



The interaction of temperature and precipitation determines productivity and diversity in a bunchgrass prairie ecosystem

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Abstract

Over the past century at the National Bison Range, temperature has increased by 0.6 °C, and annual precipitation has decreased by 26%, despite increases in May–June precipitation over the past 35 years. Limited experimental work to date has explored plant responses produced by the interaction of changes in both temperature and precipitation, and of the existing studies, none have focused on the endangered bunchgrass ecosystem. Using a 2-year climate change manipulation experiment, we show that bunchgrass productivity increased with supplemental growing season precipitation, while warming alone exerted no significant effect. More importantly, the ratio of June precipitation to minimum temperature, a representation of the interaction of climate variables, predicted bunchgrass productivity better than either climate variable individually. This ratio acted as a surrogate index reflecting increased evapotranspiration with rising temperatures and thus better predicting soil moisture available for plant growth. Experimental warming over the summer led to significantly lower plant species richness and biodiversity, while increased precipitation, when applied over the entire summer, counteracted some of these declines. Warming also led to greater and more rapid plant senescence over the summer, resulting in greater litter production [an increase of 47.82 ± 17.82 (\pm SE) percentage points] and potential fire risk. Given the simultaneous changes in precipitation and temperature predicted for the next century, multi-factor experiments are essential to understand how ecosystems will respond to future climate scenarios.

Keywords Climate change · Grassland conservation · Experimental warming · Biodiversity · Primary productivity

Introduction

Global climate change is increasing average annual temperature and is modifying precipitation and its seasonal patterns of interaction with temperature (Intergovernmental Panel on Climate Change 2013). These changes are projected to affect ecosystem net primary productivity (NPP) by altering water and possibly nutrient availability, as well as their seasonal distributions (Cleland et al. 2007). In addition, this may affect biodiversity, which can further modify NPP

through biodiversity's support of ecosystem function (Sala et al. 2000; Vitousek 1994; Chapin et al. 2000; Cardinale et al. 2012). Consequently, bottom-up effects on food webs may change. Semi-arid grasslands are especially susceptible to seasonal changes in temperature and precipitation (Intergovernmental Panel on Climate Change 1990), which may affect global carbon balance as grasslands comprise 31–43% of ice-free land surfaces (Zhou et al. 2012).

When seasonal temperature and precipitation simultaneously change, the effect of these new combinations on grassland NPP and its seasonal distribution, through plant senescence, are not easily predicted using single-factor experimental manipulations (Wu et al. 2011; Fay et al. 2011). The few simultaneous manipulations of temperature and precipitation (Wu et al. 2011) indicate less severe effects on NPP than single-factor studies, as responses are not additive (Flanagan et al. 2013; Shaw et al. 2002). We hypothesize that precipitation and temperature need to be combined as a ratio to reflect evapotranspiration, as a given amount of precipitation will provide less water for plant growth as

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temperature increases (Manske 2001), while temperature alone will increase plant senescence (Cleland et al. 2007; Belovsky and Slade pers. comm.).

To address simultaneous seasonal changes in temperature and precipitation in a grassland ecosystem, we conducted a multi-factor climate manipulation experiment in bunchgrass prairie at the National Bison Range (NBR, MT, USA). The factorial design allowed us to vary temperature, precipitation, and seasonality of precipitation independently and in combination to address NPP and biodiversity effects. Bunchgrass prairie is the intermountain valley grasslands between the Rocky and Cascade Mountains that today are one of the most endangered North American ecosystems (< 1% of its original area: Johnson and O'Neil 2001). Over the past 100 years, climate at this location has exhibited a 0.6 °C increase in average annual temperature and a 26% decline in precipitation, although May–June precipitation has increased over the last 35 years (Belovsky and Slade pers. comm.).

Methods

Study site

In 2014 and 2015 experimentation was conducted in a 1 ha area of bunchgrass prairie within a subsection of the National Bison Range (Elevation: 832 m; UTM coordinates: 713570E 5248100N). The site was dominated by grasses (96%: predominantly *Poa pratensis* and *Pascopyrum smithii*), and its soil was predominantly clay.

Experimental design

Five 9 m² (3 m × 3 m) enclosures were located randomly at the site. Each enclosure consisted of a frame, covered by lumite insect netting, that was constructed of 2.54 cm PVC pipe surrounded by 46 cm aluminum flashing buried 25 cm in the soil. The flashing excluded herbivorous rodents and roots from the surrounding area, while the netting excluded insect herbivores. The enclosure was divided into six 1 m² plots (three on each side) that were separated by aluminum flashing to isolate roots and a 1 m wide central corridor for access. One side of each enclosure was warmed passively using plastic louvre slats located above the enclosure to reduce infrared radiation loss and increase daily minimum temperatures (Germino and Smith 1999; Aronson and McNulty 2009; Sherwood et al. 2017). Nighttime temperatures are predicted to increase faster than daytime temperatures, as cold extremes are reduced and the diurnal temperature range contracts (Knowles et al. 2006; Intergovernmental Panel on Climate Change 2007). The 1 m wide central corridor served as a buffer between warmed and ambient temperature treatment plots. Each side of the enclosure had a

1 m² plot with ambient precipitation, a 1 m² plot with a 20% increase in June precipitation (supplemental precipitation), and a 1 m² plot with a 20% increase in June–August precipitation (extended supplemental precipitation). A weather station (National Geographic Deluxe) at the site measured precipitation to determine the supplemental precipitation that was provided weekly using a spray pump to ensure even distribution over the plot. If no rain fell within a week, average weekly rainfall for the period over the past 10 years was used to determine supplemental precipitation.

Measurements

Temperature was measured every 15 min in the warmed and ambient zones using data loggers (HOBOTemp) (Risch and Frank 2007). Soil moisture was measured using gypsum blocks buried 15 cm in the soil in plots and a soil moisture probe (Hydrosense).

ANPP (aboveground net primary productivity) was measured nondestructively using a CROPSCAN, Inc. multispectral radiometer. Biweekly radiometer readings were taken at three locations in each 1 m² treatment plot (Pearson et al. 1976; Milton 1987) from late May–mid-October. The radiometer was held at a height (0.71 m) to measure a 0.10 m² area. The radiometer readings measured percent reflectance of radiation at 660 and 830 nm, which were used to calculate the normalized difference vegetation index (NDVI) with the following formula:

$$\text{NDVI} = \frac{\text{Percent reflectance}_{830} - \text{Percent reflectance}_{660}}{\text{Percent reflectance}_{830} + \text{Percent reflectance}_{660}}$$

NDVI measurements were then correlated with living plant biomass using a site and date-specific regression. Each regression was based on radiometer readings of 3 to 5–0.10 m² reference plots adjacent to the study location which were selected to range from very low to very high plant abundances. Green vegetation in each reference plot was clipped, separated between grass and dicot, dried for 48 h at 60 °C, and weighed. Regressions averaged an *r* of 0.72 (± 0.03 SE; range: 0.55–0.92). Relative abundances of grass and dicot were based on clippings from these reference plots and used to apportion total ANPP between grass and dicot. ANPP is the sum of all increases in biomass from May to September.

We also quantified the die-off (plant senescence) that occurs over the late summer months after peak production in June. Percent plant senescence over the summer was determined from the ANPP data as $\left(1 - \frac{\text{lowest observed green biomass}}{\text{peak observed green biomass}}\right) \times 100$ (Belovsky and Slade pers. comm.). By subtracting $\frac{\text{lowest observed green biomass}}{\text{peak observed green biomass}}$ (the proportion of the total green biomass that remains after

die-off) from 1, we have a measure of how much of the June productivity peak was lost to die-off.

Vegetation composition was measured in June and September using a point frame sampler (Daubenmire 1947). Vegetation data were collected at 100 points (25 in each quadrant) in each 1 m² treatment plot. Plant individuals located at each point were identified to the species, or in the absence of a vascular plant individual, the point was classified as bare soil, litter, or moss/lichen. Data were used to calculate species richness, litter cover, and Shannon diversity.

Statistics

Data analyses were conducted using the R statistical software (Rstudio Team 2014). ANOVAs were employed to determine the effects of treatments on environmental conditions within the enclosures and randomized block (RB) ANOVAs were employed to examine factorial experimental results after data normality was ascertained. The block effect was used to account for potential underlying variation in replicate vegetation, despite efforts to place enclosures on a homogenous area of bunchgrass prairie. This factor was significant ($P < 0.05$) unless otherwise specified. Linear models (LM) were employed to examine hypothesized mechanistic explanations. Interaction terms were not significant ($P > 0.05$) unless specified.

Results

Minimum daily air temperature was significantly higher in the warming treatment plots in both 2014 and 2015 (ANOVA: $F = 43.76$, $df = 1$, $P < 0.001$). In 2014, the temperature was increased by 0.677 ± 0.002 °C (\pm SE) and in 2015, by 0.758 ± 0.001 °C (\pm SE), which did not differ between years (ANOVA, $F = 3.05$, $df = 1$, $P = 0.08$). The temperature in the ambient temperature treatment plots did not significantly differ from the ambient temperature outside of the experimental enclosures (ANOVA, $F = 1.36$, $df = 5$, $P = 0.27$). Soil moisture increased from $6.32 \pm 0.61\%$ (\pm SE) to $7.21 \pm 0.45\%$ (\pm SE) with supplemental precipitation in 2014 (ANOVA, $F = 9.89$, $df = 1$, $P = 0.002$, soil moisture data log transformed). The soil moisture in the ambient precipitation treatment plots did not significantly differ from the soil moisture outside the enclosures in 2014 (ANOVA, $F = 0.30$, $df = 1$, $P = 0.59$, soil moisture data log transformed). Extreme soil desiccation in 2015 prevented accurate soil moisture readings.

Supplemental precipitation significantly increased total ANPP, while the seasonality of supplemental precipitation (applied only in June versus June–August) had no effect (Table 1; Fig. 1a, b). ANPP with ambient precipitation was 245.12 ± 9.45 g/year/m² (\pm SE), while ANPP with supplemental precipitation was 262.67 ± 7.35 g/year/m² (\pm SE). The warming treatment applied over the summer months did not have a significant effect on total ANPP. Total ANPP was

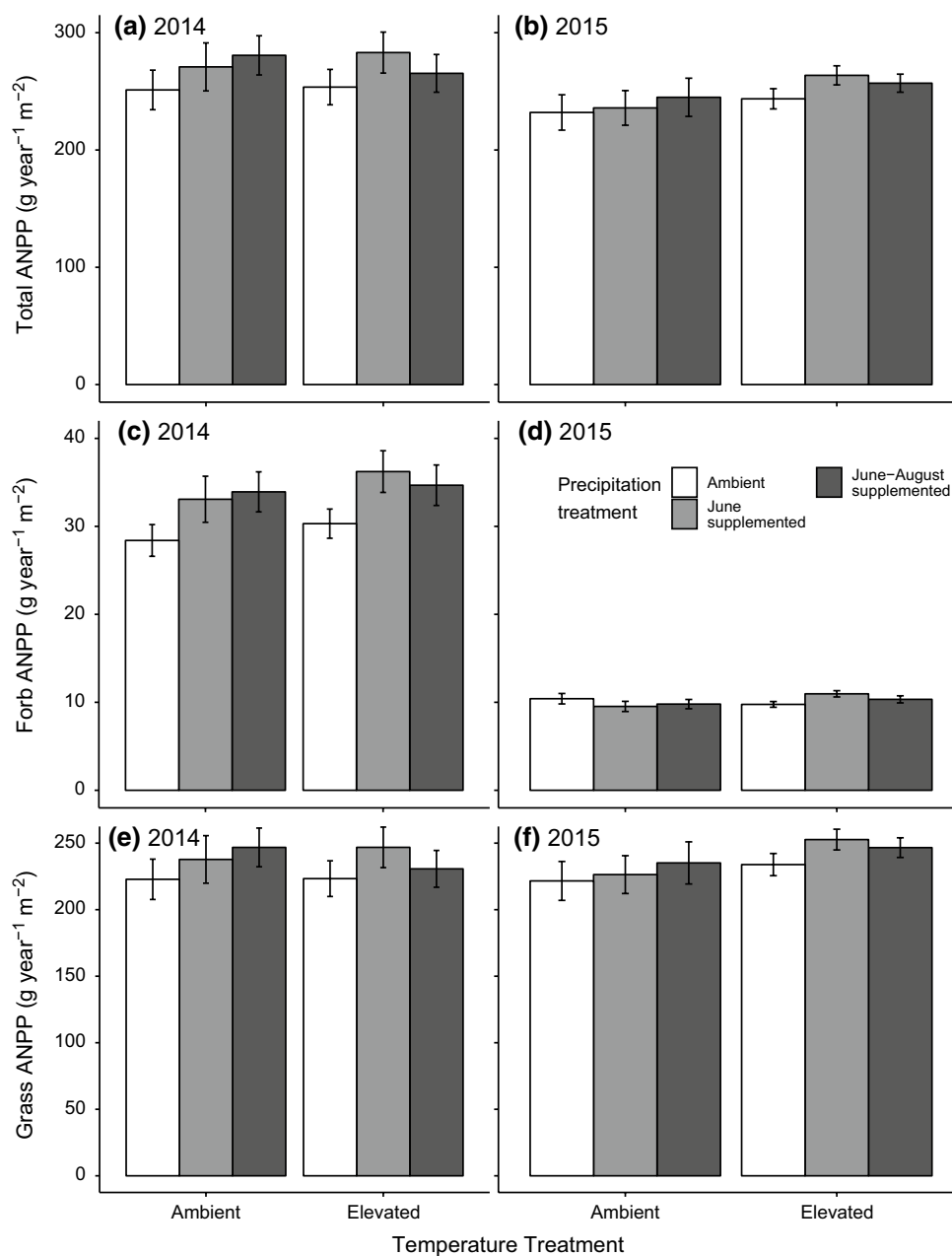
Table 1 Randomized block ANOVA results for ecosystem response variables—total ANPP, grass ANPP, forb ANPP, senescence, litter, Shannon diversity, and species richness

	Total ANPP			Forb ANPP			Grass ANPP					
	<i>df</i>	<i>F</i> value	<i>P</i>	<i>df</i>	<i>F</i> value	<i>P</i>	<i>df</i>	<i>F</i> value	<i>P</i>			
Temperature	1	2.32	0.13	1	1.97	0.17	1	2.09	0.16			
Seasonality	1	1.73	0.19	1	1.49	0.23	1	1.56	0.22			
Precipitation	1	7.20	0.01*	1	6.93	0.01*	1	6.34	0.02*			
Year	1	14.73	$\leq 0.001^*$	1	713.77	$\leq 0.001^*$	1	0.07	0.79			
Replicate	4	47.14	$\leq 0.001^*$	4	17.17	$\leq 0.001^*$	4	47.43	$\leq 0.001^*$			
	Senescence			Litter			Shannon diversity index			Species richness		
	<i>df</i>	<i>F</i> value	<i>P</i>	<i>df</i>	<i>F</i> value	<i>P</i>	<i>df</i>	<i>F</i> value	<i>P</i>	<i>df</i>	<i>F</i> value	<i>P</i>
Temperature	1	7.44	0.03*	1	4.60	0.04*	1	4.93	0.03*	1	4.99	0.03*
Seasonality	1	0.25	0.65	1	0.78	0.38	1	3.92	0.05*	1	12.06	$\leq 0.001^*$
Precipitation	1	1.61	0.21	1	0.18	0.67	1	0.19	0.67	1	0.67	0.42
Year	1	631.94	0.05*	1	14.00	$\leq 0.001^*$	1	1.62	0.21	1	0.61	0.44
Replicate	4	1.23	0.31	4	8.10	$\leq 0.001^*$	4	1.92	0.12	4	3.41	0.02*

Litter data and species richness data were log transformed to meet normality assumptions. Factors used in the analyses include the temperature treatment (ambient or elevated), precipitation treatment (ambient or elevated), seasonality of precipitation treatment (June or June–August), year of experimentation (2014 or 2015), and replicates (1–5)

*Significant at the 0.05 level

Fig. 1 Average ANPP (\pm SE) of the experimental warming and precipitation treatment combinations, with data presented from both years of experimentation. Data are shown for (a, b) total ANPP and with ANPP divided into (c, d) forb species and (e, f) grass species. For all three groupings, supplemental precipitation significantly increased ANPP [a $P=0.01$, b $P=0.01$, c $P=0.02$]



significantly higher in 2014. The same pattern was observed when total ANPP was broken down into grass ANPP and forb ANPP (Table 1; Fig. 1c, d, e, f). A significant interaction ($P=0.02$) between year and supplemental precipitation variables in the forb ANPP analysis indicated that supplemental precipitation only significantly increased forb ANPP in 2014.

The ratio of June precipitation to June average daily minimum temperature was a good predictor of total ANPP (LM: ratio—estimate = 5.80, $t=3.70$, $P<0.001$; Fig. 2). A significant interaction between the ratio and replicate in the linear model indicated that it was necessary to compare linear models for each replicate. Pairwise contrasts

indicated that regression slopes significantly differed between replicate 3 and replicate 1 ($P=0.03$) as well as between replicate 3 and replicate 2 ($P=0.01$). In these separate linear models, replicates 1, 2, and 5 had significant positive slope estimates ($P \leq 0.001$, $P<0.001$, and $P=0.006$, respectively), while slope estimates for replicates 3 and 4 were not significant. Analyses on the complete data set showed that the ratio of precipitation to average daily minimum temperature was a better predictor of ANPP than precipitation or temperature alone, as judged by Akaike's Information Criterion (ratio AIC: 540.18; precipitation AIC: 564.85; minimum temperature AIC: 567.95).

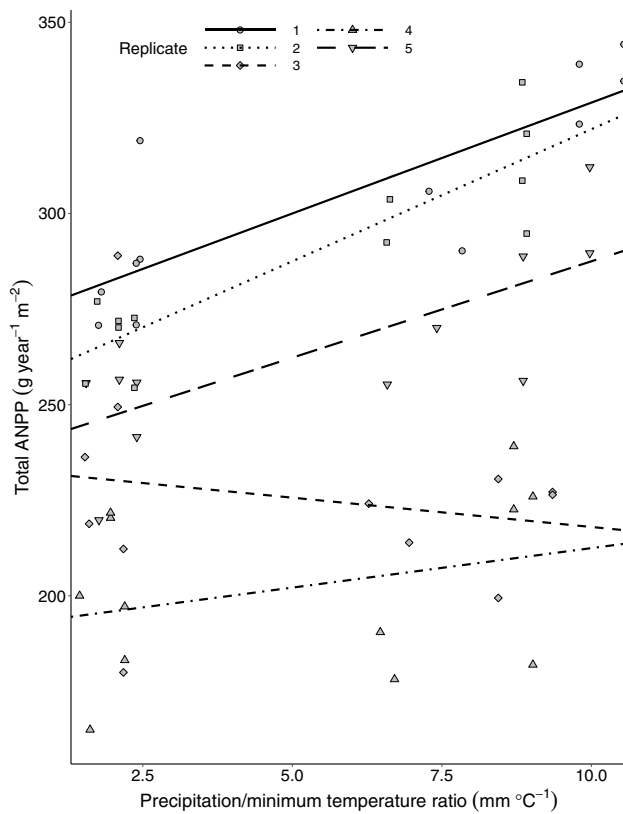


Fig. 2 Regression of total ANPP against the June precipitation to June daily average minimum temperature ratio. Separate linear regressions are shown for each replicate to account for the significant pairwise comparisons between some of the replicate slopes

Experimental warming increased plant senescence from $43.17 \pm 2.00\%$ (\pm SE) in ambient temperature plots to $45.57 \pm 2.22\%$ (\pm SE) in warmed plots (Table 1). Senescence was significantly greater in 2015 than 2014. Experimental warming also increased litter cover, the result of increased senescence (Table 1; litter data log transformed). Litter production accompanying the regular intra-seasonal die-off was increased by 47.82 ± 17.82 (\pm SE) percentage points in warmed compared to ambient temperature plots.

Warming led to significantly larger decreases in Shannon diversity than those that accompanied the regular intra-seasonal die-off (Table 1), with a $53.10 \pm 3.68\%$ (\pm SE) decrease from May to September in experimentally warmed plots and a $38.56 \pm 5.62\%$ (\pm SE) decrease from May to September in ambient temperature plots. Plots with extended supplemental precipitation had significantly lower Shannon diversity declines, a $36.67 \pm 6.26\%$ (\pm SE) decrease in diversity, compared to a $50.42 \pm 3.99\%$ (\pm SE) decrease without extended supplemental precipitation (Table 1). Species richness also decreased more from May to September with warming, but the significant interaction between warming and year variables ($P = 0.004$) indicated that this was only significant

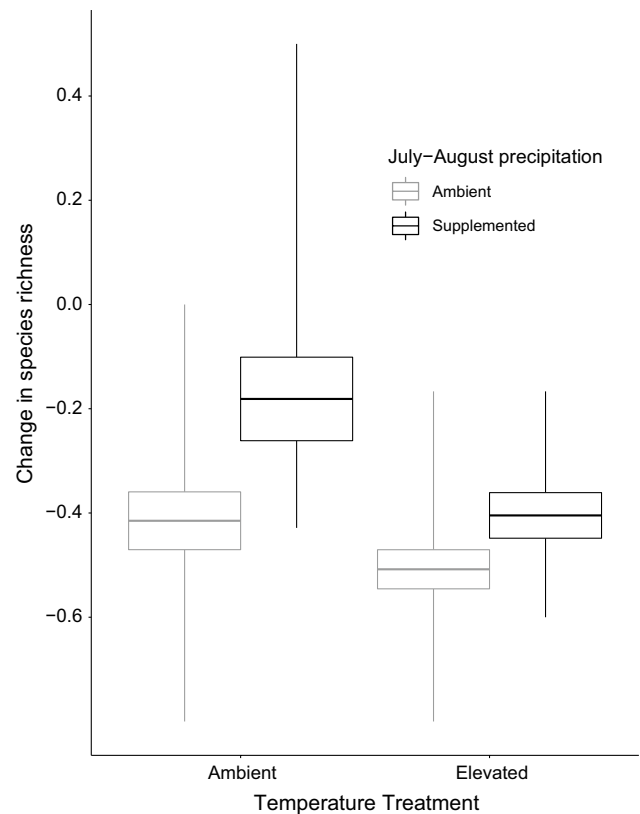


Fig. 3 Boxplot representation of the proportional change in species richness over the growing season for the experimental warming and extended supplemental precipitation treatments. In this boxplot, the box represents the mean \pm standard error. The upper whisker extends to the maximum data point, and the lower whisker extends to the minimum data point

in 2015 (Table 1; Fig. 3; richness data log transformed). Similar to diversity, the decline in species richness was significantly less with the extended supplemental precipitation treatment, $29.29 \pm 5.00\%$ (\pm SE), compared to plots without extended supplemental precipitation, $46.15 \pm 3.34\%$ (\pm SE).

Discussion

We found that ANPP increased with supplemental precipitation, when applied in June and across the whole summer, in our experimental manipulations. Senescence and the resulting increase in litter cover significantly increased in response to warming. Species richness and Shannon diversity had seasonal declines exacerbated by warming and lessened by extended supplemental precipitation. These results from our climate change manipulation experiment, on the whole, match the findings from the long-term ecological monitoring conducted at the NBR (Belovsky and Slade pers. comm.).

We hypothesize that the ratio of June precipitation to June average daily minimum temperature is critical, as

June is the time of peak plant production and a given amount of precipitation provides less water for plant growth as temperature increases due to increased evapotranspiration (Manske 2001; Belovsky and Slade pers. comm.). We used average daily minimum temperature to calculate ratio values as daily minimum temperatures were the target of the passive warming system, simulating the predicted increases in nighttime temperatures. Although studies of the effects of increasing minimum daily temperature on plant phenology and growth are less common than studies focused on average daily temperature, preliminary studies in crops show that rising minimum temperatures can have significant effects, potentially reducing biomass production and crop yield (Hartfield et al. 2011; Hartfield and Prueger 2015). Our ratio acts as a surrogate index, not a direct measure of evapotranspiration, reflecting how water available for plant growth is moderated by changes in temperature. Ratio values were highly correlated ($r=0.93$, $P<0.0001$) with precipitation minus Thornthwaite and Mather's potential evapotranspiration (P-PE), another measure of moisture excess or deficiency.

Grass and forb ANPP exhibited similar responses to experimental treatments as total ANPP, increasing with supplemental precipitation. Belovsky and Slade (pers. comm.) found that increases in ANPP over the course of their 35-year study were primarily driven by increases in grass ANPP, with grasses comprising $77.0 \pm 2.3\%$ (\pm SE) of total ANPP. We found that grasses remained the dominant functional group, with forb ANPP now accounting for only $6.0 \pm 2.0\%$ (\pm SE) of plot productivity. The time frame of the current study was too short to detect fine-scale plant community composition changes; however, Belovsky and Slade (pers. comm.) found that increases in grass ANPP were accompanied by increases in drought tolerant graminoid species such as wheat grasses (*Pseudoroegneria spicata*, *Pascopyrum smithii*), which have increased by 381% over the past 30 years.

Warming exacerbated the intra-seasonal die-off the bunchgrass prairie experiences, resulting in greater litter production. Though fire risk is historically low, elevated litter production combined with the increased probability of lightning with higher temperatures could alter bunchgrass fire dynamics (Romps et al. 2014; Belovsky and Slade pers. comm.).

Diversity and richness declines that occurred with the intra-seasonal die-off were amplified with warming. The seasonality of precipitation was also significant in determining the magnitude of the diversity and richness declines. Extended supplemental precipitation, which was applied into late summer, lessened intra-seasonal declines; however, historic climate data indicate that rainfall is becoming concentrated in early summer events (Belovsky and Slade pers. comm.). Without the late summer–early fall rains, the

bunchgrass prairie may experience exacerbated intra-seasonal diversity and richness declines.

Our results can be compared to those from climate manipulation experiments in other grassland ecosystems. Work at Konza Prairie (Kansas, USA) found increased precipitation led to increased cover and productivity, with a more significant response in drier areas of the tallgrass prairie (Collins et al. 2012). Climate change experiments at annual grasslands in Jasper Ridge (California, USA) found that supplemental precipitation increased total species richness and forb ANPP, with little effect on grasses (Zavaleta et al. 2003). In a meta-analysis of 85 global climate change experiments representing woody and herbaceous vegetation types, Wu et al. (2011) showed that increased precipitation increased ANPP by 28% on average. There is largely a qualitative agreement on the positive effect of increased precipitation on productivity in grassland ecosystems. The magnitude of this positive response, which likely depends on the level of water stress in the grassland, merits further study.

Grassland responses to experimental warming are more variable, but like precipitation, may be dependent on climate, with drier ecosystems showing larger ANPP responses to warming (Rustad et al. 2001; Fay et al. 2011; Wu et al. 2011). Fay et al. (2011) found that warming caused a ~5% decrease in tallgrass ANPP at Konza Prairie. At Jasper Ridge, Dukes et al. (2005) found no effect of warming on production, but suggested that warming may instead exert its effect on plant phenology by driving earlier senescence. Similarly, we found that warming alone exerted its effect through increased senescence and decreased species richness, not through effects on ANPP.

The response of plant productivity to individual climate change treatments has been well studied, but only 6 of the 85 studies in Wu et al.'s (2011) meta-analysis examined responses produced by the interaction of changes in precipitation and temperature. These multi-factor experiments found that the combined effects of changes in precipitation and temperature on productivity could not be solely predicted from the isolated effects of these climate variables (Wu et al. 2011). Our study supports this finding by illustrating the predictive value of the precipitation to minimum temperature ratio in the bunchgrass prairie, where increases in precipitation are moderated by increases in temperature. Belovsky and Slade (pers. comm.) noted in their long-term study that bunchgrass ANPP required more precipitation with temperature increases to compensate for evaporation. We have attempted to better quantify the interaction between temperature and precipitation using a ratio of their values, rather than assuming that their effects are additive. Future climate research could test the predictive value of this ratio in other grassland ecosystems.

The significance of water availability in xeric grasslands, demonstrated by the predictive value of the precipitation to

minimum temperature ratio, in combination with the historic trend of decreased annual precipitation, poses a new and exacerbating threat to an already threatened ecosystem. The seasonality of future changes in precipitation, in conjunction with annual climate trends, will be vital in determining future trends in bunchgrass productivity. Despite warming and annual decreases in precipitation, increases in June precipitation may provide the increased water availability necessary to stimulate ANPP.

Most importantly, we must remember that these changes in climate will not occur in isolation. Increased ANPP with increased June precipitation could support the population of grazing wildlife. However, the associated increase in senescence biomass due to warming and increased ANPP may put the ecosystem at risk. Fire suppression tactics may be necessary to preserve this threatened ecosystem and the bison-grazing habitat it provides while minimizing the risk of fire for surrounding agricultural areas.

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Author contribution statement All authors designed the study. ZV carried out field work, lab analyses, and data analysis. GB provided input on data analysis. ZV wrote the first draft of the manuscript, and all authors contributed to subsequent revisions.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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