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Legacy effects of a regional drought on aboveground net primary production in six central US grasslands

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Abstract Global climate models predict increases in the frequency and severity of drought worldwide, directly affecting most ecosystem types. Consequently, drought legacy effects (drought-induced alterations in ecosystem function postdrought) are expected to become more common in ecosystems varying from deserts to grasslands to forests. Drought legacies in grasslands are usually negative and reduce ecosystem function, particularly after extended drought. Moreover, ecosystems that respond strongly to drought (high sensitivity) might be expected to exhibit the largest legacy effects the next year, but this relationship has not been established. We quantified legacy effects of a severe regional drought in 2012 on postdrought (2013) aboveground net primary productivity (ANPP) in six central US grasslands. We predicted that (1) the magnitude of drought legacy effects measured in 2013 would be positively related to the sensitivity of ANPP to the 2012 drought, and (2) drought legacy effects would be negative (reducing 2013 ANPP relative to that expected given normal precipitation amounts). The magnitude of legacy effects measured in 2013 was strongly related ($r^2 = 0.88$) to the sensitivity of ANPP to the 2012 drought across these six grasslands. However, contrary to expectations, positive legacy effects (greater than expected ANPP) were more commonly observed

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than negative legacy effects. Thus, while the sensitivity of ANPP to drought may be a useful predictor of the magnitude of legacy effects, short-term (1-year) severe droughts may cause legacy effects that are more variable than those observed after multiyear droughts.

Introduction

Drought, defined meteorologically as a "prolonged absence or marked deficiency of precipitation" (IPCC 2013), has shaped the structure and functioning of grasslands globally, particularly those in central North America (Woodhouse and Overpeck 1998; Clark et al. 2002). Severe droughts, and climate extremes more broadly (Smith 2011), are expected to increase in frequency and intensity with climate change, and there is evidence that drought severity has already increased (Dai 2011; 2013; Ponce-Campos et al. 2013; Trenberth et al. 2014; Griffin and Anchukaitis 2014; Cook et al. 2015). In general, drought results in a decline in ecosystem functions such as aboveground net primary production (ANPP) and soil CO_2 flux (Hoover et al. 2014; Shi et al. 2014). Drought also alters structural attributes, such as tiller and rooting density (Plaut et al. 2013; Reichmann et al. 2013), which can have prolonged postdrought effects on ecosystem function.

Drought legacies, defined as alterations in resources or ecosystem properties that continue to affect an ecosystem postdrought (sensu Yahdjian and Sala 2006), can be negative or positive (Sala et al. 2012), and thus can either exacerbate or offset (partially) the negative effects of drought on ecosystem function. Negative drought legacies, characterized by reduced ANPP after a drought relative to that expected, may occur when there is a soil moisture deficit that persists after the drought (despite increased precipitation inputs), or if there is drought-induced mortality of plants or senescence that constrains ANPP responses after drought has subsided (Yahdjian and Sala 2006; Sala et al. 2012; Reichmann et al. 2013). Positive drought legacies, when ANPP is higher than expected after a drought (Seastedt and Knapp 1993),

have been linked to increased light availability (Slik 2004) or elevated soil nitrogen (N) availability after drought (Whitford et al. 1995; Reynolds et al. 1999; Hofer et al. 2017). From an analysis of long-term records of precipitation and ANPP in 16 grasslands, Sala et al. (2012) concluded that drought legacies are predominantly negative in grasslands worldwide. A recent analysis of forest tree growth after drought led to a similar conclusion (Anderegg et al. 2015). The impact of drought legacies is predicted to be positively related to drought severity and the magnitude of ecosystem responses to drought (Yahdjian and Sala 2006; Smith 2011); thus, negative drought legacies are expected to become more pronounced in the future as drought severity intensifies.

Grassland ecosystems, which cover > 30% of Earth's terrestrial surface, are ideal study systems for assessing the impacts of drought and subsequent drought legacies on ANPP because most are water-limited ecosystems (Noy-Meir 1973; Webb et al. 1978; Sala et al. 1988) and are highly responsive to changes in precipitation (Knapp and Smith 2001; Hsu et al. 2012). In 2012, grasslands in the central US experienced a severe and extensive drought (the fourth largest drought since 1895) characterized by a ~40% reduction in growing season precipitation across the region (Knapp et al. 2015). Taking advantage of the regional uniformity of these precipitation reductions, Knapp et al. (2015) assessed ecosystem sensitivity to the 2012 drought of six native grassland ecosystems ranging from a desert grassland in New Mexico to a mesic tallgrass prairie in Kansas. The sensitivity of ANPP to drought varied twofold among these six grasslands and was negatively correlated with mean annual precipitation (MAP), a pattern that is consistent with previous models predicting the high sensitivity and responsiveness of xeric ecosystems to drought (Huxman et al. 2004; Diffenbaugh et al. 2008).

The differential drought sensitivity observed across the major grasslands of the central US, combined with a return to average precipitation in 2013 (Table 1), provided an opportunity to assess the legacy effects of the 2012 drought on ecosystem function (ANPP) in 2013. We tested two hypotheses: (1) that legacy effects of drought in these grasslands would be negative (Sala et al. 2012) given the severity of the 2012 drought (rated as severe to extreme, http://www.

Table 1 Site characteristics for six central US grasslands affected by the 2012 regional drought. (Color figure online)
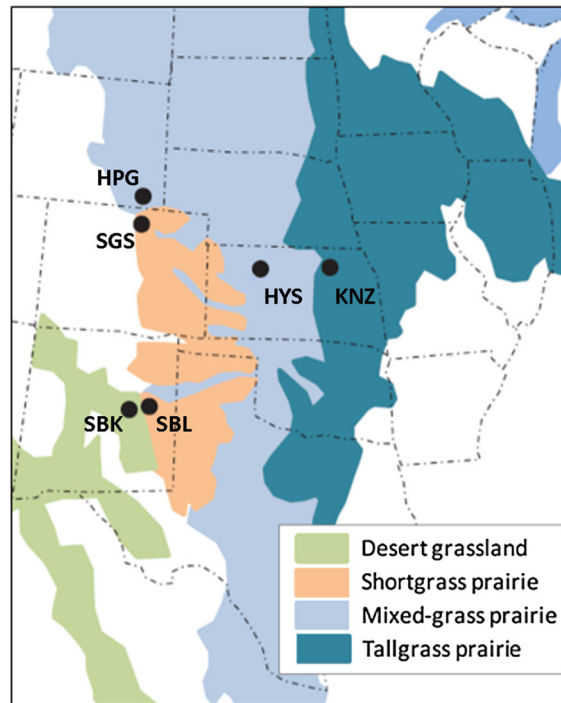

Site[a]		MAP (mm)	MAT (°C)	Mean ANPP (g m^{-2})	2012 PPT (mm)	2013 PPT (mm)	2012 ANPP (g m^{-2})	2013 ANPP (g m^{-2})	2012 SPEI
SBK	Sevilleta black grama	244 ± 39	13.4	98 ± 39	187	251	34 ± 6	243 ± 17	− 1.49
SBL	Sevilleta blue grama	257 ± 52	13.4	66 ± 26	195	299	19 ± 3	189 ± 20	− 1.49
SGS	Shortgrass Steppe	366 ± 30	9.5	94 ± 16	189	362	42 ± 2	126 ± 20	− 2.16
HPG	High Plains Grassland	415 ± 44	7.9	137 ± 30	232	447	69 ± 3	69 ± 3	− 2.4
HYS	Hays Agricultural Research Center	581 ± 96	12.3	246 ± 57	362	547	159 ± 9	245 ± 12	− 1.82
KNZ	Konza Prairie	864 ± 74	13	413 ± 42	569	787	250 ± 8	492 ± 16	− 1.57

MAP (± 95% CI), MAT, and mean aboveground net primary production (ANPP; g m^{-2} ± 95% CI). Mean ANPP and MAP were calculated excluding 2012 and 2013 values. ANPP (± SE for plot variability) and precipitation (PPT) amounts are shown for 2012 and 2013. SPEI was calculated for the site-specific 2012 growing season. Climatic data were taken from the nearest NOAA sites or from LTER rain gages. See Figs. S1 and S2 for distributions of long-term ANPP and precipitation data

[a]Sites include a desert grassland [Sevilleta National Wildlife Refuge, dominated by black grama, *Bouteloua eriopoda* (C$_4$)—SBK] and a southern Shortgrass Steppe [Sevilleta National Wildlife Refuge, dominated by blue grama (*Bouteloua gracilis* (C$_4$))—SBL] in New Mexico; a northern Shortgrass Steppe [Central Plains Experimental Range, dominated by *B. gracilis*—SGS] in Colorado; a northern mixed-grass prairie [High Plains Grassland Research Center, codominated by *Pascopyron smithii* (C$_3$) and *B. gracilis*—HPG] in Wyoming; as well as a southern mixed-grass prairie [Hays Agricultural Research Center, codominated by *P. smithii*, *Bouteloua curtipendula* (C$_4$), and *Sporobolus asper* (C$_4$)—HYS], and a tallgrass prairie [Konza Prairie Biological Station, dominated by *Andropogon gerardii* (C$_4$) and *Sorghastrum nutans* (C$_4$)—KNZ] in Kansas

droughtmonitor.unl.edu/), and (2) that differences in drought sensitivity among these grasslands would be positively related to the *magnitude* of the legacy effects observed, regardless of whether legacies were positive or negative (Yahdjian and Sala 2006; Smith 2011) (Fig. 1).
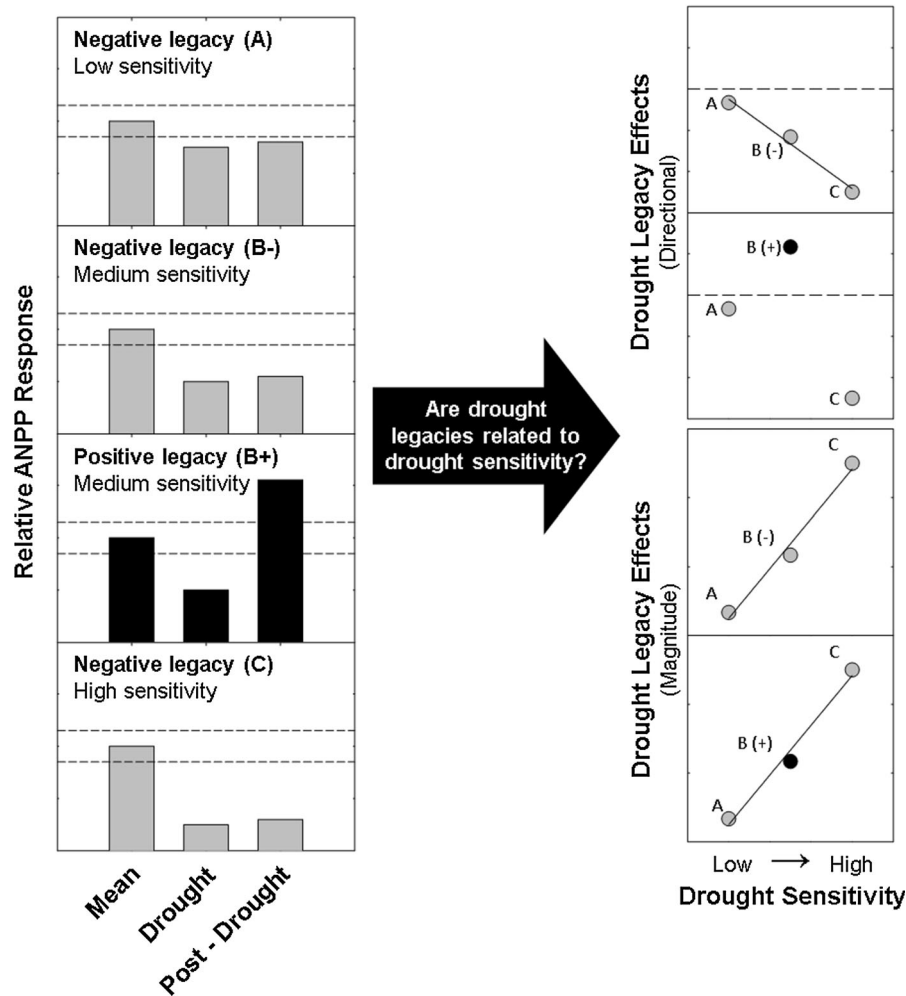
Fig. 1 Hypothetical ANPP responses of three grasslands varying in drought sensitivity (from the least to most sensitive: A, B, C) and potential legacy effects. Depicted on the left are differential responses of aboveground net primary productivity (ANPP) for each site during a drought year and a postdrought year. Long-term mean ANPP with 95% CI (dashed lines) is also shown for reference. Assuming the drought was of equal magnitude across all sites and precipitation in the postdrought year was near average, drought sensitivity and legacy effects can be calculated as anomalies from the long-term mean ANPP (i.e., % deviation) in the drought year and postdrought year, respectively. Legacy directionality is indicated as anomalies above (+) or below (−) the 95% CI for mean ANPP. As predicted by Sala et al. (2012), negative legacy effects are shown across all sites; however, an alternative positive legacy effect of similar magnitude is shown for the site with medium drought sensitivity (B+). Potential cross-site relationships between drought sensitivity and legacy effects (depicted on the right) can incorporate negative (filled gray circle) and positive (filled black circle) legacy effects or simply focus on the magnitude of the legacy effect by plotting the absolute value of the postdrought ANPP response. (The dashed line in the "directional" relationship represents zero legacy effect with positive legacies being above the line and negative legacies below it). The relationship between the responsivenesses of ecosystems during a post drought is more accurately visualized using the drought legacy magnitude

Materials and methods

Study sites

Potential legacy effects of the 2012 drought were measured in 2013 in the same six grassland ecosystems used by Knapp et al. (2015) to determine drought sensitivity. These six sites encompass the major grassland types in the central US spanning a west–east MAP gradient of 244–863 mm (> threefold difference) as well as a north–south mean annual temperature (MAT) gradient of 6.8 °C (Table 1). Soil

textures across these sites vary from sandy to clay loams (Burke et al. 1989, 1991; Kieft et al. 1998). ANPP was quantified in ungrazed pastures in 2012 and 2013. Apart from the two mixed-grass prairie sites (HYS and HPG; Table 1), which were lightly grazed two years prior to this study, these sites had not been grazed by domestic herbivores for > 10 years prior to the 2012 drought. The tallgrass prairie site (KNZ) is subjected to frequent (annual) prescribed fire, a common management practice in the region that has replaced the frequent wildfires that historically maintained the structure and function of this grassland (Knapp et al. 1998).

ANPP and climate data

From each grassland site, historical ANPP data were compiled from the literature or from online data sources and combined with ANPP measured at each site in 2012 and 2013. ANPP was also measured in 2014 and 2015 to provide a more robust measure of long-term mean ANPP and ensure that ANPP pre- and postdrought (after the single legacy year) were similar. This resulted in 8–32 years of data for each site (see Knapp et al. 2015 for additional details on data sources). Corresponding data on annual precipitation amounts were taken from on-site rain gages when available or retrieved from the nearest NOAA weather station (http://www.ncdc.noaa.gov/). Both long-term mean ANPP and MAP were calculated excluding data from the 2012 drought year and 2013 legacy year.

Estimates of ANPP were based on end-of-season or peak biomass harvests for the SGS, HPG, HYS, and KNZ sites. In contrast, biomass was estimated allometrically twice during the growing season for the two Sevilleta sites (SBK and SBL) using species-specific equations with changes over time used to estimate ANPP (Muldavin et al. 2008). Succulent plant ANPP was not included in productivity estimates and was a relatively minor component of the vegetation in most plots. Sample sizes and specific plot dimensions varied slightly depending on the study prior to 2012. In 2013, all aboveground biomass was harvested at the end of the growing season from three 0.1-m^2 quadrats randomly located within thirty 4-m^2 plots for SGS, HPG, HYS, and KNZ ($n = 90$ quadrats/site). Similarly, ANPP was estimated using species-specific allometric equations from four 1-m^2 quadrats within ten 4-m^2 plots for SBK and SBL ($n = 40$ quadrats/site)

(Muldavin et al. 2008). In all cases, biomass produced in previous years (easily identified by gray coloration) was excluded from estimates of the current year ANPP.

Data analysis

Long-term datasets were used to calculate mean ANPP and precipitation, with 95% confidence intervals (CI), for each site. The relative ANPP responses in 2012 (drought sensitivity) and 2013 (drought legacy effects) were calculated as anomalies from mean ANPP:

$$\text{Drought sensitivity} = \left| \frac{2012\text{ANPP} - \text{Mean ANPP}}{\text{Mean ANPP}} \right|$$

$$\text{Drought legacy effects} = \frac{2013\text{ANPP} - \text{Mean ANPP}}{\text{Mean ANPP}}$$

This measure of legacy effects was justified as 2013 precipitation amounts fell within the 95% CI of MAP at five of the six sites (a significant 9% reduction from MAP was observed at KNZ in 2013), thus average ANPP would be expected in the absence of legacy effects (Table 1). Legacy effects were considered statistically significant if 2013 ANPP was above (positive legacy) or below (negative legacy) the 95% CI for the site-specific long-term mean of ANPP. Drought sensitivity is shown as the absolute value of 2012 ANPP anomalies; thus, higher values indicate higher sensitivity. A general linear model was used to determine whether the drought sensitivity magnitude (i.e., absolute value) was related to the drought legacy effects (including directionality); however, second regression analysis was included using the magnitude (absolute value of drought legacy effects) to observe potential relationships between relative ANPP responses that may be hidden due to legacy directionality (Fig. 1).

The magnitude of drought legacy effects was also regressed against variables that have been shown to be predictive of lagged ANPP responses to precipitation. These included the difference in precipitation between the drought and recovery years relative to MAP for each site ([2013 Precipitation − 2012 Precipitation]/ MAP) as well as the Standardized Precipitation Evapotranspiration Index (SPEI) (Yahdjian and Sala 2006). SPEI, a common measure of drought severity,
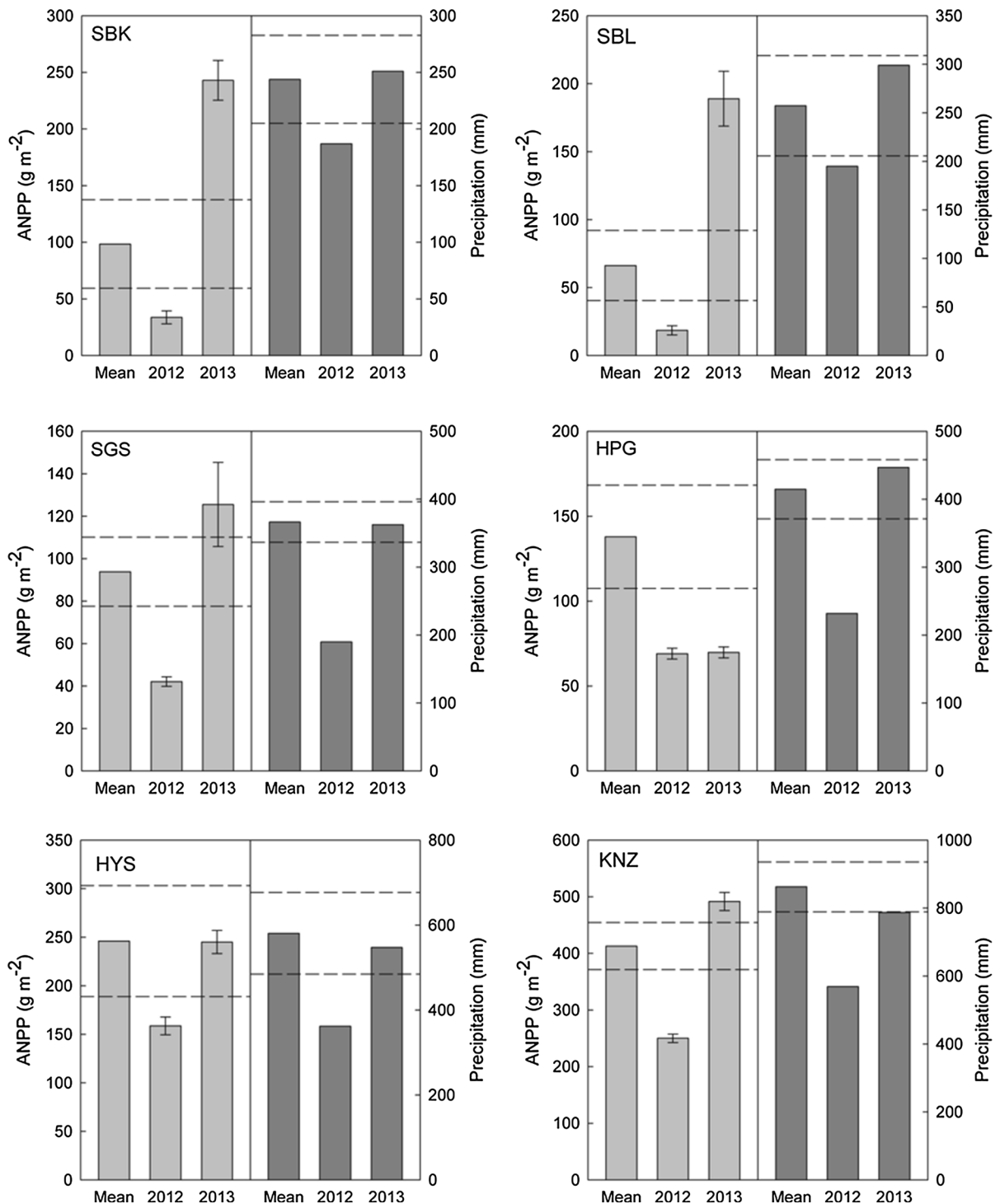
was calculated for the 2012 growing season defined separately for each site (April–September for SGS, HPG, HYS, and KNZ and April–October for SBK and SBL; Knapp et al. 2015). All regression analyses and CI were calculated in R version 3.4.0.

Results

The drought in 2012 reduced ANPP in all six grasslands relative to the long-term mean, ranging from a 35% reduction in the southern mixed-grass prairie (HYS), the least drought sensitive site, to > 65% reductions in both Sevilleta sites, SBL and SBK, the most drought sensitive sites (Fig. 2). Despite near average precipitation in 2013, ANPP deviated significantly from the long-term mean at most sites, ranging from a 49% relative *reduction* in the C3-dominated northern mixed-grass prairie (HPG) to a > 145% relative *increase* at both SBL and SBK (Fig. 2).

Contrary to our predictions, we observed positive drought legacy effects on ANPP more frequently than negative legacy effects across these six grasslands (Fig. 2). Legacy effects (i.e., significant deviations from the expected mean ANPP, given average precipitation levels) were evident in four of the six grasslands (SBK, SBL, HPG, and KNZ; Fig. 2). Three of these legacy effects were positive (SBK, SBL, and KNZ), with a negative legacy effect observed at HPG. There was no observable drought legacy effect on ANPP in the southern mixed-grass prairie (HYS) or shortgrass prairie (SGS). It is worth noting that 2013 was the most productive year on record for the Sevilleta sites (14 and 16 years of LTER data for SBL and SBK, respectively), despite receiving an average amount of annual rainfall.

Drought legacy effects were significantly correlated with drought sensitivity across these six grassland sites (Fig. 3a). This positive relationship was much stronger when drought sensitivity was regressed against the magnitude of legacy effects, irrespective of legacy directionality ($R^2 = 0.88$; Fig. 3b). The variability in the magnitude of legacy effects across sites

was much higher than the variability in drought sensitivity (ANPP anomaly range of 0.36 and 1.85 for 2012 and 2013, respectively; Fig. 3). The magnitude of drought legacy effects was not correlated with either SPEI or the difference in precipitation between the drought and postdrought years, two variables commonly used to explain drought legacy effects on ANPP (Table S1; Yahdjian and Sala 2006). Finally, we saw no evidence of any lagged effects of the 2012 drought on ANPP in 2014 or 2015, although precipitation during these years was less comparable across sites than in 2012 and 2013.

Discussion

Drought legacies can extend the influence of drought well beyond its meteorological occurrence. Legacy effects of drought, and more broadly the lagged effects of antecedent precipitation on current year ecological processes (Ogle et al. 2015), have been widely reported to be negative (Yahdjian and Sala 2006; Sala et al. 2012; Reichmann et al. 2013; Anderegg et al. 2015); however, positive effects, as well as a complete lack of drought effects on postdrought function, have also been reported (Seastedt and Knapp 1993; Slik 2004; Hermance et al. 2015; Wagg et al. 2017). For example, an experimentally induced 2-year extreme drought elicited extreme ANPP responses (significantly rare compared to historical responses; Smith 2011) in the Konza tallgrass prairie, yet there was no postdrought legacy effect on ecosystem function (ANPP) the next year (Hoover et al. 2014). Thus, greater understanding of the potential relationship between the sensitivity of ecosystems to drought and legacy effects of drought is needed, particularly given the forecasted increase in drought severity and frequency (Dai 2011; 2013).

In this study, we observed legacy effects of the severe 2012 regional drought on ecosystem function (ANPP) in 2013 and, as predicted by Smith (2011), we found a strong correlation between the ecosystem drought sensitivity and the magnitude of the legacy effect observed postdrought (Fig. 3b). Although Sala et al. (2012) concluded that drought legacies are predominately negative in grasslands, positive legacies were observed in half of the grasslands studied here (Fig. 2). A significant negative legacy effect was observed in only one grassland, HPG, the site with the
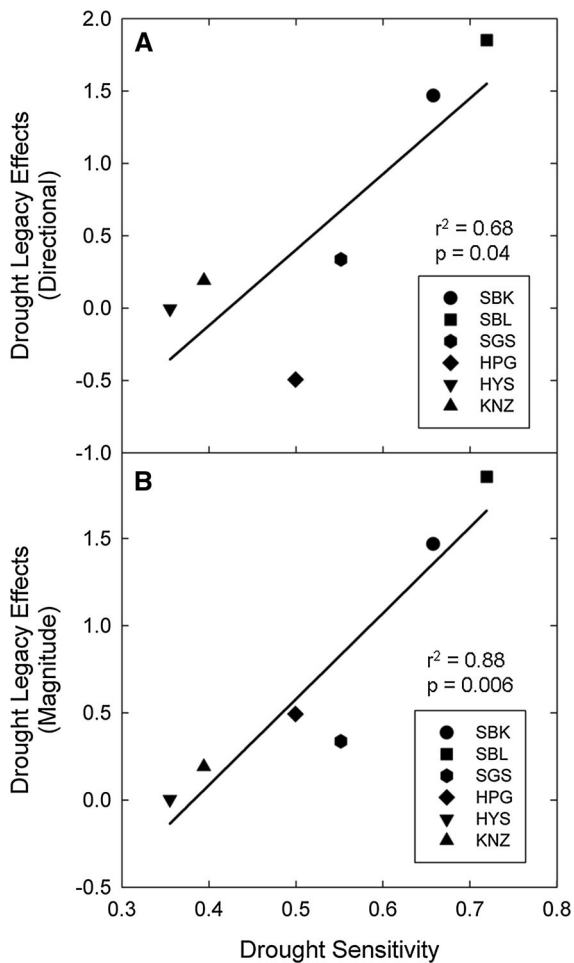
Fig. 3 The relationship between drought sensitivity and legacy effects across six central US grasslands (**a**). Both positive and negative ANPP anomalies are included in this "directional" relationship. The relationship between drought sensitivity and legacy effects is more accurately presented and strengthened when the magnitude of the legacy effects is shown (**b**). See Table S1 for linear model results. By calculating the magnitude, or absolute value, of ANPP anomalies, the responsiveness of ANPP in the drought year can be compared to responsiveness in the recovery year, irrespective of directionality. This relationship suggests that a large ANPP response to a 1-year severe drought may lead to a large ANPP response in the recovery year, regardless of whether the response is positive or negative. See Table 1 for site abbreviations and Fig. S3 for the distribution of ANPP anomalies over time for each site. *Drought sensitivity* = |2012 ANPP − Mean ANPP/Mean ANPP|. *Drought legacy effects* = 2013 ANPP − Mean ANPP/Mean ANPP

highest C$_3$ grass cover. It is worth noting that HPG experienced the most severe drought in 2012, as indicated by SPEI (Table 1), which may have contributed to the negative legacy effect. As expected, no

legacy effect was detected in the grassland that was least responsive to the 2012 drought (HYS). While considerable plot-level variability in ANPP suggests a lack of legacy effects at SGS (Fig. 2—SGS), the mean for 2013 ANPP was well above the long-term mean. Additionally, Hermance et al. (2015) observed a positive legacy effect of the 2012 drought in the Shortgrass Steppe of Colorado (SGS) based on NDVI estimates of plant production in 2013. ANPP values at the two Sevilleta sites (SBK and SBL) were historically high in 2013 (Fig. S3), which we attribute to drought legacy effects; however, rainfall patterns in 2013 likely played a role in this system, where ANPP is highly responsive to the timing and size of rain events in the late summer monsoon season (Muldavin et al. 2008).

Although negative drought legacies have several potential mechanisms, results from field experiments suggest that plant mortality or loss of meristematic tissues (stems, buds, tillers, etc.) during extreme or prolonged drought can be particularly important for constraining plant growth postdrought, even when abundant precipitation is available (Yahdjian and Sala 2006; Reichmann et al. 2013). Indeed, meristem limitation has been proposed as a mechanism limiting production responses to increased precipitation in many chronically water-limited ecosystems (Knapp and Smith 2001; Dalgleish and Hartnett 2006). Although we did not attempt to quantify plant mortality or meristem density after the 2012 drought, observations made at each site during end of season sampling did not reveal any obvious increases in plant mortality. It is likely that drought of extended duration or greater severity would be required for such plant mortality and increased meristem limitation to occur.

Positive drought legacies are most commonly attributed to higher soil N availability postdrought, a result of continued N-mineralization but reduced N-uptake during drought (Seastedt and Knapp 1993; Whitford et al. 1995; Reynolds et al. 1999; Yahdjian et al. 2006; Sala et al. 2012; Hofer et al. 2017). Indeed, N dynamics are highly correlated with variation in NPP among grasslands globally (Stevens et al. 2015). Although Reichmann et al. (2013) showed that N-addition could not offset the negative effects of drought-induced meristem reductions, the effects of N-fertilization may become apparent if plant mortality is minimal, such as during a 1-year drought.

It is tempting to conclude that relatively short-term (1-year) severe droughts are more likely to lead to positive legacy effects whereas long-term, or more extreme droughts that cause mortality, will result in negative legacy effects; however, there is abundant evidence that negative drought legacy effects can result from single-year droughts (Oesterheld et al. 2001; Sala et al. 2012; Fig. 2—HPG). This variability in legacy effects of short-term drought may be particularly pronounced in more water-limited ecosystems where rainfall timing and event size are strong determinants of the variability in ANPP, soil N availability and drought sensitivity (Heisler-White et al. 2008; Yaseef et al. 2009, 2012; Cherwin and Knapp 2012; Petrie et al. 2015).

Precipitation is expected to become more variable in the near future, with the frequency of both short-term (1-year) and long-term droughts increasing (Dai 2011; 2013; Ponce-Campos et al. 2013; Trenberth et al. 2014; Griffin and Anchukaitis 2014; Cook et al. 2015). A clear understanding of how the magnitude and directionality of legacy effects on ecosystem function differ between short versus long-term droughts is crucial given the implications for carbon storage and nutrient cycling. This is especially true within arid and semiarid ecosystems, such as grasslands, which often experience both short- and long-term droughts (Ahlström et al. 2015). The strong correlation between the sensitivity of ANPP to drought and the magnitude of drought legacy effects the following year suggests that greater understanding of the determinants of differential ecosystem sensitivity to drought will also provide insight into ecosystem function post-drought.

Author contributions AKK, MDS, and SLC conceived the experiment, while AKK and RJGN designed and conducted the analysis. EMD, MJ, CJWC, SLC, and MDS contributed to data acquisition. RJGN and AKK wrote the manuscript, and all authors edited, read, and approved the final manuscript.

References

Ahlström A, Raupach MR, Schurgers G, Smith B, Arneth A, Jung M, Reichstein M, Canadell JG, Friedlingstein P, Jain AK, Kato E, Poulter B, Sitch S, Stocker BD, Viovy N, Wang YP, Wiltshire A, Zaehle S, Zeng N (2015) The dominant role of semi-arid ecosystems in the trend and variability of the land CO_2 sink. Science 348:895–899

Anderegg WRL, Schwalm C, Biondi F, Camarero JJ, Koch G, Litvak M, Ogle K, Shaw Shevliakova E, Williams AP, Wolf A, Ziaco E, Pacala S (2015) Pervasive drought legacies in forest ecosystems and their implications for carbon cycle models. Science 349:528–532

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

Cherwin K, Knapp A (2012) Unexpected patterns of sensitivity to drought in three semi-arid grasslands. Oecologia 169(3):845–852

Clark JS, Grimm EC, Donovan JJ, Fritz SC, Engstrom D, Almendinger JE (2002) Drought cycles and landscape responses to past aridity on prairies of the northern Great Plains, USA. Ecology 83:595–601

Cook BI, Ault TR, Smerdon JE (2015) Unprecedented 21st century drought risk in the American Southwest and Central Plains. Sci Adv 1:e1400082

Dai A (2011) Drought under global warming: a review. WIREs Clim Change 2:45–65

Dai A (2013) Increasing drought under global warming in observations and models. Nat Clim Change 3:52–58

Dalgleish H, Hartnett D (2006) Below-ground bud banks increase along a precipitation gradient of the North American Great Plains: a test of the meristem limitation hypothesis. New Phytol 171:81–89

Diffenbaugh NS, Giori F, Pal JS (2008) Climate change hotspots in the United States. Geophys Res Lett. https://doi.org/10.1029/2008GL035075

Griffin D, Anchukaitis KJ (2014) How unusual is the 2012–2014 California drought? Geophys Res Lett 41:9017–9023

Heisler-White JL, Knapp AK, Kelly EF (2008) Increasing precipitation event size increases aboveground net primary productivity in a semi-arid grassland. Oecologia 158(1):129–140

Hermance JF, Augustine DJ, Derner JD (2015) Quantifying characteristic growth dynamics in a semi-arid grassland ecosystem by predicting short-term NDVI phenology from daily rainfall: a simple four parameter coupled-reservoir model. Int J Remote Sens. https://doi.org/10.1080/01431161.2015.1103916

Hofer D, Suter M, Buchmann N, Lüscher A (2017) Nitrogen status of functionally different forage species explains resistance to severe drought and post-drought overcompensation. Agric Ecosyst Environ 236:312–322

Hoover DL, Knapp AK, Smith MD (2014) Resistance and resilience of a grassland ecosystem to climate extremes. Ecology 95:2646–2656

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 (2013) Climate change 2013. The physical science basis. In: Stocker TF, Qin D, Plattner GK, Tignor MMB, Allen SK, Boschung J, Nauels A, Xia Y, Bex V, Midgley PM (eds) Working group I contribution to the fifth assessment report of the intergovernmental panel on climate change. Cambridge University Press, Cambridge

Kieft TL, White CS, Loftin SR, Aguilar R, Craig JA, Skaar DA (1998) Temporal dynamics of soil carbon and nitrogen resources at a grassland-shrubland ecotone. Ecology 79:671–683

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, Carroll CJW, Denton EM, La Pierre KJ, Collins SL, Smith MD (2015) Differential sensitivity to regional-scale drought in six central U.S. grasslands. Oecologia 177:949–957

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

Noy-Meir I (1973) Desert Ecosystems: environment and Producers. Ann Rev Ecol Syst 4:25–51

Oesterheld M, Loreti J, Semmartin M, Sala OE (2001) Interannual variation in primary production of a semi-arid grassland related to previous-year production. J Veg Sci 12:137–142

Ogle K, Barber JJ, Barron-Gafford GA, Bentley LP, Cable JM, Huxman TE, Loik ME, Tissue DT (2015) Quantifying ecological memory in plant and ecosystem processes. Ecol Lett 18:221–235

Petrie MD, Collins SL, Litvak ME (2015) The ecological role of small rainfall events in a desert grassland. Ecohydrology. https://doi.org/10.1002/eco.1614

Plaut JA, Wadsworth WD, Pangle R, Yepez EA, McDowell NG, Pockman WT (2013) Reduced transpiration response to precipitation pulses precedes mortality in a pinon–juniper woodland subject to prolonged drought. New Phytol 200:375–387

Ponce Campos GE, Moran MS, Huete A, Zhang Y, Bresloff C, Huxman TE, Eamus D, Bosch DD, Buda AR, Gunter SA, Scalley TH, Kitchen SG, McClaran MP, McNab WH, Montoya DS, Morgan JA, Peters DPC, Sadler EJ, Seyfried MS, Starks PJ (2013) Ecosystem resilience despite large-scale altered hydroclimatic conditions. Nature 494:349–352

Reichmann LG, Sala OE, Peters DP (2013) Precipitation legacies in desert grassland primary production occur through previous-year tiller density. Ecology 94:435–443

Reynolds JF, Virginia RA, Kemp PR, de Soyza AG, Tremmel DC (1999) Impact of drought on desert shrubs: effects of seasonality and degree of resource island development. Ecol Monogr 69:69–106

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

Seastedt TR, Knapp AK (1993) Consequences of non-equilibrium resource availability across multiple time scales: the transient maxima hypothesis. Am Nat 141:621–633

Shi Z, Thomey ML, Mowll W, Litvak M, Brunsell NA, Collins SL, Pockman WT, Smith MD, Knapp AK, Luo Y (2014) Differential effects of extreme drought on production and respiration: synthesis and modeling analysis. Biogeosciences 11:621–633

Slik JWF (2004) El Niño droughts and their effects on tree species composition and diversity in tropical rain forests. Oecologia 141:114–120

Smith MD (2011) An ecological perspective on extreme climatic events: a synthetic definition and framework to guide future research. J Ecol 99:656–663

Stevens CJ, Lind EM, Hautier Y, Harpole WS, Borer ET, Hobbie SE, Seabloom EW, Ladwig LM, Bakker JD, Chu C, Collins SL, Davies KF, Firn J, Hillebrand H, La Pierre KJ, McDougall AS, Melbourne BA, McCulley RL, Morgan J, Orrock JL, Prober SM, Risch AC, Schultz M, Wragg PD (2015) Anthropogenic nitrogen deposition predicts local grassland primary production worldwide. Ecology 96:1459–1465

Trenberth KE, Dai A, van der Schrier G, Jones PD, Barichivich J, Briffa KR, Sheffield J (2014) Global warming and changes in drought. Nat Clim Change 4:17–22

Wagg C, O'Brien MJ, Vogel A, Scherer-Lorenzen M, Eisenhauer N, Schmid B, Weigelt A (2017) Plant diversity maintains long-term ecosystem productivity under frequent drought by increasing short-term variation. Ecology 98(11):2952–2961

Webb W, Szarek S, Lauenroth W, Kinerson R, Smith M (1978) Primary Productivity and Water Use in Native Forest, Grassland, and Desert Ecosystems. Ecology 59:1239–1247

Whitford WG, Martinez-Turanzas G, Martinez-Meza E (1995) Persistence of desertified ecosystems: explanations and implications. Environ Monit Assess 37:319–332

Woodhouse CA, Overpeck JT (1998) 2000 years of drought variability in the central United States. Bull Am Meteorol Soc 79:2693–2714

Yahdjian L, Sala OE (2006) Vegetation structure constrains primary production response to water availability in the Patagonian steppe. Ecology 87:952–962

Yahdjian L, Sala OE, Austin AT (2006) Differential controls of water input on litter decomposition and nitrogen dynamics in the Patagonian steppe. Ecosystems 9:128–141

Yaseef NR, Yakir D, Rotenberg E, Schiller G, Cohen S (2009) Ecohydrology of a semi-arid forest: partitioning among water balance components and its implications for predicted precipitation changes. Ecohydrology 3(2):143–154

Yaseef NR, Yakir D, Schiller G, Cohen S (2012) Dynamics of evapotranspiration partitioning in a semi-arid forest as affected by temporal rainfall patterns. Agric Forest Meteorology 157:77–85