THESIS

THE TIMING OF GROWING SEASON DROUGHT AND ITS EFFECTS ON ABOVE- AND

BELOWGROUND PRODUCTION IN A MESIC GRASSLAND

Submitted by

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ABSTRACT

THE TIMING OF GROWING SEASON DROUGHT AND ITS EFFECTS ON ABOVE- AND

BELOWGROUND PRODUCTION IN A MESIC GRASSLAND

As a consequence of climate change, both the timing and amount of precipitation

ecosystems receive are expected to be altered. In general, regions that are relatively dry are

expected to get drier and the timing of seasonal drought – defined as a prolonged absence or

marked deficiency of precipitation – is expected to change. Although drought in general has been

extensively studied, particularly in grasslands, we know little about how natural ecosystems will

respond to shifts in the timing of growing season drought. In this study I investigated the

response of both above- and belowground net primary production (ANPP & BNPP) to reductions

in precipitation in a mesic, tallgrass prairie in NE Kansas. Experimental plots were subjected to

one of three drought treatments (25% reductions in the average growing season precipitation

[GSP]) imposed either in late spring, early summer or mid-summer. A control treatment that

received the mean GSP and a wet treatment that received 130% of the mean GSP were included

to assess drought responses. In all treatments, I measured soil moisture, soil N and P content,

canopy light interception and plant community composition in addition to ANPP and BNPP. I

expected that ANPP would be more sensitive to drought than BNPP based on evidence from past

studies that have almost always found a positive correlation between precipitation and ANPP,

while trends with BNPP are less clear. I also hypothesized that early summer drought would

cause the highest reduction in net primary production (ANPP + BNPP), because soil moisture

would likely still be high in the late spring from late winter and early spring snow/rain, lessening the effect of reduced precipitation inputs. Moreover, because annual ANPP approaches its maximum by summer, I expected the mid-summer drought to affect NPP the least. I found that without considering timing, a 25% growing season drought reduced ANPP relative to the control by 18-26%, while ANPP in the control and wet treatment was not significantly different. Early summer and mid-summer drought resulted in significant reductions in ANPP (~25%) relative to control plots, but late spring drought did not reduce ANPP significantly despite similar reductions in soil moisture across all treatments. In contrast, neither drought nor wet treatments altered BNPP significantly. Because soil nutrients may increase during drought and plant functional type diversity may buffer productivity responses to drought, I investigated the role these played in determining responses to the treatments imposed. I found that soil nutrients were positively related to ANPP only in the wet treatment; conversely, diversity was negatively related to ANPP in the ambient and drought treatments, but not the wet treatment. I conclude that timing does play an important role in determining ecosystem response to drought with periods of no rain that occur earlier in the year having less of an impact than those that occur later. Furthermore, differences in responses between ANPP and BNPP were striking and need to be accounted for when projecting productivity responses of grasslands to climate change.

ACKNOWLEDGEMENTS

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CHAPTER ONE:

INTRODUCTION TO GRASSLAND ECOSYSTEMS AND DROUGHT

Grassland biomes cover 30 to 40 % of the world's terrestrial surface (Lieth 1978; White et al. 2000; Sala 2001). These extensive ecosystems provide a number of important services such as forage for native and domestic ungulates, soil carbon storage and even a refuge for pollinators (Hönigová et al. 2012). In addition, grasslands are one of the biomes that have been most extensively altered by humans, primarily for agriculture and food production (Woodward 2008). Indeed, temperate grasslands have been ranked as the biome with the highest conservation risk (Hoekstra et al. 2005).

In their third assessment report the IPCC indicated that grasslands will be amongst the most vulnerable ecosystem to climate change (Fischlin et al. 2007); however, grasslands may also have the capability to serve as buffers against increased CO_2 buildup in the atmosphere (Soussana et al. 2004; Singh et al. 2010). Given the extent of their global distribution, it is estimated that grasslands are the most carbon rich of the terrestrial biomes; grasslands have even greater carbon stocks than forests (Hourghton 2007; Wolf et al. 2011). With careful management, grasslands could trap even more CO_2 (Allard et al. 2007). Grasslands accumulate carbon by absorbing more CO_2 than they release into the atmosphere through respiration. Carbon is gained by grasslands through plant vegetative growth, otherwise known as net primary productivity (NPP). NPP has two components: aboveground growth consisting principally of leaves and stems (ANPP), and belowground growth consisting principally of roots and rhizomes (BNPP). We know much more about the patterns and controls of ANPP than BNPP in grasslands

and in most terrestrial biomes. In grasslands the carbon captured by aboveground biomass is very labile and cycles each year with vegetation die-back, but belowground biomass is a more stable pool (Gilmanov et al. 2003: Soussana et al. 2004). As much as 85% of all the carbon in grassland systems is stored below ground (Neary et al. 1990), and even after death, carbon from belowground biomass often remains as soil organic matter, sometimes for thousands of years (Trumbore 2000).

Grassland productivity is principally determined by three major factors (Woodward 2008): fire (Briggs and Knapp 1995; Bond et al. 2005), grazing (Scholes and Archer 1997; Fuhlendorf et al. 2001; Koerner and Collins 2014) and climate (primarily precipitation, but to a lesser extent temperature) (Sala et al. 1988; Knapp and Smith 2001; Gill et al. 2002). The first two factors can be extensively managed by humans if needed (Sankaran 2005; Hönigová et al. 2012). Fire initially removes biomass, and its effect on ANPP varies from slightly negative to neutral in semi-arid grasslands (Scheintaub et al. 2009) to positive impacts on ANPP in mesic grasslands (Neary et al. 1990, Towne and Kemp 2008). Positive effects are a result of release from light limitation (Seastedt and Knapp 1993; Turner and Knapp 1996), particularly limitation resulting from litter (Lamb 2008) as well as increased plant available nitrogen in soils which allows for increased plant growth (Seastedt and Knapp 1993; Turner and Knapp 1996; Anderson et al. 2006). Grazing can also have a stimulatory effect on ANPP (Frank 2007; Xu et al. 2014), but this depends upon the intensity of grazing (Frank 2007; Koerner et al. 2014). Light grazing often increases biomass both above- and belowground (Frank et al. 2002; Ingram et al. 2008; Post and Pedersen 2008; Hafner et al. 2012) and heavy grazing generally has a detrimental effect on ANPP (Pandey and Singh 1992; Ingram et al. 2008; Kolbl et al. 2011; Wolf et al. 2011).

Precipitation, which undergoes natural, yearly fluctuation (Chen et al. 2012), cannot be managed to either maintain or increase ANPP to influence the world's carbon terrestrial carbon stores.

At large spatial scales mean annual precipitation (MAP) may be the single most important driver in determining ANPP (Sala et al. 1988; Knapp and Smith 2001; Hsu et al. 2012). However, this may be an indirect effect where MAP determines which species are present and which are absent (La Pierre 2013), because species tend to grow in environments that have climatic conditions to which they are well adapted (Davis and Shaw 2001). Plants are extremely plastic organisms, but there is a limit to a species' structural flexibility when it comes to responding to climatic variation (Yahdjian and Sala 2006). This may explain why yearly fluctuations in annual precipitation are not as strong of a predictor of ANPP locally as MAP is of ANPP at a regional scale (Lauernroth and Sala 1992; La Pierre 2013).

Beyond the three major drivers, other factors are important to ANPP as well, such as disease (Etzold et al. 2014), diversity (Bai et al. 2004; Polley et al. 2013; Chang and Smith 2014), past land use (Preger et al. 2010; Frescet et al. 2014) and nutrient availability (Robertson et al. 2009; Wei et al. 2014). Nutrient limitation on ANPP is likely to become particularly important in more mesic systems or in wet years when plants are less likely to be water stressed (Bai et al. 2004; Huxman et al. 2004; Hsu et al. 2012).

As previously noted, most research has focused on ANPP largely because aboveground biomass is much easier to measure than belowground biomass and it represents a key economically important ecosystem service (forage). However, it is equally important to understand controls on BNPP because this hidden component of NPP provides important services as well: carbon storage as addressed earlier, soil stabilization (Gyssels et al. 2005), and

nutrient cycling (Hendricks et al. 1993; Gordon and Jackson 2000; Hönigová et al. 2012). There are insufficient data detailing how BNPP responds to climatic variation, but when BNPP data are available, research shows that the strong relationship between ANPP and MAP is not mirrored belowground at the regional scale (Gill et al. 2002; McCulley et al. 2005; Wilcox et al. 2014). Locally the relationship between precipitation and BNPP seems more nuanced. A number of studies have found a strong positive correlation between precipitation input and BNPP (Jastrow et al. 2000; Wang et al. 2007; Kang et al. 2013; Xu et al. 2013). However, a significant body of evidence also points to there being no relationship (Sindhøj et al. 2000; Byrne et al. 2013; Kong et al. 2013) or an inconsistent relationship (Fan et al. 2008; Anderson et al. 2010; Wu et al. 2011; Xu et al. 2012; Frank 2007) between the two. Temperature, however, emerges as an important factor controlling BNPP both locally (Zhou et al. 2012; Xu et al. 2013; Xu et al. 2014), and regionally (Gill et al. 2002). In the future, atmospheric CO_2 enrichment may also increase belowground growth (Jastrow et al. 2000; Dener et al. 2003; Anderson et al. 2010; Xu et al. 2012; Xu et al. 2013; Xu et al. 2014).

ANPP and BNPP do not exist in isolation from one another (Benning and Seastedt 1997). Plants partition their biomass to best take advantage of limited resources. Belowground partitioning can decrease at high soil moisture levels as plants trade off extensive root systems for additional leaf area to aid in light competition (Xu et al. 2013). Furthermore, when nutrients such as available nitrogen and phosphorous are scarce, partitioning to belowground biomass may increase (Wang et al. 2007; Li et al. 2011).

What is known about the drivers of ANPP and BNPP in grasslands may be subject to revision in coming years as a result of anthropogenic climate change. Due to a shifting and increasingly intense hydrological cycle globally, precipitation is expected to become more

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variable both within and among years (Weltzin et al. 2003; Meehl et al. 2006; IPCC 2013). There are three distinct ways that precipitation variation could affect productivity in grasslands, some of which have received a fair amount of attention. Additionally, some combination of these possibilities may occur. Precipitation may increase (Groisman et al. 1999) or decrease significantly (Wetherald and Manabe 1995; Held and Soden 2006). Precipitation may become more variable with more frequent or more extreme events on both the wet and dry end of the spectrum (Karl et al. 1995; Sheshukov et al. 2011). Lastly, historically wet and dry periods may shift either earlier or later in the year (Kunkel and Liang 2004; Christensen et al. 2007; Kunkel et al. 2013). The final category has received very little attention in terms of its effect on NPP and is the focus of the present study.

Objectives

My primary objective was to determine if the seasonal timing over which within-season drought occurs in a mesic grassland changes how ANPP and BNPP respond to precipitation reductions as well as determine if ANPP and BNPP respond differently to these changes. To address this objective, I conducted a field experiment at a well-studied, mesic, tallgrass prairie in NE Kansas at the Konza Prairie Biological Station (KPBS). I used rainout shelters (Figure 1) to divert approximately 25% of mean growing season precipitation (GSP) away from experimental plots, an infrequent, but not unreasonable severity of drought. At KPBS, droughts of this intensity have occurred 16 times since l891. I used GSP because it has been found to have more predictive power for ANPP in this system than MAP (La Pierre et al. 2011). Droughts were timed so that they began either in late spring (April-June), early summer (May-July), or mid-summer (June-July). Responses in the drought treatments were compared to those in a control treatment, which received the long-term mean GSP, and a wet treatment, which received 130%

of mean GSP. Including both of these treatments allowed me to maximize my ability to distinguish potentially subtle drought responses even late in season when the tallgrass ecosystem experiences natural drying (Knapp et al. 2002; Wilcox et al. 2014). Water was added to the wet treatment weekly via hand watering from a well on site (Figure 2). Also, to increase my understanding of the complex interactions inherent in a natural system I assessed the roles played by other factors that may influence the precipitation/productivity relationship. The covariates I measured included light canopy penetration, soil moisture, nitrogen and phosphorous availability, previous years' production and plant functional type diversity.

The site I selected for this experiment was in an upland, infrequently burned site that was burned the spring before treatments were initiated. This location had several advantages. Soils in upland sites do not retain water as well as lowland sites (Knapp et al. 2001), resulting in decreased soil moisture, which allowed for effective implementation of the drought treatments. Additionally, at KPBS precipitation has a larger effect on ANPP in burned sites than unburned ones (Briggs and Knapp 1995). Furthermore, between infrequently burned and annually burned sites the former have been found to demonstrate more pronounced drought responses (Koerner and Collins 2014).

Figure 1. A rainout structure just after it was installed in April, 2013 on the recently burned 4B watershed at KPBS. The roof was constructed with clear, polycarbonate plastic and was 2.5 x 2.5 m. A drainage tube collected runoff from the roof and shunted it out of the plot. The plot was trenched to 0.5 m and a plastic liner was installed to prevent belowground infiltration from outside of the plot. Late spring drought roofs were in place April 20 – June 22 , early summer drought roofs were in place May 22 – July 2, and mid-summer drought roofs were in place June 22 – July 26. The goal of each drought treatment was to exclude ~ 150 mm of precipitation.

Figure 2: Water addition in the 4B watershed at KPBS via hand-held wand and flow meter in a wet treatment plot in late June. Water was applied weekly to these plots so that they received 130% (~800 mm) of the growing season mean rainfall and stayed consistently wet. Water application began in June 1 and continued through August 31, 2013.

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CHAPTER TWO:

DROUGHT TIMING DETERMINES PRODUCTIVITY RESPONSES IN A MESIC GRASSLAND[1]

SUMMARY

Global climate models forecast an intensification of the global hydrological cycle with

droughts becoming more frequent and severe, as well as occurring at times of the year when they

have not been historically common. Drought, defined as a prolonged period of precipitation

deficiency, is a common feature of most temperate grasslands, yet we know little about how

shifts in the 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. Drought treatments (25% reduction from the mean growing

season precipitation [GSP]) were imposed by erecting temporary rainout shelters in late spring,

early summer or mid-summer (n=10 plots/ treatment). These treatments were compared to a

control (long-term average GSP) and a wet treatment (130% of the long-term average GSP

respectively). We hypothesized that ANPP would be more responsive to drought than BNPP, and

that productivity would be reduced the most by early summer drought. Without reguard to

timing, drought reduced ANPP relative to the control and wet treatments, while the latter two did

not differ significantly. Early summer and mid-summer droughts resulted in the greatest

reductions in ANPP relative to control plots, while drought in the late spring did not significantly

reduce ANPP, despite similar reductions soil moisture over the entire growing season. In

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contrast, neither the drought nor wet treatments altered BNPP. We measured soil nutrients and plant diversity in each plot because of their influence on productivity in grasslands. Increased nutrient availability coincided with increased ANPP in the wet treatment, but increased diversity was more strongly related to decreased production in the drought and control treatments. Overall, drought timing played an important role in determining production responses, with late spring drought having no impact on end of season productivity – perhaps because there was time for substantial recovery. Furthermore, because ANPP and BNPP responded differently to drought, both should be considered in climate change forecasts of ecosystem services.

INTRODUCTION

Global climate models project an increase in drought frequency and intensity as a result of anthropogenic climate change over the next hundred years (Weltzin et al. 2003; Meehl et al. 2006; IPCC 2013). Drought has been defined as a 'prolonged absence or marked deficiency of precipitation' (Heim et al. 2002, IPCC 2013), and these dry periods have shaped most of the world's grasslands for thousands of years (Sala 2001; Prentice et al. 1991; Forman et al. 2001). While the frequency and severity of drought varies considerably between grasslands (Chen et al. 2012), mean annual precipitation (MAP) has long been recognized as a driver behind aboveground net primary productivity (ANPP) at broad spatial scales (Sala et al. 1988; Knapp and Smith 2001; Hsu et al. 2012). However, the relationship between precipitation and ANPP is much weaker locally (Lauenroth and Sala 1992; Knapp and Smith 2001). 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 (Yang et al. 1998; 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, after plants have had time to grow extensively (Stahle and Cleaveland 1988; Sala et al. 1995; Sala 2001; Seneviratne et al. 2002), but climate models forecast the drought window to move earlier in some regions (Christensen et al. 2007; Kunkel et al. 2013). If future droughts were to occur during more vulnerable periods for determining growth, ANPP could be severely reduced (Heitschmidt and Vermeire 2006; Jongen et al. 2011; da Silva et al. 2012). Despite the potential importance of drought timing as a determinant of productivity, we know little about how shifts in drought periods will affect ecosystems (but see Bates et al. 2006 and Heitschmidt and Vermeire 2006).

In this study, our goal was to assess how shifting the timing of moderate growing season drought will affect grassland productivity in a mesic, tallgrass prairie in NE Kansas. We used an experimental framework to quantify responses to a 25% reduction in mean growing season precipitation (GSP) imposed at three different periods during the growing season (late spring, early summer and mid-summer). 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). Responses in both ANPP and belowground net primary productivity (BNPP) to drought were compared to a control treatment that received the long-term average of GSP as well as a wet treatment (130% of the long-term average GSP). The wet treatmentwas 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 mid-summer drought treatment (Borken and Matzner 2009).

With this experiment we tested two hypotheses. First, *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) expected with early summer drought. Second, ANPP would be more sensitive to drought than BNPP in all drought treatments.* We expected in late spring that high levels of soil moisture (Knapp et al. 2002; Seneviratne et al. 2002; Craine et al. 2012) would lessen the effect of reduced precipitation inputs, whereas the mid-summer drought would also have reduced effects on productivity because most growth has occurred by summer in this grassland (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; Zhou et al. 2012) but equivocal trends with BNPP (Jastrow et al. 2000; Derner et al. 2003; Byrne et al. 2013; Kong et al. 2013).

METHODS

Study Site

Research was conducted at that Konza Prairie Biological Station (KPBS), a Long Term Ecological Research (LTER) site located in in NE Kansas in the Flint Hills region of the Central

US ($39°05′35″$N, $96°33′31″$W). This 3,487 ha native, unplowed grassland is at the western edge

of the historic tallgrass prairie distribution (Samson et al. 2004) and the dominant vegetation

includes perennial, C_4 grass species such as *Andropogon gerardii* and *Sorgastrum nutans* with

common C_3 forbs including *Solidago missouriensis* and *Aster oblongifolius.* For our study, we

selected an upland site that had burned ~ every 4 yrs since 1983. The site was burned on 13 April

2013 (Konza Prairie LTER data set, KFH011). Soils at this site are Florence silt loam (Reichman

1988), relatively rocky and with depth to bedrock estimated at ~ 50 cm. Average growing season

(April 1 – September 30) rainfall over 25 years was 614 mm (National Climate Data Center's

Global Historical Climatology Network, Manhattan, KS: station ID USC00144972).

Experimental Treatments

The drought timing experiment was conducted during the 2013 growing season (April to

September) after a year in which pre-treatment data were collected. This experiment included

three drought manipulations imposed: late spring (LSP), early summer (ESM), and mid-summer

(MSM). All drought treatments received a target of 75% of the mean GSP. In addition, there was

an ambient precipitation treatment, a control treatment that received a target of the long-term

average GSP (614 mm) and a wet treatment (WET) that received a target of 130% of the long-

term average GSP. The latter two treatments were imposed by manually adding water to each

plot on a weekly basis throughout the growing season as needed (see below). Because we added

very little water to the control treatments (~ 76 mm total) and the total GSP received for both

treatments was within the 95% confidence interval around the mean GSP for KPBS, we

combined these treatments in subsequent analyses. See Table 1 for the actual dates of the

treatments and how much precipitation each treatment received.

Each of the three drought (DRT) treatments and the WET treatment had 10 replicates while the AVG treatment (combined control and ambient treatments) had 20. Sampled plots were 1 m x 1 m, but the treatments were applied to a 2.5 x 2.5 m area to avoid edge effects. Droughts were imposed by erecting 2.5 m x 2.5 m clear polycarbonate, Dynaglas Plus® roofs over the plots (PALRAM Industries LTD, Kutztown, PA, USA). 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. All plots were hydraulically isolated by trenching a 6 x 6 m area around them to a depth of 0.4 m, which was then lined with impermeable plastic (6 mil Husky Polyethylene Sheeting, Home Depot, USA). See Supplemental Figure 1, for plot layout. 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 dropped below average. The max added in one week was 39 mm. Similar additions were applied to the AVG treatment when necessary to bring it up to the long term mean precipitation for a week.

Data Collection

Precipitation and Soil Moisture

Climate data for the 2013 growing season was downloaded from NOAA 's National Climatic Data Center and consisted of daily totals of rainfall 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 was collected late April through September in a subset of the plots using 20 cm Ech2o soil moisture probes (Model EC-20, Decagon Devices, Pullan, WA, USA). Soil

moisture was collected in five replicates of each of the DRT treatments, eight replicates for the AVG treatment, and three replicates for the WET treatment. Probes were calibrated with periodic gravimetric soil samples (Wilcox et al. 2014).

Net Primary Production

In 2012 and 2013, ANPP was estimated by harvesting aboveground biomass at its peak (late August in 2012 and mid September in 2013). For each year non-overlapping 0.1 m^2 quadrats were randomly located in each plot: three quadrats in 2012 and two in 2013. 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 hours and weighed. Values from the two quadrats were pooled.

BNPP in 2013 was estimated by harvesting fine root biomass from root in-growth cores similar to those used by Wilcox et al. (2014). Two cores were installed in each plot and values were later pooled at the plot level. The cores were 5 cm in diameter 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 in-growth cores. The cores were placed into the ground in holes made by a 5 cm auger and then filled with the pre-sieved soil, which was then compressed manually to emulate natural compaction. In-growth cores were installed on 11 May, 2013 and removed in 7 September, 2013, a period expected to capture the majority of root growth (Persson 1979; Hayes and Seastedt 1987; Sindhøj et al. 2000; Anderson et al. 2010). Cores were then eluted to separate roots from soil. The roots were dried for 48 hours at 60°C and weighed. The ash weight of samples was

obtained by heating them in a muffle furnace for four hours at 450ºC to separate remaining biomass from soil. The weight of the soil was then subtracted from the initial weight of the samples to determine final biomass.

Vegetation canopy light interception was used as a non-destructive estimate of ANPP and canopy structure (Monteith and Moss 1977; Gamon et al. 1995). Light measurements were collected biweekly from plots with no drought shelters starting in June 29, 2013. Measurements were made with an AccuPAR LP-80 Ceptometer (Decagon Devices, Inc., Pullman, WA, USA). Three readings were taken at ground level, and then at 20 cm above the surface to capture differences in canopy structure. One light reading per plot was taken above canopy so that percent of available photosynthetic radiation could be calculated.

Plant Functional Type Diversity

Diversity was determined from the biomass data by binning the collected biomass by plant functional type (PFT): C_4 grasses, C_3 grasses, forbs and woody vegetation. Simpson's diversity index (Simpson 1949) was calculated as,

$$SDI = \sum \left(x_i / \sum (x) \right)^2$$

Where x_i is the proportion of biomass belonging to any one PFT. SDI is a value between zero and one and increases with increasing diversity.

Soil Nitrogen and Phosphorus

To determine total soil N and available (extractable) P concentrations, soil samples were taken in both August 15 2012 and April 20 2013 in each plot. Each sample consisted of three 2 cm cores taken to a depth of 10 cm and then composited. Soil samples were sent to the Kansas

State University Soil Lab for analysis where percent bulk nitrogen and ppm available phosphorous were determined.

To assess soil N availability, resin bags (n = 2 per plot) were installed to a depth of 10 cm and in place from 17 May to 11 October 2013. Resin bags were constructed using 5 g of Dowex® hcr-w2 cation-exchange resin and 5 g of Dowex® 1x8-100 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 hours to ensure that the nitrogen was all in solution. The elution was then filtered using Whatman 20 Filters 11-12 cm and analyzed using OI analytical flow analyzer (Baer et al. 2003). We interpreted high extractable N 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 R version 3.0.2. (http://www.r-project.org/). 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 data sets used in this analysis the maximum number of outliers removed via this procedure was three. The mean was 0.66 and the mode was 0.

Treatment differences for all variables were determined using mixed-model ANOVA in a randomized block design. The treatment difference models were fit for ANPP, BNPP and NPP both at the level of treatment type: wet, average and drought (WET=WET, AVG= AVG, and LSP+ESM+MSM=DRT) and treatment level (WET, AVG, LSP, ESM, MSM). Pairwise

differences were determined by rerunning the models above with a fixed-effect ANOVA where block is treated as a factor and using a method suggested by Herberich et al. (2010). This method accurately estimates multiple comparisons while being robust to differences in distribution, lack of homogeneity in variance and uneven sample size. All covariates were also regressed on ANPP and BNPP using general linear regression ANOVA with block as a random factor, except when data was analyzed to determine if N and P were more important for predicting production in wetter treatments. In this case, because there was no replication within blocks, nutrient values were centered by block so that relatively higher, versus relatively lower differences could be compared within a treatment.

To better understand the complex processes interacting with ANPP and BNPP in a natural system, AICc model selection was applied to find best models for production from all of the covariates measured in this experiment, and where possible, their interactions. Model selection was conducted for both ANPP and BNPP as well as on canopy light interception (as a proxy for ANPP) at four different sampling periods (Jun 29 – Sept 9). A major focus of the modeling process was to determine if models that included precipitation parsed by drought period (DP) improved fit of models over GSP alone. Additionally, it was of interest to determine if any other variables, such as nutrients interacted with precipitation. Independent variables included in the global models were: previous year ANPP, previous and current PFT diversity, bulk soil N and soil plant available P concentration from 2013 and their interactions with precipitation. When BNPP was being modeled ANPP was included as an independent variable and vice versa. Model selection was also done using soil moisture instead of precipitation to see if outcomes changed when a more direct representation of soil available water was used. Model

selection used the glmulti package in R. See Supplementary section for more detailed description of modeling process.

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 = 74% of mean GSP, ESM = 72% of mean GSP, MSM = 76% of mean GSP; Figure 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. Average daily precipitation tends to decrease during the growing season; we anticipated, therefore, 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 it required 62 days to exclude ~25% of mean GSP for the LSP treatment, 40 days for the ESM and only 35 days for MSM (Table 1; Supplementary Figure 3). 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, AWE01), growing season dry periods of such an extensive duration have occurred only twice in the last 30 years, thus these droughts represented unusually long dry periods. Although the pattern of natural precipitation inputs was unexpected in 2013, mean air temperature increased during each treatment period as expected (Table 1). We also nearly achieved our target for the WET treatment (130% of mean GSP) by adding enough water from June through August to increase inputs to 128% of GSP (Figure 1). Finally, the AVG treatment

(combined control and ambient precipitation treatments) was within 5% of mean GSP (105%, Figure 1).

The WET treatment had significantly higher growing season soil moisture than the combined DRT treatments with the AVG treatment intermediate between these two. When the drought timing treatments were assessed individually, only the LSP drought treatment was significantly drier than the WET treatment (p=0.028) despite similar precipitation inputs for all drought treatments (Figure 2a). The LSP treatment was, however, the drought in which all rainfall was excluded for the longest period of time.

We also assessed average soil moisture during each drought period: late spring, early summer, mid-summer (Figure 2b). Average daily soil moisture when the LSP roofs were in place did not differ significantly by treatment (Figure 2b). The WET treatment had significantly higher soil moisture than the LSP treatment during the early summer drought and the MSM treatment during the mid-summer drought.

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 WET and AVG treatments (p<0.01), which were not significantly different from each other (Figure 3, top, inset). By contrast, BNPP did not differ between any of the treatments (Figure 3, bottom). ANPP and BNPP were not related to each other (p=0.32) indicating that no consistent pattern in partitioning by treatment. When ANPP and BNPP were summed to evaluate NPP there were no significant treatment differences (Supplementary Figure 2), likely because of the increased variance caused by BNPP estimates and the trend for BNPP to respond opposite of ANPP (Figure 3, bottom,

inset). Additionally, no differences were found when ANPP was analyzed for treatment response by plant functional type.

The timing of drought resulted in slight differences in ANPP (Figure 3). While ANPP did not differ significantly between the drought treatments, the smallest reduction in ANPP was measured in the LSP drought whereas the greatest reduction was evident in the MSM drought treatment. This resulted in the ESM and MSM treatments having significantly lower ANPP values than the WET and AVG treatments ($p<0.05$) while the LSP treatment did not differ significantly ($p>0.05$) (Figure 3, top). BNPP (Figure 3, bottom) and NPP (Supplementary Figure 2) were unaffected by drought timing.

Given that end of season ANPP measurements might underestimate drought impacts because late summer growth could mask early season reductions, we used canopy light interception at the soil surface as a proxy for ANPP (e.g., canopy light interception was strongly negatively correlated with ANPP at the end of the growing season; Supplementary Figure 3) to assess production responses immediately after each of the drought periods ended. Directly after the LSP, ESM and MSM droughts canopy light interception in each drought treatment was significantly higher than in the corresponding WET treatment (Figure 4, top; $p<0.05$), indicating that biomass was significantly higher in the latter. Canopy light interception in the respective drought treatment was also significantly higher than in the AVG treatment after the ESM and MSM droughts (Figure 4, top; $p<0.001$). Despite strong treatment effects immediately after the roofs were removed, by the end of the season most of the differences in canopy light interception between the treatments had disappeared. Only the MSM treatment was still significantly different from the AVG and WET treatments ($p<0.02$; Figure 4, bottom). The recovery made by the LSP and ESM treatments post-drought may have been facilitated by the large fraction of the

GSP that fell after these droughts ended, 57% for the LSP treatment and 47% for the ESM treatment. However, even though 38% of the GSP still fell after the MSM roofs were removed, these plots were unable to make a full recovery. This was despite the fact that the largest rain event of the season fell the week after the MSM treatment was removed (128.8 mm, Supplementary Figure 5).

Plant Functional Type Diversity and ANPP

There was no evidence for a legacy effect on NPP as no significant relationships between previous year ANPP and either ANPP (p=0.28) or BNPP (p=0.10) were found. There was, however, a relationship between PFT diversity in 2013 and ANPP; plots with higher diversity tended to have lower production (p<0.0001), at least in the DRT and AVG treatments. No correlation was found between 2012 PFT diversity and ANPP, nor between PFT diversity in 2012 and 2013 (p=0.34). BNPP was not associated with PFT diversity in either year nor was NPP.

Soil Nutrients

Significantly more available nitrogen, in the form of ammonium and nitrate, was captured by the resin bags in the DRT treatments than in either the WET or AVG treatments (Supplementary Figure 6). While nitrogen capture by the different DRT treatments did not differ significantly there was variation that resulted in the LSP drought treatment not capturing significantly more nitrogen than capture in either the WET or AVG treatments, while the ESM and MSM treatments did. Overall there was a negative correlation between ANPP and the amount of active nitrogen absorbed by resin bags (p<0.001). Therefore, the lower nitrogen capture in the LSP as compared to the ESM and MSM droughts may have been a result of the

extra growth that occurred after the end of the drought treatment. In contrast to available nitrogen and ANPP, there was no relationship between nitrogen and BNPP (p=0.72).

Bulk nitrogen and active phosphorous levels in the soil did not differ between treatments (p>0.05), and no relationship between nutrients and BNPP was found. However, higher values of ANPP were correlated with higher ambient levels of bulk nitrogen and active phosphorous in the WET treatment (Supplementary Figure 7). This provides evidence that when water is not limiting, nutrients levels may become more important for determining ANPP.

Modeling NPP

ANPP and Precipitation

Although the focus of our experiment was on the impact of drought timing on NPP, we used a model selection approach to assess how other factors known to influence productivity in grasslands and be affected by drought – such as soil nutrients, community diversity, legacy effects, etc – might influence production responses and therefore provide insight on the potential causes behind timing induced drought responses. Such models can also increase mechanistic insight by assessing whether interactions exist between precipitation and other variables.

All best models for ANPP included the following variables: active phosphorous, bulk nitrogen, PFT diversity values in both 2012 and 2013, and a water term. Included timing by parsing precipitation into the amount of rain that fell during each drought period (DP) did not produce better models than including only GSP. This indicates that the direct effects of timing on drought had diminished by end of season for predicting ANPP. When interactions were included, models were further improved by adding a nitrogen and phosphorous interaction and a water interaction with either phosphorous, bulk nitrogen or PFT diversity to the predictors.

The AICc values of models for ANPP that included soil moisture terms were not directly comparable with those that included precipitation terms because soil moisture was only measured in a subset of plots and therefore a reduced data set had to be used (n=26). However, the covariates included in the best models were consistent between precipitation and soil moisture models, except that including DP soil moisture terms improved model fit, while DP precipitation terms did not. This indicates timing may affect ANPP through greater soil drying later in the season even when total rainfall is the same. Due to limited replication, models including interaction terms between soil moisture and the other variables could not be considered.

Canopy light interception at ground level was used as a non-destructive proxy for ANPP. Models selected using light interception as a proxy for biomass were generally simpler than those selected for ANPP directly. All included only 2013 PFT diversity and a water term. Including DP precipitation improved model fit directly after the ESM and MSM droughts, but DP precipitation did not improve fit for light interception models after the LSP drought. This indicates that the timing and quantity of rainfall is important later in the growing season, but not early on. Additionally, including DP precipitation for models of light interception at end of season did not improve fit over strictly GSP models. Hence it seems that the timing of drought was useful for predicting mid-season biomass, but became less important as the season progressed, potentially because plants had time to recover biomass after the droughts ended. Early in the season timing of precipitation may be unimportant because soils remain wet from late winter snow/rain.

BNPP

Best AICc models for BNPP included phosphorous, bulk nitrogen, 2012 and 2013 PFT diversity and when interactions were included, a phosphorous and nitrogen interaction term. However, best models included neither DP precipitation or GSP as water terms. However, when soil moisture was used as a water term, DP soil moisture models produced better fits than the growing season soil moisture models. This indicates that timing of soil drying may have a small influence on production belowground.

Previous year production and current year production

No legacy effect for previous year's production was seen as a term in any of the best models for ANPP, BNPP or light as a proxy for aboveground biomass. Additionally, ANPP was never a predictor for models of BNPP and BNPP was never a predictor for models of ANPP. This indicates that there neither appears to be evidence for a trade-off between above- and belowground production nor for a legacy effect.

DISCUSSION

Climate change models predict not only an increase in the variability and extremity 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 when precipitation may, or may not, occur (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 timing 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; da Silva et al. 2012). Therefore, altering the timing of rainfall has the potential to severely affect 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). Some work has found that net ecosystem carbon exchange is sensitive to rainfall timing (Chou et al. 2008; Jongen et al. 2011). We conducted an experiment that manipulated precipitation amount and drought timing in a tallgrass prairie in NE Kansas. We found that ANPP was positively related to increasing precipitation and that timing of drought significantly influenced ANPP, with later droughts having a larger effect than droughts earlier in the growing season. BNPP was unaffected by any precipitation alteration. We also found that nutrients and PFT diversity were important predictors of both ANPP and BNPP. These patterns could be seen most clearly aboveground, ANPP was positively correlated with nitrogen and phosphorous in the WET treatment.

Unlike some previous studies (Kätterer et al. 1995; Frank 2007; Wu et al. 2011; Kang et al. 2013) we found no response in BNPP to the imposed precipitation treatments, though this was not unprecedented (Sindhøj et al. 2000; Gill et al. 2002; Anderson et al. 2010; Kong et al. 2010; Byrne et al. 2013). However, since BNPP has been found to be positively correlated with precipitation in experimental alterations in an Oklahoma tallgrass prairie (Xu et al. 2012; Xu et al. 2013; Xu et al. 2014) and another site at KPBS (Wilcox et al. 2014), these results were still somewhat surprising. Most of these studies augmented or decreased rainfall by 50%, so perhaps a 25% reduction and a 30% increase in precipitation were not enough to trigger a belowground response.

ANPP, on the other hand, was positively correlated with precipitation amount as has been found in almost all studies (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 biomass in the drought treatments were fairly consistent, though on the high end, of changes observed as a result of within season precipitation manipulation at KPBS ±17% to 21% (Knapp et al. 2002; Hoover et al. 2014; Wilcox et al. 2014). Interestingly, while ANPP was reduced in the DRT treatments, it did not correspondingly increase in the WET treatment. There is some presiedent for this finding. Hsu et al. (2012) found that ANPP sensitivity to mean precipitation declines in ecosystems after MAP exceeds 600 mm. Over wide spatial scales Huxman et al. (2004) found that the relationship between ANPP varies less with precipitation as MAP increases. Even prolonged wet periods may not cause major changes in vegetation. Collins et al. (2012) found only a moderate increase in plant cover even after many years of irrigation at KPBS. However, reduced sensitivity to ANPP to precipitation in wet years or climates is not universal. Knapp and Smith (2001) found that across a number of biomes the ANPP increase in wet years was more substantial than the corresponding ANPP decrease in dry years.

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 in a natural setting, found that in a cool season grassland an early-season drought was the only drought period to cause a biomass reduction. Our results from a native, unplowed, C_4 grassland better match the findings from the agricultural system. While ANPP in the three drought treatments did not significantly differ it did progressively decrease from LSP, ESM, to MSM. As

a result the LSP treatment had ANPP intermediate between the other DRT treatments and the AVG and WET treatments. In addition, using canopy light interception as a proxy for biomass we found that even directly after the LSP drought there was not as much of a reduction in biomass as compared to the AVG and WET treatments as would later be found after the ESM and MSM droughts, indicating that plants were less affected by drought at this time of year. This coincides well with results from agricultural studies; early season drought also caused the least amount of leaf area reduction in wheat (Hafid et al. 1998).

Extending our analysis of canopy light interception data through time, we found that biomass reductions had largely disappeared by end of season in both the LSP and ESM drought treatments indicating a high capacity for recovery. This may have been the result of the build up of available nitrogen in the drought plots (Borken and Matzner 2009; McCully et al. 2009), which could then be used for growth once water limitation was removed (Epstein et al. 1998). We found a correlation between available nitrogen and ANPP in the LSP drought plots which is consistent with this mechanism. Additionally, the tallgrass ecosystem has a long history of drought (Hayden 1998; Forman et al. 2001) and its species may be well adapted to cope with this type of disturbance. Drought resistant plants tend to display plasticity in timing of growth. A strong determinant of drought resistance is the ability to slow growth when conditions are poor in exchange for rapid growth when conditions improve (Simane et al. 1993). Rapid growth rates in favorable periods also seem to be connected with ability to maintain leaf area over unfavorable ones (Hafid et al. 1998).

We found that drought timing had no effect at all on BNPP. Since no research has been previously conducted in this area, it is not known how general this finding will prove to be. We were only able to sample BNPP down to 15 cm due to extensive limestone at our site, a factor

that may have affected our estimates of BNPP responsiveness to manipulation of both precipitation timing and quantity. At KPBS only 50-65% of the root biomass is captured by measuring the 0-15 cm soil layer (Wilcox et al. 2014). If there was extensive repartitioning of roots to deeper depths under drought conditions (Sindhøj et al. 2000: Derner et al. 2003), this effect may have been missed and account for the lack of treatment differences seen in BNPP.

Much of the uncertainty surrounding the drivers of productivity might be explained by considering additional factors known to influence ecosystem function. The most important covariates included in this study were soil nitrogen and phosphorous availability. The idea that nutrients become more important drivers of NPP as available water in ecosystems increases has been around for over 20 years (Scholes 1994; Austin and Vitousek 1998; Huxman et al. 2004). While no relationship between either phosphorous or nitrogen and ANPP was found across all treatments, ANPP in the WET treatment was positively correlated with the presence of both nutrients. This indicates that nutrient limitations on ANPP were greater when water was not limiting (Kätterer et al. 1995; Wang et al. 2007), consistent with much past research (Wang et al. 2007; Li et al. 2011; Klaus et al. 2013; Kong et al. 2013; La Pierre 2013), though not all (Lamb 2008). While no direct relationships between the sampled nutrients and BNPP were detected, as with models for ANPP, bulk nitrogen and phosphorous and, where possible, their interaction were included in the best models selected for BNPP. This suggests that nutrients likely played some role in determining BNPP even though a straight forward relationship wasn't found. Previous research has found nitrogen's relationship with BNPP to be complicated. Nitrogen and BNPP have been found to be negatively correlated (Li et al. 2011; Kang et al. 2013), positively correlated (Kätterer et al. 1995; Benning and Seastedt 1997; Wang et al. 2007), or not correlated at all (Epstein et al. 1998; Lamb 2008; Kong et al. 2013). Less research has been done on the

relationship between phosphorous and NPP, but several studies found that higher NPP was linked with higher phosphorous levels (Ostertag 2001; Klaus et al. 2013).

PFT diversity (both from 2012 and 2013) was an important term in all best models for ANPP and BNPP in this experiment. It has often been suggested that diversity acts as a buffer against disturbances in ecosystems (Bai et al. 2004; Nielsen et al. 2011; Polley et al. 2013). However, at least in the short term, that seems unlikely in this system as PFT diversity was negatively correlated with ANPP. The idea of diversity serving as a buffer might be more applicable in the long term. If only a small number of species respond to fluctuations in precipitation and if precipitation is highly variable, this should lead to a shift away from those species over time, but not a strong reduction in ANPP because other species will gradually compensate (Baez et al. 2013). The fact that ANPP was also influenced by 2012 PFT diversity indicates that there may be a carryover effect from year to year making this type of shift more likely. Though strangely 2012 and 2013 PFT diversity were not correlated.

In exploring novel territory on the response of ANPP and BNPP to amount and timing of growing season precipitation, this study suggests avenues and considerations for future research. For instance, it would be valuable to better examine the relationship between soil moisture and NPP. The present study lacked sufficient replication to properly investigate the soil moisture/NPP relationship, and it appears that the soil moisture interface may be the key to understanding potential effects of drought timing on BNPP. Additionally, more long-term BNPP data sets are needed so that we can get a better idea of the temporal variability in belowground growth and how this compares to the variability aboveground (only one such study exists to our knowledge, Milchunas and Lauenroth 2001).

Conclusion

      Based on this study, reduction in precipitation can have a large effect on ANPP but not BNPP in the mesic, tallgrass prairie. Increases in precipitation above the norm have no effect either above- or belowground. Timing of precipitation seems to play a noticeable role in determining ANPP responses, 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 quite severe where summer droughts are expected to be more frequent. Since ANPP and BNPP respond differently to changes in water availability these differences should be accounted for in future modeling work

Table 1: Summary of the amount of water received by each treatment at KPBS in 2013 as well as the timing of when rainfall was excluded by roofs or water was applied. The mean air temperature during the period of time over which each treatment was in place is also shown. The AVG treatment is associated with the mean air temperature for the entire growing season: April 1- September 30, 2013. The AVG (bold) treatment is a composite of the control and long term mean (MEAN) treatment. There values are included here for references. The control and MEAN were not significantly different from one another, nor from the actual long term mean (614 mm).

Treatment	Precipitation Received (mm)	Percent of Long Term Average	Mean Air Temperature (^{o}C)	Timing
WET	788	128%	24.0	Weekly (Jun 1 – Aug 31)
AVG	**643**	**105%**	**20.2**	**-**
MEAN	681	111%	-	as necessary (Jun 1-Aug 31)
CONTROL	605	98%	-	-
LSP	455	74%	18.2	Apr 20 – Jun 22
ESM	444	72%	22.4	May 22 – Jul 2
MSM	467	76%	25.2	Jun 22 – Jul 26

Table 2: Results of the regressions analyses for ANPP and BNPP and their relationship with nutrients: available soil N (collected by the resin bags), bulk soil N and available soil P. Block level differences existed, but could not be used as a random factor due to lack of replication. To account for this, and allow for accurate comparison across blocks, nutrient values were standardized by setting the mean value for each block to zero prior to analyses. F is for F-statistic, P is for p-value and d f stands for degrees of freedom

Effect	d f	ANPP		BNPP	
Active Nitrogen Flux		F	P	F	P
WET	1	0.22	0.65	1.20	0.31
AVG	1	0.12	0.73	1.6	0.22
LSP	1	**12**	**0.018**	0.0092	0.93
ESM	1	0.073	0.79	0.093	0.77
MSM	1	0.035	0.86	0.016	0.90
Bulk Nitrogen					
WET	1	**5.7**	**0.043**	0.034	0.86
AVG	1	0.43	0.52	0.61	0.45
LSP	1	0.096	0.77	0.90	0.37
ESM	1	0.077	0.79	0.30	0.61
MSM	1	0.48	0.51	0.63	0.45
Active Phosphorous					
WET	1	**7.2**	**0.028**	0.23	0.65
AVG	1	0.019	0.89	0.83	0.38
LSP	1	1.8	0.23	1.28	0.29
ESM	1	1.8	0.22	0.33	0.58
MSM	1	2.1	0.18	1.09	0.33

Table 3: Multifactor models were used to explain patterns seen in ANPP and its proxy canopy light interception. Comparisons between models that included terms for precipitation based off the entire growing season (GS) and models that included precipitation parsed by how much fell in each drought period (DP) were of particular interest. ANPP and end of summer light interception models were based off of all 60 plots included in this experiment. End of drought period light interception models used 40 plots in their analysis and soil moisture models used a reduced data set from only 26 plots. Where replication permitted, interactions were evaluated as well. P=active phosphorous, N=bulk nitrogen, D12=2012 PFT diversity, D13 =2013 PFT diversity, PNI=nitrogen and phosphorous interaction, GSW=growing season precipitation, LW = late spring precipitation, EW= Early summer precipitation, MW = mid-summer precipitation, GSSM = growing season soil moisture, LSM = late spring soil moisture, ESM = early summer soil moisture, MSM = mid-summer soil moisture, WD13I= water and 2013 PFT diversity interaction, WPI = water and phosphorous interaction, WNI= water and nitrogen interaction, WPNI.= water, nitrogen and phosphorous interaction. Horizontal lines separate comparable AICc values. Bold text demarcates best models.

	Global Model	Best Model selected	AICc value
ANPP Precipitation	GS	ANPP = 1 + GSW + P + N + D13 + D12	559.7
	GS and interactions	**ANPP = 1 + WN + PNI + P + N + D13 + D12 (WN is interchangeable with WPNI, and WD13I)**	**547.1**
	DP	ANPP = 1 + MW+ P + N + D13 + D12 (MW is interchangeable with EW)	558.4
ANPP Soil moisture	GS	ANPP ~ 1 + GSSM + P + N + D13 + D12	234.0
	DP	**ANPP = 1 + ESM + P+ N+ D13 + D12 (MSM is interchangeable with ESM)**	**220.5**
Light Interception	After LSP Drought- GS	JUN29LIGHT = 1 + GSW + D13	-45.9
	DP	JUN29LIGHT = 1 + EW + D13	-47.0
	After ESM Drought- GS	JUL10LIGHT = 1 + GSW	-58.3
	DP	**JUL10LIGHT = 1 + EW**	**-60.5**
	After MSM Drought- GS	AUG1LIGHT = 1 + GSW + D13	-77.7
	DP	**AUG1LIGHT = 1 + MW + D13**	**-94.4**
	End of Season- GS	SEP9LIGHT = 1 + GSW + D13	-93.5
	DP	SEP9LIGHT = 1 + EW + D13	-93.4

Table 4: Multifactor models were used to explain patterns in BNPP. Comparisons between models that included terms for precipitation based off the entire growing season (GS) and models that included precipitation parsed by how much fell in each drought period (DP) were of particular interest. Precipitation based models used all 60 plots included in this experiment. Soil moisture models used a reduced data set from only 26 plots. Where replication allowed interaction terms were also considered. P=active phosphorous, N=bulk nitrogen, D12=2012 PFT diversity, D13 =2013 PFT diversity, PNI=nitrogen and phosphorous interaction, GSW=growing season precipitation, LW = late spring precipitation, EW= early summer precipitation, MW = mid-summer precipitation, GSSM = growing season soil moisture, LSM = late spring soil moisture, ESM = early summer soil moisture, MSM = mid-summer soil moisture, WD13I= water and 2013 PFT diversity interaction, WPI = water and phosphorous interaction, WNI= water and nitrogen interaction, WPNI.= water, nitrogen and phosphorous interaction. Horizontal lines separate comparable AICc values. Bold text demarcates best models.

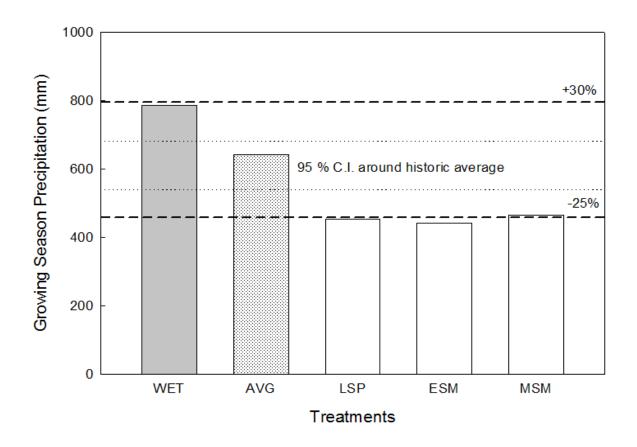|	Global Model	Best Model Selected	AICc value
BNPP Precipitation	GS	BNPP = 1+P + N + D13 + D12	588.7
	GS and interactions	**BNPP = 1 + PNI + P + N + D13 + D12**	**576.7**
	DP	BNPP = 1 + P + N + D13 + D12	588.7
BNPP Soil Moisture	GS	BNPP = 1 + P+ N + D13 + D12	234.3
	DP	**BNPP = 1 + MSM + P + N + D13 + D12**	**218.4**

Figure 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.
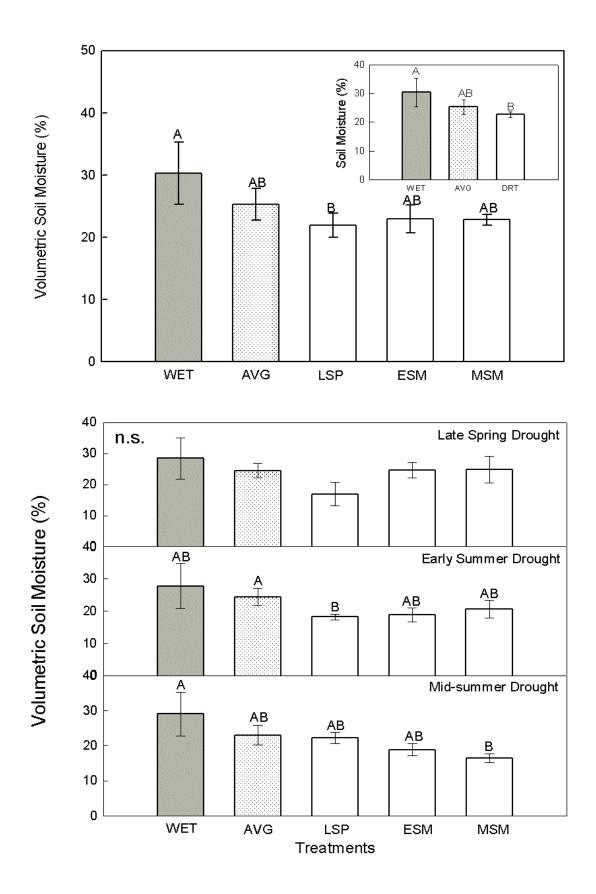
Figure 2: (top) Mean percent volumetric soil moisture for each treatment for entire growing season. Letters indicate significant differences between treatments adjusted for multiple comparisons. Error bars are 95% confidence intervals around the mean. Inset: Mean difference in soil moisture for entire growing season based on treatment type, with all the LSP, ESM and MSM drought treatments all combined into a single DRT treatment. (bottom) Mean volumetric soil moisture over the course of the three different drought periods: late spring, early summer and mid-summer. Each drought period excluded an approximately equal amount of precipitation: ~150 mm of rainfall or about 25% of the long-term growing season average. Some overlap in timing existed between the drought periods. The late spring drought and the early summer drought overlapped for 30 days and the early summer and the mid-summer drought overlapped for 10 days. Irrigation began half way through the early season drought period and continued until the end of August. No treatment differences were seen in soil moisture during the late spring drought period. For the later droughts letters demarcate treatment differences adjusted for multiple comparisons.
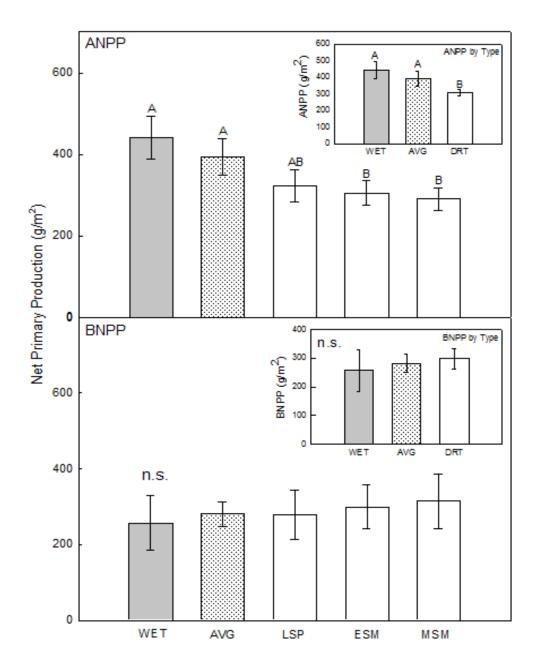
Figure 3: ANPP (top) and BNPP (bottom) for each treatment. Significant differences between treatments adjusted for multiple comparisons are indicated by letters. Error bars indicate 95% confidence interval around the mean. Top inset: ANPP values binned by treatment type, with LSP, ESM and MSM drought treatments combined into a single DRT treatment. Bottom inset: BNPP values combined across drought timing treatments.
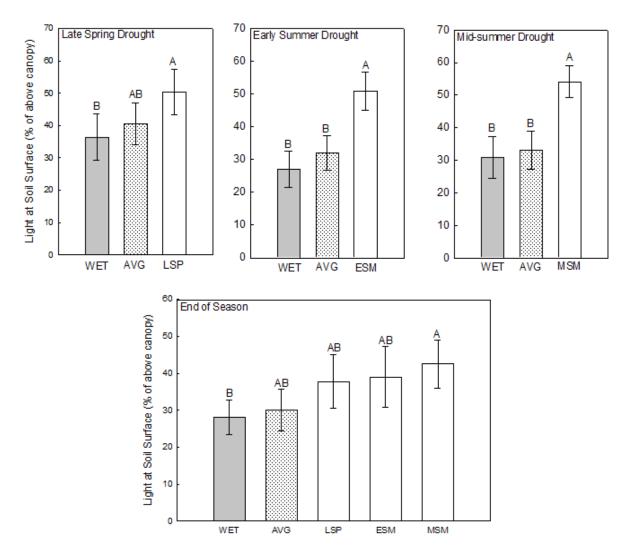
Figure 4: Canopy light interception to soil surface, as a proxy for aboveground biomass (see Supplementary Figure 3 for the relationship between ANPP and canopy light interception). Higher canopy light interception corresponds to lower ANPP. Top: Canopy light interception is shown directly after each drought period has ended (roofs removed) and values in the respective drought treatment are compared to those in the WET and AVG treatments. Letters indicate significant differences between treatments adjusted for multiple comparisons and 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).

CHAPTER TWO:

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CHAPTER THREE:

SUMMARY AND DIRECTIONS FOR FUTURE RESEARCH

Driven in large part by increasing atmospheric CO_2 levels and land use change, climate projections for the future unanimously call for rising temperatures and altered precipitation amounts and patterns (IPCC 2013). Due to the expected intensification of the global hydrological cycle, forecasts are for more variable precipitation regimes (Weltzin et al. 2003; Meehl et al. 2006), though there is much debate about the nature of future precipitation changes (Trenberth et al. 2003; Watanabe et al. 2012; Huang et al. 2013). One possibility is that the season when precipitation falls, or does not (i.e., short-term drought), will shift from its historic norm, without the overall total amount of precipitation changing (Kunkel and Liang 2004; Christensen et al. 2007; Brunsell et al. 2010; Kunkel et al. 2013). Changes in the seasonality of precipitation have been investigated in some agricultural systems (Simane et al. 1993; Hafid et al. 1998; da Silva et al. 2012), but little research has been done to investigate how sensitive ecosystems are to changes in the timing of short-term drought during the growing season (but see Bates et al. 2006 and Heitschmidt and Vermeire 2006). Thus, there is little basis for making predictions regarding future ecosystem response to such changes.

In the mesic, tallgrass prairie of NE Kansas precipitation generally falls mostly early in the growing season (Hayden 1998) and the ecosystem regularly experiences short-term periods of seasonal droughts during later months (Stahle and Cleaveland 1988; Rhee and Carbone 2007; Craine et al. 2012). If a different precipitation pattern were to prevail, it is not known how this system would respond. In this study I imposed moderate droughts at three different periods

during the growing season: late spring, early summer and mid-summer and then monitored how net primary productivity responded, both above- and belowground (ANPP &BNPP).

Droughts were instituted by installing polyurethane roofs over treatment plots, and leaving them in place until 25% of the mean growing season precipitation (GSP) was excluded, ~ 150 mm. The drought timing treatments were compared to control plots, which received mean GSP, and water addition plots that received a total of 130% of the mean GSP. ANPP was collected by clipping at the end of the season and BNPP was collected using root in-growth cores that remained in the ground from May to September. Additionally, light interception by vegetation at ground level was monitored biweekly to determine canopy structure and serve as a non-destructive proxy for biomass.

A number of other ecosystem characteristics are influenced by drought and have been found to have an effect on production. These include soil moisture (Seneviratne et al. 2002), nutrient availability (Benning and Seastedt 1997; McCully et al. 2009; Bloor and Bardgett 2012), plant diversity (Bai et al. 2004; Bloor and Bardgett 2012) and legacy effects (Haddad et al 2002). Because interactions between these covariates may influence the way ANPP and BNPP respond to drought timing I monitored these and included them in my analysis to further investigate patterns in production response to drought timing using AICc multimodel inference.

Drought was found to have an overall negative effect on ANPP, but no corresponding reduction in BNPP was found. Additionally, no treatment response was seen in NPP. Early summer and mid-summer droughts caused larger reductions in ANPP than the late spring drought. Timing of drought had no effect on BNPP or net primary production (ANPP+BNPP).

Using light as a proxy for aboveground biomass, large reductions in vegetation were seen directly after each drought treatment was removed. Reductions resulting from the late spring drought were less severe, than those from later droughts. However, all drought treatments were able to partially recover once water stress was removed. Timing of precipitation only played a small role in canopy structure by end of season. Including precipitation binned by treatment period improved fit of models on light interception only for early summer and mid-summer models. Timing of drought did not improve model fit for the late spring measurements or those collected at end of season.

While neither ANPP or BNPP was increased in the water addition plots over the control, a positive correlation was seen between overall ANPP and phosphorous and nitrogen in the water addition treatment. This indicates that in this system nutrients become more limiting when water is readily available. It is, however, likely that nutrients always play a role even when water is scarce since all best AICc models for ANPP and BNPP included nutrient terms.

PFT diversity also appears to be closely tied to production in this ecosystem, as it was included as a term in all best models. High diversity plots have lower ANPP than low diversity ones. PFT diversity's relationship with BNPP is less clear.

Many questions regarding the importance of drought timing on ecosystems remain to be addressed. A principal concern that needs to be examined is the importance of drought timing over a wide geographic extent. Ecosystem sensitivity to variation in the number and size of precipitation events varies considerably across biomes (Knapp and Smith 2001; Gerten et al. 2004; Hsu et al. 2012). Even the importance of precipitation for determining ANPP varies by ecosystem (Huxman et al. 2004; Cherwin and Knapp 2012). As such, it is important to examine

the effect of changing short-term drought timing in many systems to learn which will prove sensitivity and how prevalent this sensitivity will be. Incorporating this information will improve models of ecosystem response to climate change.

Also, while much is known about the natural drivers and variation of ANPP from year to year (Sala et al. 1988; Lauenroth and Sala 1992; Hsu et al. 2012; La Pierre 2013), less work has been done with BNPP (Milchunas and Lauenroth 2001; Zhou et al. 2012). This is largely due to the difficulty in effectively sampling belowground biomass. Many more long-term BNPP data sets are needed world wide for a better understand of natural fluctuations in and drivers of belowground plant growth.

It would also be valuable to consider how other ecosystem services may be affected by change in the seasonality of precipitation. A likely candidate for sensitivity to change in the timing of precipitation is an ecosystem's ability to benefit pollinators. If shifts in precipitation change flowering phenology (Liancourt et al. 2012; Meineri et al. 2014; Giuliani et al. 2014), this might affect the foraging of native bees and other insects pollinators (Severns and Moldenke 2010).

Examining the effects of precipitation over a longer time period would also yield useful insights. This study was only conducted over a single growing season and precipitation in the central US is historically quite variable (Chen et al. 2012), therefore short-term shifts in precipitation timing are not particularly rare and generally result in reductions in biomass equivalent to those found in this study (Knapp et al. 2002; Wilcox et al. 2014). However, longer term changes in precipitation can result in ANPP shifts of over 60% (Knapp et al. 2012; Hoover et al. 2014). Shifts in precipitation as a result of climate change are expected to persist for

decades to centuries (IPCC 2013) or even thousands of years (Archer 2008). Therefore, understanding how ecosystems respond to chronic shifts in precipitation timing would be valuable.

Lastly, while precipitation is certainly an important driver of production in grasslands, other processes, such as grazing and fire (Briggs and Knapp 1995; Koerner et al. 2014), play large roles as well. These processes also include more potential for effective management (Bestelmeyer et al. 2004; Borghesio 2014). Therefore, it would be of use to know how they interact with changing the seasonality of short-term drought so that more effective response strategies for maintaining grassland productivity can developed.

CHAPTER THREE:

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APPENDIX

Corrected Akaike Information Criteria (AICc) Analysis

Modeling was performed to determine if including the timing and amount of precipitation, instead of simply the amount, improved prediction of biomass. Additionally, model selection allows for inference of the importance of other ecosystem variables such as nutrients and diversity that are both affected by drought and are tied to NPP.

Model selection was conducted with ANPP, BNPP and light interception (a biomass proxy) as dependent variables. Independent variables included previous year ANPP (PYANPP), previous (D12) and current PFT diversity (D13), bulk soil nitrogen (N) and soil available phosphorous (P) concentration. When BNPP was being modeled ANPP was included as an independent variable and vice versa. The global models were constructed using either precipitation from the entire growing season (GS) or precipitation binned by drought period (DP) to account for timing of precipitation input: LSP, ESM and MSM drought periods. Additionally, a growing season global model was fit that included water interaction terms with BNPP/ANPP, 2013 PFT diversity, N, P, and P*N. This could not be duplicated with the seasonal global model due to insufficient replication. See Supplementary Table 2 for complete info on global models before selection.

Direct precipitation is not always a good representation plant water stress, particularly if temperatures are high and humidity is low, which results in high evapotranspiration. In these cases it is often more useful to consider soil moisture as a measure of water stress (Knapp et al. 2008). Soil moisture global models similar to those used in the precipitation models above were analyzed; the GS model used average season-long soil moisture while the DP models used

average soil moisture terms for each of the three drought periods. Due to limited replication (n=26) interactions could not be evaluated, nor could AICc values from the soil moisture models be compared directly to the precipitation based models.

Lastly, the GS precipitation and DP global models were run on canopy light interception as a dependent variable at four different points throughout the growing season (June 29 – Sept 9). This allowed for inference on the importance of precipitation timing while the treatments were still in progress. The same independent variables were included as before, except that interactions were again excluded due to limited replication (n=40 in most cases, n=60 end of season).

Best models were determined from each global model based on automated model selection using the glmulti function from the glmulti package. Linear mixed-effect regressions were specified with block as a random factor, using the lme funtion in R. The glmulti package is a wrapper that generates all possible models from a specified function (i.e. lme) and then selects the best models based on an Information Criterion (Calcagno 2013). In this case the AICc was used and five best models were automatically generated from each global model. Models with lower AICc values were deemed better; however, models with an AICc difference of 2 or less were considered a tie (Burnham and Anderson 2002). In cases of a tie the model with the least number of terms was chosen as the better model for reasons of parsimony.
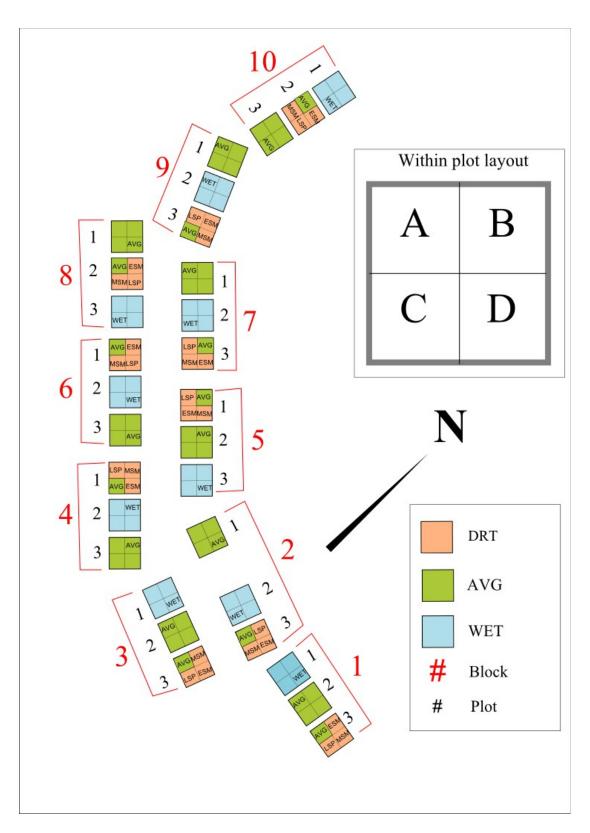
Supplementary Table 1: Global models before glmulti selection was preformed including all independent variables. P=active phosphorous, N=bulk nitrogen, D12=2012 PFT diversity, D13 =2013 PFT diversity, ANPP=aboveground net primary productivity, BNPP=belowground primary productivity, PYANPP=previous year ANPP, PNI=nitrogen and phosphorous interaction, GSW=growing season precipitation, LW = late spring precipitation, EW= early summer precipitation, MW = mid-summer precipitation, GSSM = growing season soil moisture, LSM = late spring soil moisture, ESM = early summer soil moisture, MSM = mid-summer soil moisture, WD13I= water and 2013 PFT diversity interaction, WPI = water and phosphorous interaction, WNI= water and nitrogen interaction, WPNI.= water, nitrogen and phosphorous interaction. Horizontal lines separate comparable AICc values. Sample size for each model selection is denoted under the n column.

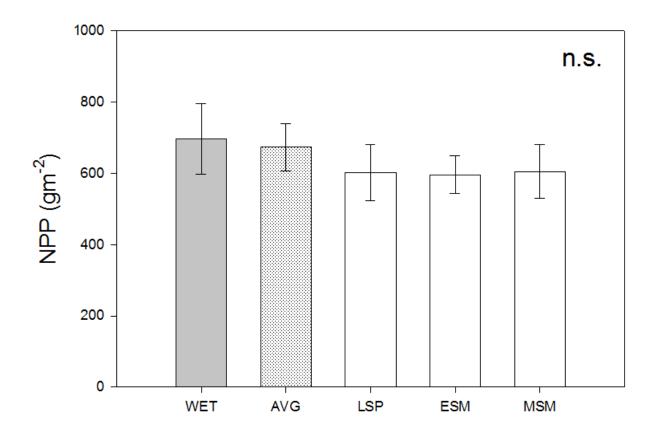| Dependent Variable	Model type	Independent variables	n
ANPP	GS precipitation	P, N, D12, D13, BNPP, PYANPP, GSW	60
	GS precipitation with interactions	P, N, D12, D13, BNPP, PYANPP, GSW, WD13I, WPI, WNI, WPNI	60
	DP precipitation	P, N, D12, D13, BNPP, PYANPP, LW, EW, MW	60
	GS soil moisture	P, N, D12, D13, BNPP, PYANPP, GSSM	26
	DP soil moisture	P, N, D12, D13, BNPP, PYANPP, LSM, ESM, MSM	26
Light Interception	GS precipitation	P, N, D12, D13, BNPP, PYANPP, GSW	40
After LSP Drought	DP precipitation	P, N, D12, D13, BNPP, PYANPP, LW, EW, MW	40
Light Interception	GS precipitation	P, N, D12, D13, BNPP, PYANPP, GSW	40
After ESM Drought	DP precipitation	P, N, D12, D13, BNPP, PYANPP, LW, EW, MW	40
Light Interception	GS precipitation	P, N, D12, D13, BNPP, PYANPP, GSW	40
After MSM Drought	DP precipitation	P, N, D12, D13, BNPP, PYANPP, LW, EW, MW	40
Light Interception	GS precipitation	P, N, D12, D13, BNPP, PYANPP, GSW	60
End of Season	DP precipitation	P, N, D12, D13, BNPP, PYANPP, LW, EW, MW	60
BNPP	GS precipitation	P, N, D12, D13, ANPP, PYANPP, GSW	60
	GS precipitation with interactions	P, N, D12, D13, ANPP, PYANPP, GSW, WD13I, WPI, WNI, WPNI	60
	DP precipitation	P, N, D12, D13, ANPP, PYANPP, LW, EW, MW	60
	GS soil moisture	P, N, D12, D13, ANPP, PYANPP, GSSM	26
	DP soil moisture	P, N, D12, D13, ANPP, PYANPP,LSM, ESM, MSM	26

APPENDIX:

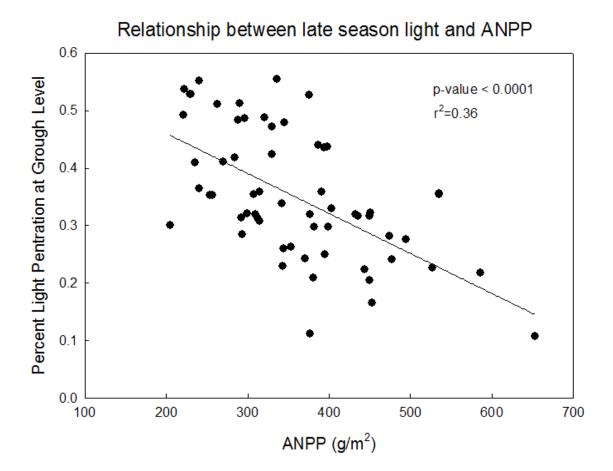REFERENCES: Corrected Akaike Information Criteria (AICc) Analysis

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Supplemental Figure 1: Shows actual plot layout of treatments. Treatment abbreviations occupy the actual subplot over which each treatment was applied in 2013.
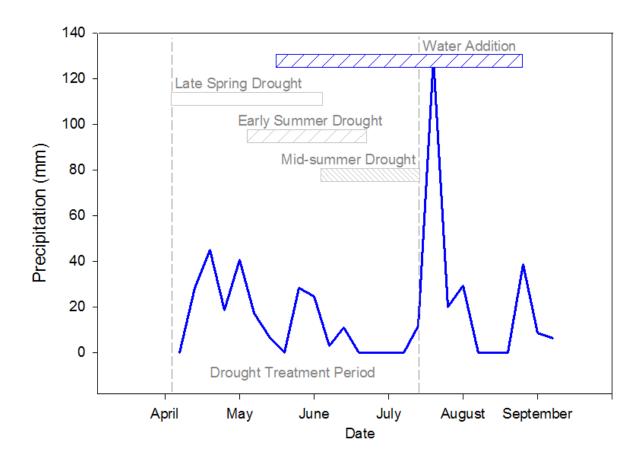
Supplementary Figure 2: Net Primary Productivity (ANPP+BNPP) for each treatment. Error bars indicate 95% confidence interval around the mean.
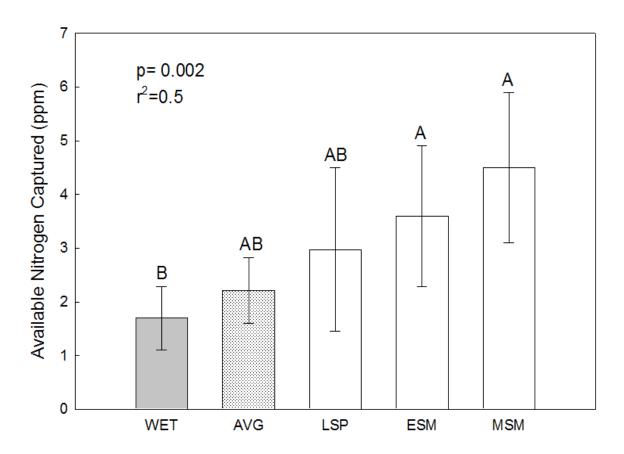
Supplementary Figure 3: Correlation between end of season (Sept 9) canopy light interception

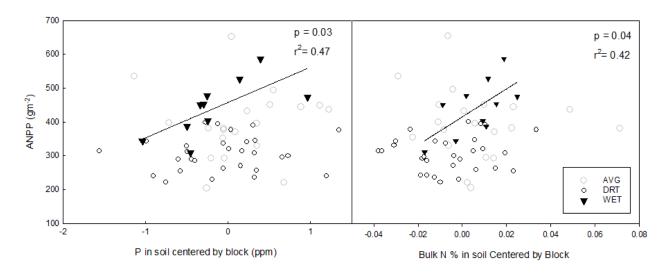and ANPP. Solid line is the linear best of the regression.

Supplementary Figure 4: Canopy light interception to soil surface over the course of the growing

season. Boxes indicate the period of time over which drought treatments were applied; The LSP

drought began April 20 so its entire duration is not shown on the graph. Light measurements

were only taken when no drought shelter was present, so measurements in the ESM and MSM

drought treatments begin later. Letters indicate significant differences in light penetration

between treatments at a single time period. Each column of letters marked by an arrow should be

compared separately.

Supplementary Figure 5: Weekly precipitation over the course of the growing season. Dashed vertical lines indicate the temporal extent of all drought treatments. Grey boxes indicate the time over which each drought treatment was applied; a blue box indicates the extent of irrigation in the WET treatment. During their respective periods drought treatments received no rain. Drought treatments stayed in place until ~150 mm of rain was excluded from each treatment. When no treatment was in effect all plots received ambient rain.

Supplementary Figure 6: Available nitrogen in the form of ammonium and nitrate captured by resin bags (17 May – 11 Oct). More nitrogen captured in resin bags was interpreted as less uptake by plants and microbes. Letters indicate significant treatment differences accounting for multiple comparisons. Error bars inidcate 95% confidence intervals.

Supplementary Figure 7: Regressions of P (left) and N (right) to ANPP split up by treatment type (WET, AVG, DRT). Timing was not included in this analysis. To account for block differences without being able to include block as a random factor when treatments were divided this way, all data was centered by block before analysis. P and N in the DRT and AVG treatments were not significantly related to ANPP, while positive correlations were found with both nutrients in the WET treatment. Regression lines, coefficients of determination and p-values refer to the WET treatment regressions.