

Differential sensitivity to regional-scale drought in six central US grasslands

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Abstract Terrestrial ecosystems often vary dramatically in their responses to drought, but the reasons for this are unclear. With climate change forecasts for more frequent and extensive drought in the future, a more complete understanding of the mechanisms that determine differential ecosystem sensitivity to drought is needed. In 2012, the Central US experienced the fourth largest drought in a century, with a regional-scale 40 % reduction in growing season precipitation affecting ecosystems ranging from desert grassland to mesic tallgrass prairie. This provided an opportunity to assess ecosystem sensitivity to a drought of common magnitude in six native grasslands. We tested the prediction that drought sensitivity is inversely related to mean annual precipitation (MAP) by quantifying reductions in above-ground net primary production (ANPP). Long-term ANPP data available for each site (mean length = 16 years) were used as a baseline for calculating reductions in ANPP, and drought sensitivity was estimated as the reduction in ANPP

per millimeter reduction in precipitation. Arid grasslands were the most sensitive to drought, but drought responses and sensitivity varied by more than twofold among the six grasslands, despite all sites experiencing 40 % reductions in growing season precipitation. Although drought sensitivity generally decreased with increasing MAP as predicted, there was evidence that the identity and traits of the dominant species, as well as plant functional diversity, influenced sensitivity. A more comprehensive understanding of the mechanisms leading to differences in drought sensitivity will require multi-site manipulative experiments designed to assess both biotic and abiotic determinants of ecosystem sensitivity.

Keywords Climate change · Primary production · Precipitation · Functional diversity · Long-term ecological research

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Introduction

Climate change forecasts include alterations in climatic means, greater climatic variability, and increases in the frequency of climatic extremes such as floods, droughts and heat waves [Intergovernmental Panel on Climate Change (IPCC) 2007, 2012; Smith 2011]. Of the latter, drought defined by the IPCC as a “prolonged absence or marked deficiency of precipitation”, is likely to have the most severe, immediate and long-term impact on terrestrial ecosystems (e.g., Weaver and Albertson 1936; Weaver 1954; Breshears et al. 2005). Thus, understanding ecosystem responses to drought is critical and heightened by expectations that future droughts will be more intense and greater in extent than those experienced in the last century (Trenberth et al. 2014).

Typically, the ecological impacts of drought are assessed at the site level through the study of natural drought (e.g., Tilman and El Haddi 1992; Frank 2007; Debinski et al. 2010) or by experimentally imposing precipitation deficits (e.g., Heitschmidt et al. 2005; Shinoda et al. 2010; Misson et al. 2010; Cherwin and Knapp 2012; Reichmann et al. 2013). While most ecosystems and key ecosystem processes respond negatively to drought (e.g., Wu et al. 2011; Hoover et al. 2014; but see Jensen et al. 2003 and Emmett et al. 2004 for notable exceptions), the magnitude of the response of different ecosystems can vary dramatically both within and among biomes (Grime et al. 2000; Weltzin et al. 2003; Luo et al. 2008; Cherwin and Knapp 2012; Byrne et al. 2013). Reported differences in responses to drought among ecosystems could be caused simply by variation in the magnitude of drought experienced for any particular site (Fraser et al. 2013) or by inherent differences in ecosystem sensitivity to drought (Smith et al. 2009). Because most observational and experimental drought studies vary in drought severity, and often in the response variables measured, it can be challenging to quantify ecosystem sensitivity in comparable ways.

The 2012 drought in the Central US was one of the most widespread on record (the fourth largest drought since 1895) and was relatively uniform with regard to severity across most of the grassland region of the central and southern plains states [National Oceanic and Atmospheric Administration (NOAA) National Climatic Data Center, <http://www.ncdc.noaa.gov/sotc/briefings/201209.pdf>]. As a consequence, this regional scale drought provided a unique opportunity to coordinate response measurements and assess ecosystem sensitivities across a range of grassland types. Grasslands are valuable model ecosystems for assessing differential drought sensitivity. They are highly responsive to variation in precipitation (Knapp and Smith 2001; Hsu et al. 2012) and previous research has shown that mean annual precipitation (MAP) correlates strongly with regional patterns of aboveground net primary production (ANPP) across a variety of different grassland types (Sala et al. 1988). Moreover, both short-term and decadal-scale droughts have been important historically in these ecosystems (Weaver and Albertson 1936; Weaver 1954; Tilman and El Haddi 1992; Woodhouse and Overpeck 1998).

Here we assess responses in ANPP, as a key measure of ecosystem function, to the 2012 drought in six distinct grasslands. These grasslands all have multi-year records of ANPP (mean length = 16 years) and thus there is site-based context for assessing their responses to the 2012 drought. Because the magnitude of drought was similar across ecosystems ranging from desert grassland (<250 mm MAP and low productivity) to tallgrass prairie (>850 mm MAP and high productivity), we were able to test the hypothesis that ecosystem sensitivity to drought is inversely related

to MAP (Huxman et al. 2004). Specifically, we predicted that the xeric, less productive grasslands would respond more negatively to drought than mesic, productive ecosystems. The mechanism that Huxman et al. (2004) proposed to explain this pattern is that as MAP increases, other resources become more limiting to ecosystem processes and thus sensitivity to alterations in precipitation will decrease. This contrasts with the prediction that vegetation chronically exposed to water limitations should be stress tolerant and more resistant to drought (Grime et al. 2000). Drought sensitivity was assessed by directly measuring the reduction in ANPP in 2012 (relative to long-term mean ANPP) per millimeter reduction in precipitation. This is particularly timely in light of recent conflicting projections of global-scale drought-sensitivity patterns, based on the normalized difference vegetation index and other proxies for ANPP. These have both supported (Vicente-Serrano et al. 2013) and contradicted (Liu et al. 2013) the sensitivity patterns hypothesized by Huxman et al. (2004).

Materials and methods

Study sites

Responses in ANPP to the 2012 drought were assessed at six native North American grasslands (Table 1). These encompassed the major grassland types in the Central US with black grama-dominated desert grassland [*Bouteloua eriopoda*; Sevilleta National Wildlife Refuge, black grama site (SBK)] and southern shortgrass steppe [dominated by *Bouteloua gracilis*; Sevilleta National Wildlife Refuge, blue grama site (SBL)] in New Mexico; northern shortgrass steppe [*B. gracilis*; Central Plains Experimental Range (SGS)] in Colorado; northern mixed grass prairie [co-dominated by *Pascopyron smithii*, *B. gracilis*; High Plains Grasslands Research Center (HPG)] in Wyoming; and southern mixed grass prairie [co-dominated by *Pascopyron smithii*, *Bouteloua curtipendula*, *Sporobolus asper*; Hays Agricultural Research Center (HAYS)]; as well as tallgrass prairie [*Andropogon gerardii*, *Sorghastrum nutans*; Konza Prairie Biological Station (KNZ)] in Kansas. Four of these grasslands were located at US National Science Foundation funded Long-term Ecological Research (LTER) sites [Sevilleta (SBK and SBL), Shortgrass Steppe (SGS) and Konza Prairie (KNZ) LTER sites], thus were especially well characterized with regard to soils, plant communities, climate and key ecosystem processes. As expected for sites arrayed across the Central US and a large precipitation gradient, soil texture varied from sandy to clay loams (Burke et al. 1989, 1991). None of the sites had been managed for grazing for at least 15 years and only the KNZ site was annually burned—a typical management practice for this historically important

Table 1 Site characteristics for six Central US grasslands impacted by the 2012 drought

Site	Grassland type	MAP (mm)	GSP (mm)	GSP-CV (%)	MAT (°C)	GST (°C)	ANPP ^a (g m ⁻²)	Years ^b
SBK ^c	Desert	246	163 (162)	48.5	13.4	19.3	89.7	14
SBL ^c	Shortgrass	246	163 (157)	48.5	13.4	19.3	63.7	11
SGS ^d	Shortgrass	375	293 (277)	33.5	9.5	16.4	88.9	27
HPG ^e	Mixed	400	303 (290)	32.8	7.9	14.6	116.2	9
HAYS ^f	Mixed	584	426 (396)	34.7	12.3	20.8	208.2	8
KNZ ^g	Tallgrass	892	652 (651)	29.8	13.0	21.4	391.9	29

Mean annual precipitation (MAP), growing season precipitation (GSP), mean annual temperature (MAT) and growing season temperature (GST) are based on 30-year means for 1982–2012. Values in parentheses are the average GSP for the years for which aboveground net primary production (ANPP) data were available

SBL Sevilleta National Wildlife Refuge, blue grama site; SBK Sevilleta National Wildlife Refuge, black grama site; SGS shortgrass steppe, Central Plains Experimental Range; HPG High Plains Grasslands Research Center; Hays Hays Agricultural Research Center; KNZ Konza Prairie Biological Station; CV coefficient of variation

^a Mean for each site

^b Number of years ANPP data were available

^c Buxbaum and Vanderbilt (2007) (for additional information)

^d Lauenroth and Burke (2008) (for additional information)

^e Dijkstra et al. (2010) (for additional information)

^f Heisler-White et al. (2009) (for additional information)

^g Knapp et al. (1998) (for additional information)

driver of tallgrass prairie structure and function (Knapp et al. 1998). Additional site information can be found in Tables 1 and S1 (Electronic Supplementary Material).

Across these grasslands, MAP (1982–2012 time period) varied by >threefold and mean growing season precipitation (GSP; April–September for SGS, HPG, HAYS and KNZ, April–October for SBK and SBL) varied by >fourfold (Table 1). We focused much of our analysis on GSP because it accounts for 66–79 % of MAP at all sites and it was during this period that the 2012 drought reached its maximum extent and was most uniform. For each of these grasslands, we compiled past estimates of ANPP (Table S1, Electronic Supplementary Material) from plant communities similar to and adjacent to those sampled in 2012. In total, 98 years of past ANPP data were available, with data for individual sites ranging from 8 to 29 years. We verified that average annual and GSP for the years with ANPP data were similar to 30-year means for each site. Precipitation in these “ANPP years” differed by an average of 3.6 % from the long-term mean (range 0.15–7.0 %; Table 1) and wet and dry years were distributed normally. We concluded that these ANPP data were from years that were representative of the longer term climatic record and thus, we used these data for calculating a baseline average value of ANPP for each grassland.

ANPP and climatic data

Long-term ANPP estimates varied by site with regard to the method used and sampling intensity, but in general biomass

was harvested at the time of peak biomass or near the end of the growing season at SGS (see Lauenroth et al. 2008 for specific details), HPG (Morgan et al. 2011), HAYS and KNZ (Briggs and Knapp 1995), whereas biomass was estimated twice a year from species-specific allometric estimations at SBK and SBL (Muldavin et al. 2008). In 2012, all aboveground biomass was harvested from three 0.1-m² quadrats randomly located within thirty 6-m² plots for SGS, HPG, HAYS and KNZ, or estimated allometrically from four 1-m² plots in thirty 6-m² plots for SBL and SBL. Only current-year production was used to estimate ANPP.

Climatic data were retrieved from NOAA's National Climate Data Center (<http://www.ncdc.noaa.gov/>). The nearest station with a complete 30-year record (1982–2012) was selected and on-site records were compared to the NOAA data sets to ensure statistical similarity and provide complete climate data records (see Electronic Supplementary Material).

Data analyses

For each grassland we estimated responses to the 2012 drought by calculating absolute reductions in ANPP from the long-term site mean as well as relative reductions expressed as a proportion of the long-term mean. Drought sensitivity was determined following the approach of Huxman et al. (2004) and others (Aanderud et al. 2011; Jin and Goulden 2014) as the response of a variable (ANPP) to a unit change in a driver (millimeters of precipitation).

Although Huxman et al. (2004) estimated sensitivity from the slope of the relationship between ANPP and MAP, we calculated drought sensitivity as:

$$(\text{Mean ANPP} - 2012 \text{ ANPP}) / (\text{Mean GSP} - 2012 \text{ GSP})$$

where mean ANPP was based on historical ANPP data, and mean GSP is the average GSP for the years in which mean ANPP was measured. Regression analyses were conducted to relate ANPP to growing season and annual precipitation. Similarly, 2012 drought responses and drought sensitivity were regressed with long-term ANPP and precipitation variables. All analyses were conducted using R version 3.0.2 (<http://www.r-project.org/>).

Results

2012 Drought and ANPP responses

Although the distance separating these grasslands exceeded 900 km north to south and east to west across the Central US, each grassland was subjected to a remarkably similar ~40 % reduction in GSP in 2012 (Fig. 1). As expected during drought years, growing season air temperatures were ~2 °C warmer than average at all sites (Fig. 1, inset).

At a regional scale, mean ANPP for these grasslands was strongly related to MAP ($p < 0.0001$, $r^2 = 0.84$), as was 2012 ANPP with 2012 precipitation ($p < 0.0001$, $r^2 = 0.98$; Fig. 2). Importantly, the slopes of these two relationships (0.47 and 0.65, respectively) bracketed the slope (0.6) of the MAP-ANPP relationship developed by Sala et al. (1988) for the Central US. Thus, regional relationships between ANPP and precipitation for these six grasslands were consistent with those from a larger and more extensive ANPP data set. Similarly, we related GSP from each site to mean ANPP, as well as 2012 GSP vs. 2012 ANPP. We found robust relationships across the six sites (ANPP = $-32.1 + 0.60 \times \text{GSP}$, $r^2 = 0.79$, $p < 0.0001$ for mean ANPP; ANPP = $-60.9 + 0.78 \times \text{GSP}$, $r^2 = 0.95$, $p = 0.0009$ for 2012 ANPP).

Drought responses for individual grasslands were quantified by comparing 2012 ANPP to the long-term mean ANPP at each site. Across the six grasslands, mean ANPP varied from ca. 60–400 g m⁻² (Table 1). As expected when comparing sites that differed in mean ANPP by more than sixfold, the greatest absolute reduction in ANPP in response to a 40 % reduction in GSP occurred at KNZ (Fig. 2, inset). This reduction in ANPP (145 g m⁻²) was greater than mean productivity for many of the other grasslands (Table 1). Thus, because those sites are incapable of responding to a similar degree, we calculated relative drought responses (reductions in ANPP proportional to the mean) as a comparable response metric. When 2012 drought responses were

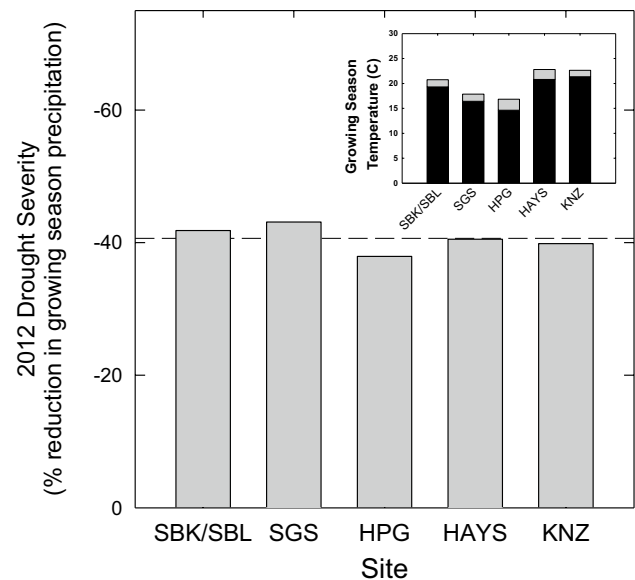


Fig. 1 Relative reduction in 2012 growing season precipitation expressed as a percent of the long-term mean for six grasslands in the Central US. The overall mean reduction in precipitation for the six sites was 40.6 % (range = 38–43; dashed line). Inset Mean growing season air temperature (black bars) and the growing season temperature for 2012 (grey bars) for these six grasslands. The mean increase in temperature across all sites was 1.7 °C (range = 1.3–2.2). Note that because Sevilleta National Wildlife Refuge, black grama site (SBK) and Sevilleta National Wildlife Refuge, blue grama site (SBL) are located about 5 km apart at the Sevilleta Long-term Ecological Research site, historical climatic data are identical. SGS Central Plains Experimental Range, HPG High Plains Grasslands Research Center, HAYS Hays Agricultural Research Center, KNZ Konza Prairie Biological Station

assessed in this way, the two grasslands at the Sevilleta site (SBK and SBL) responded to a 40 % reduction in growing season rainfall with >60 % relative reductions in ANPP. In contrast, the southern mixed-grass prairie (HAYS) was the least responsive grassland to drought with a 24 % reduction in ANPP (Fig. 2). Across sites, there was a general trend for relative drought responses to be inversely related to site productivity and precipitation (Fig. 2), although these relationships were not statistically significant.

Drought sensitivity

Drought sensitivity was estimated by calculating the reduction in ANPP (g m⁻²) per millimeter reduction in GSP. Based on this metric, the two Sevilleta grasslands were the most sensitive (>0.7 g m⁻² mm⁻¹) to a 40 % reduction in precipitation, with the HAYS grassland the least sensitive (<0.4 g m⁻² mm⁻¹, Fig. 3). Huxman et al. (2004) reported an inverse relationship between sensitivity of ANPP to change in precipitation (g m⁻² mm⁻¹) and MAP (Fig. 3, inset) and we found the same general pattern (Fig. 3).

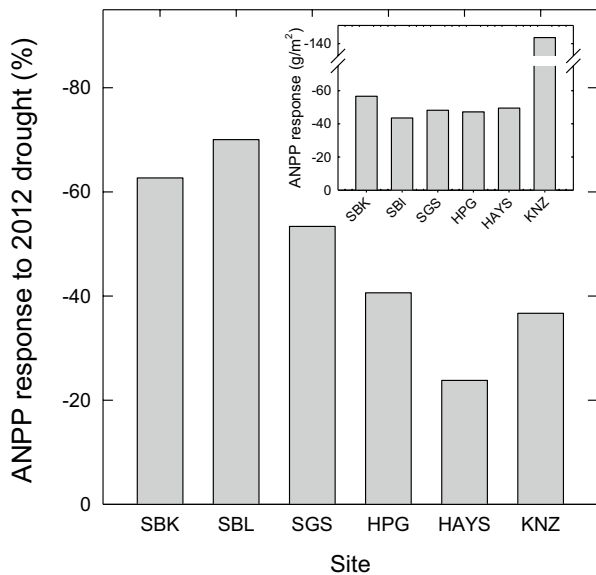
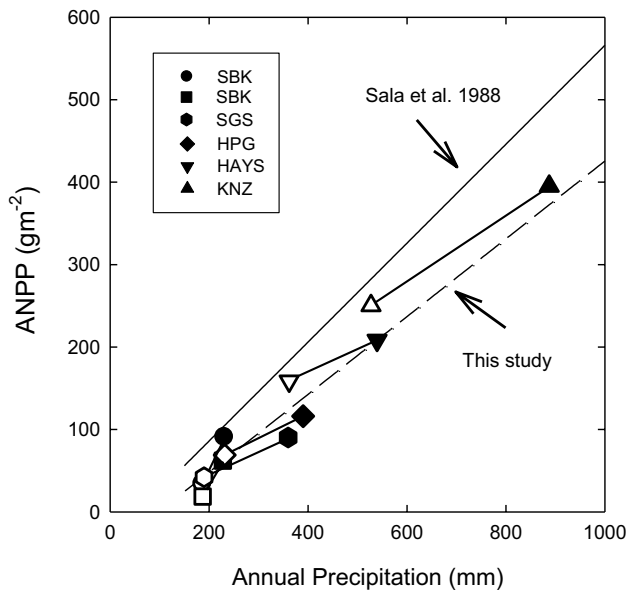


Fig. 2 *Top* relationship between mean annual precipitation (MAP) and aboveground net primary production (ANPP) for six grasslands in the Central US. *Closed symbols* denote average ANPP at each site based on historical data and the *dashed line* represents a linear regression for these data ($ANPP = -46.1 + 0.47 \times MAP$, $p < 0.0001$, $r^2 = 0.84$). ANPP in 2012 at each site is shown by the *open symbols* with *lines* connecting these values to average ANPP for ease of comparison. The relationship between 2012 annual precipitation and 2012 ANPP (not shown) was $ANPP = -87.9 + 0.65 \times \text{Annual precipitation}$, $p < 0.0001$, $r^2 = 0.98$. Also shown for comparison is the relationship between ANPP and MAP from Sala et al. (1988) developed for the entire Central US grassland region ($ANPP = -34 + 0.6 \times MAP$, $r^2 = 0.90$). *Bottom* two measures of ANPP response to the 2012 drought. The relative response was calculated as the percent reduction in 2012 relative to the long-term mean ANPP for each grassland, whereas the absolute response (*inset*) is the difference between 2012 ANPP and the long-term mean. Note that the pattern for absolute response is dominated by the magnitude of ANPP at the most productive grassland (KNZ). For other abbreviations, see Fig. 1

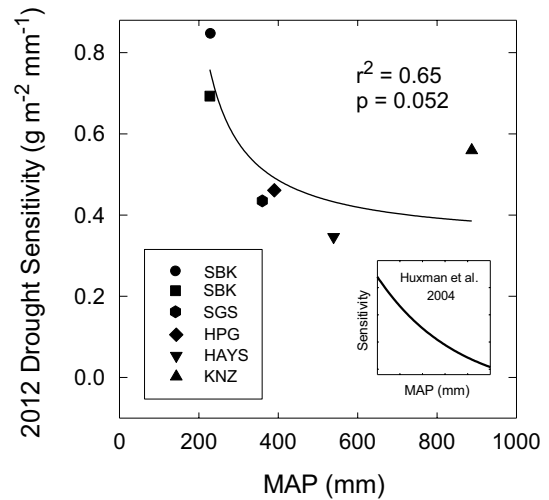


Fig. 3 Relationship between MAP and drought sensitivity for six grasslands in the Central US. Drought sensitivity was calculated as the deviation in 2012 ANPP from average ANPP (based on historical data) per millimeter reduction in 2012 precipitation from average. Equation describing the pattern across sites is: $Sensitivity = 0.329 \times MAP / (-128.9 + MAP)$. Site abbreviations are defined in Table 1. *Inset* relationship between MAP and ecosystem sensitivity to precipitation change as proposed by Huxman et al. (2004) is shown for comparison ($sensitivity = 0.388 \times [1 - \exp(-0.0022 \times MAP)]$). For abbreviations, see Figs. 1 and 2

Moderate exceptions to the pattern occurred at KNZ, the grassland with the highest MAP and the third highest estimated sensitivity to drought ($0.56 \text{ g m}^{-2} \text{ mm}^{-1}$), and at HAYS, which had the lowest sensitivity and the second highest MAP (HAYS). Although ANPP and MAP were strongly correlated (Fig. 2), we found no statistically significant relationship between mean ANPP and ecosystem sensitivity to drought.

Discussion

Despite abundant evidence that ecosystems differ dramatically in their responses to climate change in general, and drought in particular (Parton et al. 1995; Grime et al. 2000; Weltzin et al. 2003; Jónsdóttir et al. 2005; Gerten et al. 2008; Luo et al. 2008; Sitch et al. 2008; Heisler-White et al. 2009; Cherwin and Knapp 2012), our understanding of the mechanisms determining why some ecosystems respond more than others is far from complete (Smith et al. 2009). A key impediment to progress has been that most climate change studies are conducted uniquely with regard to the magnitude of treatments, variables measured and spatial and temporal scales studied (Fraser et al. 2013). Thus, it is difficult to disentangle the role of differences in ecosystem sensitivity from the many other factors that may result in different responses. This has led to recent calls for

coordinated multi-site experiments that control the magnitude of the driver (drought) in order to assess differences in ecosystem sensitivity to climate change (Smith et al. 2009; Luo et al. 2011; Knapp et al. 2012; Fraser et al. 2013).

In this study, we quantified an important ecosystem process (ANPP) with comparable methods across six distinct grassland types (Table 1). These grasslands ranged from desert grasslands to mesic tallgrass prairie, but all were exposed to a similar magnitude of growing season drought (Fig. 1). This allowed us to directly test a conclusion made by Huxman et al. (2004) that sensitivity to precipitation change will be inversely related to MAP. Testing this prediction is important for several reasons. First, the Huxman et al. (2004) sensitivity model (Fig. 3, inset) was based on ANPP responses to interannual variability in precipitation, including both wet and dry years. However, ANPP may not respond symmetrically to years with above- and below-average precipitation (Knapp and Smith 2001; Munson et al. 2013), and thus responses to severe drought may not be predictable based on general sensitivity patterns to precipitation. Second, although the analysis of Huxman et al. (2004) was based on data sets that encompassed a range of wet and dry years at each site, sensitivity estimates were based on slopes of precipitation-ANPP relationships rather than on responses to the same magnitude of precipitation deviation at all sites. The slopes of these relationships will likely vary depending on the degree of climatic extremes experienced. Finally, recent research that has attempted to assess sensitivity to drought at global scales has relied on proxies for ANPP, such as tree rings or remotely sensed vegetation indices, rather than direct measures of ANPP (Liu et al. 2013; Vicente-Serrano et al. 2013).

In general, we found that both absolute and relative responses to drought (Fig. 2) and estimates of ecosystem sensitivity to drought (Fig. 3) were consistent with Huxman et al.'s (2004) conclusion that xeric sites would be more sensitive to drought. It is important to note that we adopted the IPCC definition of drought, which emphasizes marked precipitation deficits. However, increased temperatures (Fig. 1) and high potential evapotranspiration also characterize droughts. In addition, it has been argued that drought severity for any particular ecosystem should be scaled to the historical variability it has experienced (Vicente-Serrano et al. 2010). The standardized precipitation evapotranspiration index (SPEI) includes these additional drought attributes (Vicente-Serrano et al. 2010). We determined 2012 SPEI values for all six grasslands (Fig. S1, Electronic Supplementary Material) and regressed these against drought responses (absolute and relative) and drought sensitivity. We found no significant relationships, and indeed, the two grasslands with the greatest drought responses and sensitivity (SBK, SBL) experienced the lowest SPEI, whereas the SGS grassland was subjected to the most severe drought

based on this index. Thus, drought intensity as defined by the SPEI, is not a strong driver of this regional pattern. Similarly, legacy effects of previous year's precipitation have been reported to affect current year's ANPP responses to precipitation in grasslands (Sala et al. 2012; Reichmann et al. 2013). We also quantified precipitation amounts in the year previous to the drought for each grassland (Fig. S1) and found no evidence that patterns of drought responses or sensitivity across these six grasslands were consistently related to previous year's precipitation. For example, the two grasslands with the highest drought sensitivity (SBK, SBL) and the grassland with the lowest sensitivity (HAYS) all experienced below-average precipitation (ca. 30–40 %, Fig. S1) during the previous year. Thus, although both legacy effects and drought attributes included in the SPEI may play a role in site-level responses, they do not explain the regional pattern of drought sensitivity we observed.

Our study confirms the pattern of sensitivity reported by Huxman et al. (2004) and these results are consistent with those of Heisler-White et al. (2009) who showed that more xeric grasslands were more sensitive to precipitation event size than more mesic grassland. However, evaluating the mechanisms determining differential sensitivity of ecosystems to drought is a challenge, particularly for uncontrolled natural experiments. There are insights, however, that can be drawn from this study that relate to several purported mechanisms of differential ecosystem sensitivity. Two pairs of grasslands are particularly valuable in this regard: (1) the two adjacent grasslands at the Sevilleta LTER site (SBK and SBL) that have different dominant species [and slightly different soil types (Buxbaum and Vanderbilt 2007)] but experience essentially the same climate; and (2) the two blue grama-dominated grasslands in central New Mexico and northern Colorado (SBL, SGS) that experience very different climates. At the Sevilleta LTER site, greater drought sensitivity of the desert black grama (SBK) vs. the blue grama grassland (SBL) does not support the hypothesis that stress tolerance mechanisms in desert vegetation would lead to greater resistance to drought (Grime et al. 2000). Instead, greater drought sensitivity in the black grama grassland is consistent with Munson et al. (2013), who reported that black grama and blue grama had different climate thresholds at which they increased or decreased in cover with interannual variability in precipitation. In general, black grama exhibited an asymmetric response to precipitation variability, decreasing more under drought than it increases under higher rainfall (Báez et al. 2013), and when severe drought crosses the climate threshold for black grama, this species was found to respond dramatically.

In this case of the two blue grama-dominated grasslands (SBL, SGS), drought sensitivity was much higher at the Sevilleta vs. the SGS grassland in northern Colorado. This pattern of differential sensitivity is consistent with

the hypothesis that as MAP increases, other resources become more limiting, and thus sensitivity to precipitation decreases (Huxman et al. 2004). Moreover, blue grama is at the edge of its range as a dominant grass at SBL thus, it is more likely to be sensitive to environmental variation at its physiological limits than blue grama populations further north. In contrast, this pattern is not consistent with the idea that ecosystems historically exposed to high environmental variability will respond less than ecosystems subjected to less variability (Grime et al. 2000). The coefficient of variation (CV) of precipitation at the Sevilleta is almost 1.5 times greater than at the SGS (Table 1), yet the SBL blue grama grassland was more sensitive to drought. Across all six grasslands, the CV of GSP varied by more than 2.5-fold, but there was no significant correlation between CV and sensitivity.

Finally, the least responsive and least drought-sensitive grassland was the southern mixed grass prairie at HAYS (Fig. 3). Such low drought sensitivity was surprising given that this grassland also experienced a 12-month period of below-average precipitation prior to the 2012 drought (Fig. S1). Previous research suggests that legacy effects of prior drought years exacerbate rather than mute responses to drought (Oesterheld et al. 2001). Nonetheless, Byrne et al. (2013) also reported low sensitivity to 3 years of experimental drought in this grassland, and Vicente-Serrano et al. (2013) noted that vegetation intermediate between arid and humid regions (such as the mixed grass prairie at HAYS) responds to drought over longer time scales than other ecosystems. Plant communities at HAYS include high abundances of grass species such as the C_4 shortgrass dominant *B. gracilis* from more arid grasslands, as well as mesic-adapted C_4 tall grasses such as *A. gerardii* and *Schizachryum scoparium*, from the mesic tallgrass prairie (Albertson and Tomanek 1965). Thus, this grassland has higher trait diversity relative to the other grasslands with only semi-arid grasses (SGS) or mesic tall grasses (KNZ) dominating. Diversity in functional composition has been proposed as an important mechanism buffering ecosystem responses to drought (Díaz and Cabido 2001). Such diversity can stabilize productivity via species asynchrony, which occurs when species' responses compensate for each other (e.g., Hautier et al. 2014). Hallett et al. (2014), however, found that stabilizing mechanisms in grasslands varied across a precipitation gradient, with compensatory dynamics among multiple species most important in more arid grasslands. Hallett et al. (2014) argued that dominant species are more important for stabilizing production in sites with higher MAP. Thus, the diversity of dominant grasses at HAYS may be particularly important for buffering this grassland's response to drought.

In summary, we have shown that patterns of drought sensitivity across six grasslands in the Central US, spanning

desert grassland to tallgrass prairie, generally conform to the hypothesis that sensitivity is inversely related to MAP. Although we were unable to explicitly test for mechanisms driving the more than twofold differences in ecosystem sensitivity to the 2012 drought, both abiotic and biotic mechanisms are likely responsible. For example, the reduction in drought sensitivity with increasing MAP is consistent with the co-limitation mechanism of Huxman et al. (2004). In contrast, there was no evidence that ecosystem sensitivity to drought was influenced by past climatic variability. There was evidence supporting the importance of biotic attributes influencing ecosystem sensitivity. The grassland plant community that was most resistant to drought (lowest ecosystem sensitivity) was the most functionally diverse whereas the identity of the dominant plant species clearly impacted sensitivity when climatic characteristics were similar. A plurality of mechanisms determining drought sensitivity of ecosystems is not unexpected. But to improve forecasts of ecosystem responses to environmental change, multi-site mechanistic experiments designed to assess the relative importance of biotic and abiotic determinants of ecosystem sensitivity to climate change are needed.

Author contribution statement AKK and MDS conceived of the study; KJL and SLC contributed data; CJWC and EMD conducted the analysis; AKK, CJWC and EMD wrote the manuscript; MDS, KJL, SLC edited the manuscript.

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References

- Aanderud ZT, Schoolmaster DR, Lennon JT (2011) Plants mediate the sensitivity of soil respiration to rainfall variability. *Ecosystems* 14:156–167
- Albertson FW, Tomanek GW (1965) Vegetation changes during a 30-year period in grassland communities near Hays, Kansas. *Ecology* 46:714–720
- Báez S, Collins SL, Pockman WT, Johnson JE, Small EE (2013) Effects of experimental rainfall manipulations on Chihuahuan Desert grassland and shrubland plant communities. *Oecologia* 172:1117–1127

- Breshears DD, Cobb NS, Rich PM, Price KP, Allen CD, Balice RG, Romme WH, Kastens JH, Floyd ML, Belnap J, Anderson JJ, Myers OB, Meyer CW (2005) Regional vegetation die-off in response to global-change type drought. *Proc Natl Acad Sci USA* 102:15144–15148
- Briggs JM, Knapp AK (1995) Interannual variability in primary production in tallgrass prairie: climate, soil moisture, topographic position and fire as determinants of aboveground biomass. *Am J Bot* 82:1024–1030
- Burke IC, Yonker CM, Parton WJ, Cole CV, Schimel DS, Flach K (1989) Texture, climate, and cultivation effects on organic matter in grassland soils. *Soil Sci Soc Am J* 53:800–805
- Burke IC, Kittel TGF, Lauenroth WK, Snook P, Yonker CM (1991) Regional analysis of the central Great Plains: sensitivity to climate variation. *Bioscience* 41:685–692
- Buxbaum CAZ, Vanderbilt K (2007) Soil heterogeneity and the distribution of desert and steppe plant species across a desert-grassland ecotone. *J Arid Environ* 69:617–632
- Byrne KM, Lauenroth WK, Adler PB (2013) Contrasting effects of precipitation manipulations on production in two sites within the central grassland region, USA. *Ecosystems* 16:1039–1051
- Cherwin K, Knapp A (2012) Unexpected patterns of sensitivity to drought in semi-arid grasslands. *Oecologia* 169:845–852
- Debinski DM, Wickham H, Kindscher K, Caruthers JC, Germino M (2010) Montane meadow change during drought varies with background hydrologic regime and plant functional group. *Ecology* 91:1672–1681
- Díaz S, Cabido M (2001) Vive la différence: plant functional diversity matters to ecosystem processes. *Trees* 16:646–655
- Dijkstra FA, Blumenthal D, Morgan JA, Pendall E, Carrillo Y, Follett RF (2010) Contrasting effects of elevated CO₂ and warming on nitrogen cycling in a semiarid grassland. *New Phytol* 187:426–437
- Emmett BA, Beier C, Estiarte M, Tietema A, Kristensen HL, Williams D, Peñuelas J, Schmidt IK, Sowerby A (2004) The response of soil processes to climate change: results from manipulation studies across an environmental gradient. *Ecosystems* 7:625–637
- Frank DA (2007) Drought effects on above- and belowground production of a grazed temperate grassland ecosystem. *Oecologia* 152:131–139
- Fraser LH, Henry HAL, Carlyle CN, White SR, Beierkuhnlein C, Cahill JF Jr, Casper BB, Cleland E, Collins SL, Dukes JS, Knapp AK, Lind E, Long R, Luo Y, Reich PB, Smith MD, Sternberg M, Turkington R (2013) Coordinated distributed experiments: an emerging tool for testing global hypotheses in ecology and environmental science. *Front Ecol Environ* 11:147–155
- Gerten D, Luo YQ, Le Maire G, Parton WJ, Keough C, Weng E, Beier C, Ciais P, Cramer W, Dukes JS, Hanson PJ, Knapp AK, Linder S, Nepstad D, Rustad L, Sowerby A (2008) Modeled effects of precipitation on ecosystem carbon and water dynamics in different climatic zones. *Glob Change Biol* 14:1–15
- Grime JP, Broth VK, Thompson K, Masters GJ, Hillier SH, Clarke IP, Askew AP, Corker D, KIELTY JP (2000) The response of two contrasting limestone grasslands to simulated climate change. *Science* 289:762–765
- Hallett LM, Hsu JS, Cleland EE, Collins SL, Dickson TL, Farrer EC, Gherardi LA, Gross KL, Hobbs RJ, Turnbull L, Suding KN (2014) Biotic mechanisms contributing to the stability of primary productivity alternate along a gradient of precipitation variability. *Ecology* (in press)
- Hautier Y, Seabloom E, Borer ET, Adler P, Harpole WS, Hillebrand H, Lind E, MacDougall A, Stevens C, Bakker JB, Buckley Y, Chu C, Collins SL, Daleo P, Damschen EI, Davies KF, Fay PA, Firm J, Gruner DS, Jin VL, Klein JA, Knops JMH, La Pierre KJ, Li W, McCulley R, Melbourne BA, Moore JL, O'Halloran LR, Prober SM, Risch AC, Sankaran M, Schuetz M, Hector A (2014) Eutrophication weakens stabilizing effects of diversity in natural grasslands. *Nature* 508:521–525
- Heisler-White JL, Blair JM, Kelly EF, Harmony K, Knapp AK (2009) Contingent productivity responses to more extreme rainfall regimes across a grassland biome. *Glob Change Biol* 15:2894–2904
- Heitschmidt RK, Klement KD, Haferkamp MR (2005) Interactive effects of drought and grazing on northern Great Plains rangelands. *Rangel Ecol Manage* 58:11–19
- Hoover DL, Knapp AK, Smith MD (2014) Resistance and resilience of a grassland ecosystem to climate extremes. *Ecology* (in press)
- Hsu JS, Powell J, Adler PB (2012) Sensitivity of mean annual primary production to precipitation. *Glob Change Biol* 18:2246–2255
- Huxman TE, Smith MD, Fay PA, Knapp AK, Shaw MR, Loik ME, Smith SD, Tissue DT, Zak JC, Weltzin JF, Pockman WT, Sala OE, Haddad BM, Harte J, Koch GW, Schwinning S, Small EE, Williams DG (2004) Convergence across biomes to a common rain-use efficiency. *Nature* 429:651–654
- IPCC (2007) Climate Change 2007. The physical science basis. Contribution of Working Group I to the fourth assessment report of the Intergovernmental Panel on Climate Change. Solomon SD, Qin M, Manning Z, Chen M, Marquis KB, Avery T, Tignor M, Miller HL (eds) Cambridge University Press, Cambridge
- IPCC (2012) Managing the risks of extreme events and disasters to advance climate change adaptation. A special report of Working Groups I and II of the Intergovernmental Panel on Climate Change. Field CB, Barros V, Stocker TF, Qin D, Dokken DJ, Ebi KL, Mastrandrea MD, Mach KJ, Plattner GK, Allen SK, Tignor M, Midgley PM (eds) Cambridge University Press, Cambridge
- Jensen K, Beier C, Michelsen A, Emmett BA (2003) Effects of experimental drought on microbial processes in two temperate heathlands at contrasting water conditions. *Appl Soil Ecol* 24:165–176
- Jin Y, Goulden ML (2014) Ecological consequences of variation in precipitation: separating short-versus long-term effects using satellite data. *Glob Ecol Biogeogr* 23:358–370
- Jónsdóttir IS, Magnússon B, Gudmundsson J, Elamarsdóttir A, Hjartarson H (2005) Variable sensitivity of plant communities in Iceland to experimental warming. *Glob Change Biol* 11:553–563
- Knapp AK, Smith MD (2001) Variation among biomes in temporal dynamics of aboveground primary production. *Science* 291:481–484
- Knapp AK, Briggs JM, Hartnett DC, Collins SL (1998) Grassland dynamics: long-term ecological research in tallgrass prairie. Oxford University Press, New York
- Knapp AK, Smith MD, Hobbie SE, Collins SL, Fahey TJ, Hansen GJA, Landis DA, La Pierre KJ, Melillo JM, Seastedt TR, Shaver GR, Webster JR (2012) Past, present and future roles of long-term experiments in the LTER network. *Bioscience* 62:377–389
- Lauenroth WK, Burke IC (eds) (2008) Ecology of the shortgrass steppe: a long-term perspective. Oxford University Press, New York
- Lauenroth WK, Milchunas DG, Sala OE, Burke IC, Morgan JA (2008) Net primary production in the shortgrass steppe. In: Lauenroth WK, Burke IC (eds) Ecology of the shortgrass steppe: a long term perspective. Oxford Univ. Press, NY, pp 270–305
- Liu G, Liu H, Yin Y (2013) Global patterns of NDVI-indicated vegetation extremes and their sensitivity to climate extremes. *Environ Res Lett* 8 (2013) 025009 (11 pp) doi:10.1088/1748-9326/8/2/025009
- Luo YQ, Gerten D, le Maire G, Parton WJ, Weng ES, Zhou XH, Keough C, Beier C, Ciais P, Cramer CW, Dukes JS, Emmett B, Hanson PJ, Knapp A, Linder S, Nepstad D, Rustad L (2008) Modeled interactive effects of precipitation, temperature, and CO₂ on ecosystem carbon and water dynamics in different climatic zones. *Glob Change Biol* 14:1986–1999

- Luo YQ, Melillo J, Niu S, Beier C, Clark JS, Classen AT, Davidson E, Dukes JS, Evans RD, Field CB, Czimczik CI, Keller M, Kimball BA, Kueppers LM, Norby RJ, Pelini SL, Pendall E, Rastetter E, Six J, Smith M, Tjoelker MG, Torn MS (2011) Coordinated approaches to quantify long-term ecosystem dynamics in response to global change. *Glob Change Biol* 17:843–854
- Misson L, Rocheteau A, Rambal S, Ourcival JM, Limousin JM, Rodriguez R (2010) Functional changes in the control of carbon fluxes after 3 years of increased drought in a Mediterranean evergreen forest? *Glob Change Biol* 16:2461–2475
- Morgan JA, LeCain DR, Pendall E, Blumenthal DM, Kimball BA, Carrillo Y, Williams DG, Heisler-White J, Dijkstra FA, West M (2011) C4 grasses prosper as carbon dioxide eliminates desiccation in warmed semi-arid grassland. *Nature* 476:202–206
- Muldavin EH, Moore DI, Collins SL, Wetherill KR, Lightfoot DC (2008) Aboveground net primary production dynamics in a northern Chihuahuan Desert ecosystem. *Oecologia* 155:123–132
- Munson SM, Muldavin EH, Belnap J, Peters DPC, Anderson JP, Reiser MH, Gallo K, Melgoza-Castillo A, Herrick JE, Christiansen TA (2013) Regional signatures of plant response to drought and elevated temperature across a desert ecosystem. *Ecology* 94:2030–2041
- NOAA National Climatic Data Center. <http://www.ncdc.noaa.gov/sotc/briefings/201209.pdf>
- Oosterheld M, Loreti J, Semmartin M, Sala OE (2001) Inter-annual variation in primary production of a semi-arid grassland related to previous-year production. *J Veg Sci* 12:137–142
- Parton WJ, Scurlock JMO, Ojima DS, Schimel DS, Hall D, Coughenour M, Garcia Moya E, Gilmanov TG, Kamnalrut A, Kinyamario JJ, Kirchner T, Kittel T, Menaut JC, Sala OE, Scholes RJ, van Veen J (1995) Impact of climate change on grassland production and soil carbon worldwide. *Glob Change Biol* 1:13–22
- R Core Team (2014) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna <http://www.R-project.org/>
- Reichmann LG, Sala OE, Peters DPC (2013) Precipitation legacies in desert grassland primary production occur through previous-year tiller density. *Ecology* 94:435–443
- Sala OE, Parton WJ, Joyce LA, Lauenroth WK (1988) Primary production of the central grassland region of the United States: spatial pattern and major controls. *Ecology* 69:40–45
- Sala OE, Gherardi LA, Reichmann L, Jobbágy E, Peters D (2012) Legacies of precipitation fluctuations on primary production: theory and data synthesis. *Philos Trans R Soc B* 367:3135–3144
- Shinoda M, Nachinshonhor GU, Nemoto M (2010) Impact of drought on vegetation dynamics on the Mongolian steppe: a field experiment. *J Arid Environ* 74:63–69
- Sitch S, Huntingford C, Gedney N, Levy PE, Lomas M, Piao SL, Betts R, Ciais P, Cox P, Friedlingstein P, Jones CD, Prentice IC, Woodward FI (2008) Evaluation of the terrestrial carbon cycle, future plant geography and climate-carbon cycle feedbacks using five dynamic global vegetation models (DGVMs). *Glob Change Biol* 14:2015–2039
- Smith MD (2011) An ecological perspective on extreme climatic events: a synthetic definition and framework to guide future research. *J Ecol* 99:656–663
- Smith MD, Knapp AK, Collins SL (2009) A framework for assessing ecosystem dynamics in response to chronic resource alterations induced by global change. *Ecology* 90:3279–3289
- Tilman D, El Haddi A (1992) Drought and biodiversity in grasslands. *Oecologia* 89:257–264
- Trenberth KE, Dai A, van der Schrier G, Jones PD, Barichivich J, Briffa KR, Sheffield J (2014) Global warming and changes in drought. *Nature Climate Change* 4:17–22
- Vicente-Serrano SM, Begueria S, Lopez-Moreno JJ (2010) A multi-scale drought index sensitive to global warming: the standardized precipitation evapotranspiration index. *J Clim* 23:1696–1718
- Vicente-Serrano SM, Gouveia C, Camarero JJ, Begueria S, Trigo R, Lopez-Moreno JJ, Azorin-Molina C, Pasho E, Lorenzo-Lacruz J, Revuelto J, Moran-Tejeda E, Sanchez-Lorenzo A (2013) Response of vegetation to drought time-scales across global land biomes. *PNAS* 110:52–57
- Weaver JE (1954) North American prairie. Johnsen, Lincoln
- Weaver JE, Albertson FW (1936) Effects on the great drought on the prairies of Iowa, Nebraska, and Kansas. *Ecology* 17:567–639
- Weltzin JF, Loik ME, Schwinning S, Williams DG, Fay PA, Haddad BM, Harte J, Huxman TE, Knapp AK, Guanghui L, Pockman WT, Shaw MR, Small EE, Smith MD, Smith SD, Tissue DT, Zak JC (2003) Assessing the response of terrestrial ecosystems to potential changes in precipitation. *Bioscience* 53:941–952
- Woodhouse CA, Overpeck JT (1998) 2000 years of drought variability in the central United States. *Bull Am Meteorol Soc* 79:2693–2714
- Wu Z, Dijkstra P, Koch GW, Peñuelas J, Hungate B (2011) Responses of terrestrial ecosystems to temperature and precipitation change: a meta-analysis of experimental manipulation. *Glob Change Biol* 17:927–942