Multiple global change drivers show independent, not interactive effects: a long-term case study in tallgrass prairie

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Abstract:

Ecosystems are faced with an onslaught of co-occurring global change drivers. While frequently studied independently, the effects of multiple global change drivers have the potential to be additive, antagonistic, or synergistic. Global warming, for example, may intensify the effects of more variable precipitation regimes with warmer temperatures increasing evapotranspiration and thereby amplifying the effect of already dry soils. Here, we present the long-term effects (11 years) of altered precipitation patterns (increased intra-annual variability in the growing season) and warming (1 °C year-round) on plant community composition and aboveground net primary productivity (ANPP), a key measure of ecosystem functioning in mesic tallgrass prairie. Based on past results, we expected that increased precipitation variability and warming would have additive effects on both community composition and ANPP. Increased precipitation variability altered plant community composition and increased richness, with no effect on ANPP. In contrast, warming decreased ANPP via reduction in grass stems and biomass but had no effect on the plant community. Contrary to expectations, across all measured variables, precipitation and warming treatments had no interactive effects. While treatment interactions did not occur, each treatment did individually impact a different component of the ecosystem (i.e., community vs. function). Thus, different aspects of the ecosystem may be sensitive to different global change drivers in mesic grassland ecosystems.

Keywords: Altered precipitation | Annual net primary production (ANPP) | Compound global change drivers | Plant community | Warming

Article:

Introduction

Global change drivers are altering ecosystem function in complex and varied ways (Turner et al. 2020; Avolio et al. 2020). Moreover, global change drivers are not occurring in isolation (Tylianakis et al. 2008; Leuzinger et al. 2011), and in combination their effects may be additive (i.e., not interact), antagonistic (dampen one-another's effects), or synergistic (amplify one-another's effects). Thus, studies that examine multiple co-occurring global change drivers are critical for predicting their full effects on ecosystem structure and functioning. Recent synthesis work has shown that plant community responses to global change drivers tend to be larger when global change drivers are manipulated in combination (Komatsu et al. 2019). Importantly, global change is multifaceted and includes change in both plant resources and non-resource environmental factors (Vitousek 1994), and a non-resource manipulation-like temperature or mowing can interact with global change driver-driven resource changes to magnify (Koerner and Collins 2014) or dampen its effect (Avolio et al. 2021).

Climate change models predict an increase in global average air surface temperature by 1.5 °C within the next 20 years (IPCC 2021), with these increases already evident (e.g., 7 of the last 10 years are the warmest on record (Blunden and Boyer 2021)). In addition, climate change models predict an intensification of the global hydrological cycle (IPCC 2021). Indeed, observed precipitation trends worldwide support predictions of increased precipitation extremes (Durack et al. 2012; Marvel et al. 2017; Yettella and Kay 2017; Hawcroft et al. 2018). These extremes are associated with shifts in intra-annual rainfall patterns often characterized by increased heavy rainfall events from high energy convective systems, fewer events overall (thus more dry days), and longer intervening dry periods between events.

(Karl and Trenberth 2003; Huntington 2006; Min et al. 2011; Janssen et al. 2014). Warming and intensified precipitation regimes could be expected to act additively or synergistically, perhaps by amplifying feedback cycles (Brook et al. 2008; Yuan and Chen 2015; Jackson et al. 2016) with warmer days increasing evapotranspirational fluxes and thereby amplifying the effect of already dry soils. Such synergistic effects of combining warming and altered precipitation variability is likely to be particularly important for ecosystems that are already water-limited, such as grasslands (Sala et al. 1988; Knapp and Smith 2001).

While the ecological effects of experimental manipulations of precipitation and temperature frequently are studied independently, the combination is rarer. Globally, climate change will lead to both gains and losses of species that vary with region (Vellend et al. 2013; Harrison 2020), and the magnitude of change in richness at a site will depend in part on current temperature and aridity, with more arid sites showing decreases and colder sites showing increases in richness with warming (Sommer et al. 2010; Harrison 2020). Similarly, at a global scale warming is predicted to increase ANPP by 19% (Rustad et al. 2001); however, this positive influence tends to be in colder latitudes (Rustad et al. 2001) with warming decreasing ANPP (Wu et al. 2021) or having no significant effect on ANPP (Wang et al. 2019) in most temperate grasslands. In addition, there is now abundant evidence that event size, number, and timing each may influence ecological responses independent of total precipitation amount (e.g., Cherwin and Knapp 2012; Kulmatiski and Beard 2013; Avolio and Smith 2013; Eekhout et al. 2018; Hammerl et al. 2019; Chen et al. 2019; Mitchell et al. 2020; Post and Knapp 2021). For example, increased precipitation variability resulted in increases in forb abundance and richness in tallgrass prairie, (Knapp et al. 2002; Jones et al. 2016), as well as decreased ANPP (Knapp et al. 2002; Fay et al. 2011; Slette et al. 2021), even though total precipitation was not altered. These studies show how the independent effects of precipitation variability and warming can be significant, yet how global change drivers interact to impact plant community structure and function remains under explored.

To address how forecast changes in precipitation variability and warming impact grassland ecosystem function and plant community dynamics we monitored species composition, ANPP, and stem densities in the Rainfall Manipulation Plots (RaMPs) for 11 years. The Rainfall Manipulation Plots were established in 1997 to manipulate intra-annual rainfall variability in native tallgrass prairie. The Rainfall Manipulation Plots treatments increased rain event size while decreasing event frequency, relative to ambient rainfall patterns, without altering total growing season rainfall (Fay et al. 2000). This increased intra-annual variability a greater number of high soil moisture pulses throughout the growing season (Knapp et al. 2002; Fay et al. 2011). In 2003, a warming treatment was initiated which increased ambient temperatures by ~ 1–2 °C year round (Fay et al. 2011). Overall, we hypothesized that (1) warming and altered precipitation would additively interact to impact composition, structure, and function of the plant community, and (2) the effects of treatments on the plants would be moderated by how warming and increased precipitation variability affected soil moisture variability.

Methods

Study Site

Konza Prairie Biological Station (Konza), located in the Flint Hills of northeastern Kansas, is a 3,487-ha native unplowed tallgrass prairie Long-Term Ecological Research site. Perennial C4 grasses including Andropogon gerardii and Sorghastrum nutans dominate the plant community, accounting for the majority of herbaceous primary productivity (Knapp et al. 1998), while subdominant forbs generally yield the diversity (Collins and Glenn 1991). With a mean annual precipitation of 835 mm/year and monthly air temperature in July of 27 °C the climate is temperate. Approximately 75% of precipitation falls as rain during the May–Sept growing season, but variation from average precipitation patterns is common, both in yearly totals and seasonal distribution (Hayden 1998).

Experimental design and data collection

The Rainfall Manipulation Plots (RaMPs) experiment ran from 1998 to 2013 in lowland native tallgrass prairie (Slette et al. 2021). Twelve fixed-location rainout shelters, arranged in three blocks, were established in 1997 with treatments beginning in 1998. All shelters excluded and collected natural rainfall inputs from the plots, and collected rainfall was then reapplied at different frequencies and different event sizes to create ambient ($n = 6$) and altered ($n = 6$) rainfall treatments. The ambient treatment mimicked size and frequency of natural rainfall events. The altered precipitation treatment increased rain event size while decreasing event frequency, lengthening the dry intervals by 50% relative to ambient patterns (Fay et al. 2000). The 50% increase in the length of dry intervals was chosen, because matched predictions by many climate change models for the region at that time (Waggoner 1989; Houghton et al. 1990). Event sizes were larger going from an average of ~ 15 mm to ~ 40 mm, with small events becoming very infrequent (Fay et al. 2011). Fay et al. (2000, 2011) provide further details on shelter design and efficacy. The altered precipitation treatment results in more variable within-season precipitation patterns and soil moisture regimes, with increased fluctuations between high and low soil water availability (Knapp et al. 2002; Fay et al. 2011). A key strength of this experiment is that there was no difference in total growing season rainfall between ambient and altered rainfall treatments, and thus, alterations in precipitation patterns and variability are not confounded by changes in total precipitation amount (Knapp et al. 2002). Nested within each rainout shelter a warming treatment which increased growing season temperature by ~ 1 °C was imposed from 2003 to experiment completion in 2013. Fay et al. (2011) detail warming infrastructure design and efficacy. The

Rainfall Manipulation Plots were located in ungrazed lowland prairie that is burned annually in late March. The dominant plant species in the plots include A. gerardii, S. nutans, and Panicum virgatum, all rhizomatous, warm-season, C4 tall grasses. Dominant perennial forbs include Solidago canadensis, Aster ericoides, and S. missouriensis. Productivity in the Rainfall Manipulation Plots averaged 725 g m−2 with approximately 25% of the productivity derived from forbs (unpublished data).

Under each Rainfall Manipulation Plot shelter, two 2 × 2 m plots were used for plant sampling (one ambient and one warmed). Precipitation amounts applied to all plots were recorded throughout the growing season each year. Volumetric soil water content was measured throughout the growing season for each year for each plot in each Rainfall Manipulation Plot using 30-cm time-domain reflectometry (TDR) probes (Campbell Scientific) buried 0.50 m from the edge of each subplot at a 45° angle to sample 0–15 cm soil depth. Data were recorded in 30-min intervals using a Campbell CR10X data logger. Each plot was divided into four 1 × 1 m subplots. In each subplot each year, we record the cover of each plant species visually estimated to the nearest 1%. We do this twice during each growing season (June and August) to capture peak cover of cool and warm season species, keeping the maximum value. All metrics were calculated using the maximum cover values of each species for the entire growing season. Cover data for each species on the 1-m2 scale (Daubenmire 1959) were used to compute standard metrics of community structure, including grass, forb, and total species richness, Shannon–Weiner diversity (Shannon 1948; Šigut et al. 2017), evenness (Evar) (Smith and Wilson 1996), all using the codyn 2.0.5 package (Hallett et al. 2016; Avolio et al. 2019). Evar was chosen as a measure of evenness as it is more decoupled from richness than other measures (Smith and Wilson 1996). Once metrics were calculated at the 1-m2 subplot level, the mean of the four subplots was taken. At the end of each growing season all aboveground biomass was collected from three 0.1 m2 plots nested within the warmed plots and external the ambient plots but directly adjacent. Biomass was sorted by growth form and weighed to determine aboveground net primary production (ANPP). As the site was annually burned with no previous years' dead material, this provides an accurate estimate of ANPP (Knapp et al. 2007). To provide an additional mechanistic response variable, stem density counts for all species were performed in two 0.1 m2 (20 × 50 cm) plots nested within two species composition subplots of each of the ambient and warmed plots within each Rainfall Manipulation Plot in early June and again in mid-August of each year. Metric calculations and all data manipulation occurred in R (v4.0.4; R Foundation for Statistical Computing, Vienna, Austria) using and tidyverse 1.3.1 (Wickham et al. 2019) packages.

Statistical analyses

Effects of precipitation treatment, warming treatment, and year on soil moisture and coefficient of variation (CV) of soil moisture (log transformed) were tested using mixed-model repeated-measures ANOVAs. Likewise, mixed-model repeated-measures ANOVAs were used to examine the effects of precipitation treatment, warming treatment, and year on ANPP (forb, grass, total) and both spring and fall stem density (forb, grass, and total) at the neighborhood (0.1 m2) scale. The effects of precipitation treatment, warming treatment, and year on plant community diversity at the stand (1 m2) scale were also tested using mixed-model repeated-measures ANOVAs. Three measures of plant community diversity were tested—richness (S), evenness (Evar), and the antilog of Shannon's diversity (H')—for the total plant community as well as forb and grass communities separately. All analyses were done using data from 2003 to 2013 except spring stem density which was missing data from 2003 and 2008 and fall stem density which was missing data from 2003, 2004, 2008, and 2011. All repeated measures mixed model ANOVAs were performed in SAS using the MIXED procedure with year as a repeated effect and precipitation and warming treatments as the main effects (v.9.3; SAS Institute, Cary, NC, US). In addition, the effects of the treatments on community composition within a given year were assessed using multivariate techniques. Due to differences in spatial arrangement between warmed and ambient temperature plots, only half the subplots were used in this analysis—keeping the two subplots of each plot which were arranged in a comparable way. The last year of data, 2013, is shown via a nonmetric multidimensional scaling plot with accompanying ADONIS and PERMDISP to test for differences in mean and dispersion, respectively. Only main effects were tested with PERMDISP as there was no significant interaction between treatments for mean differences in location (i.e., ADONIS). Multivariate analyses were conducted in R (v4.0.4) using the package vegan 2.4–2 (Dixon 2003). Finally, univariate linear regressions using the package stats 4.2.0 (R Core Team 2021) were used to explore the relationship between soil moisture and coefficient of variation of soil moisture on richness and ANPP.

Results

Treatment effects on community variables

Altered precipitation variability had a stronger impact on the plant community compared to warming (Table 1; Fig. 1). The altered precipitation treatment increased species richness and diversity. This change in richness was due to increases in both forb and grass species (Figure A2). Warming on the other hand did not have a meaningful impact on any of the three measures of plant community structure (Table 1; Fig. 1). The warming treatment did decrease richness but only in 1 out of 11 years and by less than one species, and no significant effect of warming was found on plant community evenness or diversity. Similarly, plant community composition was significantly different in the ambient vs. increased precipitation variability treatments in 7 out of 11 years [corrected for multiple comparisons using the Benjamini–Hochberg method (Benjamini and Hochberg 1995)], while plant community composition was never significantly affected by the warming treatment. As an example, in 2013, the last year of the experiment, the altered precipitation treatment significantly shifted the plant community composition (ADONIS: F.Model = 2.90570, $R2 = 0.12096$, p value = 0.01), whereas the effect of the warming treatment (ADONIS: F.Model = 0.47414, $R2 = 0.01974$, p value = 0.88) and the interaction between the two treatments (ADONIS: F.Model = 0.64257, $R2 = 0.02675$, p value = 0.74) were not significant. Altered precipitation variability also increased dispersion (PERMUTEST: $F = 9.5861$, p value = 0.004), with warming having no effect (PERMUTEST: $F = 0.744$, p value = 0.427).

Treatment effects on productivity and stem density

Although altered precipitation had greater impacts than warming on the plant community, an opposite pattern was observed for annual net primary productivity (ANPP). Aboveground net primary productivity was significantly and negatively impacted by warming, primarily due to decreases in grass biomass, while the altered precipitation treatment had no significant impact on ANPP (Table 2; Fig. 2). Similarly, stem density of the plant community in both spring and fall was significantly decreased due to warming, primarily due to a decrease in grass stem densities, while

Table 1 Effects of precipitation (precip, P), Warming (warm, W), and time (year, Yr) on plant community structure (richness (S), evenness (Evar), the antilog of Shannon's diversity (H') at the stand (1 m2) scale from mixed-model repeated-measures ANOVAs.

Variable	Richness			Evenness (Evar)			Diversity (H')		
	df	*F* value	*P* value	df	*F* value	*P* value	df	*F* value	*P* value
Precip	**1, 9.53**	**15.51**	**0.003**	1, 10	0.33	0.577	**1, 9.76**	**8.24**	**0.017**
Warm	1, 10	0.81	0.389	1, 10	4.86	0.052	1, 10	0.02	0.890
Year	**10, 50.7**	**10.07**	**< 0.001**	**10, 100**	**16.54**	**< 0.001**	**10, 50.1**	**45.33**	**< 0.001**
P*W	1, 10	0.16	0.696	1, 10	0.48	0.503	1, 10	0.28	0.611
P*Yr	10, 49.7	1.35	0.233	10, 100	0.32	0.976	10, 49.9	0.86	0.577
W*Yr	**10, 100**	**3.15**	**0.002**	10, 100	0.97	0.472	10, 100	0.83	0.605
P*W*Yr	10, 100	10, 100	10, 100	10, 100	10, 100	10, 100	10, 100	10, 100	10, 100

Data were used from 2003 to 2013. Shown are the F values and p values. Significant differences ($p \leq 0.05$) are bolded.

while the altered precipitation treatment had no effect on total stem density, grass stem density, of forb stem density (Table 3; Fig. 3).

Potential indirect effects of treatments through changes in soil moisture and soil moisture CV

Overall, the warming treatment decreased mean soil moisture, while altered precipitation increased soil moisture variability measured as CV (Table A1; Figure A1). There was no significant interaction between the warming and altered precipitation treatments on soil moisture, but both treatments significantly interacted with year. The altered precipitation treatment decreased mean soil moisture significantly in 3 of 11 years and increased soil moisture variability significantly in 6 of 11 years. Warming decreased mean soil moisture in 7 of 11 years but had mixed effects on soil moisture variability depending on the year (decrease in 1 out of 11 years and increase in 2 out of 11 years).

Overall, when either treatment produced a significant response in plants, this appeared to be driven predominantly by changes in soil moisture (Fig. 4). Across all treatments and years, higher growing season soil moisture was correlated with an increase in ANPP (ANPP = 448 + 1205*SM), while greater CV of soil moisture was negatively correlated with ANPP (ANPP = 988–698*CV). Richness was impacted only by mean growing season soil moisture, with higher soil moisture being correlated with richness (Richness = 10.84 + 12.22*SM).

Discussion

Lack of interactive treatment effects

Contrary to expectations, we detected no interactive effects of increased precipitation variability and year-round warming on any of the variables measured. While neither treatment was extreme (Smith 2011a, b), they were realistic for the predicted future (IPCC 2021). Hoover et al. (2014) also found no interactive effects of an extreme 2 year drought and an extreme 2-week heatwave, suggesting that the extremity of treatment is not the reason for a lack of interactive effects. Similarly, in a mesic semi-natural grassland in Germany, Grant et al. (2017) found no interactive effects of increased precipitation variability (summer or winter drought) and seasonal warming (summer or winter). Collectively, these findings suggest that the effects of simultaneous multiple global change drivers (e.g., increased precipitation variability and warming) may be equivalent to the individual effects in temperate ecosystems.

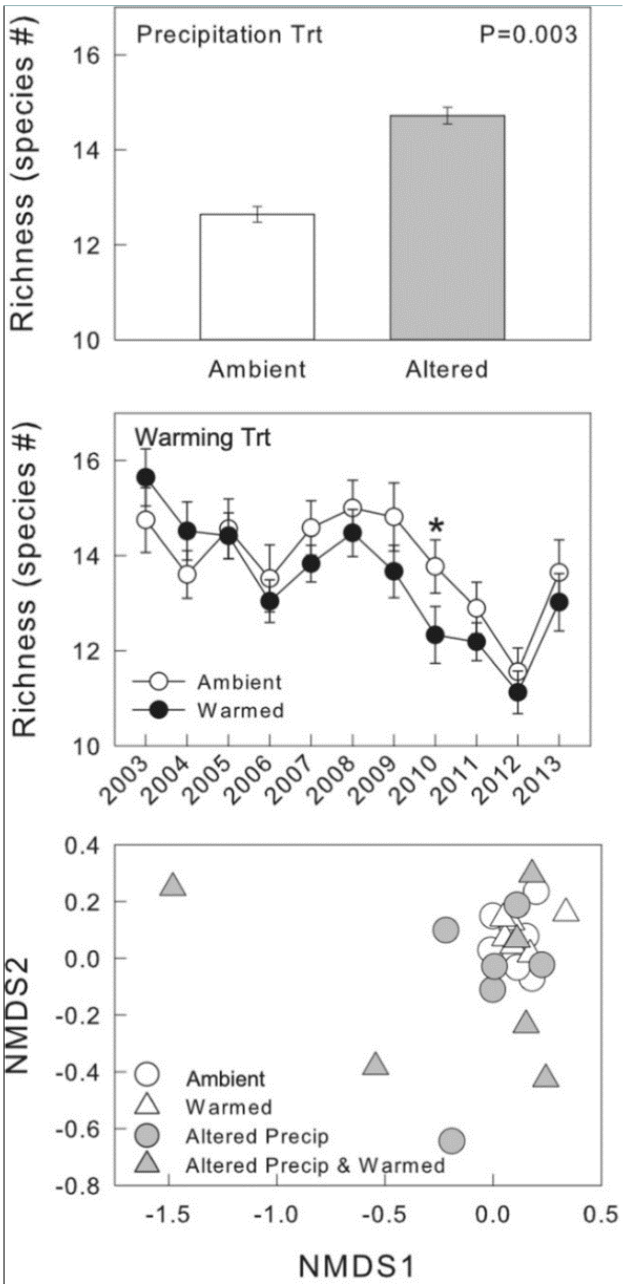

Fig. 1 Effects of precipitation and warming treatments on the plant community. Richness response to precipitation (top) and warming (middle) treatment at the stand (1 m2) level. Richness (S) was calculated per subplot (1 m2) and then averaged across the four subplots of a treatment in a Rainfall Manipulation Plot to obtain a single value for each warming treatment in a Rainfall Manipulation Plot. The interactive effects of precipitation and warming were not significant. If year X treatment was significant, trends through time are shown; however, when year X treatment was not significant, main effects are shown. See Table 1 for statistics. Shown are means with error bars representing standard error (± SE). When main effects were significant, the p value is listed in the upper left corner. N.S. not significant. When year X treatment effects were significant, * represent significant differences between the treatment and ambient in that year ($p < 0.05$). Nonmetric multidimensional space plot (bottom) of the plant community in 2013 (last year of experiment; stress = 0.124). Centroid means were significantly different due to the precipitation treatment but not the warming treatment.

Treatments independently impact different aspects of the ecosystem

Increased precipitation variability affected community composition. Richness increased due to the altered precipitation treatment, and plant community composition shifted and became more variable. Warming caused an overall decrease in ANPP, primarily driven by decreases in grass

ANPP. This corresponded with a decrease in stem density (again driven by grasses), but not changes in composition. Our findings suggest that plant community responses driven by realistic climate changes do not necessarily lead to functional responses. The responses of ecosystem functions such as ANPP to global change drivers are a result of individual plant physiological responses as well as plant community shifts. The importance of these two mechanisms may differ through time; however, both are predicted to cause changes in function (Smith et al. 2009). For example, if rainfall increases within a given year, the extant plant community all grows larger increasing ANPP, but after time, the plant species identities may shift either losing species or shifting the abundance of species causing a shift in ecosystem functioning due to the indirect effects of plant community change (Collins et al. 2012; Knapp et al. 2012; Wilcox et al. 2016). Long-term data sets which encompass plant community shifts are critical for capturing the full magnitude of global change driver effects on ANPP. However, in this study, the ANPP responses seem to correspond with changes in plant demography not compositional shifts, and even when composition shifts in abundance were observed, they do not appear to correspond with ANPP responses. Jones et al. (2016) showed the changes in composition in these plots under the altered precipitation treatment were primarily driven by an increase in forb species. Seventy-five percent of the ANPP at this site is contributed by grasses, with forbs playing a minor role in this function. Potentially, the effects of altered precipitation on this component of the community did not translate to functional changes due to the subdominant role of forbs.

Table 2 Effects of precipitation (precip, P), warming (warm, W), and time (year, Yr) on ANPP (total, grass, and forb) from mixed-model repeated-measures ANOVAs using data from 2003 to 2013.

Variable	**Total**			**Grass**			**Forb**		
	df	***F* value**	***P* value**	**df**	***F* value**	***P* value**	**df**	***F* value**	***P* value**
Precip	1, 9.99	0.10	0.762	1, 10	0.03	0.861	1, 10.2	0.31	0.588
Warm	**1, 10.1**	**11.23**	**0.007**	1, 11.4	3.50	0.087	1, 13.1	4.36	0.057
Year	**10, 74.1**	**30.79**	**< 0.001**	**10, 70.4**	**26.51**	**< 0.001**	**10, 63.3**	**26.31**	**< 0.001**
P*W	1, 10.1	0.47	0.508	1, 11.4	0.02	0.884	1, 13.1	0.19	0.672
P*Yr	10, 74.1	0.97	0.479	10, 70.4	0.58	0.825	10, 63.3	1.05	0.412
W*Yr	**10, 65.1**	**2.56**	**0.011**	**10, 62.1**	**3.55**	**0.001**	10, 71.7	0.80	0.629
P*W*Yr	10, 65.1	0.53	0.860	10, 62.1	1.40	0.202	10, 71.7	0.82	0.606

Shown are the F values and p values. Significant differences ($p \leq 0.05$) are bolded.

The negative warming effects seen here on ANPP appeared to be the direct influence of heat on primary production via changing plant photosynthesis and growth (Shaver et al. 2000; Luo 2007). Surprisingly at the same site, Hoover et al. (2014) found that 2 years of a 2-week extreme heatwave, raising temperatures ~ 7 °C, did not impact ANPP. In contrast to the findings of both Hoover et al. (2014) and this study, Grant et al. (2017), by imposing both winter and summer warming treatments, found that ANPP actually increased under warming with the strongest response occurring with winter warming. These incongruous results suggest that the timing and duration of warming may strongly impact ecosystem responses.

In addition to differences in treatment magnitudes and timing, environmental context might also influence the findings seen here. This mesic grassland receives ~ 835 mm of precipitation a year and experiences moderate levels of inter-annual variability in precipitation (Hayden 1998). It might be expected to see stronger magnitude of response to the same treatments imposed here at sites, where water is a stronger limiting factor and/or the plants are more adapted to variability in resource supply. For example, in Chihuahuan Desert grassland in New Mexico (MAP = 250 mm/year and high interannual variability), changes in rainfall timing (not mean changes) which yielded longer dry periods but bigger rainfall events increased ANPP by ~ 33% (Thomey et al. 2011). In addition, this site was annually burned throughout the experiment. Annual burning promotes the dominance of C4 grasses and limits diversity of forbs to only those that can compete with or tolerate the shade created by C4 dominance (Collins et al. 2021). Annual burning may have constrained the richness responses seen here by preventing establishment of less competitive forbs species. While a less frequent burning regime may have seen a greater magnitude of change, it is important to note that annual burning is common practice for tallgrass prairie for cattle management (Ratajczak et al. 2014). And last, it is important to consider the long-term nature of this data set. For example, others using this experiment have found significant effects of the precipitation treatment on ANPP (Knapp et al. 2002; Fay et al. 2011; Slette et al. 2021). This discrepancy is likely due differences in the years included. This analysis focuses on the years of the warming treatment only, which corresponds with the lack of response seen in Fay et al. (2011) in Phase II of this experiment. In addition, past reported differences due to precipitation variability, while significant, were small in magnitude (14% (Slette et al. 2021), 10% (Knapp et al. 2002; Fay et al. 2003)), with differences occurring more often in early years (before the scope of this analysis). This suggests that while there was an initial functional response, it diminished through time. These contexts must be taken into consideration when interpreting results from global change experiments.

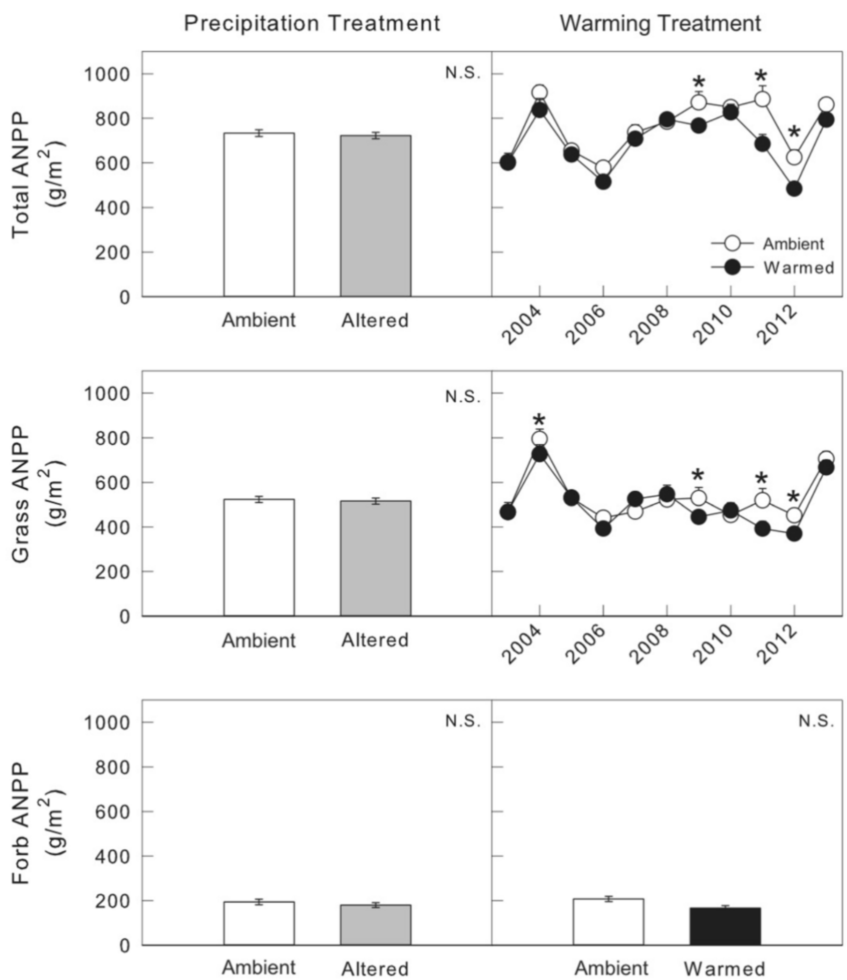

Fig. 2 Effects of precipitation (left) and warming (right) on total (top), grass (middle), and forb (bottom) annual net primary production (ANPP). The interactive effects of precipitation and warming were not significant. If year X treatment was significant, trends through time are shown; however, when year X treatment was not significant, main effects are shown. See Table 2 for statistics. Shown are means with error bars representing standard error (± SE). * represent significant differences between the treatment and ambient in that year ($p < 0.05$). N.S. not significant.

Potential indirect effects of treatments through changes in soil moisture and soil moisture CV

We hypothesized that the two treatments would yield additive effects primarily by decreasing soil moisture availability and increasing the magnitude of the dry periods. However, there were no interactive effects on either mean soil moisture or its variability which may explain why we saw no interactive effects of treatments on any of the response variables measured. We also hypothesized that treatment effects would mainly be the result of changes in soil moisture variability (i.e., CV of soil moisture). However, interestingly, mean changes in soil moisture were more strongly correlated with changes in ANPP or richness compared to changes in soil moisture CV. Both ANPP and richness increased with increasing soil moisture, suggesting that increased resource availability benefited both metrics. We hypothesize that the increased soil moisture led to increased soil resources to support more species of plants, but which species established differed by plot yielding the increased variance in composition seen.

Table 3 Effects of precipitation (precip, P), warming (warm, W), and time (year, Yr) on stem density (total, grass, and forb) at the neighborhood (0.1 m2) scale from mixed-model repeated-measures ANOVAs on spring and fall stem density measures using data from 2003 to 2013 (minus 2003 and 2008 for spring and minus 2003, 2004, 2008, and 2011 for fall due to missing data)

Season	Variable	**Total Stems**			**Grass Stems**			**Forb Steams**		
		df	***F* value**	***P* value**	**df**	***F* value**	***P* value**	**df**	***F* value**	***P* value**
Spring	Precip	1, 10.1	0.26	0.620	1, 10.2	0.09	0.772	1, 28.4	3.36	0.077
	Warm	**1, 22.1**	**18.94**	**< 0.001**	**1, 20.2**	**14.68**	**0.001**	1, 28.4	0.51	0.482
	Year	**8, 118**	**28.33**	**< 0.001**	**8, 120**	**25.37**	**< 0.001**	**8, 140**	**10.07**	**< 0.001**
	P*W	1, 22.1	2.40	0.136	1, 20.2	0.87	0.363	1, 28.4	2.64	0.115
	P*Yr	8, 118	1.21	0.302	8, 120	1.12	0.353	8, 140	1.22	0.291
	W*Yr	8, 118	0.97	0.461	8, 120	1.24	0.284	8, 140	0.75	0.645
	P*W*Yr	8, 118	0.63	0.751	8, 120	0.64	0.744	8, 140	0.48	0.872
Fall	Precip	1, 10.2	0.20	0.661	1, 10.2	0.06	0.814	1, 10.6	3.34	0.096
	Warm	**1, 16.1**	**15.41**	**0.001**	**1, 15.1**	**13.26**	**0.002**	1, 20.9	0.19	0.666
	Year	**6, 91.9**	**21.21**	**< 0.001**	**6, 92.3**	**19.84**	**< 0.001**	**6, 95.1**	**8.08**	**< 0.001**
	P*W	1, 16.1	0.99	0.335	1, 15.1	0.23	0.637	1, 20.9	3.40	0.079
	P*Yr	**6, 91.9**	**2.41**	**0.033**	**6, 92.3**	**2.26**	**0.045**	6, 95.1	1.59	0.157
	W*Yr	**6, 91.9**	**2.39**	**0.034**	**6, 92.3**	**2.57**	**0.024**	6, 95.1	0.35	0.908
	P*W*Yr	6, 91.9	0.29	0.939	6, 92.3	0.28	0.946	6, 95.1	0.22	0.971

Shown are the F values and p values. Significant differences ($p \leq 0.05$) are bolded.

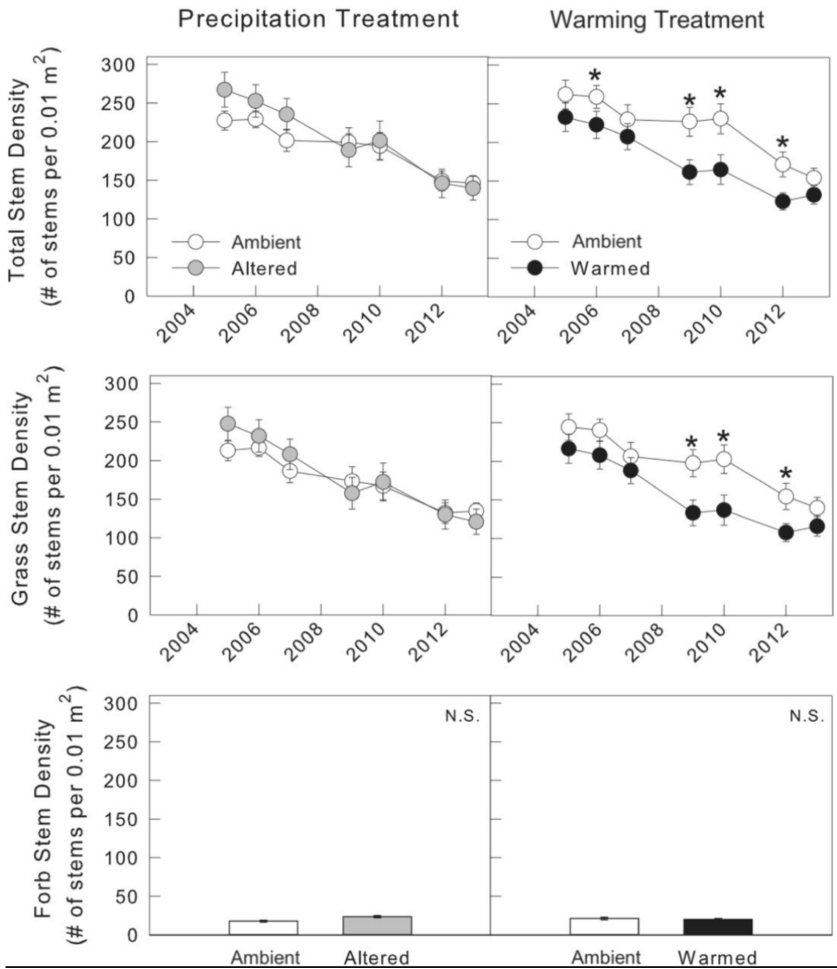

Fig 3. Effects of precipitation (left) and warming (right) treatment on total (top), grass (middle), and forb (bottom) stem density in the fall at the neighborhood (0.01 m2) scale. The interactive effects of precipitation and warming were not significant. If year X treatment was significant, trends through time are shown; however, when year X treatment was not significant, main effects are shown. See Table 3 for statistics. Shown are means with error bars representing standard error (± SE). * represent significant differences between the treatment and ambient in that year ($p < 0.05$). N.S. not significant.

Conclusions

This unique manipulation of multiple co-occurring global change drivers over more than a decade led to several important findings. First, we found no interactive effects between increased precipitation variability and warming suggesting that the effects of realistic multiple global change drivers may be equivalent to the individual effects in temperate ecosystems. Second, we found that different aspects of the ecosystem may be sensitive to different drivers (i.e., plant community was more responsive to precipitation changes, while function was more response to warming). Third, we found that changes in mean soil moisture were more closely related to changes in response variables than was the CV of soil moisture, suggesting mean might be a stronger driver than variability at the magnitudes examined here. While both warming and increased variability in precipitation, two forecast predictions of climate change, induced change in plant composition and ANPP, respectively, the magnitude of responses observed were relatively small and/or only occurred sporadically during the 11-year duration of the experiment, suggesting that on the whole, this system is relatively resistant to decade-scale changes in precipitation variability and warming. These grasslands are relatively well-adapted to climate variability, with inter-annual variability in precipitation being very large (Knapp and Smith 2001) and with a history of periodic drought (Blair et al. 2014). As long as climate shifts remain small, these grasslands appear to be resistant both in plant composition and ecosystem functioning.

Data availability

All data are publicly available on the Konza LTER website (http://lter.konza.ksu.edu/data).

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MDS, JMB, AKK conceived and designed the experiment. MLA and MDS performed the experiment, and SEK analyzed the data and wrote the manuscript. All authors contributed to analyses and edited the manuscript.

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Ethics declarations

Conflict of interest

The authors declare that they have no conflict of interest.

Ethical approval

This article does not contain any studies with human participants or animals performed by any of the authors.

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