DISSERTATION

ECOSYSTEM RESPONSES TO PRECIPITATION EXTREMES

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ABSTRACT

ECOSYSTEM RESPONSES TO PRECIPITATION EXTREMES

Predictions and recent observations of changing frequencies and intensities of climate extremes have prompted ecologists to increasingly study their ecological impacts. Rising interest in this field of research reflects growing recognition that changing climatic variability can impact ecological dynamics independent of climatic means, and that the ecological impacts of climate extremes may be of equal or greater magnitude than gradual changes in mean climate. However, recent concerns have emerged that traditional approaches used to understand and quantify relationships between climate and ecological processes may not be predictive of responses to extreme climatic conditions with no historic analog.

In this dissertation, I describe tests of current knowledge about how precipitation impacts ecosystem processes by considering how changing extremity at both intra-annual and interannual timescales impacts different components of the carbon cycle. To achieve this, I employed a novel experimental design that imposed multiple levels (n = 11 levels, n = 4 replicates), and thus a gradient, of precipitation amount and extremity within a single growing season. These manipulations were imposed within two intact ecosystems of opposing climatic backgrounds; the semi-arid steppe of Colorado (low mean productivity) and the mesic tallgrass prairie of northeastern Kansas (high mean productivity). I show that despite these ecosystems harboring differing ecological characteristics, aboveground net primary productivity was consistently more sensitive to extreme wet years than severe drought, and thus carbon gains during wet years were greater than drought-induced productivity reductions. Despite asymmetrical productivity responses to precipitation extremes in both systems, there was consistent evidence for an underlying linear relationship as best describing the response of productivity to changes in growing season precipitation within these grasslands, in agreement with current models. Coupling this experimental data with long-term records within the mesic grassland revealed strong interactions between variability in rainfall patterns within and among years. Variability in intra-annual rainfall patterns, and in particular large and more variable event sizes, acted to magnify the reductions in ecosystem functioning during drought. A systemic review of the literature adds further complexity to these dynamics from an organizational perspective, suggesting that both the response and recovery of ecosystems to climate extremes are mediated by ecological responses and interactions that propagate from the individual, population, to the community-level to collectively impact ecosystem-level functioning. Overall, my research demonstrates a critical role for changes in precipitation extremity at both intra and interannual timescales and levels of ecological organization with respect to predicting the dynamics of ecosystem functioning amid climate change.

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DEDICATION

To my mom and dad,

who have always enthusiastically supported me and my pursuits.

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CHAPTER 1: INTRODUCTION

1.1 BACKGROUND

Predictions and recent observations (IPCC 2013, Cook et al. 2015, Swain et al. 2018) of changing frequencies and intensities of climate extremes, such as heatwayes and drought, have prompted ecologists to increasingly study their ecological impacts (Allen and Breshears 1998, Ciais et al. 2005, McDowell et al. 2011, Hoover et al. 2014, Anderegg et al. 2015, Knapp et al. 2015, Wilcox et al. 2017). Observed ecological impacts of climate extremes are diverse, ranging from rapid evolution (e.g. flowering time; Franks et al. 2007) to signatures on global atmospheric CO₂ concentrations (Poulter et al. 2013, Haverd et al. 2016). Rising interest in this field of research reflects growing recognition that changing climatic variability can alter ecosystem structure and functioning independent of climatic means (Knapp et al. 2002, Gherardi and Sala 2015), and a more general consensus that the ecological impacts of climatic extremes can be greater in magnitude than gradual changes in mean climate (Niu et al. 2014). Recent concerns have thus emerged that traditional approaches used to quantify relationships between climatic drivers and ecological processes may not be predictive of responses to climatic extremes with no historic analog (Kayler et al. 2015, Knapp et al. 2017). Because of the novel pressures that changing climatic extremes and variability will impose on ecosystems, novel approaches must be considered to quantify and predict their ecological consequences.

Predicting the response of ecosystem function to expected changes in climate requires properly defined relationship between climate and ecosystem processes. In particular, terrestrial net primary productivity (NPP), as the difference between the total amount of carbon (and specifically CO₂) fixed into biomass through plant photosynthesis and lost via respiration, is a key metric of ecosystem functioning globally. By controlling the input of carbon, biomass and energy into ecosystems, NPP is a central process governing not only the carbon cycle, but a chief biological mediator of land surface feedbacks to the climate system (Churkina and Running 1998). Beyond its central ecological role, NPP also underlies the biophysical supply of critical services humans derive from ecosystems, such as forage for production cattle (Sloat et al. 2018). Consequently, a mechanistic understanding of the controls of NPP amid predicted changes in climatic variability is a critical need in terms of both basic and applied ecological knowledge, and is thus of both scientific and societal interest.

Across much of the globe, water is a primary or co-limiting resource of annual terrestrial NPP (Churkina and Running 1998, Knapp et al. 2017; Figure 1.1). As atmospheric warming continues to intensify the hydrological cycle (Huntington 2006), forecasts of both changing precipitation variability (IPCC 2013) and extremity (Cook et al. 2015) have in turn produced expectations that previous approaches relating precipitation to NPP may not be predictive of responses to future changes in precipitation regimes (IPCC 2013) and in particular extremes (Knapp et al. 2017, Luo et al. 2017). Current understanding of how precipitation impacts NPP is derived from relating NPP to changes in precipitation either *temporally* or *spatially*. Site-based, i.e., within-ecosystem, records that measure and relate interannual variation in precipitation and NPP (temporal models) typically yield a linear relationship between precipitation and NPP (Figure 1.1), once data have been collected for a sufficient period of time (e.g. 10 years). However, in moving from deserts to forests, i.e., xeric to mesic ecosystems, the slope of the temporal relationship between precipitation and ANPP tends to decrease (Huxman et al. 2004; Figure 1.1). This reduced slope in mesic systems has been attributed to biogeochemical factors, and thus movement from historically dry to wet ecosystems results in other resources, such as light or soil

nutrient availability, co-limiting NPP in concert with water availability. The consequence of this dynamic is a hypothesized and documented decreasing sensitivity of NPP to changes in precipitation as mean annual precipitation increases (Huxman et al. 2004, Wilcox et al. 2017).

Across large (e.g. continental) spatial scales, climatic gradients of annual precipitation have also allowed ecologists to relate mean precipitation with mean productivity, denoted as spatial models (Fig 1.1). When viewed across spatial scales, the relationship between precipitation and NPP yields an overall higher slope than temporal models, yet a clear saturating relationship between precipitation and productivity driven by the most mesic ecosystems (Figure 1.1), further indicative of the increased influence of other resources or factors other than water limiting NPP in mesic ecosystems (Huxman et al. 2004). However, by covering continental-scale gradients in climate and thus an array of ecosystem types, spatial models necessarily incorporate long-term climatic influences on ecosystem properties and thus large changes in soil texture, resource availability, and vegetation composition and structure into their predictions. As a consequence, spatial models are likely to have limited utility in predicting responses of any one ecosystem to precipitation change. For example, due to meristem density, growth, and/or leaf area constraints, a semi-arid grassland would likely be more limited in NPP responses to a growing season of 2000 mm than a deciduous forest. So-called "vegetation constraints' within ecosystems have been hypothesized to limit the response of NPP to precipitation within-sites (Yahdjian and Sala 2006), suggesting an eventual saturation of the aboveground fraction of NPP (ANPP) responses to precipitation at the site-level (Knapp et al. 2017). Recent evidence further points to a preserved preference for the use of temporal models, and thus a linear relationship, over spatial models in benchmarking NPP-precipitation relationships for ecosystem models (Estiarte et al. 2016). Therefore, the focus of my dissertation research has been on addressing the limitations and testing

the predictions of current temporal models of NPP-precipitation relationships amid forecast changes in precipitation extremes.

Like spatial models, temporal models also harbor limitations with respect to how data is produced, and thus the underlying inferences of these model's predictions. The first limitation in temporal models is the potentially confounding influence of variability and changes in biotic or abiotic conditions through time. This is a consequence of the decadal timescales in which data collection is needed to build a robust temporal precipitation-NPP relationship. This point is particularly relevant given current rates of human-driven changes in global biogeochemistry (Viotusek 1998, Williams et al. 2007, Smith et al. 2009, IPCC 2013). Such change and variability may occur through gradual, chronic drivers (e.g. gradual increases in atmospheric CO₂ and temperature; Smith et al. 2009), or variability produced by 'legacies' of previous-year productivity and precipitation (Sala et al. 2012, Reichmann et al. 2013, Yahdjian and Sala 2006). It may thus be the case that systems now exhibit differential sensitivity to precipitation than in the past (e.g. 30 years ago), hindering the predictive power of temporal models when looking towards the future.

The second constraint is the limited representation of statistically extreme climatic conditions, which are by definition rare (e.g. above and below the 99th and 1st percentile, respectively), in 'long-term' (e.g. 30-year) ANPP-precipitation datasets. Indeed, datasets of thirty years in duration are not likely to capture the full range of climatic variability historically experienced within a region, and thus the underlying NPP-precipitation relationship (Fig. 1.2). Because of this limitation, it has been proposed that when precipitation levels of greater magnitude are fully included models of precipitation and productivity, previously defined linear relationships of precipitation-NPP may shift towards nonlinearity (Knapp et al. 2017, Luo et al. 2017), potentially due to either vegetation growth potential (Yahdjian and Sala 2006) or biogeochemical

(Huxman et al. 2004) limitations, particularly under the wettest conditions. There is further evidence to suggest that NPP may be differentially, i.e., asymmetrically, sensitive to dry versus wet years (Knapp and Smith 2001, Wilcox et al. 2017, Zhang et al. 2017, Chapters 2 and 3 this Dissertation), yet to date much of these inferences are derived from responses to nominal precipitation variability. While current understanding suggests a greater relative sensitivity to increases in precipitation (Knapp and Smith 2001, Wilcox et al. 2017, but see Zhang et al. 2017), tests of this have not fully been applied within the context of responses to precipitation extremes, likely due to limited experiments imposing both wet *and* dry extremes (but see Wilcox et al. 2017). It has thus been suggested that when responses to extremes are incorporated, a greater relative sensitivity of NPP to severe drought will emerge in concert with a shift towards a nonlinear relationship (Knapp et al. 2017).

The third limitation of temporal models is that rainfall patterns within-years can vary dramatically from to year to year. Differences in rainfall patterns within years may explain, in part, why rain use efficiency of ecosystem productivity, i.e., NPP per unit of rainfall, can vary as much as two-fold for similar precipitation amounts (chapter 4; Figure 4.3). Despite the fact that temporal models incorporate variability in rainfall patterns, temporal models have produced a limited understanding about the relative contribution of rainfall patterns versus amounts with regard to how precipitation impacts ecosystem productivity. Experimental approaches directly manipulating rainfall patterns (Knapp et al. 2002, Heisler-White et al. 2008, Wilcox et al. 2014) and total amounts (Hoover et al. 2014) have provided clear support the notion that both total precipitation amounts and within-year variability in rainfall patterns collectively impact ecosystem functioning. Yet surprisingly, these two predictions of future climate change (IPCC 2013, Cook et al. 2015, Swain et al. 2018) have been studied in relative isolation, and thus little attention has been paid to

the interaction between changes in extremes in terms of total precipitation amounts (e.g. Hoover et al. 2014) and rainfall patterns within-years (e.g. Heisler-White et al. 2008).

Limited investigation concerning the interactive effects of changes in total precipitation amounts and within-year rainfall patterns on ecosystem function may be, in part, a product of current experimental approaches (Hoover et al. 2018; Figure 1.2a). Experiments in climate extremes research have typically employed few-factor well-replicated designs intended primarily for analysis of variance (ANOVA). Such experimental designs typically consistent of a treatment and ambient control (e.g. drought and control), and thus only explore the relative effect of two factors (Fig. 1.2a). By only exploring the relative effect of precipitation extremity or variability, such data are not particularly useful in understanding underlying NPP-precipitation relationships or incorporating into ecosystem models. This calls for alternative approaches to predict responses of ecosystem functioning to forecast changes in precipitation regimes and extremes (IPCC 2013, Cook et al. 2015, Swain et al. 2018)

Since the early 2000's, ecologists have advocated for the use of more statistically powerful and informative experimental designs in the form of regression experiments when both the independent and independent factors of interest are continuous (Gotelli and Ellison 2004, Cottingham et al. 2005). Because regression experiments impose a treatment gradient (Figure 1.2b), such designs are thought to preferable over few-factor approaches (when both dependent and independent variables are continuous) for multiple reasons. First, regression experiments and analyses are generally more statistically powerful and efficient than traditional ANOVA approaches, as regression analyses require fewer degrees of freedom and parameters for analysis. Second, as ecological research continues to move towards computational approaches and an emphasis on the utilization of data to improve models (Medlyn et al. 2015), the time for the advent

of regression experiments may be ripe. Specifically, data produced from these experimental designs can be readily incorporated into ecological models (Cottingham et al. 2005), while at the same time avoiding the pitfalls of temporal and spatial approaches. By lowering replication per treatment level and increasing the number of treatment levels, regression experiments result in a treatment *gradient* that can simultaneously achieve two key advances over ANOVA designs; 1) the ability to produce surface response of precipitation and ecosystem functions, and 2) the ability to explicitly incorporate multiple levels of climatic extremity in these gradients (Fig. 1.2b).

While it is unclear how often and in what form regression experiments have been utilized in ecological research since initials calls for its use in the early 2000's, it is clear this design has not been fully applied to climate extremes research. This is despite more recent calls in the literature for the need to impose gradients of climatic extremity in ecological experiments (Smith 2011, Kayler et al. 2015), further reflecting the potential utility of applying regression experiments to climate extremes research. Together, the limitations of spatial, temporal, and traditional experimental approaches with respect to predicting ecosystem responses to precipitation extremes have provided a substantial portion of the motivation for my dissertation research. At the same time, the clear utility of regression experimental designs has motivated the approaches I have utilized to answer my research questions and address current limitations. Below I provide an overview of my dissertation research with a summary of each chapter.

1.2 DISSERTATION OVERVIEW

The goal of my dissertation research has been to improve an understanding of how terrestrial ecosystems will respond to forecast changes in precipitation variability (e.g. altered rainfall patterns) and extremity (e.g. severe growing season drought). This goal has involved investigating the response of ecosystem functions (e.g. NPP and soil respiration) and the

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mechanisms underpinning those responses in order to achieve specific research objectives related to testing the predictions and mechanisms of current temporal models. To achieve my objectives, I utilized experiments in the field setting, long-term observational data, and a broad literature review. Below I outline in greater detail these components of my dissertation.

Focus on precipitation extremes. My dissertation, and the inferences produced, are primarily focused on predicted changes in precipitation variability, and in particular growing season precipitation. I chose to focus on precipitation for multiple reasons. First, because water is a primary limiting resource for terrestrial ecosystem productivity across much of the globe (Churkina and Running 1998; Fig. 1.1), changes to the dynamics of its availability – whether through patterns of its delivery (Knapp et al. 2002, Heisler-White et al. 2008, Craine et al. 2013, Wilcox et al. 2014, Gherardi and Sala 2015) or total/mean amounts (Huxman et al. 2004, Hoover et al. 2014) – are expected to have large consequences for the functioning of terrestrial ecosystems (Knapp et al. 2008, Allen et al. 2010, Reichstein et al. 2013). The role of precipitation as a key resource within terrestrial ecosystems also contrasts with temperature, which is classically viewed as a modifier of resource consumption (Tilman 1982) and has been shown to be less of a driver of ecosystem dynamics than water availability in the C₄ (heat-adapted) dominated grasslands of my research (Hoover et al. 2014, Hoover et al. 2017). Second, growing seasons are critical climate periods of biological activity within grasslands (Craine et al. 2013), and thus changes to the dynamics of water availability during such periods (e.g. May - August) can have large impacts on ecosystem dynamics. As a consequence, changes to growing season precipitation, and thus water availability is often viewed as the primary determinant in the structure and function of grassland ecosystems (Sala 1988, Knapp and Briggs 1995. Fig. 1.1), and informs my study systems and research approach.

Study systems. For my experimental research, my study systems were two climatically distinct grassland ecosystems of the central United States. In general, grasslands are highly responsive to precipitation change both within and among-years (Knapp and Smith 2001, Knapp et al. 2002, Heisler-White 2008, Wilcox et al. 2017), as water availability is viewed as the primary resource limiting productivity across this biome (Sala et al. 1988; Fig.1.1). This notion is confirmed through both spatial assessments relating within-biome net primary productivity and total annual precipitation amount (Sala et al. 1988), as well as site-based temporal relationships of interannual precipitation and productivity (Sala 2012), where both approaches yield an underlying linear relationship.

For the two field experiments I conducted, I selected two grassland ecosystems of the central US with differential sensitivity to precipitation change (Heisler-White et al. 2009, Knapp et al. 2015, Wilcox et al. 2015); the mesic tallgrass prairie of northeastern Kansas (Konza), and the semi-arid shortgrass steppe of northern Colorado (SGS). These ecosystems exhibit both similarities and differences in ecological characteristics, as both systems are generally water-limited and characterized by vegetation structure that is dominated in cover and productivity by perennial C_4 grasses. Yet importantly, key differences between these systems, such as soil texture and evaporative demand, are viewed as underpinning empirically observed differential sensitivity to precipitation change (Knapp et al. 2008).

Mean annual precipitation (MAP) of Konza is ~892 mm, while MAP of SGS is ~375 mm, with an opposite trend in atmospheric evaporative demand observed that reflects the east to west aridity and productivity gradient within the central US grassland biome (Sala et al 1988). A second key difference between these systems is soil texture. The mesic Konza is characterized by fine-textured soil and thus high soil water holding capacity, while SGS is defined by coarse textured

soils and thus low water holding capacity. These differences in evaporative demand and soil texture have critical implications for differences in the ecohydrology of these ecosystems and consequently productivity responses to precipitation (*sensu* inverse soil texture hypothesis; Sala et al. 1988) and thus future climate change (Heisler-White et al. 2009). For example, large rainfall events are observed to have rapidly diminishing productivity returns within Konza (Knapp et al. 2002), yet by contrast, can lead to increases in productivity within SGS (Heisler-White 2008) due to the alleviation of chronic water stress within these regions (Knapp et al. 2008). Such differences highlight the diversity of ecosystem types and responses to climate changes even within a single biome (Heisler-White et al. 2009, Wilcox et al. 2015), and underscore the importance of conducting site-level experiments across ecosystems to account for such contingency.

1.3 SUMMARY OF CHAPTERS

This dissertation consists of four research chapters in addition to this introductory chapter. In chapter 2, I apply the replicated regression experimental design within an intact, semi-arid grassland ecosystem located in the shortgrass steppe of Colorado (1.3b). I explore effects of a large growing season precipitation gradient on both vegetation structure and ecosystem functions (aboveground NPP (ANPP) and soil respiration), conducted in 2017. Within these regions, vegetation structural constraints have been posited and observed to impose a limitation on the response of aboveground ANPP to increases in precipitation (Laurenroth et al. 1992, Yahdjian and Sala 2006). This suggests than when precipitation extremes are experienced, an underlying nonlinear saturating response of ANPP to precipitation gradient (n =11 levels) resulted in and underlying linear response of ANPP, with this relationship conserved when related to soil moisture. Soil respiration responses to precipitation were weakly linear, yet more strongly nonlinear when related

to soil moisture. Both processes were more sensitive to positive, i.e., wet, precipitation extremes as opposed to severe drought (positive asymmetry). I observed unexpected evidence for rapid vegetation structural change not predicted by the hypothesis of "vegetation constraints". This shift, while unexpected, was driven by large increases in forb production at the wet ends of the precipitation gradient. As a result, positive asymmetry in forb production increased the sensitivity of this ecosystem to wet precipitation extremes, as well as the amount of variability explained in the underlying ANPP-precipitation relationship within this ecosystem.

In chapter 3, I utilize the same experimental design within a mesic grassland (Fig. 1.3a), focusing on the same key three components: vegetation structure, soil respiration, and ANPP across a precipitation gradient (n = 11 levels) that spanned the wettest to driest growing seasons in the 112-year record. Within mesic ecosystems, biogeochemical constraints, such as soil nitrogen or light resource co-limitation, are posited to constrain the response of ANPP to precipitation (Huxman et al. 2004). In contrast to this, I observed a linear relationship best explained the response of ANPP to both precipitation and soil moisture availability, while a nonlinear relationship was observed for soil respiration in response to both drivers. ANPP exhibited large positive asymmetry to precipitation extremes, while in contrast soil respiration exhibited near symmetrical responses to precipitation structure as a result of the precipitation manipulation. Thus, both semi-arid and mesic ecosystems were functionally similar in their responses to growing season precipitation amount and extremity, yet not in their structural, i.e., plant compositional, responses.

In Chapter 4, I utilize my experiment in mesic grassland (Fig. 1.3a) to explore the effects of another component of predicted climate change; changing rainfall patterns *within years*.

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Because both mean rainfall event size and the timing between events was relatively constant for a given total precipitation amount across the whole gradient for my experiment, this served as a "null model" for within-year rainfall patterns that was deployed across a gradient of total growing season amounts. I thus sought to compare the "uniform" experimental rainfall patterns to ambient patterns with regard to their effect on ecosystem productivity. Here, I focused on the rain use efficiency of ANPP (RUE), calculated as the change in ANPP (g/m²) per unit of total growing season rainfall (mm). I show that variable rainfall patterns have minimal effects on RUE during wet years, yet increasingly large, negative impacts on RUE during years of drought in this ecosystem. Analysis of rainfall patterns from the long-term site record during the driest years revealed that large rainfall events, in terms of their contribution to both rainfall variability and percentage of total precipitation, acted to reduce the RUE of ecosystem productivity during drought within this ecosystem.

Finally, in chapter 5 I conduct a literature review to gain a broader understanding of the impacts of climate extremes in both herbaceous-dominated and forest ecosystems. In this chapter, I explored how the stresses imposed by a variety climate extremes (not just precipitation) produce impacts through different levels of ecological organization, from individual physiology or growth to the ecosystem level, such as net primary productivity. I find a high degree of variability in responses at lower levels of organization, and thus a lack of reliability in predicting the ecosystem-level consequences of climate extremes from assessment of individual growth or physiology. Important mechanisms linked to high variability in individual, population and community-level response dynamics appear to often operate when an ecosystem is under climatic extremity, which can increase ecosystem stability in response to and/or recovery from climate extremes.

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1.4 FIGURES



Precipitation

Figure 1.1. Illustration of temporal versus spatial relationships of aboveground net primary productivity (ANPP) and precipitation (annual or growing season). Spatial gradients, which span an array of ecosystems, result in a steep ANPP-precipitation slope across water limited systems and a strong linear relationship across the grassland biome, the study system of my dissertation, confirming the primary role of precipitation in driving the functioning of grasslands. When incorporating the most mesic ecosystems (e.g. temperature forests), a saturating dynamic emerges between precipitation and productivity, as other resources become co-limiting to productivity. Temporal models, by relating interannual variability in precipitation. These models typically yield a linear relationship as best describing the relationship of ANPP and precipitation within-sites, with the steepness of the slope, and thus the sensitivity of ANPP to precipitation, decreasing in moving from water-limited to more mesic ecosystems.



Figure 1.2. Illustrative comparison of ANOVA versus regression-based experimental designs, specifically with respect to their application to climate change research. Traditional precipitation manipulation experiments have employed few factors (a), and thus have been primarily intended for analysis of variance (ANOVA), with the goal of addressing whether a process of interest significantly differs between discrete treatment levels of interest (e.g. drought and control). Yet the regression design, by imposing a treatment *gradient*, offers greater statistical power through regression analyses while also offering the potential to elucidate surface responses and relationship between a given climatic driver (e.g. precipitation) and ecological processes (e.g. ANPP).



Figure 1.3. The field experiments utilized in this dissertation research in the mesic tallgrass prairie (a) and the shortgrass steppe (b). These experiments occurred in consecutive years (2016 and 2017), with standardized experimental design, protocols, and data collection across sites.

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¹CHAPTER 2: SEMI-ARID ECOSYSTEM SENSITIVITY TO PRECIPITATION EXTREMES: WEAK EVIDENCE FOR VEGETATION CONSTRAINTS

2.1 OVERVIEW

In semi-arid regions, vegetation constraints on plant growth responses to precipitation (PPT) are hypothesized to place an upper limit on net primary productivity (NPP), leading to predictions of future shifts from linear to saturating NPP-PPT relationships as increases in both dry and wet PPT extremes occur. I experimentally tested this prediction by imposing a replicated gradient of growing season PPT (GSP, n = 11 levels, n = 4 replicates) – ranging from the driest to wettest conditions in the 75-year climate record - within a semi-arid grassland. I focused on responses of two key ecosystem processes: aboveground NPP (ANPP) and soil respiration. Both processes exhibited greater sensitivity to wet versus dry GSP extremes, with no evidence for a saturating relationship in the response of ANPP and soil respiration to GSP. Underlying these responses was rapid plant compositional change driven by increased forb production and cover as GSP transitioned from moderate to extreme wet conditions. This compositional shift increased both the sensitivity of ANPP to wet GSP extremes and the amount of variability explained in the underlying ANPP-GSP relationship. My findings challenge the hypothesis of vegetation constraints, and add complexity to predicting responses of semi-arid ecosystems in a future of intensified PPT extremes.

2.2 INTRODUCTION

Semi-arid regions exhibit high intrinsic sensitivity to precipitation (PPT) (Huxman et al. 2004, Haverd et al. 2016). This sensitivity can range from rapid plant physiological responses to

¹ In review at *Ecology*

small (< 5 mm) rainfall events (Sala and Lauenroth 1982) to regional increases in gross primary production during wet years (Haverd et al. 2016) that produces signatures on the global carbon cycle (Ahlstrom et al. 2015, Poulter et al. 2014). In the last decade, a major advance in understanding contemporary climate change has been increased confidence in attributing anthropogenic influences on the water cycle, updated to 'very likely' in the most recent AR [5] IPCC assessment. More specifically, gradual warming is expected to increase the frequency of wet and dry years and PPT extremes as the water-holding capacity of the atmosphere increases (IPCC 2013). These insights call for focused investigations concerning how semi-arid regions will respond to predicted changes in both precipitation means, extremes and variability, as this has clear relevance for understanding future carbon cycle dynamics that now extend from local to global scales.

A necessary step in projecting how terrestrial ecosystems will respond to changes in precipitation requires properly defined relationships of PPT and net primary productivity (NPP) (Knapp et al. 2017, Estiarte et al. 2016). Central to understanding carbon cycling in semi-arid regions is an understanding of the controls of aboveground NPP (ANPP) (Parton et al. 2012). Within semi-arid grasslands of North America, long-term data records, i.e. temporal models, indicate a linear relationship between interannual ANPP and PPT (Huxman et al. 2004, Sala et al. 2012), and a greater relative sensitivity of ANPP to wet versus dry years when compared to ANPP during years of average PPT (Knapp and Smith 2001, Wilcox et al. 2017). Although prior research suggests a high sensitivity of semi-arid ecosystems to changes in precipitation in general (Heisler-white et al. 2008, Haverd et al. 2016), an important limitation arises from the utilization of site-based long-term records to parametrize ANPP-PPT relationships that are tasked with projecting responses of these ecosystems to future climate change (Knapp et al. 2017).

Despite the labor and time-intensive (e.g. decades) nature of collecting data for temporal models, there is often a limited representation of statistically extreme climatic conditions (e.g. above and below the 99th and 1st percentiles, Smith 2011), relative to the entire historical (e.g. 100yr) distribution of climate variability within a region. This suggests that current temporal models may not be appropriate for predicting changes in precipitation extremes, particularly if climatic conditions with no historical analog are experienced. It has been proposed that when PPT extremes are included in these models, currently defined linear ANPP-PPT relationships may shift to nonlinear (Knapp et al. 2017). Such nonlinear responses to extremes may be particularly likely in semi-arid ecosystems, where meristem, tiller or general growth potential limitation are posited to impose a "vegetation constraint" on the response of ANPP to PPT (Knapp and Smith 2001, Yahdjian and Sala 2006, Reichman et al. 2013,), which is thought to underlie the weaker temporal versus spatial ANPP-PPT relationship (Lauenoth and Sala 1992, Sala et al. 2012). However, despite being considered a critical factor in ecosystem responses to PPT, tests of vegetation constraints are challenging and thus relatively rare (but see Yahdjian and Sala 2006). This raises questions as to both the nature and mechanisms of semi-arid responses to future increases in the magnitude of PPT extremes, as well as their directionality.

To improve understanding of semi-arid ecosystem responses to changes in PPT amount and extremity, I employed a novel experimental approach that exposed an intact semi-arid grassland ecosystem to an experimental gradient of PPT amount and extremity within a single growing season. Although ecologists have advocated replicated regression experimental designs when both the dependent and independent variable are continuous factors (Cottingham et al. 2005, Gotelli and Ellison 2013), only recently have these recommendations taken notice for their application to climate change research (Smith 2011, Kayler et al. 2015). In these experiments, statistical power is generated through the number of treatment levels and thus the gradient, rather than the number of replicates per level, however replication adds additional power (Cottingham et al. 2005). Utilizing this research approach, I directly imposed a gradient of growing season (June – August) PPT (GSP) amount and extremity (n = 11 levels, n = 4 replicates per level), ranging from the driest to wettest conditions ever recorded in the 75-year PPT record for the region. This replicated regression design allowed us to produce a dataset comparable to that of a replicated 11year long-term dataset used for a temporal model. Yet importantly, my design also allowed us to include multiple levels of precipitation extremity not included in current temporal models of ANPP-PPT within my study region.

My study sought to answer two key questions concerning the responses of two ecosystem processes - ANPP and soil respiration - to changes in both GSP amount *and* extremity: 1) are the relative sensitivities of these processes greater to extreme wet, i.e., 'positive asymmetry', versus dry, i.e., 'negative asymmetry' (Knapp et al. 2017), growing season conditions? And 2) do these processes exhibit linear or nonlinear responses to PPT and soil moisture when multiple levels of extremes are included? Despite evidence for positive asymmetry to nominal precipitation variability within this ecosystem (Knapp and Smith 2001), I hypothesized a greater relative sensitivity of these processes to the driest versus wettest GSP extremes after incorporating of multiple levels of extremity at both ends of the precipitation gradient. In concert with this negative asymmetry I expected to see an underlying nonlinear, saturating relationship of ANPP and soil respiration across the entire GSP and soil moisture gradient (Knapp et al. 2017), with the former driven by limitations of dominant grass growth potentials at the highest GSP inputs, indicative of hypothesized vegetation constraints.

2.3 METHODS

Study site. Field research was conducted at the Central Plains Experimental Range (formerly the Shortgrass Steppe LTER) located in northern Colorado (40.83° N 104.72° W) within an ungrazed (grazing removed in 2012) and unburned site. Relatively low but highly variable PPT defines the region, with mean annual PPT ~375 mm and mean annual temperature ~ 9.5° C (Knapp et al. 2015). The region is further characterized by coarse textured soils (average bulk density of ~ 1.41 g/m², Haverd et al. 1984), with vegetation structure and productivity controlled by perennial C₄ grasses, particularly the species *Bouteloua gracilis* (Burke and Lauenroth 2008) and *Buchloe dactyloides* within my study site.

Experimental design and treatments. I experimentally imposed both reductions and increases in GSP (Fig. 2.1A) from 1 June – 31 August 2017, relative to median levels of PPT for this time period (141.86 mm). More specifically, I utilized a replicated regression design (Cottingham et al. 2005, Gotelli and Ellison 2013) to produce an extensive and replicated gradient of PPT amount and extremity within a single growing season. There were 11 levels of GSP in my experiment, which included the 1st, 5th, 10th, 15th, 25th, 50th, 75th, 85th, 90th, 95th, and 99th percentiles of the long-term (1939 - 2014) growing season PPT record, calculated utilizing daily PPT data retrieved from the long-term climate dataset from the Central Plains Experimental Range headquarters weather station (supplemental data) and the quantile function in R.

Experimental plots were 2 x 2 m with a $1-m^2$ sampling plot located in the center, and thus 0.5 m buffer zone to account for any blow in and edge effects. Plots were arranged in a randomized complete block design (2 blocks) and were spaced ~2 m apart, with each block containing two replicates of each precipitation level and n = 4 replicates per each GSP percentile level in total. In mid-May of 2017, full roof polycarbonate rainout shelters (2.2 x 2.2 m) angled at a starting height

of 1 m sloped to ~ 0.8 m (against the prevailing westward winds) were installed to exclude ~100% of ambient rainfall. Water additions on all plots began the first week of June 2017, with each 4-m^2 sheltered plot watered weekly according to its GSP treatment level. Watering for GSP levels under the 50th percentile occurred over one day, while all other levels were watered over two days in equal amounts to avoid excessive lateral flow. Watering occurred in the evenings to minimize evaporative losses and was conducted by hand utilizing a gas-powered water pump according to methods of Felton et al. (In review). Water was supplied from a regional water delivery service and stored in on-site tanks (Mcdonalds Farms INC., Frederick, CO).

Abiotic data. To estimate the mean impacts to growing season soil moisture availability across the experimental precipitation gradient, I repeatedly sampled soil volumetric water content to 20 cm depths within each plot from 20 June – 28 August of 2017. Measurements were taken once weekly before water additions within the center of each 1-m^2 sampling plot utilizing a portable soil moisture probe (Hydrosense II, Campbell Scientific, Logan UT). These weekly measurements were also taken at the same time as soil CO₂ flux measurements. Soil moisture probe values were calibrated to site-level soil conditions utilizing collected soil samples of known gravimetric water content and bulk density. *In situ* plant inorganic nitrogen (N) availability was assessed during the middle of the 2017 growing season (3 July – 11 July 2017). Plant N availability was measured utilizing portable anion and cation exchange membrane probes (Western Ag Innovations Inc., Saskatoon, Canada). The membrane of these probes was vertically inserted ~5 cm into the soil profile, and remained in the soil for the time period 3 July – 11 July 2017 in order to allow exposure to one rainfall event for each treatment level.

Carbon cycle data. To estimate the response of soil respiration, I conducted measurements of *in situ* soil CO₂ flux. Soil CO₂ flux measurements were taken mid-day (1100-1400) every two

weeks for the time period 20 June to 16 August of 2017 utilizing a LI-6400-09 portable gas exchange system (LI-COR Biosciences, Lincoln, Nebraska, USA). Measurements were taken from a 10-cm diameter poly vinyl chloride (PVC) collar inserted 10 cm into the soil profile within the same corner of each $1-m^2$ sampling plot. Collars were installed in late May of 2017. To minimize confounding temporal effects, the order of measurements was alternated each sampling campaign (e.g. plot 1 to 44 versus plot 44 to 1). Duration of each measurement was partly contingent on flux values (e.g. larger flux = longer duration of measurement), yet was typically near one minute. Prior to measurements, any aboveground plant biomass inside the collars was clipped and removed to isolate soil CO₂ efflux.

Aboveground net primary productivity (ANPP) was estimated at the end of the 2017 growing season in early September. ANPP was measured by clipping all aboveground vegetation to the soil surface within two 0.1-m^2 quadrats located in the center of each 1-m^2 sampling plot. After clipping, biomass was dried at 60°C for at least 72 hours and then sorted in the lab to separate previous and current-year graminoid and forb biomass. After sorting, biomass was weighed to the nearest 0.01 g and the two quadrat values from each plot were averaged to yield a single plot value for ANPP. I assessed community composition at the end of the 2017 growing season (first week of September) within each 1-m^2 sampling plot for both the extreme dry (1^{st} and 5^{th} , n = 8) and wet treatments (95^{th} and 99^{th} , n = 8) as well as the 50^{th} percentile level (n = 4). Composition was assessed aerially as percent cover of each plant species to a resolution of 1%.

Statistical analyses. Treatment impacts to soil moisture were quantified using linear regression, with mean soil moisture regressed against total PPT amount. The same approach was utilized to relate PPT and soil moisture to soil N levels. I utilized two metrics to quantify the sensitivity of ANPP and soil respiration to wet versus dry GSP extremes. First, I conducted

Cohen's D effect sizes (pooled standard deviation) of the mean analyses, calculating the divergence of dry (1^{st} and 5^{th} percentile combined) and wet (95^{th} and 99^{th} percentile combined) extremes from 'nominal' levels of ppt ($15^{th} - 85^{th}$ percentiles combined) for both ANPP (grass + forb) and soil respiration. Effect size magnitude thresholds – which can be positive or negative - were classified according to Cohen (1992). Second, I defined 'asymmetry' to GSP extremes as:

$$a_p = \left(\left(\overline{F}_{+p} - \overline{F} \right) - \left(\left(\overline{F} - \overline{F}_{-p} \right) \right) / \overline{F}$$

Where \overline{F} represents the mean value of responses between the 15th and 85th percentiles (i.e., nominal variability) while \overline{F}_{+p} and \overline{F}_{-p} represent the mean values at the 95th and 99th percentiles and the 5th and 1st percentiles (i.e., extremes), respectively. A positive value indicates that the absolute response (increase) was greater for extreme wet conditions (positive asymmetry), while a negative value indicates the response (decrease) was greater for extreme dry conditions (negative asymmetry), relative to nominal variability. Consistent with effect sizes, I calculated a_p for both ANPP (grass + forb) and soil respiration. However, I further partitioned my ANPP a_p calculation into grass and forb functional group ANPP responses. To evaluate if carbon cycle responses to PPT and soil moisture were best explained by linear or nonlinear relationships, I tested whether linear or nonlinear least squares regression models best fit the responses for ANPP (grass alone and grass + forb) and soil respiration. I used Akaike's information criteria (AIC) model weights as MY metric of model fits. Outliers were identified for model selection utilizing outlier tests with Bonferroni adjusted P-values for both types of ANPP and soil respiration responses to GSP and soil moisture separately.

I used permutational multi-variate analysis of variance with Bray-Curtis distance metrics, and additionally similarity percentages, to determine if the GSP treatment subsets affected plant community composition. These subsets included extreme dry (combined 1st and 5th percentiles,

median (50th percentile), and extreme wet (combined 95th and 99th percentiles) portions of the GSP gradient. All analyses were conducted within the R statistical software environment (R 3.2.1 GUI 1.66 Snow Leopard build).

2.4 RESULTS

My experimental GSP gradient resulted in a significant gradient of mean plot-level soil moisture availability (P < 0.001, $R^2 = 0.89$, Fig. 2.1A), with a weak effect of GSP or soil moisture on mid-season soil nitrogen availability (Fig. 2.2). However, I was unable to detect an effect of GSP or soil moisture on mid-season soil nitrogen availability. Soil respiration exhibited positive asymmetry to precipitation extremes (Fig. 2.3A inset), with a greater relative sensitivity to wet versus dry extremes ($a_p = 0.09$, Fig. 2.3a inset). This result is consistent with the medium versus large effect sizes for respiration responses to dry (-0.74) versus wet (0.92) extremes, respectively. ANPP exhibited evidence for larger positive asymmetry than soil respiration, again with a similar trend observed in effect sizes (Fig. 2.4). More specifically, while both wet and dry extremes exhibited large effect sizes (>0.08) in ANPP relative to ANPP at nominal (15th - 8th percentile) inputs, the magnitude of the effect was largest for wet extremes (Figure. 2.4). Partitioning a_n values into grass versus forb ANPP responses revealed dramatically greater positive asymmetry of forb ($a_p = 0.68$) than grass ANPP ($a_p = 0.13$), primarily due to near zero productivity at severe drought. As a consequence, the high sensitivity of forbs to wet extremes operated, in part, to increase the positive asymmetry of total ANPP ($a_p = 0.18$, Fig. 2.4b).

Soil respiration exhibited significant responses to both GSP and soil moisture gradients (Fig. 1). For responses to GSP, there was weak evidence against a linear relationship (Fig. 2.3a, Table 2.1). However, there was strong support in favor of a nonlinear relationship when related to soil moisture availability (Fig. 2.3b, Table 2.1). For ANPP, a greater amount of variability in the
response to PPT was explained when including both grass and forb responses ($r^2 = 0.55$) versus the response of grass ANPP alone ($r^2 = 0.47$). A similar result was observed for responses to soil moisture, which explained more variability in ANPP than GSP (Fig. 2.5). AIC model weights indicated no evidence for a nonlinear model in the response of ANPP to precipitation and soil moisture. This result was consistent when analyzing forb + grass ANPP or grass ANPP alone (Table 4.2), providing no evidence against a linear relationship of ANPP with GSP.

By the end of the growing season, plant community composition differed between extreme dry versus wet GSP treatments (P = 0.078; Fig. 2.6). Similarity percentages showed that compositional differences between extreme dry and wet tails were driven by differences in the cover of the two C₄ grasses that dominate throughout the site, *B.gracilis* and *B.dactiloyides*, yet also the biennial invasive forb *Melilotus officinalis*. Similarity percentages also suggest that the transition to increasing forb cover - primarily the biennial invasive *M.officinalis* - occurred in between moderately and severely wet conditions. For example, the cover of *M.officinalis* averaged 0.5 and 4.25% in extreme dry and median plots, respectively, while averaging 29.62% in extreme wet plots. This dynamic is further supported by the high positive asymmetry of forb ANPP and in total suggests that increases in forb cover and productivity occurred 1) under extreme wet conditions and 2) were driven primarily by a single forb species.

2.5 DISCUSSION

Predictions of future increases in wet and dry years and PPT extremes have led to growing interest in how such changes in PPT may influence current understanding of relationships between ANPP and PPT, leading some to suggest shifts from currently defined linear ANPP-PPT relationships towards an underlying nonlinear relationship (Estiarte et al. 2016, Knapp et al. 2017). Within semi-arid ecosystems, vegetation constraints have been hypothesized (Lauenroth and Sala 1992, Sala et al. 2012) and observed (Yahidjian and Sala 2006, Reichmann et al. 2013) as a key mechanism limiting ANPP, particularly with respect to increases in PPT (Yahdjian and Sala 2006). Such constraints invoke meristematic, tiller, leaf area, and overall growth limitations of dryland vegetation to water availability, and thus a potential for saturation in ANPP responses under increases in both dry and wet PPT extremes (Estiarte et al. 2016, Knapp et al. 2017). In contrast to my hypothesis of greater a relative sensitivity in ANPP and soil respiration to dry versus wet GSP extremes, I find clear evidence of positive asymmetry of these ecosystem processes to GSP extremes. In addition, I find no evidence to reject an underlying linear relationship of these two ecosystem processes with GSP within a semi-arid grassland.

Both my metrics of asymmetry in ANPP and soil respiration responses to GSP extremes yielded similar conclusions, that is, of a greater relative sensitivity to extreme wet versus dry growing season conditions. Despite hypothesizing negative asymmetry to GSP extremes, my ANPP result is consistent with previous findings within semi-arid grassland regions to nominal PPT variability (Knapp and Smith 2001, Haverd et al. 2016, Wilcox et al. 2017, but see Zhang et al. 2017), attributed to the low mean productivity and pulse-response behavior of semi-arid vegetation to PPT (Huxman et al. 2004, Haverd et al. 2016). Positive asymmetry in ANPP was evident in both grass and forb functional groups, yet this positive asymmetry was far higher for forbs, both in cover (Fig. 2.6) and productivity (Fig. 2.4). Despite the variable contribution of forbs to ANPP across plots, the high sensitivity of forbs to wet conditions detectably increased the positive asymmetry of total ANPP to GSP extremes (Fig. 2.5). Therefore, rapid compositional change occurring within one growing season increased the sensitivity of total ANPP within this ecosystem to GSP and in particular wet extremes (Fig. 2.4).

Less tested and thus understood is the relative sensitivity of semi-arid soil respiration to PPT extremes. Zhang et al. (2017) found greater sensitivity of soil respiration to decreases than increases in precipitation in the semi-arid steppe of China, however their results may reflect baseline differences in aridity (higher in North American steppe) and thus ecohydrology between Inner Mongolian and North American semi-arid grasslands. Growing season conditions within the semi-arid steppe of Colorado are defined by chronic water stress that is periodically relieved by rainfall events (Lauenroth and Bradford 2006). Munson et al. (2010) found soil respiration within the semi-arid steppe of North America to increase with increasing rainfall event size, though their range of event sizes (2 -10 mm) was smaller than my study (3 - 22 mm). Net carbon losses from soils via physical displacement of CO_2 , mineralization, and microbial growth (Huxman et al. 2004) tend to immediately follow rainfall events in semi-arid regions (Parton et al. 2012), underscoring the pulse-response behavior of carbon fluxes within semi-arid regions to rainfall events (Nor-meir 1972). Moreover, because ANPP within the shortgrass steppe can increase with rainfall event size - independent of total GSP amount (Hesiler-White et al. 2008) - it is not surprising that soil respiration would also exhibit positive asymmetric responses to GSP extremes, particularly given that the majority of carbon within these regions is stored belowground (Burke and Lauenroth 2008).

Although it is clear that vegetation structure changes over large spatial and climate gradients (Huxman et al. 2004, LaPierre et al. 2016, Knapp et al. 2017), I find evidence for the potential of rapid within-site compositional change, here driven by the response of an opportunistic, non-native forb species to consistently wet growing season conditions. Rapid compositional shifts in response to increased resource availability were documented in earlier studies within this grassland (Hyder 1975, Laurenroth and Dodd 1978), suggesting that plant

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community structure in semi-arid regions is dynamic and can fluctuate with resource variability. Underlying this may be, in part, the high a prevalence of bare ground microsites embedded in plant communities within semi-arid systems (Vinton and Burke 1995), which can result in both low light limitation and space for opportunistic species to take advantage of resource pulses, particularly increases in soil moisture availability.

Interactions between resource pulses and opportunistic species underlies the fluctuating resource hypothesis of plant invasion (Davis et al. 2000), and here was found to influence both the sensitivity of ecosystem ANPP to GSP extremes and the ANPP-GSP relationship (Fig. 2.5). Yet the small AIC differences between linear and nonlinear ANPP-GSP models (despite greater degrees of freedom in the nonlinear model), suggests a potential emergence of a nonlinear relationship given a longer duration or greater magnitude of dry and/or wet PPT extremes, as my manipulation occurred during a small yet critical climate period (June - August). Nevertheless, my findings here of rapid compositional change challenges the hypothesis of vegetation constraints of ANPP within drylands (Yahdjian and Sala 2006), and underscores the value of site-based experiments to account for ecological contingencies may occur during climatically extreme years.

Relating ANPP and soil respiration to soil moisture can add clarity to productivity responses of semi-arid regions to wet years. Whereas soil respiration exhibited a saturating relationship with soil moisture (Fig. 2.3), total ANPP (grass + forb) showed no clear signs of saturation (Fig. 2.5B), which can drive large gains in ANPP during wet years (Knapp and Smith 2001, Haverd et al. 2016). My results thus indicate that the high sensitivity of this ecosystem to wet years can have clear implications for an understanding of carbon cycle dynamics within drylands. Such sensitivity has relevance not only within drylands, as non-palatable forb productivity may be facilitated during wet years, yet also to global scales as these regions continue

to drive variability in the land CO_2 sink (Poulter et al. 2014, Ahlstrom et al. 2015). As a consequence, I suggest that a deeper understanding of the contingencies driving carbon cycle dynamics within semi-arid regions amid future changes in PPT extremes is a particularly pressing research need.

In conclusion, utilizing a replicated regression experimental design, I assessed the sensitivity of an intact semi-arid ecosystem to an extreme GSP gradient within a single growing season, ranging from the driest to wettest conditions in the historical record. My results provide evidence for greater relative sensitivity in both ANPP and soil respiration responses to wet versus dry GSP extremes within a semi-arid grassland. Limitations in the growth potential of dryland vegetation, such as through low plant densities, have been hypothesized to impose a constraint on ANPP responses to PPT increases (Yahdjian and Sala. 2006, Sala et al. 2012), which in turn could shift the ANPP-PPT relationship towards a nonlinear, saturating dynamic under future increases in the magnitude of PPT extremes (Knapp et al. 2017). However, I found no evidence to reject a linear ANPP-GSP relationship, and that the ANPP-GSP relationship can be impacted by rapid plant compositional change during wet years. This result appears to be, in part, driven by the inherent positive asymmetry of ANPP to GSP extremes (Fig. 2.4), which was magnified by increased forb productivity and cover at the wet end of the GSP extremity gradient. I posit saturating versus linear responses of soil respiration and ANPP to soil moisture, respectively, drives large productivity gains during wet years in semi-arid regions (Poulter et al. 2014). As a result, the high sensitivity of this semi-arid ecosystem to extreme wet years - both in structure and function – indicates large increases in productivity, with implications for understanding carbon cycle dynamics within these regions.

2.6 TABLES

Process	Driver	Model	DF	AIC	Weights	R-squared
Soil respiration Soil	Precipitation	Linear	3	703.061	0.58	0.28
respiration	Precipitation	Nonlinear	4	703.75	0.42	
respiration	Soil moisture	Linear	3	594.42	0.06	0.53
respiration	Soil moisture	Nonlinear	4	588.90	0.94	

Table 2.1. Model summaries of soil respiration responses to precipitation and soil moisture

 Table 2.2. Model summaries of ANPP responses to precipitation and soil moisture

Process	Driver	DF	Model	AIC	Weights	R-squared
ANPP grass +						
forb	Precipitation	3	Linear	374.48	0.62	0.55
ANPP grass +						
forb	Precipitation	4	Nonlinear	375.44	0.38	
ANPP grass +						
forb	Soil moisture	3	Linear	385.98	0.60	0.60
ANPP grass +						
forb	Soil moisture	4	Nonlinear	386.81	0.40	
ANPP grass	Precipitation	3	Linear	359.093	0.65	0.47
ANPP grass	Precipitation	4	Nonlinear	360.93	0.35	
ANPP grass	Soil moisture	3	Linear	372.88	0.69	0.53
ANPP grass	Soil moisture	4	Nonlinear	374.44	0.31	

2.7 FIGURES



Figure 2.1. (A) Relationships between percentiles from the long-term (75-year) June-August Precipitation record and precipitation amount, which was experimentally added. (B) The impact of precipitation amount added on soil moisture availability in the upper 20 cm of the soil profile (\mathbb{R}^2 of mean response to precipitation amount = 0.89). Error bars denote the standard error of the mean.



Figure 2.2. (A) Relationships between precipitation amount and inorganic soil nitrogen (N) availability in the upper layers (top 5 cm) of the soil profile. Soil nitrogen (summed NO₃⁻ and NH₄⁺) is expressed as *u*gN absorbed per 10 cm per week. (B) Relates average soil moisture availability in the upper 20 cm of the soil profile with soil nitrogen availability. For both of these regressions, there was evidence that the influence of water availability impacted nitrogen availability (Precipitation; P = .075, Soil moisture; P = .022), yet for each metric, water availability explained a low percentage of variation in nitrogen soil availability (Precipitation; R² = .052, Soil moisture; R² = .10).



Figure 2.3. Relationship of soil respiration with growing season precipitation (GSP; June – August) and soil moisture. (A) relates mean values of soil respiration total GSP amounts. Error bars denote the standard error of the mean. Inset shows the positive asymmetry of soil respiration to GSP extremes, indicative of a greater relative sensitivity to wet versus dry GSP extremes. (B) relates flux values to soil moisture availability to 20 cm depths. Although there was no evidence against a linear fit for responses to GSP, a clear nonlinear saturating relationship was supported for soil respiration responses to soil moisture (Table S2).



Figure 2.4. Quantification of the type and magnitude of ANPP responses to dry versus wet growing season precipitation (GSP) extremes. For both graphs the mid-line represents nominal GSP amounts (between $15^{\text{th}} - 85^{\text{th}}$ percentiles). (A) depicts the magnitude of effect (Cohen's D effect size) that each extreme had relative to values at nominal levels of GSP variability. Error bars denote 95% confidence intervals while grey lines denote the cutoff for 'large' effect sizes at +/- 0.8. (B) Depicts the type of ANPP asymmetry to GSP extremes, which in all cases suggests a greater relative sensitivity to extreme wet vs. dry years.



Figure 2.5. Response of aboveground net primary productivity (ANPP) to growing season precipitation (GSP) and soil moisture gradients during the 2017 experiment, where in all cases a linear model was the best fit of the relationship (Table S1). I separated ANPP into grass (C, D) and grass + forb (A and B) responses. Overall, ANPP exhibited consistent evidence for linear responses to both metrics of water availability (A – D), yet there was evidence that incorporating the responses of forbs considerably increased the variance explained in ANPP responses to both GSP (A vs. C) and soil moisture (B vs. D).



Figure 2.6. Nonmetric multi-dimensional scaling of plant communities within the three treatment subsets: Extreme dry, median, and extreme wet growing season precipitation (GSP). By the end of the growing season, there was evidence of community divergence (see results). This divergence was driven, in part, by both variability in the cover of the dominant grasses yet most notability by increased in the cover of the biennial, non-native forb *M.offinialis*. Similarity percentages demonstrated this transition primarily occurred between the median and extreme wet conditions, as opposed to extreme dry to median levels of GSP.

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²CHAPTER 3: CARBON CYCLE RESPONSES WITHIN A MESIC GRASSLAND TO AN EXTREME GRADIENT OF PRECIPITATION

3.1 OVERVIEW

Growing evidence indicates that ecosystem processes may be differentially sensitive to dry versus wet years, and that current understanding of how precipitation affects ecosystem processes may not be predictive of responses to precipitation extremes. In an experiment within a mesic grassland, I addressed this uncertainty by assessing the responses of two key ecosystem processes - aboveground net primary production (ANPP) and soil respiration - to an extreme gradient of growing season precipitation amount and extremity. In this experiment, I imposed 11 precipitation amounts within a single growing season, ranging from the lowest to highest amounts recorded in the 112-year historical record (1^{st} to 99th percentiles, n = 4 replicates per level). Across treatments, this experimental precipitation gradient linearly increased soil moisture availability in the rooting zone (upper 20 cm). ANPP sensitivity was greatest to extreme increases in precipitation, with an underlying linear response to both the precipitation and consequent soil moisture gradient. By contrast, soil respiration responses to extremes were symmetrical with near equally large responses to both positive and negative precipitation extremes, yet a clear saturating response to increasing precipitation and soil moisture. These results highlight the differential of sensitivities of production and respiration to positive versus negative precipitation extremes at the site level. Identification of such differential sensitivities among these two ecosystem processes, and the consequences this has for their underlying relationships with precipitation, is critical for the parameterization of models

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charged with forecasting the dynamics of ecosystem processes amid predicted increases in precipitation extremes.

3.2 INTRODUCTION

A key climate change prediction is an increase in the interannual variability of precipitation, with consequent increases in the frequency and severity (or extremity) of dry and wet years (IPCC 2012). Such changes to precipitation regimes are expected to differentially impact terrestrial carbon cycling dynamics (Ciais et al. 2005, Knapp et al. 2008, Reichstein et al. 2013, Shi et al. 2013, Poulter et al. 2014, Ahlstrom et al. 2015, Frank et al. 2015). Indeed, there is growing evidence that ecosystem processes, such as primary production, may be more sensitive to dry versus wet years (*negative asymmetry*) or vice versa (*positive asymmetry*; Knapp and Smith 2001, Wu et al. 2011, Haverd et al. 2016, Wilcox et al. 2017). However, current understanding of how precipitation affects ecosystem processes (derived from spatial or temporal relationships) does not fully incorporate the potential for such asymmetric responses, particularly in response to *extremes*. As a consequence, it is evident that our ability to project how ecosystem processes will respond to predicted changes in precipitation is constrained by a limited understanding of the impacts of climatically extreme dry *and* wet years.

While there is increasing evidence for positive asymmetry - a greater relative response to wet vs. dry years (Knapp and Smith 2001, Wu et al. 2011, Haverd et al. 2016, Wilcox et al. 2017), there is still limited evidence for negative asymmetry - a greater relative response to dry vs. wet years (Zscheliger et al. 2014, Zhang et al. 2017). Nevertheless, such asymmetric responses to interannual precipitation variability provide support for the notion that production responses may have the potential to diverge from the consistently linear prediction of temporal models based on long-term relationships between interannual precipitation variability and production (Huxman et

al. 2004, Sala et al. 2012). This divergence from previously defined linear relationships may be particularly pronounced when precipitation deviations become extreme (Knapp et al. 2017a), such as beyond the 5th and 95th percentiles of the historical record (Smith 2011). However, temporal models often do not include such extreme values, given that temporal records of both precipitation and production are limited in duration and thus their representation of climatic variability, extremity, and the consequent ecological responses. Because of such limitations, novel approaches to assess the sensitivity of ecosystems to future changes in precipitation that include both positive and negative extremes are needed (Smith 2011, Knapp et al. 2017b).

Over a single growing season, I exposed an intact, mesic grassland ecosystem to an experimental gradient of precipitation amount and extremity. Utilizing a replicated regression experimental design (Cottingham et al. 2005, Gotelli and Ellison 2013), this gradient ranged from the 1st and 99th growing season precipitation percentiles of the 110-year record, employing 11 levels with four replicates per each level (Fig. 1). This experimental design allowed us to test - for the first time - the sensitivity of an intact ecosystem to large changes in precipitation *within a single growing season*. My goals were to 1) assess whether the magnitude of impacts on ANPP and soil respiration differed between extreme negative vs. positive deviations in precipitation (evidence for asymmetry), and 2) test the temporal model prediction that ANPP, and additionally soil respiration, exhibits a linear relationship with precipitation, with an emphasis on the distributional tails, i.e., extremes, of the 110-year precipitation record.

Because my experiment occurred within a mesic grassland, I hypothesized that impacts to ANPP and soil respiration would be greatest in response to extreme drought relative to positive (wet) extremes, and thus that these processes would exhibit negative asymmetry in response to precipitation extremes. I expected this negative asymmetry to be driven by the dominant control and limitation of soil moisture availability under extreme drought in this ecosystem (Hoover et al. 2014), and the hypothesized increased importance of other resource co-limitations, such as nitrogen and light, as soil moisture limitation is eliminated under extreme wet conditions (Huxman et al. 2004). Finally, with the specific inclusion of precipitation extremes in the experimental gradient (e.g. 1st, 5th, 95th and 99th percentiles), I expected to see nonlinear, saturating responses emerge across the precipitation gradient in both carbon cycling processes that deviates from the linear prediction of the temporal model.

3.3 METHODS

Experimental site. This experiment was conducted at the Konza Prairie Biological Station during the and 2016 growing season (May - August, Fig. 1a). The Konza Prairie is a 3487-ha biological reserve of native unplowed tallgrass prairie located in the Flint Hills region of northeastern Kansas. This region is characterized by warm, wet growing seasons and cold, dry winters. Mean annual temperature at the Konza prairie is ~13° C, while mean annual precipitation is ~892 mm, of which that vast majority occurs during the growing season. I selected an upland, annually burned watershed with fine-textured florence soils (bulk density of ~1 g/cm³) to conduct the experiment. Mean daily potential evapotranspiration during the manipulation period was 4.89 mm/day (AWE01 Konza LTER dataset). The plant community composition of this upland sites is dominated by rhizomatous perennial warm-season C₄ grasses, in particular the species *Andropogon gerardii, Sorghastrum nutans* and *Schizachryium scoparium*, with lesser abundant forb and graminoid species contributing to the majority of plant species richness (Knapp et al. 1998).

Experimental design and treatments. I used a replicated regression experimental approach (Cottingham et al. 2005, Gotelli and Elison 2013) within a randomized block design (n = 2 blocks,

n = 2 replicates per treatment per block) to produce a gradient of growing season precipitation amount. In these experimental designs, statistical power is generated primarily from the treatment gradient, and thus the number of levels, rather than the number of replicates per treatment levels, with regression analyses also requiring fewer degrees of freedom than traditional few-factor ANOVA designs (Cottingham et al. 2005). However, adding replication to each precipitation level (n = 4) added increased statistical power to my experimental design and subsequent analyses. Each precipitation level corresponded to a specific percentile of the 1900 - 2012 daily precipitation records for Manhattan, KS from the NOAA National Climatic Data Center (now Global Historical Climatology Network) and additionally the Kansas State University Weather Data Library (see Hoover et al. 2014). Precipitation levels ranged from the 1st (driest) to the 99th (wettest) percentiles of the 112-year record. Percentiles were calculated for total precipitation amounts from the time period May 7^{th} – August 31^{st} utilizing the quantile function in R. The precipitation gradient ranged from under 200 mm to over 1000 mm, with 11 levels in total (Fig. 1b). When compared to how data is produced through temporal approaches (using interannual precipitation amounts), my experiment gradient is comparable to 11 years-worth of data produced within a single growing season.

The target precipitation percentile amounts were achieved utilizing 100% rainfall exclusion shelters deployed on a large scale (Fig. 1a). Polycarbonate roofs (2.2 x 2.2 m) were mounted on to four fence T-posts to exclude all ambient rainfall. Shelter roofs were sloped from a height of 100 cm to \sim 70 cm to allow for rainfall drainage into gutters attached to tubing, which shunted rainfall away from the study site. Experimental plots were 2 x 2 m with a nested 1 x 1 m sampling plot, which produced a \sim 0.7 m buffer zone. Experimental plots were spaced 2 m apart, with all shelters sloped in the same direction (west) against the prevailing winds. I simulated rainfall events on a

weekly basis by conducting water additions, with amounts varying each month according to monthly differences in precipitation amount based on the long-term 112-year record. Monthly amounts were calculated by multiplying the long-term monthly mean by the percent difference of each growing season precipitation percentile from the growing season mean. This approach resulted in an efficient way to achieve total growing season precipitation percentile amounts. Water additions were performed in the evening (after 17:00) to minimize evaporative losses, and were accomplished utilizing a gas-powered water pump connected to nearby water tanks filled with water supplied from a local aquifer. I utilized flow meters (Great Plant Industries, Wichita, KS) to measure the amount of water to add to each plot, converting mm to gallons per 4-m². All plots under the 50th precipitation percentile were watered over one day, while all plots in the 50th percentile and above were watered over two days to avoid excessive overland flow.

Soil volumetric water content was repeatedly measured during June - August to 20 cm depths, where the bulk of root biomass is located in upland sites within this ecosystem (Nippert et al. 2012). Soil moisture measurements were taken utilizing a portable Hydrosense II moisture sensor (Campbell Scientific, Logan UT), and were measured randomly within the 1-m² sampling plot once per week prior to water additions. Calibrations were performed by comparing probe values to known gravimetric water content values from soil samples within the site across a range of moisture levels following the methods of Dietrich and Smith (2016) and Wilcox et al. (2015). In addition, I also assessed changes to photosynthetic active radiation, soil inorganic nitrogen availability and net photosynthesis of the dominant grass (ESM1 for detailed methods).

Carbon cycle responses. Aboveground net primary production (ANPP) was estimated at the end of the growing season in early September of 2016. Due to this site being burned annually every spring, assessing ANPP provided strong inference about the impacts of the treatments on

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primary production. To estimate ANPP, all aboveground biomass was clipped at ground level within two 0.1-m² quadrats located in the center of each 1-m² sampling plot. The two measurements for each plot were then averaged. Aboveground biomass was field-sorted to graminoid, forb and woody plant functional groups. Biomass was then immediately dried at 60°C for 48 hours and weighed to the nearest 0.01 g. Woody biomass, which represented a small proportion of total ANPP, was excluded from data analysis.

Measurements of *in situ* soil respiration were taken every two weeks in June, July and August of 2016. A LI-8100 portable gas exchange system (LI-COR Biosciences, Lincoln, Nebraska) was used to take measurements from two locations in each plot. At the beginning of the growing season (late April), two PVC collars (10 cm diam.) were installed diagonally in opposite corners within each nested $1-m^2$ sampling plot. Measurements occurred at least three days after water additions. On the day prior to measurements, any aboveground plant biomass inside the collars was clipped and removed to isolate CO_2 efflux. Flux values were recorded over a 45 second period, with measurements taken between 11:00 and 14:00. Soil moisture and temperature measurements were taken at the same time as soil respiration. Soil temperature was measured to 10 cm depths at the center of each sampling plot utilizing a thermocouple attached to the LI-8100 gas exchange system.

Plant community composition was assessed in 2016 via aerial percent cover estimates during early September. Percent aerial cover was estimated to the nearest 1 or 5% for each species separately, following the methods of Koerner et al. (2014).

Statistical analyses. I utilized two approaches to quantify asymmetry in carbon cycle responses to positive versus negative precipitation extremes. Similar to Haverd et al. (2016), I defined asymmetry as:

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$$a_p = \left(\overline{F}_{+p} - \overline{F}\right) - \left(\overline{F} - \overline{F}_{-p}\right)/\overline{F}$$

Where \overline{F} denotes the mean value of responses between the 15th and 85th precipitation percentiles (i.e., nominal variability), while \overline{F}_{+p} and \overline{F}_{-p} denote the mean values at the 95th and 99th percentiles and the 5th and 1st percentiles (i.e., extremes), respectively. A positive value indicates that the relative response was greater for extreme wet conditions (positive asymmetry), while a negative value indicates the relative response was greater for extreme dry conditions (negative asymmetry). To compliment this approach, I calculated Cohen's D effect sizes (pooled standard deviation) for the same precipitation levels, quantifying the effect sizes for *both* wet and dry precipitation extremes.

To evaluate if carbon cycle responses to precipitation and soil moisture were predominantly linear or nonlinear, I tested whether linear or nonlinear least squares regression models best fit the responses of ANPP and soil respiration to both precipitation amount and soil moisture availability. I used Akaike's information criteria (AIC) model weights to provide inference on linear versus nonlinear model fits. I utilized a linear mixed effect model framework (Ime function, MASS package) for model selection, which allowed me to treat plot nested within block as the random effect for both ANPP and soil respiration. I conducted backward model selection (dropterm function, MASS package) and AIC values as my selection criteria. For ANPP, the full model included mean soil moisture availability to 20 cm depths, light availability in August, soil inorganic nitrogen availability during mid-July and net photosynthesis of the dominant grass. Residuals were assessed for normality, while outliers and/or influential observation were assessed via outlier tests with Bonferonni adjusted P-values (P < 0.05 cutoff).

I used permutational multivariate analysis of variance with Bray-Curtis distance analyses and similarity percentages to assess plant community composition among previously defined categories of the precipitation levels. More specifically, these subsets included extreme dry (1 - 5th percentile), nominal (15 - 85th percentiles), and extreme wet (95th - 99th percentiles). All analyses were conducted within the R statistical software environment (R 3.2.1 GUI 1.66 Snow Leopard build).

3.4 RESULTS

Mean soil moisture availability in the upper 20 cm of the soil profile increased linearly with precipitation amount ($R^2 = 0.66$, Fig. 3.1b inset), confirming my experimental manipulation produced a gradient of plant and microbial water availability. In terms of the tails of the precipitation gradient, wet extremes produced a large effect on ANPP, while dry extremes resulted in a small effect (Fig. 3.2a). As a consequence, there was strong evidence in favor of positive asymmetry to precipitation extremes for ANPP ($a_p = 0.41$, Fig. 3.2b). In contrast, soil respiration exhibited near equally large responses to dry and wet extremes (Fig. 3.2a), with this process only slightly more sensitive to dry versus wet precipitation extremes ($a_p = -0.027$, Fig. 3.2b). Therefore, soil respiration exhibited near symmetry in response to precipitation extremes.

A linear model was selected as best explaining ANPP responses to both precipitation and soil moisture, with both drivers explaining equal amounts of variation in this process (Fig. 3.3, Table 3.1). For soil respiration, model weights demonstrated consistent evidence in favor of a nonlinear model, and thus this process exhibited saturating responses to both precipitation and soil moisture (Fig. 3.4, Table 3.2). Stepwise selection resulted in soil moisture alone as the most parsimonious predictor of ANPP responses. Notably, the inclusion of light availability into the model slightly lowered the AIC value (499.59 to 489.3). Yet the incorporation of light availability,

either as a main or interactive effect with soil moisture, did not significantly change the model with soil moisture as the sole predictor (P > 0.1 in both cases). Stepwise selection for soil respiration yielded the interaction of soil moisture and temperature as the best model, with a positive and negative relationship of moisture and temperature with respiration, respectively. This result is consistent with a highly significant interactive effect of temperature and soil moisture on soil respiration (P < 0.0001). Plant community composition did not differ among treatment subsets within years (Bray-Curtis dissimilarity, P = 0.70), and was driven largely by the abundance of the three dominant C₄ grass species in both years.

3.5 DISCUSSION

Precipitation is a key determinant for the structure and functioning of many terrestrial ecosystems (Knapp et al. 2017a), and thus systems are likely to be sensitive to predicted changes in the sign, magnitude or variability of this driver (Weltzin et al. 2003, Knapp et al. 2008, Poulter et al. 2014, Ahlstrom et al. 2015, Gherardi and Sala 2015, Felton and Smith 2017). A growing body of evidence indicates that ecosystem production is differentially sensitive to wet versus dry years, leading some to suggest that current temporal models of precipitation-production relationships, of which are consistently linear, may need reconsideration (Knapp et al. 2017a, Luo et al. 2017). This notion is heightened when considering predicted increases in the frequency and magnitude of precipitation extremes (IPCC 2012), which are posited to shift the relationship of precipitation and production towards a nonlinear fit (Knapp et al. 2017a). Such nonlinear response dynamics may be particularly prone to emerge if extreme conditions in precipitation with no historical analog are experienced by ecosystems (Smith 2011, Kayler et al. 2015).

To address these uncertainties, I deployed a gradient of growing season precipitation amount and extremity within an intact mesic grassland ecosystem, and assessed the responses of both aboveground net primary production (ANPP) and soil respiration. I found that soil respiration and ANPP exhibited differential sensitivity to both precipitation amount and extremity, with precipitation-driven impacts to soil moisture in the rooting zone as the key determinant of these dynamics. In contrast to my expectations, soil respiration exhibited near symmetrical responses to precipitation extremes, while ANPP responses provided strong evidence of positive asymmetry. Furthermore, while soil respiration exhibited clear saturating responses to both precipitation and soil moisture as hypothesized, the responses of ANPP were consistently linear.

Positive asymmetry in ANPP is consistent with previous observations within this ecosystem (Knapp and Smith 2001). I suspect that the apparent greater sensitivity of ANPP to single-year wet extremes may be driven by multiple mechanisms. First, drought-buffering mechanisms that enhance precipitation use efficiency, such as soil moisture carry-over from the previous year, plant physiological adjustments, and their interaction may prevent strong declines in ANPP during dry years in mesic ecosystems. At the same time, high growth rates of herbaceous vegetation (such as the C₄ grasses dominant within this study) matched with low light limitation through annual burning and high growing season temperatures (Taylor et al. 2017), all enable large aboveground growth responses to soil moisture surpluses.

In contrast, metabolic processes such as root and soil microbial respiration may have maximum rate limits that are rapidly achieved at high soil moistures. For example, whereas low soil moistures constrain substrate-microbe interactions to reduce respiration and overall cellular activity, saturated soil conditions may facilitate substrate mobilization to a degree that exceeds the physiological capacity of soil microbes (Moyano et al. 2013). Near saturated soil conditions may also reduce aeration and thus produce frequent anoxic conditions that limit oxygen diffusion for root and microbial respiration, further restricting soil respiration at the highest precipitation inputs.

In general, these characteristics portend divergent sensitivities of production (i.e. indeterminate plant growth) and respiration (i.e. metabolism) processes to precipitation extremes within this ecosystem, with respiration tending towards equal or negative asymmetry while production tending towards positive asymmetry. Such dynamics likely inform, in part, the nonlinear versus linear response dynamics of soil respiration and ANPP, respectively, to water availability in my study.

Although model selection yielded the interaction of soil moisture and temperature as the most parsimonious model for drivers of soil respiration, it is likely that the effect of soil temperature on soil respiration depended on soil moisture availability and indirectly on plant cover. I observed a negative relationship between soil respiration and temperature that is inconsistent with the generally accepted understanding of this relationship (Lloyd and Taylor 1994). However, higher soil temperatures occurred in drought plots due to lower plant cover and greater light penetration to the soil surface (Fig. S3), which I hypothesize produced an indirect effect that both increased soil temperatures and exacerbated evaporative soil moisture losses. I thus suggest that soil moisture, rather than temperature, was the dominant driver of soil respiration in my experiment, consistent with previous findings within this ecosystem (Hoover et al. 2016). Therefore, soil moisture was likely the dominant driver of the observed linear ANPP and saturating soil respiration responses to precipitation in this study.

The response of ANPP to precipitation exhibited a slope that is higher than predicted by some temporal models (Estiarte et al. 2016), however the amount of variation in ANPP explained by precipitation with this experiment is similar to earlier observations within annually burned sites of this particular ecosystem (Briggs and Knapp 1995). Because ANPP largely tracked soil moisture availability (Fig. 3b), my results reinforce the critical links between how precipitation translates to

soil moisture availability, which I suggest can also potentially alter an understanding about the underlying relationship between precipitation and production. For example, experimental manipulations of larger yet less frequent rainfall events - without attendant changes to total growing season precipitation amount - were documented to reduce ANPP within the ecosystem of this study (Knapp et al. 2002). By extension, such dynamics impacted the temporal ANPP - precipitation relationship of this ecosystem. This effect has been attributed to how intra-annual precipitation translates to temporal variability in soil moisture in the rooting zone (Knapp et al. 2008). Although my experiment was not designed to manipulate intra-annual precipitation variability, it is evident that within-growing season rainfall regimes can have consequences for understanding interannual relationships between ANPP and precipitation, an area of research warranting further exploration. Nevertheless, my results support the notion that impacts to soil moisture availability may be the underlying determinant for the realization of ANPP responses to changes in precipitation regimes and extremes across many terrestrial ecosystems (Heisler-White et al. 2008, Knapp et al. 2008, Gherardi and Sala 2015).

In total, my experimental results underscore the differential sensitivities of production and respiration to changes in both growing season precipitation amount and extremity at the site level. These differences may ultimately reflect the different timescales upon which metabolism versus biomass production operate on and respond to changes in soil moisture availability. Yet such differences are critical to elucidate for proper forecasts of ecosystem responses to future changes in precipitation as the atmosphere warms. In particular, I observed no evidence against a linear ANPP-precipitation relationship within this ecosystem, and thus am not able to reject the linear prediction of current temporal models. I posit that for clear nonlinearity in ANPP responses to precipitation to emerge within this ecosystem, multi-year periods of extremity (Hoover et al. 2014)

or levels of extremity with no historical analog must occur (Kayler et al, 2015). For example, Hoover et al. (2014) observed reductions in ANPP to be three-fold greater in the second year of an extreme drought, suggesting cumulative impacts, such as soil moisture depletion, carried over to further constrain ANPP in the second year. Indeed, Knapp et al. (2017a) only produced a nonlinear temporal relationship between ANPP and interannual precipitation within annually burned sites (similar to the one in this study) after incorporating both a multi-year extreme drought and extreme wet years beyond the amount of this study (e.g. 1400 mm).

I suspect that if my experimental gradient included a precipitation level such as 1400 mm, clear saturation or even declines in ANPP responses to precipitation and soil moisture would have occurred. Thus, for single year extremes, it is likely that nonlinear responses of ANPP within this ecosystem may be difficult to detect due to the lack of time to produce cumulative effects on ecosystem properties other than soil moisture, such as soil nitrogen and/or light availability. In addition, biotic and abiotic buffering mechanisms under drought, and high sensitivity of herbaceous vegetation to soil moisture surpluses, may render a tendency toward a linear relationship for single-year changes in precipitation as well as positive asymmetry to precipitation extremes. As a result, I suggest that a promising avenue of future research concerns investigating how key characteristics of precipitation and more generally climate extremes, such as the sign, magnitude, and/or duration, will independently and interactively impact ecosystem functions.

3.6 TABLES

Model	Driver	AIC	AIC diff	AIC weight
Linear	Precipitation	495.76	0	0.7
Nonlinear	Precipitation	497.31	1.55	0.32
Linear	Soil moisture	496.12	0	0.7
Nonlinear	Soil moisture	497.72	1.6	0.30

Table 3.1. Summary of model selection output for ANPP responses to both precipitation and soil moisture. Values are rounded to two decimals places.

Table 3.2. Summary of model selection output for soil respiration responses to both precipitation and soil moisture. Values are rounded to two decimal places.

Model	Driver	AIC	AIC diff	AIC weight
Linear	Precipitation	1004.98	35.34	2.12e-08
Nonlinear	Precipitation	969.64	0	1.00e+00
Linear	Soil moisture	865.90	39.17	3.13e-09
Nonlinear	Soil moisture	826.73	0	1.00e+00

3.7 FIGURES



Figure 3.1. A) The 2016 field experiment at the Konza Prairie Biological Station in northeastern, Kansas. B) Relationship between growing season (May – August) precipitation percentiles from the long-term record and total growing season precipitation amounts added. Specific emphasis was placed on the distributional tails of the long-term record. Inset is the relationship between precipitation amounts and mean soil moisture availability during the growing season, which resulted in linear relationships ($R^2 = 0.66$). Standard errors on each point are too small to be visible.



Figure 3.2. The two approaches used to quantify asymmetric responses of ANPP and soil respiration to precipitation extremes. For both graphs the mid-line represents values at nominal precipitation amounts (between $15^{\text{th}} - 85^{\text{th}}$ precipitation percentiles). (a) depicts the magnitude of effect (Cohen's D effect size) that each extreme had relative to values at nominal levels of precipitation variability. Error bars denote 95% confidence intervals while grey lines denote the cutoff for 'large' effect sizes at +/- 0.8. (b) Depicts the relative responses to extreme such that a positive or negative values indicates responses were relatively larger for extreme wet or dry treatments.



Figure 3.3. Response of aboveground net primary production (ANPP) to precipitation amount (a) and soil moisture availability (b) during the experiment. ANPP exhibited consistent evidence for a linear response to water availability, in terms of both precipitation and soil moisture. R^2 values were generated from linear models.



Figure 3.4. Relationship of soil respiration with precipitation and soil moisture. (a) relates mean values of soil respiration (June - August) with total growing season (May – August) precipitation amounts. Error bars denote standard errors of the mean. (b) relates flux values to soil moisture availability to 20 cm depths. For both of these approaches, a clear nonlinear, saturating relationship emerged between soil respiration and water availability.

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³CHAPTER 4: ECOSYSTEM FUNCTION IS MOST SENSITIVE TO PRECIPITAION VARIABILITY DURING DROUGHT

4.1 OVERVIEW

Periods of water scarcity and abundance occur in all terrestrial ecosystems, and with continuing intensification of the global hydrological cycle, the frequency of extreme wet and drought years, as well as variability in the timing and size of rainfall events, are both predicted to increase. Yet despite longstanding recognition of the importance of both resource amount and variability, we lack fundamental understanding of how their interactions affect ecosystem functioning. Here I quantify this interaction in a native grassland ecosystem by experimentally eliminating temporal variability in growing season rainfall (imposing uniform rainfall event timing and size) over a wide range of total precipitation amounts, including simulated extreme wet and dry years. In this 2-yr study, I focused on responses in rain use efficiency [RUE = aboveground net primary productivity (ANPP) per mm rainfall], an integrative metric of ecosystem functioning. I contrasted experimental results based on uniform rainfall patterns with a long-term (32-yr) record of RUE that incorporates natural variability in rainfall patterns and amount for this grassland. From these data, I show for the first time that rainfall variability reduces ecosystem function primarily during drought, with RUE reduced by 35% during the most extreme drought years. In contrast, when precipitation is abundant variability in event size and timing has little impact on RUE. Further analysis of the long-term record indicated that historically, the lowest RUE in dry years was recorded when maximum rain event sizes were large, and a greater proportion of total rainfall was derived from large events. Thus, increases in rainfall variability and specifically more frequent

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extreme precipitation events, as forecasted by climate models, can be expected to magnify the negative impacts of drought on ecosystem functioning.

4.2 INTRODUCTION

The structure and functioning of all ecosystems are mediated by a relatively few abiotic constraints and limiting resources (e.g. temperature, water, and nutrients; Churkina and Running 1998, Nemani et al. 2003). The availability of these resources through time (e.g. diurnally or seasonally) can be highly variable or relatively predictable, and much foundational theory in population and community ecology incorporates the constraints and consequences of resource fluctuations through time (Hutchinson 1961, Huston 1979, Chesson 1986). Similarly, we know that temporal variability in limiting resources, such as water, can affect key ecosystem functions, including aboveground net primary productivity (ANPP; Knapp et al. 2002, Gherardi and Sala 2015), with regional-scale precipitation anomalies now linked to variability in the global carbon cycle (Poulter et al. 2014, Haverd et al. 2016). What we lack, however, is an understanding of how resource variability interacts with resource amount to affect ecosystem functioning. This is a critical limitation, as ecosystems are experiencing alterations in both resource amounts and variability globally, in ways that have no historic analog (Williams and Jackson 2007, Smith et al. 2009, IPCC 2013).

Water availability is the primary resource limiting terrestrial ecosystem function across much of the globe (Churkina and Running 1998, Seddon et al. 2016), and precipitation regimes are forecast to become more variable at intra-annual to decadal time scales, linked to a warming atmosphere (IPCC 2013). Quantifying the consequences of this increased variability will be particularly critical for ecosystems where periods of water limitation are common, such as in grasslands (Sloat et al. 2018). Grasslands are among the most extensive biomes on earth, covering

approximately 30% of the terrestrial surface (Parton et al. 2012) while providing essential ecosystem services (Sloat et al. 2018). Growing evidence suggests that changes to the variability of rainfall patterns can alter grassland productivity independent of total rainfall amounts (Knapp et al. 2002, Heisler-White et al. 2008). However, while shifts in the timing, size, and distribution of rainfall events have all been shown to alter ecosystem function (Knapp et al. 2002, Heisler-White et al. 2012), there is considerable variation in the direction of this sensitivity among ecosystems (Heisler-White et al. 2009). For example, fewer yet larger rainfall events may either increase (Hesiler-White et al. 2008) or decrease (Knapp et al. 2002) productivity in semi-arid versus mesic grasslands, respectively. This suggests that more variable rainfall patterns may interact with changes in total or mean rainfall amount. Unfortunately, much of our understanding of how precipitation variability impacts ecosystem function is anecdotal or based on experiments that alter variability at a single precipitation level (Knapp et al. 2002). As a consequence, the relative influence of rainfall pattern versus amount on ecosystem function is poorly understood.

Here I report the results of a two-year rainfall manipulation experiment conducted within an intact, C₄ dominated mesic grassland in NE Kansas (Knapp et al. 1998). Although past experiments in this and other grasslands have quantified effects of increased variability in rainfall inputs on ecosystem function (Knapp et al. 2002, Heisler-White et al. 2008, Hesiler-White et al. 2009, Wilcox et al. 2014, Gherardi and Sala 2015), I opted to *eliminate* temporal variability in rainfall inputs by keeping both the size of rainfall events and the amount of time between events constant (Fig. 4.1a). I deployed this manipulation across a well-replicated experimental gradient (Cottingham et al. 2005) of growing season precipitation (GSP) amount (9-11 treatment levels). These spanned the driest to wettest years in the 112-year (1900 - 2012) precipitation record for this region. The experiment was repeated in adjacent sites during the 2015/16 growing seasons. I focus my analysis on responses in rain use efficiency (RUE), quantified as the change in ANPP (g/m^2) per mm of GSP. This metric describes how efficiently the primary limiting resource within this ecosystem (water) is utilized for ecosystem function (ANPP).

4.3 METHODS

Study site. This study was conducted at the Konza Prairie Biological Station (KPBS), a long-term ecological research site and 3487 ha preserve of native tallgrass prairie located in northeastern Kansas (39°N 96°W). This region is characterized by warm, wet growing seasons and cold, dry winters. Mean annual temperature is 13° C while annual precipitation for this region is 892 mm, of which the majority occurs during the growing season (e.g., April – August). High variability in interannual precipitation is an inherent feature of this region, which has been shown to drive the highest interannual variability in aboveground net primary productivity within North American ecosystems (Knapp and Smith 2001). I focused mu study within ungrazed annually burned (spring) upland sites, where C₄ grasses dominate the plant community and contribute largely to aboveground productivity (Knapp et al. 1998).

Experimental design. I conducted two independent growing season (defined here as May – August) rainfall manipulation experiments in neighboring (< 50 m apart) upland sites in 2015 and 2016. I utilized a replicated regression experimental design, where statistical power is generated primarily from the treatment gradient (Cottingham et al. 2005). I imposed 9 and 11 precipitation levels in 2015 and 2016, respectively. This design allowed us to produce a replicated gradient of precipitation amounts (n = 4 replicates per each treatment level) within a single growing season, resulting in 36 and 44 experimental plots in 2015 and 2016, respectively. Precipitation levels corresponded to total growing season precipitation amounts derived from specific

percentiles of the 112-year (1900-2012) record for this region based on daily precipitation data for Manhattan, KS obtained from the NOAA National Climatic Data Center (now Global Historical Climatology Network) and the Kansas State University Weather Data Library (climate data, supplemental information). These percentiles ranged from the 1st (driest) to 99th (wettest).

In order to control growing season rainfall variability, I utilized 2.2 x 2.2 m polycarbonate (~10% reduction in photosynthetic active radiation) rainfall manipulation shelters to exclude 100% of ambient rainfall. Shelters were placed over 4-m^2 experimental plots, with a nested 1-m^2 sampling plot. I then performed weekly water additions for each precipitation level during the evening (after 17:00, to minimize evaporative losses) in order to keep the timing between rainfall events constant. Weekly rainfall amounts were calculated by multiplying long-term monthly means by the % deviation of each growing season percentile from the long-term growing season mean, and then dividing this amount by 4 (5 in June) to correspond to each weekly rainfall event amount and conserve monthly historical amounts. This approach resulted in minimal week-to-week variation in rainfall event sizes for each treatment level, while also keeping the amount of time between rainfall events constant (Fig. 1a).

Site-specific climate data. To compare my experimental manipulation with ambient precipitation patterns, I utilized data from the long-term (1984 – 2015) site record for KPBS. I used rainfall data collected from three rain gauges located in different watersheds across KPBS. Daily rainfall data from two rain gauges (in watersheds 20B and N1B), each approximately half a mile away from the long-term ANPP transects (one to the north and one the south), were averaged to yield a single value for each day (which should represent rainfall received at the ANPP transects more accurately than any single rain gauge dataset). Prior to averaging, all gaps and missing data points in each of these 2 daily rainfall records were filled using data from the rain gauge located

in the KPBS headquarters area (approximately 3 miles from the ANPP transects), which records data more regularly and frequently than the 2 closer gauges. Rainfall events \leq 4 mm were converted to 0 mm, as they are considered ineffective in this system (Gilliam et al. 1987). Consistent with the experimental dataset, days of consecutive rainfall were summed together and treated as single rainfall events. I focus here on rainfall patterns and total amounts between May and August, corresponding with my experimental manipulation.

Aboveground net primary productivity. Aboveground net primary productivity (ANPP) was estimated by harvesting all aboveground biomass in early September, the time when peak vegetation growth typically occurs (Knapp et al. 1998). For both the experimental and long-term observational studies, ANPP was harvested via clipping all aboveground biomass to the soil surface. Because both observational and experimental studies occurred in an ungrazed annually burned upland site, harvesting of all aboveground biomass provided a reliable indicator for annual ANPP and carbon flow within this grassland. For the experiment, I clipped vegetation within two 0.1-m² quadrats located within the center of each 1-m² sampling plot that were then averaged to yield a single value per plot. For the observational transects in upland, annually burned (spring) sites. ANPP within each transect was then averaged to yield 4 replicates for each year. After harvesting, biomass was immediately dried at 60° C for at least 48 hours and weighed to the nearest 0.01 g.

Statistical analyses. Rain use efficiency of ANPP (RUE) was calculated as the change in dry mass of aboveground net primary productivity (g/m^2) per unit change in mm of total growing season (May – August) precipitation (GSP). Although experimental RUE differed significantly between years, this was driven by consistently higher ANPP in 2015 versus 2016, with the

underlying RUE-precipitation pattern similar between years. Therefore, I averaged precipitation (total amounts and rainfall attributes) and ANPP values (from the same percentiles) for both years in order to produce a single relationship of experimental RUE and GSP. Because I employed two additional treatment levels in 2016 (25^{th} and 75^{th} precipitation percentiles), I combined these with the 50th percentile treatment. This allowed me to robustly represent RUE responses around median inputs of growing season precipitation. In total, this resulted in n = 14 data points contributing to my median precipitation level, and an average of n = 8 data points for each of the other eight precipitation levels (n = 9 treatment levels total for analysis). This yielded a robust, replicated dataset (equivalent to a 14-year temporal dataset) to examine relationships between GSP and RUE.

For the observational data, a single averaged value for ANPP for each year (1984 - 2015), along with precipitation, resulted in 32 data points. I tested fits between linear and second order polynomials for the response of RUE to GSP for both the experimental and long-term observational record, utilizing Akaike information criteria (AIC) as my metric for linear versus nonlinear model selection (AIC function in base R). To further explore the effects of rainfall variability on RUE during dry years, I quantified specific rainfall attributes during years of low GSP (May – August precipitation < 500 mm) using the long-term observational data. I calculated mean event size, the coefficient of variation (% CV) of event size, maximum event size, and average number of consecutive (>1) dry days (CDD). In addition, I developed a metric to represent the percent of total GSP derived from excess rainfall, or in other words, water delivered by large rainfall events that was not used by the system. This metric quantified the percent of total GSP that was derived from large rainfall events above and beyond a 30 mm per event size threshold, hereafter referred to as $R_{>30}$. For example, a 50 mm event would produce 20 mm of excess rainfall. I chose 30 mm as my threshold for a 'large' rainfall event because this represented the midpoint

of average rainfall event size between my median and 85th percentile treatment levels (Fig. 2). All correlations between precipitation variables were quantified utilizing pearson correlation coefficients.

Multiple regression model selection for correlates of RUE (backwards and forwards AIC selection, stepAIC function, MASS package in R) was conducted utilizing all precipitation attributes (Table 4.1) including total GSP as a predictor variable. Multicollinearity among predictor variables in the initial full model was assessed by calculating the variance inflation factor (vif function, MASS package in R) for each predictor variable, and was found to be high. Removal of CV of event size and mean event size, the two predictor variables with the highest vif values, reduced all vif values of the remaining predictor variables in the model below 5, and thus I chose to include total GSP, maximum event size, $R_{>30}$, and CDD for model selection. Collinearity between the two selected predictor variables in the final model was found to be low (vif values of 1.25). For all analyses, I removed one year (1989), as this was the second year of a severe drought, yet I have maintained this point in Fig. 2. All analyses were conducted within R statistical software (R 3.4.2 GUI 1.70 El Capitan build (7434)).

4.4 RESULTS AND DISCUSSION

My experimental manipulations produced strong impacts to soil moisture in the rooting zone (0-20 cm; Nippert et al. 2012, Fig. 4.1), with differences in rainfall patterns relative to ambient conditions (Fig. 4.2a), while also Experimentally imposed rainfall event size ranged from 11.1 to 61.7 mm across treatment levels (Fig. 4.2b), with event size increasing linearly with total GSP amount (Fig. 4.2b inset). For ambient rainfall patterns, the range of mean event size was similar (17.9 to 62.8 mm) yet less strongly correlated with total GSP (R = 0.56, P < 0.001). As expected, variability in GSP event size (quantified as the coefficient of variation, %CV) was dramatically

greater (~20 fold) for ambient vs. experimental precipitation patterns (Fig. 4.1b). Event size variability, however, was not significantly related to mean event size in either case (Fig. 4.1b). Overall, my experimental manipulation reduced %CV of event size by 93% relative to what this ecosystem has experienced historically, and because events occurred at regular intervals through the growing season, variability in both the size and timing of rainfall events was virtually eliminated.

I compared patterns of RUE under experimental conditions of minimal variability in event size and timing with RUE measured under ambient conditions with naturally varying rainfall patterns. The latter was possible because of a long-term (32-year) ANPP-precipitation record from a site adjacent to my experiment. This long-term dataset spans a range of GSP amounts similar to the range imposed in the experiment (see methods for further details). For both datasets, a nonlinear response of RUE to GSP amount was apparent (Fig. 4.2), in which RUE increased as growing season conditions became drier, consistent with ecophysiological and ecohydrological theory (Good et al. 2017), as well as previous assessments of such relationships (Huxman et al. 2004, Wilcox et al. 2017). However, the increase in RUE in dry years was much greater when rainfall patters were uniform versus naturally variable (Fig. 4.3). Indeed, differences in experimental versus observational RUE were negligible at the wet end of the GSP gradient, but RUE began to diverge strongly between experimental and long-term values when GSP decreased below 500 mm (Fig. 4.3). For instance, at the lowest GSP input of 182 mm, uniform rainfall patterns increased RUE by 53% relative to ambient patterns (Fig. 4.3). This overall pattern indicates that the influence of rainfall variability on RUE - here negative - is magnified as growing seasons become drier. On average, this negative effect of rainfall variability on RUE resulted in a

24% lower ANPP for the long-term record when compared to the experiment (Fig. 4.3 inset), even though both had the same average GSP (442.7 ± 24.1 (SE) vs. 471.5 ± 92.5 , respectively).

To identify specific attributes of rainfall patterns that could be linked to variability in RUE independent of rainfall amount, I conducted a detailed analysis of the long-term ambient ANPPprecipitation record for this ecosystem (see methods). This was not possible within my experimental framework because of strong covariation between event size and GSP amount, and because event number did not vary (Fig. 4.1b). I focused on a subset of years (23) in the long-term record when precipitation amounts were < 500 mm because this is where the greatest impact of rainfall variability was evident (Fig. 2). Moreover, in these dry years RUE varied by nearly twofold at similar total precipitation amounts (Fig. 2). I quantified characteristics of rainfall regimes that have previously been shown to impact productivity and RUE within this and other grassland ecosystems (Knapp et al. 2002, Heisler-White et al. 2008, Heisler-White et al. 2009, Thomey et al. 2010, Wilcox et al. 2014, Gherardi and Sala 2015, Wilcox et al. 2017), including mean event size, CV of event size, maximum event size, and the average number of consecutive dry days (CDD). To provide an index of 'excess rainfall', I also calculated the percent of GSP that fell after a 30 mm/event threshold was exceeded, hereafter referred to as $R_{>30}$ (see methods for further details).

To reduce multicollinearity among these initial predictor variables (Table 4.1), I removed mean and %CV of event size and utilized GSP, maximum event size, CDD and $R_{>30}$ for model selection of RUE. From this full model, GSP (partial R = -0.38) and maximum event size (partial R = -0.64; Fig. 4.4a) were selected as the best predictors of variation in RUE (model $R^2 = 0.54$). Although not selected in the final model, $R_{>30}$ was also significantly negatively correlated with RUE (Fig. 4.4b). Collectively, this analysis suggests that large precipitation events, which increase precipitation variability (Fig. 4.4a inset) and are expected to increase with climate change¹, reduce growing season RUE within this ecosystem. Thus, when a greater percentage of total GSP is derived from larger rainfall events during dry years, RUE can be expected to be reduced (Fig. 4.4).

My results provide novel insight towards predicting the ecological impacts of climate change. It is well established that climate change will increase rainfall variability at both intra- and interannual time scales (IPCC 2013), necessitating a more complete understanding of how changing variability in this key limiting resource interacts with precipitation amount. Yet prior to this study, these two temporal scales of precipitation change have only been studied in isolation (Knapp et al. 2002, Heisler-White et al. 2008, Gherardi and Sala 2015), with most focused on quantifying the impacts of precipitation amount on ecosystem function (Knapp et al. 2001, Huxman et al. 2004, Good et al. 2017). Now, by experimentally removing variability in rainfall events across a wide gradient of total precipitation amounts, I have quantified for the first time differential sensitivity in ecosystem function to changing rainfall patterns contingent on total amount. This portends a future where more variable event sizes, and a greater proportion of rainfall derived from extreme precipitation events, can be expected to magnify the negative impacts of drought on ecosystem functioning within this and potentially many other ecosystems.

4.5 TABLES

Table 4.1. Pearson correlation coefficients of RUE and the different rainfall attributes for years with < 500 mm of total growing season precipitation (May – August, GSP). RUE denotes the rain use efficiency of aboveground net primary productivity (ANPP per mm of GSP). CDD denotes the average number of consecutive (>1) dry, or zero precipitation days during the growing season. CV of event size represents the coefficient of variation of event size. % Excess rainfall denotes the percentage of rainfall contributed to total GSP after a 30 mm/event threshold. For these calculations, rainfall occurring over consecutive days was summed and treated as a single event. Bolded values indicate significant correlations at p-value ≤ 0.05 .

	RUE	GSP	Mean event size	CV of event size	Maximu m event size	CDD
GSP	-0.56					
Mean						
event size	-0.33	0 49				
CV of	0.55	0.47				
	0.52	014	0.056			
event size	-0.55	.014	-0.050			
Maximum	0.50	0.45	0.44	0.00		
event size	-0.72	0.45	0.44	0.80		
~~~~						
CDD	0.14	-0.49	0.43	0.05	0.1	
% Excess						
rainfall	-0.55	0.35	0.76	0.57	0.79	0.40

# 4.6 FIGURES



**Figure 4.1.** Relationship between precipitation amount and % volumetric water content to 20 cm soil depths ( $R^2 = 0.91$ ). Soil moisture was measured according to a standardized protocol in both years during the June – August period utilizing a portable 20 cm probe (Campbell Scientific, Logan, UT) that was calibrated to site-level soil conditions. Measurements occurred each week prior to experimental rainfall events by inserting the probe into the middle of the 1-m² sampling plot. Precipitation and soil moisture values are averaged across the two years of the experiment.



**Figure 4.2.** Illustrative comparisons of naturally variable and experimentally even (uniform) rainfall patterns. Example of differences between ambient and experimental rainfall patterns are shown for years with similar total growing season precipitation (GSP) amounts (a). The experimental dataset is from 2016, while the ambient rainfall pattern is from a year (1990) with comparable GSP (both ~ 400 mm). The dashed horizontal line represents my cutoff for a "large" rainfall event (30 mm), in which rainfall from single events above this cutoff (R_{>30}) is posited to *not* be used by the system (see methods). Comparison of experimental versus ambient relationships of mean event size and the coefficient of variation (% CV) of rainfall event size (b). For both datasets, mean event size was not predictive of CV of event size. However, my experimental rainfall regime represented, on average, a 93% reduction in variability of rainfall event size relative to natural variability. Inset demonstrates how experimental event size was collinear with total GSP (Pearson's *R* =1.0).



**Figure 4.3.** The impact of naturally variable rainfall patterns on the rain use efficiency (RUE) of ecosystem productivity. Relative to ambient and more variable patterns, uniform rainfall patterns, i.e., weekly events with similar amounts, had null impacts on RUE during wet years, yet dramatic positive effects during the driest years. RUE was calculated as the ratio of aboveground net primary productivity (ANPP) to growing season precipitation (GSP). Relationships of GSP and RUE for both rainfall regimes were best explained by a nonlinear fit (AIC criteria, second-order polynomial models). However, the evidence against a linear relationship was far stronger for uniform (AIC model difference: 9.1) versus ambient patterns (AIC model difference: 1.79). Inset shows the average ANPP between variable and uniform rainfall patens, in which variable rainfall patterns reduce ANPP by an average of 24%. Error bars denote the standard error of the mean.



**Figure 4.4.** Attributes of natural rainfall variability and their effect on rain use efficiency (RUE) of ecosystem productivity. In addition to total growing season precipitation, maximum event size was the variable selected as best explaining impacts to RUE (see Fig. 2), with a significant negative effect (a). Inset shows the strong correlation (Pearson correlation coefficient) with CV of event size, suggesting large events are related to increased event size variability. Shown here is the correlation between maximum event size and RUE. To further explore the effect of large events, I quantified the % of excess rainfall ( $R_{>30}$ ) that contributed total growing season precipitation (b). This attribute also resulted in a significantly negative relationship with RUE. Together, these insights suggest that a greater percentage of total GSP derived from large events can reduce RUE during years when water availability becomes limiting.

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# ⁴CHAPTER 5: INTEGRATING PLANT ECOLOGICAL RESPONSES TO CLIMATE EXTREMES FROM INDIVIDUAL TO ECOSYSTEM LEVELS

# 5.1 OVERVIEW

Climate extremes will elicit responses from the individual to the ecosystem level. However, only recently have ecologists begun to synthetically assess responses to climate extremes across multiple levels of ecological organization. I review the literature to examine how plant responses vary and interact across levels of organization, focusing on how individual, population, and community responses may inform ecosystem-level responses in herbaceous and forest plant communities. I report a high degree of variability at the individual level, and a consequential inconsistency in the translation of individual or population responses to directional changes in community- or ecosystem-level processes. The scaling of individual or population responses to community or ecosystem responses is often predicated upon the functional identity of the species in the community, in particular the dominant species. Further, the reported stability in plant community composition and functioning with respect to extremes is often driven by processes that operate at the community level, such as species niche partitioning and compensatory responses during or after the event. Future research efforts would benefit from assessing ecological responses across multiple levels of organization, as this will provide both a holistic and mechanistic understanding of ecosystem responses to increasing climatic variability.

⁴ Felton, Andrew J., and Melinda D. Smith. "Integrating plant ecological responses to climate extremes from individual to ecosystem levels." *Phil. Trans. R. Soc. B* 372.1723 (2017): 20160142.

## **5.2 INTRODUCTION**

An emergent consequence of global climate change has been the increase in the frequency and severity of climate extremes (IPCC 2012). Climate extremes, such as drought, heavy precipitation, heat waves and cold snaps, have the potential to produce large impacts to ecosystem dynamics (Easterling 2000, IPCC 2012, Ummenhofer and Meehl 2017). However, the type and magnitude of ecological impacts resulting from climate extremes, both within (Hoover et al. 2014) and among (Knapp et al. 2015) ecosystems are highly variable (Smith 2011). With regard to plant responses, the variation can range from changes to species population genetics (Franks et al. 2007), altered local species richness (Tilman and El Haddi 1992), rapid shifts in ecotone boundaries (Allen and Breshears 1998) to continental-scale reductions in gross primary production (Ciais et al. 2005).

Implicit in these examples is the necessary consideration of the scale of the measurement. Ecologists have long recognized that the scale of an observation (e.g. temporal, spatial or level of organization) can significantly influence conclusions about the underlying processes determining a pattern (Levin 1992). It is also often the case that certain processes determine patterns observed at different scales (Wu 1999), as 'fast' process (e.g. respiration) at fine scales and 'slow' processes (e.g. succession) operating at broader scales can affect and feedback to each other (Levin 1992, Holling 1996). These notions apply equally to ecosystem responses to climate extremes. For example, high sensitivity or alterations at fine scales, such in plant physiology, can underlie and buffer impacts to broad scale processes, such as in net primary production (Jentsch et al. 2011, Hoover et al. 2014a). Therefore, an understanding of the cross-scale interactions between different levels of ecological organization (e.g., individual, population or community) within an ecosystem may inform variability in ecosystem-level responses to climate extremes (Smith 2011).

Prior efforts to scale from individual to ecosystem-level processes have considered the metabolic rate (Allen et al. 2005), size and/or density (Enquist 2002) of organisms. Suding et al. 2008 proposed that community dynamics often complicate scaling up from the individual level, and that plant community processes may be scaled to ecosystem productivity by relating species abundances with their functional traits. Only recently have ecologists begun to explicitly consider how responses to climate extremes at lower ecological levels, such as individual mortality, will scale to ecosystem-level processes such as carbon and water cycling (Anderegg et al. 2016). Nevertheless, despite calls in the literature as a research need (Smith 2011), experimental or observational approaches that measure responses to climate extremes across multiple levels of ecological organization are relatively rare (Fig. 5.1).

Climate extremes will initially impact plant community and ecosystem processes via either physiological (Levitt 1972) or mechanical (Saurez and Kitzberger 2010) impacts to individuals that produce the initiating conditions for responses (Wu 199, Smith 2011) at the population or community level (Fig. 5.2). Smith 2011 proposed that ecosystem responses to climate extremes consists of three integrative hierarchical (i.e. ordered) pathways; i) the immediate physiological and growth impact to individuals, ii) demographic changes to species abundances (community response) and iii) mortality/loss of species and replacement with novel species. Polley et al. 2014 extended this framework by proposing that climate change, here climate extremes, will impact ecosystem function as a consequence of the response and effect traits of individuals, and how the climatic conditions alters the relative abundance of these traits in the community (community effect).

A response trait is considered to be a trait that may drive changes in the composition of species in the plant community, while an effect trait produces detectable feedbacks on ecosystem

function (Polley et al. 2014). For example, a trait that is highly responsive to drought stress, such as flowering in mesic grassland, may also have detectable feedbacks effects on ecosystem productivity due to the large investment of carbon in flowering stalks (Dietrich and Smith 2016). However, response and effect traits of plants may not necessarily be tightly coupled, and thus those traits responsible for driving plant community compositional change during or after an extreme may not translate to detectable impacts on ecosystem function, such as productivity (Suding et al. 2008, Polley et al. 2014). For example, traits that are highly sensitive to stress, such as photosynthetic responses to drought, may buffer impacts to ecosystem productivity by increasing water use efficiency of species in the community. Further, if there is high intraspecific or interspecific variation among genotypes or species sensitivities to an extreme, the extant functional diversity within the community may also operate to stabilize ecosystem functions (Tilman and Downing 1994). Thus, the fundamental links between processes occurring across levels of organization in an ecosystem suggests that their dynamics will be highly interactive both during and after periods of climatic extremity (Fig. 5.2).

In the following literature review I assess how plant responses to climate extremes vary and potentially interact across levels of ecological organization. In particular, I focus on studies that have considered response and/or recovery dynamics from climate extremes across the individual, population, community and ecosystem level in herbaceous and forest plant communities. As a consequence, my review was not intended to assess how ecological responses to climate extremes differ across spatial (Knapp et al. 2015) or temporal scales (Haddad et al. 2002, Sala et al. 2012) of which are increasingly relevant and likely warrant their own independent reviews. I acknowledge that forest and herbaceous plant dynamics – of which may include species turnover, productivity, and sensitivity to global change drivers - can vary considerably between

these ecosystem types as these dynamics operate on differential timescales. Rather, the focus of my review was to assess how information propagates across levels of organization within an ecosystem during and/or after periods of extreme climatic stress, and secondarily to see if the characteristics of these systems or the extremes may contribute to the observed dynamics.

While climate extremes are generally defined as statistically extreme or unusual climatic conditions (e.g. heat waves or droughts), extreme climate events (ECEs) have been defined in a number of ways - both from climatic and ecological perspectives (Gutschik and BassirRad 2003, Smith 2011, NAS 2016, van de Pol et al. 2017). Indeed, these varying definitions, as well as the multiple different research approaches historically employed (e.g. observational vs. experimental), underscore the challenges in attaining a general understanding of the ecological and evolutionary consequences of climate extremes (van de Pol et al. 2017). For the purposes of this review, I consider experimental, observational and opportunistic studies that assessed plant responses to climatically extreme conditions irrespective of the magnitude of the ecological responses. As a result, I do not limit my review to the climatic driver and ecological response definition proposed by Smith 2011, or to an organismal focused definition, such as proposed by Gutshick and BassirRad 2003. Instead, my approach was motivated towards improving an understanding of the ecological mechanisms that may underlie the variability in ecosystem resistance and resilience to periods of climatically extreme conditions. Thus, for this review, I employ the climatological definition outlined in the 2016 Attribution of Extreme Weather Events in the Context of Climate Change.

Overall, this review has the underlying goal to synthesize past research findings and contribute to advancing a more integrative understanding about the role of responses at different levels of ecological organization in determining ecosystem response to and recovery from climate

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extremes. I sought to understand how the responses of processes occurring at lower levels, such as at the individual or population level, may inform higher-order responses at the community and/or ecosystem level. Finally, another key objective of this review was to generate recommendations for researchers interested in mechanistically assessing ecosystem responses to climate extremes, and in particular the dynamics of ecosystem responses to climate extremes across levels of ecological organization.

# 5.3 SCALING INDIVIDUAL PLANT RESPONSES TO THE POPULATION AND COMMUNITY

The immediate impacts to ecosystem processes are likely to be driven by changes to physiological processes induced by the stress of a climate extreme (Smith 2011). Physiological adjustments in plants (e.g. rapid changes to stomatal aperture) operate to avoid the potentially irreversible functional damages a climatic stress can impose (Levitt 1972) and the associated fitness costs to the organism (Gutschick and BassirRad 2003). Physiological impacts to individuals will vary by the type of climate extreme experienced (Levitt 1972). Force-driven mechanical damage is also of considerable importance in forest ecosystems exposed to high-energy storms (Saurez and Kitzberger 2010), or as a result of secondary consequences of climate extremes such as fire or flooding. In general, the stresses induced by climate extremes tend to produce greater impacts on plant performance than gradual climate change (Reyer et al. 2013) despite their shorter timescales. As a result, such events are posited to more likely reduce plant productivity and increase the probability of mortality (Niu et al. 2014).

Expectations that individual responses to climate extremes may scale to trajectories of plant population or community compositional change are based on the assumption that species and genotypes differ in their sensitivities to environmental changes. Indeed, a large body of literature

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suggests that variability in the responses of key organismal traits associated with fitness, survival or the life histories of individuals will impact demographic and population-level dynamics, and that such links may occur through multiple pathways (van Tienderen 2000, Jongejans et al. 2010, McLean et al. 2016). Moreover, the degree of change to plant community diversity (e.g. richness) or composition (e.g. species relative abundances) produced by a climate extreme should be an emergent property produced by differential responses and sensitivities of individual genotypes or species in the community, and the impact of the climate extreme on their relative abundances. Thus, genotypes within populations and species or functional groups within the community with differential sensitivities to a particular climate extreme presents a mechanistic pathway for directional changes to plant community diversity, composition and likely productivity.

Plant species in both forest and herbaceous ecosystems possess high variation in their physiological stress tolerances (Allen and Breshears 1998, Craine et al. 2012, Marechaux et al. 2015). As a result, there is evidence of differential sensitivity among plant genotypes (Reusch et al. 2005, Avolio and Smith 2013), species (Allen and Breshears 1998, Marchand et al. 2006, Hoover et al. 2014, Lloret et al. 2016) and functional groups (Debinksi et al. 2010, Hoover et al. 2014, Hoover et al. 2015) to climate extremes. Liu et al. 2015 observed large variation in long-term drought impacts to tree growth in depending on the species considered in Mediterranean forest communities, with fruit production and growth largely impacted in certain species and others not affected. Similarly, Hoover et al. 2014a observed differential sensitivity to repeated droughts and heatwaves between the  $C_3$  and  $C_4$  co-dominant plant species. This led to asymmetric impacts to species population sizes and thus a reordering of species abundances in the community following the extreme (Hoover et al. 2014a, Table 5.1). Interestingly, this variability also appears in other guilds besides plant. For example, Palmer et al. 2017 reported that even closely related

species within butterflies, moths and bird guilds varied significantly in what climatic conditions elicited extreme population responses. Thus, it has become increasingly clear that what is extreme for one species may not necessarily be extreme for another.

The observed variability in species sensitivity to climate extremes can be argued to underlie - and likely scale to - important plant community-level processes, such as niche complementarity. Through genotypes and/or species occupying different ecological niches, the temporal stability of ecosystem function is posited to be maintained in the face of environmental variation due to certain genotypes or species performing more optimally under different conditions (Tilman 1999). Such a dynamic has been observed to decrease the temporal stability among species population dynamics within the community, yet increase the temporal stability of plant community productivity (Tilman 1996).

Yet despite evidence for differential sensitivities among plant genotypes and species to climate extremes and evidence for compositional changes (Hoover et al. 2014), it is still rare that these observations scale to large community-level changes in species composition due to a single episode of climatic extremity (but see Allen and Breshears 1998, Hoover et al. 2014). Directional changes to species composition that is driven by differential sensitivities among species may be most likely if a plant species' vulnerability to a climate extreme is matched with a low population size, as was observed in Minnesota grassland communities following drought (Tilman and El Haddi 1992). However, non-random losses of species with low population sizes will likely not scale to large changes to community composition or productivity that is distinguishable from background variability (Smith and Knapp 2003, Smith 2011). It is often the case that there are reported physiological or phenotypic impacts to individuals that do not produce detectable impacts on plant population or community composition and ecosystem productivity (Fay et al. 2008,

Kreyling et al. 2008). For example, despite evidence of widespread tissue dieback in individuals, Kreyling et al. 2008 observed plant community productivity to be unaffected by both drought and heavy precipitation events. Moreover, high phenotypic plasticity in key traits associated with demographic processes (e.g. seed size) may also partially buffer negative impacts to the population-level during or after environmental stress (Jongejans et al. 2010).

There is also increasing evidence for high intraspecific variability in species responses to extremes, of which has been observed to be of equal or even greater magnitude than interspecific variation (Malyshev et al. 2016). High intraspecific variability may be influenced by ecotypic and genetic variation within a species (Bejerkehnlein et al. 2011, Avolio and Smith 2013, Matias et al. 2014, but see Theil et al. 2012). High intraspecific trait variation has thus been posited to contribute to post-extreme shifts in community-weighted trait means irrespective of gains or losses of species from the community (Jung et al. 2014). As a consequence, the impacts to individuals may not necessarily provide a single pathway for detecting impacts to population dynamics (McLean et al. 2016), and thus changes in community composition resulting from a climate extreme.

Variability in individual responses to climate extremes will be further driven by the ecological context in which the organism exists, in which plant responses may be modified by competitive interactions, soil mineral nutrient availability or trophic interactions such as herbivory (Valladares et al. 2017). Thus, the detection of individual or population responses to climate extremes must also consider co-occurring ecological drivers (Solow 2017). Moreover, plant communities also exhibit a certain degree of stochasticity in terms of the trajectories of species demography. For example, Kreyling et al. 2014 reported that even when multiple identical plant communities were exposed to the European drought and heatwave of 2003, the successional development of the communities followed multiple different pathways. Therefore, it is clear that

high variability at lower ecological levels of organization, such as individual or population responses, may further complicate efforts to scale-up these responses to community- and ecosystem-level responses to climate extremes.

## 5.4 THE ROLE OF SPECIES FUNCTIONAL IDENTITY

Approaches designed to relate individual and/or population responses to alterations in community composition or ecosystem function must first consider both the population size and functional identity of a species in the community. This is so because a species' functional identity within the community is likely to modify the strength of interactions between individual and population responses to a climate extreme with community or ecosystem level responses (White et al. 2000). There is evidence to suggest that focusing assessment on the responses of functionally important species in the community can inform, at least in part, variability in community and ecosystem responses to climate extremes (Hoover et al. 2014a). As terrestrial plant communities are commonly structured according to an abundance hierarchy (Whittaker 1965), highly abundant or dominant species are hypothesized to drive community and ecosystem processes (Grime 1998). This perspective has been extended to ecosystem-level responses to climate extremes, as decreased performance or changes to the population size of dominant species are likely to produce detectable impacts to processes that occur at the community and ecosystem level (Gitlin 2006, Smith 2011).

Research in forest communities has demonstrated that climate extreme impacts on the dominant tree species can impact the diversity of forest plant communities and alter community-level processes (Kane et al. 2011). Due to the large influence of forests on the global carbon cycle (Pan et al. 2011), how climatically induced widespread tree mortality (Breshears et al. 2005, Bigler et al. 2007) will impact the composition and productivity of forest ecosystems is a topic of increasing interest (Anderegg et al. 2012, Martinez-Vilalta et al. 2012). Dominant tree species are

an important structural component in forest ecosystems that significantly modify the physical environment. Consequently, widespread mortality, reduced growth or defoliation of a dominant tree species is expected to alter the ecology of the understory environment (Royer et al. 2011), and as a consequence likely impact the extant species in the community.

Defoliation or mortality of the dominant tree species due to climate extremes has been observed to impact plant community composition as a result of increased performance and richness of shade-intolerant understory species due to increased canopy openness and light availability (Rich et al. 2008, Kane et al. 2011, Saurez et al. 2012, Saura-Mas et al. 2015). This dynamic may scale to the ecosystem level if understory species are able to offset productivity declines of the dominant species. Differential sensitivities among co-dominant trees to a climate extreme (Barbeta et al. 2013) can alter the age structure and successional status of the ecosystem if one co-dominant species experiences a mortality threshold and the other does not (Mueller et al. 2005). Such changes to age structure or the successional state of vegetation may then impact the sensitivity of the ecosystem to future extremes (Kroel-Dulay et al. 2015). Changes to dominance hierarchies due to differential sensitivities may further impact ecosystem productivity via competitive releases of a co-dominant (Cavin et al. 2013), and may generate longer-term impacts to the composition of the community (Allen and Breshears 1998). Due to the long temporal scales of forest ecosystem dynamics and tree life histories, climatically induced mortality events and loss of dominant trees may permanently alter the structure, distribution and function of the ecosystem. For example, a severe drought in the 1950's produced a rapid and seemingly permanent two km shift in the piñon -juniper woodland ecotone boundary within the Southwestern United States (Allen and Breshears 1998).

However, it is important to consider that the timescales of recovery of forest ecosystems from these mortality events may exceed the shorter timescales of many ecological studies, resulting in the perception of permanent change. This highlights the need to understand the timescales of extreme events impacts (e.g. shorter-term mortality events) vs. the longer timescales of recovery dynamics in ecosystems with long-lived species. In other words, with short-term extremes events, such as drought, there is likely to be a mismatch in the timescale of dynamics driven by physiological (short-term growth) vs. demographic responses (short to long-term regrowth and recruitment dynamics) and alterations in physical processes that may modify these responses over time. Indeed, there is extensive knowledge of shorter-term responses of ecosystems to disturbances and climate extremes, as well as understanding of century-scale dynamics as observed from pollen records during glaciation cycles, but our understanding of dynamics at medium timescales and the mechanisms determining these dynamics remains limited.

In grasslands, dominant plant species are a common attribute of the ecosystem, and can drive ecosystem productivity irrespective of species richness (Smith and Knapp 2003). For example, Arnone et al. 2011 found grassland community production responses to heat wave to be driven primarily by the dominant  $C_4$  grass. Dominant species have also been observed to drive rapid recovery in ecosystem function following extreme drought (Weaver 1954, Hoover et al. 2014a). Similarly, in arctic shrublands decreased shoot growth of the dominant shrubs due to an extreme heat wave was observed to be linked to decreases in gross primary production (Bokhorst et al. 2011). Gradual decreases in the performance of the dominant species in response to 'press' type climatic extremity may further impact community composition by gradually facilitating increased abundance of initially subordinate species, as was observed in the response of the semiarid shortgrass steppe to prolonged drought (Evans et al. 2011). Thus, ecologically dominant species and their responses to climate extremes have the potential to influence the trajectories of community and ecosystem responses in both forest and herbaceous plant communities, despite the fact that these systems operate on differential temporal scales.

There is also emerging evidence that functionally distinct species, such as nitrogen fixing legumes, can modify neighboring species responses and potentially influence community-level processes despite their relatively low population sizes. For example, Khan et al. 2014 found the presence of legumes to facilitate the performance of neighboring species in the community under heavy precipitation, which in turn may have contributed to the stabilizing of aboveground productivity observed in the experiment. Similarly, the presence or absence of legumes has been reported as a determinant in community resistance to the same type of climate extreme (De Boeck et al. 2011, Dreeson et al. 2014). As such, functionally important species in the community that are not the dominant may also have the potential to impact individual, community and potentially ecosystem responses to climate extremes.

In total, there is evidence to suggest that ecologically and functionally dominant species can largely influence the response and/or recovery of community and ecosystem-level processes to climate extremes. However, species with other functional roles in the community, despite their low population sizes, may also have the potential to impact community and ecosystem responses to an extreme. Due to the directional nature of climate change, and forecast increases in the magnitude of climate extremes, such as with global change-type droughts (Breshears et al. 2005), declines in the performance or abundance of dominant species may occur as stress thresholds are more commonly experienced (Mitchell et al. 2014). Declines in the performance or abundance of dominant species (Evans et al. 2011), and thus may portend a reordering of species abundances in the community and changes to ecosystem-level

processes (Smith et al. 2009). As such, reordering of species due to climate extremes, potentially driven by demographic responses of the dominant species (Fig. 5.2), may become an increasingly important pathway of change for plant community and ecosystem processes (Lloret et al. 2012).

It must also be noted that plant communities exhibit varying degrees of species dominance (Whittaker 1965). Thus, differential mechanisms besides dominance may operate in communities where species abundances are more evenly distributed or species turnover is high. On this issue, the well-documented relationship between plant biodiversity with ecosystem functioning and stability (Tilman et al. 2001, Tilman et al. 2006, Isbell et al. 2011) suggests that such dynamics are likely to operate in plant communities during and/or after periods of climatic stress. As a result, efforts that scale individual species responses to ecosystem responses to climate extremes will likely undermine the complexity of processes occurring at the community level.

# 5.5 SCALING COMMUNITY RESPONSES TO ECOSYSTEM PRODUCTIVITY

As climate change progresses, climate extremes are likely to become an increasingly important determinant in the structure (richness, diversity or composition) of plant communities. Indeed, there is evidence that climate extremes can impact the species diversity and composition of plant communities (Tilman and El Haddi 1992, Allen and Breshears 1998, Smart et al. 2014, Saura-Mas et al. 2015, Concilio et al. 2015, dos Santos et al. 2015, Zeiter et al. 2016). However, there is still little evidence that climate extremes often induce large changes to plant community composition (Lloret et al. 2012), and thus large vegetation shifts following climate extremes are currently the exception rather than the norm (Allen and Breshears et al. 1998). Although functional resistance to climate extremes is often low, rapid recovery and thus stability in ecosystem function is evident across systems (Dreeson et al. 2014, Hoover et al. 2014, but see Haddad et al. 2002). The paucity in large compositional or functional changes appears to be often driven, in part, by

context-dependent community-level processes that act to stabilize plant community structure and/or function in response to, or recovery from climate extremes (Jentsch et al. 2011, Grant et al. 2014, Hoover et al. 2014a).

The composition of interacting plant species within a community can greatly modify the response of both individual organisms and ecosystem productivity to a climate extreme (Kreyling et al. 2008, Fry et al. 2013, Gellesch et al. 2015, Urbina et al. 2015, Arredondo et al. 2016). While it is clear that ecologically dominant species can often drive trajectories of ecosystem response and recovery, a large body of evidence supports biodiversity as an ecological property of plant communities that increases their functional stability (Tilman et al. 2001, Tilman et al. 2006, Isbell et al. 2011). The diversity-stability hypothesis is rooted in the multifunctional advantage of niche partitioning among species, in which functional diversity among species is an emergent property of variability in the environment (Tilman 1982, Tilman 1999). Indeed, these trade-offs in stress tolerance and responses to climatic extremes have been reported to increase both local (Silverton et al. 1999) and regional diversity (dos Santos et al. 2015) patterns of plant communities within forest and herbaceous ecosystems. As alluded to earlier, stability in ecosystem productivity may also be driven by reduced stability at lower ecological levels, such as with species population dynamics (Tilman 1996, Tilman 1999). Thus, the high variability that is evident at the individual or population level may provide a pathway to stabilize community composition (Lloret et al. 2012) or ecosystem productivity (Jentsch et al. 2011) with respect to increases in climatic extremity and variability.

There is evidence to suggest that plant communities with greater species richness tend to be more functionally resistant to climate extremes (Tilman and Downing 1994, Kahmen et al. 2005, Bloor and Bardgett 2012, Mariotte et al. 2013, van Rooijen et al. 2015), thus supporting the diversity-stability hypothesis. Community-level mechanisms of resistance appear to be, in part, driven by niche separation via differential functional responses among species to an extreme event. For example, Mariotte et al. 2013 reported that even with declining performance of the dominant species under drought, subordinate species were able to maintain carbon uptake and therefore partially compensate for productivity declines. Niche partitioning has also been reported to occur due to morphological or temporal separations among species in soil water resource acquisition under drought stress. Such differential acquisition strategies can partially reduce competition for soil moisture and stabilize carbon uptake (Lebourgeois et al. 2013). Differential drought sensitivity of co-dominant trees may also relax competitive interactions between species, allowing compensatory growth of the less sensitive species to occur that offsets growth reductions of the other species, as was observed within mixed stands of deciduous forest (Cavin et al. 2013).

However, plant communities with greater species richness may also potentially have negative (Pfisterer and Schmid 2002, Van peer et al. 2004, Lloret et al. 2007, Fischer et al. 2016) effects on ecosystem stability under climatic extremity. Both the sampling and niche complementarity effect of biodiversity have been reported to decrease the resistance of ecosystem productivity to climate extremes. The sampling probability effect suggests that biodiversity and ecosystem function relationships may be often driven by the chance of a plant community containing a highly productive species (Huston 1997). Yet just as more species-rich communities may have a greater probability of containing highly productive species, such highly productive species may exhibit functional trade-offs and thus be highly sensitive to a particular climate extreme.

As a consequence, this dynamic has been observed to decrease the resistance of ecosystem productivity to an extreme (Pfisterer and Schmid 2002). Similarly, niche complementarity in soil

water resource use has been reported to produce a greater draw down in total soil water availability, and thus heighten interspecific competition, increase plant water stress and decrease the performance of species in the community (Van peer et al. 2004). However, these examples appear to currently be the exception rather than the rule. Interestingly, Lloret et al. 2007 observed changes in the diversity-resistance relationship in response to drought in moving across climatic gradients, with positive relationships in water limited sites, and more negative relationships in wetter sites. This result suggests a potentially key role for the climatic context in which species and communities have evolved for contributing to variability in the relationship between species richness and resistance to climate extremes.

Resilience, i.e., the rate and magnitude of recovery, in ecosystem productivity following climate extremes has been reported to be driven by compensatory and demographic responses of species in the community following the climate extreme (Hoover et al. 2014a). As stated earlier, widespread mortality of dominant trees in forests due to extreme events can promote recruitment and growth of light-limited understory species in the community (Saura-Mas et al. 2015, Lloret et al. 2016), which can partially offset reductions in ecosystem productivity while at the same time altering community composition. For example, Lloret et al. 2016 observed mortality following a climate extreme to be positively correlated with seedling recruitment in Mediterranean shrublands. Thus, mortality or reduced performance of species in the community presents a potential pathway for other species in the community to compensate and offset productivity declines and drive ecosystem recovery, thereby enhancing stability in function.

In contrast, Isbell et al. 2015 observed a lack of evidence for increased resilience in productivity with higher plant species diversity across grassland biodiversity experiments. Reductions in species richness also often do not preclude full recovery in productivity in native
grassland plant communities (Tilman and El Haddi 1992, Hoover et al. 2014a). However, diversity-dependent ecosystem recovery following extremes is also often reported (Reusch et al. 2005). Thus, there appears to be lack of generality in the effect of plant diversity on ecosystem resilience to climate extremes. On this issue, ecosystem resilience to climate extremes may be a process in plant communities that is more strongly driven by both post-extreme abiotic conditions and the functional traits of the surviving species in the community, irrespective of species richness (Smith and Knapp 2003, but see Tilman 1997, Van Ruijvan et al. 2010). More specifically, resource availability following relaxation of the extreme and the capacity of the surviving species to respond to those conditions will likely drive ecosystem resilience (Hoover et al. 2014a, Tilman and el Haddi 1992). Nevertheless, high resilience in community composition does not appear to be requisite for high resilience in ecosystem function following climate extremes, yet this may vary by case and warrants further exploration.

Another community-level process that may contribute to stability in ecosystem processes under climatic extremity is the beneficial interactions between species that can develop during a climate extreme, such as facilitation (Lloret et al. 2013). Shifts from competitive to facilitative interactions between species due to increases in abiotic stress underlie the stress gradient hypothesis (Michalet et al. 2013). Although there is evidence to suggest the existence of beneficial interactions between species under climatic extremity, these dynamics are ecologically context dependent. For example, whether species interactions were facilitative, competitive or neutral in response to drought and heavy rainfall depended on community compositional context in European grassland (Grant et al. 2014). Saccone et al. 2009 found that facilitation of understory nurse seedling during heat wave depended on soil moisture status, with facilitation disappearing under low soil moisture. Further, the presence of legumes has been observed to benefit neighboring plants under heavy rainfall via increased nitrogen availability, yet this effect may lessen or disappear under extreme drought (Khan et al. 2014). Thus, it is still unclear the role that species interactions will play with respect to community and ecosystem responses to climate extremes.

## 5.6 SPECIES INVASIONS AND CLIMATE EXTREMES

The entry of novel species into the community due to the community-level impacts of a climate extreme may become a stronger determinant of plant community change as the frequency and severity of extremes increases. As such, climate extremes have been posited to potentially facilitate species invasions via multiple mechanisms (Diez et al.2012), of which there is some supporting evidence. Mortality of species in the community may produce 'invasion windows' that reset plant community development (Jimenez et al. 2011). This resetting of community dynamics has been observed to facilitate the entry of novel species into the community, in large part due to space creation (Dreeson et al. 2015).

Mortality of individuals and space creation may also generate a pulse of resources during or after a climate extreme that facilitates the establishment of novel species into the community (Manea et al. 2016), as predicted by the fluctuating resource hypothesis (Davis et al. 2000). Indeed, extreme wet years have been observed to potentially facilitate plant invasions (Koerner et al. 2015), likely due to increased inorganic nitrogen availability via increased mineralization (Concilo et al. 2015). Extremes such as drought may also induce alterations to soil properties that promote exotic performance over natives (Mesiner et al. 2013). Heightened performance of exotics under climatic extremity may then lead to community compositional changes, with consequences for ecosystem productivity (Caldeira et al. 2015).

However, plant communities may also possess a high degree of structural resistance to invasion during or following extremes, of which varies depending on the degree to which the properties of the community (e.g. species richness) are altered. Invasion resistance appears to be predicated in part on both the species composition and richness of the community and the type of climate extreme. For example, Kreyling et al. 2008 reported a nearly two-fold increase in invasion under heavy rainfall as opposed to drought, yet with the degree of invasion generally reduced in more diverse communities. Similarly, Sheppard et al. 2012 reported high variability in whether drought or heavy rainfall facilitated exotic performance. Establishment success of native versus exotic seedlings has also been demonstrated to depend on whether a temperature extreme was positive or negative (Hou et al. 2014), suggesting there will be important interactions between the type of climate extreme and the traits of the invaders. Thus, whether or not climate extremes will facilitate plant invasions is likely to be contingent upon the type of extreme, how the extreme modifies the species composition and abiotic conditions of the community and the functional attributes of the invader.

## 5.5 INTEGRATING RESPONSES ACROSS ECOLOGICAL SCALES

Studies that employ multi-scale approaches are valuable in demonstrating the importance of a holistic understanding of ecosystem responses to changing climatic variability (Knapp et al. 2002) and extremity (Jentsch et al. 2011, Hoover et al. 2014a, De Boeck et al. 2016). The magnitude of response to a climate extreme will likely vary with the ecological level of organization (e.g. 'fast' individual versus 'slow' community responses). Thus, an understanding of the relative sensitivities among scales may contribute insight towards the relation of each scale to one another, and contribute understanding towards the variability in ecosystem resistance and resilience to climate extremes. However, multi-scale studies employing greater than two ecological organizational levels are relatively rare (Fig. 5.1). The utility of multi-scale approaches in understanding ecosystem responses to climate extremes can be best demonstrated by those experiments that have assessed responses across multiple levels of organization, from the individual, population, community to the ecosystem level.

From a response perspective, Jentsch et al. 2011 observed negligible effects of a statistically extreme five-year growing season drought on both above and belowground ecosystem productivity in herbaceous plant communities. However, responses at the physiological were pervasive, which included reduced net photosynthesis, lower leaf water potentials and alterations to leaf C:N consistent with drought stress. At the plant community level, the experiment observed interspecific compensatory responses in species' morphology, in particular tiller outputs, that contributed to the stabilization in community productivity. These dynamics occurred without large structural changes in plant community composition. Thus, this experiment supports the hypothesis of stabilizing mechanisms within plant communities under climatic extremity (Lloret et al. 2012), and in particular the notion that processes that operate and interact across lower levels of organization may contribute to the stabilization of different ecosystem functions.

From a recovery perspective, Hoover et al. 2014a and (Table 5.1) observed plant water status, net photosynthesis and productivity responses of the dominant grass species to generally correspond with large reductions in aboveground net primary productivity in response to extreme drought. However, despite low ecosystem resistance to climate extremes and near local extinction of the dominant forb species, demographic compensation of the dominant grass following the extreme drove full recovery in ecosystem productivity (Table 5.1). Thus, while physiological and growth responses were partially linked with declines in ecosystem productivity and low resistance, it was community-level processes via demographic compensation of species following the extreme that largely drove full recovery and thus the stability of ecosystem production to drought. Furthermore, while drought responses interacted across scales in this ecosystem, heat wave

impacts were not detectable beyond physiological responses, despite both events being statistically extreme with regard to the long-term climate record (Hoover et al. 2014a for methods). Yet importantly, the underlying characteristics of each extreme also differed, as the drought lasted the entirety of the growing seasons, while the heat wave occurred for two weeks during the middle of each growing season. Nevertheless, Jentsch et al. 2011 and Hoover et al. 2014a and b demonstrate that interactions between lower ecological levels can underlie and inform ecosystem-level responses to and recovery from climate extremes. Additionally, responses to climate extremes at lower levels, such as in physiology, may not always be detectable at the ecosystem level depending on the type of climate extreme the system was exposed to, and the underlying characteristics of the extreme (e.g. magnitude or duration). In total, these results suggest that the organizational dynamics of scale within an ecosystem are likely to differ depending on the type of climatic stress experienced by the system (Table 5.1).

# 5.6 SYNTHESIS, CONCLUDING REMARKS, AND RECOMMENDATIONS FOR RESEARCH

Research on the ecology of climate extremes has emerged as a frontier in climate change research. Although the number of ecological studies on climate extremes continues to grow (Jentsch et al. 2011, Bailey et al. 2016, Ummenhofer et al. 2017), it is evident that both experimental and observational approaches often focus on one ecological level, and less often assess responses to an extreme climate period across multiple levels of ecological organization (Fig. 5.1). my review suggests that an understanding of ecosystem responses to climate extremes will be heightened by consideration of cross-scale interactions. This is so because it is often the case that variability, sensitivity or changes observed at one level (e.g. physiology or population),

can mechanistically act to reduce variability at other levels, such as ecosystem productivity (Tilman 1996, Jentsch et al. 2011, Hoover et al. 2014a), either during or after a climate extreme.

Within any given ecosystem, the variability of ecological responses is likely to decrease in moving from the individual, population, community to the ecosystem level. It also is clear that the efficacy of upscaling individual or population responses to the community or ecosystem level largely depends on the functional identity and/or population size of a species within the community. The literature to date has provided support for the notion that the responses of dominant species can feed into, and impact plant community and ecosystem responses to climate extremes. Yet equally relevant are biodiversity-driven dynamics at the community level that may operate in concert with the responses of dominant species. Community-level processes such as niche partitioning (in resource acquisition or stress tolerance) and demographic compensation, both during and after extremes, are ecological mechanisms that can heighten the stability of plant community composition or function to climate extremes.

As a consequence of these dynamics, I contend that studies focused on responses at one ecological level do so at the potential risk of overlooking contributing drivers to the variability of the response at that level, at least from an organizational perspective. Variability in the response of ecosystem productivity to climate extremes is likely to, in part, be determined by how individual, population and community processes respond, interact and integrate during and/or after the extreme period. Indeed, extreme climate periods often do not elicit large ecosystem level responses (Smith 2011). Yet, negligible impacts of a climate extreme on higher-order ecosystem-level functions do not necessarily mean that the system has not been detectably impacted at lower levels of organization. More pronounced impacts at lower levels, such as individual plant physiology or morphology, may underlie or portend interactions between population- and

community-level processes. These dynamics can further add explanatory power to responses at the ecosystem level, such as net primary productivity (Jentsch et al. 2011). However, I posit that different insights into the variability of ecosystem responses may be attained by scaling-down and decomposing ecosystem-level responses into its smaller components (top down approach), versus scaling-up and integrating fine-scale responses to understand broader components (bottom up approach), as has been the focus of this review. Thus, assessing how top-down versus bottom-up research approaches compare in terms of ecological response dynamics to climate extremes warrants further exploration.

Future research efforts focused on scaling individual responses to climate extremes to community or ecosystem processes ought to focus assessment on the responses of functionally distinct species in the community (e.g. dominant species), and relate those responses to the broader context of community and ecosystem responses. Thus, a deeper understanding of how current ecological dominants, i.e., those species with large population sizes, will respond to novel climatic stress may provide insight to the potential pathways and trajectories of change in community composition and/or productivity. Prior research also suggests that community-level properties and processes such as functional diversity, beneficial interactions and species invasions, all have the potential to modify community and ecosystem resistance and resilience to climate extremes.

Community ecology in particular is often described as having a 'black box' of complexity and contingency (Vellend 2010). Indeed, such complexity appears to apply equally well to climate extremes. On this notion, I stress the need for deeper investigation into how processes and species interactions within (e.g. competition) and among (e.g. dispersal) communities may scale to impact the stability of community composition and ecosystem function, both locally and regionally, during and after climate extremes. This follows the concept that non-random community compositional changes are likely to be a mechanistic pathway for mediating changes to ecosystem function that operate in synergy with environmental change drivers (De Laender et al. 2016), such as climate extremes. In addition, greater attention toward integrating population- and communitylevel processes into impact-oriented investigations of ecosystem-level responses to climate extremes will be critical in bridging individual to ecosystem responses (Fig. 5.2). Indeed, while the complexities of studying the impacts of climate extremes across levels of organization underscore the challenges in studying their dynamics, such complexity also signifies the importance of a holistic approach in assessing their ecological consequences.

## 5.7 TABLES

**Table 5.1.** Adapted from Hoover et al. 2014a, in which both a statistically extreme drought and heat wave were imposed on an intact grassland ecosystem over a two-year period, and responses across multiple levels of ecological organization were assessed. Checked boxes indicate detectable impacts to that ecological level, while unchecked boxes signify no detectable effects. The experimental results demonstrate how responses can propagate across levels of organization during and after a climate extreme, and how both individual and community level processes may both scale to the ecosystem level. Of equal importance is how two types of climate extremes yielded different dynamics; while responses cascaded across multiple levels of organization for extreme drought, the impacts from heat wave were not detectable beyond the physiological level. Such differences may very well be attributed to differential durations of the extremes, as the heat waves were of much shorter durations than the drought. Dynamics of how responses propagate across levels of organization within an ecosystem during or after an extreme likely differ depending on the type of climate extreme, as well as the underlying characteristics of the extreme.

Level of Organization	Drought	Heat Wave
<b>Individual</b> Physiological impacts on the dominant C ₄ grass species were evident for both drought and heat wave. However, only drought impacts translated to changes in growth rates and propagated to impacts in higher-order ecological processes.	Physiological 1 – Morphological 1 – Growth 1 –	Physiological ☑ – Morphological ☑ – Growth □
<b>Population</b> Asynchrony in species' population dynamics was driven by differential sensitivity to extreme drought. This lead to near local extinction of the co-dominant forb, with subsequent increases in the abundance of the dominant $C_4$ grass species.	Dominant species ☑ + Co-Dominant ☑ –	Dominant species
<b>Community</b> Re-ordering of species abundances in the community lead to altered species composition and diversity in the community following extreme drought.	Compositional change ☑	Compositional change □
<b>Ecosystem</b> Low resistance to extreme drought did not preclude full recovery in ecosystem productivity. Recovery was driven, in part, by community-level processes via demographic compensation of the dominant C ₄ grass following extreme drought.	Response ☑ – Recovery ☑ +	Response

## **5.8 FIGURES**



**Figure 5.1.** The number and type of study in terms of the ecological levels of organization that were assessed for the period 2000-2016. Inset is the data re-organized to more generally demonstrate the number of levels that studies have assessed. To date, ecological studies have typically focused assessment of responses to climate extremes at one ecological level, most notably the responses of individuals (e.g. physiology). What is clear is that studies that assess greater than two levels are comparatively rare, with the number of studies a decreasing function of the number of levels assessed. Studies were found and reviewed via a Web of Science and Google Scholar literature search utilizing the key words: climate extreme, plant, population, community, ecosystem. I then ran a separate search replacing climate extreme with drought because this extreme has been of much focus in ecology.



**Figure 5.2.** Conceptual diagram of how responses propagate across levels of ecological organization during and after a climate extreme. A climate extreme will initially impact individuals through physiological or mechanical damage that may impacts growth and fitness. Consequent downstream impacts to demographic processes may produce changes to population sizes that will feed into community compositional changes, particularly if the species that is impacted is the dominant species or has a large initial population size. Abundance shifts or local extinction of species may be partly offset by community level processes, such niche partitioning or demographic compensation, that can then drive stability in the response or recovery of different ecosystem functions.

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### **CHAPTER 6: CONCLUSIONS**

Atmospheric warming and consequent intensification of the global hydrological cycle (Huntington 2005) has led to forecasts of future changes in precipitation regimes (IPCC 2013). Specifically, future precipitation regimes are expected to be characterized by greater interannual variability in wet and dry years and extremes such as drought (Cook et al. 2015), as well as more subtle changes within years to the size and timing of individual rainfall events (IPCC 2013). Such alterations to precipitation regimes have led ecologists to question whether current understanding of how precipitation impacts ecosystem functioning, such as net primary productivity (NPP), may change under more variable and extreme weather patterns (Estiarte et al. 2016, Knapp et al. 2017, Luo et al. 2017). Current baseline understanding of how precipitation impacts NPP is derived from large spatial or within-site temporal relationships of NPP and precipitation, with a current preference for temporal relationships in benchmarking ecosystems models (Estiarte et al. 2016). Yet temporal relationships, i.e., temporal models, are limited with respect to predicting responses of ecosystem functioning to projected changes in precipitation extremes. Such limitations in temporal models, outlined in brief below, have provided much of the motivation for my dissertation research.

Due to the limited duration of data collection (e.g., 30 years), temporal models often do not capture the full change of historical climatic variability within a region. As a consequence, such models can be considered to characterize the response of NPP, or other ecosystem functions, to nominal precipitation variability. This raises the question as to how such models may perform in predicting responses to the most extreme precipitation deviations in the historical record, or perhaps more pressing, to extremes conditions with no historic analog (Kayler et al. 2015, Knapp

et al. 2017), particularly amid growing evidence for differential sensitivity of NPP to dry versus wet years (Knapp and Smith 2001, Wilcox et al. 2017, Zhang et al. 2017). Second, within-year rainfall patterns can vary dramatically among years, and the documented influence of precipitation patterns within-years on ecosystem functioning within grasslands (Knapp et al. 2002, Heisler-White et al. 2008, Heisler-White et al. 2009, Wilcox et al. 2015) warrants deeper investigation into how rainfall patterns interact with total precipitation amounts (Chapter 4, this dissertation). Yet to date, these two components of forecast precipitation change have been studied in relative isolation.

In this dissertation, I sought to answer three key, non-exclusive questions concerning limitations of current temporal models in an effort to improve understanding of how grassland ecosystems will respond to future changes in precipitation variability and extremity: 1) How do changes in precipitation extremes in terms of total amounts impact ecosystem functioning, the underlying relationship ecosystem processes with precipitation, and is there differential sensitivity of ecosystems with contrasting climatic backgrounds?; 3) How do within-year rainfall patterns modify the sensitivity of ecosystem functioning to total precipitation amounts?

*Ecosystem responses to precipitation amount and extremity*. In chapters 2 and 3, I assessed responses of two key ecosystem functions (aboveground net primary production; ANPP and soil respiration) to a gradient of growing season precipitation amount and extremity within two distinct grassland ecosystems: the semi-arid steppe of Colorado and the mesic tallgrass prairie of Kansas. Despite different climatic and edaphic characteristics of these grasslands, as well as different dominant plant species controlling ANPP, both ecosystems exhibited greater relative sensitivity of ANPP to extreme increases in precipitation versus extreme reductions, relative to nominal (e.g. 25th - 85th percentiles) inputs, at least for single-year extremes. This result suggests high sensitivity

of grassland primary production to extreme wet years, and supports previous reports of ANPP responses to nominal (Knapp and Smith 2001) and more extreme (Wilcox et al. 2017) precipitation deviations, as well as the hypothesis that the marginal cost of deploying new tissue during resource pulses is less than abscission during drought (Sala et al. 2012). Yet this is also in contrast to my hypothesis of greater relative sensitivity to the most extreme precipitation reductions driven by large water stress, with concurrent saturation at the most extreme increases in precipitation. I was additionally unable to find strong evidence in support of soil nitrogen (or light in the tallgrass prairie) resource co-limitation within either grassland, or of vegetation constraints specifically within the semi-arid steppe.

*Within-year rainfall patterns.* In chapter 4, I utilized a 2-year manipulation within the tallgrass prairie to test how rainfall patterns within years may impact the sensitivity of ecosystem function (rain use efficiency of ANPP) to total precipitation amounts. This multi-year experiment imposed a gradient of total precipitation amounts eliminated variability in rainfall patterns by keeping the timing and size of rainfall events virtual constant. This served as a null model of variability in within-year rainfall patterns, which allowed me to contrast the effects of this manipulation on ecosystem function with a long-term record of similar precipitation amounts, yet considerably high variability in natural rainfall patterns. What this study shows is that as the ecosystem is saturated during wet years, the impact of variability in rainfall patterns on ecosystem function is reduced. Yet as conditions move towards drought and thus the primary limiting resource (water) within this ecosystem becomes increasingly scarce, the sensitivity of this system to variability in rainfall patterns increases. Within this mesic ecosystem, I found that variability in rainfall patterns - here large events - acts to magnify reductions in ecosystem function during drought by decreasing the efficiency by which rainfall is utilized for productivity.

My results are in general support of previous findings within this mesic grassland (Knapp et al. 2002, Fay et al. 2003). Larger events, and a consequent greater percentage of total rainfall being derived from them, is likely to lead to two nonexclusive consequences for mesic ecosystem ecohydrology and functioning. The first is a high percentage of ineffective rainfall relative to total rainfall due to runoff or deep soil percolation, especially within the shallow upland soils of my study, where the bulk of root water uptake is restricted to the top 20 cm of the soil profile (Nippert et al. 2012). Second, because the majority of rainfall is derived from single large events, intermittent periods between these events during the growing season likely result in increased water stress due to lower mean soil moisture in the rooting zone (Knapp et al. 2008). Indeed, this dynamic will be influenced by the timing of these large events (Craine et al. 2013), and I highly suspect interactions between patterns and amounts differ across ecosystems of historically different water balances (e.g. deserts versus forests). I further suspect that the relationships I observed between within-year rainfall patterns, total amounts, and ecosystem functioning may change as a certain magnitude of drought intensity is experienced and thus a threshold is surpassed, as recently demonstrated by Due et al. 2018. Identification of such thresholds, as well as how interactions between among and within-year rainfall variability differ across ecosystems of different climatic backgrounds, are areas of research I contend warrant greater attention.

*The role of ecological contingency*. Despite ecology being a relatively young science, the lack of predictability and laws in ecology has historically been a key source of frustration for ecologists, and has pushed some to recommend focusing on large spatial scales to increase degrees of generality in ecological relationships, and presumably predictability (Lawton 1999). In contrast, the seemingly built-in contingency of ecological dynamics has led others to *refute* the notion of ignoring details and focusing all efforts on generality or large spatial scales (Simberloff 2004). My

work and findings here supports the latter idea, in that a truly predictive understanding of how these ecosystems will respond to precipitation change can be best understood within the context of characteristics specific to the ecosystem. Greater relative sensitivity to extreme precipitation increases and support for an underlying linear relationship within both ecosystems was observed, yet the reasons behind these convergent responses likely varies between these two ecosystems. In general, at the wet ends of my precipitation gradient I suspect that low light limitation and high growth potentials of herbaceous vegetation produces high NPP sensitivity to growing season soil moisture surpluses, consistent with hypotheses outlined in Knapp and Smith 2001. However, low light limitation was driven by different factors within each grassland.

The shortgrass steppe attains low light limitation primarily due to low mean ANPP, and thus leaf area, of these regions. Low ANPP reflects frequently low levels of plant water availability in this ecosystem (due to both low precipitation inputs and high evaporative losses), supporting water as the primary resource limiting NPP, as I was also unable to detect a strong impact of precipitation on soil nitrogen availability. Thus, the low mean productivity, low light limitation, and high sensitivity to precipitation and moisture pulses (Heisler-White et al. 2008) within the semi-arid steppe likely underlies the observed large gains in NPP during wet years in semi-arid regions (Haverd et al. 2016). The experiment within the tallgrass prairie occurred within an annually burned (spring) watershed, a common management practice that increases forage productivity and its sensitivity to precipitation (Briggs and Knapp 1995). Frequent burning may also lead to low nitrogen availability and thus my inability to detect an effect of soil moisture on nitrogen availability (Knapp et al. 1998). As a consequence of spring burning, this watershed experiences low light limitation throughout most of the growing season. And despite this system having relatively high mean productivity - in contrast to the semi-arid steppe - soil moisture

carryover from snowmelt or previous-year precipitation may also assist in partially buffering the system to single-year drought episodes, preventing large declines and thus greater relative sensitivity to drought.

Together, these dynamics enable large increases in NPP during wet years with this mesic grassland and add clarity to my experiments results. Though not an exhaustive discussion of the contingencies within these ecosystems, they highlight, in my view, that site-based assessments and knowledge are a critical component to understanding, and preparing for how particular ecosystems will respond to precipitation change. These and other contingencies during extremes (Chapter 5 this dissertation), pose a challenge in the downscaling of continental-scale spatial relationships of precipitation and ecosystem function to any one particular site, as other factors come into play that mediate the sensitivity of ANPP to precipitation within-sites. Yet at the same time, such contingencies underscore the utility and value of site-based data collection and experiments in ecological research.

*Concluding thoughts and future directions.* It is likely that a linear model will not hold in explaining the responses of ANPP to precipitation with respect to future precipitation regimes (IPCC 2013), particularly if extremes increase in magnitude beyond historically experienced within these regions. Indeed, my finding of clear saturation in soil respiration responses to water availability within the tallgrass prairie reflects the limitations in the response of ecosystem processes to water availability, and suggests limitations on other ecosystem processes, such as ANPP, may eventually arise as well. This raises the question as to what may cause shifts towards nonlinearity within these systems, holding the aforementioned contingencies constant within both systems. I suspect that my findings reflect the dynamics of these systems' responses to single-year extremes, given that these extremes are not necessarily outside the bounds of what has been

historically experienced within these regions, as the precipitation percentiles were derived from long-term records. This leads to two key characteristics of extremes that warrant further exploration and can be achieved through the replicated regression experimental design I have employed in this dissertation: the magnitude and duration of climatically extreme periods.

Both of these characteristics of climate extremes - the magnitude and duration - reflect my thought that conditions with little to no historic analog will be needed to alter ecosystem properties (e.g. soil moisture or nitrogen availability) to a degree that pushes the ecosystem beyond a response threshold. In other words, extreme climatic conditions of longer durations or greater magnitudes (e.g. % precipitation reductions) than historically experienced may be needed to produce ecological responses that deviate from our current understanding of eco-climatic relationships derived from nominal climatic variability. Holding the timescale of my manipulation constant (e.g. one growing season), I hypothesize that greater deviations of precipitation than in my experiment - both increases and decreases - will be needed to push the system towards nonlinearity and greater relative sensitivity to severe drought. Consistent flooding during severe wet years, and consequent saturating of soil, would likely place an upper limit and the response of NPP, whether through initial hypothesized vegetation growth limitations (Yahdjian and Sala 2006), clear depletion of co-limiting resources such as light or nitrogen (Huxman et al. 2004), or metabolic stress imposed by hydric soil conditions (Knapp et al. 2017).

There is also evidence that the duration of a climatically extreme period can produce cumulative impacts on ecosystem function. As discussed in chapter 3, Hoover et al. 2014 found drought-induced ANPP reductions to be far greater in the second year of severe drought. This suggests that cumulative stress effects through time, whether via depletion of carbohydrate reserves, or simply the carryover of soil moisture depletion into the second year, can magnify the impact of precipitation reductions on ecosystem functioning. I suggest that future work can address the role of the magnitude and duration of precipitation extremes quite efficiently through the replicated regression experimental design. My findings in this dissertation suggest these characteristics are likely to be of critical consideration in understanding the impact of precipitation extremes within the two grasslands I have studied, and potentially many other grasslands. Utilizing the regression design, interannual-level characteristics can also be crossed with manipulations of within-year rainfall patterns (e.g. larger and fewer events) across a large gradient of total precipitation amounts, and be manipulated for multiple years. As my research points to a critical role of these characteristics in impacting the responses of these ecosystems to extremes, future work can be directed towards elucidating their independent and interactive effects on ecosystems. Such knowledge is critical not only from a theoretical and ecological perspective, yet is needed to understand, predict, and prepare for how future changes in precipitation regimes will impact the services humans derive from ecosystems.

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