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Contrasting effects of precipitation manipulations in two Great Plains plant communities

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Abstract

Question: Anthropogenic climate change is altering temperature and precipitation in grasslands worldwide. As grasslands are primarily water-limited, these changes in climate will likely have dramatic impacts on ecosystem function and community structure, yet the magnitude of change and the types of species favoured may differ among ecosystems or even among local communities within ecosystems. How much might plant community responses to altered precipitation vary at two sites within one grassland region?

Location: Semi-arid and sub-humid natural grasslands in the US Great Plains.

Methods: At two sites we used rainfall shelters and irrigation to create irrigation, drought and control treatments. We measured changes in species composition, richness, Shannon's diversity, evenness and cover by plant functional groups across 4 yr (2008–2011).

Results: The semi-arid grassland community was relatively insensitive to precipitation manipulations, and in the few cases where there was a significant relationship between treatment precipitation and the response variable, the slope of the relationship was weak. In contrast, the sub-humid grassland community was very sensitive to changes in treatment precipitation throughout the experiment, and responded more strongly, and negatively, to drought compared to irrigation.

Conclusions: The differing sensitivity of the dominant species to altered precipitation amount appears to largely determine the overall differences in community response at these sites. The variable responses we observed within a single grassland region highlight the challenge of forecasting community impacts of climate change.

Introduction

Recent predictions of climate change, including an increase in temperature and changes in precipitation timing and quantity (IPCC 2013) have sparked interest in understanding how ecosystems will respond to these abiotic drivers (Clark et al. 2001; Huxman et al. 2004). A growing body of research (Knapp & Smith 2001; Liu et al. 2013; Vicente-Serrano et al. 2013; Knapp et al. 2015a) suggests that global change will not affect ecosystems uniformly – temperature and precipitation changes will vary across regions, and their ecological impact will depend on an ecosystem's sensitivity to these climate parameters.

Much of the ecosystem sensitivity research has focused on the grassland biome. Water is a primary driver of community structure and ecosystem processes in this system (Noy-Meir 1973), meaning that the grassland biome may be particularly sensitive to predicted changes in precipitation (Knapp & Smith 2001; Huxman et al. 2004). Further, both observational and experimental studies conducted at multiple sites within the grassland biome have demonstrated that specific sites may have differing sensitivities to predicted changes in climate (Knapp & Smith 2001; Hsu et al. 2012; Byrne et al. 2013; Knapp et al. 2015a; Wilcox et al. 2015). While these studies provide predictions for future provisioning of ecosystem goods and services

(Chapin et al. 2000), they focus primarily on differences in the sensitivity of net primary production to changes in climate, but do not provide information on the corresponding sensitivity of plant community composition. This is a significant gap in our knowledge, as the sensitivity of plant community composition to changes in climate may have implications for ecosystem functioning (Hooper & Vitousek 1997; Tilman et al. 1997; Isbell et al. 2011), community stability (McNaughton 1977; Tilman & Downing 1994) and intrinsic conservation value.

The Great Plains of North America is an ideal location for studying the effects of global change on grassland plant communities. It contains little topographic complexity, with temperature varying smoothly south to north and precipitation varying east to west. The range of climates within the region allows comparisons with grasslands worldwide (Lauenroth et al. 1999). Climate models predict that the region will warm substantially (1.1–4.3 °C) during the 21st century (IPCC 2013). Associated predictions of precipitation changes are less certain and range from small increases to small decreases, either exacerbating or ameliorating water limitation in the region. Substantial warming, even with small increases in precipitation, will result in a net drying effect in the region (Lauenroth & Bradford 2011). Any changes in precipitation will likely have profound effects on ecosystem dynamics, whether climate change increases or decreases soil water (Weltzin et al. 2003).

While many studies have found a consistent response of grassland production to experimentally manipulated precipitation, plant community composition and diversity respond inconsistently. In observational studies, plant species richness was positively related to precipitation across North American grasslands, but the relationship was much weaker through time at individual sites (Adler & Levine 2007; Cleland et al. 2013). Some precipitation manipulation experiments have found a positive relationship between increased precipitation and species richness and diversity (Sternberg et al. 1999; Zavaleta et al. 2003; Stevens et al. 2006; Yang et al. 2011), while other studies have found a negative effect (Suttle et al. 2007; Engel et al. 2009). Some studies found that drought decreases species diversity (Grime et al. 2008; Koerner & Collins 2014), and still other studies found that drought (Knapp et al. 2002) or irrigation (Collins et al. 2012) had no or little effect on species richness. One potential explanation for these idiosyncratic responses is that community dynamics may depend on the climate response of the dominant species. Two sites located within the same grassland ecosystem but dominated by different species might respond quite differently to a similar change in precipitation.

Here, we report the influence of precipitation manipulation on plant community composition and structure at two grasslands in the Great Plains. We are interested in these two sites because they occupy different ends of the natural precipitation gradient across the Great Plains, and previous observational studies and a rainfall manipulation experiment demonstrated that the sensitivity of ANPP to precipitation differed between the two sites (Lauenroth & Sala 1992; Paruelo et al. 1999; Byrne et al. 2013). Our 4-yr study explored the response of individual species, functional groups and community diversity to both increased and decreased precipitation. Specifically, we were interested in the following questions: (1) how do changes in precipitation affect plant community structure and composition in semi-arid and sub-humid grasslands; (2) do the dominant species and functional groups at the two sites display similar responses to changes in precipitation; and (3) does irrigation or drought cause a larger change in important plant community characteristics at each site?

Methods

Study sites

We conducted our study at two sites within the US Great Plains, both classified in the temperate steppe division of the Bailey ecoregion classification system (Bailey 1983, 1989). The strong climatic gradient within the region leads to distinct plant communities. We imposed drought and irrigation treatments at each site to create large differences in growing season precipitation, rather than to simulate a specific future precipitation scenario. These experiments were set up independently, and as such the experimental design is not identical between sites. However, the experiments provide a unique opportunity to investigate the effects of rainfall manipulations within two distinct plant communities in a large geographic biome.

Our first site is located within the semi-arid shortgrass steppe (SGS) at the Shortgrass Steppe Long Term Ecological Research site (40°49′ N, 104°46′ W) in northern CO. Mean annual precipitation is 341 mm and mean annual temperature is 8.2 °C. The plant community is dominated by the short-stature C_4 grass *Bouteloua gracilis*, which typically accounts for 80–90% of plant cover in this ecosystem (Milchunas et al. 1989). Common sub-dominant species include the perennial graminoid *Carex eleocharis* and forb *Sphaeralcea coccinea*, and the dwarf shrubs *Artemisia frigida*, *Eriogonum effusum* and *Gutierrezia sarothrae*. The soils are Aridic Argiustolls and patches of bare ground are prevalent. Livestock grazing has been excluded from the site for several decades.

The second site is located within the sub-humid southern mixed grass prairie (MGP), further east and south along the climatic gradient of the region. The site is located at the Fort Hays State University College Farm, in west-central Kansas (38°52′ N, 99°23′ W). Mean annual precipitation is 583 mm and mean annual temperature is

12.1 °C. The differences in climate result in a very different plant community from that of the SGS. The plant community includes a mixture of tall-, mid- and short-stature C_4 grasses, but the clear dominant species at the study site is the tall-stature grass *Schizachyrium scoparium*, which accounted for 55–75% of total plant cover in the control plots during the experiment. *Andropogon gerardii*, also a tall-stature grass, is a common sub-dominant species. Forbs are quite diverse at the site, and the dwarf shrub *G. sarothrae* is also common. The soils are very shallow Typic Argiustolls, with underlying fractured limestone bedrock. Livestock grazing was excluded at the site beginning in 2007, the year prior to the initiation of the experiment.

Experimental design

At the SGS site, we selected 45 1.0-m^2 plot locations with similar abundances of the dominant species, *B. gracilis*, and associated sub-dominant species (*C. eleocharis*, *A. frigida* and *G. sarothrae*). The median density and basal area of *B. gracilis* ramets is 16 plants·m^{-2} and 325 cm^2·plant^{-1} there (Aguilera & Lauenroth 1993), leading us to choose 1.0 m^2 as an appropriate plot size. We randomly assigned a treatment (drought or control) to 30 of the plots in May 2008. We imposed drought by creating 15 rainfall shelters designed to intercept approximately 60% of incoming rainfall (Yahdjian & Sala 2002). The drought shelters are described in detail in Byrne et al. (2013). Drought shelters were present on plots during the May–Sept growing season, and were taken down during the dormant period. We removed any dust or bird droppings from the shelters before reassembling them each May. In May 2009, we initiated an irrigation treatment in the remaining 15 1.0-m^2 plots. Throughout the growing season we calculated the weekly long-term average rainfall for the site, and added the difference between the observed rainfall and double the weekly long-term average rainfall once weekly by hand using watering cans. This amounted to an additional 92, 179 and 148 mm of water added during the 2009–2011 growing seasons.

At the MGP site, we selected two blocks of nine plots, each block separated by 0.5 km in late March 2008. We randomly assigned each plot to one of three precipitation treatments: drought, control and irrigation. Each plot was 2.0 m × 8.0 m; long sides oriented with the slope. We constructed six 4.0 m × 10.0 m rainfall shelters that were designed to intercept 50% of incoming ambient rainfall. The drought shelters are described in detail in Byrne et al. (2013). Drought shelters were permanent and left up year-round. We applied water with a pump system from a holding tank connected to a network of soaker hoses (2008 and 2009) or drip lines (2010 and 2011). We used municipal water low in nitrates. Once a week throughout the

growing season (April–September) we applied the long-term average weekly precipitation, regardless of the actual rainfall received during the week, totaling an addition of 380 mm of water during the growing season each year.

Abiotic data

For the SGS, we obtained meteorological data from the Central Plains Experimental Range headquarters, located approximately 2 km from the field site. For the MGP, we obtained meteorological data from a National Climatic Data Center (NCDC) weather station (HAYS 1S) located approximately 5 km from the field site. We combined daily ambient precipitation data with supplemental irrigation and excluded rainfall amounts to calculate precipitation treatment totals for each year of the study. We monitored volumetric soil water content (θ_v) every 4 h in a subset of plots to evaluate the effectiveness of drought and irrigation treatments. All probes were installed perpendicular to the soil surface and remained in place for the duration of the experiment. Because our sensors were only in the shallowest soil layers (10 or 5 cm, respectively), the data are most useful to verify that our treatments enhanced or reduced soil water (Appendix S1).

To interpret our experimental treatments in the context of longer-term precipitation records at each site, we calculated an estimate of treatment intensity using the methods described in Knapp et al. (2015b). For each site, we compiled annual precipitation records from 1909 through the 2011 calendar year. At the SGS, reliable local precipitation data were not available until 1939, so for 1909–1938 we used PRISM (parameter-elevation regressions on independent slopes model; PRISM Climate Group, Oregon State University http://prism.oregonstate.edu, created 26 Apr 2016), a knowledge-based interpolation program that generates continuous climate surfaces based on weather station data and topographic variables (Daly et al. 1994). We then calculated the normalized precipitation for our treatments each year using the equation $X_n = \frac{(X_{i,t}-\mu)}{\sigma}$, where X_n is the normalized precipitation value, $X_{i,t}$ is the individual value for year i within treatment t, and μ and σ are the mean and SD of the historical 102-yr precipitation data sets from each site. We compared these calculated values to the 10th (extreme drought) and 90th (extreme wet) percentiles of the historical data sets, as in Knapp et al. (2015b).

Biotic data

We measured plant species composition at peak biomass (first week in Aug at the SGS; last week in Jul at the MGP) by visually estimating canopy cover of each species within each plot. At the SGS, we estimated canopy cover

for the entire 1.0-m^2 plot, while at the MGP we did so in ten 0.1-m^2 subplots within each 16.0-m^2 plot. In the 2011 growing season, we split the drought and irrigation treatments in half for another experiment, and therefore we estimated canopy cover in five 0.1-m^2 subplots within each 6.0-m^2 plot. We recorded species richness (number of species·m^{-2}) at the sites by surveying each plot completely twice each growing season; once in early May to capture the cool season species, and again in late Jul or early Aug to capture the warm season species. At the SGS, we report richness as the number of species recorded in each 1.0-m^2 plot, while at the MGP we report richness as the sum of species present in five 0.1-m^2 subplots each year in order to compare across years. We note that this is an overestimate of richness at the 0.5-m^2 scale, since plots are not contiguous.

We defined dominant species as those that made up the majority of cover in the plant communities, and sub-dominant species as the species with the second highest cover, which were also common across treatments. We divided plants into different functional groups on the basis of growth form: graminoids, forbs and dwarf shrubs. We excluded dwarf shrubs from our analyses due to low (<10%) and inconsistent cover among plots. We also grouped ruderal species together to assess if water manipulation affected invasion. We defined ruderals as species that quickly responded to disturbances (Grime 2001). This included short-lived, fast-growing native and non-native species often considered undesirable by range managers (Appendix S2). We described patterns of community structure using richness (number of species per 1.0 m^2 or 0.5 m^2 for the SGS and MGP, respectively), Shannon-Weiner diversity index (H') and Pielou evenness index (E).

Statistical analysis

To answer our research questions, we needed to compare the sensitivity of response variables at each site to precipitation. A traditional ANOVA, which provides a qualitative but not quantitative test of treatment effects, cannot address this goal. However, we did use a mixed model ANOVA to identify the response variables that are affected by precipitation treatments at each site. We then modelled the quantitative effects of precipitation on these responses using regression. Below, we first describe methods for the ANOVAs and then methods for the regressions.

We conducted mixed model ANOVAs in the Statistical Analysis System (v 9.2; Cary, NC, US) with a repeated measure design. We compared AIC values (Akaike information criterion; Burnham & Anderson 2002) of models with several autoregressive error terms and chose the model with the lowest AIC value. For the SGS, we conducted t-tests for response variables in 2008 between the

drought and control treatments, but conducted an ANOVA for the remaining years (2009–2011) when all three treatments were present. The fixed effects in the model were treatment, year and their interaction, while the random effects were plot and the plot by treatment interaction. The model with the lowest AIC value included a heterogeneous autoregressive process in the error term. For the MGP, the fixed effects in the mixed model ANOVA were block, treatment, the block by treatment interaction, year and the year by treatment interaction. We included plot and the plot by year interaction as random effects. The model with the lowest AIC value did not include an autoregressive error term. To rule out the possibility that the lack of change in aggregate species richness was masking turnover of rare species, at the SGS we also calculated Jaccard similarity indices for pair-wise treatment comparisons using presence–absence data. We report the results of the ANOVAs in Appendix S3.

To compare the sensitivity of our vegetation variables to imposed treatments, we replaced the categorical variable "treatment" from our mixed model ANOVA above with the continuous variable, estimated treatment normalized precipitation (henceforth "normalized precipitation"), calculated using the methods of Knapp et al. (2015b). At each site and for each vegetation response variable, we created LMM using the fixed effects that were significant for each site and response variable, and we report the estimated coefficient of the normalized precipitation effect on each response variable.

To compare the magnitude of response to drought or water addition, we calculated a new response variable, the log response ratio, $\ln(R_i) = \ln\left(\frac{X_{ij}}{\bar{X}_{ic}}\right)$, where X_{ij} is the observed quantity for variable i in each experimental plot j, and $\bar{X}_{ic}$ is the mean response of the variable i in the control treatment. R is a unit-less measure of the experimental effect and can help us understand the magnitude of change for each variable that results from manipulation. We used the absolute value of the natural logarithm of R. The natural logarithm of R has a more normal sampling distribution than R (Hedges et al.1999), and using the absolute value allowed all differences from the control to be positive numbers, so we could compare the magnitude of the response directly. Because each treatment had year-to-year consistency in the sign (either + or −), the use of absolute values did not bias analyses and allowed comparison of effect sizes between the treatments whether the effects were increases or decreases relative to the control. We used the same mixed model ANOVAs described above to analyse the response ratio data, and when treatment effects were significant, we made specific comparisons between treatments using the LSMEANS statement. We excluded ruderals, shrubs and the sub-dominant species at the short-grass steppe, *Carex eleocharis*, from this analysis since cover

for these species and functional groups were variable among plots, and many plots lacked these species and functional groups. Unless otherwise stated, the level of significance for all statistical tests was $P < 0.05$.

Results

Precipitation manipulations

At the SGS, annual precipitation ranged from 330 to 436 mm and growing season precipitation ranged from 176 to 282 mm during our experiment (Appendix S4). Assuming 60% interception by the rainfall shelters, the drought plots received roughly 40% of these growing season totals (70–113 mm). The irrigation treatment increased growing season totals to between 355–386 mm, an increase of 71% over mean annual precipitation.

At the MGP, annual precipitation ranged from 474 to 727 mm and growing season precipitation ranged from 306 to 495 mm during our experiment (Appendix S4). Assuming 50% interception by the rainfall shelters, the drought plots received roughly 50% of the annual precipitation totals (237–364 mm), since the shelters were up year-round. The irrigation treatment increased growing season totals to between 686–875 mm, an increase of 61% over mean annual precipitation.

At both sites, the precipitation treatments led to clear differences in soil water content (Appendix S1). Treatment differences were smallest during the high precipitation portion of the growing season and largest during the driest portion (July, August and September) as soils dried in the drought and control treatments, while soil water was replenished by weekly water addition in the irrigation treatment.

Normalized precipitation

Interpreted within the historical probability distribution of annual precipitation at the SGS, extreme dry or wet years in the 102-yr record (<10th percentile or >90th percentile) had normalized precipitation values of −1.06 and 1.35, respectively. Three of the 4 yr of drought exceeded the 10th percentile, while all 3 yr of irrigation exceeded the 90th percentile (Appendix S5). At the MGP, extreme dry or wet years in the 102-yr record (<10th percentile or >90th percentile) had normalized precipitation values of −1.17 and 1.21, respectively. All 4 yr of drought and irrigation exceeded the 10th and 90th percentiles, respectively (Appendix S5).

Sensitivity of species richness, evenness and Shannon's diversity to changes in precipitation

Species richness was not affected by treatment at the SGS (Appendix S3a), and was insensitive to normalized precipitation (Table 1). Our analysis of Jaccard similarity indices indicated that there was not a shift in species composition among treatments at the SGS (Appendix S6a), meaning that the negligible change in richness did not mask a turnover of species within treatments. In contrast, Shannon's diversity and evenness differed among some treatments and years, and with the year × treatment interaction (Appendix S3a). There was a positive linear relationship between normalized precipitation and Shannon's diversity and evenness (Table 1), although the slope of the relationship was low (0.01 for both).

At the MGP, species richness, Shannon's diversity and evenness were all affected by the treatments (Appendix S3b). Each variable responded significantly, and negatively, to changes in normalized precipitation (Table 1). Richness was the most sensitive to changes in normalized precipitation (−0.23 slope), and species evenness, although significant, was the least sensitive (−0.01 slope). At both sites, there were significant temporal differences in the response variables (Appendix S3).

Sensitivity of total canopy cover and cover by functional group to changes in precipitation

Treatment did not affect total cover, graminoid cover or forb cover at the SGS, although there was a year × treatment interaction for all three response variables (Appendix S3a). Total cover and graminoid cover were both insensitive to changes in normalized precipitation at the SGS (Table 1). There was a small (0.41 slope), but significant, positive linear relationship between normalized precipitation and forbs (Table 1).

In contrast, at the MGP treatment significantly affected total and graminoid cover (but not forb cover), and the year × treatment interaction was also significant for these two variables (Appendix S3b). There was a strong positive linear relationship between normalized precipitation and

Table 1. Slope of relationship between treatment normalized precipitation and vegetation variables at the shortgrass steppe (SGS) and mixed grass prairie (MGP) in linear mixed effects models. F values in parentheses.

Site Response Variable	SGS Slope	MGP Slope
Species Richness (S)	−0.57 (1.58)[n.s.]	−0.23 (37.35)***
Species Evenness (E)	0.01 (4.78)*	−0.01 (2.85)[+]
Shannon Diversity (H')	0.01 (3.69)[+]	−0.06 (31.68)***
Total Cover	0.02 (0.33)[n.s.]	2.87 (147.98)***
Graminoid Cover	−1.19 (0.82)[n.s.]	3.04 (132.09)***
Forb Cover	0.41 (4.74)*	0.36 (2.14)[n.s.]
Dominant Species Cover	0.48 (5.08)*	1.47 (27.49)*
Sub-Dominant Species Cover	−1.68 (1.71)[n.s.]	1.78 (32.71)*
Ruderal Species Cover	0.92 (4.09)*	0.50 (2.27)[n.s.]

n.s., not significant.
[+]$P < 0.1$, *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

total (2.87 slope) and graminoid (3.04 slope) cover, while forbs were insensitive to changes in treatment precipitation (Table 1). At both sites, there were year-to-year fluctuations in cover for all three response variables (Appendix S3).

Sensitivity of dominant, sub-dominant and ruderal species to changes in precipitation

At the SGS, our treatments affected cover of the dominant species, *B. gracilis*, but not the sub-dominant species *C. eleocharis* or ruderal species, and there was a significant year × treatment interaction for *C. eleocharis* and ruderal species (Appendix S3a). There was a small, positive linear relationship between normalized precipitation and percentage cover of *B. gracilis* (0.48 slope; Table 1). Cover of the sub-dominant species was insensitive to changes in normalized precipitation, while ruderal species responded fairly strongly and positively to changes in normalized precipitation (0.92 slope).

At the MGP, our treatments affected cover of the dominant species, *S. scoparium*, and the sub-dominant species, *A. gerardii*, but not ruderal species. The year × treatment interaction was significant only for the sub-dominant species (Appendix S3b). There was a strong, positive linear relationship between normalized precipitation and percentage cover of the dominant (1.47 slope) and sub-dominant (1.78 slope; Table 1) species. Ruderal species were insensitive to changes in precipitation at the MGP (Table 1). At both sites there was notable inter-annual variation in the cover of the dominant and sub-dominant species, while cover of ruderals was not affected by year at the MGP (Appendix S3).

Magnitude of response to drought and water addition

There was no difference between the absolute value of the drought and irrigation treatment responses at the SGS for any of the variables measured (Appendix S7a). For species richness, evenness and Shannon's diversity, the response to drought was small, and negative, while the response to irrigation was negative in some cases and positive in others (Fig. 1). For total, graminoid, forb and dominant species cover, the response to drought was negative, and the response to irrigation tended to be positive, although this was not always the case (Fig. 2). The dominant species, *B. gracilis*, had a positive response to both irrigation and drought (Fig. 2).

In contrast to the SGS, at the MGP drought tended to have a larger treatment response than irrigation throughout the experiment, with few exceptions (Appendix S7b). Irrigation consistently decreased richness, while drought tended to have a small positive effect. The response to

irrigation was much larger than the response to drought in 2010 and 2011 (Fig. 1). In contrast, drought increased species evenness and Shannon's diversity, while irrigation had a small negative effect (Fig. 1) The response to drought was larger than the response to irrigation in 2010 and 2011 for species evenness, and only in 2011 for Shannon's diversity (Fig. 1).

There were consistent differences in the absolute value of the treatment responses for total, graminoid and forb cover at the MGP (Appendix S7b). For total and graminoid cover, drought had a consistent negative effect, while irrigation had a consistent positive effect, and the response was stronger to drought than irrigation in 2009–2011 (Fig. 2). Forbs, in contrast, tended to respond negatively to irrigation and positively to drought (Fig. 2). The dominant and sub-dominant species at the MGP generally responded negatively to drought, and positively to irrigation, with few exceptions. In 2009 and 2010, the magnitude of the
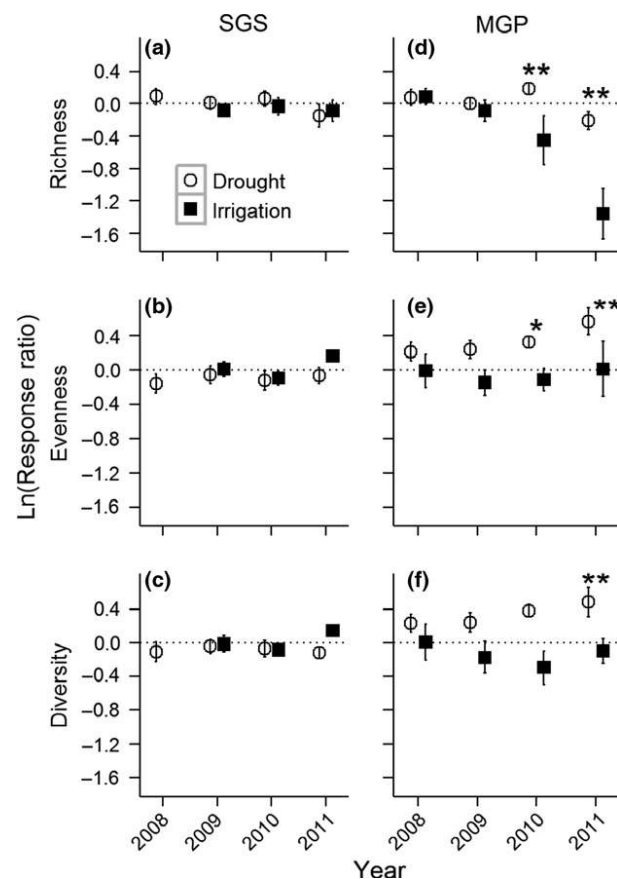
Fig. 1. Relative change (Ln response ratio ± 95% CI) in species richness, evenness and Shannon diversity at the shortgrass steppe (**a, b, c**) and mixed grass prairie (**d, e, f**) in the drought and water addition treatments. Statistical analysis performed on the absolute value of the Ln response ratio for each variable, and presented in Appendix S6. $^+P < 0.1$, $^*P < 0.05$, $^{**}P < 0.01$.
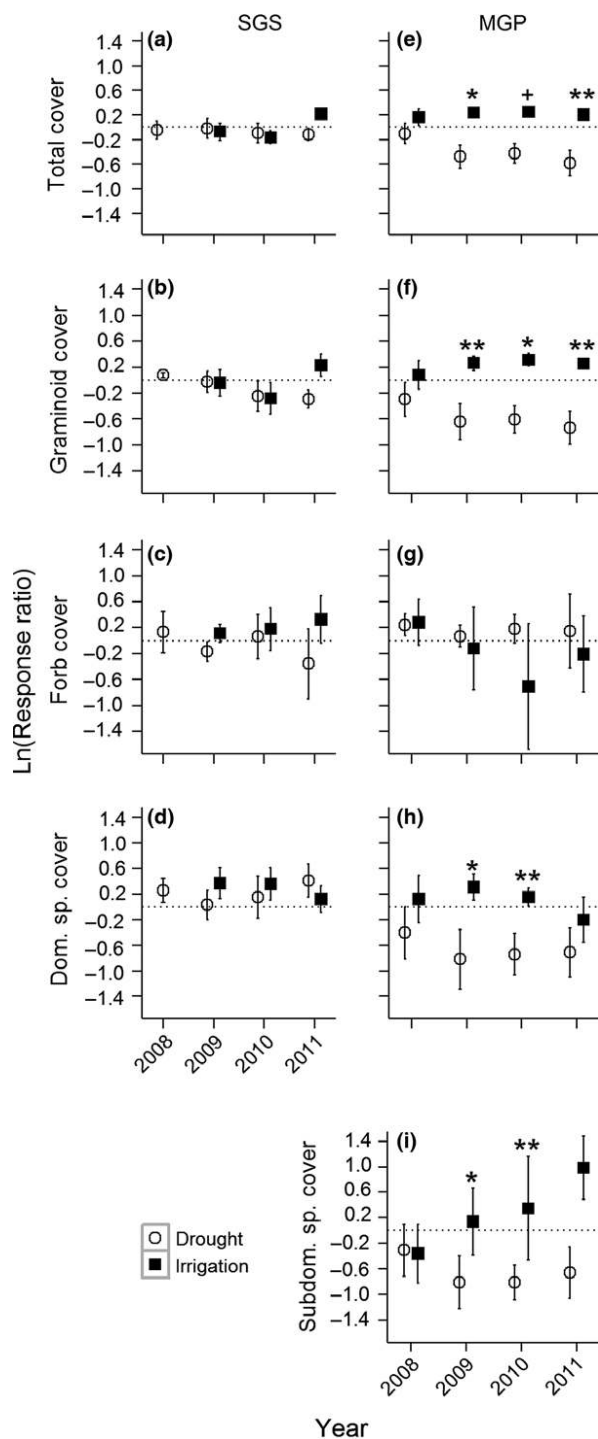
Fig. 2. Relative change (Ln response ratio ± 95% CI) in total, graminoid, forb and dominant species (*B. gracilis*) cover at the shortgrass steppe (**a, b, c, d**) and total, graminoid, forb and dominant (*S. scoparium*) and sub-dominant (*A. gerardii*) species at the mixed grass prairie (**e, f, g, h, i**) in the drought and water addition treatments. We excluded the sub-dominant species at the shortgrass steppe from this analysis due to low and variable cover among plots for this species. Statistical analysis performed on the absolute value of the Ln response ratio for each variable, and presented in Appendix S6. $^{+}P < 0.1$, $^{*}P < 0.05$, $^{**}P < 0.01$.

response to drought was larger than the response to irrigation for both response variables (Fig. 2, Appendix S7b).

Discussion

Climate models project warming and changes in precipitation in the Great Plains during the 21st century (IPCC 2013), yet community sensitivity to these predicted changes may vary across and within biomes. We found that our two grassland sites displayed different sensitivities to changes in precipitation, and the responses of functional groups and individual species varied between sites. Some of the results were expected, yet others were counter-intuitive. Our results highlight the idiosyncratic nature of plant community responses to climate change and the challenge of predicting those responses.

Sensitivity of plant community structure and composition

Our treatments had very different effects on species richness, Shannon's diversity and evenness at the two sites. At the SGS, richness was not affected by normalized precipitation, and while evenness and Shannon's diversity were positively related to normalized precipitation, the slope was very low, indicating low sensitivity to changes in precipitation (Table 1). While the lack of sensitivity at the SGS was somewhat surprising, previous research in semi-arid grasslands has produced similar results. An 11-yr experiment at the SGS found that under extreme drought it took 4 yr to reduce species richness (Evans et al. 2011). Likewise, richness, diversity and evenness were not altered after 2 yr of drought in the semi-arid Patagonian steppe, except in the most extreme (80% rainfall reduction) treatment (Yahdjian & Sala 2006). It appears that a ~ 60% reduction or increase in growing season precipitation is not sufficient to greatly alter community structure and stability in 4 yr. Milchunas & Lauenroth (1995) also found time lags in responses of SGS plant communities to nutrient and water enrichment treatments.

In contrast to the SGS, richness, evenness and Shannon's diversity were all negatively related to normalized precipitation at the MGP. Notably, the relationship between richness and normalized precipitation was strongly negative (−0.23 slope), and irrigation dramatically reduced richness from 15 to five species per 0.5 m² from 2008–2011 (data not shown). One explanation for this pattern of decreased richness in the irrigation treatment is competition from the dominant and sub-dominant grass species, *S. scoparium* and *A. gerardii*. Indeed, percentage cover of these two species responded strongly and positively to increases in normalized precipitation (1.47 and 1.78 slope, respectively; Table 1). Increased grass cover

may have created low light conditions unsuitable for many short-stature forbs, as observed in the tallgrass prairie (Turner & Knapp 1996), although alternative explanations for the forb response cannot be excluded (Adler & HilleRisLambers 2008; Adler et al. 2013).

Sensitivity of plant functional groups and dominant species to changes in precipitation

At the SGS, only forbs were affected by changes in normalized precipitation, while total and graminoid cover were insensitive to these changes, although our rainfall manipulations resulted in "extreme" precipitation values interpreted within the historical precipitation record (Table 1, Appendix S5a). In contrast, forbs were insensitive to changes in normalized precipitation at the MGP while total cover and cover of graminoids responded strongly, and positively, to increases in treatment precipitation (2.87 and 3.04 slope, respectively; Table 1).

The differing sensitivities of total and graminoid cover to changes in precipitation at our two sites may be partly explained by vegetational constraints (Paruelo et al. 1999). The SGS is dominated by drought-resistant species, especially the dominant species, *B. gracilis* (Mueller & Weaver 1942; Hyder 1975). The bunchgrass's lack of rhizomes and stolons makes it difficult for individual genets or tillers to respond quickly to favourable water conditions (Weaver & Albertson 1943). The slow response time is demonstrated by the low but significant slope relating normalized precipitation to *B. gracilis* cover (0.48 slope; Table 1). In contrast, the vegetation at the MGP is dominated by grass species with a range of traits. The taller, dominant grass species can adjust total cover or leaf area index faster than the drought-tolerant short grasses and were therefore able to respond more rapidly to changes in soil water, as evidenced by the higher slope values relating normalized precipitation to cover by the dominant (1.47) and sub-dominant (1.78) grass species at the MGP (Table 1). Our results confirm previous research during and after the great drought of the 1930s that recorded much larger changes in the plant communities of the tall and mixed grass prairies than in the shortgrass steppe (Weaver 1954).

Changes in total and graminoid cover were largely driven by the response of the dominant grass species at each site. Previous research at the SGS has shown that the dominant species, *B. gracilis*, plays an important role in maintaining community structure (Milchunas et al. 1990) and stability (Sasaki & Lauenroth 2011). Singh et al. (1996) found that at small scales (<3 m²) the presence of *B. gracilis* constrained species richness. Indeed, our treatments had only a small effect on this drought-tolerant species; and likewise species richness, evenness and net primary production (Byrne et al. 2013) were insensitive to changes in precipitation over our

experiment. Interestingly, *B. gracilis* responded positively to both water addition and drought (Fig. 2), again providing support to the statement that *B. gracilis* maintains community structure, even when perturbations occur.

At the MGP, the dominant species, *S. scoparium*, and the sub-dominant species, *A. gerardii*, both appeared to be important drivers of changes in community dynamics. The sub-dominant species was more sensitive to changes in normalized precipitation than the dominant species (1.78 vs 1.47 slope, respectively). *Andropogon gerardii* has higher moisture requirements than *S. scoparium* (Weaver 1954; Knapp 1984). Further, plant physiological measurements taken in 2009 in our experiment showed that *A. gerardii* was less drought-tolerant than *S. scoparium*; experiencing higher limitations to photosynthesis and less ability to lower its water potential (Maricle & Adler 2011). If *A. gerardii* has such low tolerance to drought, why was it more sensitive to changes in normalized precipitation than *S. scoparium*, as indicated by the higher slope value? We hypothesize that this change in community structure was driven by competitive interactions between the dominant and sub-dominant species. In the more mesic tallgrass prairie, *A. gerardii* is considered a dominant species, making up just under 40% of total cover (Silletti & Knapp 2001). Apparently our irrigation added enough additional water to make *A. gerardii* a better competitor with *S. scoparium*. These results suggest that in times of above-average soil water availability, the structure of the MGP and other ecosystems that include species with a range of traits (both wet- and dry-adapted species) may change significantly.

Does water addition or drought cause a larger change in important plant community characteristics at each site?

Interestingly, there were no differences in response magnitude between drought and irrigation at the SGS despite the fact that the normalized precipitation value was larger in the irrigation treatment than the drought treatment for all 3 yr of the experiment (Appendix S5a). The weak community response indicates the shortgrass steppe ecosystem may be resistant to climate change in the short term, as previous research has shown (Evans et al. 2011). In contrast, at the MGP, the magnitude of response to drought tended to be much larger than the response to irrigation, with the exception of species richness, which had a higher (and negative) response to irrigation. Like the SGS, the normalized precipitation value was larger in the irrigation treatment than the drought treatment at the MGP in all but the final year of the experiment (Appendix S5b). These results suggest that the MGP may be particularly vulnerable to the longer, multi-decadal droughts predicted in the future (Cook & Seager 2010).

Caveats

Our objective for this study was not to simulate a specific climate change scenario, but rather to create large differences in growing season precipitation among treatments. The two sites were initially set up as independent experiments, thus there are methodological differences between the two sites (growing season rainfall shelters at the SGS and year-round rainfall shelters at the MGP). While it is possible that these methodological differences may have influenced our results, the sites both receive the majority of annual precipitation during the summer growing season, when shelters were up at both sites. Previous research has shown that growing season, more so than annual precipitation, has a larger effect on grassland plant communities in terms of important variables such as ANPP (Robinson et al. 2013). Further, by calculating normalized treatment precipitation at each site, we see that our imposed treatments exceeded the 10th and 90th percentile for extreme dry and wet years in the 102-yr historical record for all treatment years at both sites, except the first year at the SGS. By evaluating the slope of the relationship between normalized precipitation and vegetation variables at each site, we were still able to investigate plant community sensitivity to precipitation, despite methodological differences.

An additional caveat is that our design does not replicate historical extreme precipitation years, where extreme wet years are typically the result of the addition of several very large daily precipitation events, while extreme dry years are typically the result of the absence of several large precipitation events (Sala et al. 1992; Knapp et al. 2015b). Rather, our drought treatment decreased all precipitation events by the same amount. Further, our irrigation treatment added a consistent amount of water each week throughout the growing season, rather than adding a few very large precipitation events. These are artifacts of our experiment, and the results should be interpreted with caution, but some important general patterns still emerge.

Conclusions

Our results have two important implications for predicting the magnitude of temperate grassland responses to anthropogenic climate change. First, we found that our two sites, located within the same biome, differed markedly in their response to similar relative changes in growing season precipitation. The SGS was moderately insensitive to changes in growing-season precipitation, and there was not a difference in the absolute magnitude of the response to irrigation or drought. The MGP, in contrast, was much more sensitive to changes in precipitation, and tended to respond more dramatically to drought than to water addition, except in the case of species richness, which

responded more strongly to irrigation. The differences in community responses between our two sites highlight the importance of multi-site studies to refine our knowledge of the mechanisms and generalities of community response to climate change at the biome level. Second, our study suggests that both direct and indirect components of climate change can play important roles in regulating plant community response to climate change. At the SGS, cover of the dominant species did not change significantly over the 4-yr experiment, and likewise, we saw few changes in other species. At the MGP, composition changed dramatically, reflecting direct effects of the experimental treatments along with interactions among plant species and other unknown indirect effects, such as disease or soil aeration. If we are to accurately predict biodiversity and ecosystem responses to global change, we must improve our understanding of both the direct and indirect impacts of climate change in natural ecosystems and apply these interactions to ecological forecasting models. Given the importance of grassland and savanna ecosystems worldwide, the complexity of both within-site and across-biome community responses to predicted climate changes warrants future experiments to improve our understanding of community and ecosystem dynamics within the grassland biome.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Daily growing season volumetric soil water content (θ_v) at each site.

Appedix S2. Percentage cover of species considered ruderal at each site.

Appendix S3. Effects of treatment (T), year (Y), and the T × Y interaction on plant community parameters at each site.

Appendix S4. (a) April and growing season (May – September) precipitation received at the shortgrass steppe,

and (b) growing season (April – September) precipitation received at the mixed grass prairie, during the experiment years (2008 – 2011) and long term monthly growing season precipitation.

Appendix S5. Normalized treatment precipitation at each site.

Appendix S6. Jaccard similarity index for pair-wise treatment comparisons at each site.

Appendix S7. Results of mixed model ANOVA for natural logarithm of the response ratio at each site.