DISSERTATION

SENSITIVITY OF A SEMI-ARID GRASSLAND TO EXTREME PRECIPITATION EVENTS

Submitted by

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ABSTRACT

SENSITIVITY OF A SEMI-ARID GRASSLAND TO EXTREME PRECIPITATION EVENTS

Rising global temperatures due to climate change are intensifying the hydrological cycle, resulting in larger and more frequent extreme rain events, or deluges. Dryland ecosystems are predicted to be especially sensitive to this change in precipitation pattern because, in these water-limited systems, ecological processes are largely controlled by infrequent water pulses and deluges represent an extreme precipitation pulse. Therefore, my dissertation examined how the semi-arid shortgrass steppe of eastern Colorado responds to deluge timing and size. Using field experiments, I applied deluge events to grassland plots that varied in seasonal timing (early, middle, or late growing season) and magnitude (moderate – extreme event sizes), and quantified ecosystem response. I also conducted an observational study to determine if these plot-level results could be scaled to the larger shortgrass steppe landscape. I identified natural deluges in the historical precipitation record and related spatial variation in precipitation to post-deluge canopy greenness via satellite imagery. My field experiments showed that the shortgrass steppe is extremely responsive to large rain events, with most measured variables exhibiting a substantial increase following an applied deluge event. Measured variables included soil moisture, soil respiration, and above and belowground net primary production (ANPP & BNPP), as well as growth and flowering of the dominant grass species, *Bouteloua gracilis* (blue grama). However, response magnitude depended on both deluge timing and size. The shortgrass steppe was most responsive to a mid-growing season (July) deluge, and ecosystem processes generally increased linearly with increasing deluge size, with limited evidence for response saturation. My observational study exhibited similar patterns at the landscape-scale, suggesting that these experimental plot-level results can be scaled to the larger shortgrass steppe landscape, despite greater variation in soil texture, grazing regime, and plant community. Overall, my dissertation research suggests that semi-arid ecosystems could be well-adapted to the increase in rainstorm size and frequency predicted with climate change; however, the magnitude of the ecosystem response depends on intra-seasonal precipitation patterns, including deluge timing and size. These findings have important implications for predicting both local ecosystem services (e.g., forage production) and global carbon cycling under altered precipitation regimes.

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DEDICATION

To my parents,

who taught me to love nature and science.

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CHAPTER 1: INTRODUCTION

Atmospheric concentrations of greenhouse gases, such as carbon dioxide (CO_2) and methane (CH_4), are rising at alarming rates due to emissions from anthropogenic sources including industry, transportation, and land degradation (IPCC, 2013). This is causing the Earth to warm, with average global temperatures predicted to increase by as much as 2.6-4.8°C by the end of the 21st century without significant emissions reductions (IPCC, 2013). One consequence of a warmer atmosphere is an overall intensification of the hydrologic cycle: for every 1°C increase in temperature, the water-holding capacity of the atmosphere increases by about 7% (Trenberth, 2011). As a result, many parts of the world are already experiencing significantly altered rainfall patterns, especially more frequent precipitation extremes, such as droughts and large rainstorms (Huntington, 2006; Groisman & Knight, 2008; Donat et al., 2016). These extreme events have dire consequences for both natural ecosystems and society, such as crop and livestock failure, water insecurity, and loss of biological diversity (Mantyka-pringle et al., 2012; Prăvălie, 2016; Gaur & Squires, 2018: Eekhout et al., 2018; Klemm et al., 2020). Therefore, it is important to understand how ecosystems respond to these precipitation extremes in order to more accurately forecast future impacts on both ecological function and society.

Dryland ecosystems, such as grasslands, are predicted to be especially sensitive to these changes in rainfall regime because they are inherently water limited (D'Odorico & Porporato, 2006). Drylands cover about 45% of the Earth's land area (Prăvălie, 2016) and provide many important ecosystem services, such as habitat for culturally and economically important plants and animals (Abberton et al., 2010; Pendall et al., 2018). They also serve as significant carbon sinks because CO_2 is absorbed by plants and held in biomass and soil, effectively removing it from the atmosphere (Pendall et al., 2018). However, dryland ecosystems are extremely sensitive to rainfall amount, as evidenced by the well-established positive linear relationship between average annual precipitation and total plant growth, measured as aboveground net primary production (ANPP), across most grassland ecosystems (Sala et al., 1988; Huxman et al., 2004). This tight association between water input and ecosystem function suggests that a shift in precipitation regime could significantly impact many ecosystem processes in these water-limited environments.

A recent study assessed drought sensitivity across a gradient of grassland types (from desert grassland to tallgrass prairie) and found the driest grasslands to be most sensitive to reduced precipitation (Knapp et al., 2015a). This is likely due to several factors. First, more mesic grasslands are often co-limited by other resources besides water, making them less sensitive to changes in precipitation (Huxman et al., 2004). Second, xeric (arid and semi-arid) grasslands experience larger inter-annual variability in precipitation (Gherardi & Sala, 2019; Morin et al., 2020), so the native plants are well-adapted to rapid changes in water availability (Knight 1973; Sala et al., 1982). For example, in the semi-arid shortgrass steppe of eastern Colorado, the dominant grass species (*Bouteloua gracilis*) senesces its aboveground tissue during drought but can quickly re-grow new leaves after a rainstorm (Menke & Trlica, 1981; Hazlett, 1992; Parton et al., 2012). This results in highly variable year-to-year ANPP based on annual rainfall pattern and amount and leads to the observed extreme reduction in productivity under drought conditions. In fact, due to their extreme sensitivity to water inputs, semi-arid ecosystems account for a large portion of inter-annual variation in global carbon uptake (Poulter et al., 2014; Ahlstrom et al., 2015). Therefore, it is of both regional and global importance to understand how semi-arid ecosystems respond to altered precipitation regimes caused by climate change.

While numerous studies have assessed the response of semi-arid ecosystems to drought events (e.g., Evans & Burke, 2013; Griffin-Nolan et al., 2018; Luo et al, 2019; Carroll et al., 2021), few have assessed their response to the opposite extreme, large rain events. This represents a critical knowledge gap given the mounting evidence that large rain events, or deluges (defined as statistically large rain events, cf. Smith, 2011), are increasing in magnitude and frequency across many parts of the world (IPCC, 2013; Janssen et al., 2014; Monier & Gao, 2015). In fact, most of the central and northeastern regions of the United States, including all of the Great Plains, are already experiencing increases in both deluge size and frequency (Mallakpour & Villarini, 2017). Given their observed sensitivity to altered precipitation (Knapp et al., 2015a, Maurer et al., 2020), semi-arid ecosystems could be especially affected by this change in rainfall regime. In these chronically water-limited systems, a single deluge significantly increases total annual rainfall (Sala et al., 1992; Knapp et al., 2015b), yet it is unclear how effective precipitation delivered via a deluge might be at stimulating ANPP and other ecosystem processes.

Results from several prior experiments suggest that semi-arid ecosystems might respond positively to large rain events (Lauenroth & Sala, 1992; Heisler-White et al., 2008; Cherwin & Knapp, 2012; Wilcox et al., 2015). In these dry systems, ecological processes are largely driven by infrequent precipitation events that temporarily elevate soil moisture (Noy-Meir, 1973; Schwinning & Sala, 2004), and deluges cause substantial soil moisture pulses. For example, Heisler-White et al. (2008) manipulated growing season rainfall patterns in the shortgrass steppe of eastern Colorado and found that water applied as a few large events increased ANPP more than the same amount applied as more frequent, smaller events. Large rain events promote deeper soil water infiltration, proportionally reducing evaporative losses and increasing plant-available water (Loik et al., 2004; Knapp et al. 2008; He et al., 2012). In addition to event size, the timing of precipitation inputs can also influence ecosystem processes, with results from past studies suggesting that early-season rainfall stimulates greater plant growth than does late-season rainfall in the shortgrass steppe (Derner & Hart 2007; Derner et al. 2008; Parton et al. 2012; Morgan et al. 2016). Given this demonstrated sensitivity to intra-annual precipitation patterns, it seems likely that semi-arid ecosystems could also respond strongly to deluge events. Therefore, my dissertation examined the impact of deluge timing and size on key ecological processes in the semi-arid shortgrass steppe of Colorado.

In the following chapters, I describe three separate field experiments, as well as an observational study using remote sensing data, to understand how the shortgrass steppe responds to deluge events. All of my research was conducted at the Central Plains Experimental Range (CPER), a 62.7 km^2 tract of shortgrass steppe owned by the United States Department of Agriculture-Agricultural Research Service (USDA-ARS) located in northeastern Colorado (40.8422, -104.7156). Since prior studies have reported a lack of biomass response to late-season water inputs (Derner & Hart 2007; Parton et al., 2012), my first field study aimed to measure the sensitivity of plant growth and ANPP to late-season deluges of varying magnitude (Chapter 2). Building on those results, my second field experiment assessed how the seasonal timing (early, middle, or late growing season) of a single deluge altered key ecological processes in the shortgrass steppe (Chapter 3). My third field study quantified ecological responses to deluge size (moderate – extreme), with the aim of identifying event size thresholds beyond which ecological processes saturate (Chapter 4). Finally, Chapter 5 describes an observational study in which I identified natural deluges in the long-term precipitation record and related spatial variation in precipitation across the CPER to post-deluge canopy greenness (normalized difference vegetation index, NDVI) via satellite imagery. The goal was to determine if the results from my small-scale deluge experiments (Chapters 2-4) could be scaled up to the larger shortgrass steppe landscape. Through this research, I hoped to elucidate how semi-arid ecosystems respond to extreme rain events, such as those predicted for the future, in order to better understand how these altered rainfall patterns might affect both regional and global carbon cycles.

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CHAPTER 2: PLANT GROWTH AND ABOVEGROUND PRODUCTION RESPOND DIFFERENTLY TO LATE-SEASON DELUGES IN A SEMI-ARID GRASSLAND[1]

2.1 Summary

Semi-arid ecosystems are strongly water-limited and typically quite responsive to changes in precipitation amount and event size. In the C_4-dominated shortgrass steppe of the Central US, previous experiments suggest that large rain events more effectively stimulate plant growth and aboveground net primary production (ANPP) than an equal amount of precipitation from smaller events. Responses to naturally occurring large events have generally been consistent with experimental results, with the exception of large events occurring later in the growing season (e.g., August). These have been reported as less effective at increasing net C uptake, despite temperatures optimal for C_4 plant growth. Because atmospheric warming is increasing the frequency of statistically extreme rain events (deluges) throughout the growing season, how late-season deluges affect semi-arid ecosystems remains to be resolved. We applied deluges in August of three sizes (1.0-2.5 times average August precipitation) to assess the potential for late-season deluges to stimulate plant growth and ANPP. These late-season deluges led to significant "green-up" of this grassland, with new leaf production and an increase in flowering of the dominant grass species. Further, these responses increased as deluge size increased, suggesting that larger or multiple deluges may lead to even greater growth responses. However, despite strong plant-level responses, no increase in ANPP was measured. Our results confirm that aboveground plant growth in the C_4-dominated shortgrass steppe does respond to

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[1] Post, A.K., & Knapp, A.K. (2019). Plant growth and aboveground production respond differently to late-season deluges in a semi-arid grassland. *Oecologia*, 191(3), 673-683.

late-season deluges; however if there is an increase in plant biomass, net accumulation aboveground is minimal at this time of year.

2.2 Introduction

Warming air temperatures are intensifying the hydrologic cycle globally, resulting in more frequent extreme events that range from extended periods of drought to more frequent large individual precipitation events or deluges (Huntington, 2006; Groisman & Knight, 2008; IPCC, 2013; Donat et al., 2016). There is evidence that an increasing proportion of precipitation now occurs as large rain events in many parts of the world (Easterling et al., 2000; Groisman & Knight, 2008; Groisman et al., 2012; Kunkel et al., 2013; Janssen et al., 2014; Monier & Gao, 2015; Mallakpour & Villarini, 2017). While a wide range of ecosystem types will be affected by intra- and interannual alterations in precipitation patterns globally (Weltzin et al., 2003; Knapp et al., 2008; Jentsch & Beierkuhnlein, 2008), arid and semi-arid systems are expected to be the most responsive (Diffenbaugh et al., 2008; Ahlstrom et al., 2015). In these ecosystems, ecological processes are largely controlled by the pulsed nature of individual precipitation events (Noy-Meir, 1973; Reynolds et al., 2004; Schwinning & Sala, 2004), and deluges (defined as events of statistically extreme magnitude, cf. Smith, 2011) represent an extreme precipitation pulse.

In arid and semi-arid ecosystems, where water limits most ecological processes and aboveground net primary production (ANPP) is strongly correlated with precipitation (Sala et al., 1988; Lauenroth & Sala, 1992; Knapp & Smith, 2001; Huxman et al., 2004; Bai et al., 2008; La Pierre et al., 2016), the occurrence of a single large precipitation event can significantly increase total annual precipitation (Sala et al., 1992) and potentially impact many aspects of ecosystem function (plant growth, phenology, soil respiration, etc.). Sensitivity to precipitation event size has been particularly well-documented in the semi-arid shortgrass steppe of North America. For example, Lauenroth and Sala (1992) showed that moderate-sized precipitation events (15-30 mm) explained the most interannual variability in long-term records of ANPP, with the inclusion of smaller events adding only minimal strength to the model. Moreover, Heisler-White et al. (2008, 2009) manipulated growing-season rainfall patterns in the shortgrass steppe and found that water applied as a few large events increased ANPP more than the same amount applied as more frequent, smaller events. While these studies indicate that larger precipitation events are more effective at increasing ANPP in the shortgrass steppe than more frequent, smaller rain events, small events do stimulate plant physiological processes and soil respiration (Sala & Lauenroth, 1982; Huxman et al., 2004; Parton et al., 2012).

In addition to precipitation event size affecting ecosystem processes in the shortgrass steppe, the timing of precipitation inputs is critical. In this ecosystem, spring moisture is especially important for plant growth (Derner & Hart, 2007; Derner et al., 2008; Parton et al., 2012; Morgan et al., 2016). In fact, Parton et al. (2012) reported that precipitation in April-June affects ANPP much more than July-August precipitation. Thus, late-season precipitation is often assumed ineffective for increasing aboveground plant biomass (Sala et al., 1992; Parton et al., 2012). Indeed, measurements before and after naturally occurring large precipitation events indicate that the ecosystem becomes a strong C sink in response to deluges in June, but has a variable response to August deluges, switching between a C source and sink depending on the deluge size (Parton et al., 2012). Unfortunately, differing antecedent conditions (e.g., rainfall, temperature, green leaf area) prior to naturally occurring deluges makes drawing inferences from such observational studies a challenge.

Intensification of the hydrological cycle is increasing event size both early and late in the growing season. But because uncertainty in ecological responses is greater for late-season deluges, we assessed the sensitivity of plant growth and productivity to late-season deluges of varying magnitude. In this undisturbed, native shortgrass steppe, we expected to measure positive responses in plant growth and ANPP to deluges given that August is the second warmest month of the year in this C_4 grassland, and that these responses would increase as deluge size increased. Such outcomes may necessitate extending the presumed period of effective precipitation for stimulating key ecosystem services (C sequestration, forage production) as deluges become more frequent.

2.3 Methods

2.3.1 Site Description

Research was conducted at the Central Plains Experimental Range (CPER) located in northeastern Colorado, USA (40.8422, -104.7156). The CPER, operated by the United States Department of Agriculture – Agricultural Research Service (USDA-ARS), is representative of the shortgrass steppe biome. Mean annual precipitation is 321 mm, with about 70% falling during the summer months (May – September), and mean annual temperature is 8.6°C (Lauenroth & Sala, 1992). Average ANPP is ~100 g m^{-2} (Lauenroth & Sala, 1992). The dominant grass species is *Bouteloua gracilis* (blue grama), accounting for as much as 90% total plant cover (Milchunas et al., 1989). This dominant grass is one of few shortgrass steppe species active late in the growing season, and is well-adapted to stochastic rain patterns, exhibiting opportunistic growth following water inputs (Dickinson & Dodd, 1976; Sala et al., 1982; Schwinning & Sala, 2004). Soils at our study site are classified in the Ascalon series (Aridic

Argiustolls; https://soilseries.sc.egov.usda.gov/) with a sandy clay loam texture (Sala et al., 1992).

2.3.2 Experimental Design and Treatments

We established twenty 0.5 x 0.5 m plots in a relatively flat area protected from livestock grazing for > 10 years. Since grass cover in this semi-arid ecosystem can be patchy, each plot was centered around a single *B. gracilis* tuft of similar size (~ 13 cm in diameter). Interannual variability in precipitation can be quite high in this and most semi-arid ecosystems (Knapp & Smith, 2001), so to control for antecedent conditions and reduce the possibility of a naturally wet year rendering the system unresponsive to experimental deluges, we erected rainout shelters over all the plots on May 1, 2016. Shelters were 0.5 m tall, and measured 1.22 x 1.22 m, creating a 0.36 m buffer around each plot. They were constructed from PVC (polyvinyl chloride) frames with clear corrugated polycarbonate roofs (Suntuf, Palram Americas) angled slightly to allow for intercepted rain to drain away. To prevent surface water flow into plots, we used aluminum flashing to create a barrier 10 cm outside the perimeter of each plot. Flashing was installed to a depth of 10 cm and extended 5 cm aboveground. The shelters remained in place for the duration of the experiment.

We assessed the influence of the shelters on environmental conditions by measuring light transmission and air temperature beneath the roofs. We used a 1-m linear quantum light sensor (Decagon AccuPAR, model LP-80) to measure photosynthetically active radiation (PAR) just above plant height both inside and outside of 10 shelters at noon on a sunny day in mid-July. Air temperature was measured in four plots every hour using iButtons (iButtonLink Technology, model DS1921G) installed 0.3 m above the ground. The iButtons were shielded from direct sunlight and attached to a wooden stake with an arm that extended over the plots to measure temperature at the plot center. Four additional iButtons were installed outside of the plots to measure ambient temperature.

Plots were randomly assigned to one of three watering (deluge) treatments or to the control treatment (N = 5 plots/treatment). The three watering treatments, based on the long-term rainfall record (1980 – 2015) from a nearby NOAA weather station (Nunn, CO; 40.7063, -104.7833) were average August rainfall (36 mm, Fig. 2.1), one standard deviation above average August rainfall (64 mm), and two standard deviations above average August rainfall (92 mm). Each treatment was applied as two distinct events (see below) so that individual rain events varied from 18 mm to 46 mm. The magnitude of such deluges has historic precedent in this semi-arid grassland. Indeed, despite relatively low monthly average precipitation in August, individual precipitation events often exceeded the monthly average precipitation total historically (Fig. 2.1). Control plots received no water during the month of August. The four treatments are referred to by the total amount of water added: 0 mm (control), 36 mm, 64 mm, and 92 mm.

Deluges were added as two events approximately 2 weeks apart to maintain an extended period of relatively wet soils, and thus maximize the potential for this ecosystem to respond to substantial late-season water availability. For example, the 36 mm treatment was applied as two separate 18 mm watering events on August 3, 2016 and August 19, 2016. Our selection of two temporally distinct deluge events in August has historic precedent at our site, with such a pattern occurring in about one in eight years. Water was applied to the entire area within the aluminum flashing buffer (0.7 x 0.7 m) using watering cans. Our goal was not to simulate characteristics of deluges from ecohydrological or meteorological perspectives (e.g., infiltration and runoff rates that vary with raindrop size and rainfall intensity), but rather the soil moisture consequences of large rain events, which result in significant and extended periods of soil moisture recharge in this ecosystem (Parton et al., 2012).

2.3.3 Measured Responses

Volumetric soil water content was measured approximately weekly in the center of each treatment plot from May-September using a handheld 20-cm depth time-domain reflectometry (TDR) probe (Campbell Hydrosense II). This instrument integrates soil moisture over the top 20 cm of the soil, a depth corresponding to the rooting zone for species at this site (75% of total root biomass is within the upper 20 cm), including *B. gracili*s (90% of root biomass) (Milchunas & Lauenroth, 1989; Nelson et al., 2004). Concurrently, we also measured ambient soil moisture outside the plots. More frequent measurements (every 1-4 days) were made directly following each deluge addition.

We assessed sensitivity to deluges by measuring responses in a variety of ecologically relevant attributes, including plant growth, canopy greenness, and ANPP. We considered an attribute to be "sensitive" if it showed a significant change after the deluge additions. We focused our measurements on the dominant species, *B. gracilis*, since it accounts for the majority of plant cover, so monitoring its deluge sensitivity is key to understanding the larger ecosystem-level response. Most measurements began just before or within a day of when experimental deluges were added.

Canopy greenness has been linked to many aspects of plant function (Homolová et al., 2013). The normalized difference vegetation index (NDVI) is a commonly used metric in remote sensing to track ecosystem-level greenness, which has a strong correlation with plant production and ecosystem C uptake, especially in grassland systems (Paruelo et al., 1997; Wang et al., 2003; Morgan et al., 2016). At a smaller-scale, digital repeat photography has been successfully used to calculate another index of plant greenness, the green chromatic coordinate (GCC, described in detail below). GCC is strongly correlated with NDVI, successfully bridging the gap between scales (Migliavacca et al., 2011; Browning et al., 2017; Vrieling et al., 2018). GCC has also been correlated with leaf area index and green biomass and has been used to predict ecosystem-level gross primary production (C uptake) in grassland systems (Migliavacca et al., 2011; Toomey et al., 2015).

We tracked the green-up response of the grassland by taking weekly digital images of the central *B. gracilis* tuft of each treatment plot using a Sony cyber-shot digital camera (model DSC-WX100). Roofs were temporarily removed to photograph the plots. Camera settings remained constant and the camera was always positioned 0.3 m above the ground. To standardize lighting, we shadowed the plots while taking pictures. In addition to photographing the treatment plots, we also recorded images of *B. gracilis* plants (N = 5) outside of the plots as an ambient comparison. All plots were photographed six times between August 2 and September 19, but the plots receiving the two wettest treatments (64 and 96 mm) were photographed an additional two times later in the season, as they remained green longer.

We calculated the GCC from each picture as an index of greenness. Digital images are stored as pixels that each have a numerical value of green, blue, and red intensity to determine its apparent color. The GCC uses those color intensities to compute the greenness relative to the total brightness for each pixel as: green / (red + blue + green) (Filippa et al., 2016). By using a ratio, this metric accounts for variation in image lighting. To minimize the influence of the background soil, we cropped each image to include only pixels from the central *B. gracilis* tuft in each plot. We used the package EBImage (Pau et al., 2010) in R to extract the green, blue, and red intensities and calculate GCC for each pixel. We then took an average of all the pixels in each picture to compute mean GCC.

Similar to GCC, measuring changes in live tiller and leaf densities allows for real-time tracking of plant response to water inputs, supplementing ANPP samples collected at the end of the growing season. Prior research has shown that tiller density accounts for a large portion of variability in ANPP in a tallgrass prairie (Hartnett & Fay, 1998), and tiller density and individual tiller production (measured as leaf density) are the strongest drivers of ANPP response to precipitation inputs in an arid grassland (Reichmann & Sala, 2014). Furthermore, tiller emergence is dependent on the availability and activation of belowground meristems (buds), one of the largest constraints on the biomass response of grasslands to rain pulses (Knapp & Smith, 2001; Dalgleish & Hartnett, 2006). Therefore, tracking vegetation structure, in the form of tiller and leaf dynamics, provides insights into the potential limitations on plant growth following a late-season water input.

Responses in live tiller and leaf density of *B. gracilis* were measured by establishing a 1.5-cm-wide transect across the longest diameter of the central *B. gracilis* tuft in each plot. At 1-2 week intervals, we counted the number of live tillers and leaves located within the transect. A leaf was considered alive if it was at least 50% green, and a tiller was considered active if any leaf originating from its base was at least partially green. We divided the leaf and tiller counts by the area of each transect (1.5 cm x diameter of *B. gracilis* tuft) to calculate tiller and leaf density (number per cm^2). All plots were counted five times between August 4 and September 19, but the plots receiving the two largest deluges (64 and 96 mm) were counted an additional two times later in the season, as they remained active longer.

We sampled for ANPP when all aboveground plant tissue had senesced at the end of the season. During late September, we harvested all plant biomass present in each 0.5 x 0.5 m plot. Biomass was sorted to functional group (grass, forb/woody) in the field. Samples were dried at 60°C for 48 hours and then processed to remove all plant material from the previous year (identified by grey color). Since grass flowering has shown sensitivity to precipitation inputs and can account for a significant portion of aboveground biomass in grassland systems (Craine et al., 2010; La Pierre et al., 2011; Moore & Lauenroth, 2017), *B. gracilis* flowering stalks in the samples were separated, counted, and weighed. All dried biomass was weighed to the nearest 0.01 g to determine ANPP. Finally, to assess whether late-season deluges impact forage nutritional quality, a portion of each dried ANPP sample (grass functional group only) was analyzed for carbon (C) and nitrogen (N) content (LECO TruMac CN Dumas analyzer, Ward Laboratories, Kearney, NE). The C:N ratio was then calculated for each sample.

2.3.4 Statistical Analyses

All analyses were performed in R (version 3.3.2) with a significance level of $p = 0.05$. For soil moisture, greenness, leaf density, and tiller density, analyses were performed on measurements taken during the defined "treatment period," from August 3 - September 19, 2016. For these data, we used the nlme package (Pinheiro et al., 2016) to run a repeated measures mixed model analysis of variance with treatment and sampling date as fixed effects, plot as a random effect, and an interaction term between sampling date and treatment. All models used an autoregressive covariance structure.

Both flowering stalk density and mass were square root transformed due to the non-normality of the data sets. Then, a Kruskal-Wallace non-parametric test (with Benjamini-Hochberg multiple-testing correction) was used to test for differences among the deluge treatments (36 mm, 64 mm, 92 mm); 95% confidence intervals were used to assess significant differences between the control and the treatment groups. A one-way ANOVA was used to analyze the ANPP data and the nutritional data sets (C content, N content, and C:N ratio).

2.4 Results

2.4.1 Environmental and Shelter Effects

We erected rainout shelters to reduce early season precipitation and prevent the plots from receiving above-average precipitation. Fortunately, 2016 was a relatively dry year— only 108 mm of precipitation (53% of the long-term average) fell from May to August. Thus, the shelters did not drastically reduce soil moisture relative to unsheltered ambient plots, with an average reduction of 3.4 ± 3.0 % (mean ± standard error) for the period prior to the August watering treatments (May 1 – August 2, Fig. 2.2). Nonetheless, the shelters were largely effective at excluding rainfall. Inspection of the soil moisture data indicates that sheltered plots experienced an increase in soil moisture after only one storm (with high winds in mid-June) prior to implementing deluge treatments. Thus, there were few differences in the measurements made in plots in the control shelters versus the surrounding grassland.

Using data from two nearby NOAA weather stations [1980-2002: Briggsdale, CO (40.6344, -104.3286); 2003-2016: Nunn 7 NNE, CO (40.8066, -104.7552)], we confirmed that the average daily maximum (28.9°C) and minimum (10.0°C) air temperatures for August 2016 (time of treatments) fell within the range of historic August temperatures (1980-2015; maximum: 27.5-33.0 °C, minimum: 9.6-14.0 °C). The shelters affected temperatures and light availability only slightly. For the period of May 13 – September 19, on average, the shelters caused 1.9 ± 1.1 °C warming during the day (7 am – 6 pm) and 0.5 ± 0.2 °C warming at night (7 pm – 6 am). Light transmission was 81.3 ± 4.8 %, which is similar to the value found by Yahdijian and Sala (2002) for their rainout shelters.

2.4.2 Treatment Effects

As expected, soil moisture peaked after each water addition in August and then gradually decreased with the magnitude of the peak proportional to the treatment size (Fig. 2.2). For the treatment period (August 3 – September 19), average soil moisture (volumetric water content) for each treatment was: 5.2 ± 1.8% (0 mm control), 12.1 ± 1.9% (36 mm), 15.8 ± 2.3% (64 mm) and 17.8 ± 4.6% (92 mm). All of the deluge treatments had significantly greater average soil moisture than the control treatment ($p < 0.01$ for all). A repeated measures mixed model ANOVA of the treatment groups (excluding the control group) showed significance for treatment, sampling date, and their interaction (Table 2.1). Following the first water addition, the 92 mm treatment had significantly greater soil moisture than the 36 mm treatment for about a week, and the 64 mm treatment had greater soil moisture for 5 days. Both larger treatments (64 & 92 mm) had significantly greater soil moisture than the 36 mm treatment again for 1-2 days after the second water addition.

All plots receiving deluges were visibly greener after the first water addition, reaching peak greenness in late August (Fig. 2.3). A repeated measures mixed model ANOVA showed significance for treatment, sampling date, and their interaction (Table 2.1). The overall increase in greenness was proportional to the treatment size. The ambient *B. gracilis* tufts (outside of shelters) remained brown for the entire month of August (which only received 11 mm of rainfall). The largest treatment (92 mm) greened most rapidly and had the highest GCC values, reaching peak greenness on Sept 2. This treatment was significantly greener than ambient for almost the entire treatment period, and significantly greener than the 36 mm treatment from Aug

22 – Sept 2. The two smaller treatments (36 & 64 mm) reached a similar maximum greenness on the same day (Aug 22), but the smallest treatment saw a more rapid decline after this date. Averaged over the treatment period, both the 64 mm and 92 mm treatments were significantly greener than ambient ($p = 0.0320$ & $p = 0.0003$, respectively), and the 92 mm treatment was significantly greener than the 36 mm treatment ($p = 0.0171$).

Consistent with GCC values, there was a rapid increase in live leaf density after the first water addition and this continued through the month of August (Fig. 2.4). A repeated measures mixed model ANOVA indicated that treatment, sampling date, and their interaction were all significant. The increase in live leaf density was proportional to the treatment size. All the treatments reached their maximum leaf density at the end of August. Leaf density was minimally increased by the 36 mm treatment and was significantly lower than the 64 mm treatment from Sept 12 – Sept 19, and lower than the 92 mm treatment from Aug 29 – Sept 12. When averaged over the treatment period, live leaf density (# cm^{-2}) for each treatment was: 36 mm = 2.62 ± 0.55, 64 mm = 4.24 ± 0.36, 92 mm = 5.52 ± 0.68. The 92 mm treatment had significantly greater average leaf density than the 36 mm treatment ($p = 0.0068$).

Live tiller density did not differ among treatments; however, a repeated measures mixed model ANOVA was significant for sampling date (Table 2.1). Thus, all deluge treatments caused an overall increase in live tiller density across the treatments, from 1.46 ± 0.15 tillers cm^{-2} on Aug 4 to 2.1 ± 0.18 tillers cm^{-2} on Aug 29 (results not shown).

Despite the clear responses above, there were no significant differences in total ANPP among the treatments ($F = 0.72$, $p = 0.5542$; Fig. 2.5). However, all the deluge treatments did have slightly higher average ANPP values than the control treatment (0 mm (control) = 66.48 ± 3.50 g m^{-2}, 36 mm = 75.83 ± 6.19 g m^{-2}, 64 mm = 69.75 ± 7.08 g m^{-2}, 92 mm = 78.24 ± 7.87 g

m^{-2}). Responses remained non-significant when biomass was partitioned by grass and forb functional groups (data not shown). Forb biomass was nearly identical across all treatments (8.87 ± 1.34 g m^{-2}), accounting for only a small portion of total biomass (12.83 ± 2.13 %). Similarly, there were no significant differences among the treatments for biomass C content (0 mm = 40.01 ± 0.50%, 36 mm = 39.97 ± 1.01%, 64 mm = 40.11 ± 0.64%, 92 mm = 40.00 ± 0.53% ; F = 0.0075, p = 0.9991), N content (0 mm = 1.23 ± 0.08%, 36 mm = 1.08 ± 0.09%, 64 mm = 1.20 ± 0.10%, 92 mm = 1.04 ± 0.09% ; F = 1.02, p = 0.4116), or C:N ratio (F = 1.03, p = 0.4047) of the foliage harvested at the end of season (results not shown).

August deluges stimulated flowering stalk production (Fig. 2.6). The average number of flowering stalks (and flowering stalk mass) for each treatment was: 14.4 ± 4.3 stalks m^{-2} (0.23 ± 0.06 g m^{-2}) for the 36 mm deluge, 22.4 ± 11.5 stalks m^{-2} (0.41 ±0.22 g m^{-2}) for the 64 mm deluge, and 21.6 ± 8.9 stalks m^{-2} (0.51 ± 0.23 g m^{-2}) for the 92 mm deluge treatment. Because control plots had zero flowering stalks, and none of the 95% confidence intervals for the deluge treatments included zero, we conclude that all the treatments had significantly greater flowering stalk density and mass than the control plots. However, due to high variance, there were no differences among the deluge treatments for either variable (density: $X^2 = 0.08$, p = 0.9603, mass: $X^2 = 0.65$, p = 0.7239).

2.5 Discussion

Prior studies have found that early-season, rather than late-season, moisture is most effective at stimulating plant growth, C uptake, and ANPP in the shortgrass steppe (Derner & Hart, 2007; Derner et al., 2008; Morgan et al., 2016), and others have reported little response to late-season precipitation, beyond an increase in ecosystem respiration (Parton et al., 2012; Hermance et al., 2015). Since deluges are predicted to become more frequent as a result of climate change (IPCC, 2013), and semi-arid ecosystems can play a large role in global C uptake (Ahlstrom et al., 2015), the influence of changing precipitation patterns on this ecosystem has both local and global relevance. Our goal was to more rigorously assess the potential ecological impacts of late-season deluges in a semi-arid grassland. Despite adding an almost threefold increase in average August precipitation, we measured no significant increase in ANPP in response to late-season deluges. This is consistent with the results from natural rain events observed by Parton et al. (2012), even though the largest single event we added (46 mm) was ~ 2 times the size of the largest August rain event observed in their study. Thus, we can confirm that late-season precipitation, even when received as large deluges during a period when air temperatures are near their annual peak, provide only a small contribution to total ANPP in the C_4 dominated shortgrass steppe.

Parton et al. (2012) noted that net ecosystem production (ecosystem C uptake) is highly correlated with the amount of live aboveground biomass in the shortgrass steppe, even more so than soil water content. It is typical for the majority of the leaves in the shortgrass prairie to be senesced by late in the season (Knight, 1973; Parton et al., 2012; Hermance et al., 2015), and thus a lack of photosynthetically active tissue may limit the ability of the plants to quickly respond to a significant water input (Schwinning & Sala, 2004). While our experimental plots were senesced prior to imposing the first deluge treatments, green leaves were present when the second deluge was imposed. Thus, a lack of response in ANPP is less likely to be due to green leaf area limitation. Alternatively, Parton et al. (2012) suggested that shortgrass steppe plants might allocate more carbon to belowground structures late in the growing season. In response to large, late-season rain events, they observed very little increase in aboveground biomass, despite an increase in ecosystem carbon uptake, suggesting that these dominant grasses may preferentially allocate C to belowground structures during this period of the growing season. This is consistent with increases in belowground meristematic reserves in the shortgrass steppe in early fall (Dalgleish & Hartnett, 2006) and observations by Frank (2007) that semi-arid grasslands are more sensitive to precipitation below than aboveground in late summer.

Despite a lack of deluge-induced ANPP response, the shortgrass steppe ecosystem did respond to late-season precipitation in other ways. We saw substantial green-up of the dominant grass species (*B. gracilis*), with the total amount of August rainfall dictating the magnitude of response. This immediate green-up after a significant late-season water input was also observed by Hermance et al. (2015) in the shortgrass steppe. Using a remotely sensed greenness index (NDVI), they determined that the rate and magnitude of green-up following a rain event differs within the growing season. Specifically, compared to early-season rain events, the shortgrass steppe greens up faster following a late-season rainfall, but the overall magnitude of green-up is reduced. This is consistent with the rapid green-up, but minimal biomass accumulation, observed in our plots. This decoupling of ecosystem green-up and biomass production suggests that correlations between ANPP and season-long NDVI may be weakened by the inclusion of late-season green-up events.

The visible green-up was primarily driven by the production of new *B. gracilis* leaves. In fact, the 92 mm treatment resulted in 2.3 times more green leaves than the 36 mm treatment when maximum leaf density responses are compared. This indicates that late-season deluges do stimulate some aboveground biomass production, and in proportion to the amount of water received, but this was not of sufficient magnitude to significantly increase total ANPP given the spatial variability in this grassland. We anticipated that new leaf production would increase overall forage nutritional quality (higher N content), given that young leaves tend to have higher

N content than older or senesced leaves (Anten et al., 1998; Zhang et al., 2013; Yang et al., 2014). However, this was not the case, perhaps because we analyzed bulk samples of aboveground biomass and the seasonal accumulation of sensed tissue diluted the effect of newly produced leaves, which were also senescent at the time of collection. Additionally, in this system, soil N availability is typically greatest early in the growing season, and then slowly declines (Burke et al., 2008). Therefore, new leaves produced late in the season may have lower N content than leaves produced earlier in the season.

We measured a slight increase in live tiller density across all the treatments, but this response to deluges was much less striking than the increase in leaf density, suggesting that the primary response to late-season water availability is the emergence of new leaves from existing tillers. Prior research has also found limited late-season tiller emergence in *B. gracilis* (Jaramillo & Detling, 1992). This lack of tiller response lends support to the meristem limitation hypothesis (Knapp & Smith, 2001; Dalgleish & Hartnett 2006), which states that the limited number of meristems in the belowground bud bank constrains the ecosystem's ability to respond to a sudden or extreme resource pulse. Dalgleish and Hartnett (2006) found that arid and semi-arid ecosystems generally have a small belowground meristem reserve, and in the shortgrass steppe, the bud bank peaks in early spring before the initiation of plant growth, and then remains low for the rest of the summer. As a result, very few tillers are available to emerge later in the season after the initial spring growth period, even with significant rainfall. This could be a potential mechanism to explain the low rate of tiller emergence following the deluge treatments, which in turn, could limit the ANPP response.

Late-season deluges stimulated *B. gracilis* flowering stalk production. Water availability appears to tightly control flowering stalk production, as all the watered treatments flowered but the control treatment did not, despite this being the expected flowering period for this species (July-August) (Dickinson & Dodd, 1976). In agreement with our results, past studies have found *B. gracilis* to be sensitive to precipitation inputs and their timing (Dickinson & Dodd, 1976; Samuel, 1985; Giuliani et al., 2014), with a recent study noting that July-September precipitation dictates the dates of flowering initiation and termination of this species in the shortgrass steppe (Moore & Lauenroth, 2017). The complete absence of flowers in the control treatment suggests that late-season deluges can provide sufficient moisture to promote the development of reproductive structures in an otherwise dry year. In fact, *B. gracilis* has been observed to not flower at all in extremely dry years (Moore & Lauenroth, 2017). However, flowering stalks only accounted for a small portion (< 1%) of total biomass across the treatment groups, explaining the lack of impact on overall ANPP. While *B. gracilis* primarily reproduces clonally (Lauenroth et al., 1994), flowering is still important for enhancing genetic diversity (Aguado-Santacruz et al., 2004) and forage nutrition (Arzani et al., 2004; Milchunas et al., 2008), as well as acting as an indicator of sufficient resource (water) availability for investment in expensive reproductive structures.

In summary, late-season deluges did not increase ANPP in the shortgrass steppe, but they did trigger a growth response in the dominant species, with significant green-up, leaf growth, and flowering. Therefore, we conclude that the shortgrass steppe is sensitive to late-season deluges at the plant-scale, but does not demonstrate sensitivity in ecosystem-scale ANPP. We highlight two additional implications of our results. First, from an ecosystem services perspective (forage production for livestock), despite a lack of measured increase in forage quantity, late-season deluges did stimulate new leaf growth, which could benefit cattle nutrition late in the season. Our failure to detect an increase in forage quality (tissue N content from bulk aboveground biomass samples) may be due in part to the fact that all leaves were senescent at the time of sampling (collected with ANPP samples). Had measurements been taken when leaves were still green in late August, a relative increase in N content due to new leaf growth might be more evident. More research is required to quantify the effect of late-season deluges on forage quality in actively grazed systems. Second, ANPP is estimated in this, and many other herbaceous-dominated semi-arid ecosystems, from mid-season harvests of peak biomass (Knapp et al., 2007). Our results suggest that increases in late deluges will not require shifting this sampling protocol to later in the year. However, more studies are needed to determine whether this timeframe also applies to belowground NPP estimates, as it is possible that belowground responses to late-season deluges may be greater than aboveground.

2.6 Tables

Table 2.1. Summary of the repeated measures mixed model ANOVA results for several measured variables (soil moisture, canopy greenness, leaf density, tiller density) with deluge treatment, date, and their interaction as factors. Reported values include the degrees of freedom (numerator, denominator), the F-statistic, and the p-value. Significant p-values are bolded**.**

Variable	Soil Moisture			Greenness			Leaf Density			Tiller Density		
	df	F	p	df	F	p	df	F	p	df	F	p
Treatment	2, 12	4.68	**0.0314**	3, 16	3.54	**0.0386**	2, 12	5.8	**0.0173**	2, 12	2.23	0.1506
Date	14, 168	109.49	**<0.0001**	5, 80	66.93	**<0.0001**	4, 48	20.48	**<0.0001**	4, 48	7.00	**0.0002**
Treatment x Date	28, 168	6.5	**<0.0001**	15, 80	11.36	**<0.0001**	8, 48	3.43	**0.0034**	8, 48	0.82	0.5852

2.7 Figures

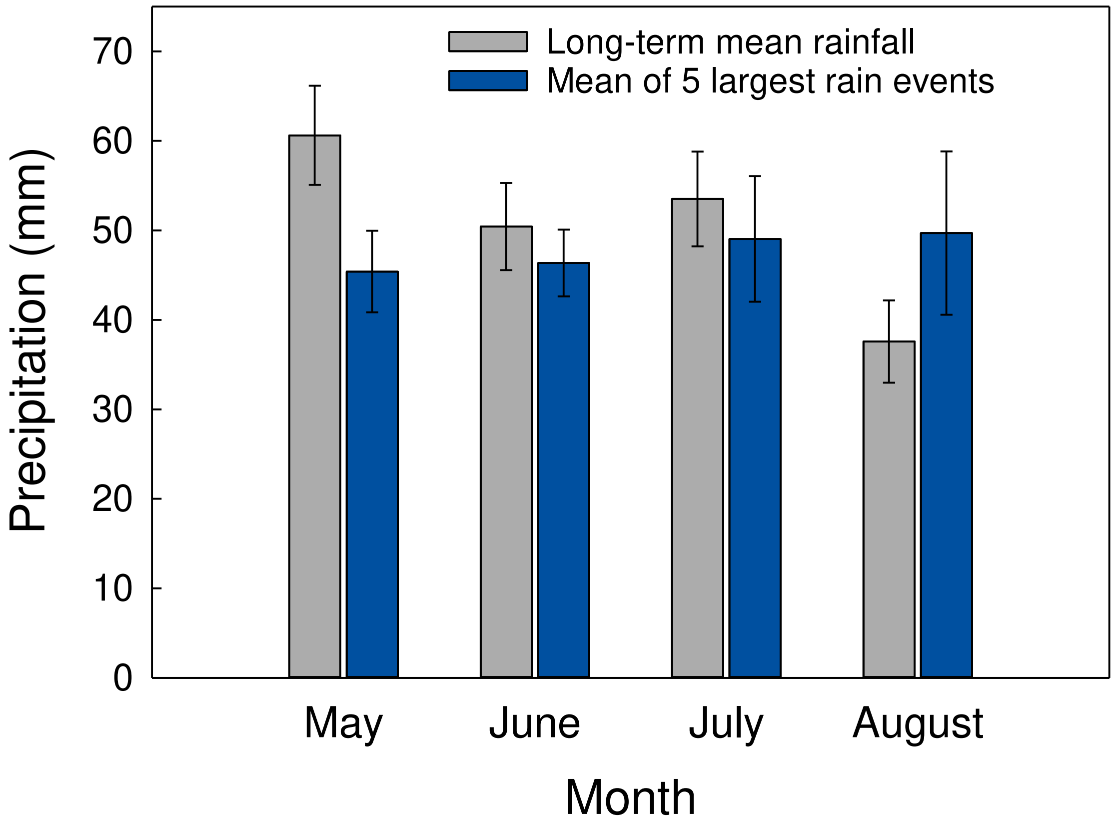

Figure 2.1. Long-term mean monthly rainfall and the mean of the five largest rain events (± SE) that have occurred each month at the CPER (1980-2017).

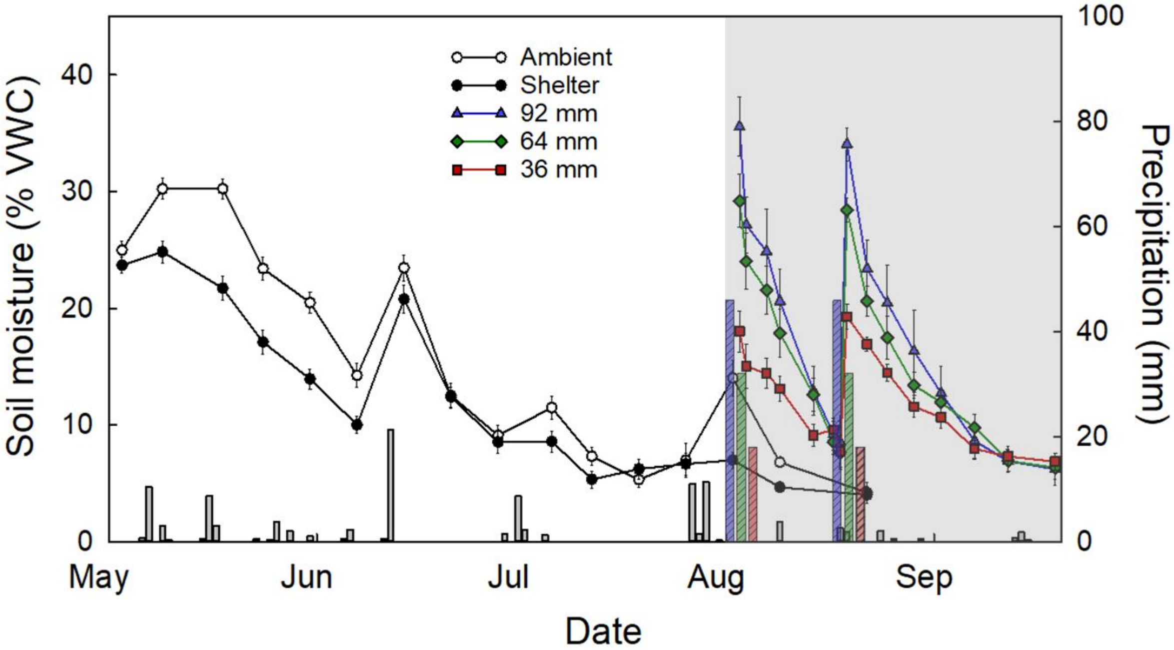

Figure 2.2. Seasonal patterns of soil moisture (lines; mean ± SE) and precipitation (bars) over the course of the 2016 growing season and in response to the deluge treatments. The grey panel denotes the deluge treatment period and hashed bars indicate the water added during the August watering treatments. Open circles represent ambient soil moisture, the filled circles represent soil moisture under the rainout shelters, and the other symbols (colored) represent soil moisture of the different treatments after water additions.

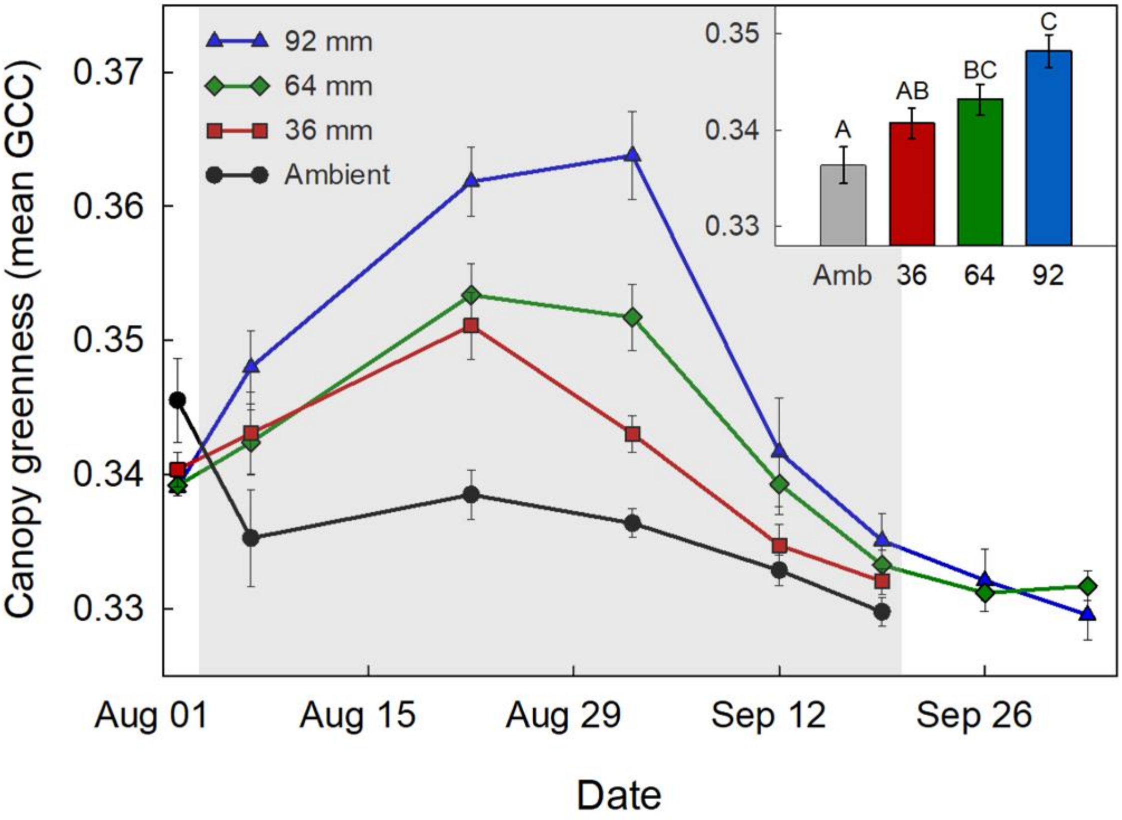

Figure 2.3. Average canopy greenness (mean ± SE), measured using the green chromatic coordinate (GCC) color index, for *B. gracilis* by treatment through time. The grey panel indicates the treatment period. The inset shows average greenness (mean ± SE) for each treatment during the treatment period. Different letters denote statistical significance.

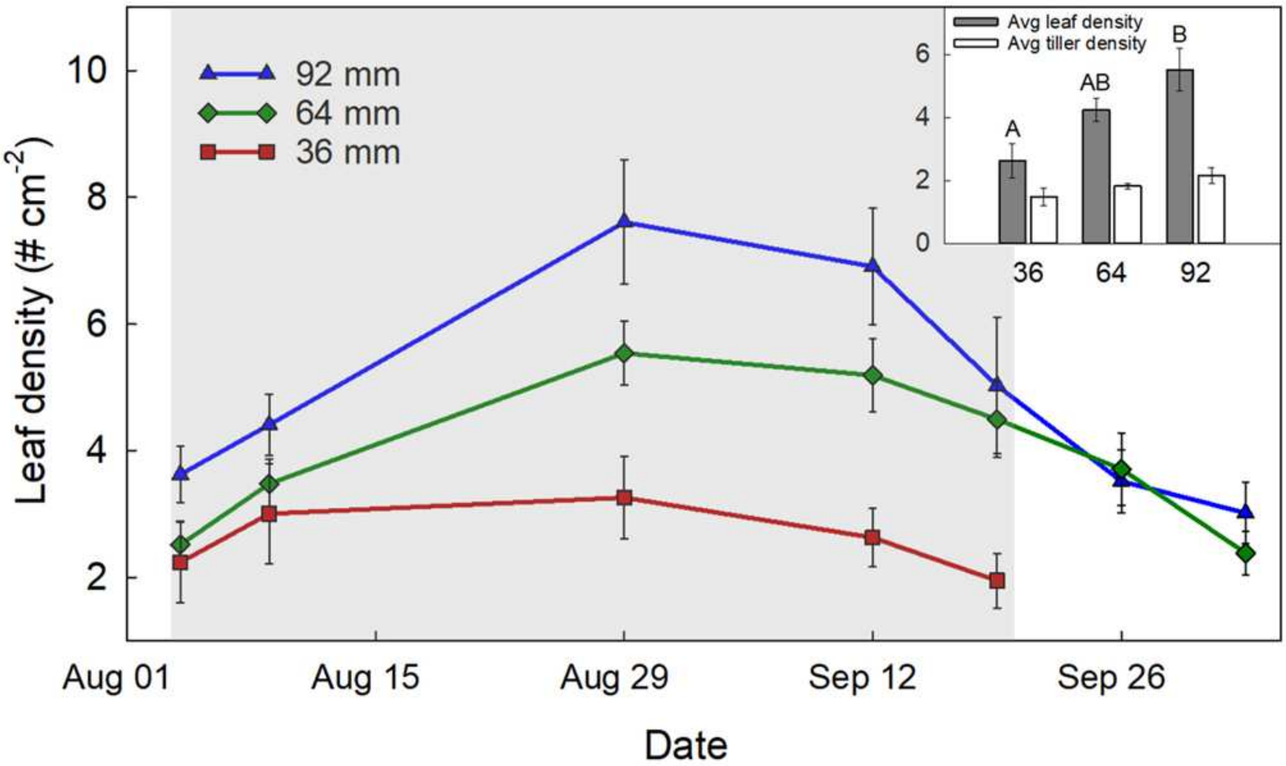

Figure 2.4. Average live leaf density (mean ± SE) of *B. gracilis* by treatment through time. The grey panel indicates the treatment period. The inset shows average live leaf and tiller density (mean ± SE) for each deluge treatment during the treatment period. Different letters denote statistically significant differences in average leaf density. Average tiller density did not differ among treatments.

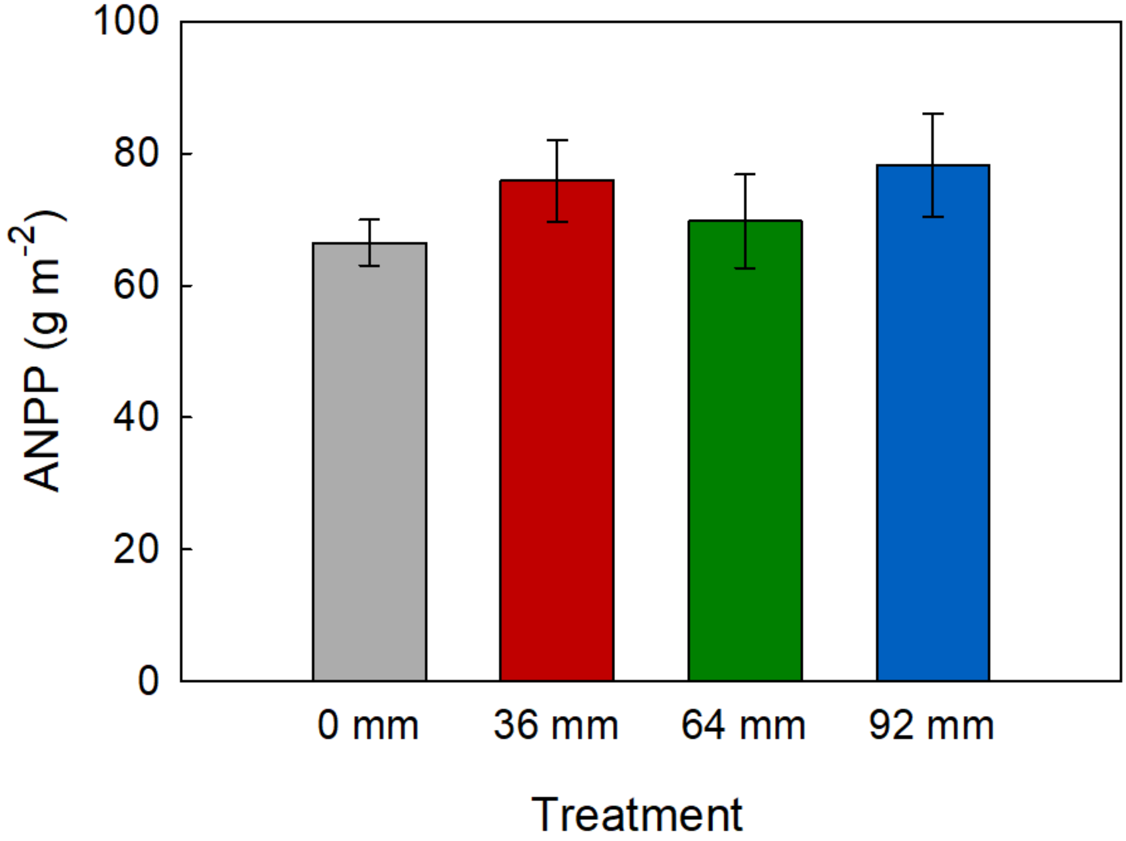

Figure 2.5. Response of ANPP (mean ± SE) in the semi-arid shortgrass steppe to the addition of late growing-season deluges of different magnitudes. There were no significance differences among deluge treatments or from the control plots (0 mm).

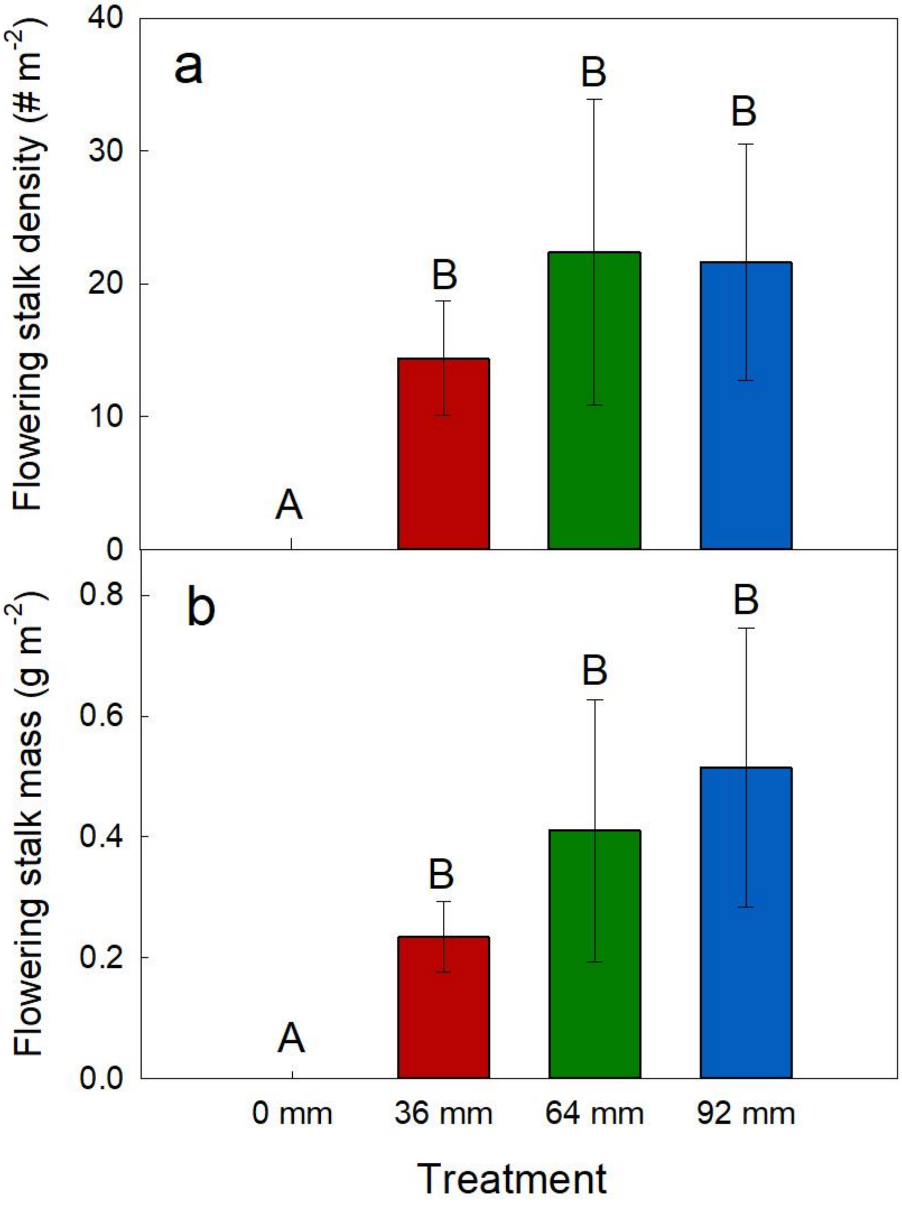

Figure 2.6. End-of-season (a) flowering stalk density and (b) mass (mean ± SE) of *B. gracilis* for each late-season deluge treatment. Different letters denote statistical significance between the treatments.

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CHAPTER 3: THE IMPORTANCE OF EXTREME RAINFALL EVENTS AND THEIR TIMING IN A SEMI-ARID GRASSLAND[2]

3.1 Summary

Climate change is intensifying the hydrologic cycle globally, increasing both the size and frequency of extreme precipitation events, or deluges. Arid and semi-arid ecosystems are expected to be particularly responsive to this change because their ecological processes are largely driven by distinct soil moisture pulses. However, since soil moisture, air temperature, and plant phenology vary throughout the growing season, deluges will likely have differing impacts on these systems depending on when they occur. We conducted a field experiment to assess how the seasonal timing (early, middle, or late growing season) of a single deluge (70 mm precipitation event) altered key ecological processes in the semi-arid shortgrass steppe of North America. Regardless of timing, a single deluge stimulated most ecosystem processes, but a deluge at mid-season caused the greatest increase in soil respiration, canopy greenness, aboveground net primary production (ANPP), and growth and flowering of the dominant plant species (*Bouteloua gracilis*). In contrast, belowground net primary production (BNPP) was insensitive to deluge timing, with a consistent BNPP increase in all the deluge treatments that was almost twice as large as the ANPP response. This BNPP response was largely driven by enhanced root production at 10-20 cm, rather than 0-10 cm, soil depths. In a semi-arid ecosystem, a single deluge can have season-long impacts on many ecosystem processes, but responses can be mediated by event timing. Therefore, predicting responses of semi-arid ecosystems to more dynamic precipitation regimes, and subsequent impacts on the global carbon

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[2] Post, A.K., & Knapp, A.K. (2020) The importance of extreme rainfall events and their timing in a semi-arid grassland. *Journal of Ecology*, 108(6), 2431-2443.

budget, will require knowledge of how deluge magnitude, frequency, and timing are being altered by climate change.

3.2 Introduction

Warming air temperatures are intensifying the hydrologic cycle, resulting in altered weather patterns and more frequent extremes, such as droughts and large rainstorms (Huntington, 2006; Groisman & Knight, 2008; IPCC, 2013; Donat et al., 2016). Drought and its impact on terrestrial ecosystems is arguably the most studied climate extreme (Slette et al., 2019), but there is growing evidence that heavy rain events are increasing in frequency and magnitude in many parts of the world (Easterling et al., 2000; Groisman & Knight, 2008; Groisman et al., 2012; Kunkel et al., 2013; Janssen et al., 2014; Monier & Gao, 2015; Mallakpour & Villarini, 2017). Unfortunately, our understanding of the ecological consequences of large individual rain events, or deluges (defined as statistically extreme, large magnitude events, cf. Smith, 2011), is only beginning to emerge (e.g., Manea & Leishman, 2018; Eekhout et al., 2018; Chen et al., 2019; Hammerl et al., 2019; Zhang et al., 2019). While it is expected that changes in deluge frequency will impact most ecosystems to some degree (Weltzin et al., 2003; Knapp et al., 2008; Jentsch & Beierkuhnlein, 2008), it is likely that arid and semi-arid ecosystems will be disproportionately affected (Diffenbaugh et al., 2008; Ahlstrom et al., 2015). In these water-limited systems, ecological processes are largely driven by infrequent precipitation events that elevate soil moisture (Noy-Meir, 1973; Reynolds et al., 2004; Schwinning & Sala, 2004), and deluges cause significant soil moisture pulses.

In arid and semi-arid ecosystems, aboveground net primary production (ANPP) is strongly correlated with annual precipitation (Sala et al., 1988; Lauenroth & Sala, 1992; Knapp & Smith, 2001; Huxman et al., 2004b; Bai et al., 2008; La Pierre et al., 2016). Yet, while a single deluge increases total annual rainfall in these dry systems (Sala et al., 1992; Knapp et al., 2015), it is unclear how effective precipitation delivered via a deluge might be at stimulating ANPP and other ecosystem processes. Results from several prior experiments suggest that large rain events are often more effective than smaller events in arid and semi-arid ecosystems (Heisler-White et al., 2008, 2009; Thomey et al., 2011; Peng et al., 2013; Zeppel et al., 2014; Wilcox et al., 2015). This is likely because large events have relatively lower losses of water to interception and evaporation compared to smaller rain events (Loik et al., 2004; Knapp et al., 2008), and consequently, proportionally more water is available for plant growth and other ecosystem processes.

However, deluges can also saturate soil water holding capacity and increase runoff, reducing effective precipitation (Ye et al., 2016). Further, if soils become anaerobic, some ecosystem processes could be negatively affected (Knapp et al. 2008, Hao et al., 2017). Indeed, other studies have found ANPP to be unresponsive to large precipitation events (Hao et al., 2017; Post & Knapp, 2019), or decrease under a precipitation regime with deluges (Robertson et al., 2009; Liu et al., 2012; Zhang et al., 2013; Liu et al., 2017, Manea & Leishman, 2018). In US arid grasslands, for example, Zhang et al. (2013) reported that heavy rain events reduced remotely sensed estimates of ANPP.

These differing responses to deluges may be due, in part, to when an extreme precipitation event occurs (Reynolds et al., 2004; Ogle & Reynolds, 2004). The influence of precipitation timing on ecosystem function has been well-documented from studies that have shifted rainfall between and within seasons (Epstein et al., 1999; Huxman et al., 2004c; Robertson et al., 2009; Parton et al., 2012; Peng et al., 2013; Prevey & Seastedt 2014; Zeppel et al., 2014; Morgan et al., 2016). However, these studies focused on precipitation totals and did not measure responses to individual events. Given that temperate semi-arid ecosystems have seasonally dynamic soil moisture, air temperature, and plant phenology, they will likely be sensitive to deluge event timing, but this has yet to be experimentally assessed.

To address this, we conducted a field experiment in the semi-arid shortgrass steppe of eastern Colorado. We asked the following questions: 1) What is the impact of a single large rain event (deluge) on ecosystem processes in the shortgrass steppe? And 2) How does deluge timing affect these ecosystem responses? Based on prior observations in this system (Heisler-White et al., 2008; Parton et al., 2012; Hermance et al., 2015; Post & Knapp 2019), we predicted that deluges would significantly enhance most ecosystem processes and that early-season deluges would be more effective than deluges later in the season because the dominant grasses are more physiologically active early in the growing season (Monson et al. 1986, Morgan et al., 2016).

3.3 Materials and Methods

3.3.1 Site Description

Research was conducted in an undisturbed, native shortgrass steppe ecosystem located at the United States Department of Agriculture – Agricultural Research Service (USDA-ARS) Central Plains Experimental Range (CPER) in northeastern Colorado (40.8422, -104.7156). Mean annual precipitation is 321 mm, with about 70% occurring during the summer months (May-September), and mean annual temperature is 8.6°C (Lauenroth & Sala, 1992). Average ANPP is ~100 g m^{-2} (Lauenroth & Sala, 1992), and the dominant C_4 grass, *Bouteloua gracilis* (blue grama), accounts for up to 90% of total plant cover (Milchunas et al., 1989). Soils at the experimental site are classified in the Ascalon series (Aridic Argiustolls; https://soilseries.sc.egov.usda.gov/) with a sandy clay loam texture (61% sand, 17% silt, 22%

clay) and 6.4% organic matter (Soil, Water, and Plant Testing Laboratory, Colorado State University).

3.3.2 Experimental Design and Treatments

We applied a deluge treatment (70 mm event) to 32 1-m^2 plots in a relatively flat location at a site that had been protected from large ungulate grazing for 6 years prior to the experiment. Previously, the site was moderately grazed by domestic livestock (M. Johnston, pers. comm.). Plots were spaced at least 3 m apart and aluminum roof flashing was installed 20 cm outside the perimeter of each plot. Flashing was inserted to a depth of 10 cm belowground and extended 5 cm aboveground. Clear corrugated polycarbonate roofs (Suntuf, Palram Americas, 2.44 m by 3.05 m) were temporarily erected over all the plots during each deluge addition (see below). Thus, there was a 0.7 to 1.0 m buffer between the roof edge and the plot edge. Roofs were installed 1 m above ground level, and slightly angled to allow for water drainage away from plots.

To assess the influence of the shelters on ambient environmental variables, temperature and light readings were taken both underneath and just outside the shelters. From May 2 – Sept 25, 2017, hourly air temperature was recorded using iButtons (iButtonLink Technology, model DS1921G) placed within and adjacent to the study plots (n = 2 each). They were shielded from direct sunlight and extended over the plots to measure temperature at the plot center 40 cm above ground level. Photosynthetically active radiation (PAR) was measured just above plant height both under and adjacent to 10 shelters at noon on a sunny day in mid-July using a 1-m linear quantum light sensor (Decagon AccuPAR, model LP-80).

Plots were randomly assigned to one of three deluge treatments or to the Ambient group (n = 8 plots/treatment). The treatments included the addition of a deluge in either the early (June

10-12), mid (July 11-13), or late (August 8-10) part of the 2017 growing season (referred to hereafter as Early, Mid, or Late treatments). Ambient plots did not receive additional rainfall.

We analyzed summer (June-August) precipitation data from a nearby NOAA (Nunn, CO; 40.7063, -104.7833) weather station from 1980-2016 to quantify the statistical distribution of precipitation event sizes and select the magnitude of the applied deluge treatment. For this analysis, we excluded rain events less than 2 mm and combined consecutive rain days into a single rain event, as in this region, rain days tend to be clustered (Bertolin & Rasmussen, 1969) and have an additive effect on ecosystem processes (Loik et al., 2004). Since our goal was to simulate future deluge events that are expected to become larger and more frequent, we chose a statistically extreme 70 mm event (98.6th percentile of historic event size, Fig. A1.1). We added the deluge over a 3-day period, with 40 mm applied on the first day, and 15 mm on each of the next two days. Water was applied using a hand-held watering wand attached to a flow meter and pump to deliver potable water from a local water delivery service (McDonald Farms Enterprises, Frederick, CO). Added water met US EPA drinking water standards and thus was not a significant source of nitrogen compared to annual atmospheric inputs (Burke et al. 2002; Burke et al., 2008) and was well below nitrogen critical load estimates for regional grasslands (Symstad et al. 2019).

To prevent an unpredictable natural rainstorm from confounding the treatments, roofs were erected over all the plots 2-3 days before each deluge addition and remained for 10-12 days after. Roofs were then removed to allow for ambient rainfall the rest of the growing season. The relatively small quantities of ambient rain that fell when the roofs were erected (see results) was added back to all of the plots within one week of the roofs being removed, using the same watering method as described above.

3.3.3 Measured Responses

In all plots, we monitored soil moisture, soil CO_2 efflux (respiration), canopy greenness, and above and belowground net primary production (ANPP & BNPP). In addition, leaf growth, leaf water potential, and flowering of the dominant species, *B. gracilis,* was recorded.

Soil moisture and soil respiration were measured weekly for the duration of the experiment (May 1 – Sept 21). More frequent measurements (every 1-3 days) were made immediately following a deluge addition. Soil moisture was measured to a depth of 20 cm in the center of each plot via a time-domain reflectometry (TDR) probe (Campbell Hydrosense II). Values were calibrated to the soil texture of the study site using gravimetric soil moisture measurements of multiple ($n = 6$) soil cores collected at various soil moisture levels. To monitor soil respiration, permanent PVC collars (10 cm diameter) were installed in bare soil areas, at the mid-point between *B. gracilis* patches. Collars were installed in each plot at the beginning of the growing season to a depth of 2.4 cm and extended 2 cm above the soil surface. Before each measurement, minor amounts of aboveground vegetation within the collar were clipped and removed. Soil CO_2 efflux from each collar was measured at midday (10 am – 2 pm) at ambient CO_2 concentration, temperature, and humidity using a 6400-09 soil flux chamber attached to an LI-6400 (LI-COR, Lincoln, NE). Concurrently, soil temperature was measured just outside of the collar to a depth of 10 cm.

Changes in plot greenness were monitored weekly (excluding weeks when the roofs were in place) via repeat digital photography. For each photograph, the camera (Sony cyber-shot digital camera, model DSC-WX100, 2496 x 1872 pixel resolution) was positioned directly over the center of each plot at a 90° angle, 1.2 m above the ground surface to capture the entire 1-m^2 plot. Each picture was then cropped to the upper right corner (0.25 m^2) of each plot (to avoid the influence of markers elsewhere in the plots), re-sized to standardize the number of pixels (500 x 450 pixels), and then assessed for greenness based on the green chromatic coordinate (GCC) index. This index computes greenness relative to the total brightness of each pixel using the following formula: green / (red + blue + green) (Filippa et al., 2016). By using a ratio, this metric accounts for variation in image lighting. Using the package EBImage (Pau et al., 2010) in R, we calculated the GCC for each pixel in an image, and then averaged all the image pixels to obtain mean GCC.

Because *B. gracilis* accounts for the majority of plant cover in the shortgrass steppe, we focused on growth and flowering of this species. Before the first deluge addition, we marked three *B. gracilis* tillers, each from spatially separate plant crowns, within each plot. Every 1-2 weeks (Jun 12 – Sept 7), all live leaves (at least 50% green) on each marked tiller were counted and measured. For each tiller, the lengths of all the green leaves were summed to obtain a measure of total green leaf length per tiller, which we use as a metric of *B. gracilis* plant growth. The three tillers within each plot were averaged to obtain a plot-level value. The Late treatment plots were measured one additional week (Sept 14) since tillers in this treatment remained green longer. Upon the appearance of the first *B. gracilis* flowering stalks in early July, we counted the number of flowering stalks in each plot weekly through mid-August. We completed visual assessments of plant species cover within each plot in early July to use as a covariate in the analysis of *B. gracilis* flowering density.

To monitor the influence of the deluges on plant water status, pre-dawn and midday leaf water potentials of *B. gracilis* were measured. Measurements were made 1-2 days prior to each deluge treatment, the day after water additions concluded, and once a week for the next two weeks thereafter. Measurements were only made in the plots actively receiving a treatment at the time and in the Ambient plots (n = 8 plots each), therefore, three sets of measurements were made during the growing season coinciding with the Early, Mid, and Late deluge treatments. Leaf water potential was measured with a Scholander pressure bomb (PMS instruments) on 1-2 leaves per plot.

Belowground net primary production (BNPP) was measured using 20 cm depth root in-growth cores (Pérez-Harguindeguy et al., 2013). This depth was chosen as it has been shown that 75% of roots at this site are found within the top 20 cm of the soil profile (Milchunas & Lauenroth, 1989). The cores were made from 2 mm fiberglass window screen formed into hollow cylinders 22 cm in length with a diameter of 5 cm. Soil was collected from a location adjacent to the study site to a maximum depth of 20 cm. Soil was then air dried, sieved, and hand-picked to remove any remaining roots prior to filling the mesh cylinders. One core per plot was installed on May 6, 2017 to a depth of 20 cm (2 cm remained above the soil surface). To standardize, all cores were placed in between grass crowns. Cores were removed at the end of the growing season in mid-September and temporarily stored in plastic bags at 40°C. During processing, cores were cut in half so that root production could be assessed at two depth intervals, 0-10 cm and 10-20 cm. Each segment was then washed through two sieves (2 mm & 0.5 mm), and roots on the larger sieve were collected. In order to separate smaller roots from other detritus, material left on the smaller sieve was rinsed into a bin of water and roots floating at the surface were hand-picked. All roots were dried in a 60°C oven for two days and then weighed to the nearest 0.0001 g.

At the end of the growing season (mid-Sept), all plots were sampled for aboveground net primary production (ANPP). In each plot, we harvested all biomass within two 0.1 m^2 quadrats. During this process, biomass was sorted by functional group (grass, forb) and *B. gracilis* flowering stalks were separated. All biomass was dried at 60°C for two days, and then sorted to remove biomass from previous years (distinguished by grey color). Samples were weighed to the nearest 0.01 g.

3.3.4 Statistical Analyses

All analyses were performed in R (version 3.3.2). Soil moisture, soil respiration, GCC, leaf length, and flowering were subjected to a repeated measures mixed model analysis of variance with treatment and sampling date as fixed effects, plot as a random effect, and an interaction term between sampling date and treatment (nlme package, Pinheiro et al., 2019). All models used an autoregressive covariance structure. Some datasets were log transformed to meet model assumptions.

We conducted additional analyses to quantify the impacts of each deluge addition. We refer to the 28-day period following each water addition as the "treatment period" (TrtPd), beginning the first day of water application and ending when soil moisture values approximated ambient plot levels. Therefore, during this experiment, there were three TrtPds— one for each deluge treatment— as follows: Early = Jun 10 – Jul 7, Mid = Jul 11 – Aug 7, Late = Aug 8 – Sept 4. For continuously monitored variables (soil respiration, leaf length, GCC), we used the TrtPds to assess ecosystem responses directly following each deluge addition. This measure of sensitivity represents the stimulated increase above ambient conditions directly attributable to the deluge treatment. For each treatment group (Early, Mid, Late), sensitivity was estimated by subtracting the average response of the treatment plots from the average response of the Ambient plots for each day measured. Average sensitivity for each deluge treatment was determined by averaging over all the measured dates within each TrtPd (n = 2-9 dates/TrtPd, depending on variable). A one-way ANOVA and Tukey's post-hoc pairwise comparisons were used to compare the magnitude of this response among deluge treatments for each dataset.

Since flowering stalks accumulate over the season, in addition to the repeated measures ANOVA described above, we also analyzed the density and total mass of flowering stalks present at the end of the season for each treatment. In order to account for varying cover of *B. gracilis* between plots, we ran ANCOVAs on flowering stalk density and mass with treatment as a categorical factor and estimated percentage plot cover of *B. gracilis* as a covariate. A one-way ANOVA and Tukey's post-hoc pairwise comparisons were used to analyze the ANPP and BNPP data sets. T-tests were used to compare BNPP at different depth intervals. Finally, we used t-tests to analyze differences in water potential between treatment and ambient plots within each TrtPd, separated by sampling time (pre-dawn and midday).

3.4 Results

3.4.1 Environmental and Shelter Effects

In 2017, Ambient plots received about average annual (Jan-Dec) precipitation (346 mm), whereas the deluge treatment plots received slightly above average annual precipitation (416 mm). However, the growing season months were drier than average (Fig. 3.1), indicating that a somewhat disproportionate amount of rain fell at other times of the year. Based on the historic record (1980-2018), mean total rainfall for Jun-Aug at this site is 139 ± 9 mm, but the Ambient plots only received 78.5 mm during this period in 2017. In contrast, the deluge plots received about average summer rainfall (148.5 mm; Fig. A1.2). Since little precipitation occurred while the roofs were erected, we only needed to add back a total of four small rain events to the plots following the removal of the roofs (28.5 mm total, one event after the Early and Late deluges, and two events after the Mid deluge - see methods, Fig. 3.1).

There were minimal environmental impacts from the rainout shelters; they caused no change in ambient air temperature (data not shown), and an average reduction of 16.4 ± 5.4 % in photosynthetically active radiation for the 12-15 days they were in place for each deluge event. Similar light reductions from rainout shelters have been found in other studies (Yahdjian & Sala, 2002; Zhang et al., 2017), and Loik et al. (2019) found shelters to have little measurable effect on plant function, including leaf temperature, photosynthesis, and stomatal conductance.

3.4.2 Treatment Effects

As expected, soil moisture increased immediately after each deluge event, and then gradually decreased over the next 20-30 days (Fig. 3.1). Compared to Ambient plots, soil moisture was, on average, 5.6 ± 0.7% (mean ± SE) higher during the Early TrtPd, 8.2 ± 1.2 % higher during the Mid TrtPd, and 7.1 ± 0.4 % higher during the Late TrtPd. A repeated measures mixed model ANOVA indicated that sampling date ($p < 0.001$) and the interaction between sampling date and treatment ($p < 0.001$) influenced these patterns (Table 3.1). Soil moisture was elevated ($p< 0.05$) above ambient levels for 17, 17, and 30 days for the Early, Mid, and Late treatments, respectively.

Consistent with soil moisture, soil respiration increased immediately after each deluge addition, peaking at approximately the same maximum efflux value for each treatment (Fig. 3.2). Treatment ($p = 0.023$), sampling date ($p < 0.001$), and their interaction ($p < 0.001$) influenced these patterns (Table 3.1). When averaged over all sampling dates (May 1 – Sept 21), all the deluge treatments had greater growing season soil respiration (μmol CO_2 m^{-2} s^{-1}) than Ambient (Early: $p = 0.0161$, Mid: $p = 0.0386$, Late: $p = 0.0534$). However, when just the treatment period was considered, soil respiration was increased the most after the Mid deluge ($p = 0.010$). During their respective TrtPds, on average, Early was 1.5 ± 0.11, Mid was 2.20 ± 0.33, and Late was 1.05 ± 0.26 μmol CO_2 m^{-2} s^{-1} higher than Ambient (Fig. 3.2 inset).

Regardless of seasonal timing, all treatments exhibited significant green-up after a deluge event, with maximum greenness measured between 17-24 days post-deluge (Fig. 3.3a). Treatment ($p = 0.008$), sampling date ($p < 0.001$), and their interaction ($p < 0.001$) all influenced greenness patterns (Table 3.1). To compare greenness across the entire growing season, values were averaged over all sampling dates for each treatment (May 1 – Sept 7). Overall, Early and Mid were greener than Ambient ($p = 0.012$ & $p= 0.001$, respectively), and canopy greenness was stimulated the most by the Mid treatment, especially compared to Late ($p = 0.015$). Similarly, immediately after the deluge additions, Mid exhibited the greatest green-up during its TrtPd, slightly more than Early ($p = 0.071$, Fig. 3.3a inset).

Consistent with plot green-up, leaf growth increased after each deluge (Fig. 3.3b). For total green leaf length per tiller, sampling date ($p < 0.001$) and the interaction between sampling date and treatment ($p < 0.001$) influenced patterns of growth (Table 3.1). Compared to Ambient, the greatest increases in leaf length were measured on sampling dates after the Mid and Late deluge treatments. Mid showed the greatest immediate response to a deluge by exhibiting more leaf growth during its respective TrtPd than either Early ($p = 0.019$) or Late ($p = 0.043$). During their respective TrtPds, on average, Early had 3.24 ± 1.36, Mid had 10.75 ± 1.39, and Late had 3.81 ± 2.46 cm greater total leaf length per tiller than Ambient (Fig. 3.3b inset).

During the growing season, both the Early and Mid deluge treatments stimulated *B. gracilis* flowering (Fig. 3.3c), with sampling date ($p < 0.001$) and the interaction between sampling date and treatment ($p < 0.001$) influencing patterns (Table 3.1). However, there was no response of flowering stalk density with the late-season deluge. Accounting for variable *B.*

gracilis plot cover, at the end of the season, flowering stalk mass (F = 2.60, p = 0.072) and density (F = 4.49, p = 0.011) also varied by treatment. The mid-season deluge stimulated the most flowering, with slightly greater end-of-season flowering stalk mass than Ambient (p = 0.061), and greater flowering stalk density than all other treatments (Ambient: p = 0.023, Early: p =0.058, Late: p = 0.001; Fig. 3.3c inset).

Both pre-dawn and midday water potential of *B. gracilis* increased relative to Ambient after each deluge addition ($p < 0.01$ for all; Fig. A1.3). However, during the TrtPds, Mid and Late exhibited greater increases relative to Ambient (Midday water potential increase: Mid = 2.20 ± 0.97 MPa; Late = 2.65 ± 0.99 MPa) than did Early (Early = 0.42 ± 0.08 MPa).

When deluge plots (regardless of timing) were compared to control plots, deluges stimulated ANPP by 28.4% (p= 0.003). However, timing was important— the Mid deluge treatment resulted in the largest increase in total ANPP compared to Ambient (37% increase, p = 0.008; Fig. 3.4). Early and Late increased ANPP to a lesser degree (~24% increase for both, p = 0.129 and p = 0.130, respectively). Total ANPP values were: Early = 102.34 ± 6.90 g m^{-2}, Mid = 113.18 ± 6.80 g m^{-2}, Late = 102.30 ± 6.06 g m^{-2}, Ambient = 82.49 ± 4.64 g m^{-2}. When ANPP was assessed by functional group, grass production responded similarly, with the Mid treatment greater than Ambient (p = 0.016). Across all the treatments, forbs only accounted for a small portion of total ANPP (1.40 ± 0.38 %) and there was no difference between the treatments (p = 0.276). Similarly, flowering stalks accounted for only a small proportion of total biomass (5.49 ± 0.76%).

Despite differences in aboveground production, total BNPP (0-20 cm) did not differ between the treatments (F = 1.9356, p = 0.150, Fig. 3.4). Further, there was no difference when partitioned and analyzed by depth (Shallow: 0-10 cm and Deep:10-20 cm; data not shown).

However, when all deluge treatments were combined (called "Deluge"), deluges stimulated total belowground production (Deluge = 117. 26 ± 8.86 g m^{-2}, Ambient = 78.74 ± 9.03 g m^{-2}; t = -2.13, p = 0.043). This belowground response was about twice as large as the overall aboveground response (BNPP ~ 50% vs ANPP ~ 28% increase). When analyzed by depth increment, deluges caused greater deep root production than Ambient (Deluge = 44.27 ± 4.62 g m^{-2}, Ambient = 24.73 ± 3.46 g m^{-2}; t = -2.0973, p = 0.046), but this was not the case for shallow root production (Deluge = 72.99 ± 6.38 g m^{-2}, Ambient = 54.01 ± 9.43 g m^{-2}; t = -1.41, p = 0.170; Fig. 3.5).

3.5 Discussion

Understanding how expected increases in extreme precipitation events (deluges) will impact ecosystem processes in semi-arid ecosystems is critical given the significant role these water-limited systems have in the global carbon (C) cycle (Jones, 2010; Poulter et al., 2014; Ahlstrom et al., 2015). However, evidence to date has been mixed regarding how large precipitation events impact various ecosystem functions (e.g., Heisler-White et al., 2008; Hao et al., 2017; Liu et al., 2017). Therefore, we conducted a field experiment to assess key ecosystem responses to a deluge event, and to determine if deluge timing might partially explain this reported discrepancy. Results from our study showed that the shortgrass steppe is responsive to a single deluge event at any point in the growing season (early, middle, and late), with marked increases in multiple measures of ecosystem function. However, deluge timing influenced response magnitude. In contrast to our hypothesis that the ecosystem would be most responsive to an early-season deluge, the mid-season deluge caused the greatest increase in almost all measured responses.

3.5.1 Plant Growth Responses

Soil moisture peaked after each deluge addition, triggering a rapid increase in *B. gracilis* leaf growth and overall canopy greenness. While these plant responses occurred after all deluge treatments, they were most pronounced following the mid-season deluge. Previous studies have found similar increases in plant growth and canopy greenness following large precipitation events (Parton et al., 2012; Li et al., 2013; Hermance et al., 2015; Moore et al., 2015; Morgan et al., 2016), but very few have addressed event timing. In the shortgrass steppe ecosystem, early season rainfall (Apr-Jun) is generally considered most effective at stimulating plant growth (Derner & Hart, 2007; Parton et al., 2012). However, our findings suggest that large isolated events might deviate from this pattern, with later season deluges stimulating either greater (Mid) or at least equivalent (Late) growth compared to early-season deluges. Consistent with our results, Hermance et al. (2015) quantified the relationship between precipitation timing and plant response in the shortgrass steppe using remotely sensed greenness measurements (NDVI) and reported that the magnitude and rate of canopy green-up was influenced by rain event timing. Further, there are reports of increases in both *B. gracilis* plant growth and canopy greenness following late-season deluge events, even as late as mid-September (Moore et al., 2015; Post & Knapp, 2019). Overall, plant growth in the shortgrass steppe appears to be extremely sensitive to deluge timing.

The effect of deluge timing was even more pronounced in the flowering response of *B. gracilis*; the early- and mid-season deluges increased flowering, but the late-season deluge did not. Consistent with the leaf growth response, the Mid deluge caused the greatest stimulation, with flowering stalks accounting for ~7% of total ANPP by mass. Prior studies have found flowering of *B. gracilis* to be extremely responsive to water inputs (Dickinson & Dodd 1976;

Samuel, 1985; Giuliani et al., 2014), with July-September precipitation amount dictating the dates of flowering initiation and termination (Moore & Lauenroth, 2017). However, given the typical flowering period for *B. gracilis* is July-August (Dickinson & Dodd, 1976), it is surprising that the Late deluge (in mid-August) did not trigger greater flowering, as observed in a previous study (Post & Knapp, 2019). Such variation in response may be linked to antecedent soil moisture conditions. While the plots in the previous study were droughted before the late-season deluge, our plots received ambient precipitation, allowing the Ambient and Late treatment plots to initiate flowering prior to the late deluge addition. This might have rendered the plots less responsive to late-season water inputs. Nonetheless, flowering of the dominant plant species is sensitive to when deluges occur during the growing season.

3.5.2 Ecosystem Carbon Dynamics

Soil respiration in semi-arid systems is highly responsive to rain events and their size, with large events generally causing greater CO_2 efflux (Huxman et al., 2004a; Chen et al., 2008; Munson et al., 2010; Song et al. 2012). A recent study in the Mongolian semi-arid steppe found that rain pulses account for approximately 40% of total growing-season soil respiration (Yan et al., 2014). Similarly, following each of the applied deluges, soil respiration immediately increased and remained above ambient for at least a month, causing elevated seasonal values across all treatments (Fig. 3.2). This extended response duration is especially striking when compared to smaller rain events (10 mm) at the same site, which only increased soil respiration for two days (Munson et al., 2010). Timing also influenced the response, with the Mid deluge causing the greatest immediate stimulation. However, soil respiration remained elevated for almost the entire growing season following the Early deluge, causing the Early and Mid deluges to have similar season-long values. Therefore, a single deluge was able to increase seasonal soil respiration, but earlier deluges (Early and Mid) caused a greater increase than a deluge later in the season. Such dynamic temporal responses have been found in other arid and semi-arid ecosystems, with larger soil respiration increases following an early-season rain pulse than a late-season one (Chou et al., 2008; Song et al., 2012; Wang et al., 2019). This dampened response to late-season deluge events could be attributed to decreased root activity as plants begin to senesce towards the end of the growing season (Knight, 1973; Parton et al., 2012). Overall, these results suggest that the largest CO_2 efflux from the ecosystem (soil respiration) is strongly influenced by deluge events and their timing, with potential implications for shifts in total ecosystem C balance (Huxman et al, 2004c; Morgan et al., 2016; Song et al., 2019).

Because this study occurred during a relatively dry year (growing-season precipitation was 56% of long-term average), a single deluge was able to "rescue" ANPP. In other words, a deluge event was able to transform ANPP from below average (Ambient = 82 g m^{-2} vs. long-term average ANPP ~100 g m^{-2}, cf. Lauenroth & Sala, 1992) to average-year values (102-113 g m^{-2} for deluge treatments), regardless of event timing. While other studies have observed an increase in plant production as a result of increased rain event size (Heisler-White et al., 2008; Wilcox et al., 2015; Liu et al., 2017), our study extends this ANPP response to a single precipitation event, and is similar to ANPP responses remotely sensed after large isolated rain events in a Chinese arid ecosystem (Li et al., 2013). Furthermore, deluge timing dictated the magnitude of impact. Consistent with the other ecosystem responses, ANPP was most sensitive to the mid-season deluge; compared to the Ambient plots, the Early and Late deluges resulted in a 24% increase in ANPP, whereas the Mid deluge led to a 37% increase. This suggests that, in order to make accurate predictions of C sequestration in semi-arid ecosystems, precipitation event size and timing must be considered.

In contrast, belowground production was insensitive to deluge timing, exhibiting a consistent increase (~50%) in all the deluge treatments. This response was almost twice as large as measured aboveground. Past studies have found BNPP to peak at different points in the growing season depending on prior precipitation patterns (Bai et al., 2010; Kong et al., 2013), suggesting that root production is more sensitive to precipitation amount than to precipitation timing. More notably, deluges influenced rooting depth, disproportionately stimulating deep (10-20 cm) over shallow (0-10 cm) root production. In fact, compared to the Ambient plots, the treatment plots had 80% greater deep root biomass, but only 36% greater shallow root biomass (a non-significant increase). In contrast, a study in the Mongolian semi-arid steppe found that increased precipitation stimulated more shallow than deep root production (Zhang et al., 2019). This study, along with others (Milchunas & Lauenroth, 2001; Hui & Jackson, 2006; Zeppel et al., 2014) propose that plants reduce resource allocation belowground when water is not limiting, decreasing deep root production. However, our results suggest the opposite – elevated soil moisture from a deluge disproportionally increased deep root production. This difference could be due to the pattern of precipitation addition—Zhang et al. (2019) increased the size of each ambient precipitation event throughout the growing season (resulting in many smaller rainfall additions), whereas we added a single large event. A deluge may result in deeper water infiltration into the soil, stimulating deep root production to access this water source, whereas smaller rain events remain in the upper soil layers, stimulating shallow root production (Sala et al., 1992). Deeper infiltration also results in reduced evaporative loss, potentially resulting in more available water for plant growth and total C uptake (Loik et al., 2004). Importantly, deep root production might contribute to increased long-term soil C sequestration (Jones & Donnelly, 2004; Jones, 2010). It is unknown how increased deep root biomass might affect plant response to rain events later in the season, or even in future years, but it likely contributes to the observed plant legacy effect from one year to the next (Sala et al., 2012).

3.5.3 The Unique Nature of Mid-Season Deluges

With the exception of BNPP, ecological processes were most responsive to a mid-season deluge in this semi-arid grassland. We conjecture that this striking mid-season response could be a combination of several factors. First, at the time that the Early deluge was added, soil moisture was still relatively high due to the abundant spring rainfall that is common for this region (Sala et al., 1992; Parton et al., 2012). Therefore, a large rain pulse when soil moisture is typically less limiting to plant growth would not be expected to strongly increase ecosystem function. Note that the Early deluge caused a much smaller increase in plant water status than did the later deluges (Fig. A1.3). Additionally, prior research at this location has found that soil temperature limits plant growth in the early growing season, but that soil moisture is more limiting later in the growing season when it tends to be hotter and drier (Sala et al., 1992; Moore et al., 2015). A deluge can provide a much-needed increase in soil moisture in the mid and late growing season, but by late growing season, senescing plants are likely less able to physiologically respond to a large water input (Schwinning & Sala, 2004; Parton et al., 2012). Therefore, we posit that the mid-growing season represents the ideal combination of relatively low soil moisture and physiologically active plants for the ecosystem to most effectively utilize the water from an opportune deluge event. Of course, it is possible that this mid-season effect could be altered by atypical seasonal precipitation patterns in other years.

3.5.4 The Importance of Deluges in Semi-Arid Ecosystems

Globally, semi-arid ecosystems are proposed to be strong determinants of interannual variability in total C uptake (Ahlstrom et al., 2015). This is largely due to their sensitivity to precipitation, causing them to fluctuate between a net C source and sink depending on rainfall pattern and amount (Parton et al., 2012; Scott et al., 2015; Morgan et al., 2016). Therefore, the response of semi-arid ecosystems to precipitation extremes (drought and deluge) is critical to the global C budget. Research has shown that these systems become a significant C source during periods of drought (Nagy et al., 2007; Scott et al., 2015; Ma et al., 2016), but less is known about the effect of deluge events on semi-arid ecosystem C balance. In general, precipitation events stimulate the largest sources of both ecosystem C release (soil respiration) and uptake (plant growth), but large events typically promote net C uptake in semi-arid systems by stimulating plant growth (Fig. 3.4) and photosynthesis (Kurc & Small, 2007; Bachman et al., 2010; Guo et al., 2016) more than soil respiration. In contrast, small rain events disproportionately stimulate soil respiration over plant processes, resulting in a net C release (Huxman et al., 2004c; Parton et al., 2012). Consistent with this, observations from CO_2 flux towers indicate that years with large rain events tend to have greater total C uptake in semi-arid grasslands (Parton et al., 2012). This suggests that large precipitation events play a crucial role in promoting C sequestration in these systems, and that an increase in the frequency of deluges, as well as shifts in their timing, may significantly alter net ecosystem C fluxes. Furthermore, these patterns are likely to be similar in semi-arid systems subject to grazing, as multiple studies have shown that light to moderate grazing has little impact on the net C budget of semi-arid ecosystems (LeCain et al., 2002; Reeder & Schuman 2002; Morgan et al., 2016), with precipitation being a much stronger determinant of C fluxes than grazing (Jamiyansharav et al., 2010; Morgan et al., 2016).

Additionally, compared to more mesic or xeric ecosystems, semi-arid systems are likely the most responsive to extreme precipitation events (Piao et al., 2019). In these systems, plant cover is relatively high and deluges alleviate the largest limitation to plant growth (water) by causing an extended period of above-average soil water content (Knapp et al., 2008; Heisler-White et al., 2009). In contrast, more xeric systems, such as deserts, may lack sufficient plant cover to elicit a sizable autotrophic response, at least in the short-term (Knapp & Smith 2001), and more mesic systems, such as humid prairies and forests, may be either unresponsive to deluges or even adversely affected (Reichstein et al., 2013, Ye et al., 2016).

3.5.5. Conclusions

Our results indicate that the shortgrass steppe can be quite responsive to deluge events. A single deluge may be able to promote sufficient plant production to “rescue” the ecosystem during a drought year, with corresponding impacts on both ecosystem C uptake and forage production for cattle. Moreover, deluge timing strongly influences the magnitude of the ecological response, with a mid-season deluge event causing the greatest overall stimulation, as indicated by measures of soil respiration, canopy greenness, leaf growth, flowering, and ANPP. While BNPP was not sensitive to deluge timing, deluges may promote deeper root production, possibly increasing soil C sequestration and contributing to plant legacy responses. Many studies have focused on ecosystem response to changes in rainfall pattern and amount (Knapp et al. 2002, Fay et al., 2003; Heisler-White et al., 2008, 2009; Wilcox et al., 2015; Liu et al., 2017), but our results exemplify the impact that a single large rain event can have on season-long ecosystem dynamics in a semi-arid system. Accurately forecasting the response of semi-arid ecosystems to climate change, and consequently their impact on the global C budget, will require knowledge of how the magnitude, frequency, and timing of deluges might be altered in the future.

3.6 Tables

Table 3.1 Summary of the repeated measures mixed model ANOVA results for several measured variables (soil moisture, soil respiration, canopy greenness, green leaf length, flowering) with deluge treatment, date, and their interaction as factors. Reported values include the degrees of freedom (numerator, denominator), the F-statistic, and the p-value. Significant p-values ($p<0.05$) are bolded**.**

Variable	Soil Moisture			Soil Respiration			Greenness			Green Leaf Length			Flowering		
	df	F	p	df	F	p	df	F	p	df	F	p	df	F	p
Treatment	3, 28	0.44	0.729	3, 28	3.71	**0.023**	3, 28	4.90	**0.008**	3, 28	2.21	0.109	3, 28	1.68	0.193
Date	20, 552	184.80	**<0.001**	17, 468	166.35	**<0.001**	15, 412	160.90	**<0.001**	8, 224	75.75	**<0.001**	6, 168	54.41	**<0.001**
Treatment x Date	60, 552	10.34	**<0.001**	51, 468	5.07	**<0.001**	45, 412	23.90	**<0.001**	24, 224	5.46	**<0.001**	18, 168	4.48	**<0.001**

3.7 Figures

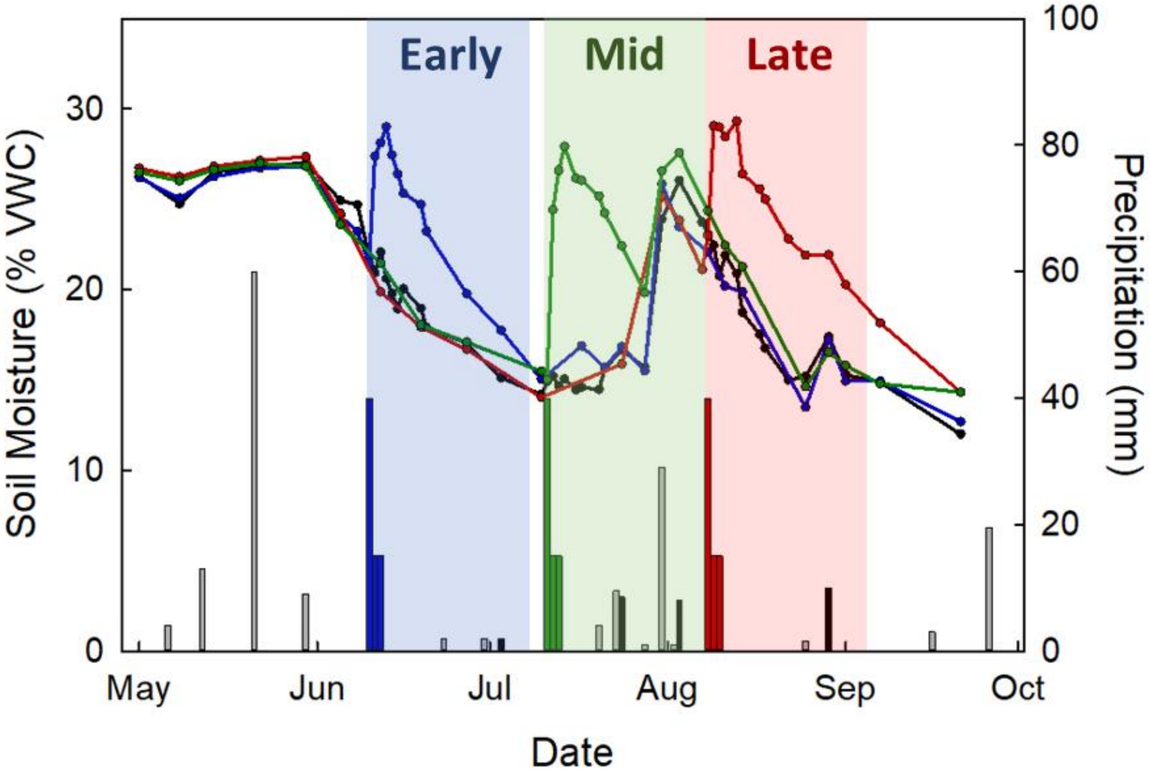

Figure 3.1. Seasonal patterns of average soil moisture by treatment (lines) and precipitation (bars) over the course of the 2017 growing season. The black line is ambient soil moisture throughout the growing season, and the colored lines exhibit soil moisture of the three deluge treatments. The grey bars indicate ambient rain events, the black bars indicate ambient rain events added back once the rainout shelters were removed, and the colored bars indicate water added during the deluge treatments. The colored panels denote the deluge treatment periods.

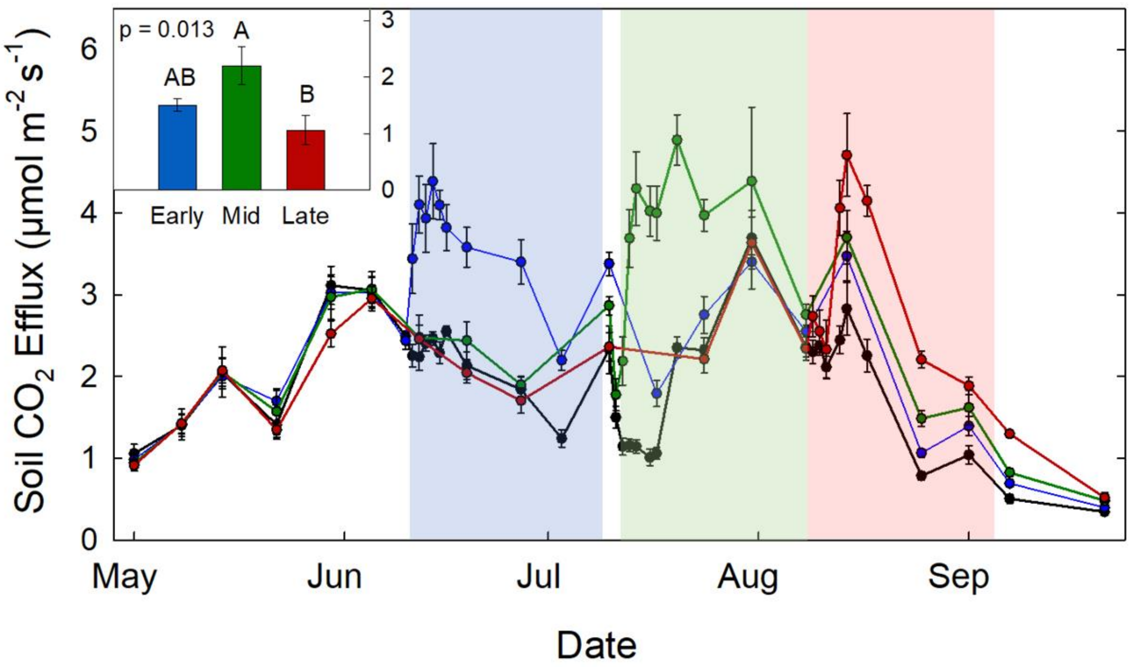

Figure 3.2. Seasonal patterns of soil respiration by treatment (mean ± SE). The black line is Ambient, blue is Early, green is Mid, and red is Late. Colored panels indicate the deluge treatment periods. The inset shows the average increase (stimulation above Ambient) in soil respiration (mean ± SE) during each treatment period. Different letters denote statistical significance ($p<0.05$).

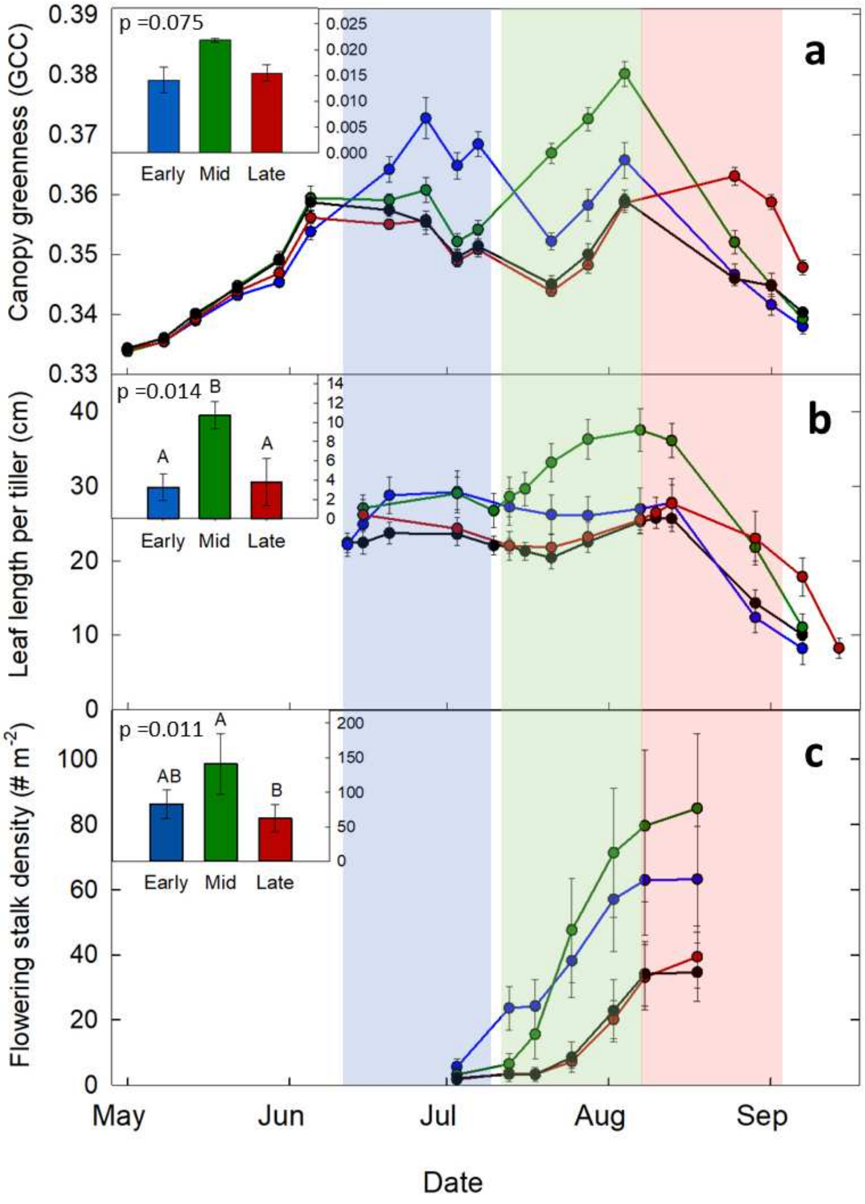

Figure 3.3. Seasonal patterns of (a) canopy greenness, (b) *B. gracilis* green leaf length per tiller, and (c) *B. gracilis* flowering stalk density (mean ± SE for all). For all, the black line is Ambient, blue is Early, green is Mid, and red is Late. Colored panels indicate the deluge treatment periods. Insets a and b show the average increase (stimulation above Ambient) in greenness and leaf length during each treatment period. Inset c shows flowering stalk density from the end-of-season ANPP samples. Different letters denote statistical significance ($p<0.05$).

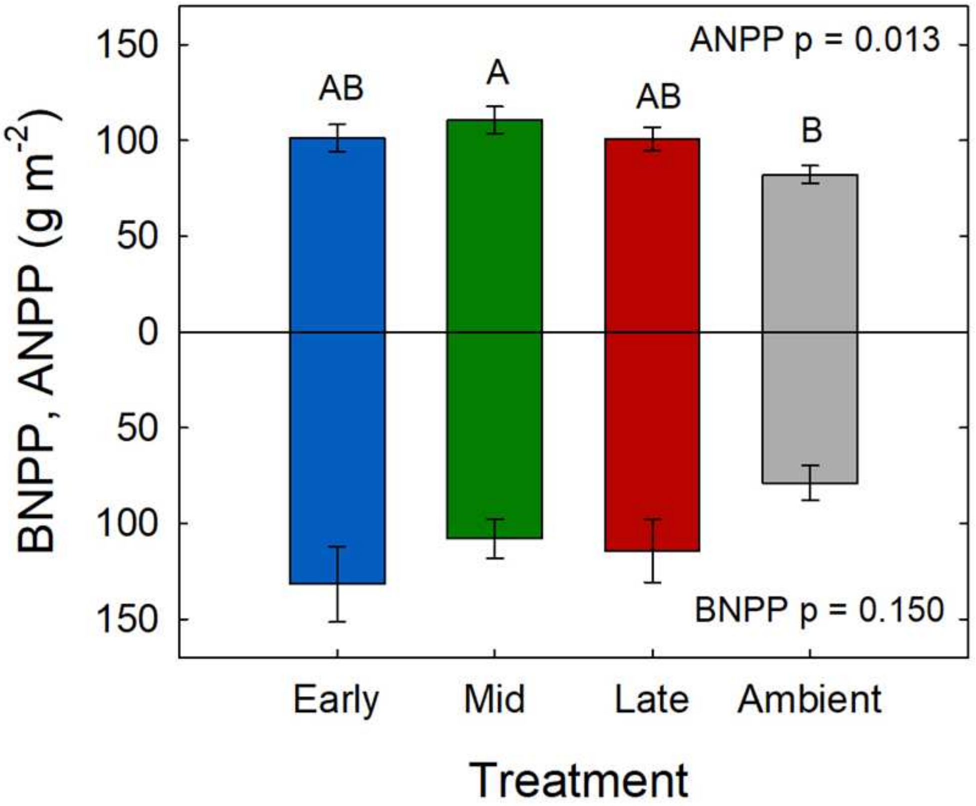

Figure 3.4. Response of ANPP (top) and BNPP (bottom; mean ± SE for both) to the addition of either an early, mid, or late growing-season deluge. For ANPP, different letters denote statistical significance ($p<0.05$). There were no significant differences between treatments for BNPP.

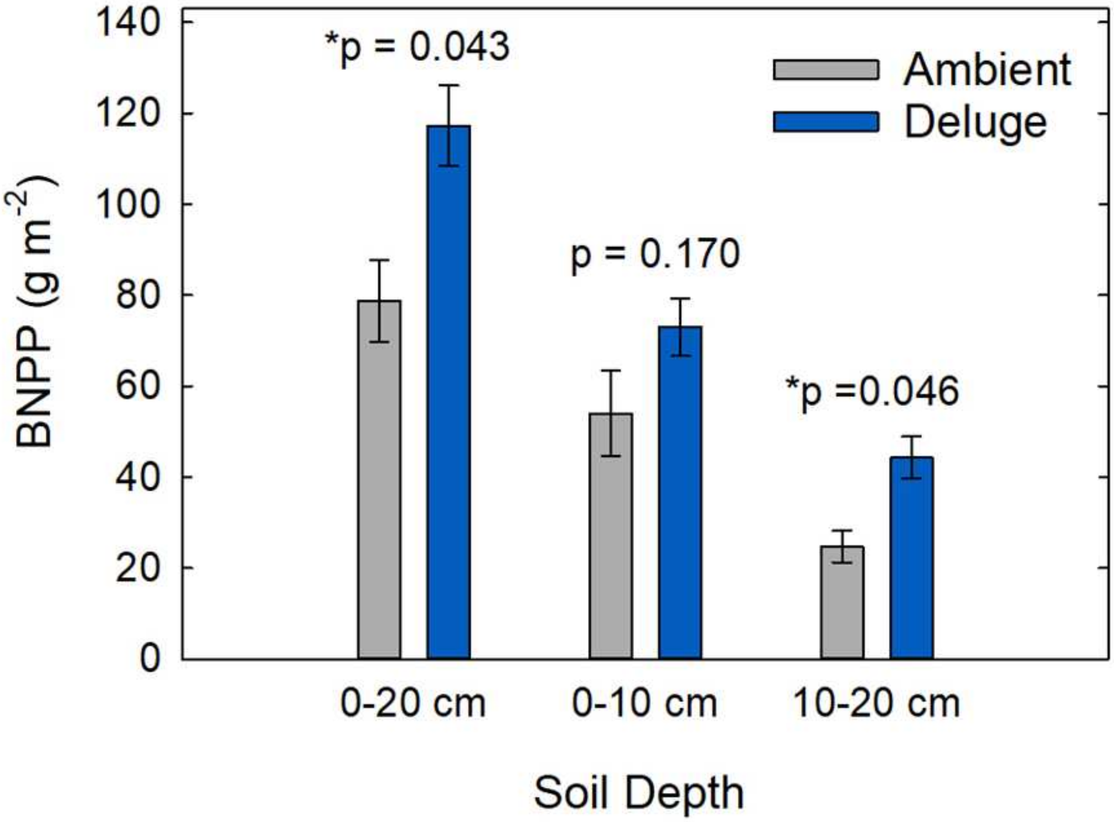

Figure 3.5. BNPP (mean ± SE) of combined deluge treatments (Early + Mid + Late = "Deluge") compared to Ambient, split by depth. P-values with an asterisk indicate statistical significance ($p<0.05$) between a set of bars.

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CHAPTER 4: HOW BIG IS BIG ENOUGH? SURPRISING RESPONSES OF A SEMI-ARID GRASSLAND TO INCREASING DELUGE SIZE[3]

4.1 Summary

Climate change has intensified the hydrologic cycle globally, increasing the magnitude and frequency of large precipitation events, or deluges. Dryland ecosystems are expected to be particularly responsive to increases in deluge size, as their ecological processes are largely dependent on distinct soil moisture pulses. To better understand how increasing deluge size will affect ecosystem function, we conducted a field experiment in a native semi-arid shortgrass steppe (Colorado, USA). We quantified ecological responses to a range of deluge sizes, from moderate to extreme, with the goal of identifying response patterns and thresholds beyond which ecological processes would not increase further (saturate). Using a replicated regression approach, we imposed single deluges that ranged in size from 20 to 120 mm (82.3rd to > 99.9th percentile of historical event size) on undisturbed grassland plots. We quantified pre- and post-deluge responses in soil moisture, soil respiration, and canopy greenness, as well as leaf water potential, growth, and flowering of the dominant grass species (*Bouteloua gracilis*). We also measured end of season above and belowground net primary production (ANPP, BNPP). As expected, this water-limited ecosystem responded strongly to the applied deluges, but surprisingly, most variables increased linearly with deluge size. We found little evidence for response thresholds within the range of deluge sizes imposed, at least during this dry year. Instead, response patterns reflected the linear increase in the duration of elevated soil moisture (2-22 days) with increasing event size. Flowering of *B. gracilis* and soil respiration responded

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[3] Post, A.K., & Knapp, A.K. (2021) How big is big enough? Surprising responses of a semi-arid grassland to increasing deluge size. *Global Change Biology*, 27, 1157-1169.

particularly strongly to deluge size (14- and 4-fold increases, respectively), as did ANPP and BNPP (~60% increase for both). Overall, our results suggest that this semi-arid grassland will respond positively and linearly to predicted increases in deluge size, and that event sizes may need to exceed historical magnitudes, or occur during wet years, before responses saturate.

4.2 Introduction

Climate change is intensifying the hydrologic cycle worldwide, causing increased drought severity and duration, as well as larger and more frequent extreme precipitation events (Huntington, 2006; Groisman & Knight, 2008; IPCC, 2013; Donat et al., 2016). While many studies have focused on the ecological impacts of drought (Slette et al., 2019), far fewer have assessed ecosystem response to large rain events, or deluges (defined as statistically large rain events, cf. Smith, 2011). An increase in extreme precipitation events is now considered a robust fingerprint of climate change (Hegerl et al., 2015), and in many parts of the world, there are documented increases in deluge magnitude and frequency (Easterling et al., 2000; Groisman et al., 2012; Kunkel et al., 2013; Janssen et al., 2014; Monier & Gao, 2015; Mallakpour & Villarini, 2017), with attendant consequences for key ecological processes (Zhang et al., 2013; Eekhout et al., 2018; Chen et al., 2019; Hammerl et al., 2019; Mitchell et al., 2020). Drylands, including arid and semi-arid ecosystems, are expected to be particularly sensitive to alterations in precipitation pattern (Diffenbaugh et al., 2008; Ahlstrom et al., 2015; Maurer et al., 2020). In these water-limited systems, ecological processes are largely driven by discrete rain events that result in soil moisture pulses (Noy-Meir, 1973; Reynolds et al., 2004; Schwinning & Sala, 2004), and deluges are expected to cause extremely large pulses.

Since they are water-limited, arid and semi-arid ecosystems exhibit a strong positive relationship between annual precipitation and aboveground net primary production (ANPP; Sala et al., 1988; Lauenroth & Sala, 1992; Knapp & Smith, 2001; Huxman et al., 2004a; Bai et al., 2008; La Pierre et al., 2016). Even a single deluge event can substantially increase annual rainfall in these dry systems (Sala et al., 1992; Knapp et al., 2015), and thus stimulate plant growth and impact other ecosystem processes (Lauenroth & Sala 1992; Heisler-White et al., 2008; Li et al., 2013; Guo et al., 2015; Post & Knapp 2020). Typically, large rain events more effectively increase soil moisture than equivalent water inputs via multiple small rain events (Heisler-White et al., 2008; Knapp et al., 2008; Zeppel et al., 2014; Guo et al., 2015). This is because large events have lower proportional losses to evaporation, and unless edaphic conditions lead to significant run-off, cause greater infiltration of moisture into the soil, resulting in more plant-available water (Loik et al., 2004; Huxman et al. 2004b; Knapp et al., 2008; He et al., 2012; Lauenroth & Bradford, 2012). Consistent with the above, several studies have found plant growth and ANPP in semi-arid ecosystems to be sensitive to event size (Heisler-White et al., 2008; Chen et al., 2009; Thomey et al., 2011; Peng et al., 2013; Wilcox et al., 2015; Guo et al., 2016; Post & Knapp, 2019).

However, for most ecological processes, there is likely an upper limit to this observed response with increasing event size, beyond which the system is unable to effectively utilize additional water from a single precipitation event (Huxman et al., 2004b). For example, an extremely large deluge might elicit a limited ecosystem response due to saturated, anoxic soils (Knapp et al. 2008, Hao et al., 2017) or because vegetation growth rates are maximized and cannot respond to additional precipitation (Lauenroth & Sala, 1992; Smith & Knapp, 2001). This could result in a saturating, rather than a linear, relationship between ANPP and rain event size. In many ecosystems, this saturating response pattern manifests as “negative asymmetry,” in which ecological processes exhibit greater reductions under dry conditions than increases under equivalent wet conditions (Hsu et al., 2012; Hsu & Adler, 2014; Wilcox et al., 2017; Du et al., 2020; Yang et al., 2020). Semi-arid systems have exhibited inconsistent evidence for such asymmetric responses (Haverd et al., 2017; Zhang et al., 2017; Wu et al., 2018; Felton et al., 2019; Yang et al. 2020). For example, Zhang et al. (2017) applied a range of growing season precipitation (GSP) amounts in a semi-arid grassland and found that gross primary productivity decreased substantially when GSP was reduced, but did not respond to increased GSP, thereby exhibiting a saturating response with rainfall amount (negative asymmetry). In contrast, Felton et al. (2019) applied a gradient of GSP to a semi-arid grassland, spanning the driest to the wettest years on record (1st – 99th percentile), and reported a linear precipitation-ANPP relationship with no evidence of saturation. However, both of these studies focused on seasonal rainfall totals and not on individual event size. Given that individual precipitation events are increasing in magnitude (IPCC, 2013), it is important to understand the relationship between event size and ecosystem processes in order to accurately predict the response of semi-arid ecosystems to climate change.

To better understand how increasing deluge size will affect ecosystem function, we conducted a field experiment to assess the influence of single deluge events, varying in size from moderate to extreme, on key ecological processes in the shortgrass steppe of NE Colorado (USA). Our goals were to quantify relationships between deluge size and ecological function in this water-limited ecosystem, and from these response patterns, identify event size thresholds at which ecosystem processes saturate.

4.3 Materials and Methods

4.3.1 Site Description

Research was conducted at the United States Department of Agriculture – Agricultural Research Service (USDA-ARS) Central Plains Experimental Range (CPER) in northeastern Colorado (40.8422, -104.7156). This undisturbed, native shortgrass steppe ecosystem has a mean annual precipitation of 321 mm, with about 70% occurring during the summer months (May-September), and a mean annual temperature of 8.6°C (Lauenroth & Sala, 1992). Average ANPP is ~100 g m^{-2} (Lauenroth & Sala, 1992), and the dominant C_4 grass, *Bouteloua gracilis* (blue grama), can account for up to 90% of total plant cover (Milchunas et al., 1989). Soils at the experimental site are classified in the Ascalon series (Aridic Argiustolls; https://soilseries.sc.egov.usda.gov/) with a sandy clay loam texture (61% sand, 17% silt, 22% clay) and 6.4% organic matter (Soil, Water, and Plant Testing Laboratory, Colorado State University). Field capacity is about 27% volumetric water content (Saxton & Rawls, 2006).

4.3.2 Experimental Design and Treatments

During the 2018 growing season, we applied single deluge events of varying size (20-120 mm) to 28 1-m^2 plots. Plots were located in a relatively flat area previously subjected to moderate livestock grazing but that had been protected from large ungulate grazing for 7 years prior to the experiment (M. Johnston, USDA-ARS, pers. comm.). Plots were spaced at least 3 m apart, and aluminum roof flashing was installed 20 cm outside the perimeter of each plot to a depth of 10 cm and extending 5 cm aboveground. To prevent the confounding effects of an unpredicted natural rain event, we erected rainout shelters over all the plots 7 days prior to the deluge addition and removed them 12 days after the conclusion of the deluge treatment. The roofs were constructed from clear corrugated polycarbonate (Suntuf, Palram Americas, 2.44 m by 3.05 m) with a 0.7 to 1.0 m buffer between the roof edge and plot edge. Roofs were installed 1 m above ground-level and angled slightly to direct water drainage away from the plots. Previous research indicates that the shelters only moderately reduce transmission of photosynthetically active radiation (PAR; average reduction of 16.4 ± 5.4 %, Post & Knapp, 2020) and have minimal effects on the microclimate and plant responses (Loik et al., 2019).

The experiment employed a replicated regression design with plots randomly assigned to one of six deluge treatments, or to the ambient treatment (referred to as "0 mm") that did not receive a deluge addition (n = 4 plots/treatment). The deluge treatments included the addition of a single rain event that was either 20, 40, 60, 80, 100, or 120 mm in size. Deluges were added in the mid-growing season (Jul 10-12) when the shortgrass steppe is highly responsive to large water inputs (Post & Knapp, 2020). Our goal was to include deluge sizes representing large rain events that occur relatively frequently in this ecosystem (20 mm), as well as historically unprecedented deluges that might occur in the future as the climate changes (120 mm). Therefore, based on the historical precipitation record from a nearby NOAA weather station (1980-2017; Nunn, CO; 40.7063, -104.7833), we selected event sizes that spanned the 82.3rd to > 99.9th percentile of summer (Jun-Aug) rain event sizes for this location (Fig. 4.1a). For this analysis, we excluded rain events less than 2 mm (Heisler-White et al., 2008); although small events can temporarily stimulate plant physiological activity (Sala & Lauenroth, 1982), they are largely ineffective at promoting plant growth (Sala et al., 1992). We then combined consecutive rain days into a single rain event because, in this region, rain days tend to be clustered (Bertolin & Rasmussen, 1969) and have an additive effect on ecosystem processes (Noy-Meir, 1973; Loik et al., 2004).

During a natural deluge event, the amount of runoff (and run-on) that occurs varies according to local topography, soil type, and soil surface characteristics, as well as plant cover, rainfall intensity, and antecedent soil moisture conditions (D'Odorico & Porporato, 2006; Liu et al., 2011; Zhao et al., 2013; Fischer et al., 2015). Our goal was to control for these variables and focus on deluges that only differed in size. Thus, we minimized runoff by applying deluge treatments over a 1-3 day period, adding a maximum of 40 mm in a single day. As a result, the 20 and 40 mm events were fully applied the first day of watering, the 60 and 80 mm events were applied over two days, and the 100 and 120 mm events were applied over three consecutive days. For each plot, deluge treatments were applied to the entire area within the flashing buffer (1.4 x 1.4 m) using a hand-held sprayer attached to a flow meter and pump. We used potable local water (McDonald Farms Enterprises, Frederick, CO) that met US EPA drinking water standards. Therefore, added water was not a significant source of nitrogen relative to typical annual atmospheric inputs (Burke et al., 2002; Burke et al., 2008) and well below nitrogen critical load estimates for regional grasslands (Symstad et al., 2019).

4.3.3 Measured Responses

Over the course of the growing season, we monitored soil moisture and canopy greenness, as well as leaf growth, leaf water potential, and flowering of the dominant species, *B. gracilis*. We also measured soil CO_2 flux (respiration) because it represents one of the largest carbon fluxes in semi-arid ecosystems (Huxman et al., 2004b). At the end of the growing season, we assessed above and belowground net primary production (ANPP, BNPP). Methods generally followed protocols in Post & Knapp (2020).

Soil moisture and soil respiration were measured weekly throughout the growing season (soil moisture: May 1 - Aug 21, soil respiration: May 8 - Aug 21) with more frequent measurements (every 1-3 days) directly after the deluge addition. Soil volumetric water content (VWC) was measured at the plot center and integrated over the top 20 cm of soil using a time domain reflectometry (TDR) probe (Campbell Hydrosense II). Measurements were corrected for soil texture of the site using gravimetric soil moisture measurements (Post & Knapp, 2020). To monitor soil respiration, a permanent PVC collar (10 cm diameter) was installed in each plot at the beginning of the growing season to a depth of 2.4 cm and extending 2 cm aboveground. To standardize, collars were placed in areas of bare soil between *B. gracilis* crowns. Before each measurement, any aboveground vegetation growing inside the collar was clipped and removed. For consistency, soil CO_2 efflux was always measured midday (10 am – 2 pm) at ambient CO_2 concentration, temperature, and humidity using a 6400-09 soil flux chamber attached to an LI-6400 (LI-COR, Lincoln, NE). Concurrently, soil temperature was measured just outside of the collar to a depth of 10 cm.

Using repeat digital photography, we assessed weekly changes in plot canopy greenness. For each image, a Sony cyber-shot digital camera (model DSC-WX100, 2496 x 1872 pixel resolution) was positioned directly above the plot at a 90° angle to photograph the upper right corner (0.25 m^2) of each plot. This location was chosen to avoid the influence of markers placed elsewhere in the plots. Images were analyzed using the R package EBImage (Pau et al*.*, 2010) to calculate the average green chromatic coordinate (GCC) of the pixels in each photograph. See Post & Knapp (2020) and Seyednasrollah et al. (2019) for more details on this method. Because GCC is a ratio, it is robust to variations in image lighting, thus we did not observe any impact of the shelters on greenness measurements.

We monitored growth and flowering of the dominant grass species, *B. gracilis*, in response to the deluge addition. In early June, three tillers from spatially separate *B. gracilis* crowns were identified and marked in each plot. Every 1-2 weeks (Jun 7 – Aug 14), we counted and measured the live (at least 50% green) leaves on each tiller. The lengths of the green leaves were summed for each tiller to obtain a measure of total live leaf length per tiller. We then multiplied this number by average *B. gracilis* leaf width (1.9 ± 0.2 mm, n = 106 leaves) to estimate live leaf area per tiller. The three tillers within each plot were averaged to obtain a plot-level value. Starting in mid-June (before the appearance of the first *B. gracilis* flowering stalks), we counted the number of flowering stalks present in each plot to determine flowering density (# flowering stalks/m^2) through the end of the season (Aug 21).

We also monitored *B. gracilis* plant water status in response to the deluge treatments by measuring pre-dawn and midday leaf water potential. Measurements were taken 4 days prior to the deluge addition, the day after watering treatments concluded, and then weekly for the following three weeks. However, due to plant senescence, the 0 mm treatment was only sampled once, and the 20 mm was only sampled twice, after the deluge addition. Each time, we measured 1-2 leaves per plot from 2-3 plots per treatment using a Scholander pressure chamber (PMS instruments). Leaves were stored in the dark in humid bags and measured within 1 hour of collection.

Belowground net primary production (BNPP) was measured using 30 cm depth fine-root in-growth cores (Pérez-Harguindeguy et al., 2013). This depth accounts for 80% of roots found at this site (Sims et al., 1978; Liang et al., 1989). Methods are described in Post & Knapp (2020), but briefly, we used 2 mm fiberglass window screen formed into hollow cylinders with a 5 cm diameter. These were filled with root-free soil collected from a location adjacent to our site. One core per plot was installed in between grass crowns on May 10, 2018 to a depth of 30 cm. Cores were removed at the end of the growing season in late August and temporarily stored in plastic bags at 40° C. Each core was divided into three depth intervals (0-10 cm, 10-20 cm, 20-30 cm), which were processed separately. Each segment was rinsed through 2 sieves (2 mm and 0.5 mm), and roots on the larger sieve were collected. Material remaining on the smaller sieve was rinsed into a bin of water and roots floating at the surface were hand-picked. Samples were dried at 60° C for two days and then weighed to the nearest 0.0001 g.

At the end of the growing season (late August), we sampled aboveground net primary production (ANPP). In each plot, all plant material from two 0.1 m^2 quadrats was harvested and sorted by functional group (grass, forb). *B. gracilis* flowering stalks were also separated. Biomass samples were dried at 60°C for two days, sorted to remove biomass from previous years (distinguished by grey color), and weighed to the nearest 0.01 g.

4.3.4 Statistical Analyses

All analyses were performed in R (version 3.6.3). In order to capture the full treatment effect, for continuously measured variables, we analyzed the average response during the 28-day period following the deluge addition. We refer to this as the response period (ResPd), beginning the first day of the deluge addition and concluding approximately when soil moisture of the largest treatments returned to ambient levels (Jul 10 – Aug 7). Fortunately, only one small precipitation event (4 mm) fell on the plots during the ResPd, so soil moisture dynamics were primarily the product of deluge size. Measurements of soil moisture, soil respiration, canopy greenness, and leaf area from each plot were averaged over the ResPd (n = 3-8 dates, depending on variable). These plot-level averages were then regressed against the size of the deluge treatment each plot received. Additionally, to observe changes in response pattern through time, we also assessed the response of these variables on each individual sampling date within the

ResPd. For each date a variable was measured, we fit a linear regression between the single-day response and deluge size.

Since flowering stalk density is cumulative over the growing season, instead of using the ResPd average, we used maximum flowering density of each plot during the ResPd as the response variable. Likewise, linear regression was used to assess treatment effects on ANPP and BNPP. For water potential, because some treatments could not be measured on all days (due to senescence, see above), we performed separate linear regressions for each date and sampling time (pre-dawn and midday). For each dataset, outliers were identified using the function "outlierTest" in R (Bonferroni-adjusted p-values < 0.05) and removed before analysis. Only 2 out of 316 data points were identified as outliers.

To identify the deluge size that resulted in response saturation, we also fit non-linear regressions to each dataset. Since we expected to observe a plateau for each response, we used the "nls" function in R with a self-starting command (SSasymp) to fit an asymptotic regression model with the equation: $y = a + (R_0 - a)e^{-cx}$, where a is the horizontal asymptote, R_0 is the y intercept, and c is the rate constant. We also fit a quadratic model to each dataset to identify evidence of non-linearity (concave or convex). These non-linear models were also fit for individual sampling dates within the ResPd for the continuously measured variables. We used Akaike Information Criterion (AIC) values and weights to compare linear and non-linear models and determine the best-fit model for each dataset.

4.4 Results

4.4.1 Precipitation Amounts

The 2018 growing season was drier than normal, with 43 mm of precipitation during the summer months (Jun-Aug, 30-year mean = 139 ± 9 mm). However, 4 small events occurred when the roofs were erected, totaling 8 mm, so the ambient plots only received 35 mm (~25% of the long-term average). With the deluge addition, treatment plots received between 55-155 mm of summer rainfall in total, and annual precipitation in the plots varied from 202-322 mm. Therefore, plots receiving the largest deluge treatment (120 mm) received average annual rainfall (321 mm).

4.4.2 Treatment Effects

Response patterns were assessed at two timescales— on a daily basis (individual sampling dates) and cumulatively over the period of time that deluges impacted soil moisture (ResPd). As expected, soil moisture increased after all the deluge additions, with soil moisture maxima and duration of elevation corresponding to treatment size (Fig. 4.1b). Soil moisture at all sampling dates during the ResPd ($n = 8$ dates) exhibited a linear relationship with deluge size, except for one (Jul 26, 16 days post-deluge), when the quadratic model (convex) was a slightly better fit (Fig. A2.1). Similarly, when averaged over the 28-day ResPd, soil moisture increased linearly with deluge size ($p < 0.001$, $R^2 = 0.54$; Fig. 4.1c). The linear model was a better fit than either non-linear models (asymptotic regression and quadratic; Table A2.1). Additionally, the average duration of elevated soil moisture (defined as VWC at least 3% higher than ambient) increased linearly with deluge size ($p < 0.001$, $R^2 = 0.86$; Fig. A2.2), with the smallest (20 mm) treatment response lasting 2 days, and the largest (120 mm) treatment response lasting 22 days.

B. gracilis leaf water potential also increased rapidly following the deluge addition, but its relationship with deluge size changed through time. For both pre-dawn and midday measurements, the first two dates following the deluge addition (3 and 8 days post-deluge) exhibited a saturating relationship with deluge size ("pseudo" $R^2 = 0.72\text{-}0.96$; Table A2.2, Fig. 4.2). However, by 15 and 23 days post-deluge, linear regressions better explained the data (p =

0.002-0.052, $R^2 = 0.28$-0.55), except for the last midday measurement (23 days post-deluge), when a convex (quadratic) relationship best fit the data ($p = 0.005$, $R^2 = 0.62$; Table A2.2, Fig. 4.2).

Soil respiration and canopy greenness both increased rapidly following the deluge application (Fig. 4.3a,b) and showed similar daily responses (respiration: $n = 8$ dates, greenness: $n = 4$ dates). Both exhibited evidence of response limitation to the largest deluges (80-120 mm) only on the first sampling date after the deluge addition (respiration = 3 days, greenness = 7 days post-deluge). On this date, greenness showed a generally saturating relationship with deluge size, whereas soil respiration was inhibited by the largest deluge treatments, resulting in a concave relationship. This response limitation was temporary, however, as both responses became linear (or very slightly convex) for the rest of the ResPd (Figs. A2.3 & A2.4). When averaged over the ResPd, both soil respiration and canopy greenness increased linearly with deluge size (respiration: $p < 0.001$, $R^2 = 0.88$; greenness: $p < 0.001$, $R^2 = 0.70$; Fig. 4.3d,e), and the linear model was a better fit than the non-linear models for both (Table A2.1). Similarly, average leaf area during the ResPd was also best explained by a linear model ($p = 0.004$, $R^2 = 0.28$; Table A2.1, Fig. 4.3f), but unlike the other variables, leaf area exhibited a consistent linear response with deluge size for each individual day measured ($n = 3$ dates, Fig. A2.5).

Total ANPP and BNPP both increased linearly with deluge size (ANPP: $p < 0.001$, $R^2 = 0.61$; BNPP: $p = 0.020$, $R^2 = 0.20$; Fig. 4.4a, Table A2.1). Additionally, they exhibited similar magnitudes of increase, with the largest treatment (120 mm) resulting in 61% greater ANPP and 58% greater BNPP relative to the ambient (0 mm) treatment. As a result, the slopes of the relationships of ANPP and BNPP with deluge size did not differ from each other ($p = 0.27$). When ANPP was separated by functional group, grass ANPP exhibited a similar linear relationship as total ANPP ($p < 0.001$, $R^2 = 0.57$, data not shown), but forbs only accounted for a small portion of total biomass (5.0 ± 0.7 %) and exhibited no relationship with deluge size ($p = 0.19$, data not shown). When BNPP was separated by depth increment (Shallow: 0-10 cm, Middle: 10-20 cm, Deep: 20-30 cm), BNPP in the Shallow depth was significantly related to deluge size ($p = 0.009$, $R^2 = 0.24$), whereas the Middle and Deep layers did not respond to increasing event size (Middle: $p = 0.29$, $R^2 = 0.04$; Deep: $p = 0.08$, $R^2 = 0.11$; Fig. A2.6). However, if BNPP is contrasted between treatment extremes (0 mm vs. 120 mm), there was evidence of increased fine root production in the Deep soil layer in response to the largest deluge ($p = 0.01$).

Finally, *B. gracilis* flowering density increased strongly with deluge size ($p < 0.001$, $R^2 = 0.40$), with almost no flowering stalks in the 0 mm treatment increasing to a density of 22 flowering stalks m^{-2} in the largest deluge treatment (Fig. 4.4b). Again, a linear model better explained the data than the non-linear models (Table A2.1).

4.5 Discussion

The consequences of climate change-induced increases in the frequency and magnitude of large rain events (IPCC, 2013; Donat et al., 2016) are especially important to understand in semi-arid systems given their importance to the global carbon cycle (Poulter et al., 2014; Ahlstrom et al., 2015). We assessed key ecosystem responses to single deluge events of varying magnitude, with the goal of identifying response thresholds beyond which ecological processes would not increase further with larger deluge sizes. Contrary to our expectations, both above and belowground processes primarily increased linearly with deluge size, even with events that exceeded historical magnitudes. The ecosystem exhibited an impressive ability to respond to a large volume of water delivered in a short period of time, thus we saw little evidence of response saturation or asymmetry. This suggests that the shortgrass steppe has the potential to effectively utilize water from the extreme deluges forecast for the future.

4.5.1 Ecological Responses to Deluge Size

During the 28-day response period (ResPd) following the deluge addition, soil respiration, canopy greenness, and leaf area all increased linearly with deluge size, consistent with the soil moisture response. Similarly, at the end of the season, ANPP, BNPP, and flowering also exhibited a linear relationship with deluge size. ANPP and canopy greenness both had similar values for the two largest deluges (100 mm and 120 mm), suggesting a response plateau may have been reached, but the overall lack of evidence for saturation was striking. Impressively, the shortgrass steppe ecosystem was able to utilize a volume of water equivalent to a third of mean annual rainfall (321 mm) delivered as a single event. Soil respiration and *B. gracilis* flowering were the most responsive ecosystem processes; compared to ambient, the largest deluge stimulated a 4-fold increase in soil respiration and an impressive 14-fold increase in flowering.

Although comparable studies are limited, there is evidence for both linear and saturating responses to large precipitation events. Li et al. (2013) assessed ecosystem response to natural rain events and found a linear relationship between event size and remotely sensed estimates of productivity (NDVI). Guo et al. (2016) observed gross primary production (GPP) to increase linearly with rain event size, but Chen et al. (2009) found GPP to saturate around 50-75 mm events. Similarly, there is evidence of both linear and saturating responses of soil respiration with increasing rain event size (Chen et al., 2008; Chen et al., 2009; Munson et al., 2010; Song et al., 2012). A greater number of studies have assessed ecosystem response to seasonal or annual precipitation totals, but have also found variable results, with ANPP, BNPP, and soil respiration exhibiting either a linear or saturating relationship with precipitation amount (Kong et al., 2013; Hsu & Adler, 2014; Zhu et al., 2016; Wilcox et al., 2017; Wu et al., 2018; Ru et al., 2018; Hao et al., 2019; Du et al., 2020). Our results are consistent with a season-long rainfall manipulation also conducted in this semi-arid grassland. Felton et al. (2019) found ANPP and soil respiration to increase linearly with growing season precipitation, even at extreme values (1st – 99th percentile of long-term precipitation record). This suggests that the shortgrass steppe is highly responsive to rainfall amount, whether precipitation is delivered as an individual event or as multiple events over the growing season, with no evidence of saturation even at extreme precipitation levels.

It is important to note, however, that responses were timescale dependent. For the continuously measured variables, ResPd averages were linear with deluge size (as discussed above), but daily responses did show some evidence of non-linearity at these shorter time scales. Immediately following the deluge addition, water potential and greenness exhibited saturation at the largest event sizes, and soil respiration may have been inhibited (concave relationship). This initial saturation was likely caused by several different mechanisms. For water potential, maximum plant hydration was achieved by a 40 mm event (Fig. 4.2), so any larger event was unable to elicit a greater response. For canopy greenness, there was clearly a time lag required for plant growth to fully respond to deluges (Fig. 4.3b), and for soil respiration, the largest events likely caused temporary anoxic conditions, reducing soil CO_2 efflux. Prior studies have shown that soil microbial (heterotrophic) respiration is limited by saturated soil conditions (Chen et al., 2009; Du et al., 2020; Yang et al., 2020), but plant root (autotrophic) respiration could also be affected (Ben-Noah & Friedman, 2018). As the soils dried, and with more time to respond, these daily relationships became linear, and in some cases slightly convex as the smallest deluge treatment plots ceased responding. In contrast, soil moisture and leaf area were consistently linear at both the daily and ResPd timescales. This highlights the importance of considering response duration, in additional to response magnitude, in order to understand the full ecological impact of a deluge event (Schwinning & Sala 2004). Indeed, previous studies have found rain event size to correlate with the duration of various ecological responses, including plant green-up (Li et al., 2013), soil respiration (Chen et al., 2008; Munson et al., 2010; Song et al., 2012), and gross primary production (Guo et al., 2016). Similarly, deluge size determined the duration of the ecological responses measured in our experiment.

This extended response duration was likely a direct consequence of the water holding capacity of the soil at our study site—larger deluges caused the soil profile to remain wet for a longer period of time. In fact, the difference between treatments was striking; the smallest deluge (20 mm) elevated soil moisture (0-20 cm depth, where 75% of roots are located, Milchunas & Lauenroth, 1989) for only 2 days, whereas the largest deluge (120 mm) elevated soil moisture for 3 weeks. Therefore, plots receiving larger deluges had a much longer response window, allowing for increased plant growth (above and belowground) and flowering, as well as greater total soil respiration. While the duration of the soil moisture response is impressive, similar results have been reported in other studies of semi-arid ecosystems— a 40 mm event elevated soil moisture for 18 days (Guo et al., 2016) and a 70 mm event for 17-30 days (Post & Knapp 2020). Larger rain events recharge deeper soil layers (He et al., 2012), proportionately reducing losses to evaporation and increasing plant transpiration (Loik et al., 2004; Lauenroth & Bradford 2012, Guo et al., 2015). However, soil texture is important; the sandy clay loam soil texture at our study site allowed for sufficient water storage within the root-available zone, with limited losses to deep infiltration (Sala et al., 1992; Saxton & Rawls, 2006). In contrast, when Hao et al. (2017)

applied a large rain pulse, soil moisture was only briefly elevated, which they attributed to water loss due to deep infiltration in the sandy soil at their study site. Consequently, ANPP was unresponsive to their applied rain pulse. This highlights the importance of considering soil texture when assessing ecosystem deluge response.

Finally, our results support the response hierarchy framework described by Schwinning and Sala (2004), in which rain event size determines the number of ecological processes that are triggered in semi-arid ecosystems. According to this framework, after a rain event, the first measurable ecological response is an increase in soil moisture. If that increase is large enough, plant water potential increases over the next several hours and days (Fig. A2.7a). This increase in plant water status can stimulate greater physiological activity (carbon uptake via photosynthesis), which if elevated for an extended period of time, results in new leaf production (Fig. A2.7b,c) and eventually increased plant biomass. In our study, the smaller deluges (20-60 mm) successfully triggered these initial responses, as exhibited by the saturating relationships of water potential with deluge size (Fig. 4.2), but impacted subsequent ecosystem responses to a lesser degree, resulting in relatively smaller increases in leaf production and ANPP.

4.5.2 Above vs Belowground Response

Above and belowground production exhibited similar responses to increasing deluge size— both increased at similar rates and the largest deluge increased productivity by ~60% relative to the ambient treatment (Fig. 4.4a). We were surprised by this consistent response given that prior precipitation addition studies have found ANPP and BNPP to differ in response magnitude, although again, patterns have been inconsistent. For example, Wilcox et al. (2015) found BNPP to be more responsive to increased precipitation than ANPP in the shortgrass steppe, and a recent review of experimental grassland manipulations found BNPP to increase linearly, but ANPP to saturate, with precipitation amount (Wilcox et al., 2017). Alternatively, an observational study in a semi-arid grassland found ANPP to be more responsive to annual precipitation than BNPP (Milchunas & Lauenroth, 2001).

The above studies focused on annual or seasonal precipitation totals, whereas our study addressed responses to single deluges. Our results indicate that ANPP and BNPP responded nearly identically to rainfall from a single deluge addition. This is in contrast to the results of a previous study which reported BNPP to be twice as responsive as ANPP to a deluge event (Post & Knapp, 2020). This inconsistency in plant growth allocation is a challenge to resolve but could be related to differing antecedent precipitation patterns and soil moisture conditions between the two studies.

4.5.3 Context and Interpretation

This experiment was conducted in a naturally dry year (annual precipitation was 63% of long-term average), so only the plots receiving the largest deluge treatment (120 mm) experienced long-term average annual precipitation (321 mm). The remaining plots experienced below-average precipitation. This may have rendered the shortgrass steppe ecosystem especially sensitive to deluge events and could contribute to the observed linear responses to increasing deluge size. If this study were conducted in an average or above-average rainfall year, increased baseline soil moisture conditions might cause the system to achieve its maximum response potential (saturation) with the larger deluge additions. However, a prior experiment in this system suggests that at least some ecosystem responses (ANPP, soil respiration) continue to increase linearly with precipitation amount, even with extreme amounts of rainfall (Felton et al., 2019). We would expect that response saturation thresholds must exist for this ecosystem, but identifying them may require larger deluges, especially during dry years.

The extreme drought conditions in the ambient treatment highlight an additional insight from this experiment— a single deluge event was able to stimulate ANPP from below-average levels (ambient = 60 g/m^2) to average-year values (120 mm = 97 g/m^2 vs long-term average ANPP ~ 100 g/m^2, cf. Lauenroth & Sala, 1992). A similar magnitude increase (~60%) was observed for BNPP. This "drought-rescue" effect of large rain events has been observed in prior experiments in the shortgrass steppe (Cherwin & Knapp, 2012; Post & Knapp, 2020). Our study confirms that a single deluge can elicit this rescue response to extreme drought in semi-arid ecosystems.

One other caveat for interpreting our results is that we prevented run-off during the deluge additions. Run-off, even from large precipitation events, is fairly uncommon at our study site (Lauenroth & Bradford, 2006), but it could be more substantial in other locations, depending on soil texture, surface conditions, and plant cover (D'Odorico & Porporato, 2006; Zhao et al., 2013; Fischer et al., 2015). In such cases, larger deluges could result in proportionally more water loss to run-off than smaller events (Liu et al., 2011; Zeppel et al., 2014), leading to apparent ecosystem response saturation. This saturation would not be caused by an inability of the system to utilize large water inputs, but rather by the redistribution of water from large deluges to lower topographic locales via run-off. For example, Peters et al. (2012) found a grassland playa to be unresponsive to annual precipitation amount due to substantial water redistribution via overland flow. Run-off from deluge events could also cause additional ecological impacts, such as increased soil erosion and nutrient depletion (Turnbull et al., 2011; Wang et al., 2019). Since an increase in extreme rain events could result in more frequent run-off in some ecosystems (Zeppel et al., 2014), it is important that future research address the influence of deluge events in a variety of natural systems.

4.5.4 Conclusions

Semi-arid ecosystems have been reported to strongly influence interannual variability in global carbon uptake (Ahlstrom et al., 2015), thus, our findings have broader implications for the global carbon cycle. The role of large rain events in semi-arid systems has been previously established; average rain event size is often a strong predictor of ANPP (Lauenroth & Sala, 1992; Swemmer et al., 2007; Li et al., 2015; Post & Knapp 2020), and therefore, ecosystem carbon uptake (Parton et al., 2012; Peng et al., 2013; Guo et al., 2015). Our results suggest that the size of individual deluge events may also influence total carbon sequestration of semi-arid ecosystems. Thus, as climate change increases rainstorm magnitude and frequency (IPCC, 2013), semi-arid ecosystems could be well-adapted to respond to this shift in precipitation pattern with consequences for both local ecosystem services (forage production) and global carbon uptake.

4.6 Figures

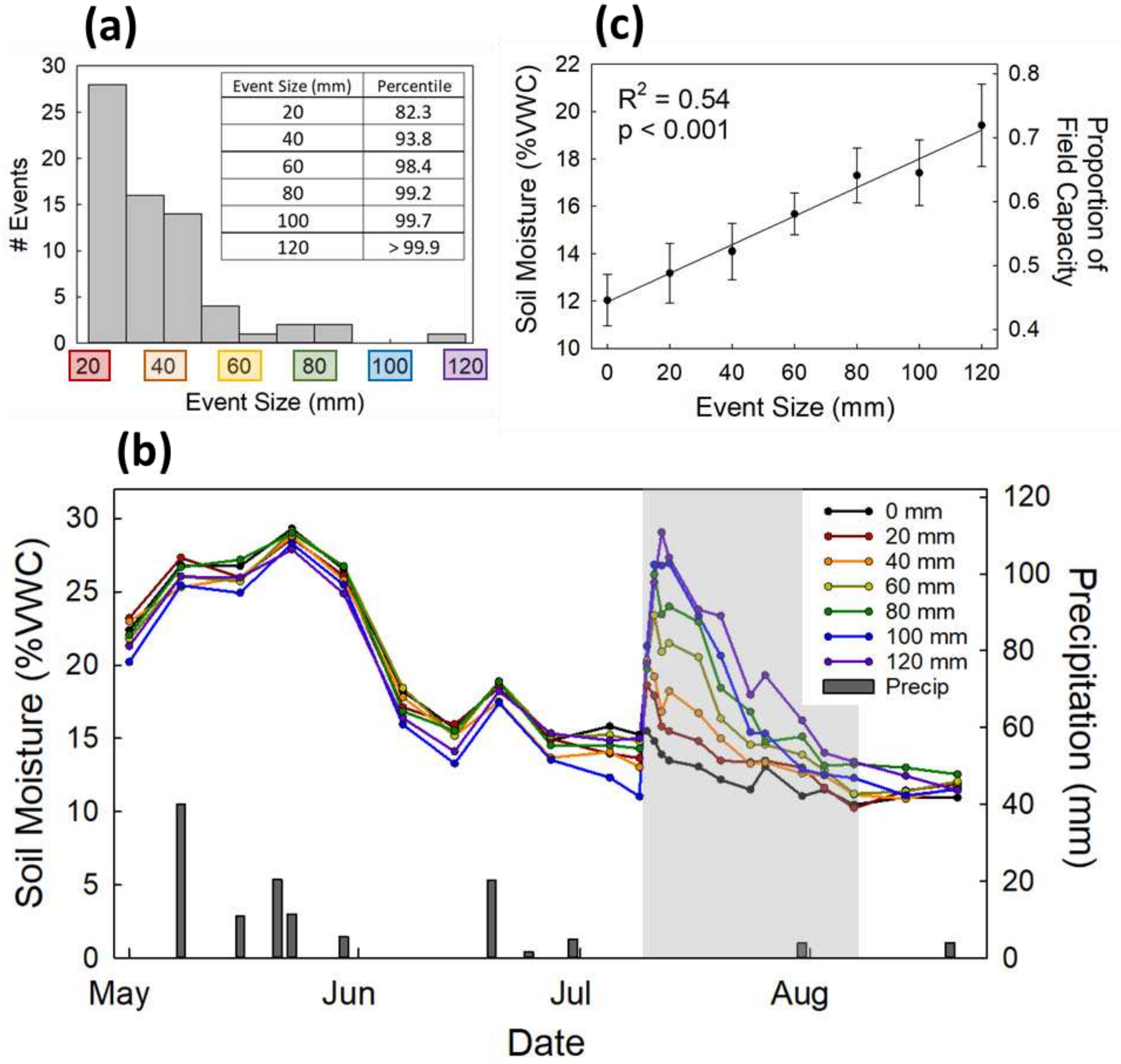

Figure 4.1. (a) Historical distribution (1980-2017) of large rain events (≥ 20 mm) during the summer months (Jun-Aug) at the CPER. The colors match the applied treatments in panel b. The inset shows the percentile ranking of each deluge treatment based on the summer rainfall record of all rain events ≥ 2 mm. (b) Average soil moisture by treatment (lines) and ambient precipitation (bars) over the course of the 2018 growing season. The grey panel denotes the 28-day response period (see text for definition). (c) Average soil moisture (mean ± SE) of each treatment during the response period and the corresponding proportion of field capacity (27% VWC).

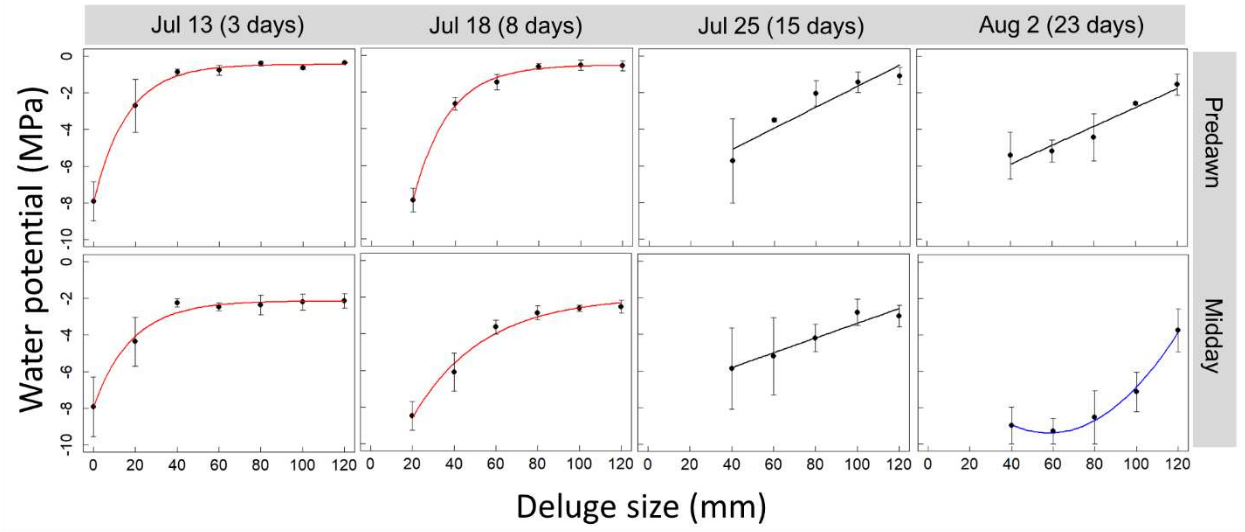

Figure 4.2. Pre-dawn (upper) and midday (lower) leaf water potential (mean ± SE) of *B. gracilis* at several timepoints after the deluge treatments. Panels increase in the number of days since the deluge application (parenthesis in top label) from left to right. Red lines indicate a better saturating fit, black lines a better linear fit, and blue lines a better convex (quadratic) fit.

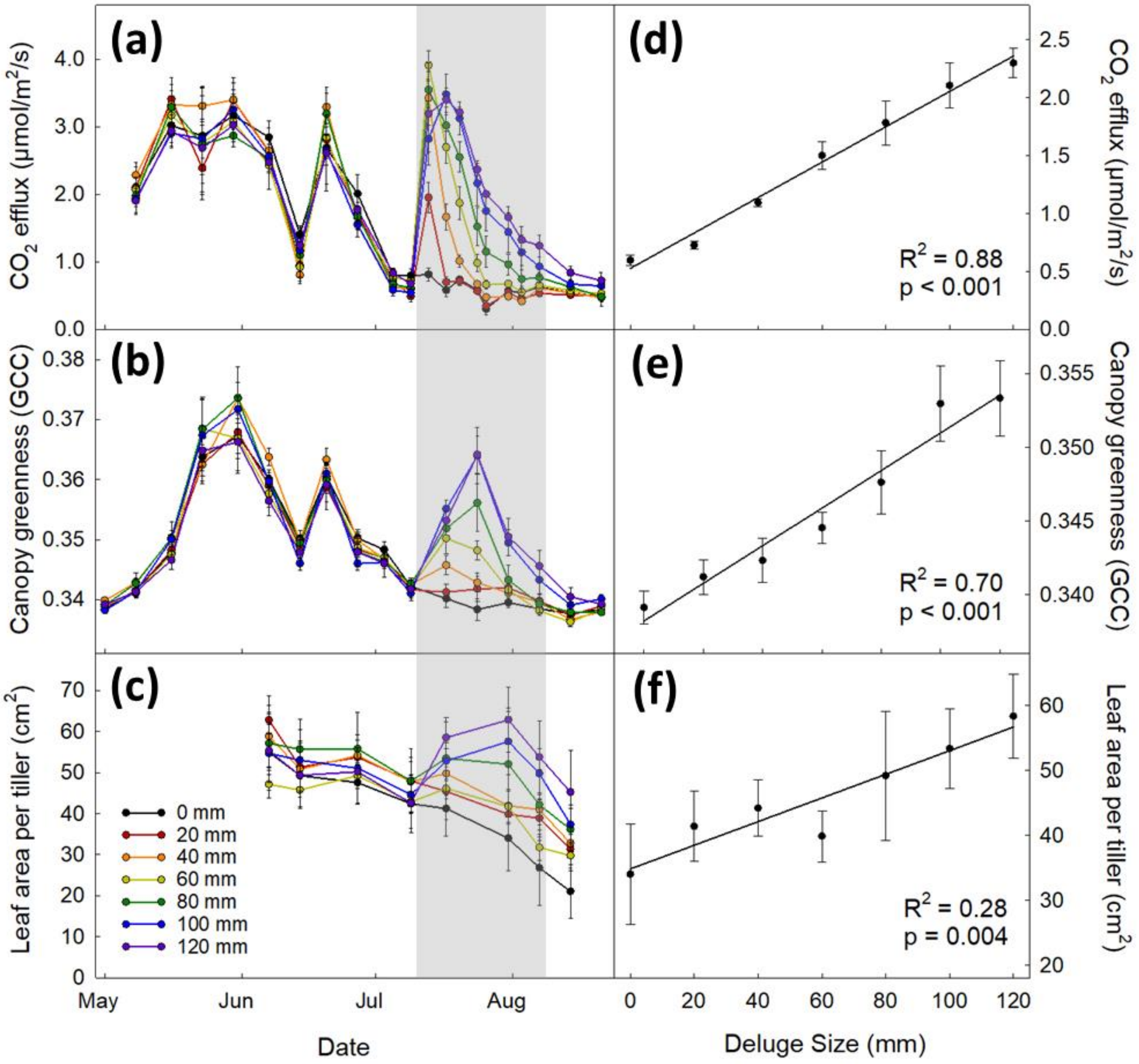

Figure 4.3. (a-c) Seasonal patterns (mean ± SE) of (a) soil respiration, (b) canopy greenness, and (c) *B. gracilis* green leaf area per tiller by treatment (colored lines). The grey panel indicates the response period. (d-f) Average (mean ± SE) of each measured attribute over the response period. A linear model was the best fit for all the relationships.

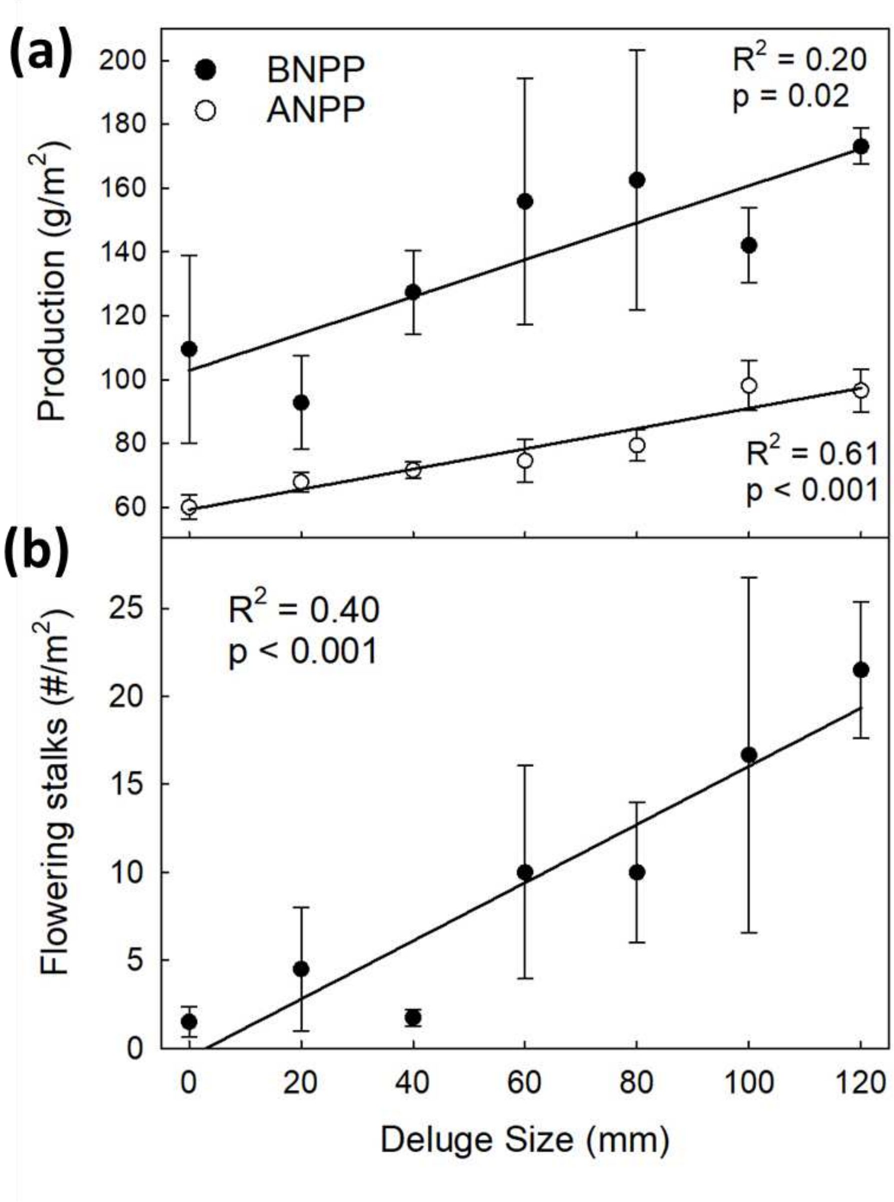

Figure 4.4. (a) Response (mean ± SE) of ANPP (unfilled circles) and BNPP (filled circles) to the deluge treatments. The slopes are not significantly different ($p = 0.27$). (b) Maximum flowering stalk density (mean ± SE) of each treatment during the 2018 growing season. A linear model was the best fit for all the relationships.

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CHAPTER 5: SEMI-ARID GRASSLANDS AND EXTREME PRECIPITATION EVENTS: DO EXPERIMENTAL RESULTS SCALE TO THE LANDSCAPE?

5.1 Summary

The frequency and magnitude of deluges (extremely large rain events) are increasing globally as the atmosphere warms. Small-scale experiments suggest that semi-arid grasslands are particularly sensitive to both the timing and size of deluge events. However, the assumption that plot-scale results can be extrapolated across landscapes with variable soil textures, plant communities, and grazing regimes has seldom been tested, despite being key to forecasting regional consequences of precipitation extremes. We used precipitation data from an extensive rain gauge network to identify natural deluges (mean size = 60 ± 31 mm, 1984–2012) that occurred across a ~60 km^2 heterogeneous native shortgrass steppe landscape in Colorado. We then related spatial variation in deluge precipitation to post-deluge responses in canopy greenness (normalized difference vegetation index, NDVI) via satellite imagery. Consistent with results from experiments, this semi-arid grassland was most sensitive to mid-growing season deluges, and post-deluge canopy greenness usually increased linearly (67% of the time) with increasing deluge size. This suggests that aboveground productivity in these semi-arid systems will likely increase, rather than asymptote, with forecasted increases in deluge size. Importantly, differences in grazing regime did not significantly alter deluge responses, indicating that these patterns are robust to this widespread management practice.

5.2 Introduction

Rising global temperatures are intensifying the hydrological cycle (Huntington, 2006; IPCC, 2013), resulting in more frequent large rain events, including deluges (statistically extreme rain events, cf. Smith, 2011). Indeed, many parts of the world are already experiencing increases in rain event size, as well as deluge frequency (Kunkel et al., 2013). Dryland ecosystems are expected to be particularly sensitive to this change in precipitation pattern because their ecological processes depend strongly on discrete rain events (pulses) that alleviate chronically low soil moisture (Noy-Meir, 1973; Schwinning & Sala, 2004).

Past research in dryland ecosystems suggests that precipitation delivered as large events increases productivity more effectively than multiple small rain events (Lauenroth & Sala, 1992; Heisler-White et al., 2008). This is because large events promote deeper soil water infiltration, thereby limiting the amount of water lost to evaporation and increasing the amount available for plant uptake (Loik et al., 2004; Knapp et al. 2008). Additionally, observations and recent experiments suggest that dryland systems are sensitive to both the timing and size of deluge events (Parton et al., 2012; Peng et al., 2013). For example, in the semi-arid shortgrass steppe (SGS) of Colorado, productivity was stimulated most by a deluge at mid-growing season relative to deluges of the same size occurring earlier or later in the season (Post & Knapp, 2020). Further, although a threshold event size might be expected (beyond which ecosystem responses saturate), productivity responses to experimental deluges increased strongly and linearly even as deluge size reached historical maxima (Post & Knapp, 2021).

A long-standing concern in ecology is how well results from experimental plot-level studies scale to larger landscapes (Knapp et al., 2018). While evidence for consistency in plot-to-landscape patterns has been mixed (e.g., Leuzinger et al., 2011; Wilcox et al., 2016), scaling results from deluge experiments is particularly challenging due to the difficulty of replicating factors that impact soil water infiltration and runoff (Lauenroth & Burke, 2008; Hoover et al., 2021). Scaling challenges include replicating natural rainfall intensities, capturing realistic ranges in topographic and soil variability, and including differences in grazing regime and plant community composition (Milchunas et al., 1989; Burke et al., 1999; Porensky et al., 2017).

Here, we assessed responses to naturally occurring deluges across the 62.7 km^2 Central Plains Experimental Range (CPER) in NE Colorado, a SGS ecosystem with significant spatial variation in soils and grazing management, and where several small-scale deluge experiments have been conducted (Post & Knapp 2019, 2020, 2021). This allowed us to directly compare responses to simulated deluges at the plot scale to natural deluges at the landscape scale. We identified isolated deluge events that occurred at the site using historical data from a spatially extensive rain gauge network. We then related spatial variation in precipitation to subsequent responses in canopy greenness (via the normalized difference vegetation index, NDVI) as a surrogate for aboveground net primary production (ANPP, Hermance et al., 2015). Our goal was to test two general predictions from past experiments (Post & Knapp 2020, 2021): (1) that ANPP responses to deluges would vary seasonally, with the greatest sensitivity at mid-growing season, and (2) that ANPP would increase linearly as precipitation event/deluge size increased.

5.3 Methods

5.3.1 Site Description

The study area was the Central Plains Experimental Range (CPER, United States Department of Agriculture-Agricultural Research Service), a 62.7 km^2 tract of native SGS located in NE Colorado (40.8422, -104.7156). Mean annual precipitation is 321 mm, and most rainfall (70%) occurs as patchy, often intense convective storms during the warm months (May-September; Lauenroth & Sala, 1992; Lauenroth & Burke, 2008). As a result, spatial variation in precipitation within a single growing season is often large (Augustine, 2010). While most rain events are small (83% are $\leq$ 10 mm), these account for only 41% of total growing season rainfall;

therefore, infrequent large rain events are important in this ecosystem (Sala & Lauenroth, 1982). Mean annual temperature is 8.6°C, and average ANPP is ~100 g/m^2 (Lauenroth & Sala, 1992). The dominant plant species is a C$_4$ grass, *Bouteloua gracilis* (blue grama), but there is substantial variation in plant community composition within the site, largely due to differences in long-term grazing regimes (Lauenroth & Burke, 2008; Porensky et al., 2017). The most common ecological site is classified as Loamy Plains (ID: R067BY002CO; nrcs.usda.gov), and soil texture varies significantly across the CPER (Burke et al., 1999).

5.3.2 Precipitation Data

The CPER contains a network of 30 manual rain gauges distributed across the site (Fig. 5.1a), and since 1939, precipitation has been recorded during the growing season (May-September), usually within 24 hours of a rain event (Augustine, 2010). To verify rainfall dates, we cross-validated this dataset with a daily precipitation record from the National Atmospheric Deposition Program (NADP, 1980-present, Hoover et al., 2021). Some gauges were missing data for select days, but all our analyses included data for at least 24 of the 30 gauges.

We used the above dataset to identify isolated summer (June-September) deluge events. We define a deluge as a statistically large event based on the long-term rainfall record (Post & Knapp, 2021). The average monthly deluge size included in this study ranged from 47-70 mm (Table 5.1), representing event sizes that exceed the 90th percentile based on the long-term precipitation record (Post & Knapp, 2021). For this analysis, we summed precipitation from rain events that co-occurred temporally (typically over 2-4 days, Table 5.1) and considered these as single deluge events (Post & Knapp, 2021). This is because rain days tend to be clustered in the SGS and function as a single soil moisture pulse (Noy-Meir, 1973; Loik et al., 2004). For consistency in satellite imagery, we restricted our focal time period to the duration of the Landsat

5 TM, from 1984-2012. To compare ecosystem response across varying precipitation amounts, we selected deluge events that were spatially variable (average precipitation range = 27-46 mm across the 30 gauges, Table 5.1). Additionally, in order to isolate the ecosystem deluge response, we excluded deluges during periods when other rainfall events co-occurred and instead focused on rain events that were isolated in time with no significant rainfall (10 mm) measured either the week before or after the deluge. This provided a minimum 14-day "dry window," with most events having much longer dry windows (Table 5.1). We chose a 10 mm threshold because this amount of rain has little impact on plant production in this ecosystem (Lauenroth & Sala 1992; Post & Knapp, 2021). Because June was the wettest month during our study period (June-September), fewer isolated deluges were available for this month.

5.3.3 Landsat Imagery

We utilized remotely sensed images (30 m spatial resolution) from Landsat 5 TM (1984–2012, nasa.gov) to quantify the impact of deluge events on canopy greenness. Since the CPER lies at the intersection of two Landsat scenes (Path 33 Row 32 and Path 34 Row 32), images were available every 7-9 days. This temporal resolution was sufficient to achieve our goal of assessing the influence of deluge size on canopy greenness, but unfortunately, prevented us from being able to calculate precise response durations.

Using Google Earth Engine (Gorelick et al., 2017), we filtered the Landsat 5 Collection 1 Surface Reflectance imagery to select all images from approximately 2 weeks before to 4-5 weeks after each deluge event and masked low-quality pixels (cloud cover, cloud shadow) using the quality assessment band provided with each image (see Tebbs et al., 2017). We created a shapefile with a 150 m square buffer (sampling area) around each rain gauge (excluding a small grazing exclosure surrounding most gauges), which we used to extract pixels for each rain gauge location (average = 92 pixels per rain gauge, Fig. 5.1b). We calculated average NDVI for each of these rain gauge sampling areas according to Tebbs et al. (2017).

We only assessed deluge events when there was at least 1 image within the dry window before the deluge and another image at least 7 days after. Further, each image had to have a cloud-free NDVI value for at least half (15) of the gauges. From these, we calculated the relative (%) change in NDVI (%NDVI) for each rain gauge as: ((post-deluge NDVI – pre-deluge NDVI) / pre-deluge NDVI) * 100. If a deluge event had several post-deluge images available within the dry window, %NDVI was calculated for each. Analyses based on absolute change in NDVI (post-deluge NDVI – pre-deluge NDVI) to account for pre-existing differences in greenness, bare soil cover, plant litter, and standing dead vegetation across the landscape (Hermance et al., 2015) yielded nearly identical results as %NDVI.

5.3.4 Statistical Analyses

Analyses were performed in R (version 3.6.3). For each deluge event, we used linear regression to assess the relationship between rainfall amount and %NDVI across the CPER (Fig. 5.1c). We refer to the slope of this relationship as deluge "sensitivity," representing the percent change in NDVI per mm of precipitation. If a deluge event had multiple post-deluge images, we performed a separate linear regression for each and selected the one with the steepest significant slope (date with greatest sensitivity) for further analyses. For each regression model, outliers were identified using the function "outlierTest" (Bonferroni-adjusted p-values < 0.05) and removed. Only 15 of the total 1,723 %NDVI observations were identified as outliers (<0.01%).

To assess how the SGS response to a deluge event differed across the growing season, we separated deluge events by the month in which they occurred (June-September) and compared slopes (sensitivities) and R^2 values from the linear regressions described above. We used a one-way ANOVA with Tukey's post-hoc pairwise comparisons to identify monthly differences in average sensitivity (see Fig. A3.1 for additional analyses). We also determined the proportion of events with significant ($p < 0.05$) regression slopes for each month.

To determine if increasing deluge size elicited linear or saturating NDVI responses, we also fit non-linear regressions to deluge events with significant linear relationships (see above). We used the “nls” function with a self-starting command (SSasymp) to fit an asymptotic regression model: $y = a + (R_0 - a)e^{-cx}$, where a is the horizontal asymptote, R_0 is the y intercept, and c is the rate constant. We compared linear to non-linear models using Akaike Information Criterion (AIC) values and weights.

We also assessed the influence of grazing intensity, and corresponding differences in plant composition (Porensky et al., 2017), on deluge response by focusing on three co-located pastures that have been subjected to different grazing intensities (light, moderate, or heavy) since 1939. We used an ANOVA to evaluate differences in average green-up magnitude (%NDVI) across the three pastures in response to deluge events.

5.4 Results

In total, 51 events met our criteria for being spatially variable and temporally isolated, and of those, 31 had satellite images available. The events were spread across the 4 growing-season months with the fewest in September (the driest month, Table 5.1). As expected, %NDVI was highly related to precipitation amount, with ~77% (24/31) of the deluge events exhibiting a significant linear regression slope. However, the proportion of significant deluges varied by month, with significant relationships for all deluges occurring in July and August versus only ~ 42% of deluges in June and September (Fig. 5.2a).

Average sensitivity (regression slope) and linear regression fit (R^2 value) showed similar monthly trends, with deluges in July and August generally exhibiting the strongest relationships. Sensitivity differed by month ($p = 0.023$), with sensitivity in September substantially lower than all the other months, especially July (Fig. 5.2b). Similarly, average R^2 values tended to be higher in July and August than in June or September (Fig. 5.2c). We also analyzed patterns using only events with significant regression slopes. Interestingly, this caused the monthly trends to disappear, with similar average sensitivity ($p = 0.51$) and R^2 values across all months (Fig. A3.2).

Of the deluges with significant relationships (see above), the majority of deluge events (16/24, 67%) were better fit with a linear than a saturating model relating precipitation amount to %NDVI (Fig. 5.3). Of the eight events exhibiting saturating relationships, four were in July, three in August, and one in September. Further, two of the events in July had very similar AIC values for both saturating and linear models (AIC weights = 51% vs 49% and 56% vs 44%).

Finally, the average green-up response (%NDVI) to the included deluge events did not differ between pastures that experienced different long-term grazing regimes ($p = 0.69$, Fig. A3.3).

5.5 Discussion

We utilized the natural spatial variability of large summer rainstorms to relate deluge size and timing to ecological response (NDVI) in a water-limited semi-arid grassland. We found that the strongest deluge responses were during the mid-growing season, and that canopy greenness typically increased linearly with precipitation event size. Thus, landscape-level responses (km^2 scale) largely matched those of previous small-scale (m^2 scale) deluge experiments (Post & Knapp, 2020, 2021). We elaborate on these response patterns below.

5.5.1 Response to Deluge Timing

The highest sensitivity of NDVI to precipitation amount was observed during the peak summer months, in July and August. During these months, all deluges exhibited a significant positive relationship between precipitation amount and green-up, with deluge size explaining an average of ~ 47% of variation in canopy greenness and a maximum of 86%. A smaller proportion (~ 42%) of June and September deluges exhibited a significant relationship between deluge size and canopy greenness, and relationships were generally weaker (precipitation explained ~ 21% of variation in greenness). These results are similar to those from a 1-year experiment conducted in an ungrazed site with a single soil type (Post & Knapp, 2020). They found the SGS to be most responsive to a mid-growing season (July) deluge, with deluges earlier (June) or later (August) in the season eliciting dampened ecosystem responses. By contrast, this observational study showed equally strong green-up responses to deluges in both July and August, perhaps due to variations in antecedent soil moisture and/or plant conditions (Schwinning & Sala, 2004; Sala et al., 2012).

The reduced sensitivity of the SGS to early (June) and late-season (September) deluges was likely caused by different mechanisms. Prior to deluges in July, August, and September, average NDVI was generally low due to senescent vegetation (Fig. A3.4). This senescence was likely induced by low soil moisture in July and August; thus a large rain event could initiate a substantial plant response and cause the SGS to exhibit higher deluge sensitivity. However, by September, the dominant C_4 grasses begin to senesce seasonally, limiting their ability to physiologically respond to a deluge (Schwinning & Sala, 2004; Parton et al., 2012). In contrast, the landscape was typically much greener before June deluge events, with substantially higher average pre-deluge NDVI (Fig. A3.4). The SGS usually receives considerable spring rainfall, initiating plant green-up that persists into the early summer (Parton et al., 2012). Therefore, plants are less likely to be sensitive to isolated deluges in June because the plant canopy is already actively growing and not water-limited (Fig. 5.2). Nonetheless, the SGS did respond to three deluges in June, suggesting that aboveground productivity can respond to early-season deluges, perhaps during unusually dry spring conditions. Thus, for much of the growing season (June-August), antecedent soil moisture might more strongly determine the ecosystem deluge response, rather than event timing itself.

5.5.2 Response to Deluge Size

Based on experimentally imposed deluges, Post and Knapp (2021) reported that almost all measured ecosystem responses exhibited a positive linear relationship with increasing deluge size. The results of this study are similar, with the majority (67%) of natural deluges eliciting a linear relationship between precipitation amount and canopy greenness across the landscape. However, eight of the 24 significant deluges (33%) did exhibit evidence of saturation with increasing precipitation amount, indicating a threshold beyond which more precipitation does not further stimulate ecosystem response. We expected that the largest deluges would be most likely to saturate ecosystem responses, but of the four largest deluges we assessed (each >100 mm, 2 each in July and August), two exhibited saturating relationships (1 in each month), but two did not. Likewise, the saturating deluges were evenly distributed across the growing season and showed no trends in dry window length, precipitation range, or overall change in canopy greenness (%NDVI). Previous dryland studies have also reported a mix of linear and saturating ecological responses with rain event size (Li et al., 2013; Chen et al., 2009), attributable in part to legacies from prior precipitation patterns (Sala et al., 2012).

5.5.3 Broader Implications

Our results have several important implications. First, relationships between deluge size and canopy green-up were strong despite variations in grazing intensity, soil texture, and plant community across the >60 km^2 study region. This emphasizes the overarching importance of precipitation as a primary driver of ecosystem function, and suggests that results from small-scale precipitation manipulation experiments, with inherently limited variation in these variables, can be extrapolated to more extensive semi-arid grassland regions. Second, deluges in these systems tend to exhibit high spatial variability (see Fig. 5.1a), which our results suggest will strongly affect patterns of forage quantity and perhaps quality, depending on the month of the growing season. These results can help inform adaptive grazing management strategies whereby ranchers relocate livestock to track rainfall patterns (Derner & Augustine, 2016). Finally, our results highlight the importance of considering fine-scale spatial heterogeneity in rainfall for more accurate estimates of regional carbon uptake. This is especially important in semi-arid systems where water inputs can drive “hot spots” and “hot moments” of carbon fluxes (Parton et al., 2012; Peng et al., 2013), with important implications for interannual variability in global carbon uptake (Ahlstrom et al., 2015).

5.6 Tables

Table 5.1 Summary statistics of the analyzed deluge events (1984-2012), defined as statistically large precipitation events based on the long-term rainfall record. For each month, the number of deluge events (Deluges) is reported, along with multiple deluge metrics (mean ± SD): the number of individual rain days per deluge event (Rain days), deluge size (Deluge size), range in precipitation across all the rain gauges (Precip range), the number of dry days before a deluge (Dry period before), and the number of dry days after a deluge (Dry period after). The number of days over which daily events (Rain days) were combined into a single deluge event was typically 2-4 days.

Month	June	July	August	September
Deluges (#)	7	9	10	5
Rain days (#)	1.4 ± 0.2	2.2 ± 0.4	2.0 ± 0.4	2.0 ± 0.4
Deluge size (mm)	49.4 ± 9.0	62.9 ± 9.3	70.2 ± 13.3	46.6 ± 3.9
Precip range (mm)	31.0 ± 7.1	41.6 ± 5.6	45.9 ± 8.1	26.8 ± 5.5
Dry period before (# days)	16.4 ± 3.6	17.4 ± 2.8	21.7 ± 3.8	14.6 ± 4.9
Dry period after (# days)	14.9 ± 2.3	21.4 ± 3.3	26.9 ± 5.1	28.4 ± 9.2

5.7 Figures

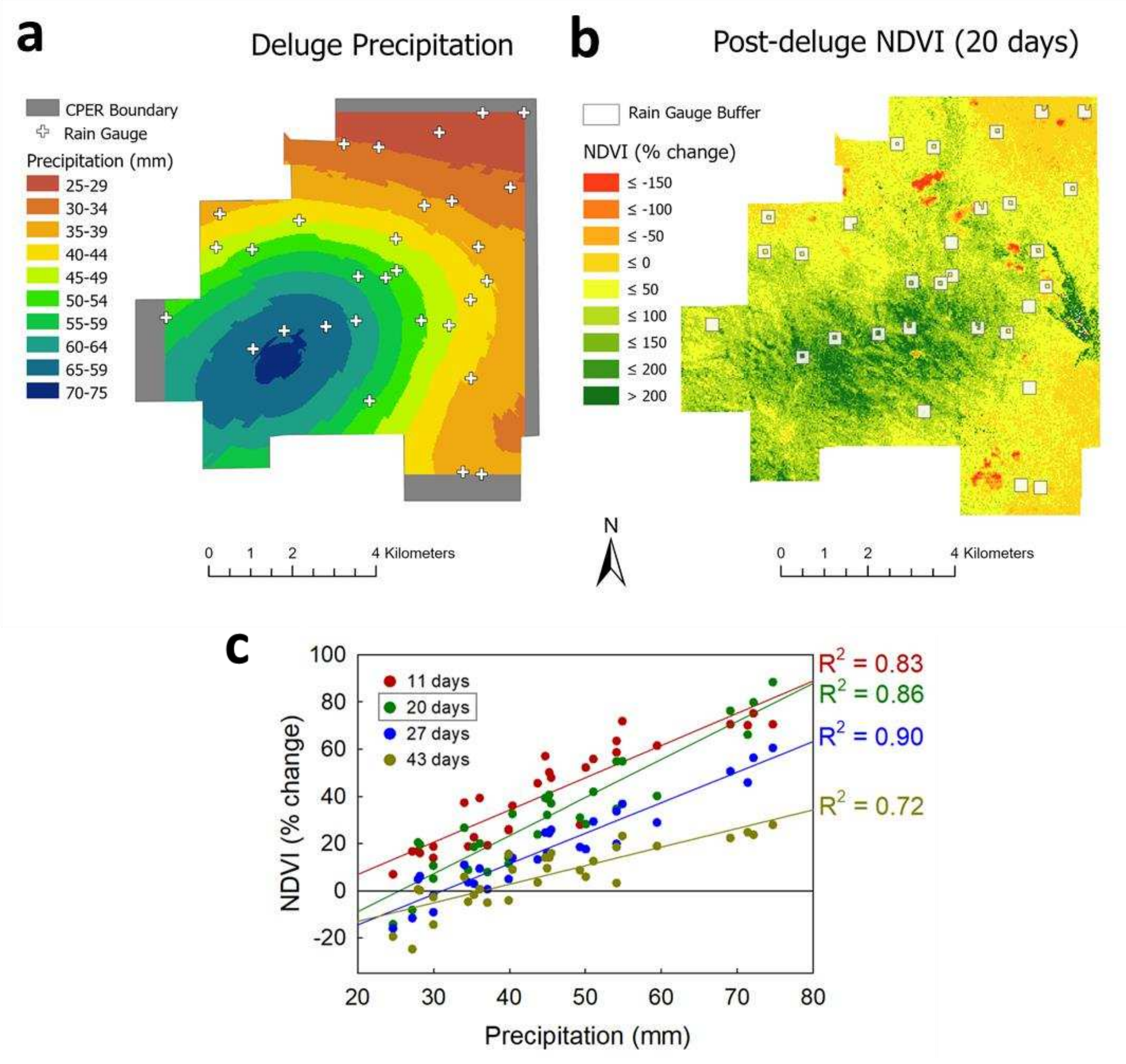

Figure 5.1. (a) Spatial distribution of precipitation amounts across the study site for an example deluge in July 2006. Also shown are locations of rain gauges (+). (b) Response of NDVI (% of pre-deluge values) 20 days after the deluge. The white boxes denote the 150 m sampling buffers around each rain gauge. (c) Linear regressions relating percent change in NDVI to precipitation amount for several image dates following the deluge event, reported as days since deluge. The image with the steepest regression slope (20 days post-deluge) is framed by a box and shown in panel b.

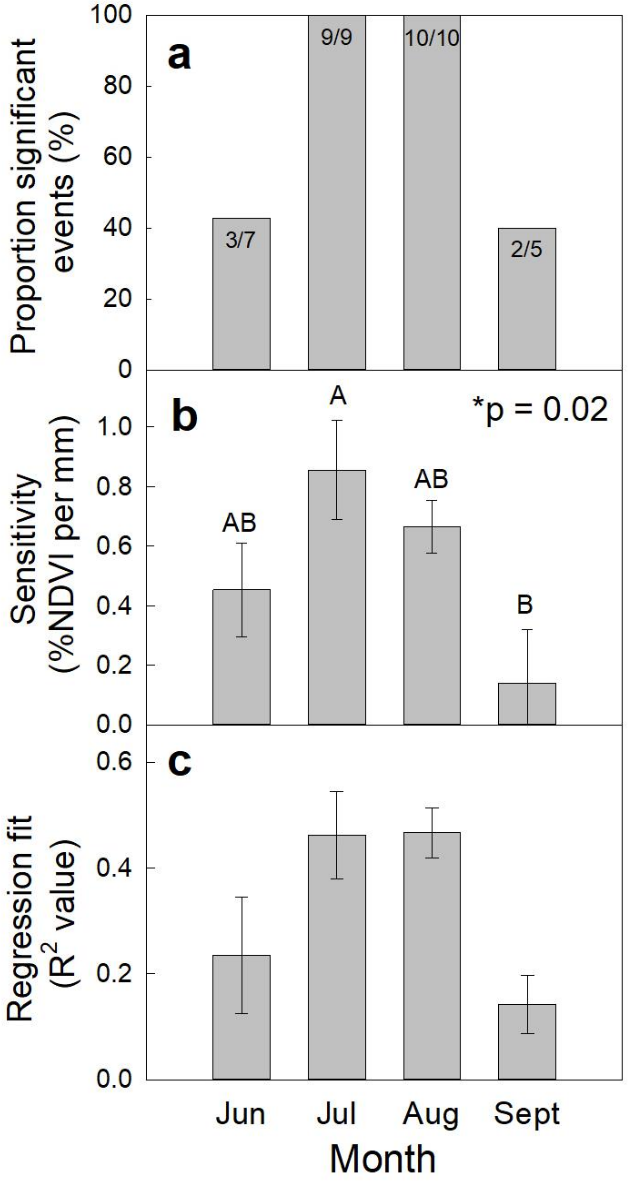

Figure 5.2. (a) Proportion of deluge events, separated by month, with a significant ($p < 0.05$) relationship between precipitation amount and post-deluge NDVI ~7-30 days post-deluge (see Fig. 5.1). Numbers in bars indicate the fraction of deluge events with statistically significant relationships (e.g., 3 of the 7 deluges in June exhibited a significant regression slope). (b) Sensitivity of NDVI to increasing precipitation, quantified as the slope of the linear precipitation-NDVI relationships (percent NDVI increase per mm of precipitation, see Fig. 5.1c) for all deluges in each month. Different letters indicate significant differences between months. (c) Average linear regression fit (R^2 value) of all deluges for each month. See Fig. A3.2 for similar analyses but limited to only statistically significant relationships.

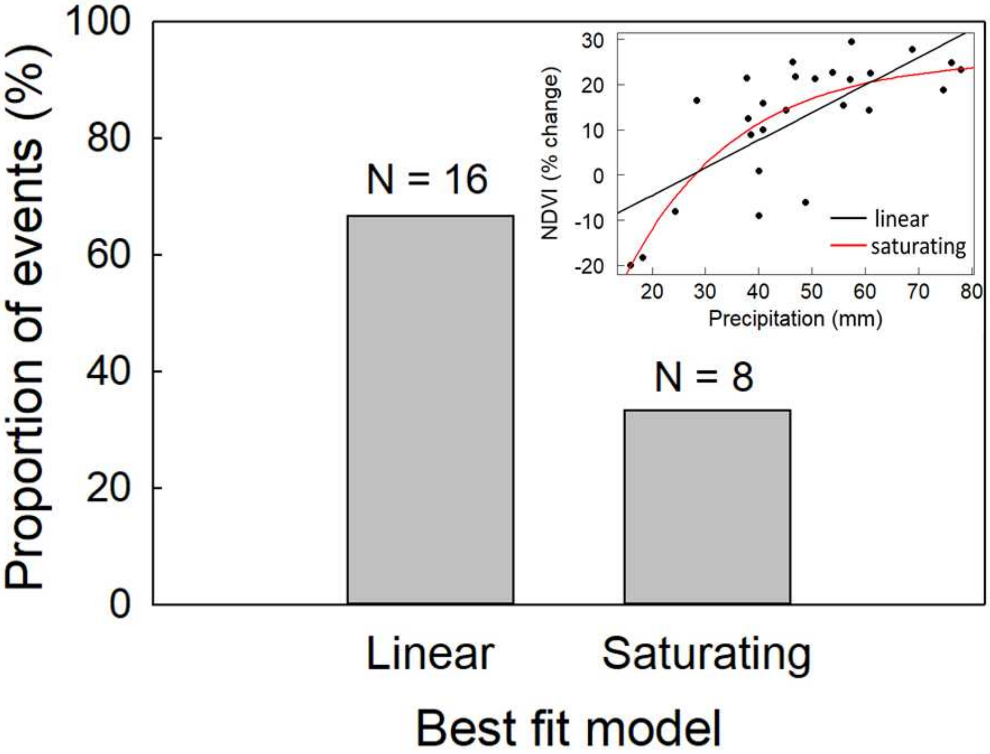

Figure 5.3. Proportion of deluges that exhibited a significant relationship between deluge size and NDVI response for which a linear versus a saturating (asymptotic regression) relationship was the best-fit model. The actual number of events is listed above each bar. Inset: example of a deluge event (August 1987) where a saturating relationship between NDVI response and precipitation amount was superior to a linear relationship.

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CHAPTER 6: CONCLUSIONS

As a result of climate change, many regions of the world are experiencing more frequent extreme precipitation events, or deluges (Huntington, 2006; IPCC, 2013). Water-limited dryland ecosystems, such as semi-arid grasslands, are predicted to be especially sensitive to this change in precipitation regime, as their ecological processes are strongly linked to sporadic water inputs (Noy-Meir, 1973; Schwinning & Sala, 2004). Yet, little is known about how these ecosystems respond to deluge events. Therefore, through several field experiments and an observational study using satellite data, my dissertation explored how the semi-arid shortgrass steppe of northeastern Colorado responds to deluge timing and size.

6.1 Research Summary

My research showed that the shortgrass steppe is generally responsive to large rain events, with sharp increases in most key ecological processes following a deluge. However, response magnitude depends on both deluge timing and size. My first field experiment (Chapter 2) applied late-season (August) deluges of varying sizes to experimental plots in the shortgrass steppe and found that the dominant warm-season grass (*Bouteloua gracilis*) responded positively, demonstrating increases in leaf growth and flowering proportional to the size of the applied deluge treatment. However, despite these strong plant-level responses, there was not a significant increase in total aboveground net primary production (ANPP; Post & Knapp, 2019). These results confirm observations made by prior studies that the shortgrass steppe exhibits a limited productivity response to late-season water inputs, perhaps attributed to seasonal plant senescence (Derner & Hart, 2007; Parton et al., 2012; Morgan et al., 2016).

Building on the results of this first experiment, my next field study (Chapter 3) assessed whether the response of the shortgrass steppe to a deluge event differs throughout the growing season. I applied a single deluge of uniform size (70 mm) to plots in either the early (June), middle (July), or late (August) growing season. The shortgrass steppe was responsive to all the applied deluges, but the mid-season deluge caused the greatest increase in soil respiration, canopy greenness, ANPP, and growth and flowering of *B. gracilis*. Only belowground net primary production (BNPP) was insensitive to deluge timing, with a consistent increase across all the deluge treatments. This striking mid-season response was likely a combination of several factors, with elevated soil moisture limiting the response early in the season and seasonal plant senescence limiting the response later in the season (Parton et al., 2012; Schwinning & Sala, 2004). Therefore, the mid-growing season represents the ideal combination of relatively low soil moisture and physiologically active plants for the ecosystem to most effectively utilize water from a deluge event. In contrast to the results of my first experiment, the shortgrass steppe did exhibit an increase in ANPP following a late-season deluge (in August). It is possible that this difference could be attributed to variations in antecedent soil moisture, as the plots in my first study were droughted prior to the deluge additions, whereas these plots were not, perhaps rendering them more responsive (Schwinning & Sala, 2004). Nonetheless, the shortgrass steppe is extremely responsive to deluge events and their timing (Post & Knapp, 2020).

My next field experiment (Chapter 4) tested the sensitivity of the shortgrass steppe to deluge size. I used a replicated regression approach to apply single deluges, ranging in size from moderate to extreme (20-120 mm), to plots in the shortgrass steppe. Surprisingly, almost all measured responses increased linearly with increasing deluge size. Measured responses included soil moisture, soil respiration, canopy greenness, *B. gracilis* leaf growth and flowering, ANPP, and BNPP. I expected to observe an upper event size limit, beyond which ecological responses could not increase further (saturate), but I found little evidence for response thresholds within the range of deluge sizes imposed. Instead, response patterns reflected the linear increase in the duration of elevated soil moisture (2–22 days) following deluges of increasing size. Only leaf water potential of *B. gracilis* exhibited evidence of response saturation at large event sizes. These results suggest that the shortgrass steppe will respond positively and linearly to predicted increases in deluge size, and that event sizes may need to exceed historical magnitudes before responses saturate (Post & Knapp, 2021).

Finally, my last study (Chapter 5) tested whether the results from my plot-scale deluge experiments could be extrapolated to the larger shortgrass steppe landscape. Using historical precipitation data from a spatially extensive rain gauge network, I identified natural deluges that occurred across a heterogeneous expanse of shortgrass steppe (Central Plains Experimental Range, ~60 km^2). I then related spatial variation in precipitation to spatial variation in post-deluge canopy green-up (normalized difference vegetation index, NDVI) via satellite imagery. The results largely matched those of my small-scale experiments (Post & Knapp 2020, 2021) – deluge response was strongest in the mid-growing season, and canopy greenness typically increased linearly with precipitation event size. Importantly, these patterns were strong despite variations in soil texture, grazing regime, and plant community composition across the study region, emphasizing the overarching importance of precipitation as the primary driver of ecosystem function in semi-arid ecosystems. Therefore, this study confirmed that results from small-scale precipitation manipulation experiments, with inherently limited variation in these variables, can be extrapolated to more extensive semi-arid grassland regions.

6.2 Implications and Future Directions

My dissertation research highlights the highly responsive nature of semi-arid ecosystems to deluge events, including event timing and size. In fact, my results suggest that a single deluge has the potential to promote enough plant growth to “rescue” the shortgrass steppe from drought, depending on the time of year (Post & Knapp 2020, 2021). Yet, most ecosystem models do not incorporate intra-seasonal rainfall patterns (Derner & Schuman, 2007; IPCC, 2013, Piao et al., 2019), a significant oversight given their sizable influence on overall carbon dynamics in dryland systems (Parton et al., 2012; Peng et al., 2013). Therefore, based on my research findings, it is crucial that future models incorporate rain event timing and size for more accurate estimates of carbon uptake in semi-arid ecosystems. Additionally, my last study (Chapter 5) exemplified the substantial spatial heterogeneity of natural deluge events, resulting in highly variable biomass production across the landscape. This adds an additional challenge for estimating regional carbon uptake (and forage production) that is not accounted for in most models. From a management perspective, Derner and Augustine (2016) suggest using adaptive grazing, whereby ranchers relocate livestock to track rainfall patterns, in order to partially mitigate the impacts of a more variable precipitation regime.

Furthermore, my experimental findings suggest that semi-arid ecosystems, such as the shortgrass steppe, might actually benefit from a precipitation regime with more frequent deluge events. Knapp et al. (2008) proposed that large events increase overall soil water availability in xeric ecosystems because they promote deeper soil water infiltration, thereby reducing the amount of water lost to evaporation. In support of this, my deluge size experiment (Chapter 4) showed that large deluges elevated soil moisture for a significantly longer period of time than did smaller deluges. For example, the smallest deluge (20 mm) increased soil moisture for 2 days, whereas the largest deluge (120 mm) caused soil moisture to remain elevated for 3 weeks (Post & Knapp, 2021). Thus, large rain events create an extended response window for water-limited ecological processes, such as plant growth and soil respiration in dry ecosystems (He et al., 2012). These results also suggest that the ability of a deluge to impact ecosystem processes is highly dependent on the water-holding capacity of the regional soils. In soils with higher drainage, water from a deluge event might leach past the primary rooting zone, rendering it ineffective for plant growth (Noy-Meir, 1973; Saxton & Rawls, 2006). Likewise, deluge events in more mesic grasslands could be less beneficial, or even detrimental, depending on background precipitation patterns. These wetter systems are often co-limited by resources other than water and rely on more frequent small rain events to maintain soil moisture and plant growth (Huxman et al., 2004; Knapp et al., 2008). Therefore, future experiments should address the impact of deluge events on ecosystems that vary in both annual precipitation and soil texture to better understand when deluges might be beneficial versus detrimental for ecosystem function.

There are several additional factors that might affect an ecosystem's deluge response that should be addressed by future studies. First, during a natural deluge event, the amount of runoff that occurs varies according to local topography, soil type, and soil surface characteristics, as well as plant cover, rainfall intensity, and antecedent soil moisture conditions (Fischer et al., 2015; Liu et al., 2011; Zhao et al., 2013; Hoover et al., 2021). My experiments controlled for these variables in order to isolate the impact of deluge event timing or size; however, factors that influence run-off and soil infiltration likely also affect plant production and carbon cycling in semi-arid ecosystems, so should be considered in future deluge studies. Second, the predicted increase in deluge magnitude and frequency will occur in tandem with other climate changes, such as longer periods of drought, increased air temperatures, and higher atmospheric concentrations of CO_2 (IPCC, 2013). Therefore, it is crucial that future experiments test how deluges will impact semi-arid ecosystems when they are experiencing simultaneous environmental stressors. Finally, these studies did not test for potential legacy effects of deluge events. Prior research suggests that current-year precipitation amount can influence future production responses (Sala et al., 2012), but the role of precipitation pattern, such as deluge timing and size, is unknown. For instance, since deluges stimulate the production of roots (perennial structures; Chapters 3 & 4), this additional belowground surface area could enhance the ability of plants to access soil water in future years.

In conclusion, my dissertation research confirmed the importance of large rain events for semi-arid ecosystems (Lauenroth & Sala, 1992; Li et al., 2015; Swemmer et al., 2007; Heisler-White et al., 2008) and, for the first time, assessed how key ecosystem processes respond to the timing and size of single deluge events. Since climate change is causing larger and more frequent extreme rain events worldwide, it is imperative that we understand how various ecosystems will respond and the resulting consequences to regional and global carbon cycles. It is especially important to understand the impact of this altered precipitation regime on semi-arid ecosystems given their disproportionately large influence on the interannual variability of global carbon uptake (Poulter et al., 2014; Ahlstrom et al., 2015). My research suggests that semi-arid ecosystems could be well-adapted to respond to this shift in precipitation pattern, but their response is dependent on both deluge event timing and size. These findings will hopefully inform and improve ecosystem carbon models, as well as assist ranchers in making more accurate predictions of regional forage production.

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APPENDIX 1

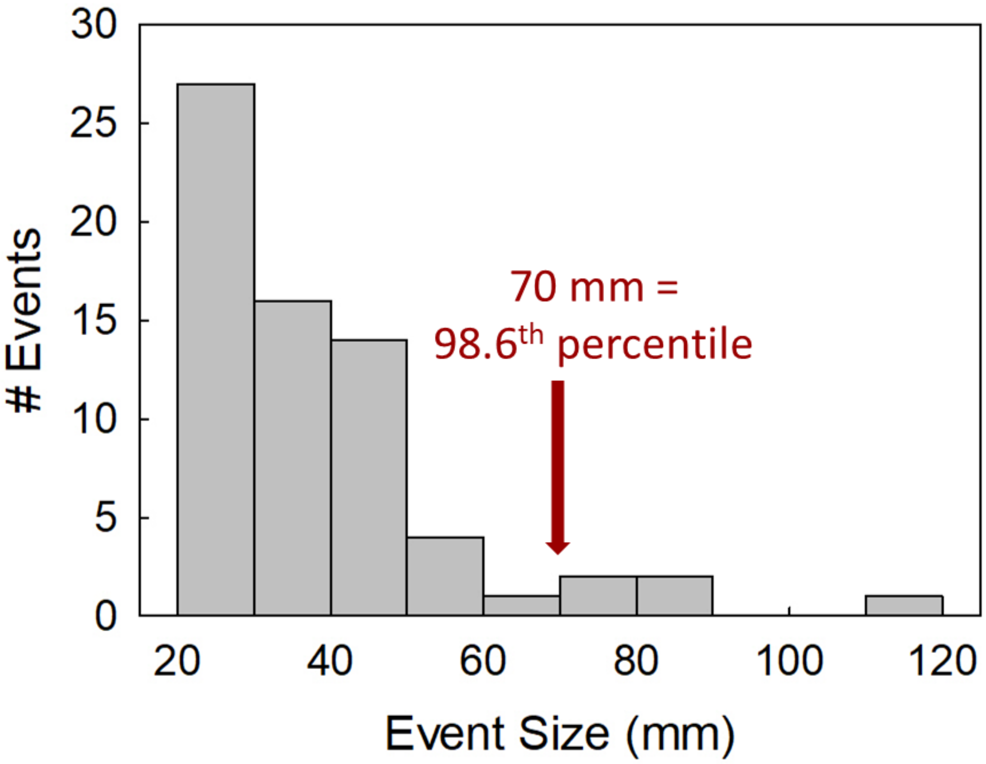

Figure A1.1 Historical distribution (1980-2016) of large rain events (≥ 20 mm) at the CPER. Consecutive rain days were combined into a single rain event; average event duration was 2.1 ± 1.1 days. The red arrow designates the size of the added deluge (70 mm), and the percentile indicates its size relative to all rainfall events (≥ 2 mm) during the same period.

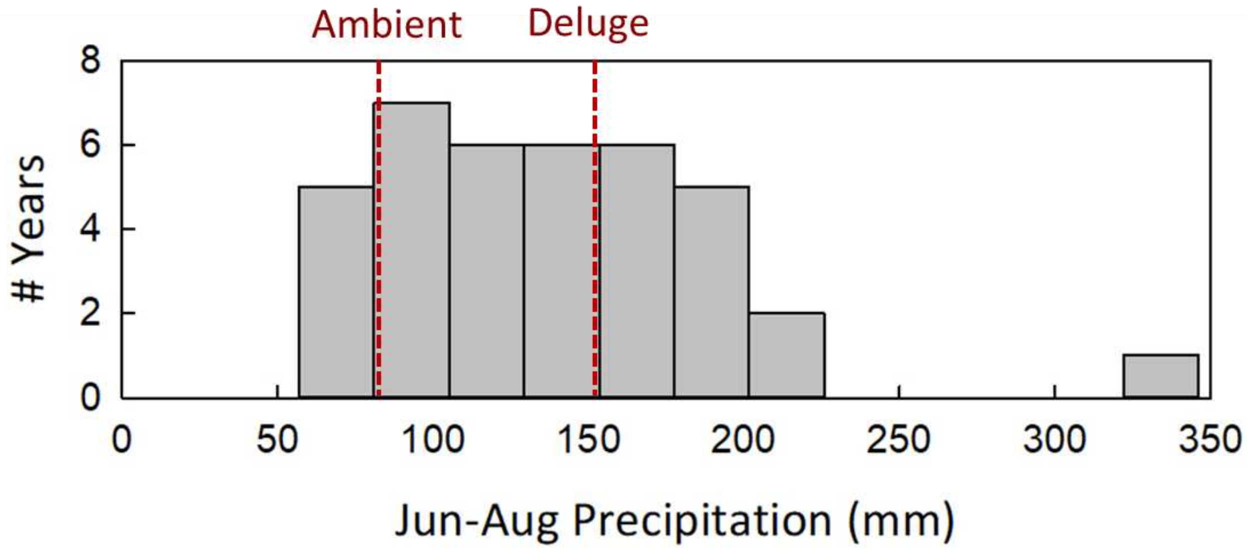

Figure A1.2. Distribution of total June-August precipitation (1980-2018), based on the historical rainfall record for the CPER. The red dashed lines indicate 2017 ambient rainfall ("Ambient") and total precipitation the deluge treatments ("Deluge") received during this period.

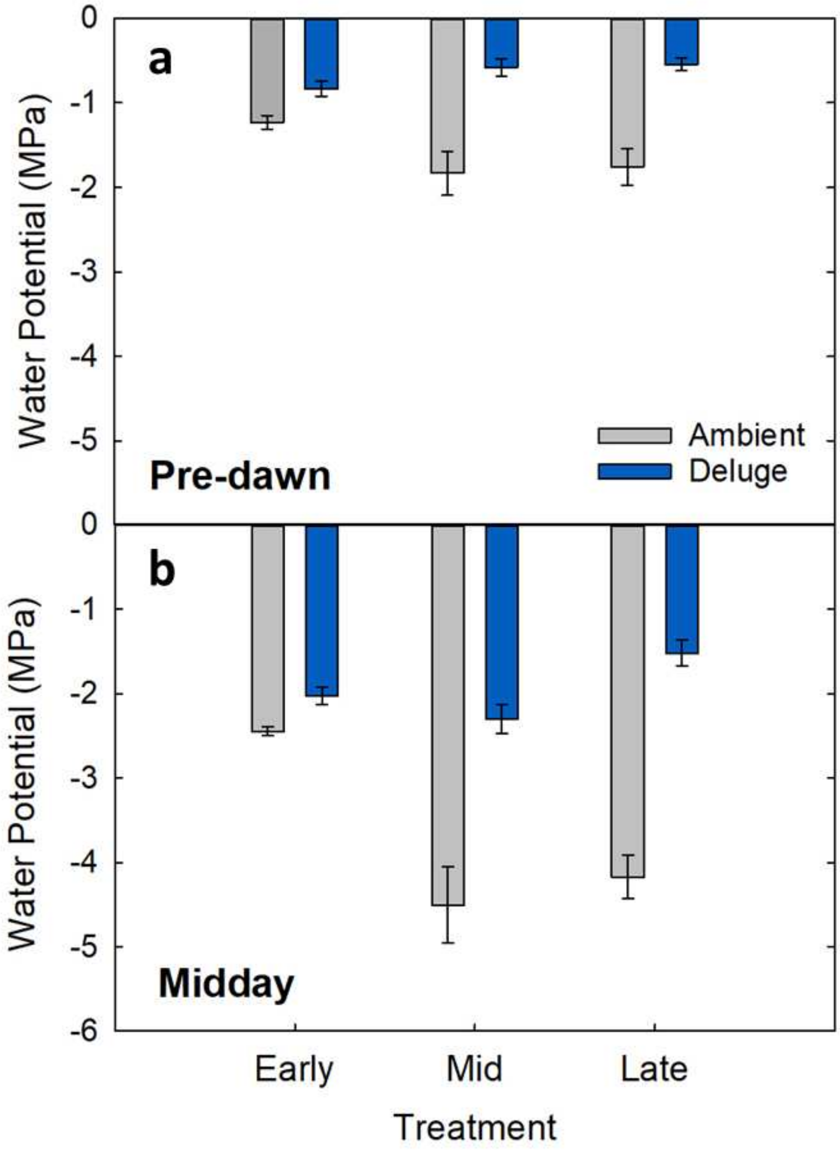

Figure A1.3. Leaf water potential (mean ± SE) of *B. gracilis* in ambient plots and the deluge treatment plots during each respective treatment period (N = 3 dates/TrtPd). The top panel (a) shows pre-dawn water potential values and the bottom panel (b) shows midday values. All pairs of values are statistically different (p<0.05) from each other.

APPENDIX 2

Table A2.1. Comparison of linear and nonlinear models (asymptotic regression, quadratic) for each measured variable versus deluge size. For continuously measured variables (soil moisture, soil respiration, greenness, leaf area), analyses were done on the ResPd average, and for flowering, on the ResPd maximum value. The degrees of freedom (df), R^2 ("pseudo" R^2 for asymptotic*), p-value (p), AIC, and AIC weights are listed for each model. The general direction of curvature (often minimal) for each relationship is also included, either concave (down) or convex (up). If the asymptotic model is not listed for a variable, it did not converge due to the non-saturating shape of the dataset. The name of the best-fit model is colored red.

*pseudo R^2 = estimated R^2 for non-linear model

Variable	Model	df	R^2	p	AIC	AIC weight	Curvature
Soil moisture	Linear	26	0.54	<0.001	130.12	0.73	up
	Quadratic	25	0.54	<0.001	132.12	0.27	
Soil respiration	Linear	26	0.88	<0.001	1.93	0.57	down
	Quadratic	25	0.88	<0.001	3.90	0.21	
	Asymptotic	25	0.88	*NA*	3.90	0.21	
Greenness	Linear	26	0.70	<0.001	-233.58	0.64	up
	Quadratic	25	0.70	<0.001	-232.46	0.36	
Leaf area	Linear	26	0.28	0.004	187.00	0.71	up
	Quadratic	25	0.28	0.015	188.83	0.29	
ANPP	Linear	26	0.61	<0.001	215.12	0.68	up
	Quadratic	25	0.62	<0.001	216.64	0.32	
BNPP	Linear	25	0.20	0.019	290.30	0.56	down
	Quadratic	24	0.21	0.063	292.17	0.22	
	Asymptotic	24	0.20	*NA*	292.20	0.22	
Flowering	Linear	25	0.40	<0.001	195.05	0.60	up
	Quadratic	24	0.43	0.001	195.86	0.40	

Table A2.2. Comparison of linear and nonlinear models (asymptotic regression, quadratic) for *B. gracilis* leaf water potential versus deluge size for each sampling time (Pre = pre-dawn, Mid = midday) and date after the deluge addition. The degrees of freedom (df), R^2 (“pseudo” R^2 for asymptotic*), p-value (p), AIC, and AIC weights are listed for each model. If there are no values listed for the asymptotic model, it did not converge due to the non-saturating shape of the dataset. The name of the best-fit model is colored red.

*pseudo R^2 = estimated R^2 for non-linear model

Date	**Time**	**Model**	**df**	**R^2**	**p**	**AIC**	**AIC weights**
July 13	Pre	Linear	19	0.48	<0.001	92.86	0.00
		Quadratic	18	0.78	<0.001	77.77	0.12
		Asymtotic	18	0.87	*NA*	66.98	0.88
	Mid	Linear	19	0.44	0.001	89.07	0.00
		Quadratic	18	0.66	<0.001	80.59	0.01
		Asymtotic	18	0.72	*NA*	76.66	0.99
July 18	Pre	Linear	16	0.64	<0.001	74.22	0.00
		Quadratic	15	0.90	<0.001	52.35	0.00
		Asymtotic	15	0.96	*NA*	38.02	1.00
	Mid	Linear	16	0.72	<0.001	65.23	0.00
		Quadratic	15	0.87	<0.001	53.90	0.60
		Asymtotic	15	0.86	*NA*	54.74	0.40
July 25	Pre	Linear	12	0.48	0.006	61.19	0.38
		Quadratic	11	0.53	0.016	61.64	0.31
		Asymtotic	11	0.53	*NA*	61.62	0.31
	Mid	Linear	12	0.28	0.052	63.18	0.56
		Quadratic	11	0.29	0.158	65.05	0.22
		Asymtotic	11	0.28	*NA*	65.08	0.22
August 2	Pre	Linear	13	0.55	0.002	57.09	0.64
		Quadratic	12	0.58	0.006	58.20	0.37
		Asymtotic	*NA*	*NA*	*NA*	*NA*	*NA*
	Mid	Linear	12	0.48	0.006	63.40	0.22
		Quadratic	11	0.62	0.005	60.91	0.78
		Asymtotic	*NA*	*NA*	*NA*	*NA*	*NA*

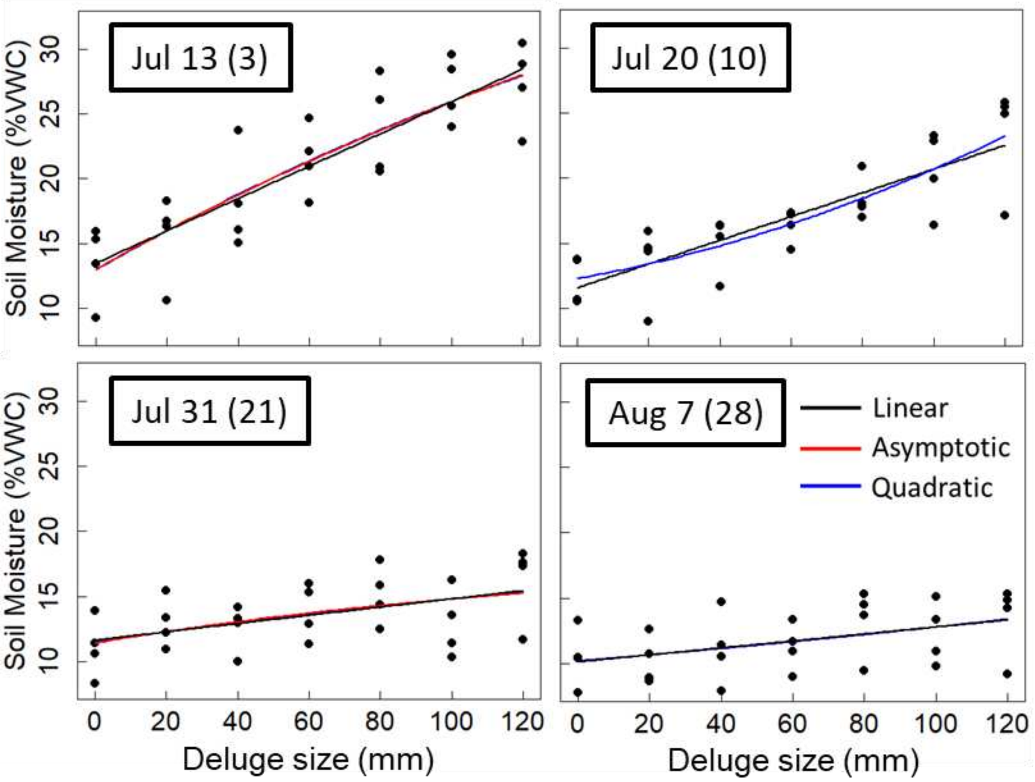

Figure A2.1. Regressions of soil moisture with deluge size for a subset of individual sampling days during the response period. The numbers in parenthesis indicate days since the deluge application. The fitted models appear in different colors. If a color is missing, the model could not be fit to the data (or overlapped with another model). In each panel, the date is framed by the color of the best-fit model. In this case, the linear model (black) is the best fit for all dates.

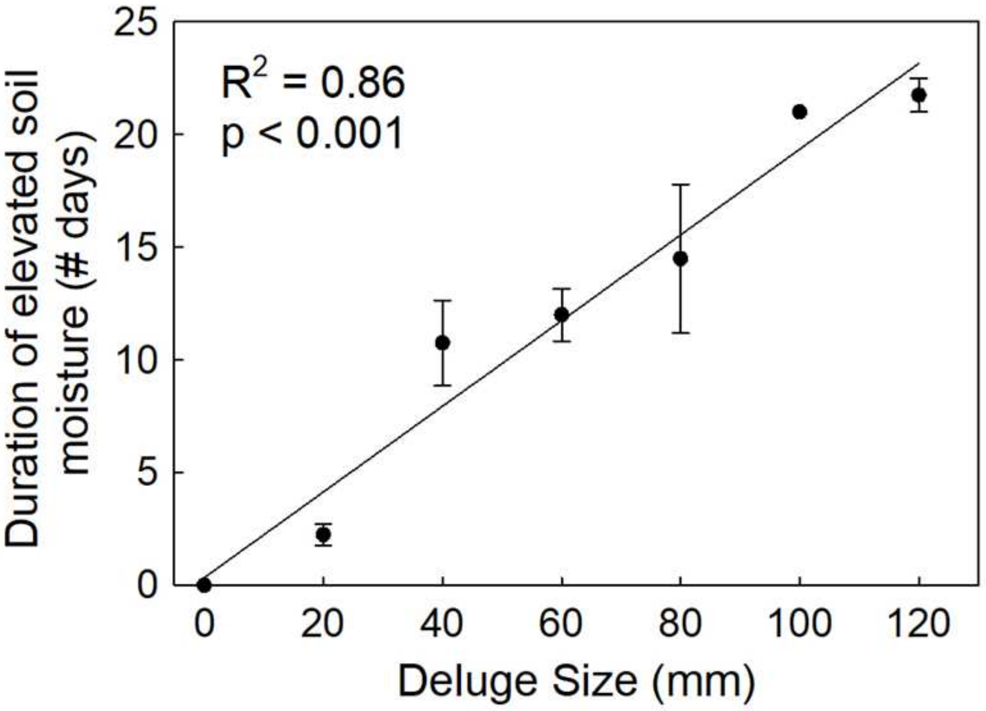

Figure A2.2. Number of days (mean ± SE) soil moisture remained elevated above ambient as a result of the deluge treatments. Soil moisture was considered elevated if it was at least 3% VWC greater than ambient (0 mm). A linear model was the best fit.

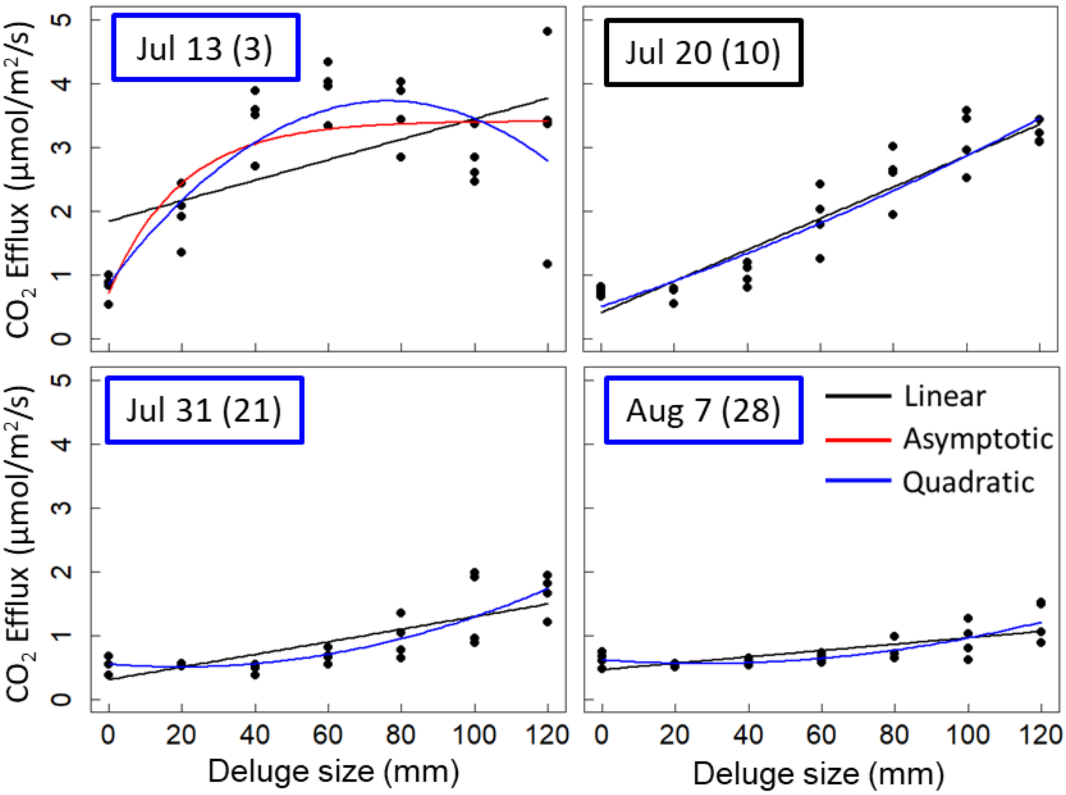

Figure A2.3. Regressions of soil respiration with deluge size for a subset of individual sampling days during the response period. The numbers in parenthesis indicate days since the deluge application. The fitted models appear in different colors. If a color is missing, the model could not be fit to the data. In each panel, the date is framed by the color of the best-fit model.

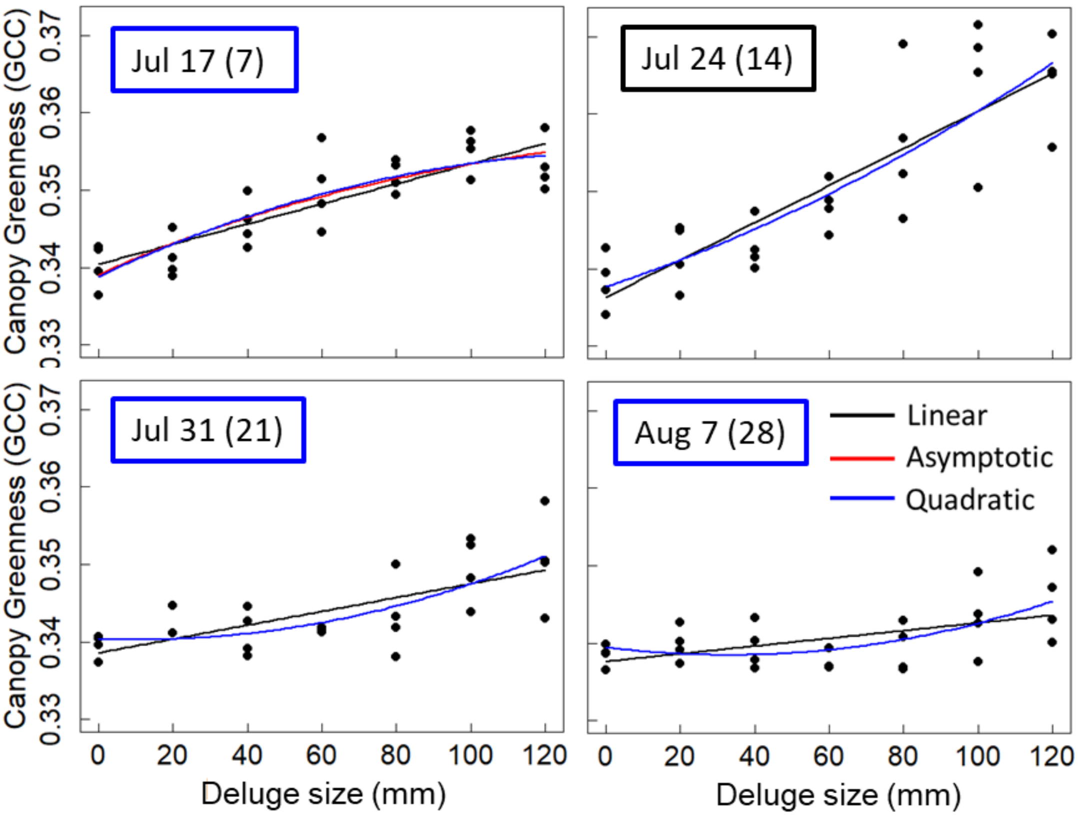

Figure A2.4. Regressions of canopy greenness with deluge size for individual sampling days during the response period. The numbers in parenthesis indicate days since the deluge application. The fitted models appear in different colors. If a color is missing, the model could not be fit to the data. In each panel, the date is framed by the color of the best-fit model.

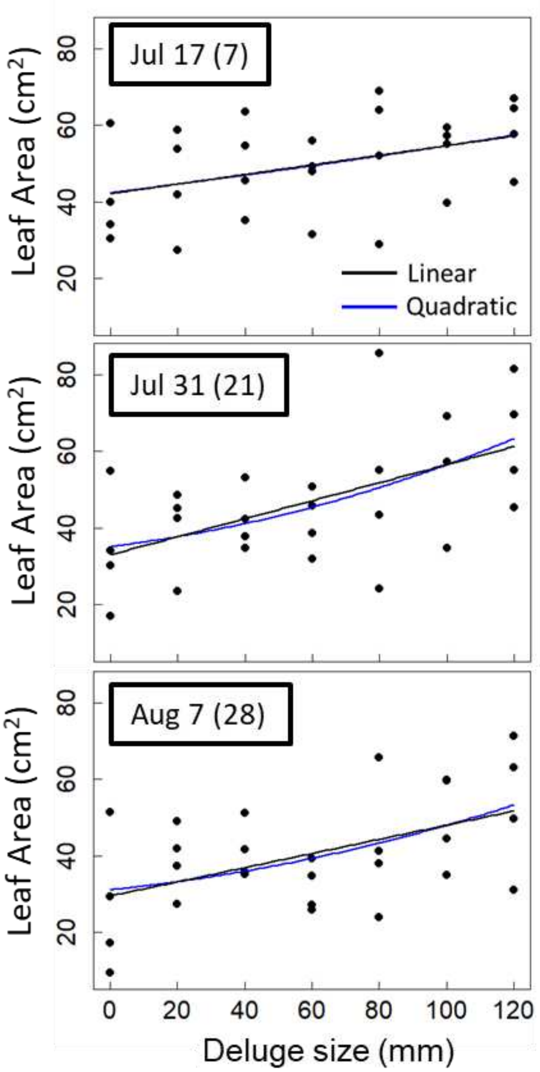

Figure A2.5. Regressions of leaf area with deluge size for individual sampling days during the response period. The numbers in parenthesis indicate days since the deluge application. The fitted models appear in different colors. The asymptotic model did not fit the data for any date, so is not shown. In each panel, the date is framed by the color of the best-fit model. In this case, the linear model (black) is the best fit for all dates.

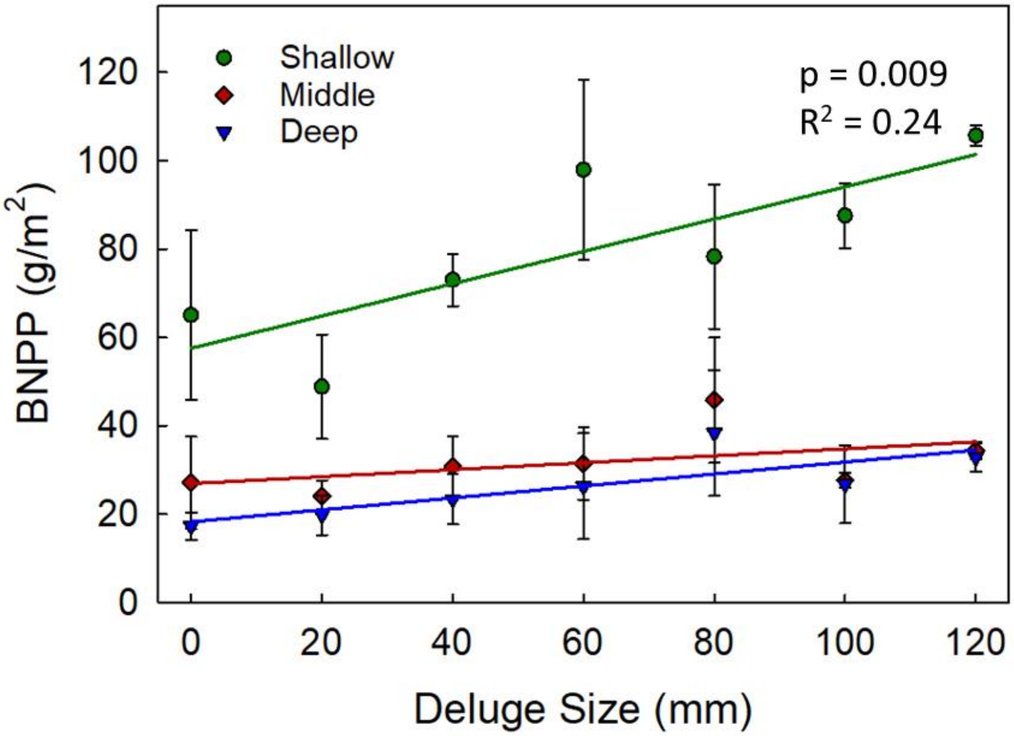

Figure A2.6. Response (mean ± SE) of BNPP to the deluge treatments, separated by depth increment: Shallow (0-10 cm), Middle (10-20 cm), Deep (20-30 cm). Only the regression slope for Shallow was significant ($p < 0.05$).

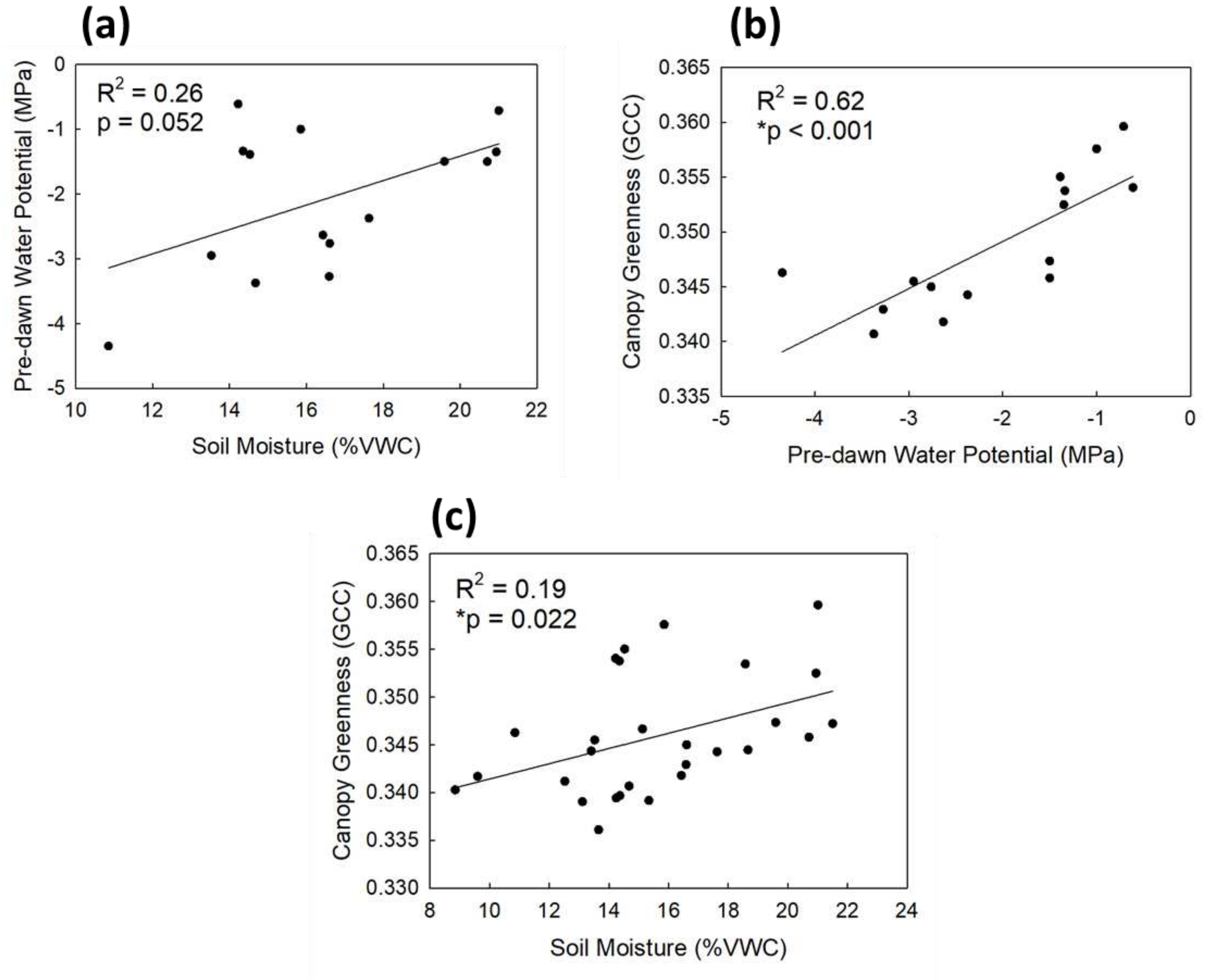

Figure A2.7. Mechanistic relationships between several measured responses following the applied deluge treatments. Each point represents the average value over the response period for a single plot†. Pre-dawn water potential is related to soil moisture (a), and canopy greenness is correlated with both pre-dawn water potential (b) and soil moisture (c). However, the stronger relationship is between water potential and canopy greenness. Asterisks denote significant slopes ($p < 0.05$).

†For pre-dawn water potential, the smallest deluge treatments (0 & 20 mm) were excluded because of missing data due to plot senescence.

APPENDIX 3

a

Type III Analysis of Variance Table with Kenward-Roger's method						
	Sum Sq	Mean Sq	NumDF	DenDF	F value	Pr(>F)
Month	826.9	275.6	3	40.33	2.6689	0.06041 .
Precip	13222.5	13222.5	1	776.74	128.0365	< 2.2e-16 ***
Month:Precip	3956.2	1318.7	3	765.8	12.769	3.779e-08 ***

b

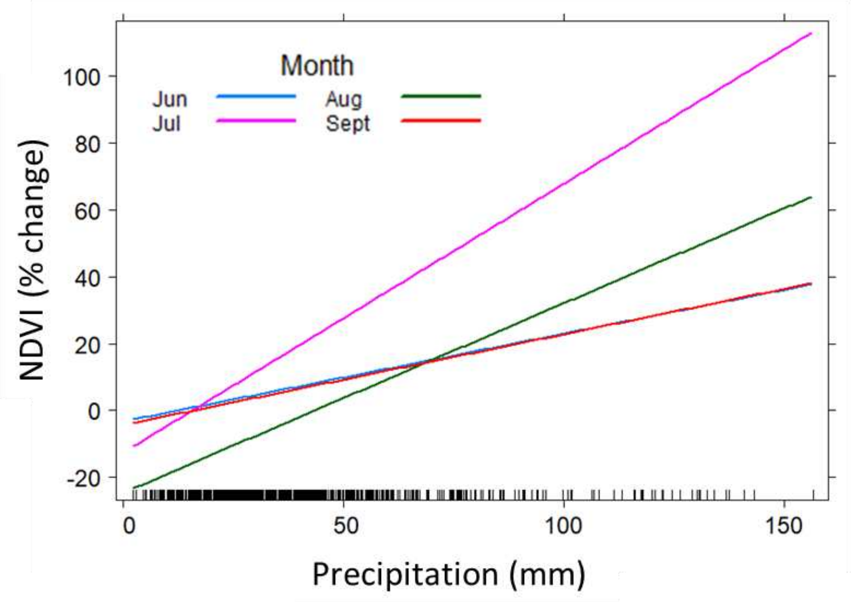

Figure A3.1. In addition to the linear regression analyses described in the methods, all deluge events were combined into a single model to confirm the observed trends. Shown are the results from a mixed model linear regression (a) with percent change in NDVI as the response variable, and precipitation amount, month, and their interaction as fixed effects, and rain gauge location and deluge event as random effects. There was a significant interaction between month and precipitation amount. This is visible in the graph of predicted values from the model (b). The black ticks along the x-axis show the distribution of precipitation amounts delivered by a deluge event to a single rain gauge location. The shortgrass steppe is more sensitive to precipitation amount in July and August (steeper slopes) than in June or September (shallower slopes), consistent with patterns in Fig. 5.2.

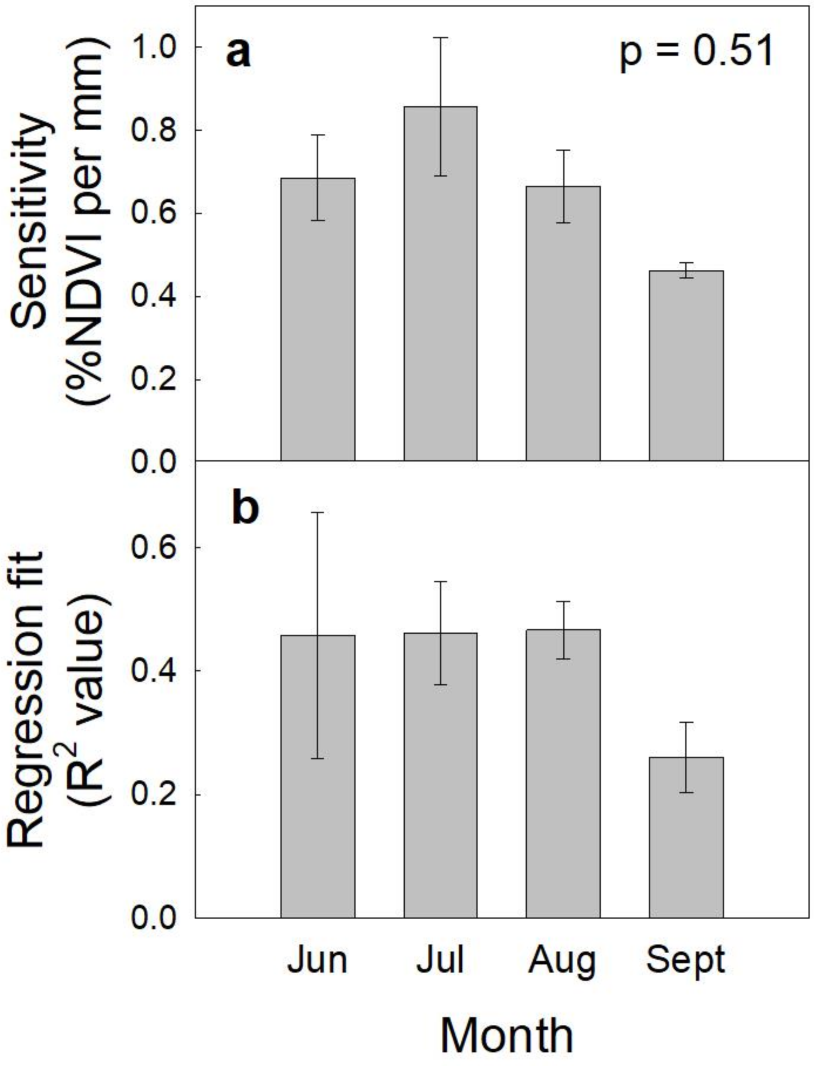

Figure A3.2. For each month, the average sensitivity (percent change in NDVI per mm of precipitation (a) and linear regression fit (R^2 value, b) for only those deluge events with significant precipitation-NDVI relationships (n = 24, see Fig. 5.1c). Average sensitivity was not significantly different between months.

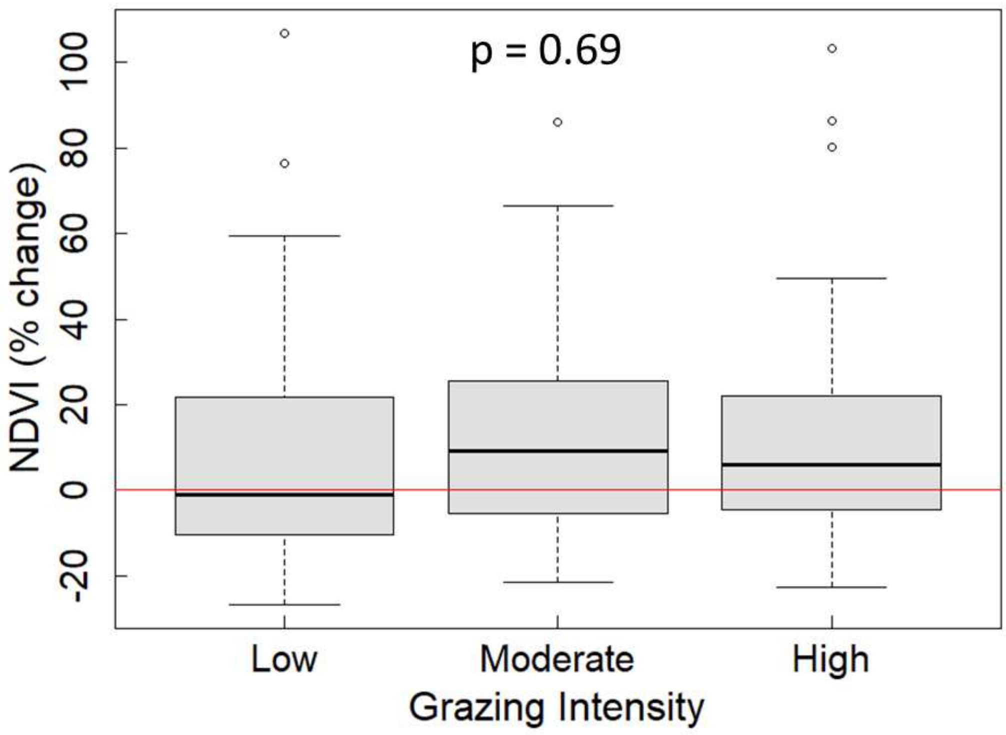

Figure A3.3. Average canopy green-up (% change in NDVI) following the analyzed deluge events for three co-located grassland sites exposed to different long-term grazing intensities.

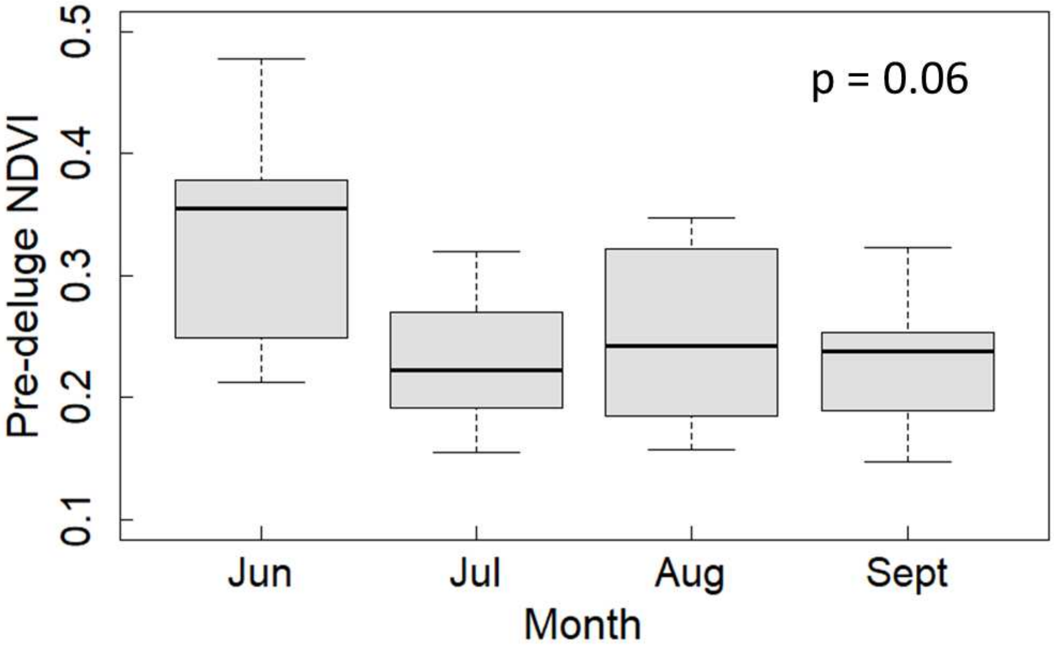

Figure A3.4. Average pre-deluge NDVI (across all rain gauges), separated by month.