periods, PPT–ANPP and ANPP_{n-1}–ANPP relationships in mesic grasslands declined from year 1 to year 2, and a positive, emergent response of ANPP_{n-1}–ANPP developed in semiarid cool grasslands from year 1 to year 3 (Table 3). The very high rate of response in semiarid warm grasslands suggests potential strong PPT_{n-1}–ANPP and ANPP_{n-1}–ANPP relationships that emerge after the first and second above-average year, respectively (Table 3). Similar to results in Table 2, the most frequent significant relationships that we found were between PPT–ANPP and ANPP_{n-1}–ANPP, yet the frequency and slope of these relationships varied between sites, and in above- and below-average periods.

4 | DISCUSSION

4.1 | PPT–ANPP relationships in the context of PPT variability

Although current year PPT has a strong influence on ANPP, the different relationships between PPT and ANPP in above- and below-average years suggest there is much variation in ANPP that is not explained by annual or seasonal PPT. Long-term data are more likely to capture a distribution of PPT that includes both above- and below-average extremes that can drive nonlinear relationships with ANPP (Peters et al., 2012), which are not necessarily observed in short-term data. For example, the central grasslands region

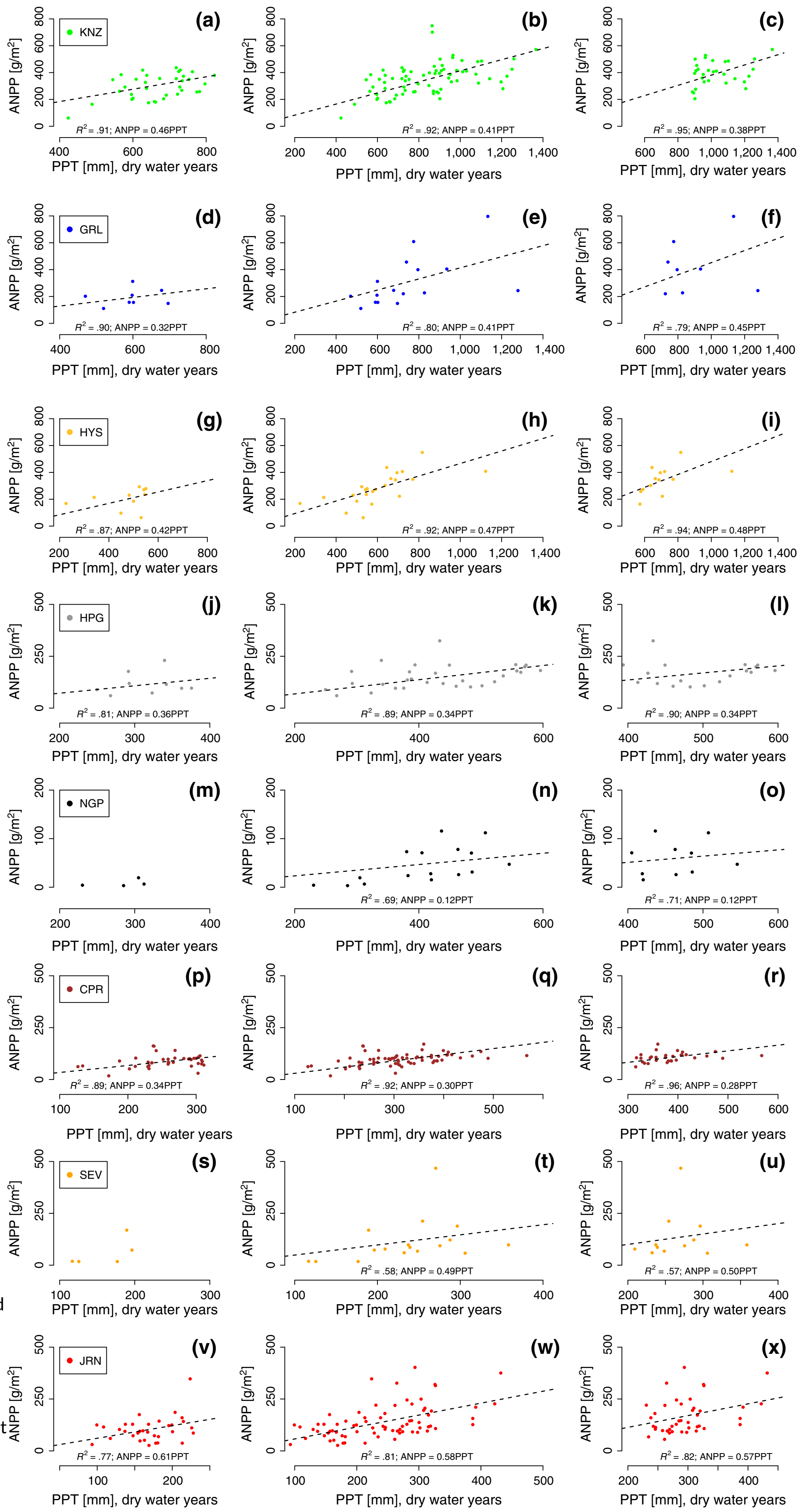

FIGURE 3 Scatterplots of aboveground net primary production [ANPP: g/m^2] and water year precipitation in above-average water years, below-average water years, and all water years for each grassland site. All regressed relationships are significant at $p < .05$, and were forced through zero [Colour figure can be viewed at wileyonlinelibrary.com]

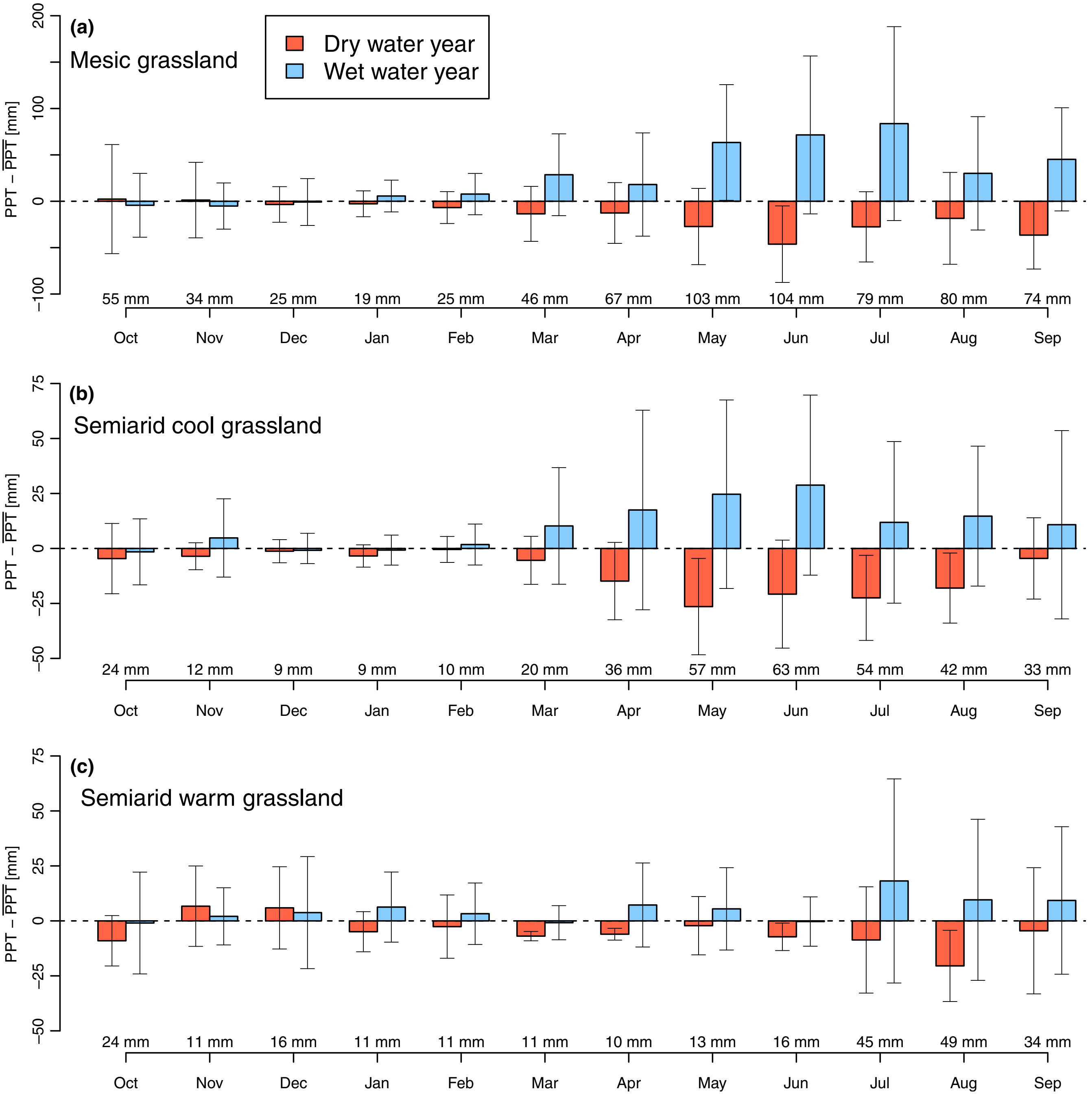

FIGURE 4 Average difference in monthly precipitation ($PPT - \overline{PPT}$) during much drier ($Pa < -1.0$) and much wetter ($Pa > 1.0$) than average average water years for mesic, semiarid cool, and semiarid warm grasslands. Average PPT from long-term site data and US Historical Climatology Network data is shown for each month, and the error bars represent one standard deviation in monthly PPT [Colour figure can be viewed at wileyonlinelibrary.com]

experiences multiyear drought ca. every 20–30 years (1930s, 1950s, 1960s–1970s, and early 2000s) that reduces plant growth and production (e.g., Knapp et al., 2015), and is reflected in long-term data collected across this region, but that may not be part of a qualitative estimate or a short-term sample period.

In general, above-average periods in all grassland types are shorter in duration (3–5 years) than below-average ones (3–10 years), similar to results found in arid grasslands (Peters et al., 2014), and multiyear periods of both type are more frequent than we expected. Multiyear above-average periods of 4+ years are less frequent than below-average periods, but 2+ year above-average periods are more frequent than below-average periods of similar duration. Although these periods are not easy to predict in a temporal sense, their effect on seasonal rainfall patterns was somewhat uniform (the wettest months experienced the greatest deviation in total rainfall), yet the positive effects of above-average conditions on grassland productivity may take longer to be realized compared to negative impacts of below-average conditions (Peters et al., 2014).

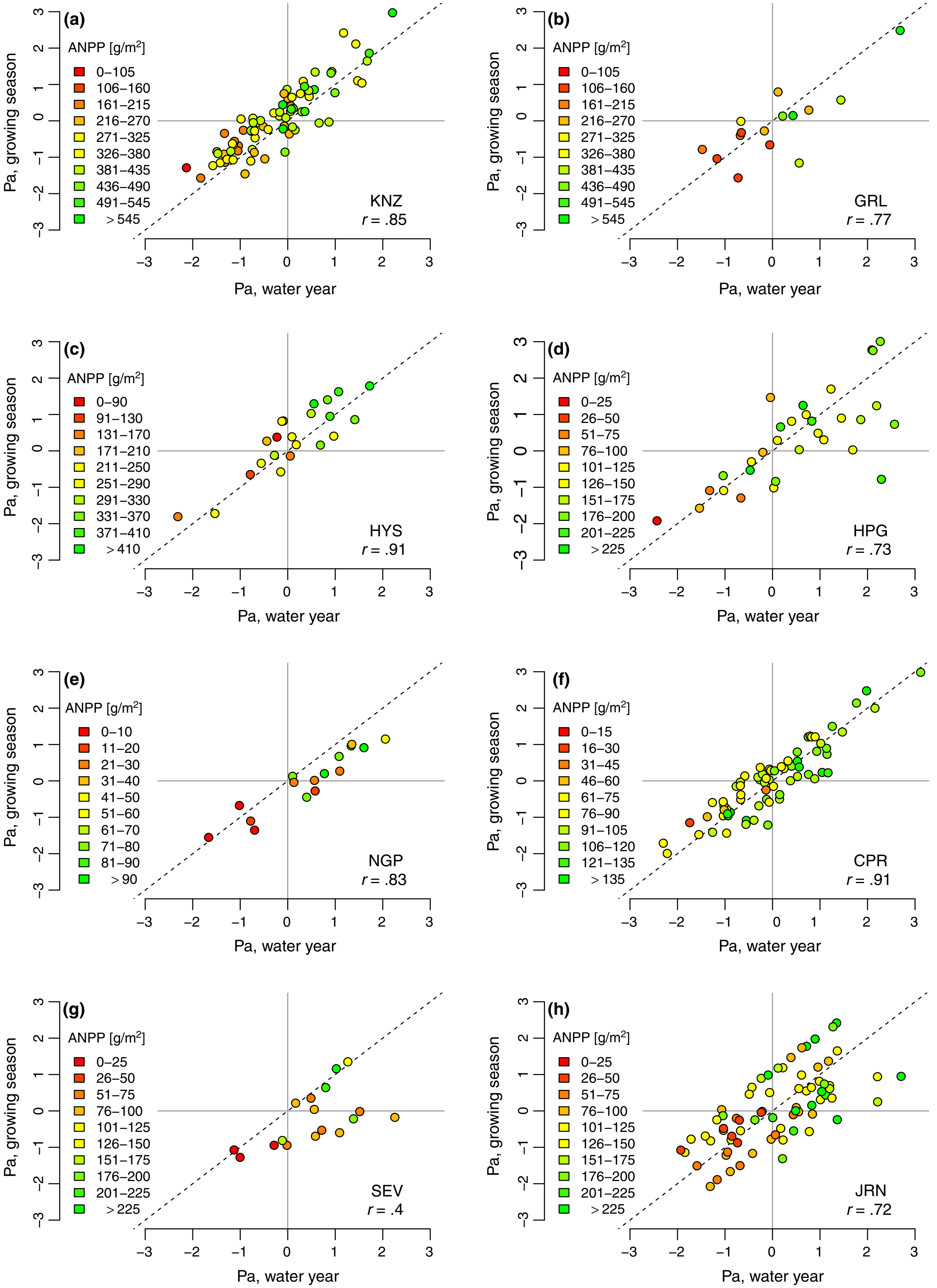

FIGURE 5 Aboveground net primary productivity [ANPP: g/m^2] plotted against water year PPT anomaly [Pa: $(\mathrm{PPT}-\overline{\mathrm{PPT}})/\sigma^2_{\mathrm{PPT}}$] and growing season Pa for each grassland site. Pearson's *r* is provided for each site and is based on the 1:1 line. The ANPP scale differs between sites [Colour figure can be viewed at wileyonlinelibrary.com]

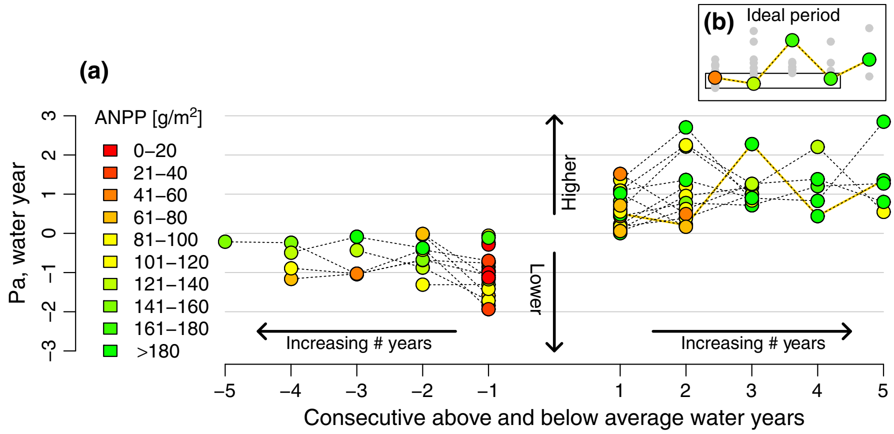

FIGURE 6 Aboveground net primary productivity [ANPP: g/m^2] and water year precipitation anomaly [Pa: $(\mathrm{PPT} - \overline{\mathrm{PPT}})/\sigma^2_{\mathrm{PPT}}$] for multiyear periods of above- and below-average water year precipitation for semiarid warm grasslands (JRN, SEV; Panel a). The dotted lines between points illustrate the temporal trace of Pa and ANPP in each individual period. The inset (Panel b) illustrates an ideal multiyear period of above-average PPT at JRN from 2004 to 2008 that supports our hypothesis, where the area bounded by the rectangle highlights three years with similar PPT, but increasing ANPP with the length of the period [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 2 R^2 correlation statistic and slope of correlation line (in parenthesis) for all above- and below-average water years and growing seasons compared to current and prior-year ($n-1$) conditions for mesic, semiarid cool, and semiarid warm grassland types

Grassland type	ANPP and PPT	WUE and PPT	ANPP and PPT$_{n-1}$	WUE and PPT$_{n-1}$	ANPP and ANPP$_{n-1}$
Below-average water year					
Mesic	0.36 (0.51)	ns	0.07 (0.15)	ns	ns
Semiarid cool	ns	ns	ns	ns	0.08 (0.25)
Semiarid warm	0.12 (0.63)	ns	ns	ns	ns
Below-average growing season					
Mesic	0.21 (0.52)	0.07 ($-8.8e^{-4}$)	0.11 (0.21)	0.06 ($4.5e^{-4}$)	0.11 (0.28)
Semiarid cool	ns	0.20 ($-3.3e^{-3}$)	ns	ns	0.15 (0.33)
Semiarid warm	ns	0.11 ($-7.2e^{-3}$)	ns	ns	ns
Above-average water year					
Mesic	0.09 (0.20)	0.11 ($-2.3e^{-4}$)	ns	ns	0.14 (0.35)
Semiarid cool	0.12 (0.27)	ns	ns	ns	0.20 (0.46)
Semiarid warm	0.09 (0.63)	ns	ns	ns	0.06 (0.31)
Above-average growing season					
Mesic	0.13 (0.37)	ns	ns	ns	0.08 (0.30)
Semiarid cool	ns	0.05 ($-6.9e^{-4}$)	ns	ns	0.17 (0.50)
Semiarid warm	0.15 (0.76)	ns	ns	ns	ns

Prior years include both above- and below-average water years and growing seasons. WUE is water-use efficiency [ANPP/PPT]. To compare legacies to current-year relationships, regressions were not forced through the origin. All reported values are significant at $p < .05$.

Fine-scale, daily to weekly patterns of rainfall play an important role in shaping grassland productivity at some sites as well (Byrne, Lauenroth, & Adler, 2013; Heisler-White et al., 2009). We expect that interannual patterns of grassland productivity are influenced by multiple, site-specific precipitation conditions including the timing of precipitation at daily timescales, the magnitude of precipitation on weekly to monthly to seasonal timescales, the duration of above- and below-average periods of years, and also the pattern and frequency of these periods and the time interval between them.

4.2 | Legacy effects and emergent responses in grasslands

Variation in PPT–ANPP for grassland types and for individual grassland sites portends to influences on grassland ANPP that are not solely captured by year-to-year variation in rainfall, such as legacies. The legacy effects of prior-year conditions on grassland productivity are only beginning to be uncovered and distinguished from additional long-term effects such as grazing (Irisarri et al., 2016), and it is

TABLE 3 Significant relationships between ANPP and current- and prior-year ($n-1$) explanatory variables of PPT and ANPP for each grassland type, summarized for all above- and below-average water years and growing seasons that were part of a multiyear period, for water years and growing seasons that were part of a multiyear period of 2 years in length, and for water years and growing seasons that were part of a multiyear period of 3 years in length

Grassland type, year	ANPP and PPT	ANPP and PPT_{n-1}	ANPP and ANPP_{n-1}
Below-average periods (all, 2-year, 3-year)			
Mesic, $n = 1$	$\frac{5}{6}$ (0.60)	$\frac{2}{6}$ (0.34)	$\frac{1}{6}$ (0.32)
Mesic, $n = 2$	$\frac{2}{6}$ (0.38)	$\frac{2}{6}$ (0.40)	$\frac{2}{6}$ (0.51)
Mesic, $n = 3$	$\frac{1}{2}$ (0.65)	$\frac{0}{2}$	$\frac{0}{2}$
Semiarid cool, $n = 1$	$\frac{0}{4}$	$\frac{0}{4}$	$\frac{2}{4}$ (0.43)
Semiarid cool, $n = 2$	$\frac{0}{4}$	$\frac{0}{4}$	$\frac{3}{4}$ (0.71)
Semiarid warm, $n = 1$	$\frac{0}{4}$	$\frac{0}{4}$	$\frac{0}{4}$
Semiarid warm, $n = 2$	$\frac{0}{4}$	$\frac{1}{4}$ (0.78)	$\frac{0}{4}$
Semiarid warm, $n = 3$	$\frac{0}{2}$	$\frac{0}{2}$	$\frac{0}{2}$
Above-average periods (all, 2-year, 3-year)			
Mesic, $n = 1$	$\frac{4}{4}$ (0.48)	$\frac{0}{4}$	$\frac{2}{4}$ (0.38)
Mesic, $n = 2$	$\frac{1}{4}$ (0.65)	$\frac{0}{4}$	$\frac{0}{4}$
Mesic, $n = 3$	$\frac{0}{1}$	$\frac{0}{1}$	$\frac{0}{1}$
Semiarid cool, $n = 1$	$\frac{1}{6}$ (0.54)	$\frac{0}{6}$	$\frac{1}{6}$ (0.49)
Semiarid cool, $n = 2$	$\frac{0}{6}$	$\frac{1}{6}$ (0.27)	$\frac{6}{6}$ (0.59)
Semiarid cool, $n = 3$	$\frac{2}{4}$ (0.36)	$\frac{0}{4}$	$\frac{2}{4}$ (0.56)
Semiarid warm, $n = 1$	$\frac{0}{6}$	$\frac{0}{6}$	$\frac{1}{6}$ (0.80)
Semiarid warm, $n = 2$	$\frac{0}{6}$	$\frac{1}{6}$ (2.79)	$\frac{0}{6}$
Semiarid warm, $n = 3$	$\frac{0}{2}$	$\frac{0}{2}$	$\frac{1}{2}$ (1.24)

Summary statistics include the proportion of significant relationships for the above periods (up to six total), and the average slope of this relationship. Grassland types and periods that are not shown did not contain enough observations for analysis. To compare legacies to current-year relationships, regressions were not forced through the origin.

not yet clear how they vary across different grassland types and time intervals. For example, Reichmann, Sala and Peters (2013a) found that prior-year density of living grass meristems accounted for as much as 40% of year-to-year variability in ANPP in a Chihuahuan Desert grassland, and Petrie, Collins, and Litvak (2015) found that reductions in nutrient production and meristem density may delay the recovery of grassland ANPP following drought in a similar desert grassland. Conversely, Sternberg et al. (2016) found only weak relationships between nonpeak seasonal grassland productivity and prior-year PPT over two decades in a Mediterranean grassland–shrubland ecosystem. Our results support the prior-year legacy effect of ANPP on productivity in both above- and below-average years for multiple grassland types, and prior-year production was in some cases more important than amount of rainfall following the first year of a multiyear above- or below-average rainfall period. In addition, relationships of ANPP to current year PPT and prior-year legacies changed throughout sequences of above- and below-average years, and new emergent responses that both supported and limited ANPP became significant. Changing legacy and emergent responses during multiyear periods indicates a shift in grassland responsiveness to external drivers that may explain some of the variability observed in PPT–ANPP relationships, and we propose that further site-based research on the legacy effect of productivity is warranted.

4.3 | Climate, ecological boundaries, and multiyear above- and below-average periods

Climate change projections for North America call for slightly reduced annual PPT in the southwestern and southern grasslands region, and slightly higher annual PPT in the central and northern grasslands (IPCC, 2013; Taylor, de Jeu, Guichard, Harris, & Dorigo, 2012), which are expected to have different effects on plant production in these regions. In addition, model simulations suggest that the occurrence of multiseason below-average rainfall periods may increase (Greene & Seager, 2016), and increasing evaporative demand is expected to increase aridity even if annual PPT does not decline (IPCC, 2013). In this context, we found that the decline in PPT required to significantly decrease ANPP is most likely to occur only during specific months that already experience relatively high rainfall— from March through October in mesic and semiarid cool grasslands, and from July through October in semiarid warm grasslands. Increasing average aridity or increased frequency of isolated below-average years may not be ecologically meaningful, however, as grasslands do not often experience degradation due to variability in climate forcings alone, even if their productivity declines (Collins et al., 2017; Hoover, Knapp, & Smith, 2014; Yao, Peters, Havstad, Gibbens, & Herrick, 2006). Instead, we hypothesize that should such climate conditions occur, the true risk of precipitation-associated climate change in grasslands lies in persistent changes to monthly rainfall that combine to change the frequency and duration of above- and below-average sequences of years, and especially in cases where these changes constitute an increase in precipitation-driven extreme events compared to historical conditions. Our results suggest that above- and below-average periods alter the relationships that govern grassland productivity, from PPT sensitivity to the potentially compounding influence of prior-year ANPP. Thus, an alteration in the frequency, magnitude, and duration of above- and below-average periods would likely instigate a shift in the relationships governing grassland productivity, and in doing so could potentially impose changes in grassland vulnerability to climate in ways that are not fully clear.

Ecosystems are most responsive to external forcings at their geographic boundary, where the local climate conditions may be less favorable for their persistence (Allen & Breshears, 1998; Gosz, 1993). For example, both semiarid warm grasslands and mesic grasslands— which exist at opposite ends of low and high annual PPT in grasslands, respectively— are vulnerable to encroachment by woody plant species and the ecological transition of grasslands to shrublands. This transition results from long-term livestock overgrazing and multiyear drought in arid grasslands (Bestelmeyer et al., 2011), compared to high PPT and reduced incidence of fire in mesic grasslands (Briggs et al., 2005; Knapp et al., 2008). An increase in the frequency of multiyear above- and below-average periods would increase the probability that these periods co-occur with additional site-specific factors and land management decisions, potentially increasing grassland vulnerability to degradation and ecological transitions (Ratajczak et al., 2017). In semiarid warm grasslands, an increase in the number or length of below-average periods would likely increase their vulnerability to desertification, which requires sustained drought combined with additional disturbances such as fire and soil erosion (Moreno-de las Heras, Turnbull, & Wainwright, 2016; Peters, Herrick, Monger, & Huang, 2010; Van Auken, 2009). Conversely, multiyear above-average periods in semiarid warm grasslands promote rapid grass recovery from disturbance and higher productivity that may be sustained for multiple years, thus increasing grass cover and limiting shrub expansion (Drewa, Peters, & Havstad, 2006; Peters et al., 2012). In mesic grasslands, an increase in the frequency of above- and below-average periods could facilitate invasion by woody plant species by supporting their clonal expansion in the case of above-average conditions, and by decreasing fire frequency (Briggs et al., 2005; Ratajczak, Nippert, & Collins, 2012). Conversely, higher levels of precipitation may not cause changes in the composition of herbaceous vegetation unless sustained over multiyear to decadal time periods (Collins et al., 2012; Knapp, Briggs, & Smith, 2012), and it is unclear to what degree and over what time periods nutrient availability may be altered by changes in the rainfall regime across the grasslands of our study (Wilcox et al., 2016). Legacy effects were not observed in below-average years in semiarid warm grasslands and these effects declined over multiple above-average years in mesic grasslands. We postulate that these declines in legacies occurred because these climatic conditions fall outside the normal range of grassland functioning. Therefore, for semiarid warm and mesic grasslands specifically, an increase in the frequency of multiyear above- and below-average periods may constitute a shift away from the climatic conditions that favor their persistence. Although below-average rainfall periods and loss of productivity may increase grassland vulnerability to other factors, such as woody plant encroachment, the effects of multiyear above-average periods are likely to be positive in degraded arid ecosystems and provide opportunities for grass recovery (Peters et al., 2012), but additional factors may influence more mesic grassland communities under similar above-average conditions.

5 | CONCLUSIONS

We used a unique set of long-term observations of ANPP and PPT from eight grassland sites to examine relationships between these variables during multiyear above- or below-average PPT periods throughout the central grasslands region, and to investigate variability in ANPP responses to above- and below-average PPT for mesic, semiarid cool, and semiarid warm grassland types. We found differences in PPT–ANPP relationships in above- and below-average years, and especially variation in ANPP not explained by PPT totals that likely are attributed to legacy effects. The correlation between ANPP and current- and prior-year conditions changed from year to year throughout multiyear periods, with some legacy effects declining, and new responses emerging. Most importantly, the influence of prior-year ANPP often increased with the length of both above- and below-average multiyear periods, whereas the influence of the amount of current-year PPT declined. Multiyear periods occurred more frequently at these sites than we expected (~51% of years), and the distribution of monthly and seasonal PPT was relatively uniform in wet and dry years. This suggests that these periods are frequent, have multiyear effects, and may explain some of the variability observed in PPT–ANPP relationships. Although it is not fully clear how a directional change in the frequency of above- and below-average years could impose a persistent change in grassland ANPP, our results emphasize the importance of legacy effects on productivity for sequences of above- vs. below-average years.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

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REFERENCES

Allen, C., & Breshears, D. (1998). Drought-induced shift of a forest-woodland ecotone: Rapid landscape response to climate variation. *Proceedings of the National Academy of Sciences of the United States of America*, *95*, 14839–14842. https://doi.org/10.1073/pnas.95.25.14839

Anderson, J., Ellis, M., von Dohlen, C., & Romme, W. (2004). *After the fires: Establishment, growth, and survival of lodgepole pine in the first decade*. New Haven, CT: Yale University Press.

Angert, A., Biraud, S., Bonfils, C., Henning, C. C., Buermann, W., Pinzon, J., . . . Fung, I. (2005). Drier summers cancel out the CO_2 uptake enhancement induced by warmer springs. *PNAS*, *102*(31), 10823–10827. https://doi.org/10.1073/pnas.0501647102

Bestelmeyer, B. T., Ellison, A. M., Fraser, W. R., Gorman, K. B., Holbrook, S. J., Laney, C. M., . . . Schmitt, R. (2011). Analysis of abrupt transitions in ecological systems. *Ecosphere*, *2*, 1–26. https://doi.org/10.1890/es11−00216.1

Briggs, J., Knapp, A., Blair, J., Heisler, J., Hoch, G., Lett, M., & McCarron, J. (2005). An ecosystem in transition: Causes and consequences of the conversion of mesic grassland to shrubland. *BioScience*, *55*, 243–254. https://doi.org/10.1641/0006-3568(2005) 055[0243:AEITCA]2.0.CO;2

Buis, G. M., Blair, J. M., Burkepile, D. E., Burns, C. E., Chamberlain, A. J., Chapman, P. L., . . . Smith, M. D. (2009). Controls of aboveground net primary productivity in mesic savanna grasslands: An inter-hemispheric comparison. *Ecosystems*, *12*, 982–995. https://doi.org/10.1007/s10021−009−9273−1

Byrne, K. M., Lauenroth, W. K., & Adler, P. B. (2013). Contrasting effects of precipitation manipulations on production in two sites within the central grassland region, USA. *Ecosystems*, *16*, 1039–1051. https://doi.org/10.1007/s10021-013-9666-z

Collins, S. L., Belnap, J., Grimm, N. B., Rudgers, J. A., Dahm, C. N., D'odorico, P., . . . Sinsabaugh, R. L. (2014). A multi-scale, hierarchical model of pulse dynamics in aridland ecosystems. *Annual Review of Ecology, Evolution and Systematics*, *45*, 397–419. https://doi.org/10.1146/annurev−ecolsys−120213−091650

Collins, S. L., Fargione, J. E., Crenshaw, C. L., Nonaka, E., Elliott, J. R., Xia, Y., & Pockman, W. T. (2010). Rapid plant community responses during the summer monsoon to nighttime warming in a northern Chihuahuan Desert grassland. *Journal of Arid Environments*, *74*, 611–617. https://doi.org/10.1016/j.jaridenv.2009.10.005

Collins, S. L., Koerner, S. E., Plaut, J. A., Okie, J. G., Brese, D., Calabrese, L. B., . . . Nonaka, E. (2012). Stability of tallgrass prairie during a 19-year increase in growing season precipitation. *Functional Ecology*, *26*, 1450–1459. https://doi.org/10.1111/j.1365−2435.2012.01995.x

Collins, S., Rudgers, J., Chung, Y., Maurer, G., Moore, D., & Muldavin, E. (2017). Climate sensitivity functions and net primary productivity: A framework for incorporating climate mean and variability. *Ecology*, in press. https://doi.org/10.1002/ecy.2136

Drewa, P., Peters, D., & Havstad, K. (2006). Population and clonal level responses of a perennial grass following fire in the northern Chihuahuan Desert. *Oecologia*, *150*, 29–39. https://doi.org/10.1007/s00442-006-0502-4

Easterling, D., Meehl, G., Parmesan, C., Changnon, S., Karl, T., & Mearns, L. (2000). Climate extremes: Observations, modeling, and impacts. *Science*, *289*, 2068–2074. https://doi.org/10.1126/science.289.5487.2068

Fierer, N., & Schimel, J. (2002). Effects of drying-rewetting frequency on soil carbon and nitrogen transformations. *Soil Biology & Biochemistry*, *34*, 777–787. https://doi.org/10.1016/S0038-0717(02)00007-X

Flanagan, L., & Adkinson, A. (2011). Interacting controls on productivity in a northern Great Plains grassland and implications for response to ENSO events. *Global Change Biology*, *17*, 3293–3311. https://doi.org/10.1111/j.1365-2486.2011.02461.x

Gang, C., Zhou, W., Wang, Z., Chen, Y., Li, J., Chen, J., . . . Groisman, P. Y. (2015). Comparative assessment of grassland NPP dynamics in response to climate change in China, North America, Europe and Australia from 1981 to 2010. *Journal of Agronomy and Crop Science*, *201*, 57–68. https://doi.org/10.1111/jac.12088

Gherardi, L., & Sala, O. (2015). Enhanced interannual precipitation variability increases plant functional diversity that in turn ameliorates negative impact on productivity. *Ecology Letters*, *18*, 1293–1300. https://doi.org/10.1111/ele.12523

Gosz, J. R. (1993). Ecotone hierarchies. *Ecological Applications*, *3*, 369–376. https://doi.org/10.2307/1941905

Greene, A., & Seager, R. (2016). Categorical representation of North American precipitation projections. *Scientific Reports*, *6*, 23888. https://doi.org/10.1038/srep23888

Gutzler, D., & Robbins, T. (2011). Climate variability and projected change in the western United States: Regional downscaling and drought statistics. *Climate Dynamics*, *37*, 835–849. https://doi.org/10.1007/s00,382-010-0838-7

Heisler-White, J. L., Blair, J. M., Kelly, E. F., Harmoney, K., & Knapp, A. K. (2009). Contingent productivity responses to more extreme rainfall regimes across a grassland biome. *Global Change Biology*, *15*, 2894–2904. https://doi.org/10.1111/j.1365-2486.2009.01961.x

Hermance, J., Sulieman, H., & Mustafa, A. (2016). Predicting intra-seasonal fluctuations of NDVI phenology from daily rainfall in the East Sahel: A simple linear reservoir model. *International Journal of Remote Sensing*, *37*, 3293–3321. https://doi.org/10.1080/01431161.2016.1196841

Hoover, D., Knapp, A., & Smith, M. (2014). Resistance and resilience of a grassland ecosystem to climate extremes. *Ecology*, *95*, 2646–2656. https://doi.org/10.1890/13-2186.1

Hoover, D., & Rogers, B. (2016). Not all droughts are created equal: The impacts of interannual drought pattern and magnitude on grassland carbon cycling. *Global Change Biology*, *22*, 1809–1820. https://doi.org/10.1111/gcb.13161

Hufkens, K., Keenan, T. F., Flanagan, L. B., Scott, R. L., Bernacchi, C. J., Joo, E., . . . Richardson, A. D. (2016). Productivity of North American grasslands is increased under future climate scenarios despite rising aridity. *Nature Climate Change*, *6*, 710–714. https://doi.org/10.1038/nclimate2942

Hulett, G., & Tomanek, G. (1969). Forage production on a clay upland range site in western Kansas. *Journal of Range Management*, *22*, 270–276. https://doi.org/10.2307/3895931

IPCC (2013). *Climate change 2013: I. The physical science basis*, London, UK: Cambridge University Press.

Irisarri, J. N. G., Derner, J., Porensky, L., Augustine, D., Reeves, J., & Mueller, K. (2016). Grazing intensity differentially regulates ANPP response to precipitation in North American semiarid grasslands. *Ecological Applications*, *26*, 1370–1380. https://doi.org/10.1890/15−1332

Jones, S., Collins, S., Blair, J., Smith, M., & Knapp, A. (2016). Altered rainfall patterns increase forb abundance and richness in native tallgrass prairie. *Scientific Reports*, *6*, 20120. https://doi.org/10.1038/srep20120

Knapp, A. K., Briggs, J. M., Collins, S. L., Archer, S. R., Bret-Harte, M. S., Ewers, B. E., ... Cleary, M. B. (2008). Shrub encroachment in North American grasslands: Shifts in growth from dominance rapidly alters control of ecosystem carbon inputs. *Global Change Biology*, *14*, 615–623. https://doi.org/10.1111/j.1365–2486.2007.01512.x

Knapp, A., Briggs, J., & Koelliker, J. (2001). Frequency and extent of water limitation to primary production in a mesic temperate grassland. *Ecosystems*, *4*, 19–28. https://doi.org/10.1007/s100210000057

Knapp, A., Briggs, J., & Smith, M. (2012). Community stability does not preclude ecosystem sensitivity to chronic resource alteration. *Functional Ecology*, *26*, 1231–1233. https://doi.org/10.1111/j.1365-2435.2012.02053.x

Knapp, A., Carroll, C., Denton, E., La Pierre, K., Collins, S., & Smith, M. (2015). Differential sensitivity to regional-scale drought in six central US grasslands. *Oecologia*, *177*, 949–957. https://doi.org/10.1007/s00442-015-3233-6

Knapp, A., Ciais, P., & Smith, M. (2016). Reconciling inconsistencies in precipitation-productivity relationships: Implications for climate change. *New Phytologist*, *214*, 41–47. https://doi.org/10.1111/nph.14381

Lauenroth, W., Burke, I., & Gutmann, M. (1999). The structure and function of ecosystems in the central North American grassland region. *Great Plains Research*, *9*, 223–259.

Lauenroth, W., & Sala, O. (1992). Long-term forage production of North-American shortgrass steppe. *Ecological Applications*, *2*, 397–403. https://doi.org/10.2307/1941874

Liang, W., Lü, Y., Zhang, W., Li, S., Jin, Z., Ciais, P., ... Su, H. (2017). Grassland gross carbon dioxide uptake based on an improved model tree ensemble approach considering human interventions: Global estimation and covariation with climate. *Global Change Biology*, *23*, 2720–2742. https://doi.org/10.1111/gcb.13592

McCulley, R. L., Burke, I. C., & Lauenroth, W. K. (2009). Conservation of nitrogen increases with precipitation across a major grassland gradient in the Central Great Plains of North America. *Oecologia*, *159*, 571–581. https://doi.org/10.1007/s00442-008-1229-1

Mendez-Barroso, L. A., Vivoni, E. R., Watts, C. J., & Rodriguez, J. C. (2009). Seasonal and interannual relations between precipitation, surface soil moisture and vegetation dynamics in the North American monsoon region. *Journal of Hydrology*, *377*, 59–70. https://doi.org/10.1016/j.jhydrol.2009.08.009

Moreno-de las Heras, M., Turnbull, L., & Wainwright, J. (2016). Seed-bank structure and plant-recruitment conditions regulate the dynamics of a grassland-shrubland Chihuahuan ecotone. *Ecology*, *97*, 2303–2318. https://doi.org/10.1002/ecy.1446

Mueller, K. E., Blumenthal, D. M., Pendall, E., Carrillo, Y., Dijkstra, F. A., Williams, D. G., ... Morgan, J. A. (2016). Impacts of warming and elevated CO_2 on a semi-arid grassland are non-additive, shift with precipitation, and reverse over time. *Ecology Letters*, *19*, 956–966. https://doi.org/10.1111/ele.12634

Nippert, J., Knapp, A., & Briggs, J. (2006). Intra-annual rainfall variability and grassland productivity: Can the past predict the future? *Plant Ecology*, *184*, 65–74. https://doi.org/10.1007/s11258-005-9052-9

Peters, D., Groffman, P., Nadelhoffer, K., Grimm, N., Collins, S., Michener, W., & Huston, M. (2008). Living in an increasingly connected world: A framework for continental-scale environmental science. *Frontiers in Ecology and the Environment*, *6*, 229–237. https://doi.org/10.1890/070098

Peters, D., Havstad, K., Archer, S., & Sala, O. (2015). Beyond desertification: New paradigms for dryland landscapes. *Frontiers in Ecology and the Environment*, *13*, 4–12. https://doi.org/10.1890/140276

Peters, D., Herrick, J., Monger, H., & Huang, H. (2010). Soil-vegetation-climate interactions in arid landscapes: Effects of the North American monsoon on grass recruitment. *Journal of Arid Environments*, *74*, 618–623. https://doi.org/10.1016/j.jaridenv.2009.09.015

Peters, D., Yao, J., Browning, D., & Rango, A. (2014). Mechanisms of grass response in grasslands and shrublands during dry or wet periods. *Oecologia*, *174*, 1323–1334. https://doi.org/10.1007/s00442-013-2837-y

Peters, D., Yao, J., & Gosz, J. (2006). Woody plant invasion at a semi-arid/arid transition zone: Importance of ecosystem type to colonization and patch expansion. *Journal of Vegetation Science*, *17*, 389–396. https://doi.org/10.1111/j.1654-1103.2006.tb02459.x

Peters, D., Yao, J., Sala, O., & Anderson, J. (2012). Directional climate change and potential reversal of desertification in arid and semiarid ecosystems. *Global Change Biology*, *18*, 151–163. https://doi.org/10.1111/j.1365-2486.2011.02498.x

Petrie, M. D., Brunsell, N. A., & Nippert, J. B. (2012). Climate change alters growing season flux dynamics in mesic grasslands. *Theoretical and Applied Climatology*, *107*, 427–440. https://doi.org/10.1007/s00704-011-0484-y

Petrie, M. D., Brunsell, N. A., Vargas, R., Collins, S. L., Flanagan, L. B., Hanan, N. P., ... Suyker, A. E. (2016). The sensitivity of carbon exchanges in Great Plains grasslands to precipitation variability. *Journal of Geophysical Research: Biogeosciences*, *121*, 280–294. https://doi.org/10.1002/2015jg003205

Petrie, M. D., Collins, S. L., & Litvak, M. E. (2015). The ecological role of small rainfall events in a desert grassland. *Ecohydrology*, *8*, 1614–1622. https://doi.org/10.1002/eco.1614

R Development Core Team (2016). *R: A language and environment for statistical computing*, Vienna, Austria: R Foundation for Statistical Computing, pp. ISBN 3–900051–07–0, http://www.R–project.org

Ratajczak, Z., D'Odorico, P., Collins, S., Bestelmeyer, B., Isbell, F., & Nippert, J. (2017). The interactive effects of press/pulse intensity and duration on regime shifts at multiple scales. *Ecological Monographs*, *87*, 198–218. https://doi.org/10.1002/ecm.1249

Ratajczak, Z., Nippert, J. B., & Collins, S. L. (2012). Woody encroachment decreases diversity across North American grasslands and savannas. *Ecology*, *93*, 697–703. https://doi.org/10.1890/11-1199.1

Reichmann, L., & Sala, O. (2014). Differential sensitivities of grassland structural components to changes in precipitation mediate productivity response in a desert ecosystem. *Functional Ecology*, *28*, 1292–1298. https://doi.org/10.1111/1365-2435.12265

Reichmann, L. G., Sala, O. E., & Peters, D. P. C. (2013a). Precipitation legacies in desert grassland primary production occur through previous-year tiller density. *Ecology*, *94*, 435–443. https://doi.org/10.1890/12-1237.1

Reichmann, L. G., Sala, O. E., & Peters, D. P. C. (2013b). Water controls on nitrogen transformations and stocks in an arid ecosystem. *Ecosphere*, *4*, 1–17. https://doi.org/10.1890/ES12-00263.1

Sala, O., Gherardi, L., Reichmann, L., Jobbagy, E., & Peters, D. (2012). Legacies of precipitation fluctuations on primary production: Theory and data synthesis. *Philosophical Transactions of the Royal Society B-Biological Sciences*, *367*, 3135–3144. https://doi.org/10.1098/rstb.2011.0347

Seastedt, T., & Knapp, A. (1993). Consequences of nonequilibrium resource availability across multiple time scales – The transient maxima hypothesis. *American Naturalist*, *141*, 621–633. https://doi.org/10.1086/285494

Sternberg, M., Golodets, C., Gutman, M., Perevolotsky, A., Kigel, J., & Henkin, Z. (2016). No precipitation legacy effects on above-ground net primary production and species diversity in grazed Mediterranean grassland: A 21-year experiment. *Journal of Vegetation Science*, *28*, 1–10. https://doi.org/10.1111/jvs.12478

Taylor, C. M., de Jeu, R. A. M., Guichard, F., Harris, P. P., & Dorigo, W. A. (2012). Afternoon rain more likely over drier soils. *Nature*, *489*, 423–426. https://doi.org/10.1038/nature11377

Van Auken, O. W. (2009). Causes and consequences of woody plant encroachment into western North American grasslands. *Journal of*

Environmental Management, *90*, 2931–2942. https://doi.org/10.1016/j.jenvman.2009.04.023

Vermeire, L., Heitschmidt, R., & Rinella, M. (2009). Primary productivity and precipitation-use efficiency in mixed-grass prairie: A comparison of northern and southern US sites. *Rangeland Ecology & Management*, *62*, 230–239. https://doi.org/10.2111/07-140R2.1

Weaver, J., & Albertson, F. (1936). Effects of the great drought on the prairies of Iowa, Nebraska, and Kansas. *Ecology*, *17*, 567–639. https://doi.org/10.2307/1932761

Wever, L., Flanagan, L., & Carlson, P. (2002). Seasonal and interannual variation in evapotranspiration, energy balance and surface conductance in a northern temperate grassland. *Agricultural and Forest Meteorology*, *112*, 31–49. https://doi.org/10.1016/S0168-1923(02)00041-2

Wilcox, K., Blair, J., Smith, M., & Knapp, A. (2016). Does ecosystem sensitivity to precipitation at the site-level conform to regional-scale predictions? *Ecology*, *97*, 561–568. https://doi.org/10.1890/15-1437.1

Williams, A. P., Allen, C. D., Macalady, A. K., Griffin, D., Woodhouse, C. A., Meko, D. M., … Dean, J. S. (2013). Temperature as a potent driver of regional forest drought stress and tree mortality. *Nature Climate Change*, *3*, 292–297. https://doi.org/10.1038/nclimate1693

Yahdjian, L., & Sala, O. E. (2010). Size of Precipitation Pulses Controls Nitrogen Transformation and Losses in an Arid Patagonian Ecosystem. *Ecosystems*, *13*, 575–585. https://doi.org/10.1007/s10021-010-9341-6

Yao, J., Peters, D., Havstad, M., Gibbens, R., & Herrick, J. (2006). Multiscale factors and long-term responses of Chihuahuan Desert grasses to drought. *Landscape Ecology*, *21*, 1217–1231. https://doi.org/10.1007/s10980-006-0025-8

Zhang, L., Wylie, B., Ji, L., Gilmanov, T., & Tieszen, L. (2010). Climate-driven interannual variability in net ecosystem exchange in the northern great plains grasslands. *Rangeland Ecology & Management*, *63*, 40–50. https://doi.org/10.2111/08-232.1

Zhang, L., Wylie, B., Ji, L., Gilmanov, T., Tieszen, L., & Howard, D. (2011). Upscaling carbon fluxes over the Great Plains grasslands: Sinks and sources. *Journal of Geophysical Research — Biogeosciences*, *116*, 1–13. https://doi.org/10.1029/2010JG001504

Zhu, K., Chiariello, N., Tobeck, T., Fukami, T., & Field, C. (2016). Nonlinear, interacting responses to climate limit grassland production under global change. *Proceedings of the National Academy of Sciences of the United States of America*, *113*, 10589–10594. https://doi.org/10.1073/pnas.1606734113

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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