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Sensitivity of productivity to precipitation amount and pattern varies by topographic position in a semiarid grassland

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Abstract. Aboveground net primary productivity (ANPP) in grasslands is an important integrator of terrestrial ecosystem function, a key driver of global biogeochemical cycles, and a critical source of food for wild and domesticated herbivores. ANPP exhibits high spatial and temporal variability, driven by a suite of factors including precipitation amount and pattern, biotic and abiotic legacies, and topographic heterogeneity. Global climate models forecast an altered hydrological cycle due to climate change, including higher precipitation variability and more extreme events, which may further increase spatiotemporal variability in ANPP. Therefore, it is essential to understand the sensitivity of this central ecosystem function to various precipitation metrics, legacies, and topographic positions to better inform sustainable grassland management. In this study, we analyzed long-term (36-yr) ANPP data collected across a topographic sequence in the semiarid shortgrass steppe of North America to examine patterns and drivers of spatiotemporal variability in ANPP. We observed that (1) ANPP varied substantially by topographic position, with greater divergence during years with high production, (2) ANPP variability was higher temporally (16-fold maximum difference across years) than spatially (4-fold maximum difference across topographic positions), (3) warm-season perennial grasses were the dominant plant functional type across all topographic positions and strongly influenced total ANPP dynamics, and (4) ANPP had strong sensitivities to current year precipitation amount and pattern that varied by plant functional type, as well as weaker sensitivities to precipitation and productivity legacies. Overall, the lowest topographic position had the highest sensitivity to precipitation, likely due to higher resource availability via the downhill movement of water and nutrients during years with high precipitation and large rainfall events. These results suggest that temporal and spatial ANPP variability in shortgrass steppe is primarily driven by the combined effects of precipitation amount and pattern during the current year, with the dominant warm-season perennial grasses governing these responses.

Key words: aboveground net primary production; legacies; precipitation; semiarid grassland; topography.

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INTRODUCTION

Aboveground net primary production (ANPP) is one of the main components of the carbon cycle, a major input of nutrition and energy into ecosystems, and a key indicator of ecosystem function (McNaughton et al. 1989, Scurlock et al. 1999). In grasslands, which cover 41% of the terrestrial land surface (White et al. 2000), ANPP is also the main source of forage for native herbivores and domesticated livestock (McNaughton et al. 1989, Haberl et al. 2007, Milchunas et al. 2008), provides habitat for other grassland fauna (Samson and Knopf 1996, Augustine and Derner 2015), and has global ecological and socioeconomic importance. ANPP has high spatiotemporal variability, driven largely by variation in precipitation, which results in two classic precipitation-ANPP models: temporal models derived from ANPP dynamics at individual locations over time, and spatial models relating ANPP to temporally averaged precipitation variation across broad geographic regions (Lauenroth and Sala 1992, Knapp et al. 2002, Nippert et al. 2006, Petrie et al. 2018, Maurer et al. 2020). To date, much less attention has been paid to understanding spatial variability within a given region or site, despite evidence that such variability is likely significant and site-specific (Milchunas et al. 1989, Briggs and Knapp 1995, Nippert et al. 2011, Stephenson et al. 2019). Global climate models forecast an increase in both precipitation variability and extremes (e.g., droughts and deluges; IPCC 2013), which may further increase ANPP variability (Hsu and Adler 2014). To predict how grassland ecosystems will respond to a more variable climate, we need to understand patterns and drivers of spatial and temporal variability in ANPP at finer spatial scales.

Grassland ANPP is highly sensitive to current year precipitation amount and pattern. At broad, regional spatial scales, ANPP is strongly correlated with mean annual precipitation (Lauenroth and Dodd 1979, Sala et al. 1988, Hsu et al. 2012, Knapp et al. 2017). For example, across the North American Great Plains, differences in mean annual precipitation can explain 90% of the variation in ANPP (Sala et al. 1988). In addition to precipitation means, ANPP is highly sensitive to extreme dry and wet years, though the responses are not always symmetrical (Knapp et al. 2017, Wilcox 2017). ANPP is also sensitive to inter- and intra-annual precipitation patterns (Milchunas et al. 1994, Knapp et al. 2002, Nippert et al. 2006, Heisler-White et al. 2008, Petrie et al. 2018, Gherardi and Sala 2019). For example, increased interannual variability in precipitation over six years reduced grass productivity by 81% in a desert grassland (Gherardi and Sala 2015). Changes in the magnitude and pattern of precipitation events within a year can also have large effects on ANPP due to changes in soil moisture availability and timing (Milchunas et al. 1994, Knapp et al. 2002, Nippert et al. 2006, Heisler-White et al. 2008, 2009).

Although current year precipitation is a major driver of grassland ANPP, biotic or abiotic legacies of prior year conditions can also have a significant effect on productivity (Sala et al. 2012, Petrie et al. 2018). In a semiarid grassland, while 39% of interannual variation in ANPP was linked to current year precipitation (Lauenroth and Sala 1992), up to one third of the unexplained variation was correlated to prior year ANPP (Oesterheld et al. 2001). Abiotic legacies, such as prior year precipitation, may influence ANPP directly through soil moisture carryover (Sherry et al. 2008, 2012, Bisigato et al. 2013), or indirectly through biotic legacies (Paruelo et al. 1999, Sala et al. 2012, Reichmann et al. 2013). Such biotic legacies can be shaped by changes in individual plants (e.g., tillers, stolons, or axillary buds; Reichmann and Sala 2014, Ott et al. 2019), or shifts in the plant community (e.g., mortality, community reordering; Smith 2011, Hoover et al. 2014). Thus, to accurately understand spatiotemporal dynamics of ANPP, it is important to account for the potential influence of such legacies.

Along with temporal variability, ANPP can vary spatially due to local topographic heterogeneity. Large over- or under-estimates of landscape-level ANPP can occur when topography is not accounted for properly (Nippert et al. 2011, Stephenson et al. 2019). In grasslands with significant topographic variation, ANPP tends to increase downhill, with the highest productivity often in the lowest topographic position (Briggs and Knapp 1995, Bork et al. 2001, Nippert et al. 2011, Stephenson et al. 2019). Previous research suggests topographic position may affect ANPP through several mechanisms (Schimel et al. 1985, Milchunas et al. 1989, Briggs and Knapp 1995, Burke et al. 1999, Bork et al. 2001, Nippert et al. 2011, Stephenson et al. 2019). First, water availability may increase downhill due to higher storage capacity (e.g., deeper soils) or through water redistribution within the landscape via surface or subsurface movement of water (Bork et al. 2001). Second, soil nutrient content may be greater at lower elevation points, with plant available nitrogen, phosphorus, and organic matter increasing downhill due to soil and geomorphic processes (Schimel et al. 1985, Burke et al. 1999). Third, and perhaps due to a combination of the previous two mechanisms, differences in plant community composition may affect the production potential of a given topographic position. For example, an increase in nutrient and water conditions downhill may favor a community of less conservative, faster growing species that may be able to produce higher ANPP for a given precipitation input (e.g., Knapp et al. 2012).

The shortgrass steppe is the most water-limited grassland of the North American Great Plains, with high interannual variability in precipitation and a strong, positive correlation between precipitation and ANPP (Lauenroth and Sala 1992, Derner and Hart 2007). Shortgrass landscapes are often characterized by gently rolling hills and flat-topped terraces (Yonker et al. 1988) in which plant communities, nutrient content, and organic matter change with topographic position (Schimel et al. 1985, Milchunas et al. 1989, Burke et al. 1999). This region has a long evolutionary history of grazing (Milchunas et al. 1988), and currently supports livestock production and other ecosystems services such as wildlife habitat and soil carbon storage (Lauenroth and Burke 2008). For producers and land managers to sustainably manage large parcels spanning varied topography, it is important to understand how topographic position influences the sensitivity of ANPP to precipitation amount and pattern. In this study, we examined a long-term (36-yr) ANPP dataset across three topographic positions (ridge, slope, and swale) in the shortgrass steppe to better understand the responses of four dominant plant functional types (PFTs) to variation in precipitation patterns and amounts. We examined the following questions:

1. How does ANPP vary by topographic position, and how is that variability influenced by plant functional type?
2. How does current year precipitation amount and pattern (e.g., total, number of events) influence ANPP by topographic position?
3. How do biotic and precipitation legacies (e.g., previous year ANPP, fall precipitation) influence ANPP by topographic position?

Methods

Site description

Research was conducted at the 6500-ha USDA-Central Plains Experimental Range, which is part of the Long-Term Agroecosystem Research (LTAR; 2012–present; https://ltar.ars.usda.gov/) network, a former Long-Term Ecological Research station (LTER, 1983–2012), and located in the shortgrass steppe of north-central Colorado, USA (40°50′ N, 104°43′ W, 1645 m above sea level). The topography is characterized by gently rolling hills, with 50% of the area upland ridges, 28% slopes, and 22% lowland swales (Senft et al. 1985). Soils have a high degree of spatial heterogeneity due to a complex geomorphic history (Yonker et al. 1988), however this study site does not span extremes in soil texture (Singh et al. 1998), and thus we focused on the effect of topography along a catena in one of the most common ecological sites, Loamy Plains (ID: R067BY002CO; NRCS 2020). The plant community included four herbaceous plant functional types (PFTs): (1) perennial, warm-season, C_4 grasses (primarily *Bouteloua gracilis* [Willd. ex Kunth] Lag ex Griffiths and *B. dactyloides* [Nutt.] J.T. Columbus), (2) perennial, cool-season, C_3 grasses (primarily *Pascopyrum smithii* [Rydb] A. Love and *Hesperostipa comata* [Trin. & Rupr.] Barkworth ssp. comata), (3) cool-season, annual grass (*Vulpia octoflora* [Walter] Rydb.), and (4) forbs (primarily *Sphaeralcea coccinea* [Nutt.] Rydb.). Shrubs, subshrubs, and cactus were present but do not represent a large component of total ANPP and were not included in this study.

Precipitation data

Daily precipitation data were obtained from a long-term (1979–2018) precipitation gauge associated with the National Atmospheric Deposition program (Site ID NTN-CO22; http://nadp.slh.wisc.edu/), located on site. Missing precipitation data were gap-filled using CPER headquarters data (1939–2018), or from the Soil Climate Analysis Network (SCAN) rain gauge (1997–2018, Site Number 2017; https://www.nrcs.usda.gov/scan/), depending on proximity and temporal overlap. Following gap-filling, precipitation data were omitted if >10% of the time series was missing for each focal time period (e.g., fall or spring).

Current year and legacy precipitation metrics were calculated annually (Table 1). Current year precipitation amount metrics included spring precipitation totals (SPRG_{ppt}; April–June) and growing season precipitation totals (GS_{ppt}; April–August). Five current year growing season precipitation pattern metrics were calculated based on Knapp et al. (2015), using only days with precipitation >2 mm. Mean daily precipitation event size (EVENTSIZE) and the number of precipitation events (EVENTS) were calculated each year (Table 1). The number of consecutive dry days (#CDD) was calculated as the average number of days between precipitation events each year (Table 1). The number of large precipitation events (#LRGEVENTS) was defined as the number of precipitation events that exceeded the 90th percentile for the total dataset (>16.7 mm; Table 1). Legacy precipitation metrics included previous cool-season precipitation ($\text{PRVCool}_{\text{ppt}}$; November–March; Table 1), previous year fall precipitation ($\text{PRVFall}_{\text{ppt}}$; September and October; Table 1), and previous year growing season precipitation ($\text{PRVGS}_{\text{ppt}}$; Prior April–August; Table 1).

Aboveground net primary productivity sampling

From 1983 to 2018, ANPP was sampled annually at three topographic positions (i.e., ridge, slope, and swale), in a moderately grazed pasture (0.6 AUM/ha stocking rate). Each year, ANPP was estimated as the peak current year biomass harvested from 15 temporary exclosures per topographic position, which were moved each year a random distance and direction prior to the grazing season. In this system, with a short growing season and dominance by warm-season grasses, peak standing biomass is a good estimate of ANPP based on comparison with ^{14}C isotope turnover method (Milchunas and Lauenroth 1992). Current year's ANPP was clipped to crown-level in August (mean harvest date DOY = 221) using a 0.25-m^2 frame (1983–2008; 2014–2018) or a 0.1-m^2 frame (2009–2012), with all data scaled to 1 m^2 for analysis. Plants were sorted to species, except from 2009 to 2012, when they were sorted to plant functional type (PFT). For this study, we only focused on PFTs to utilize all years, and thus we focus on plant dynamics from a functional perspective. Following collection, samples were oven dried at 55°C and weighed.

Analysis

To examine how ANPP varied by topographic position, year, and PFT, we ran linear mixed models for each ANPP response variable. For

Table 1. Precipitation metrics.

Category	Metric	Metric abbreviation	Unit	No. of years	Mean	SD
Current year (amount)	Spring precipitation total (April–June)	SPRG_{ppt}	mm	38	137.7	58.1
	Growing season precipitation total (April–August)	GS_{ppt}	mm	38	225.0	68.8
Current year (pattern)	Mean daily precipitation event size	EVENTSIZE	mm	38	8.6	1.9
	No. of precipitation events	#EVENTS	days	38	24.0	5.7
	No. of consecutive dry days	#CDD	days	38	7.4	2.2
	No. of large precipitation events (>90th percentile, 16.7 mm)	#LGEVENTS	days	38	2.6	1.9
Legacy (amount)	Previous cool-season precipitation total (November–March)	$\text{PRVCOOL}_{\text{ppt}}$	mm	34	47.8	21.7
	Previous fall precipitation total (prior September, October)	$\text{PRVFALL}_{\text{ppt}}$	mm	38	48.7	26.1
	Previous growing season precipitation total (prior April–August)	$\text{PRVGS}_{\text{ppt}}$	mm	37	225.8	69.5

Note: Current year precipitation metrics are for the growing season (April–August).

total ANPP, topographic positions and year (categorical) were treated as fixed factors. For absolute and relative ANPP PFT models, topographic position and PFT were treated as fixed factors. To account for repeated measures, we used a compound symmetry covariance structure with plot ID as a random grouping factor and year (continuous) as a random temporal covariate, using the nlme package in R (version 3.1-143, Pinheiro et al. 2019). To fit assumptions of normality, all ANPP values were log-transformed prior to analysis. For significant main effects or interactions ($P < 0.05$), Tukey-adjusted pairwise comparisons were made using the emmeans package (Lenth 2019).

Next, we conducted a sensitivity analysis to examine the relationship of each ANPP response variable with current year and legacy metrics across topographic positions. Both ANPP response and current year and legacy metrics were normalized prior to analysis with the following equation:

$$X_{\text{norm}} = \frac{X - X_{\min}}{X_{\max} - X_{\min}}$$

where X is a given variable (e.g., GS_{ppt}), and $X_{\max}$ and $X_{\min}$ are the maximum and minimum values for the variable, respectively. We then ran an analysis of covariance for each ANPP variable with a two-way model of each normalized metric (current year or legacy) and topographic position. We defined sensitivity based on slope (−1 to 1), and if there were significant interactions ($P < 0.05$) between a given normalized metric and topographic positions, we tested for slope differences to assess divergence in sensitivity (Appendix S1: Figs. S1, S2), using the emmeans package (Lenth 2019). Precipitation metrics are reported as mean ± SD, while ANPP and sensitivity estimates are reported as means ± SE.

RESULTS

Precipitation

Across this time series (1983–2018), mean annual precipitation was 321.5 mm, with 70% occurring during the growing season (GS_{ppt}, April–August), 43% in the spring (SPRG_{ppt}, April–June), and 15% in both the previous cool-season ($\text{PRVCool}_{\text{ppt}}$, November–March) and previous fall ($\text{PRVFall}_{\text{ppt}}$, September and October; Table 1, Figure 1). Mean event size was 8.6 (±1.9) mm, with 24 (±5.7) events occurring during the growing season (Table 1). The average number of consecutive dry days was 7.4 (±2.2) with a minimum of 4.7 d (1995) and maximum

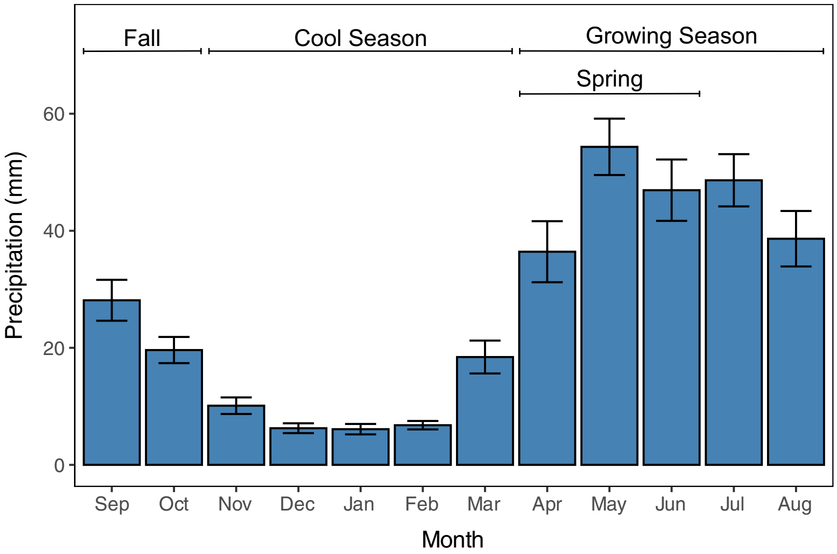

Fig. 1. Monthly precipitation. Mean monthly precipitation (± SE) from 1983 to 2018 at the Central Plains Experimental Range. Lines above bars indicate the previous fall ($\text{PRVFall}_{\text{ppt;}}$ September–October), previous cool-season ($\text{PRVCool}_{\text{ppt:}}$ November–March), spring (April–June), and growing season (April–August) periods.

of 15.7 d (2012). The average number of large precipitation events per year was 2.6 (±2.2) with a minimum of 0 events (1986, 2002, 2004), and maximum 8 events (1997; Table 1).

ANPP by topographic position

Total ANPP exhibited high interannual variability across this time series, with the swale topographic position tending to have higher production and diverge from the other two topographic positions (Fig. 2; Appendix S1: Table S1a). The lowest recorded total ANPP for all three topographic positions occurred in 2002 (ridge = 9.4 ± 1.1; slope = 9.4 ± 0.9; swale = 14.2 ± 1.5 g/m^2), while 2009 was the most productive year (ridge = 122.9 ± 9.2; slope = 129.7 ± 11.0; swale = 223.3 ± 12.0 g/m^2; Fig. 2). This resulted in maximum temporal variability in ANPP (i.e., the greatest difference within a topographic position, among years) of 13-, 14-, and 16-fold for the ridge, slope, and swale topographic positions, respectively. In contrast, maximum spatial variability (i.e., the greatest difference among topographic positions, within a year), exhibited only a 4-fold difference between the ridge and the swale in 1992 (ridge = 46.5 ± 5.9; swale = 177.8 ± 22.0).

Total ANPP differed across topographic positions ($F_{2,42} = 290$, $P < 0.001$) and the effect of topography varied among years ($F_{68,1407} = 235$, $P < 0.001$; Appendix S1: Table S1a). Total ANPP increased downhill with mean values of 57.2 (±4.0 g/m^2), 63.7 (±4.7 g/m^2), and 100.0 (±8.6 g/m^2), for the ridge, slope, and swale, respectively (Fig. 2). Mean total ANPP in the swale was 57% greater than the slope, and 75% greater than the ridge (Fig. 2, inset). The three topographic positions tended to converge in ANPP in low productivity years, (e.g., 2002 and 2012), but diverge in high productivity years (e.g., 1999 and 2009; Fig. 2).

Next, we explored how the variance in total ANPP across topographic positions was driven by variation in PFTs. We found significant interactions between topographic position and PFT for both absolute ($F_{6,1407} = 151$, $P < 0.001$; Appendix S1: Table S1b) and relative biomass ($F_{6,1407} = 322$, $P < 0.001$; Appendix S1: Table S1c). Absolute biomass of C_4 grasses did not differ between the ridge (43.3 ± 3.0 g/m^2)

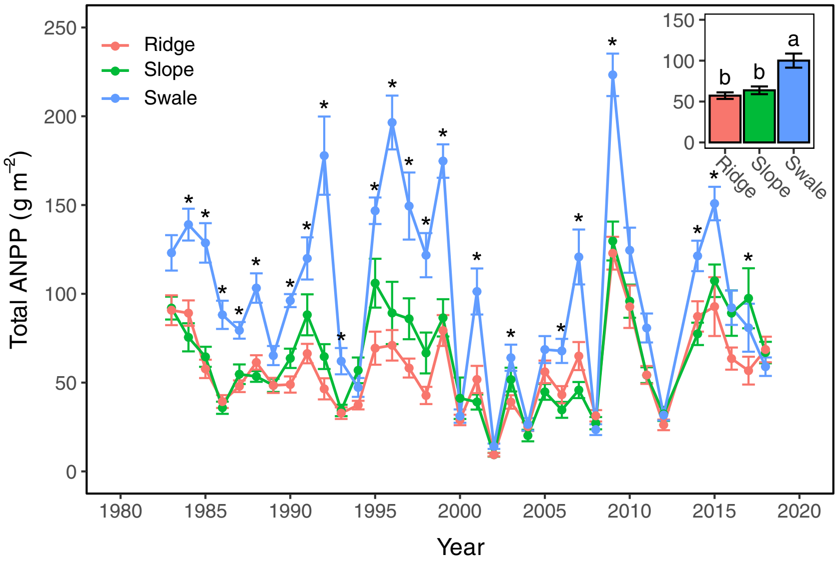

Fig. 2. Total ANPP by topographic position. Total annual net primary productivity (ANPP) by topographic position through time (1983–2018). Points indicate mean total ANPP (1 ± SE). (Inset) Mean total ANPP by topographic position across years (±SE), and asterisks indicate significant differences ($P < 0.05$) between topographic positions, within a year. Inset letters denote significant differences among topographic positions across years ($P < 0.05$).

and slope (46.4 ± 3.4 g/m^2) topographical positions but was 55% higher in swales (70.7 ± 7.2 g/m^2; Fig. 3A). Relative biomass of C_4 grasses did not vary across topographic positions and represented approximately three-quarters of total ANPP (69–79%; Fig. 3B). C_3 grasses absolute biomass was 25% lower at the ridge (9.3 ± 0.9 g/m^2) than the slope (12.3 ± 1.3 g/m^2) and swale (12.0 ± 1.4 g/m^2), with the latter two positions not differing (Fig. 3A). Relative biomass of C_3 grasses represented the second highest proportion of total ANPP. The swale (13%) and ridge (15%) topographic positions had lower relative C_3 grasses biomass than the slope (18%; Fig. 3B). Like C_4 grasses, mean absolute biomass of forbs in the swale (9.8 ± 1.4 g/m^2) was double that of either the ridge (4.4 ± 1.0 g/m^2) or slope (4.4 ± 1.1 g/m^2) topographic positions (Fig. 3A). The pattern for relative biomass of forbs was the same as absolute biomass (Fig. 3B). Annual grasses also displayed similar topographic responses as C_4 grasses and forbs with the most absolute biomass occurring in the swale (7.2 ± 2.1 g/m^2; Fig. 3A), where it represented 7% of total ANPP (Fig. 3B). Thus, in absolute terms, swales produced significantly more biomass of all four PFTs than ridges. In relative terms, the slope position contained relatively more C_3 grasses than the ridge position, while the swale position contained relatively more forbs and annual grasses than the ridge position.

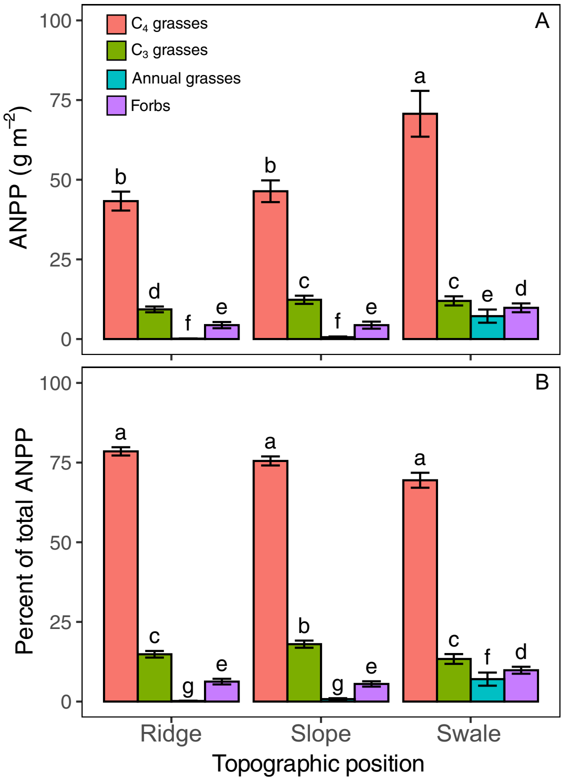

Fig. 3. ANPP by topographic position and plant functional type. Aboveground net primary productivity (ANPP) across topographic position for four herbaceous plant functional types, with (A) showing the absolute values of ANPP, and (B) showing each plant functional type as relative value of total ANPP. Bars indicate means (1 ± SE), and letters denote significant differences across topographic positions and plant functional types ($P < 0.05$).

Sensitivity to current year precipitation and legacies

Total ANPP was sensitive to current year precipitation amount and pattern, with topographic position influencing these responses for several precipitation metrics. Total ANPP was positively related to GS_{ppt}, #EVENTS and #LARGEVENTS, with higher sensitivity exhibited by the swale topographic position (Fig. 4; Appendix S1: Table S2). For example, the swale position was more than twice as sensitive to GS_{ppt} (0.76 ± 0.17; $P = <0.001$; Fig. 4) as the slope (0.36 ± 0.08; $P = <0.001$; Fig. 4) and the ridge (0.29 ± 0.07; $P = <0.001$; Fig. 4) positions were. We observed a negative relationship between total ANPP and CDD, with the swale (−0.69 ± 0.16; $P = <0.001$; Fig. 4) having higher sensitivity than the ridge (−0.24 ± 0.08; $P = 0.007$; Fig. 4), while the slope sensitivity was intermediate (−0.30 ± 0.10; $P = 0.003$; Fig. 4). Total ANPP was positively associated with $SPRG_{ppt}$ and EVENTSIZE, but the sensitivity did not vary by topographic position (Fig. 4; Appendix S1: Table S2).

Sensitivity to current year precipitation amount and pattern varied among the PFTs. C_4 grasses exhibited the same sensitivity patterns as total ANPP (see above; Fig. 4; Appendix S1: Table S2). C_3 grasses exhibited sensitivity to all metrics, but only sensitivity to GS_{ppt} and #LRGEVENTS varied by topographic position, with the swale having significantly more sensitivity than the ridge, and the slope having intermediate sensitivity (Fig. 4). Annual grasses were the only functional group with sensitivity to $SPRG_{ppt}$, but this relationship was only significant for the

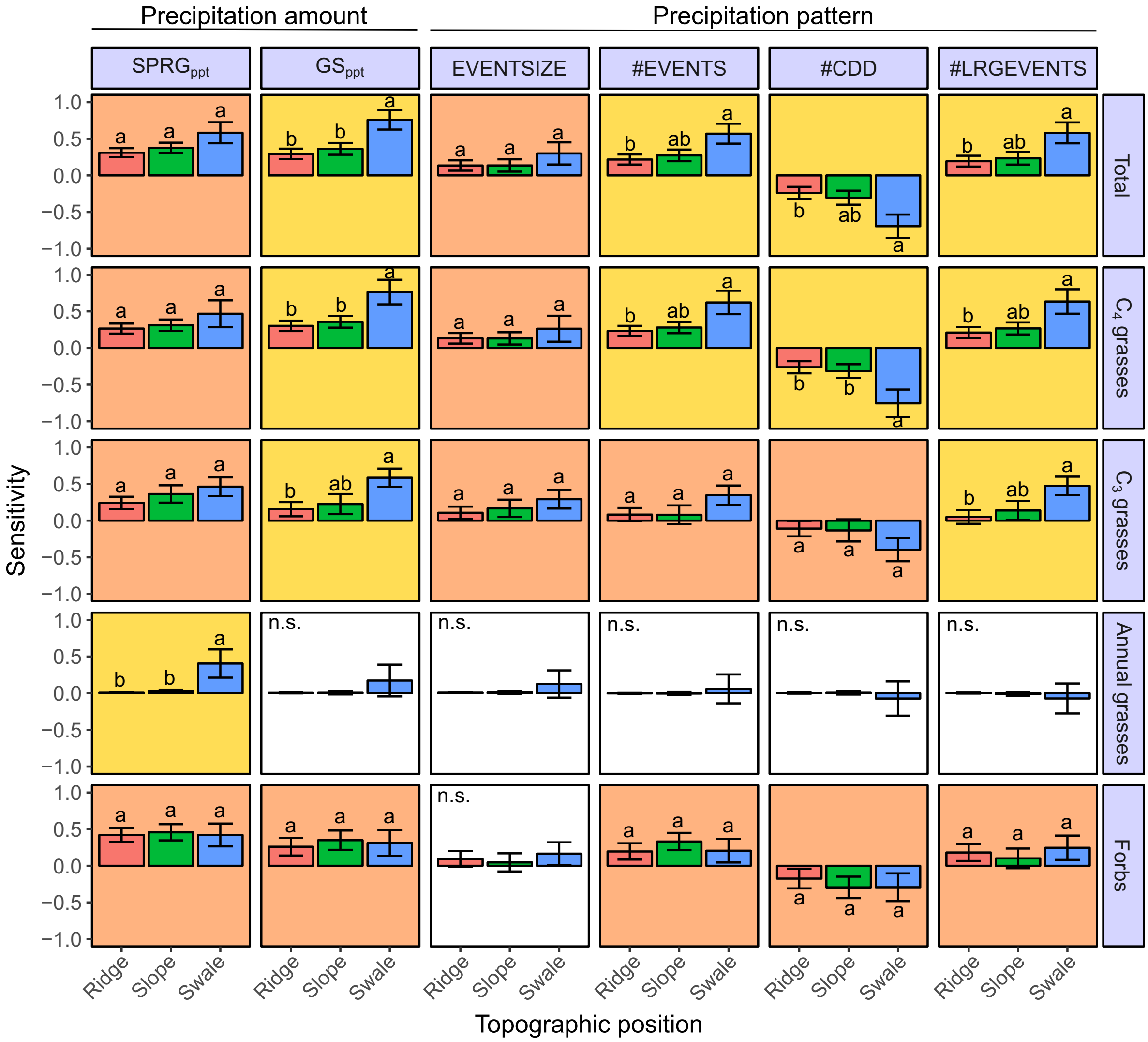

Fig. 4. Sensitivity of aboveground net primary production (ANPP) to current year precipitation. Sensitivity of productivity to current year precipitation amount and pattern across different plant functional types and topographic position. Current year precipitation amount metrics include total spring precipitation (SPRG$_{ppt}$; April–June), and total growing season precipitation (GS$_{ppt}$; April–August), while precipitation pattern metrics include mean daily event size (EVENTSIZE), the number of events (#EVENTS), the number of consecutive dry days (#CDD), and the number of large precipitation events (#LGEVENTS; >90th percentile). See Table 1 and methods text for additional info on precipitation metrics. Sensitivity is defined as the slope between a given precipitation metric and ANPP (both normalized). Positive sensitivity values indicate positive slopes, while negative sensitivity vaules indicate negative slopes. Values further from zero indicate steeper slopes. Bars represent the slope, and error bars indicate standard error estimated from the linear regression model. Figure panel background colors indicate results from analysis of covariance models (ANCOVA) for ANPP with topographic position and precipitation as predictors: white = no significant main effects of precipitation; orange = significant main effects of precipitation; and yellow = significant interaction between precipitation and topographic position. Letters denote significant differences across topographic position for each precipitation metric and plant functional type combination.

swale (0.41 ± 0.19; $P = 0.043$; Fig. 4). Forbs were sensitive to all current year precipitation metrics except EVENTSIZE; sensitivity for this PFT, however, did not differ by topographic position (Fig. 4).

Overall, we observed lower sensitivity to biotic and precipitation legacies than current year precipitation. No PFT demonstrated any sensitivity to $\mathrm{PRVCool_{ppt}}$ or $\mathrm{PRVGS_{ppt}}$ (Fig. 5; Appendix S1: Table S3). Only annual grasses had sensitivity to $\mathrm{PRVFall_{ppt}}$, with the swale having the highest sensitivity. $\mathrm{PRV_{anpp}}$ had a significant positive effect on TOTAL, C_4 grasses and C_3 grasses, but we found no differential sensitivity to this biotic legacy across topographic positions (Fig. 5; Appendix S1: Table S3). Forbs were not sensitive to any legacy metrics (Fig. 5; Appendix S1: Table S3).

DISCUSSION

We assessed how ANPP varies by topographic position in a shortgrass steppe ecosystem using long-term (36-yr) ANPP data, and determined the mechanisms driving this observed variability. We observed that (1) ANPP varied substantially by topographic position, with more divergence among positions in high productivity years, (2) temporal variability in ANPP across years (maximum 16-fold difference) was substantially greater than spatial variability across the topographic sequence (maximum 4-fold difference), (3) warm-season perennial grasses (C_4 grasses) contributed approximately 75% of total ANPP across the topographic sequence, while ANPP contributions of the subdominant PFTs (C_3 grasses, annual grasses, forbs) varied across topographic positions, and (4) ANPP exhibited strong sensitivities to current year precipitation amount and pattern, as well as some weaker sensitivities to biotic and precipitation legacies that varied by plant functional type. Collectively, our results suggest that annual ANPP in semiarid grasslands is strongly sensitive to interactions between spatial (topographic) and temporal (precipitation) variability, even at relatively fine spatial scales. Interactive effects of precipitation variability and topography on ANPP are largely driven by the effects of current year precipitation amount and pattern, with C_4 grasses dominating the plant community response.

Variation in ANPP by topographic position

The mean spatial variability in ANPP observed in this topographic sequence (1.75-fold, ridge vs. swale) is consistent with other grassland ecosystems, including increases of ~1.5-fold in sandhills prairie (Stephenson et al. 2019), ~2-fold in both tallgrass prairie (Nippert et al. 2011) and boreal grasslands (Bork et al. 2001). Downhill movement of water and nutrients, as well as topographic variation in soil texture, may contribute to this variation. In this semiarid shortgrass steppe, water is the most limiting factor to growth, followed to a much lesser degree by nitrogen (Dodd and Lauenroth 1979, Burke et al. 1997). During wet years, or large precipitation events, the redistribution of water downhill via surface or subsurface flow may provide swales with higher water availability (Bork et al. 2001). Consistent with this mechanism, we found the largest increases in production in swales relative to ridges during years with the most growing season precipitation, and in years with more large precipitation events. Previously, Heisler-White et al. (2009) showed that large precipitation events enhance ANPP on flat plains more than an equivalent amount of precipitation received as multiple small events, suggesting that larger events result in greater infiltration and retention of water in deeper soil layers. Our results suggest that large events on slopes may result in either greater runoff or subsurface flow compared to small events, leading to greater topographic variation in ANPP. Soil nitrogen, phosphorus, and organic matter also increase downslope in this grassland (Schimel et al. 1985, Burke et al. 1999), and may contribute to increased total production in swales compared to slopes and ridges in periods when water is not limiting growth.

High spatial heterogeneity in soils is common in the shortgrass steppe (Yonker et al. 1988), which may further increase spatial variability in productivity due to differences in soil water storage and losses (Singh et al. 1998). However, this study site does not span such extremes in soil texture and therefore is not likely a large contributing factor to spatial variability in productivity observed in this study (Singh et al. 1998). While we acknowledge that using a single pasture for long-term ANPP observations limits spatial replication, it also avoids the confounding

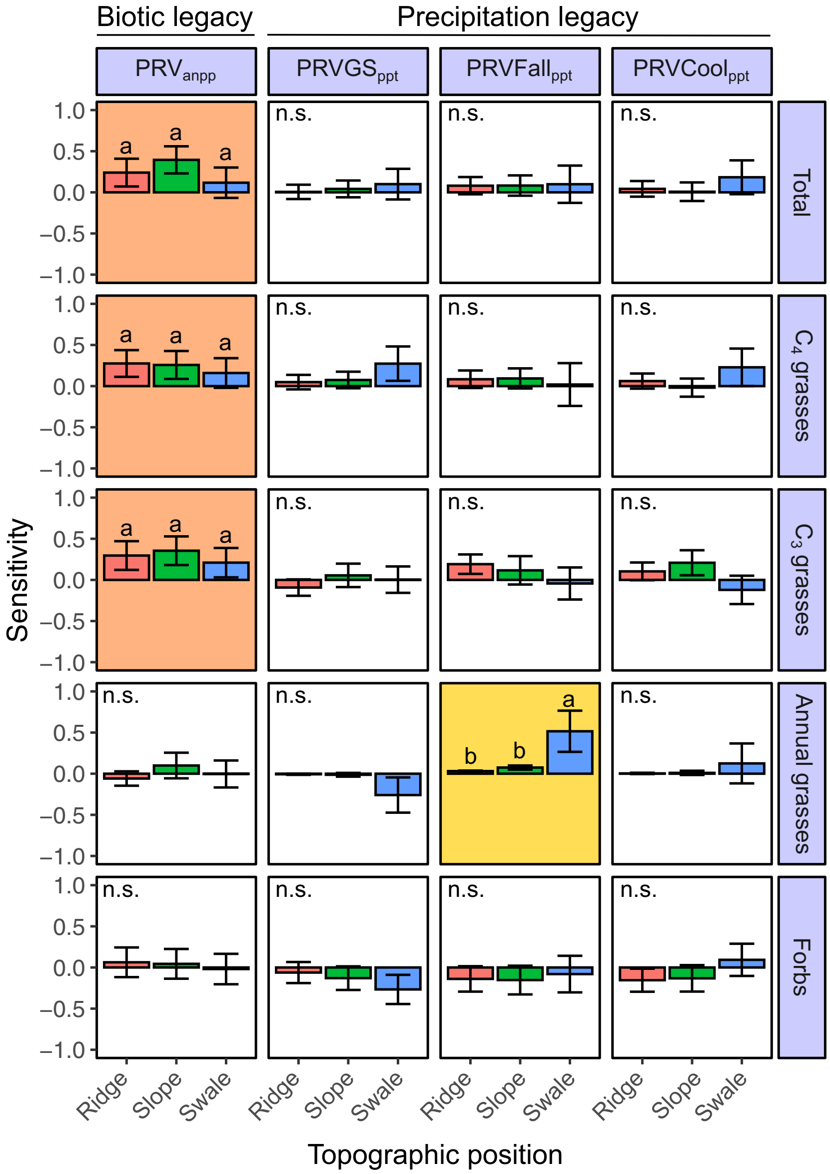

Fig. 5. Sensitivity of aboveground net primary production (ANPP) to biotic and precipitation legacies. Sensitivity of productivity to biotic and abiotic legacies across different plant functional types and topographic position. Legacy metrics include previous year's aboveground net primary productivity (PRV$_{anpp}$), previous growing season's precipitation (PRVGSppt; prior April–August ANPP), previous fall precipitation (PRVFall$_{ppt}$; prior September–October precipitation), and previous cool-season precipitation (PRVCool$_{ppt}$; prior November–March). See Table 1 and methods text for additional info on metrics. Sensitivity is defined as the slope between a given precipitation metric and ANPP (both normalized). Positive sensitivity values indicate positive slopes, while negative sensitivity values indicate negative slopes. Values further from zero indicate steeper slopes. Bars represent the slope, and error bars indicate standard error estimated from the linear regression model. Figure panel background colors indicate results from analysis of covariance models (ANCOVA) for ANPP with topographic position and legacy metric as predictors: white = no significant main effects of legacy; orange = significant main effects of precipitation; and yellow = significant interaction between legacy and topographic position. Letters denote significant differences across topographic position for each legacy metric and plant functional type combination.

effects of high spatial variability in soils, allowing us to make more defensible predictions of loamy soils, a dominant soil type of the region.

Changes in the plant community may also be a contributing factor to ANPP variation with topography. Swale positions may favor less conservative, faster growing species (such as forbs and annual grasses in our dataset), which may lead to higher total ANPP for a given precipitation amount (Knapp et al. 2012). While we did observe an increase in ANPP in the swale for both forbs and annual grasses PFTs (Fig. 3A), they contributed a relatively small amount to total ANPP, even in swales (7% and 10%, respectively, Fig. 3B). Grime's (1998) Mass Ratio theory proposes that the effect of a given species, or PFT, on ecosystem function (e.g., ANPP) is proportional to its relative abundance in the community. In terms of production, C_4 grasses heavily dominated all three topographic positions, accounting for roughly 75% of total ANPP. C_4 grasses had a proportionally large effect on variation in total ecosystem productivity, as patterns for C_4 grasses ANPP were similar to total ANPP. Therefore, we do not see evidence that differences in the relative abundance of plant functional types in this ecosystem are strong drivers of divergence in total productivity by topographic position.

Sensitivity of ANPP to current year precipitation amount and pattern

ANPP was sensitive to current year precipitation amount (Lauenroth and Sala 1992, Derner et al. 2008, Hermance et al. 2015, Irisarri et al. 2016) and pattern (Milchunas et al. 1994, Heisler-White et al. 2008, Wilcox et al. 2015). Novel here, however, is our examination of how this sensitivity varied by topographic position and was driven by complex relationships among multiple PFTs and precipitation metrics (Fig. 4). Consistent with the Mass Ratio Hypothesis (Grime 1998), sensitivity of total ANPP to precipitation mirrored that of the dominant PFT; C_4 grasses and total ANPP were both sensitive to GS_{ppt}, EVENTS, #CDD, and #LRGEVENTS (Fig. 4). Sensitivity of C_4 grasses and total ANPP varied by topographic position, with swales having the highest sensitivity, and ridge and slope sharing the same lower sensitivity (Fig. 4). Greater sensitivity of C_4 grasses and total ANPP to GS_{ppt} and #LRGEEVENTS in the swale provides support for the hypothesis that increased water availability drives higher ANPP in this landscape position. More total rainfall and more large events are likely to result in more surface and subsurface flow of water downhill to the swale, thus providing a water subsidy to this landscape position. Given that this landscape consists of closed basins and often dry ephemeral streams, little water is lost via streamflow (e.g., Frasier et al. 1995, Koler et al. 2008). Therefore, runoff loss on slopes may not have as great of an impact on landscape-level productivity, as this water movement can stimulate productivity in other local, lower topographic positions. Increased sensitivity of the swales to EVENTS and #CDD for C_4 grasses and total ANPP (Fig. 4), suggest that the precipitation patterns, not only amount, affect water availability across the toposequence. For example, increasing the duration between precipitation events (or increasing #CDD) can reduce soil moisture below critical thresholds thereby limiting plant growth and reducing ANPP (Knapp et al. 2002).

Subdominant PFTs (C_3 grasses, annual grasses, forbs) in this semiarid grassland had varying sensitivities to current year precipitation. C_3 grasses responded similarly to C_4 grasses and total ANPP, except they did not have differential sensitivity by topographic position to #EVENTS or #CDD (Fig. 4). Annual grasses were only sensitive to $SPRG_{ppt}$, which is not surprising given that they typically complete growth during this period. While forbs were sensitive to almost all current year precipitation metrics, they responded uniformly across all three topographic positions, despite their greater overall abundance in swales.

Sensitivity of ANPP to biotic and abiotic legacies

Studies of grasslands worldwide provide evidence of both abiotic legacies (e.g., carryover effects of soil moisture and/or nutrients), and biotic legacies (e.g., changes in individual plants or the community; Sherry et al. 2008, 2012, Sala et al. 2012, Bisigato et al. 2013, Reichmann and Sala 2014). In the shortgrass steppe, previous work identified the influence of biotic legacies on ANPP (Oesterheld et al. 2001, Petrie et al. 2018), and separately identified the importance of current-season precipitation amount (Lauenroth and

Sala 1992) and event size (Heisler-White et al. 2009). However, the influence of all three factors has not been evaluated in a common analytical framework. After accounting for the effects of current year precipitation metrics on ANPP precipitation sensitivity, we observed no effects of precipitation legacies on total or perennial grass ANPP (Fig. 5; Appendix S1: Table S3). We did observe precipitation legacy effects for annual grasses, which likely reflect the fact that these cool-season annuals rely on stored soil moisture to begin their life cycle in the late winter or early spring. There were biotic legacy effects of $\mathrm{PRV}_{\mathrm{anpp}}$ for total, C_4 grasses, and C_3 grasses ANPP, and these biotic legacy effects did not vary by topographic position (Fig. 5; Appendix S1: Table S3). Such legacies may be influenced by belowground structural changes to individual plants, such as tillers, stolons, axillary buds, or root systems due to water availability affecting the growth potential of plants the following year (Oesterheld et al. 2001) and at longer time scales (decadal) by species compositional changes (Milchunas et al. 1989, Augustine et al. 2017, Porensky et al. 2017). These individual plant-level responses and community dynamics are manifest together to result in ANPP being greater or less than expected with a given precipitation amount (Oesterheld et al. 2001, Reichmann and Sala 2014).

IMPLICATIONS

Understanding the patterns and drivers of ANPP has been a long-standing goal of both theoretical and applied ecologists due to the critical role of ANPP in regulating ecosystem function and provisioning food, fuel, and fiber (McNaughton et al. 1989, Fahey and Knapp 2007, Haberl et al. 2007). Across most biomes, water availability is the limiting or co-limiting factor for ANPP, and thus understanding the relationship between precipitation and productivity has long been a major research emphasis (Rosenzweig 1968, Webb et al. 1978, 1983). This effort has resulted in two classic precipitation-ANPP models: temporal models derived from individual sites over time, and spatial models across sites, averaged through time (Lauenroth and Sala 1992). However much less attention has been paid to understanding spatial variability within a given site, despite evidence that such variability is significant and likely site-specific (Briggs and Knapp 1995, Bork et al. 2001, Lauenroth et al. 2008, Nippert et al. 2011, Stephenson et al. 2019). In this study, we observed strong interactive effects of temporal and spatial variability on total ANPP at the site scale. While classic models of precipitation and ANPP account for high temporal variability, most do not account for such high within-site spatial variability, such as the 4-fold maximum spatial variability observed here, and instead often rely on a single measurement location for a site-level ANPP value. Our results show that when scaling up productivity estimates from the plot-scale to the region-scale, it is critical to account for patterns and drivers of within-site variability in productivity.

High variability in climate and range conditions make livestock management decision-making especially challenging in semiarid rangelands (Shrum et al. 2018). The distribution of large herbivores across the landscape is uneven, with factors such as distance to water or vegetation community composition affecting movement and grazing preferences (Allred et al. 2013, Bailey et al. 2015). Topography can also influence livestock behavior. For example, in the shortgrass steppe of North America, cattle grazing intensity can be two to three times greater in swales than ridge tops (Milchunas et al. 1989), likely a response to differences in forage, as observed in this topographic sequence. Results from this study highlight the importance of considering topography and its effects on plant productivity when moving livestock, establishing grazing boundaries, estimating forage production at the pasture scale or adapting practices to variation in precipitation amount and patterns.

Climate change is projected to alter the hydrological cycle through increases in precipitation variability and extremes (IPCC 2013), with uncertain impacts on the spatiotemporal dynamics of ANPP. Results from this study suggest ANPP is sensitive to growing season precipitation amount and pattern, and this sensitivity varies by topographic position. Such information is valuable in predicting responses of ecosystem function (e.g., carbon uptake) or adapting management (e.g., livestock distribution) to extreme hydrological conditions. For example, during drier years, ANPP across topographic positions will converge, while ANPP will tend to diverge during wetter years or years with more heavy precipitation events. Another key result from these long-term observations is that while legacies of prior year production do influence current year production, this effect does not vary by topographic position. Thus, increased spatial variability in ANPP is primarily driven by current year precipitation amount and pattern. Overall, this study suggests that adapting to altered precipitation due to climate change will require accurate weather forecasting of current year precipitation and highly flexible adaptive management.

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DATA AVAILABILITY STATEMENT

Data used in this manuscript are publicly available through the US Department of Agricultures' Ag Data Commons (https://dx.doi.org/10.15482/USDA.ADC/1519328).

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3376/full