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Drought timing differentially affects above- and belowground productivity in a mesic grassland

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Abstract Climate models forecast an intensification of the global hydrological cycle with droughts becoming more frequent and severe, and shifting to times when they have been historically uncommon. Droughts, or prolonged periods of precipitation deficiency, are characteristic of most temperate grasslands, yet few experiments have explored how variation in the seasonal timing of drought may impact ecosystem function. We investigated the response of above- and belowground net primary production (ANPP & BNPP) to altered drought timing in a mesic grassland in NE Kansas. Moderate drought treatments (25% reduction from the mean growing season precipitation [GSP]) were imposed by erecting rainout shelters in late spring (LSP), early summer (ESM), and mid-summer (MSM, n = 10 plots/treatment). These treatments were compared to two controls (long-term average GSP [LTA] and ambient GSP [AMB]) and a wet treatment (+30% of the long-term average GSP [WET]). We found that LSP drought did not significantly reduce ANPP relative to control plots while the ESM and MSM drought did despite equivalent reductions in soil moisture. In contrast, the WET treatment did not affect ANPP. Neither the WET nor the drought treatments altered BNPP as compared to the controls. Our results suggest that forecasts of ecosystem responses to climate change will be improved if both the seasonal timing of alterations in precipitation as well as differential responses of above- and belowground productivity to drought are incorporated into models.

Keywords Grasslands · Drought timing · Climate change · Aboveground net primary production · Belowground net primary production

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Introduction

Global climate models project an increase in drought frequency and intensity as a result of anthropogenic climate change during this century (Weltzin et al. 2003; Meehl et al. 2006; IPCC 2013). Drought has been defined as a 'prolonged absence or marked deficiency of precipitation' (Heim 2002; IPCC 2013), and these dry periods have shaped most of the world's

grasslands for millennia (Forman et al. 2001). While the frequency and severity of drought varies considerably among grasslands (Chen et al. 2012), mean annual precipitation (MAP) has long been recognized as a driver of aboveground net primary productivity (ANPP) at broad spatial scales and across multiple continents (Sala et al. 1988, 2012; Knapp and Smith 2001; Hsu et al. 2012). However, the relationship between precipitation and ANPP is much weaker locally (Lauenroth and Sala 1992; Huxman et al. 2004). One reason suggested for this is that the timing of precipitation (or its absence), as opposed to total amount, can be an important determinant of ANPP in some grasslands (Ji and Peters 2003; Svoray and Karnieli 2011; Cherwin and Knapp 2012; La Pierre 2013).

Shifts in the timing of drought are expected under some climate change scenarios (Kunkel and Liang 2004; Christensen et al. 2007; Kunkel et al. 2013). In the Central US, historically most droughts have occurred in the middle of the growing season (July–August), after plants have had time to grow extensively (Stahle and Cleaveland 1988; Seneviratne et al. 2002), but climate models forecast that the drought window may move earlier in some regions (Christensen et al. 2007; Kunkel et al. 2013). If future droughts were to occur during more vulnerable periods for plant growth, ANPP could be reduced more than expected (Heitschmidt and Vermeire 2006; Jongen et al. 2011). Despite the potential importance of drought timing as a determinant of productivity, we know little about how shifts in prolonged dry periods will affect ecosystems (but see Bates et al. 2006; Heitschmidt and Vermeire 2006). Even less is known about how drought timing may affect belowground primary productivity (BNPP).

To address these knowledge gaps, we experimentally altered drought timing (late spring, early summer, and mid-summer) to test two hypotheses (1) that drought impacts on production would vary based on the period of the growing season over which the droughts were imposed with the largest reduction in net primary production (ANPP + BNPP) occurring as a result of the early summer drought; (2) that ANPP would be more sensitive to drought than BNPP. The latter hypothesis was based on patterns observed in previous studies (see below) and the expectation that allocation of biomass to root production would be advantageous during dry periods. We also measured available soil nitrogen levels over the course of the growing season to determine if timing of drought influenced other belowground resources.

We expected that ecosystem sensitivity to an early summer drought would be highest. High levels of soil moisture would lessen the effect of reduced precipitation inputs in the late spring (Knapp et al. 2002; Seneviratne et al. 2002), whereas most growth will have already occurred in this NE Kansas grassland prior to a mid-summer drought (Paruelo and Lauenroth 1995; Briggs and Knapp 2001). Additionally, many plant species are likely adapted to mid-summer droughts (Heckathorn and De Lucia 1991; Zhang et al. 2011; Olsen et al. 2013). We predicted that ANPP would be more responsive than BNPP based on evidence from past studies that have almost always found a positive correlation between precipitation and ANPP (Briggs and Knapp 1995; Knapp and Smith 2001; La Pierre et al. 2011), but equivocal trends with BNPP (Derner et al. 2003; Zhou et al. 2012; Byrne et al. 2013; Evans and Burke 2013; Kong et al. 2013). The potential effect of drought timing on soil nitrogen level is important as increased nitrogen availability post-drought may facilitate recovery (Sala et al. 2012; de Vries et al. 2012).

Methods

Study site

Research was conducted at the Konza Prairie Biological Station (KPBS), a Long Term Ecological Research (LTER) site located in the Flint Hills region of NE Kansas in the Central US (39°05′35″N, 96°33′31″W). This 3487 ha native, unplowed grassland is at the western edge of the historic tallgrass prairie distribution (Samson et al. 2004). Representative plant communities are dominated by a few perennial, C_4 grass species such as *Andropogon gerardii* and *Sorgastrum nutans* with a much higher number of less common, C_3 forbs driving patterns of spatial and temporal diversity. For our study, we selected an upland site that had been burned in the spring around every 4 yrs since 1983. The site was burned on 13 April, 2013 (Konza Prairie LTER data set, KFH011; Briggs 1972-present). Soils at this site are Florence silt loam (Knapp et al. 1998), relatively rocky and with depth to bedrock estimated a ~ 50 cm.

MAP at the experimental site is 860 mm with mean growing season precipitation [GSP] of 610 mm (1 April–30 September) (National Climate Data Center's Global Historical Climatology Network, Manhattan, KS: station ID USC00144972 [1981–2005]).

Experimental treatments

The drought timing experiment was conducted during the 2013 growing season (April–September). This experiment included three drought manipulations imposed in late spring (LSP), early summer (ESM), and mid-summer (MSM), respectively. All drought treatments received a target of 75% of the mean GSP; growing season droughts of this severity have occurred approximately once every 8 years since 1891 (National Climate Data Center's Global Historical Climatology Network, Manhattan, KS). In addition, there were two control treatments: an ambient precipitation treatment (AMB) that received unadjusted precipitation and a long-term average (LTA) treatment that received some additional precipitation to bring its water inputs up to the 25-year mean GSP. Finally, we included a water addition treatment (WET) that received a target of +30% of the long-term average GSP. The WET treatment was included to minimize naturally occurring periods of low soil moisture that are typical of Kansas summers (Knapp et al. 2002; Seneviratne et al. 2002; Wilcox et al. 2014) and thus facilitate detecting drought impacts, particularly for the MSM drought treatment when dry periods are more likely to occur. The LTA and the WET treatments were imposed by manually adding water to each plot on a weekly basis throughout the growing season as needed (see below). Because ambient precipitation was near the long-term mean, we added very little water to the LTA treatment (~76 mm total). Thus, the total GSP received by both control treatments (i.e., LTA and AMB) was within the 95% confidence interval around the mean GSP for KPBS, allowing us to combine these treatments in subsequent analyses using contrasts. See Table 1 for the actual dates of the treatments and how much precipitation each treatment received. All treatments had 10 replicates.

Droughts were imposed by erecting 2.5 m × 2.5 m clear polycarbonate, Dynaglas Plus® roofs over the plots (PALRAMB Industries LTD, Kutztown, PA, USA) center over 1 m × 1 m sampling plots.

Initially, the roofs were installed 0.8 m above the ground, but were moved progressively upwards to a maximum of 1.2 m as the season progressed to avoid interference with the vegetation canopy. Water was added weekly to the WET treatment using water from a well on-site and a flow meter (Electronic Digital Meter, Great Plains Industries, INC., Wichita, KS, USA). A minimum of 7.3 mm was added weekly, plus additional when precipitation was below average. The maximum amount added in one week was 39 mm. Similar additions were applied to the LTA treatment when necessary to bring it up to the long-term mean precipitation for a given week.

Data collection

Precipitation and soil moisture

Climate data for the 2013 growing season were downloaded from NOAA's National Climatic Data Center and consisted of daily totals of precipitation from KPBS (station ID CD0076A4), 6 km SWW of Manhattan, Kansas. This weather station was 2.5 km north of the study site.

Soil moisture data were collected from late April through September in a subset of the plots using 20-cm soil moisture probes (Model ECH20, Decagon Devices, Pullman, WA, USA). Soil moisture data were collected in five replicates of each of the drought treatments, four replicates each for the AMB and LTA treatments, and three replicates for the WET treatment. Probes were located in the center of each 1 × 1 m plot and calibrated with periodic gravimetric soil samples (Wilcox et al. 2014).

Net primary production

ANPP was estimated by harvesting aboveground biomass at its peak (mid September in 2013). Two non-overlapping 0.1 m^2 quadrats were randomly located in each 1 × 1 m sampling plot. For each quadrat, all aboveground biomass was clipped to ground level and sorted to functional type: C$_4$ grasses, C$_3$ grasses, and forbs/woody species. Samples were then dried at 60 °C for 48 h and weighed. Values from the two quadrats in each plot were pooled.

BNPP was estimated by harvesting root biomass from root in-growth cores similar to those used by Wilcox et al. (2014). The cores were 5 cm in diameter

Table 1 Summary of the amount of water received by each treatment at KPBS in 2013 as well as the timing of precipitation exclusion or water addition. The mean air temperature during the period of time over which each treatment was in place is also shown. The LTA and AMB treatments are associated with the mean air temperature for the entire growing season: 1 April – 30 September, 2013

Treatment	Precipitation received (mm)	Percent mean GSP (%)	Mean air temperature (°C)	Timing
WET	788	129	24.0	Weekly (1 Jun–31 Aug)
LTA	681	112	20.2	As necessary (1 Jun–31 Aug)
AMB	605	99	20.2	–
LSP	455	75	18.2	20 Apr–22 Jun
ESM	444	73	22.4	22 May–2 Jul
MSM	467	77	25.2	22 Jun–26 Jul

Treatments: water addition (WET); long-term average (LTA); ambient (AMB); late spring drought (LSP); early summer drought (ESM); mid-summer drought (MSM)

and 15 cm deep and made of 2-mm fiberglass mesh, a dimension which has been shown to provide sufficient spacing to avoid impeding root in-growth (Montagnoli et al. 2014). Native soil from the study site that had been processed through a 2 mm sieve (to remove preexisting biomass and large debris) was used to fill the in-growth cores. The cores were placed into the ground in holes made by a 5-cm auger, filled with the pre-sieved soil, and then compressed manually to approximate site bulk density. In-growth cores were installed on 11 May and removed in 7 September, a period expected to capture the majority of root growth (Persson 1979; Hayes and Seastedt 1987; Sindhøj et al. 2000). Cores were then eluted to separate roots from soil. The roots were dried for 48 h at 60 °C and weighed. The ash weight of samples was obtained by heating them in a muffle furnace for four hours at 450 °C to separate the remaining biomass from soil. The weight of the soil was then subtracted from the initial weight of the samples to determine final biomass. Two cores were installed in each plot and values were later pooled at the plot level.

Vegetation canopy light interception was used as a non-destructive estimate of ANPP and canopy structure (Gamon et al. 1995) as end-of-season ANPP measurements might underestimate drought impacts because late summer growth could mask early-season reductions. To assess production responses during the growing season, light measurements were collected biweekly from plots with no drought shelters starting 29 June. Measurements were made with an AccuPAR LP-80 Ceptometer (Decagon Devices, Inc., Pullman, WA, USA). Three readings were taken at ground level. One light reading per plot was taken above the canopy so that the percent of available photosynthetic radiation could be calculated.

Soil nitrogen

To assess soil nitrogen availability, resin bags ($n = 2$ per plot) were installed on opposing edges of the 1×1 m sampling plot to a depth of 10 cm on 17 May and removed on 11 October. Resin bags were constructed using 5 g of Dowex® hcr-w2 cation-exchange resin and 5 g of Dowex® 1×8-100 anion-exchange resin (Dow Chemical Co., USA) enclosed in nylon (No nonsense, Kayser-Roth Corporation, USA). These were charged for an hour in 0.6 M HCl prior to placement in the field. Upon removal, extractable nitrogen was determined by placing each bag in 80 mL solution of 2 M KCl and agitating for 1–2 h. The elution was then filtered using Whatman 20 Filters 11–12 cm and analyzed for ammonium and nitrate using an OI analytical flow analyzer (Baer et al. 2003). We interpreted high extractable nitrogen from the resin bags as low nitrogen use by plants and microbes (Epstein et al. 1998; McCulley et al. 2009).

Statistical analysis

Statistical analyses were performed in SAS 9.3 (SAS Institute, Cary NC). Data were prepped by removing outliers using the generalized ESD test as recommended when the total number of outliers is not known (Rosner 1983). For all datasets used in this analysis, the maximum number of outliers removed via this procedure was three; zero outliers were removed from most datasets.

Analysis of variance was conducted using linear models to construct contrasts on each of the following a priori tests for ANPP, BNPP, NPP, and available nitrogen. Block and treatment were fixed factors. The contrasts of interest were the control treatments (AMB and LTA) versus each of the following treatments individually LSP, ESM, MSM, and WET. Additionally, we tested our assumption that no difference existed between AMB and LTA. Note that since AMB and LTA are compared to each of the other treatments individually these contrasts are not independent and are therefore not orthogonal. To keep experiment-wise error rate at alpha = 0.05, a Bonferroni correction for five multiple tests was applied resulting in a corrected, comparison-wise alpha level of 0.01 (Dunn 1961). Treatment differences in functional group ANPP responses to drought were investigated post hoc by contrasting: controls vs LSP, ESM, and MSM separately. Tests were performed for the following functional groups: C_3 graminoids, C_4 grasses, and forb/woody species (corrected alpha level for three multiple contrasts of 0.0167).

Contrasts were also used to examine average soil moisture over the period of time during which the drought treatments were in effect. Contrasts of interest were control treatments (AMB & LTA) versus drought treatments, control treatments versus WET treatment, WET treatment versus drought treatments, LSP versus ESM, and ESM versus MSM (corrected alpha level for five multiple contrasts of 0.01).

End-of-season (9 Sept) light canopy interception was examined using the same contrasts as ANPP. Additionally, light canopy interception was analyzed directly after each drought treatment ended (at roof removal on 29 June, 10 July, and 17 Aug). At each time point, only three contrasts were performed: WET versus controls (AMB & LTA); controls versus the treatment just removed (either LSP, ESM, MSM); and WET versus the treatment just removed. In this case, since only three contrasts were performed, a Bonferroni correction for three multiple tests was used, resulting in a comparison-wise alpha of 0.0167.

Finally, because available nitrogen may limit NPP in mesic tallgrass prairies (Knapp et al. 1998), the relationship of ANPP and BNPP to available nitrogen was investigated using ANOVA with a blocked design. Since no contrasts were tested an uncorrected alpha level of 0.05 was used.

Results

Efficacy of treatments

Our goal was to impose a 25% reduction in mean GSP at three different times during the growing season. Although we came close to meeting this target for each treatment (LSP = 75% of mean GSP, ESM = 73% of mean GSP, MSM = 77% of mean GSP; Fig. 1), the time that the roofs were in place to meet these goals varied inversely to what would be expected based on historical precipitation patterns. At KPBS, average daily precipitation tends to decrease during the growing season and we anticipated that the LSP treatment would require roofs to be in place the fewest number of days and the MSM treatment the longest. In contrast, in 2013 the LSP treatment required 62 days to exclude ∼25% of mean GSP, the ESM treatment required 40 days, and the MSM only 35 days (Table 1 and Online Resource 1). The average duration of days with no rain needed to achieve these drought treatments was 45 days. Based on long-term precipitation records (KPBS data set, AWE012; Briggs 1982-present), growing season dry periods of such an extensive duration have occurred only twice in the last 25 years, thus these droughts represented unusually
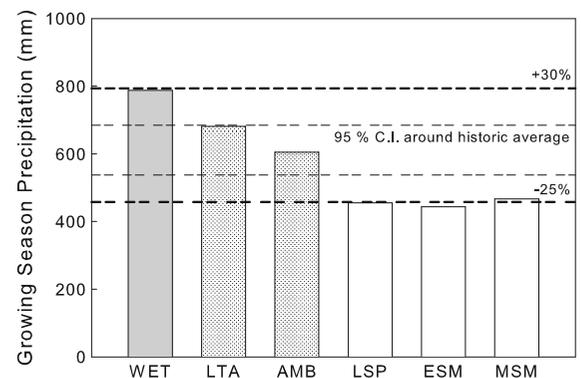

Fig. 1 Total amount of precipitation received by each treatment over the course of the 2013 growing season (April–September). *Thick*, *dashed lines* are the target amount of precipitation for the water addition and drought treatments. *Thin dotted lines* are the 95% confidence interval around the historic mean growing season precipitation based on a 25-year average (1981–2005). Treatments: water addition (WET); long-term average (LTA); ambient (AMB); late spring drought (LSP); early summer drought (ESM); mid-summer drought (MSM). Gray-scale shading provided for ease of comparison of wet versus dry treatments: *dark gray*—wet; *light gray*—control; *white*—dry

long dry periods for this ecosystem. Although the pattern of natural precipitation inputs was unexpected in 2013, mean air temperature increased over the course of the growing season as is consistent with the general climate patterns of the region. (Table 1). We also nearly achieved our target for the WET treatment (+30% of mean GSP) by adding enough water from June through August to increase inputs to 129% of GSP (Fig. 1). Finally, the AMB and LTA treatments were within the 95 confidence interval [541-682 mm] around the mean GSP (99 and 112% of the mean GSP, respectively, Fig. 1).

Soil moisture was not significantly higher in the WET as compared to the control treatments ($P = 0.22$), while both the control treatments and the WET treatment were significantly wetter than the drought treatments ($P = 0.007$ and 0.009, respectively). Relative to soil moisture in the control plots, the drought treatments (LSP, ESM, MSM) were 31, 23, and 34% drier than the controls, respectively (Fig. 2, top). There were no significant differences among the drought treatments; the ESM drought differed from neither the LSP drought ($P = 0.44$) nor the MSM drought ($P = 0.81$). Note that these comparisons were made just for the periods when roofs were deployed in the drought treatments.

Treatment effects on productivity

As predicted, ANPP and BNPP responded differently to the precipitation treatments. ANPP decreased in the drought treatments when compared to the control treatments (LSP = −18%, ESM = −23%, MSM = −26%), but only significantly so in the ESM ($P = 0.0038$) and MSM droughts ($P = 0.0009$). The WET did not result in significantly increased aboveground production compared to the controls (WET = +12%; $P = 0.12$, Fig. 3, top). By contrast, BNPP did not differ between any of the treatments (WET = −1%; LSP = 0%; ESM = +1%; MSM = +12%); Fig. 3, bottom). Furthermore, ANPP and BNPP were not related to each other ($P = 0.22$) indicating no consistent pattern in partitioning by treatment. NPP (ANPP + BNPP) was not significantly different among the treatments (Online Resource 2), likely because of the increased variance caused by BNPP estimates and the slight trend for BNPP to respond opposite of ANPP (Fig. 3, bottom). No differences in aboveground biomass were
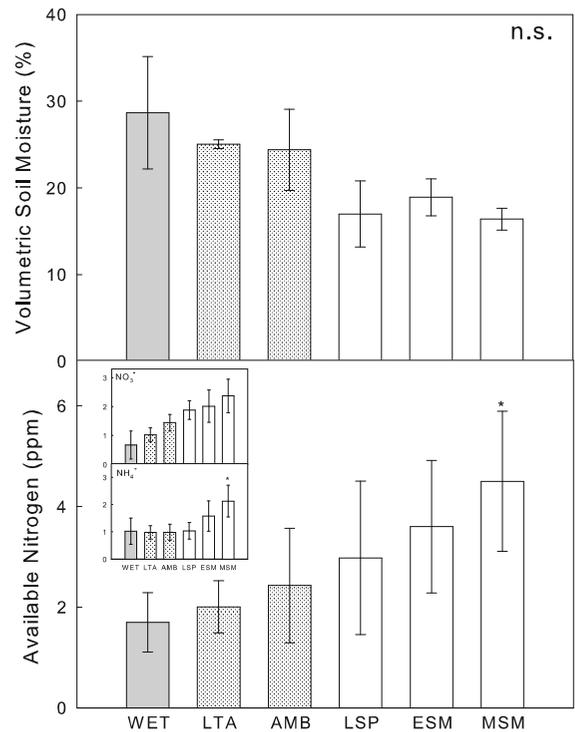
Fig. 2 (*Top*) Mean volumetric soil moisture for each treatment for the period of time when the experimental drought was in effect (22 April–26 July), for exact dates of each treatment see Table 1. *Error bars* are 95% confidence intervals around the mean. (*Bottom*) Plant available nitrogen captured by resin bags (17 May–11 Oct). (*inset*) available nitrogen data are presented separately as nitrate (NO_3^-) and ammonium (NH_4^+). *Asterisk* indicates treatments significantly different from controls (alpha level of 0.01 for five multiple tests)

found between treatments when separated by functional type for C_4 species ($Ps > 0.022$), C_3 species ($Ps > 0.54$), or forbs/woody species ($Ps > 0.51$). Plots of functional type biomass can be found in Online Resources 3.

Canopy light interception was strongly correlated with ANPP at the end of the growing season (Online Resource 4). Directly after the LSP, ESM, and MSM droughts canopy light interception in each drought treatment was significantly lower than in the corresponding AMB, LTA, and WET treatments (Fig. 4, top; $P < 0.013$) (LSP = 24%, ESM = 58%, and MSM = 49% reductions from control light interception), indicating that biomass was significantly higher in the three wetter treatments. However, by the end of the season, as in the direct ANPP data, only ESM and MSM droughts still showed reduced canopy light interception compared to the control treatments
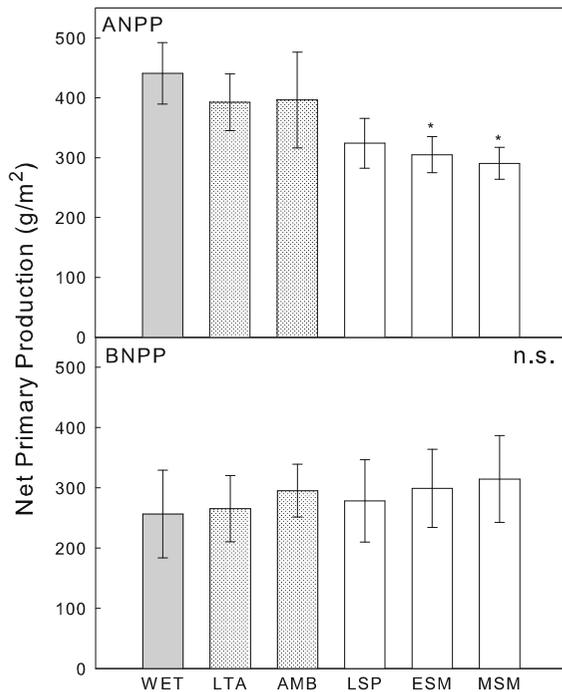
Fig. 3 Aboveground net primary production (ANPP) (*top*) and belowground net primary production (BNPP) (*bottom*) for each treatment. Treatments that are significantly different from the controls (LTA & AMB) are indicated with *asterisks*. *Error bars* indicate 95% confidence interval around the mean. Alpha level of 0.01 is used because of a Bonferroni correction for five multiple tests. See Fig. 1 legend for treatment abbreviations

(reductions in end-of-season light interception relative to controls: LSP = 26%, ESM = 30%, MSM = 42%). This indicates that the LSP drought was able to recover the biomass that it was unable to produce during the drought in the post-drought period. Light interception in the WET treatment did not differ from light interception in the control treatments during any period.

Soil nitrogen

A trend of increasing available nitrogen with decreased precipitation was evident, and it appears that the available soil N increased as the drought treatments occurred later in the season (Fig. 2, bottom). However, due to high variance, only the MSM drought was significantly higher than the controls ($P = 0.0008$). There was an increase in ammonium in the MSM drought to nearly twice as much ammonium as the controls (194%; $P = 0.0002$).

The other treatments did not have significantly more ammonium than controls. Nitrate levels did not differ across treatments ($Ps > 0.25$; Fig. 2, bottom, inset). There was a negative correlation between ANPP and available nitrogen ($P = 0.0023$). In contrast to available nitrogen and ANPP, there was no relationship between nitrogen and BNPP ($P = 0.89$).

Discussion

Climate change models predict not only an increase in the variability and severity of precipitation patterns over the course of the next century (Weltzin et al. 2003; Meehl et al. 2006; IPCC 2013), but also potential shifts in the timing of precipitation (Kunkel and Liang 2004; Christensen et al. 2007; Kunkel et al. 2013). Precipitation has long been known to be an important driver of ANPP in grasslands (Sala et al. 1988; Knapp and Smith 2001; Chen et al. 2012), but some research has shown that precipitation during certain periods of the year is a more important predictor of ANPP than others (La Pierre et al. 2011), probably because it occurs during important phenological periods for determining growth (Hafid et al. 1998; Heitschmidt and Vermeire 2006; Jongen et al. 2011). Therefore, altering the timing of precipitation has the potential to impact productivity. However, very few experiments that manipulate drought timing have been conducted in natural settings (but see Bates et al. 2006; Robertson et al. 2009), despite research indicating that net ecosystem carbon exchange is sensitive to precipitation timing (Chou et al. 2008; Jongen et al. 2011). By manipulating precipitation amount and drought timing in a tallgrass prairie in NE Kansas, we found that timing of drought significantly influenced ANPP, with later droughts having a larger effect than droughts earlier in the growing season. In contrast, BNPP was not significantly affected by any precipitation alteration. We also found that timing of drought may influence the amount of available nitrogen in the soil.

The sensitivity of ANPP to precipitation amount in our experiment was consistent with other studies in the region (Sala et al. 1988; Lauenroth and Sala 1992; Knapp and Smith 2001; Hsu et al. 2012), including many conducted at KPBS (Briggs and Knapp 1995; Knapp et al. 2002; La Pierre et al. 2011; Wilcox et al. 2014). The 18 to 26% reductions in ANPP in the
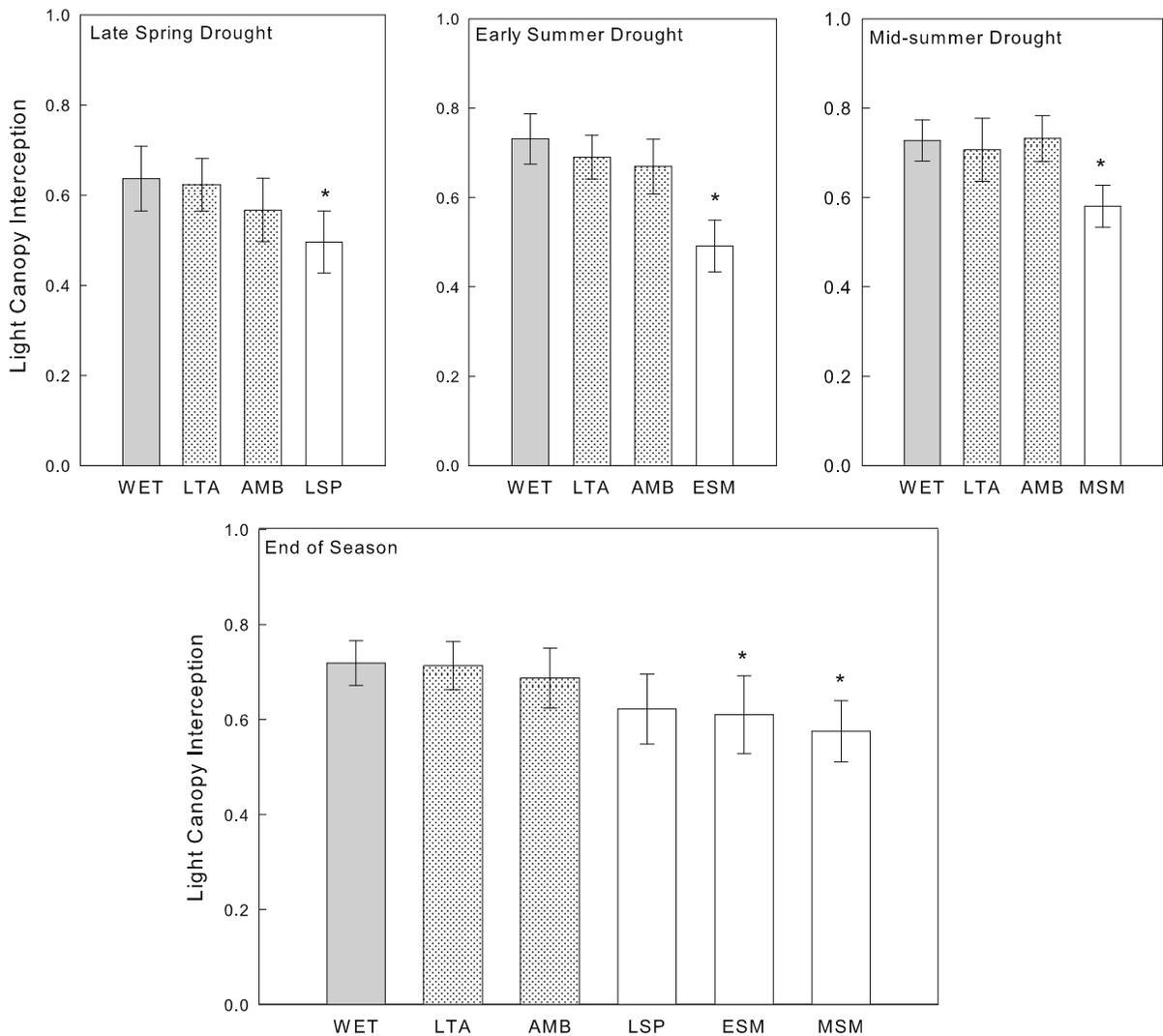
Fig. 4 Canopy light interception to soil surface, as a proxy for aboveground biomass (see Online Resource 4 for the relationship between aboveground net primary productivity (ANPP) and canopy light interception). Higher canopy light interception corresponds to higher ANPP. *Top*: Canopy light interception as measured immediately after each drought period ended (after roofs were removed). In each panel, light interception in the drought treatments was compared to that in the WET and control treatments. Treatments that are significantly different from the controls are indicated with *asterisks*, based on a Bonferroni correction for three multiple tests alpha level is 0.0167. *Error bars* are 95% confidence intervals around the mean. *Bottom*: canopy light interception at the end of the growing season at the time of biomass harvest for estimating ANPP (End-of-Season light sampling: September 9, 2013 vs ANPP harvest: September 13, 2013). Alpha level of 0.01 is used because of a Bonferroni correction for five multiple tests. See Fig. 1 legend for treatment abbreviations

drought treatments were similar, though slightly higher, than ANPP responses observed as a result of other within-season precipitation manipulations (both water additions and precipitation exclusions) at KPBS which resulted in ANPP changes of |17| to |21| % (Knapp et al. 2002; Hoover 2014; Wilcox et al. 2014). Interestingly, while ANPP was reduced in the later

drought treatments, it did not increase in the WET treatment, though it should be noted that soil moisture, a better predictor of production responses than precipitation (Fay et al. 2003), was not significantly higher in the WET treatment than the controls.

Based on results from agricultural studies conducted with wheat, a C_3 grass, one would expect

spring droughts to have the least influence on final biomass (Simane et al. 1993; Hafid et al. 1998). However, Bates et al. (2006), in one of the few studies manipulating drought timing in a natural setting, found that early-season drought in a cool season (C_3) grassland did cause a biomass reduction. Our results from a native, C_4 grassland better match the findings from the agricultural system. ANPP in the three drought treatments progressively decreased from LSP, ESM, to MSM, though only the ESM and MSM drought had significantly lower ANPP than the controls. In addition, using light canopy interception as a proxy for ANPP, we found that even directly after the LSP drought, there was a less pronounced reduction in canopy structure as compared to the reductions later observed after the ESM and MSM droughts—indicating that the LSP drought affected growth dynamics the least. Hafid et al. (1998) also found that early-season drought caused the least amount of leaf area reduction compared to later droughts in their study of wheat. From our data it is not clear why leaf area should be maintained in early but not later drought periods. We predicted that a reduced response to drought in the late spring would be the result of sustained high soil moisture levels from winter; however, soil moisture was similar across all drought periods, so it is unlikely that differences in soil moisture would be driving this difference.

Droughts early in the growing season may have reduced impacts on productivity in tallgrass prairies because there is still ample time for plants to recover and produce more biomass. The tallgrass ecosystem has a long history of drought (Knapp et al. 1998; Forman et al. 2001) and its species may be well adapted to cope with periodic drought. Drought-resistant plants tend to display plasticity in timing of growth, demonstrating the ability to grow slowly when conditions are poor and resume rapid growth when conditions improve (Simane et al. 1993). Rapid growth rates in favorable periods have been found to positively correlate with the ability to maintain leaf area during unfavorable periods (Hafid et al. 1998).

We expected the early summer drought to have a greater effect on production than the mid-summer drought because most species would have completed the majority of their growth by mid-summer (July) in this system (Paruelo and Lauenroth 1995; Briggs and Knapp 2001). However, we found that the mid-summer drought was actually the most severe in terms

of biomass reduction. A companion study conducted at the same time and in the same plots as the present study (Dietrich and Smith 2016) indicates that most of the reduction in productivity in this experiment was due to the failure of *Andropogon gerardii* to flower, indicating that the mid-season drought may have occurred during a critical period for determining flowering in this species. *A. gerardii* is a dominant species in this grassland, comprising up to 70% of the total biomass in burned sites at Konza Prairie (Knapp et al. 1998). As the dominant grass in this grassland, *A. gerardii* can exert disproportionate influence over total ecosystem response (Smith and Knapp 2003) perhaps explaining why ANPP as a whole was reduced by later season droughts, even though C_4 grasses as a whole, C_3 graminoids and forbs/woody species as functional types did not have significant reductions in aboveground biomass.

We detected no response in BNPP to the imposed precipitation treatments, consistent with some past studies in grasslands (Sindhøj et al. 2000; Gill et al. 2002; Byrne et al. 2013) but in contrast to others (Frank 2007; Wu et al. 2011; Evans and Burke 2013; Kang et al. 2013) including some in tallgrass prairie (Xu et al. 2012, 2013; Wilcox et al. 2014). However, most of these studies augmented or decreased precipitation by >50%, so perhaps, the more modest precipitation alterations in our experiment were not sufficient to trigger a belowground response. This is supported at least in part by the fact that we did not find significant soil moisture differences between the controls and the wet treatment. Another reason we may not have found a belowground response to our experimental alterations is that we only sampled BNPP to 15 cm. Although 50–65% of root biomass is captured by measuring the 0–15 cm soil layer (Wilcox et al. 2014), differential root growth at deeper depths between drought and control treatments (Sindhøj et al. 2000: Derner et al. 2003) could not be accounted for in this study. Due to the non-responsiveness of BNPP to precipitation treatments, NPP was also unaffected by either drought or water addition.

Drought effects may extend beyond the drought period and these are known as legacy effects (Sala et al. 2012). Drought timing also may affect the way ecosystem functioning recovers from drought in subsequent years. We found that the mid-summer drought had significantly more soil nitrogen than the

controls, an outcome consistent with the previous research that found reduced plant growth led to nitrogen accumulation (Epstein et al. 1998; McCulley et al. 2009). Thus, grasslands subjected to mid-summer drought could be primed for larger pulses in growth the following year than grasslands experiencing drought earlier in the season (Seastedt and Knapp 1993; Blair 1997; de Vries et al. 2012). Available soil nitrogen has been found to increase the year after drought (Seasted and Knapp 1993; Sala et al. 2012) but it is also susceptible to being leached from the system (Evans and Burke 2013). How the timing of drought might impact the differences in post-drought nitrogen levels and subsequent ANPP responses is largely unexplored and in need of an additional study.

Conclusion

We conclude that the seasonal timing of drought can significantly affect ANPP responses in this grassland, with droughts occurring earlier in the growing season causing less severe reductions in production than those that occur later. This indicates that areas where climate projections predict increased frequency of spring droughts may not see large reductions in aboveground biomass. However, production decreases might be greater than expected if summer droughts become more frequent or severe. Our results, and those of others (Wilcox et al. 2014), indicating that ANPP and BNPP respond differently to changes in water availability suggest that these differences should be accounted for in future work modeling ecosystem responses to climate change.

Compliance with ethical standards

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