

DISSERTATION

CLIMATE CHANGE AND PLANT SPECIES COMPOSITION AND COMMUNITY
STRUCTURE IN THE CENTRAL GRASSLAND REGION OF NORTH AMERICA

Submitted by

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ABSTRACT

CLIMATE CHANGE AND PLANT SPECIES COMPOSITION AND COMMUNITY STRUCTURE IN THE CENTRAL GRASSLAND REGION OF NORTH AMERICA

Precipitation and temperature are recognized as important drivers of plant community structure and function across ecosystems worldwide. The seasonality and quantity of precipitation combine with temperature to influence soil water balance, which is a primary determinant of terrestrial vegetation. Aspects of soil water balance have been shown to affect many properties of plant communities. The distribution of the earth's major biomes, for example, can be largely predicted from temperature and precipitation. Abundant evidence supports a strong relationship between actual evapotranspiration (AET) and aboveground net primary production (ANPP), and strong relationships exist between precipitation and species richness as well. Yet recent predictions of an increase in mean global temperature and changes in precipitation timing and quantity have the potential to alter terrestrial communities in novel ways by changing both the strength of abiotic controls on ecosystem processes as well as changing biotic interactions such as predation, competition, and trophic interactions in plant communities. As strongly water-controlled systems, grasslands may be particularly sensitive to predicted changes in climate. Using the central grasslands of North America as my study region, I examined how predicted changes in climate will affect soil water availability, net primary production, and species composition and community structure at study sites located in the shortgrass steppe and mixed grass prairie.

My results demonstrate that ecosystems located within the same biome may respond differently to similar changes in precipitation and temperature, primarily due to differences in

community structure, interspecific competition, and patterns of soil water availability. Simulated future soil water availability revealed greater temporal and spatial changes in available water at the mixed grass prairie than at the shortgrass steppe site. Using a soil water manipulation experiment, I found that ANPP at the shortgrass steppe was insensitive to changes in soil water, while belowground net primary production (BNPP) was sensitive to changes in soil water, although the direction of the response differed between years. I observed the opposite pattern at the more mesic mixed grass prairie site. Here, there was a rapid ANPP response to the water manipulation treatments, but BNPP was insensitive to changes in soil water availability. Likewise, the shortgrass steppe plant community was fairly insensitive to manipulated soil water, while the mixed grass prairie plant community responded rapidly to manipulated soil water. The differences in community responses between my two sites highlight the importance of multi-site studies to refine our knowledge of the mechanisms and generalities of community response to climate change at the biome level.

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Chapter 1: Introduction

Across ecosystems worldwide, precipitation and temperature are recognized as important drivers of plant community structure and function. The seasonality and quantity of precipitation combine with temperature to influence soil water balance, which is a primary determinant of terrestrial vegetation (Stephenson 1990). Soil water balance is comprised of precipitation inputs balanced by water losses in the form of evapotranspiration, runoff, and deep drainage.

Precipitation provides a direct influence on soil water balance by affecting inputs, while temperature indirectly influences water balance by controlling evapotranspiration. Aspects of soil water balance have been shown to affect many properties of plant communities. The distribution of the earth's major biomes, for example, can be largely predicted from temperature and precipitation (Holdridge 1947, Leith and Whittaker 1975, Whittaker 1975). Abundant evidence supports a strong relationship between actual evapotranspiration (AET) and aboveground net primary production (ANPP; Rosenzweig 1968, Webb et al. 1983), and strong relationships also exist between precipitation and species richness (Tilman and Haddi 1992, Givnish 1999, Adler and Levine 2007). Yet recent predictions of an increase in mean global temperature and changes in precipitation timing and quantity (Christensen et al. 2007) have the potential to alter terrestrial communities in novel ways by changing both the strength of abiotic controls on ecosystem processes as well as changing biotic interactions such as predation, competition, and trophic interactions in plant communities (Ives 1995, Suttle et al. 2007, Tylianakis et al. 2008).

Global change will not affect the earth uniformly – temperature and precipitation changes will vary across regions, and impacts will depend on an ecosystem's sensitivity to climate. As strongly water-limited systems, grasslands will likely be very sensitive to predicted changes in

precipitation and temperature (Knapp and Smith 2001, Huxman et al. 2004). Grasslands represent the potential natural vegetation cover of over 40% of the Earth's terrestrial surface; including many productive agricultural and rangeland areas worldwide (White et al. 2000). The potential sensitivity of grasslands to climate change, combined with the global ecological and agricultural importance of the biome make it an important system for testing the response of plant communities to future novel climatic conditions outside of the recent range of variability within the ecosystem (Williams et al. 2007).

The central grassland region of North America, in particular, is an ideal ecosystem for studying the effects of global change on grassland communities, as the range of climates represented within the region allows for comparisons with grasslands worldwide and there is already a strong existing knowledge of ecosystem processes present in the scientific literature. The region is bounded by the Rocky Mountains to the west and the Mississippi River to the east; the boreal forest to the north and the Gulf of Mexico to the South (Coupland 1992). Both temperature and precipitation vary greatly along the north-south and east-west gradients of the region. Mean annual precipitation ranges from less than 300 mm in the west-northwest to greater than 1,000 mm in the east-southeast. Mean annual temperature ranges from less than 2° C in the north to greater than 18° C in the south (Lauenroth et al. 1999).

Climate models predict that the central grassland region will warm substantially (3 – 4.4°C) during the twenty-first century (Christensen et al. 2007). Associated predictions of precipitation changes are less certain and range from small increases to small decreases. These changes in precipitation could either exacerbate or ameliorate water limitation in grasslands. However, previous research provides reason to believe that any changes in climate will have

profound effects on ecosystem dynamics, whether climate change increases or decreases soil water (Weltzin et al. 2003).

Several studies have already demonstrated that grasslands are sensitive to variation in precipitation. In a study spanning a variety of ecosystem types in North America, Knapp and Smith (2001) reported that aboveground production in grassland and old field ecosystems was most sensitive to precipitation variability. In an earlier observational study, Weaver and Albertson (1936) reported large and rapid changes in the species composition and total plant cover at sites in the eastern and central portions of the central grassland region in response to the drought of the 1930s, noting the largest vegetation changes in areas dominated by tallgrass species. More recently, Paruelo et al. (1999) found that precipitation use efficiency across the region was maximized at intermediate precipitation values (462 or 491 mm, depending on the data used), not the minimum or maximum represented by the shortgrass steppe or tallgrass prairie. This contrast in aboveground ecosystem response is likely due to differences in plant species traits across the region. In the driest portion of the central grassland region, the dominant species have low relative growth rates and are unable to respond quickly to interannual variation in precipitation. In the wettest portion of the region, the dominant species have higher relative growth rates and can respond more quickly to interannual variation in precipitation, but an increase in biomass or leaf area index will cause limitation by other resources; namely light or nutrients (Knapp and Seastedt 1986, Baer et al. 2003). These studies provide observational evidence of differences in sensitivity within grassland types to variations in soil water, yet we lack experimentally based evidence to support these observations across multiple ecosystem types within a single biome.

A critical ecosystem property that is sensitive to soil water availability is net primary production (NPP), the net amount of carbon removed from the atmosphere by plants. Plant production can be divided into aboveground net primary production (ANPP) and belowground net primary production (BNPP). Observational studies have found that ANPP is tightly linked to precipitation, often used as a surrogate for soil water, across the central grassland region (Sala et al. 1988), and through time with interannual variability at individual sites (Lauenroth and Sala 1992, Briggs and Knapp 1995). Although predicted changes in soil water will likely have an important impact on ANPP, there is a paucity of studies examining the effect of altered soil water on BNPP. Furthermore, we lack a regional understanding of soil water availability and its impacts on BNPP in the central grassland region (McCulley et al. 2005). Yet BNPP is an important portion of total production: it contributes 50 % or more to the total NPP of grassland ecosystems (Sims and Singh 1978, Milchunas and Lauenroth 2001), and represents a large terrestrial carbon sink (Scurlock and Hall 1998). We need to understand how NPP, not just the aboveground component, will respond to changes in soil water in order to improve models and predictions of future carbon storage and turnover in grassland ecosystems.

While changes in water availability will affect NPP in grasslands directly, species composition and diversity are also known to affect ecosystem structure and function (Wardle et al. 2000, Hooper et al. 2005, Isbell et al. 2011). The potential changes in species composition and diversity may occur directly, by changing the quantity and timing of resources, or indirectly, by altering competitive interactions among species. Several precipitation manipulation studies have observed changes in plant communities, yet there is a lack of consensus among studies in how changes in precipitation affect species composition and diversity. Additionally, most previous studies occurred at a single site and are therefore not ideally suited to test if the community

response is similar within a biome. Some precipitation manipulation experiments have found a positive relationship between increased precipitation and species richness and diversity (Sternberg et al. 1999, Zavaleta et al. 2003, Stevens et al. 2006, Yang et al. 2011), while other studies found a negative effect of increased precipitation on species richness (Suttle et al. 2007, Engel et al. 2009). One study found that drought decreased species diversity, but water addition had no effect on diversity (Grime et al. 2008), and still another study found that drought had no effect on species richness or diversity (Knapp et al. 2002). Since changes in species composition will directly influence plant NPP, with potential feedbacks to soil biogeochemical and water cycles, it is important that we can predict changes in species composition alongside changes in NPP in grasslands.

Using the central grasslands of North America as my study region, the overall goal of my dissertation research is to improve our understanding of the implications of climate change for grassland community structure and function. I will first address the most basic issue of how predicted changes in temperature and precipitation will affect plant available soil water by conducting a modeling study (Chapter 2), then I will further investigate the role of soil water availability in affecting NPP (Chapter 3) and species composition (Chapter 4) by conducting a water manipulation experiment that both increases and decreases growing season soil water. In my rainfall manipulation experiment, I focus on changes in growing season soil water, not dormant season soil water, because I expected that the plant communities at each site would be more influenced by changes in soil water during the active growing season.

I conducted both my soil water modeling and field experiment at two grassland sites in the central grassland region. The grasslands are similar in that each is dominated by native perennial C₄ grasses and soils are characterized as Argiustolls, yet there are some important

differences between them as well. Mean annual precipitation increases from west to east across the central grassland region, and mean annual temperature increases from north to south (Table 1.1). The sites occur at similar latitudes, so the main difference in climate between them is annual precipitation amount. Despite these differences, the grasslands are often lumped together in climate change modeling.

In chapter 2, I combined field data from each grassland site and a daily time step simulation model (SOILWAT; Lauenroth and Bradford 2006) to understand how soil water dynamics are affected throughout the soil profiles by the changes in temperature and precipitation from the A2 and B1 emission scenario families (Nakicenovic et al. 2000). Further, I examined the differences using “average”, “dry” and “wet” years in the historical (51 year) record to understand what rainfall conditions lead to the largest and smallest differences in soil water between current conditions and General Circulation Model predictions. In chapter 3, I measured ANPP, BNPP, and NPP at each site over 3 years (2008 -2010) to determine if there was a difference in the sensitivity of the response NPP (both the above and belowground components) to changes in soil water between sites. Further, I aimed to determine if above and belowground production respond similarly to manipulations of soil water within and across sites. In chapter 4, I investigated the response of individual species, functional groups, and community diversity to both increased and decreased soil water over 4 years (2008 – 2011). Here, I was specifically interested in whether the dominant species and functional groups at the two sites displayed similar responses to changes in soil water; and whether water addition or drought caused a larger change in important plant community characteristics at each site. Finally, I summarize my findings and present conclusions from my dissertation work in Chapter 5.

TABLES

Table 1.1. Characteristics of the two sites located across the driest portion of the Central Grassland Region.

	SGS Shortgrass Steppe LTER	HAYS Fort Hays State University
<i>Climate and Vegetation</i>		
Latitude and Longitude	40° 49' N, 104° 46' W	38° 52' N, 99° 23' W
MAP (mm)	341	583
MAT (°C)	8.2	12.1
Vegetation type	Shortgrass steppe	Mixed grass prairie
Dominant plant species	<i>Bouteloua gracilis</i>	<i>Schizachyrium scoparium</i>
<i>Soils</i>		
Taxonomy	Aridic Argiustoll	Typic Argiustoll
Textural class	Sandy loam	Loam
% Sand	79	44
% Clay	11	13

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Chapter 2. Spatial and temporal variability of soil water under simulated climate change conditions in the Great Plains of North America

SUMMARY

General Circulation Models predict that arid and semiarid ecosystems will experience, on average, drier conditions in the coming century. Many rainfall manipulation experiments have been initiated to understand the implications of drier conditions on ecosystem dynamics, but these experiments are short in duration and lack descriptions on soil water dynamics throughout the soil profile. Here, I compare simulated soil water data at two grassland sites for the past 51 years using current conditions and downscaled regional climate change predictions from the A2 and B1 family scenarios of the IPCC 2007 report to understand how future climate change may affect soil water dynamics throughout the soil profiles as well as ecosystem water balance. I found that while the IPCC predicts that the two grasslands will experience similar percentage changes in annual precipitation and temperature, the consequences of these changes on the spatial and temporal dynamics of soil water were different between sites. I was able to gain a reasonable understanding of the spatial and temporal dynamics of soil water by examining the surface layers alone at the shortgrass steppe. However, at the mixed grass prairie site, the most important changes in soil water occur deeper in the soil, from 30 -120 cm. I conclude that predicted changes in climate may have a greater impact on plant community structure and ecosystem function in more mesic grassland communities, as evidenced by the greater changes in dynamics of soil water at our more mesic mixed grass prairie site.

INTRODUCTION

Climate models predict, and studies confirm, that the earth is experiencing anthropogenic-induced changes in climate, including an increase in global temperature and changes in precipitation patterns (Christensen et al. 2007). Global change will not affect the earth

uniformly – temperature and precipitation changes will vary across regions, and responses will depend on an ecosystem’s sensitivity to climate. Grasslands are likely to be particularly sensitive to changes in precipitation patterns, as soil water availability is both the most frequent limiting resource and key control on ecosystem processes in arid and semiarid ecosystems (Noy-Meir 1973). Precipitation, often used as a surrogate for soil water, is tightly linked to important ecosystem processes in arid-semiarid regions including aboveground net primary production (Rosenzweig 1968, Webb et al. 1983, Sala et al. 1988), nitrogen availability (Burke et al. 1997), and carbon storage (Parton et al. 1987).

The central grassland region of North America is an ideal ecosystem for studying the effects of global change on grassland communities. The region represents 12.5% of North America and 2% of the Earth’s terrestrial surface (Lauenroth et al. 1999). Both temperature and precipitation vary along the north-south and east-west gradients of the region, and the range of climates represented make it comparable to similar grasslands worldwide. General Circulation Models (GCMs) predict that the central grassland region of North America will warm substantially (3 – 4.4 °C) during the twenty first century (Christensen et al. 2007, CCSP 2008). Associated predictions of precipitation changes are less certain and range from small increases to small decreases. Regardless of the uncertainty in predictions of precipitation changes, the magnitude of the predicted increases in temperature will create drier conditions (MacDonald 2010). These drier conditions will decrease soil water availability, which will likely affect ecosystem dynamics (Weltzin et al. 2003, Williams et al. 2007).

Predictions about changes in soil water availability have sparked numerous rainfall manipulation studies (Fay et al. 2003, Yahdjian and Sala 2006, Fiala et al. 2009, Heisler-White et al. 2009, Levine et al. 2010, Evans et al. 2011, Thomey et al. 2011) that aim to understand how

changes in soil water will affect ecosystem dynamics in grasslands. However, these studies are typically short in duration (1-4 years), and often lack descriptions of soil water dynamics at depths greater than 10 or 15 cm. We need to understand how predicted changes in temperature and precipitation will affect soil water over decades, and throughout the entire soil profile, to better predict the impacts of these changes on species dynamics and ecosystem structure and function.

Here, I combine field data, collected in the driest portion of the central grassland region at the shortgrass steppe and mixed grass prairie, and a daily time step simulation model (Lauenroth and Bradford 2006) to understand how soil water dynamics are affected throughout the soil profiles by the changes in temperature and precipitation from the A2 and B1 emission scenario families (Nakicenovic et al. 2000). Further, I examine the differences using “average”, “dry” and “wet” years in the historical (51 year) record to understand what rainfall conditions lead to the largest and smallest differences in soil water between current conditions and GCM predictions.

Specifically, I asked, both within and between sites; 1) Where in the soil profile do the largest and smallest differences in soil water occur in current conditions versus GCM predicted dynamics?; 2) Do the largest differences between current and GCM predicted dynamics occur in dry, average, or wet precipitation years?; and 3) What are the major differences in the temporal distribution of soil water between current and future GCM predictions?

METHODS

Study sites

I conducted this study at two sites in the driest portion of the central grassland region. The region is characterized by a continental climate, and the majority of precipitation falls during

the summer growing season. My first site was the semiarid shortgrass steppe at the Central Plains Experimental Range (CPER), 60 km northeast of Fort Collins, Colorado (40° 49' N, 104° 46' W) (Fig. 2.1a). The CPER is administered by the USDA Agriculture Research Service and is also a National Science Foundation Long Term Ecological Research site. The plant community is dominated by the short-stature C₄ grass blue grama (*Bouteloua gracilis* Willd. ex Kunth Lag. ex Griffiths) and patches of bare ground are prevalent. The dominant soil series in the region is Ascalon, a sandy loam (NRCS 2011).

My second site was the subhumid mixed grass prairie, at the Fort Hays State University College Farm, in west-central Kansas, 3 km west of Hays (38° 52' N, 99° 23' W) (Fig 2.2a). The plant community includes a mixture of tall- mid- and short- stature grasses, predominantly C₄ species. The dominant soil series in the region is Harney, a loam (NRCS 2011). Species nomenclature follows USDA Plants Database (USDA 2008). I compiled 51 years (1960-2010) of daily precipitation and maximum and minimum temperatures from the National Climatic Data Center for each site.

Model Description

I used SOILWAT, a daily time-step soil water model developed for and widely used in the shortgrass steppe ecosystem (Parton 1978). SOILWAT requires input information about initial soil water conditions, vegetation, weather, and soil properties. Vegetation inputs are mean monthly aboveground biomass, litter, proportion of aboveground biomass that is green, and the proportion of root biomass in each soil layer. Weather inputs include daily precipitation and daily maximum and minimum air temperatures, mean monthly relative humidity, mean monthly wind speed, and mean monthly cloud cover. Soil properties for each soil layer include texture (percentage sand and clay), bulk density, field capacity, wilting point, and the relative

proportions of evaporation and transpiration in each layer (relative to the entire soil profile). In this analysis, I simulated soil water in nine layers (0-10, 10-20, 20-30, 30-40, 40-50, 50-60, 60-80, 80-100, and 100-120 cm). I used weather inputs from each site and simulated the water balance in a soil profile representing the dominant soil type for the counties in which each site occur (NRCS 2011). I collected vegetation inputs from the literature. Detailed descriptions of sources for input parameters can be found in the Appendix.

From the input values, SOILWAT simulates water interception and evaporation from the canopy and litter layer, water infiltration into the soil, water flow and distribution among soil layers, and losses by bare-soil evaporation and transpiration in each layer. Parton (1978) presents a description of SOILWAT, and applications of the model can be found in Lauenroth et al. (1993), Lauenroth et al. (1994), Coffin and Lauenroth (1994), and Lauenroth and Bradford (2006, 2011).

Climate Scenarios

I ran the model under three climate scenarios: current conditions for 1960-2010 and two future conditions for 2070-2099. I used the A2 and B1 emission scenario families (Nakicenovic et al. 2000) from the special report on emission scenarios (SRES), which represent the high and low emission scenario families, respectively. I used climatewizard.org (accessed September 2011) to download future climate scenarios with monthly 1/8th-degree gridded downscaled temperature and precipitation predictions of 16 GCMs for both the A2 and B1 emission scenario families (Maurer et al. 2007). Future daily forcing consisted of current daily weather conditions (1960-2010) with multiplied proportional mean monthly precipitation changes and added absolute predicted mean monthly temperature changes for each GCM in the B1 and A2 scenario

families, for a total of 32 model runs. My future climate scenarios did not include changes in wind speed, relative humidity, cloud cover, or climatic variability.

Data Analysis

I calculated average daily available soil water in each layer across the 51 years of data using a minimum soil water potential of -1.5 MPa for current conditions and each of the 16 GCM in the B1 and A2 emission scenarios. Although I understand that plants in the central grassland region of North America can likely withdraw water from the soil at water potentials less than -1.5 MPa, there are few data to guide the choice of a minimum value. I then calculated mean daily available soil water for each scenario by taking the average of the 16 GCMs for each scenario.

To determine spatial and temporal differences in available water, I summed available water in the shallow (0 – 30 cm) and deep (30 – 120 cm) layers over the growing season (April – Sept) and the non growing season (Oct – March), and calculated total annual available water for each GCM and calculated mean available water at each different time period. I then compared the GCM ensemble mean available water at each time period to the simulated available water in current conditions. I present results with the shallow and deep soil water division for two reasons. First, changes in shallow and deep soil water resources have the potential to influence grassland ecosystem structure in different ways, and this division aids in the assessment of these possible differences. Second, this division greatly simplifies the presentation of results.

To determine the differences in dry, average, and wet years separately, I ranked annual precipitation from lowest to highest values at each site for the historical (51 year) record, then calculated mean daily soil water for each site in the ~ 25% driest and wettest years (12 years each), and the 27 middle (average) annual precipitation years.

RESULTS

Climate of the sites

The central grassland region is characterized by a continental climate with the majority of precipitation falling during the summer growing season at each site when temperatures are warmest (Lauenroth et al. 1999). This overall pattern did not change greatly under predicted climate change scenarios (Figs. 2.1 and 2.2). Mean annual precipitation for our 51-year simulations under current conditions was 338 mm, 324 mm in the A2 scenario, and 347 mm in the B1 scenario for the shortgrass steppe site (Fig. 2.1). For the mixed grass prairie site, mean annual precipitation under current conditions was 582 mm, 568 mm in the A2 scenario, and 598 mm in the B1 scenario (Fig 2.2). These changes in precipitation represented an annual decrease in precipitation of 4.0% or 2.4% for the A2 scenario, and an annual increase in precipitation of 2.6% or 2.8% for the B1 scenario at the shortgrass steppe and mixed grass prairie sites, respectively.

Both sites experienced similar increases in temperature under climate change scenarios; a mean annual increase in temperature of 4.5°C or 4.7°C for the A2 scenario, and 2.7°C or 2.8°C for the B1 scenario at the shortgrass steppe and mixed grass prairie sites, respectively. At the shortgrass steppe, mean annual temperature for the simulation under current conditions was 9.1°C, 13.6°C for the A2 scenario, and 11.9°C for the B1 scenario (Fig 2.1). At the mixed grass prairie, mean annual temperature for the simulation under current conditions was 11.8°C, 16.5°C for the A2 scenario, and 14.6°C for the B1 scenario (Fig. 2.2).

The monthly distributions of predicted changes in precipitation and temperature were similar within scenario families and between sites. Both the A2 and B1 emission scenario families predicted an increase in winter (Oct - March) precipitation at each site, and on average,

a decrease in growing season (April - Sept) precipitation at each site. The A2 scenario family predicted an average decrease in growing season precipitation of 3.0% at the shortgrass steppe and decrease of 5.9% at the mixed grass prairie, while the B1 scenario predicted very slight changes at each site (-1.7% at the shortgrass steppe and 0.09% at the mixed grass prairie). Likewise, the A2 and B1 emission scenario families predicted greater increases in summer temperatures than winter temperatures at each site.

Dry, Average, and Wet years

Annual precipitation for the 51 years of data ranged from 106 – 572 mm at the shortgrass steppe and 363 – 965 mm at the mixed grass prairie. At the shortgrass steppe, I classified all years with less than 265 mm annual precipitation “dry” (the 12 driest years), and those with more than 391 mm “wet” (the 12 wettest years). At the mixed grass prairie, I classified all years with less than 470 mm “dry”, and those with more than 640 mm precipitation “wet”. Predicted future changes in precipitation resulted in an increase in the number of “dry” years at the shortgrass steppe for the A2 scenario (15 years, SD 9) and a decrease in the number for the B1 scenario (11 years, SD 4). There was no change in the number of wet years predicted by the A2 scenario (12 years, SD 10) for the shortgrass steppe, and an increase in the number by the B1 scenario (15 years, SD 8). For the mixed grass prairie site, predicted precipitation changes resulted in an increase in the number of “dry” years (18 years, SD 15) for the A2 scenario and a decrease for the B1 scenario (10 years, 6 SD). Both the A2 and B1 scenarios predicted an increase in the number of “wet” years (15 years, 13 SD for A2 and 17 years, 10 SD for B1).

Spatial dynamics of available soil water

Spatial dynamics- Shortgrass steppe

Spatial differences in available water between simulated current conditions and GCM predicted dynamics were small. The 0 – 10 cm and 30 -120 cm soil layers had the highest percentage of available water in all time periods and model simulations. In the 12 dry years, the surface layer had the highest percentage of available soil water in all periods of the year (Table 2.1). In average years, the greatest percentage of available water was split almost equally between the surface and deep soil layers (Table 2.2). In the 12 wettest years, the deep soil layer had the greatest percentage of available water for all time periods (Table 2.3). Coefficient of variation (CV) among model ensemble means was lowest near the surface, and increased with depth (Tables 2.1-2.3).

Differences in spatial distribution of available water tended to be larger during the growing season and non-growing season than annual differences. However, these differences were not consistent between climate change scenarios. For the A2 scenario, largest differences occurred in average and wet years during the winter: a 3 or 6% increase in the percentage of available water at the surface, and a 6 or 8 % decrease in the percentage of available water in the deep soil layer for average and wet years, respectively (Tables 2.2 and 2.3). In contrast, although the largest differences for the B1 scenario also occurred during the non-growing season, they occurred during the driest years: the surface layer had a 7 % decrease in the percentage of available water, while the deep soil layer had a 7 % increase in the percentage of available water.

Spatial Dynamics- Mixed grass prairie

Similar to the shortgrass steppe, mean CV among model ensemble means was smallest near the surface and increased with depth at an annual time scale in all years except the 12 driest

and average years for the B1 scenario (Tables 2.4 – 2.6). However, this was often not the case when examining the growing season and non-growing season individually. For dry, average, and wet years, CV in the deep soil layer was often lower than the layer above, especially for the B1 scenario during the winter and the A2 scenario during the summer. Unlike the shortgrass steppe, where the highest percentage of available water tended to be in the surface layers, at the mixed grass prairie site, the deep soil layer always had the largest percentage of available water (Tables 4 – 6), in all time periods and all types of years. The small remaining percentage of available water was split fairly evenly between the 0 – 30 cm depths.

Differences in the spatial distribution of available water between current and future simulated conditions were smaller than those seen at the shortgrass steppe. Differences tended to be larger during the non-growing season than annual and growing season differences. At an annual scale, there was a 1 - 2 % increase in the percentage of available water at the surface 0 - 10 cm, and a 1 – 2 % decrease in the percentage of available water in the 30 -120 cm layer for each year type. For the A2 scenario, the largest differences occurred in average and wet years during the winter: a 3 or 2 % increase in the percentage of available water at the surface, and a 4 or 3 % decrease in the percentage of available water in the 30 -120 cm layer for average and wet years, respectively (Tables 2.5 - 2.6). Differences in growing season available water were smaller (1 -2 %) in dry and average years, and in wet years, there was no difference between current and future predicted conditions in the A2 scenario.

Differences between current conditions and the B1 scenario were greatest in dry and average years. In dry years during the growing season, there was a 2 % increase in the percentage of available water at 0 – 10 cm and a 3 % decrease in the percentage of available water available at 30 – 120 cm. In dry years during the non-growing season, there was a 1 – 2%

decrease in the percentage of available water between 10 – 30 cm, and a 3 % increase in the percentage of available water at 30 – 120 cm. In average years there was a 3 or 1 % increase in the percentage of available water at 0 – 10 cm in the growing and non-growing seasons, respectively, a 2 or 3 % decrease in the percentage of available water at 20 -30 cm, and a 2 % increase in the percentage of available water at 30 – 120 cm during the non-growing season.

Temporal dynamics of available water

Temporal dynamics- shortgrass steppe

Similar to the spatial dynamics of soil water at the shortgrass steppe, there were few differences in temporal dynamics of available water between current and climate change simulations. Differences were largest in wet years and smallest in dry years, and tended to be larger during the growing season than the non-growing season (Fig. 2.3 – 2.5). In dry years, there were no discernible differences in the temporal dynamics of available water between the control, A2, and B1 model ensembles (Fig. 2.3). In average years, there was a small decrease in available water during the early part of the growing season (May and June) for the A2 and B1 scenarios in the shallow and deep soil layers, but no discernible change in non-growing season available water (Fig 2.4). Changes were most apparent in wet years. There was a decrease in growing season available water in wet years for the A2 and B1 scenarios. In the surface layers (0 – 30 cm), the decrease was greatest during the early growing season (May and June), and greater for the A2 scenario ensemble than for the B1 scenario ensemble (Fig. 2.5, Fig 2.9). The decrease in surface growing season available water was accompanied by a slight increase in non-growing season available water for the B1 scenario (Fig 2.5), but the decrease in growing season water was much greater than the corresponding increase in non-growing season water. In the deeper soil layers, there was a decrease in both growing season and late non-growing season available

water (Fig. 2.5), especially for the A2 scenario ensemble. There was no change in early (Jan – April) non-growing season available water.

There were no large differences in frequency of days with available soil water in the surface between dry, average, and wet years. On an annual scale, the percentage of days with available water ranged from a low of 57 % in dry years to a high of 69 % in wet years under current conditions, 57 % to 66 % in the A2 scenario, and 57 % to 67 % in the B1 scenario. On a seasonal scale, the differences were small as well. In dry and wet years, the percentage of days with available water in the surface layers was least in the winter (45 – 55 % for dry and wet years, respectively) and greatest in the fall (65 – 73 % for dry and wet years, respectively), but the percentages were similar throughout the year during average years (Fig. 2.6). The differences between the percentage of days with available water under current and future predicted conditions were very small; and represented, at most, a difference of 4% during the fall in wet years (Fig 2.6).

Temporal dynamics- mixed grass prairie

Like the shortgrass steppe, differences in available water between current and future predicted dynamics were highest in wet years and smallest in dry years. However, unlike the shortgrass steppe, differences tended to be larger during the non-growing season than during the growing season (Fig. 2.7 – 2.9). For dry, average, and wet years, there was a decrease in available water at both depths during the entire year. For the B1 scenario, decreases were greater during the non-growing season than the growing season in the shallow layers (0 – 30 cm), but decreases in the deep soil layers (30 – 120 cm) were not congruent across year types. In dry years, the greatest decrease in available water occurred from Jan – July (Fig 2.7). In average years, the greatest decrease in available water occurred during mid-growing season, in June and

July (Fig 2.8). In wet years, the greatest decrease in available water occurred later in the year; in August – Dec (Fig 2.9).

Differences between current conditions and the A2 scenario were always greater than differences observed in the B1 scenario, but like the B1 scenario, differences were greatest in wet years and smallest in dry years. For the 0 -30 cm layer, there was little difference in the temporal distribution of available water across the non-growing season and growing season in dry and average years (Fig. 2.7 – 2.8). Across the year, the mean decrease in available water for dry years was 1.7 mm, and 3.3 mm for average years, with few small differences between the growing season and non-growing season. Similar to the B1 scenario, in wet years the greatest decrease in available water in the A2 scenario compared to current conditions occurred during the growing season, in June – July (Fig 2.9). Differences in available deep soil water in the A2 scenario followed the same pattern as those in the B1 scenario, although more pronounced in the A2 scenario. In dry years, the greatest decrease in available water occurred from Jan – July (Fig 2.7). In average years, the greatest decrease in available water occurred during mid-growing season, in June and July (Fig 2.8). In wet years, the greatest decrease in available water occurred later in the year; in August – Dec (Fig 2.9).

Unlike the shortgrass steppe, where the proportion of days with available water in the surface layers tended to be similar between seasons and climate change scenarios, the differences were much larger at the mixed grass prairie. While available soil water at the shortgrass steppe was slightly higher during the growing season than during the winter, at the mixed grass prairie the pattern was reversed and exaggerated. In dry, average, and wet years for current conditions, winter was the season with the greatest frequency of available soil water; ranging from 99% in wet years to 96% in dry years (Fig 2.10). Summer was the season with the lowest frequency of

available surface water under current conditions; ranging from 73 % in dry years to 97 % in wet years, representing a seasonal difference of 23 % in dry years, 12% in average years, and 3 % in wet years. There were also large differences in the percentage of days with available water between current and future predicted conditions. Differences tended to be greater during the summer and fall than during the winter and spring, although there was also a large difference in the winter for the B1 scenario (Fig 2.10). Finally, there were greater differences between the A2 and B1 scenarios at the mixed grass prairie than at the shortgrass steppe, especially during the winter and spring. The A2 scenario represented greater differences from current conditions.

DISCUSSION

The central grassland region is currently characterized by a continental climate; with the majority of precipitation falling during the summer growing season when temperatures are warmest (Lauenroth et al. 1999). This overall pattern did not change greatly under predicted climate change scenarios (Figs. 2.1 and 2.2). However, while the IPCC predicts that the two grassland sites will experience similar percentage changes in annual precipitation and temperature, the consequences of these changes on the spatial and temporal dynamics of soil water were different between sites.

Spatial dynamics of available water

Differences in the spatial distribution of available water between current and future simulated conditions were small at the shortgrass steppe, and tended to be greatest during the non-growing season (Tables 2.1 – 2.3). At most, these differences represented an increase of 8 % from current conditions, and in many cases were smaller than 8 %. Although these changes are relatively small, previous research in the shortgrass steppe has shown that non-growing season precipitation may have a disproportionately large effect on plant productivity. In an analysis of

long term production at the CPER, Milchunas et al. (1994) found that production was very sensitive to changes in cool season (Oct-April) precipitation, but only slightly sensitive to changes in growing season precipitation. Another recent study of net ecosystem production at the CPER concluded that additional precipitation during the July – Oct period would have much less of an impact on net ecosystem production than additional precipitation received during the April – June time period (Parton et al. 2012). Thus, even small changes in the spatial distribution of non-growing season precipitation may impact plant production in the shortgrass steppe.

At the mixed grass prairie site, the changes we observed in the spatial distribution of water were smaller than those observed at the shortgrass steppe. The largest changes occurred in average and wet years in the A2 scenario, but even these changes represented a small increase of 3 or 2 % in the 0 – 10 cm layer, with a corresponding decrease in deep soil water of 3 or 4 %. During dry years and during the growing season and at an annual scale for all year types, any change in the spatial distribution of available water represented a difference of 2 % or less compared to current conditions. At this more mesic site, the majority of soil water is held in the 30 -120 cm layer, and this pattern clearly will not be affected under future climatic conditions.

Temporal dynamics of available water

On average, there is very little soil water available on any day of the year at the shortgrass steppe, and this pattern did not change in simulated future conditions (Fig 2.3 – 2.5). In dry and average years, the A2 and B1 scenarios had very small differences in available water relative to current conditions. Differences were greatest in wet years, when there was a small decrease in available soil water during the growing season in the surface and deeper soil layers in the climate change scenarios, particularly the A2 scenario, compared to current conditions (Fig 2.5).

While the lack of changes in soil water conditions in dry and average years bodes well for the future stability of the shortgrass steppe ecosystem, the decrease in available growing season water in wet years, especially in the 10 - 20 and 20 – 30 cm depths, has the potential to adversely affect recruitment of the dominant species. The shortgrass steppe is dominated by a single species, the perennial C₄ bunchgrass *Bouteloua gracilis* (Willd. ex Kunth) Lag. ex Griffiths. *Bouteloua gracilis* consistently makes up 80% or more of aboveground net primary production (Milchunas et al. 1989), and previous research has shown that it plays an important role in maintaining ecosystem stability (Sasaki and Lauenroth 2011) and structure (Milchunas et al. 1990). *Bouteloua gracilis* normally reproduces vegetatively, but after large-scale disturbances it relies on seedling recruitment for reestablishment (Coffin et al. 1996). Previous work has shown that recruitment is limited to years with sufficient available water in the 0 -30 cm layer of the soil (Lauenroth et al. 1994). Wet years are more likely to have conditions favorable to *B. gracilis* recruitment, and even a small decrease in available water during the growing season under future climate change conditions may further limit the already infrequent recruitment events. Further limitation of *B. gracilis* recruitment could lead to changes in community structure and stability, including an increase in annual and ruderal species (Evans et al. 2011).

Climate change simulations at the mixed grass prairie site led to larger changes in the temporal distribution of available water in all year types. Compared to the shortgrass steppe, the percentage of days with available soil water was much higher (Fig 2.9 – 2.10), due to the larger quantity of precipitation that this wetter site receives (Fig 2.2). In dry, average, and wet years, the greatest decrease in the percentage of days with available water in the 0 – 30 cm layer in climate change scenarios compared to current conditions occurred during the summer season (Fig 2.10). For the 30 -120 cm depth, the changes in available water compared to current

conditions differed among dry, average, and wet years (Figs 2.6 – 2.8). In dry years, the greatest decrease occurred at the beginning of the year (Fig 2.6), in average years, the greatest decrease occurred during the growing season (Fig 2.7), and in wet years the greatest decrease occurred during the non-growing season (Fig 2.8). Regardless of the timing of decreased deep soil water, there will likely be less available deep soil water under future predicted conditions, throughout the year.

A decrease in deep soil water could in turn, affect species dynamics and net primary production for the mixed grass prairie site. Shrubs, forbs, and grasses have different rooting strategies that allow them to coexist by using soil water at different depths (Walter 1979; but see Ogle and Reynolds 2004 for limitations). In general, grasses have shallow, fibrous root systems that take advantage of shallow soil water, while forbs and shrubs have deeper root systems that can access both shallow and deeper soil water. Under current conditions, a study in the tallgrass prairie showed that the dominant C₄ grasses used soil water from the upper 30 cm throughout the study, irrespective of seasonal wet or dry periods, while subdominant shrubs and forbs often used deeper soil water, especially in seasonal dry periods (Nippert and Knapp 2007b, a). In the short term, these studies suggest that climate change might favor grasses over deeper rooted forbs and shrubs. Yet while the dominant C₄ grasses of the tallgrass prairie have the majority of roots in the top 30 cm, 20 -30 % of roots extend below 30 cm (Weaver and Darland 1949, Kucera and Dahlman 1968, Kitchen et al. 2009). These roots can extend to a depth of 150 cm or more in the tallgrass prairie (Weaver and Darland 1949, Weaver 1968). A decrease in the availability of deep soil water, as predicted in our climate change simulation, may change the balance between more water dependent tallgrass species and drought tolerant shortgrass species at the mixed grass prairie. Indeed, Weaver and Albertson (1936) showed dramatic changes in species composition

in the mixed grass and tallgrass prairies during the severe drought of the early 1930's, including a decrease in tall and mid-stature grasses, and an increase in drought tolerant shortgrasses. As warming and changes in precipitation are predicted to result in longer and more severe droughts in the western United States (Cook et al. 2004, MacDonald 2010, Woodhouse et al. 2010), it is likely that the mixed grass prairie will experience changes in species composition, especially if drought periods lengthen and intensify.

Although not studied here, it is important to mention rising atmospheric CO₂ as another global change factor that may indirectly affect soil water content in grasslands. Elevated CO₂ decreases stomatal conductance, which reduces plant transpiration and can result in increased plant water use efficiency and soil water content (Morgan et al. 2004). While increased CO₂ may lead to an increase in soil water, it is still unclear how changes in temperature and precipitation will combine with elevated CO₂ to affect temporal and spatial soil water dynamics in the central grassland region. In a combined elevated temperature and CO₂ study in the northern mixed grass prairie, elevated CO₂ increased annual soil water content while elevated temperature decreased it, so that there was no difference between current conditions and elevated CO₂ and temperature treatments (Morgan et al. 2011). However, this experiment did not manipulate precipitation, which is the most important determinant of soil water content. In another study, conducted in the tallgrass prairie of Texas, elevated CO₂ resulted in a shift in species composition, including an increase in the dominant tallgrass species, *Sorghastrum nutans*, at the expense of the dominant mid-stature grass, *Bouteloua curtipendula* (Polley et al. 2012). The magnitude of change depended not only on the quantity of CO₂ added, but on the texture of the soil. The largest changes in composition occurred in the coarsest textured soils, where water savings from elevated CO₂ were greatest (Polley et al. 2012). As GCM's improve, and results from CO₂

experiments become clearer, it will be important to include estimates for changes in atmospheric CO₂ concentrations in addition to changes in the timing and quantity of precipitation and temperature to improve our predictions of future soil water dynamics in grassland ecosystems.

Differences in dry, average, and wet years

At the shortgrass steppe site, the differences between current and future conditions were nonexistent in dry and average years, and small in wet years. At the mixed grass prairie site, differences were greatest in wet years and smallest in dry years. Even in average years, there were significant changes in the distribution of soil water at the mixed grass prairie site. If we consider that ecosystems are shaped by “average” conditions, an important general conclusion about climate change in grasslands can be made by comparing the relative changes in the spatial and temporal distribution of available water in these two ecosystems during average years. I found that the drier site experienced relatively few changes in soil water in average years, while the more mesic site experienced large changes in soil water in average years. Thus, in areas where relatively small changes in precipitation and temperature are predicted, as is the case in the central grassland region of North America (Christensen et al. 2007), wetter grasslands may be more sensitive to climate change than semiarid and arid grasslands.

Conclusions

Many experimental manipulations have examined the short term consequences of changes in precipitation and temperature predicted by the IPCC, but my simulation study is unique in that it provides a long term perspective on daily soil water dynamics throughout the soil profile and over a range of annual conditions (dry, average, and wet years). Field measurements of soil water are often limited to the top 10 or 30 cm of the soil profile. Although these studies increase our understanding of temporal dynamics of soil water in the shallow soils,

such shallow measurements do not elucidate changes that may occur at depth. At the shortgrass steppe site, we gain a reasonable understanding of the spatial and temporal dynamics of soil water by examining the surface layers. However, at the mixed grass prairie site, the largest changes in soil water occur deeper in the soil, from 30 -120 cm. Simulation modeling is a straightforward and easy way to greatly increase the amount of information we can get from rainfall manipulation experiments.

While we are able to make general predictions of future soil water dynamics based on the A2 and B1 ensemble means, my results indicate that there is still a large amount of variability among GCMs, as evidenced by the large coefficients of variation associated with my simulation results (Tables 1- 6). As GCMs improve, I recommend additional simulations to improve our understanding of future soil water dynamics in water-controlled ecosystems like the shortgrass steppe and mixed grass prairie.

TABLES

Table 2.1. Percentage (%) of available water by depth at the shortgrass steppe for the 12 driest years in the control, A2, and B1 scenarios for the April – Sept growing season (GS), non-growing season (W), and annual (T) time periods. For each scenario, depth percentages sum to 1. Coefficient of variation for model ensemble means shown in parentheses.

	GS	GS	GS	W	W	W	T	T	T
Depth (cm)	C	A2	B1	C	A2	B1	C	A2	B1
0-10	65 (-)	67 (8)	63 (7)	73 (-)	73 (24)	66 (18)	68 (-)	69 (9)	64 (7)
10-20	20 (-)	15 (45)	18 (22)	10 (-)	8 (38)	8 (32)	16 (-)	12 (34)	14 (25)
20-30	7 (-)	6 (71)	7 (54)	0 (-)	1 (225)	1 (129)	4 (-)	4 (70)	5 (58)
30-120	8 (-)	12 (114)	13 (125)	17 (-)	18 (138)	24 (138)	12 (-)	14 (122)	18 (130)

Table 2.2. Percentage (%) of available water by depth at the shortgrass steppe for the 27 average years in the control, A2, and B1 scenarios for the April – Sept growing season (GS), non-growing season (W), and annual (T) time periods. For each scenario, depth percentages sum to 1. Coefficient of variation for model ensemble means shown in parentheses.

	GS	GS	GS	W	W	W	T	T	T
Depth (cm)	C	A2	B1	C	A2	B1	C	A2	B1
0-10	32 (-)	35 (9)	31 (7)	49 (-)	52 (13)	47 (11)	39 (-)	43 (5)	37 (5)
10-20	19 (-)	17 (15)	17 (22)	11 (-)	13 (24)	12 (21)	16 (-)	16 (24.)	15 (18)
20-30	13 (-)	12 (56)	13 (34)	4 (-)	5 (46)	5 (40)	10 (-)	9 (50)	9 (33)
30-120	36 (-)	36 (126)	40 (102)	36 (-)	30 (128)	36 (95)	36 (-)	33 (126)	38 (99)

Table 2.3. Percentage (%) of available water by depth at the shortgrass steppe for the 12 wettest years in the control, A2, and B1 scenarios for the April – Sept growing season (GS), non-growing season (W), and annual (T) time periods. For each scenario, depth percentages sum to 1. Coefficient of variation for model ensemble means shown in parentheses.

	GS	GS	GS	W	W	W	T	T	T
Depth (cm)	C	A2	B1	C	A2	B1	C	A2	B1
0-10	18 (-)	21 (11)	19 (8)	27 (-)	34 (16)	28 (9)	21 (-)	26 (6)	22 (4)
10-20	13 (-)	13 (32)	13 (18)	5 (-)	7 (30)	6 (25)	11 (-)	11 (28)	11 (18)
20-30	11 (-)	10 (52)	10 (28)	5 (-)	4 (54)	4 (44)	9 (-)	8 (50)	8 (28)
30-120	58 (-)	55 (78)	58 (64)	63 (-)	55 (108)	62 (90)	60 (-)	55 (86)	59 (72)

Table 2.4. Percentage (%) of available water by depth at the mixed grass prairie for the 12 driest years in the control, A2, and B1 scenarios for the April – Sept growing season (GS), non-growing season (W), and annual (T) time periods. For each scenario, depth percentages sum to 1. Coefficient of variation for model ensemble means shown in parentheses.

	GS	GS	GS	W	W	W	T	T	T
Depth (cm)	C	A2	B1	C	A2	B1	C	A2	B1
0-10	7 (-)	7 (18)	7 (9)	10 (-)	10 (16)	11 (17)	8 (-)	9 (14)	9 (12)
10-20	5 (-)	6 (42)	5 (17)	8 (-)	8 (27)	8 (14)	6 (-)	7 (30)	7 (13)
20-30	4 (-)	5 (50)	4 (24)	7 (-)	7 (36)	7 (23)	5 (-)	6 (40)	6 (20)
30-120	84 (-)	82 (47)	84 (22)	75 (-)	74 (51)	74 (27)	80 (-)	78 (49)	79 (24)

Table 2.5. Percentage (%) of available water by depth at the mixed grass prairie for the 27 average years in the control, A2, and B1 scenarios for the April – Sept growing season (GS), non-growing season (W), and annual (T) time periods. For each scenario, depth percentages sum to 1. Coefficient of variation for model ensemble means shown in parentheses.

	GS	GS	GS	W	W	W	T	T	T
Depth (cm)	C	A2	B1	C	A2	B1	C	A2	B1
0-10	6 (-)	8 (13)	7 (11)	9 (-)	12 (12)	9 (18)	8 (-)	10 (9)	8 (13)
10-20	6 (-)	5 (32)	6 (16)	7 (-)	8 (25)	8 (13)	7 (-)	7 (25)	7 (12)
20-30	6 (-)	4 (38)	6 (21)	8 (-)	7 (37)	8 (18)	7 (-)	6 (35)	7 (18)
30-120	81 (-)	82 (42)	81 (28)	76 (-)	72 (47)	75 (35)	79 (-)	77 (44)	78 (31)

Table 2.6. Percentage (%) of available water by depth at the mixed grass prairie for the 12 wettest years in the control, A2, and B1 scenarios for the April – Sept growing season (GS), non-growing season (W), and annual (T) time periods. For each scenario, depth percentages sum to 1. Coefficient of variation for model ensemble means shown in parentheses.

	GS	GS	GS	W	W	W	T	T	T
Depth (cm)	C	A2	B1	C	A2	B1	C	A2	B1
0-10	6 (-)	6 (20)	6 (11)	8 (-)	10 (12)	8 (16)	7 (-)	8 (13)	7 (12)
10-20	6 (-)	6 (35)	6 (16)	7 (-)	8 (20)	8 (6)	6 (-)	7 (24)	7 (9)
20-30	6 (-)	6 (42)	6 (18)	8 (-)	9 (25)	8 (8)	7 (-)	7 (30)	7 (12)
30-120	82 (-)	83 (36)	83 (13)	77 (-)	74 (45)	76 (25)	80 (-)	78 (40)	79 (18)

FIGURES

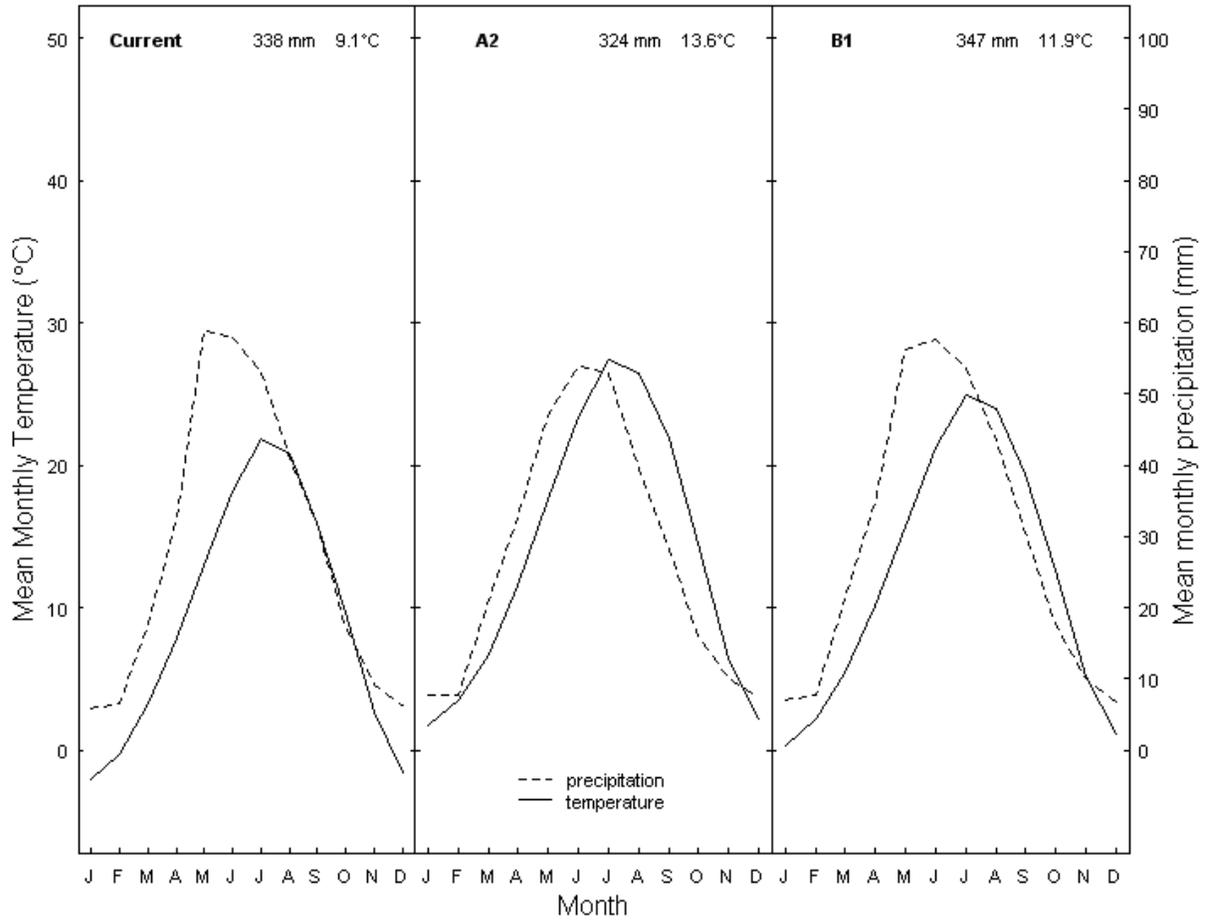


Figure 2.1. Mean monthly temperature and precipitation at the shortgrass steppe in (a) current and future predicted climate change scenarios for the (b) A2 and (c) B1 emission scenario families. Mean annual precipitation and temperature are displayed on the upper right of each panel. Error bars are removed for clarity.

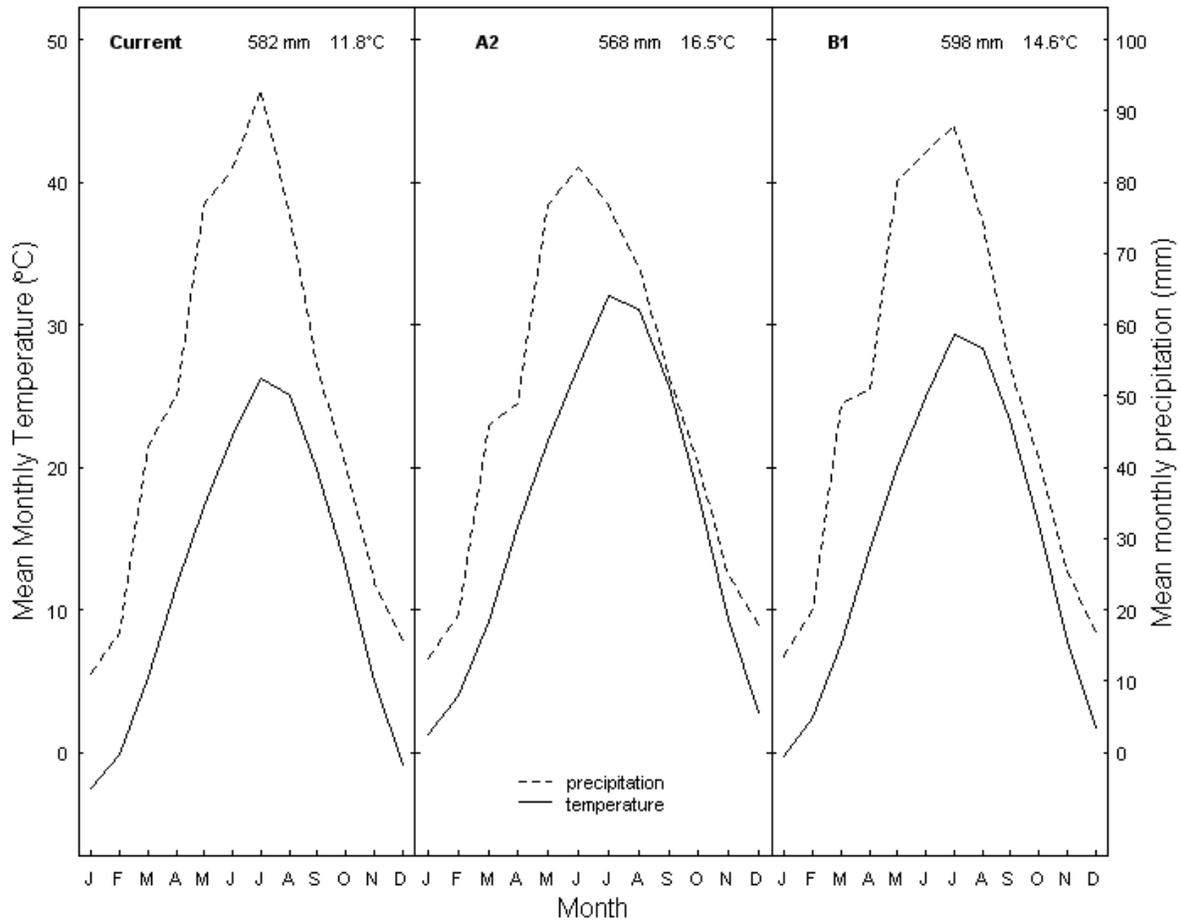


Figure 2.2. Mean monthly temperature and precipitation at the mixed grass prairie in (a) current and future predicted climate change scenarios for the (b) A2 and (c) B1 emission scenario families. Mean annual precipitation and temperature are displayed on the upper right of each panel. Error bars are removed for clarity.

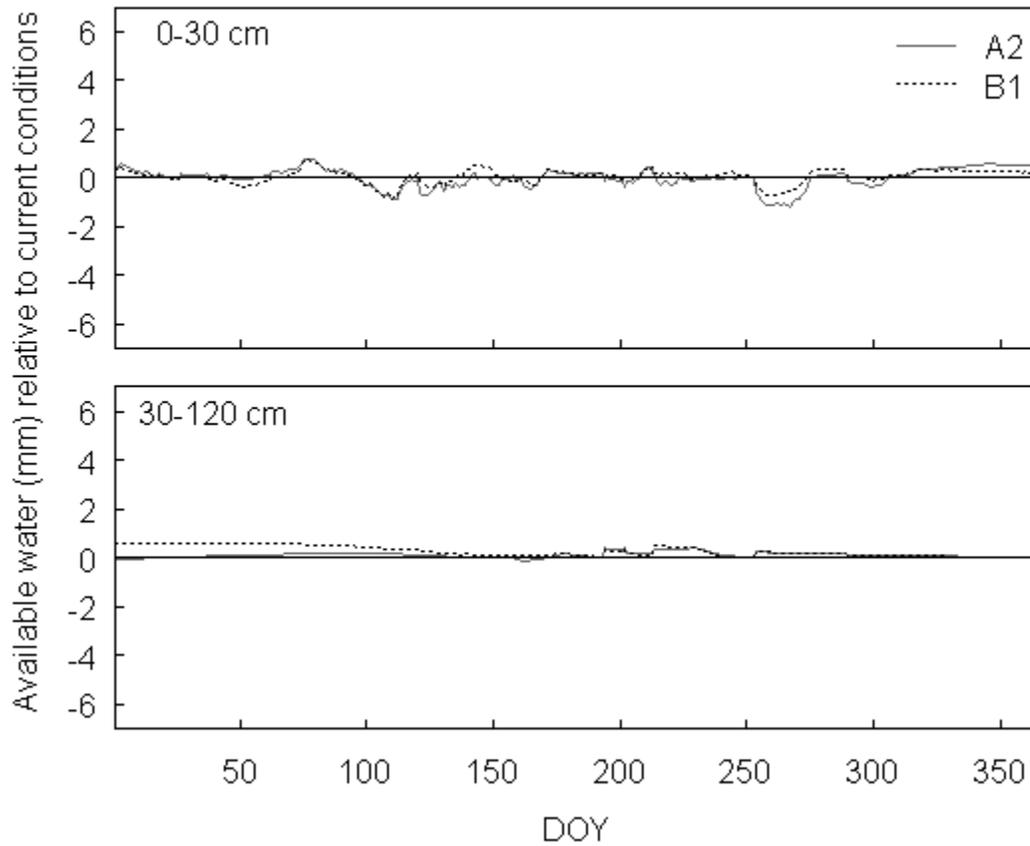


Figure 2.3. Difference between current and future predicted mean daily available soil water at the shortgrass steppe for 0 – 30 and 30 – 120 cm for the A2 and B1 scenarios for 12 driest weather years.

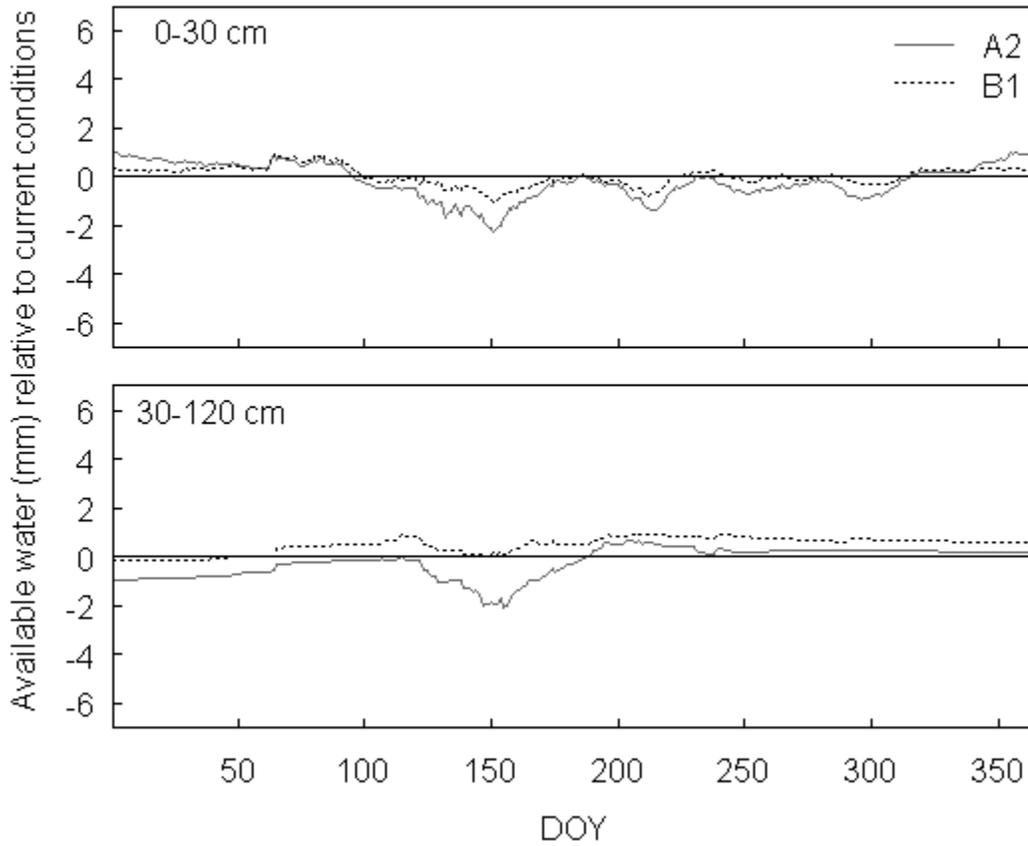


Figure 2.4. Difference between current and future predicted mean daily available soil water at the shortgrass steppe for 0 – 30 and 30 – 120 cm for the A2 and B1 scenarios for 27 average weather years.

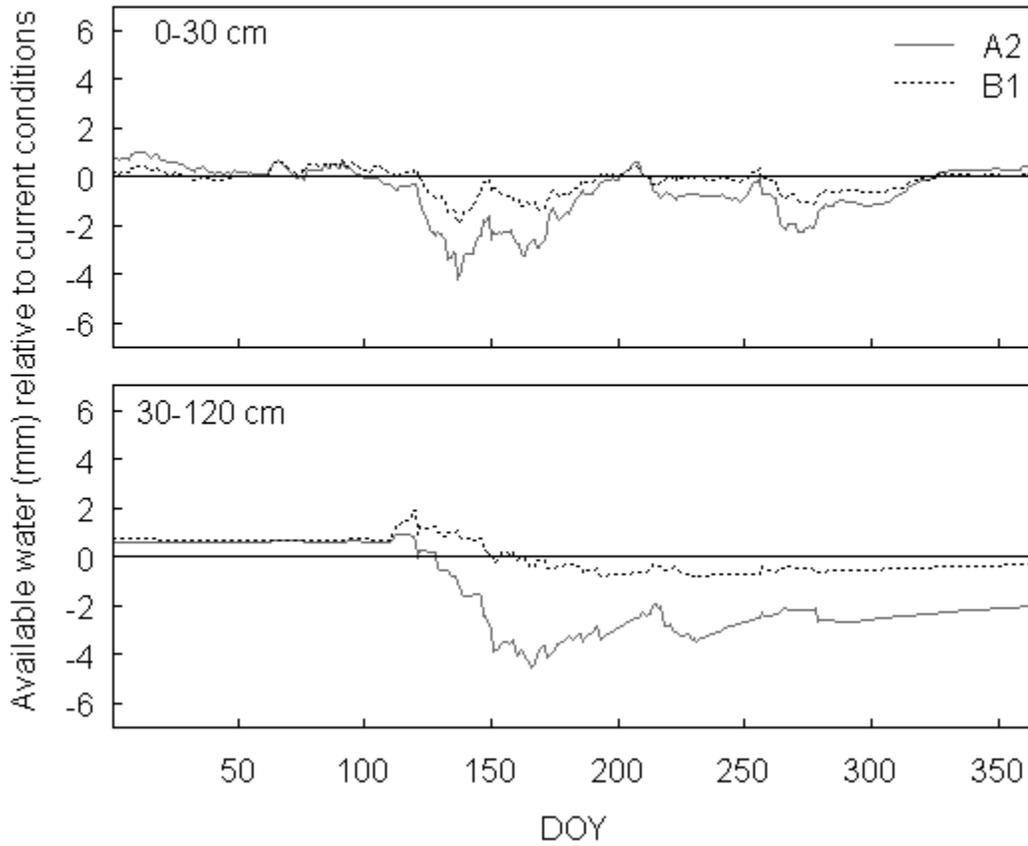


Figure 2.5. Difference between current and future predicted mean daily available soil water at the shortgrass steppe for 0 – 30 and 30 – 120 cm for the A2 and B1 scenarios for 12 wettest weather years.

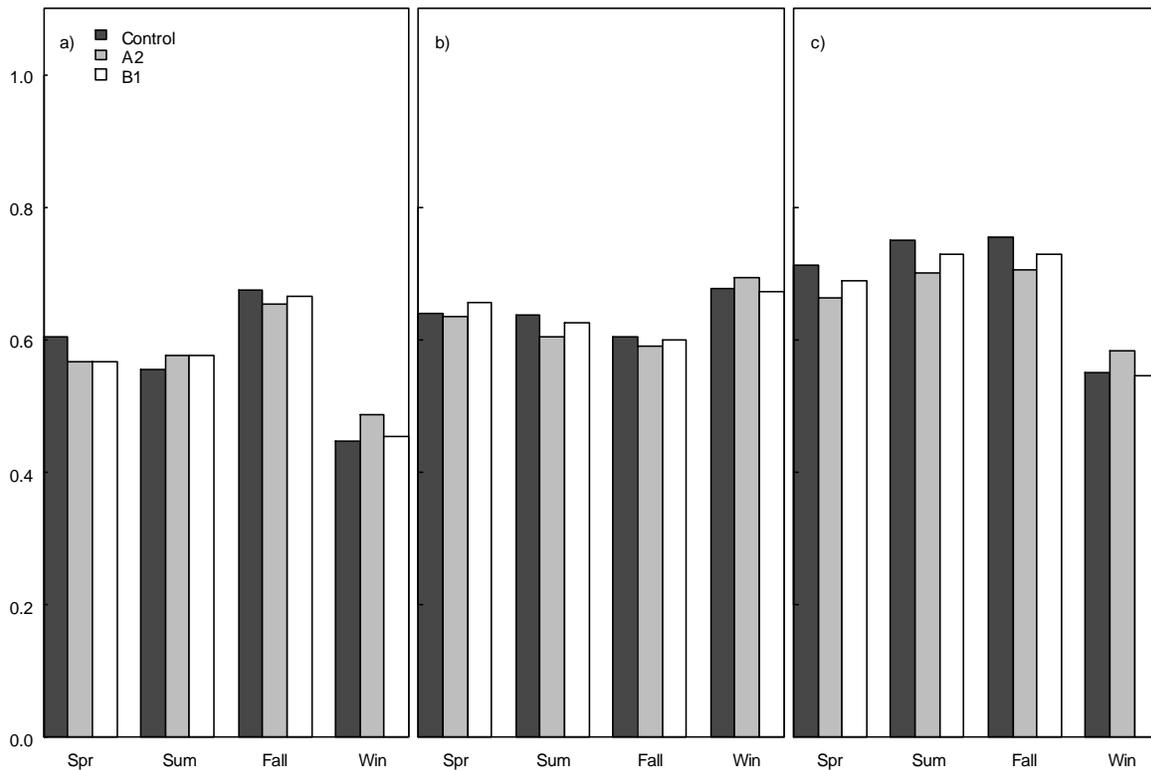


Figure 2.6. Mean frequency of days with soil water content in the top 30 cm of the soil profile greater than wilting point (-1.5MPa) during the spring (Mar – May), summer (Jun – Aug), fall (Sep – Nov), and winter (Dec – Feb) at the shortgrass steppe in dry (**a**), average (**b**), and wet weather (**c**) years for current conditions and future predicted conditions for the A2 and B1 ensemble scenarios.

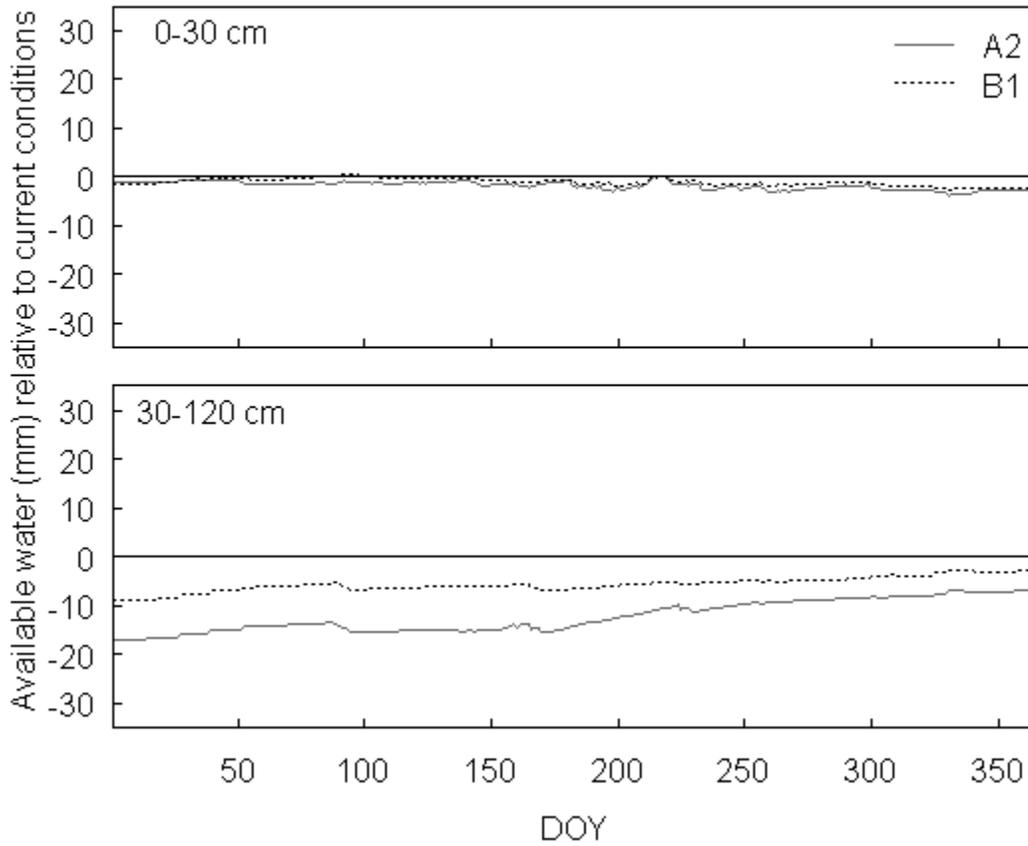


Figure 2.7. Difference between current and future predicted mean daily available soil water at the mixed grass prairie for 0 – 30 and 30 – 120 cm for the A2 and B1 scenarios for 12 driest weather years.

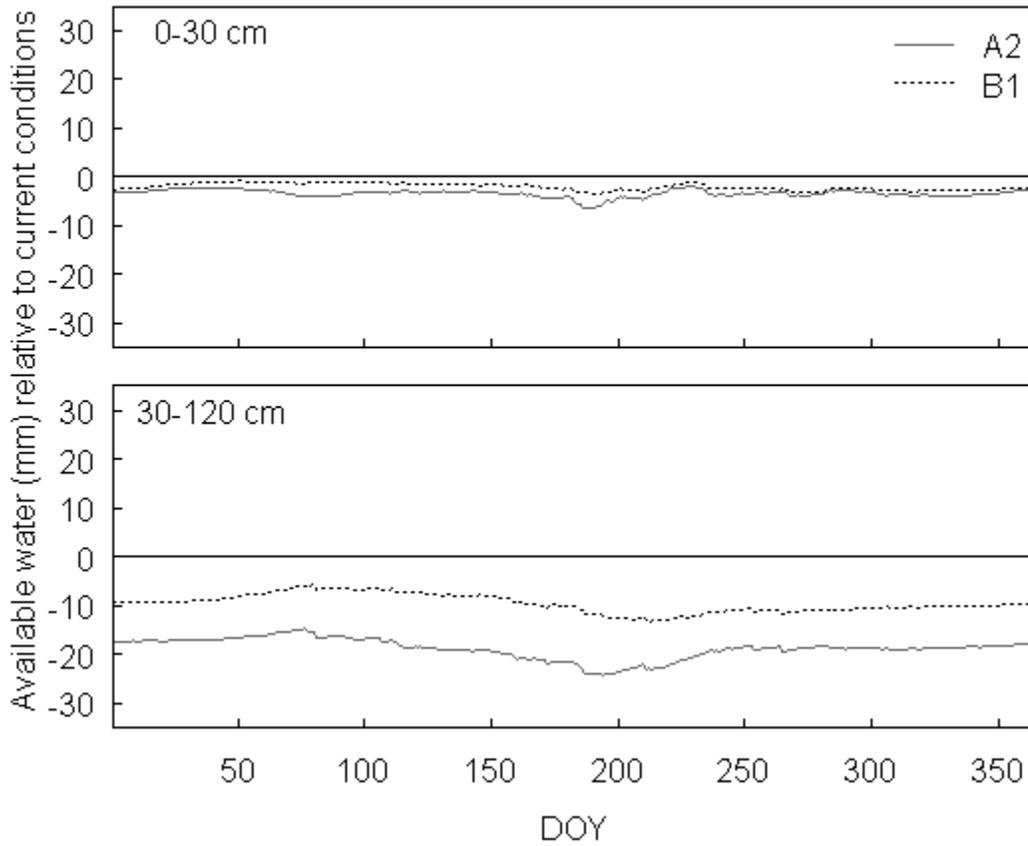


Figure 2.8. Difference between current and future predicted mean daily available soil water at the mixed grass prairie for 0 – 30 and 30 – 120 cm for the A2 and B1 scenarios for 27 average weather years.

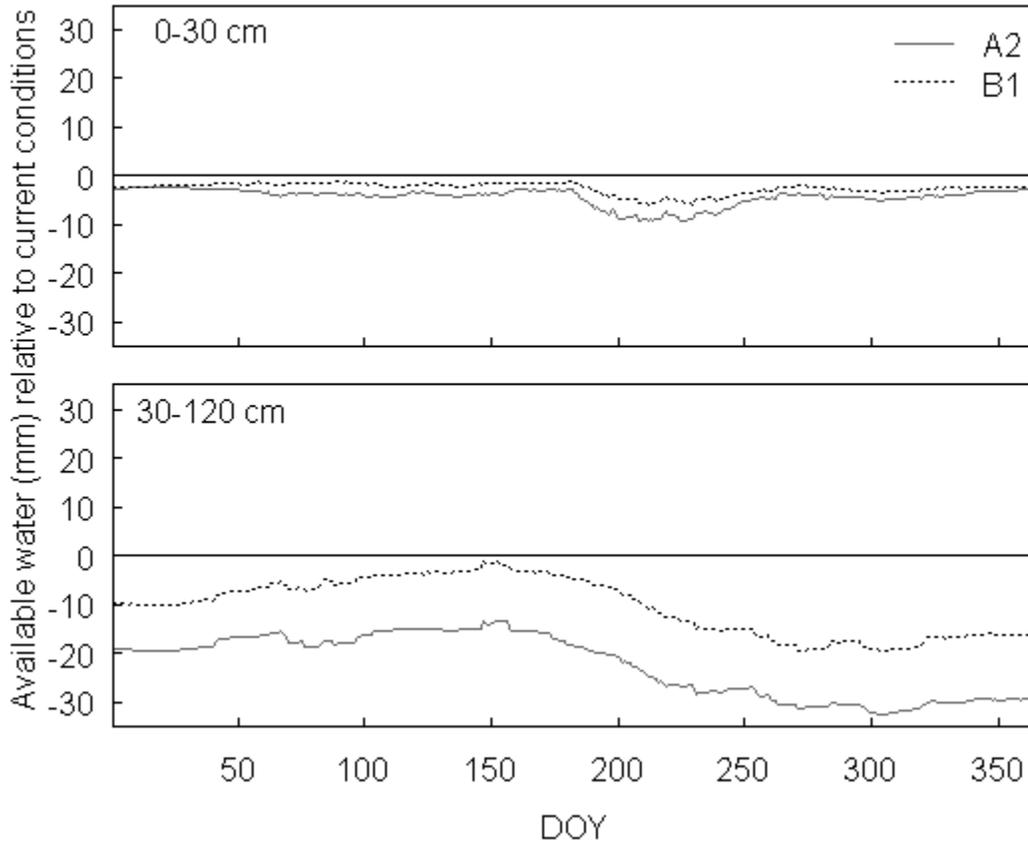


Figure 2.9. Difference between current and future predicted mean daily available soil water at the mixed grass prairie for 0 – 30 and 30 – 120 cm for the A2 and B1 scenarios for 12 wettest weather years.

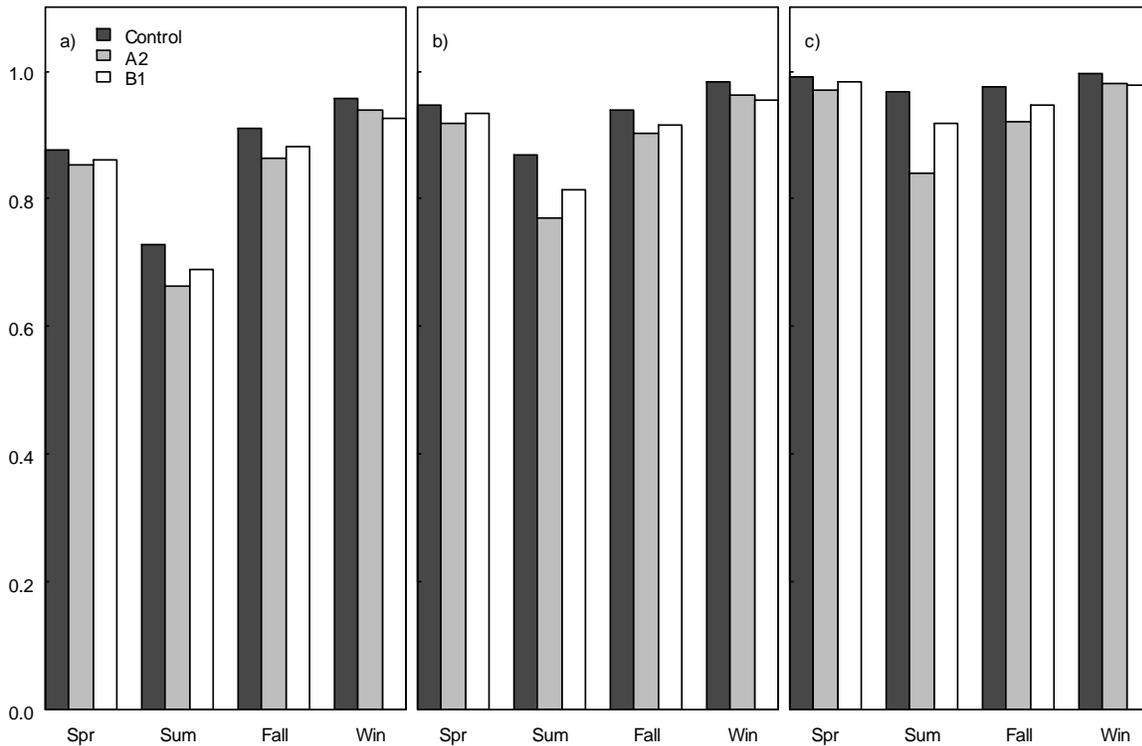


Figure 2.10. Mean frequency of days with soil water content in the top 30 cm of the soil profile greater than wilting point (-1.5MPa) during the spring (Mar – May), summer (Jun – Aug), fall (Sep – Nov), and winter (Dec – Feb) at the mixed grass prairie in dry (a), average (b), and wet weather (c) years for current conditions and future predicted conditions for the A2 and B1 ensemble scenarios.

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APPENDIX

Table A.2.1. Soil, evaporation and transpiration parameters for the shortgrass steppe site

Depth	Bulkd	Fieldc	Wiltpt	Evco	Trco	% Sand	% Clay
10	1.55	0.1976	0.0843	0.683	0.367	0.635	0.1
20	1.55	0.1976	0.0843	0.183	0.2567	0.635	0.1
30	1.4	0.2634	0.1538	0.133	0.1133	0.558	0.265
40	1.4	0.2634	0.1538	0	0.0933	0.558	0.265
50	1.4	0.2634	0.1538	0	0.0867	0.558	0.265
60	1.4	0.2634	0.1538	0	0.08	0.558	0.265
80	1.6	0.1822	0.0715	0	0.0567	0.652	0.075
100	1.6	0.1822	0.0715	0	0.0133	0.652	0.075
120	1.6	0.1822	0.0715	0	0	0.652	0.075

Table A.2.2. Soil, evaporation and transpiration parameters for the mixed grass prairie site

Depth	Bulkd	Fieldc	Wiltpt	Evco	Trco	% Sand	% Clay
10	1.34	0.3432	0.1982	0.683	0.367	0.24	0.25
20	1.34	0.3432	0.1982	0.183	0.2567	0.24	0.25
30	1.34	0.3432	0.1982	0.133	0.1133	0.24	0.25
40	1.25	0.4019	0.2654	0.0	0.0933	0.07	0.39
50	1.25	0.4019	0.2654	0.000	0.0867	0.07	0.39
60	1.25	0.4019	0.2654	0.000	0.0800	0.07	0.39
80	1.25	0.4019	0.2654	0.000	0.0567	0.07	0.39
100	1.33	0.3531	0.2066	0.000	0.0133	0.21	0.26
120	1.33	0.3531	0.2066	0.000	0.0000	0.21	0.26

Depth = (cm) lower limit of layer; layers must be in order of depth.

Bulkd = (g/cm^3) bulk density of soil in this layer.

Fieldc = (cm^3/cm^3) field capacity soil water volume/volume soil.

Wiltpt = (cm^3/cm^3) wilting point water volume/volume soil.

Evco = (frac) proportion of total bare soil evaporation from this layer.

Trco = (frac) proportion of total transpiration from this layer.

% Sand = (frac) proportion of sand in layer (0–1.0).

% Clay = (frac) proportion of clay in layer (0–1.0).

Note that the evco and trco columns must sum to 1.0 or they will be normalized.

Table A.2.3. Plant biomass and production parameters for the shortgrass steppe site.

Litter	Biomass	% Live	LAI_conv	Month
75	150	0.05	300	January
80	150	0.05	300	February
85	150	0.1	300	March
90	170	0.2	300	April
50	190	0.4	300	May
50	220	0.6	300	June
50	250	0.4	300	July
55	220	0.4	300	August
60	190	0.3	300	September
65	180	0.2	300	October
70	170	0.1	300	November
75	160	0.05	300	December

Table A.2.4. Plant biomass and production parameters for the mixed grass prairie site.

Litter	Biomass	% Live	LAI_conv	Month
300	254	0	300	January
312	260	0	300	February
235	216	0	300	March
248	244	0	300	April
266	229	0.20	300	May
170	254	0.37	300	June
249	284	0.60	300	July
203	277	0.47	300	August
272	248	0.27	300	September
207	218	0	300	October
266	216	0	300	November
217	213	0	300	December

Litter = dead leafy material on the ground (g/m^2).

Biomass = living and dead aboveground standing biomass (g/m^2).

% Live = proportion of Biomass that is actually living (0–1.0).

LAI_conv = monthly amount of biomass needed to produce LAI=1.0 (g/m^2).

Table A.2.5. Atmospheric parameters for the shortgrass steppe site.

Cld_cvr	Wnd_sp	Rel_hud	Transm_cf	Month
58	4.2	28	0.87	January
48	4.2	25	0.83	February
39	4.7	20	0.79	March
33	4.7	20	0.77	April
29	4.7	18	0.75	May
30	4.2	18	0.72	June
48	3.8	29	0.76	July
48	3.8	28	0.76	August
48	3.8	18	0.84	September
48	3.8	19	0.86	October
47	3.8	18	0.88	November
47	4.2	27	0.87	December

Table A.2.6. Atmospheric parameters for the mixed grass prairie site.

Cld_cvr	Wnd_sp	Rel_hud	Transm_cf	Month
37	4.7	67	0.87	January
37	4.7	64	0.83	February
37	5.6	63	0.79	March
40	5.6	61	0.77	April
40	5.1	62	0.75	May
30	4.7	64	0.72	June
22	4.2	60	0.76	July
29	4.2	62	0.76	August
30	4.2	57	0.84	September
30	4.2	61	0.86	October
34	4.7	62	0.88	November
38	4.7	67	0.87	December

Cld_cvr = average monthly cloud cover (%).

Wnd_spd = average monthly wind speed (m/s).

Rel_hud = average monthly relative humidity (%).

Transm_cf = transmissivity coefficient.

Sources for SOILWAT parameters

Soils

I used USDA NRCS web soil survey

(<http://websoilsurvey.nrcs.usda.gov/app/HomePage.htm>) to determine soil types in the county that each of our field sites were located in, and populated SOILWAT with the most common soil series in each county. For the shortgrass steppe site, I used the Ascalon Fine Sandy Loam, 0-6% slope from Weld County, CO. For the mixed grass prairie site, I used the Harney Silt Loam 0-1% slope from Ellis County, KS.

Production

I used the original values used to populate SOILWAT from Parton (1978) for monthly production values for the shortgrass steppe. For monthly production values at the mixed grass prairie, I used values from Lester, J. (1969). *Net shoot production and biomass transfer rates in a mature grassland ecosystem*. Unpublished master's thesis, Fort Hays State University, Hays, KS.

Wind Velocity

I took monthly wind velocity data estimated for our study sites from the National Climatic Data Center (<http://hurricane.ncdc.noaa.gov/cgi-bin/climaps/climaps.pl>).

Chapter 3: Contrasting effects of precipitation manipulations on production in two sites within the central grassland region, USA

SUMMARY

In grassland ecosystems, where soil water most frequently controls ecosystem processes, expected changes in precipitation and temperature may have dramatic effects on ecosystem dynamics. Previous observational studies have reported that aboveground net primary production (ANPP) in grasslands is very sensitive to changes in precipitation. Yet we lack experimentally based evidence to support these observations. Further, most studies have focused solely on ANPP, neglecting belowground production (BNPP). This is an important gap in our knowledge, as BNPP represents 50% or more of total net primary production (NPP) in grasslands. Here, I present results from a 3-year water manipulation experiment (2008 - 2010) at two sites in the central grassland region of North America, USA. I was successful in changing the soil water content in our treatments, but these changes resulted in different, but significant responses in ANPP and BNPP at my two sites. At the shortgrass steppe, I found that neither NPP nor ANPP was sensitive to treatment precipitation, and while I found BNPP was sensitive to changes in treatment precipitation, the direction of the response varied between years. In contrast, ANPP was very sensitive to treatment precipitation on the mixed grass prairie, while BNPP was insensitive. Based on my finding that two grassland ecosystems showed dramatically different above and belowground production responses to soil water manipulations, we cannot assume that predicted changes in climate will cause similar above and below ground production responses. Second, my results demonstrated that sites within the same region may differ markedly in the sensitivity of ANPP to changes in growing season precipitation.

INTRODUCTION

Human activities since the industrial revolution have contributed to regional and global changes in climate, including an increase in global temperature and changes in precipitation patterns (Christensen et al. 2007). Global change will not affect the Earth uniformly – temperature and precipitation changes will vary across regions, and responses will depend on an ecosystem's sensitivity to climate parameters (Knapp and Smith 2001). Thus, it is important to understand how different ecosystems may respond to future climatic perturbations. Predicting the effects of global change in grasslands is especially important, as they represent the potential natural vegetation of over 40% of the Earth's terrestrial surface (White et al. 2000) and include many productive agricultural and rangeland areas. The central grassland region of North America is an ideal ecosystem for studying the effects of global change on grassland communities. The region represents 12.5% of North America and 2% of the Earth's terrestrial surface (Lauenroth et al. 1999). Both temperature and precipitation vary along the north-south and east-west gradients of the region, and this range of climates within the region allows for comparisons with a variety of grasslands worldwide.

Climate models predict that the central grassland region of North America will warm substantially (3 – 4.4 °C) during the twenty-first century (Christensen et al. 2007; CCSP 2008). Associated predictions of precipitation changes are less certain and range from small increases to small decreases. It is still not clear how warmer temperatures and associated changes in precipitation regimes will alter ecosystem soil water patterns. However, ecosystems in the region are most frequently water limited (Noy-Meir 1973; Sala et al. 1988), and whether the predicted effects of climate changes increase or decrease soil water, previous work suggests that any change in soil water will have dramatic effects on ecosystem dynamics (Weltzin et al. 2003).

A critical ecosystem property that is sensitive to soil water availability is net primary production (NPP), the net amount of carbon removed from the atmosphere by plants. Plant production can be divided into aboveground net primary production (ANPP) and belowground net primary production (BNPP). Quantifying ANPP is a frequent goal of basic and applied ecology (Sala and Austin 2000), as estimates of ANPP are necessary to understand the global carbon balance and trophic interactions. From an applied perspective, estimates of ANPP are used to determine forage availability and stocking rates for livestock and managed wildlife populations in rangelands, and wood yield in forests. Observational studies have found that ANPP is tightly linked to precipitation across the central grassland region (Sala et al. 1988), and through time with interannual variability at individual sites (Lauenroth and Sala 1992; Briggs and Knapp 1995). This provides good reason to expect that grasslands will be responsive to predicted future changes in soil water. Indeed, recent predictions of changes in precipitation patterns and temperature have inspired field experiments to examine the effects of altered precipitation on grassland community structure and function with striking results (Grime et al. 2000; Fay et al. 2003; Zavaleta et al. 2003; Yahdjian and Sala 2006; Heisler-White et al. 2009; Jentsch et al. 2011).

Although predicted changes in soil water will likely have an important impact on ANPP, there is a paucity of studies examining the effect of altered soil water on BNPP. Furthermore, we lack a regional understanding of soil water availability and its impacts on BNPP in the central grassland region (McCulley et al. 2005). Yet BNPP is an important portion of total production: it contributes 50 % or more to the total NPP of grassland ecosystems (Sims et al. 1978; Milchunas and Lauenroth 2001), and represents a large terrestrial carbon sink (Scurlock and Hall 1998). We need to understand how NPP, not just the aboveground component, will respond to changes in

soil water in order to improve models and predictions of future carbon storage and turnover in grassland ecosystems.

Several studies have demonstrated that grasslands are sensitive to variation in precipitation, a surrogate for soil water. In a study spanning a variety of ecosystem types in North America, Knapp and Smith (2001) reported that aboveground production in grassland and old field ecosystems was most sensitive to precipitation variability. In an earlier observational study, Weaver and Albertson (1936) reported large and rapid changes in the species composition and total plant cover at sites in the eastern and central portions of the central grassland region in response to the drought of the 1930s, noting the largest vegetation changes in areas dominated by tallgrass species. More recently, Paruelo et al. (1999) found that precipitation use efficiency across the region was maximized at intermediate precipitation values (462 or 491 mm, depending on the data used), not the minimum or maximum represented by the shortgrass steppe or tallgrass prairie. This contrast in aboveground ecosystem response is likely due to differences in plant species traits across the region. In the driest portion of the central grassland region, the dominant species have low relative growth rates and are unable to respond quickly to interannual variation in precipitation. In the wettest portion of the region, the dominant species have higher relative growth rates and can respond more quickly to interannual variation in precipitation, but an increase in biomass or leaf area index will cause limitation by other resources; namely light or nutrients (Knapp and Seastedt 1986; Baer et al. 2003). These studies provide observational evidence of differences in sensitivity within grassland types to variations in soil water, yet we lack experimentally based evidence to support these observations. Further, these studies focus solely on aboveground production responses, and lack descriptions of belowground production responses.

Here, I aim to understand how changes in soil water will influence grassland ecosystem function in the driest portions of the central grassland region. I conducted a 3-year water manipulation experiment at two study sites to examine the effects of altered growing season soil water dynamics on NPP. Specifically, I experimentally increased and decreased soil water to determine if there was a difference in the sensitivity of the response NPP (both the above and belowground components) to changes in soil water between sites. Further, I aimed to determine if above and belowground production respond similarly to manipulations of soil water within and across sites. Based on previous studies, I hypothesized that NPP at the shortgrass steppe site would be less sensitive to changes in soil water than NPP at the mixed grass prairie site (Paruelo et al. 1999; Huxman et al. 2004) . Additionally, I predicted that the belowground production response would mirror the aboveground production response.

MATERIALS AND METHODS

Study sites

I conducted this study at two grassland sites in the driest portion of the central grassland region, spanning a 550 km transect from eastern Colorado to central Kansas. The region is characterized by a continental climate, and the majority of precipitation falls during the summer growing season at each site. The two grasslands are similar in that each is dominated by native perennial C₄ grasses and soils are characterized as Argiustolls, yet there are some important differences between them as well. Mean annual precipitation increases from west to east across the central grassland region, and each site occurs at different locations along this gradient. Mean annual precipitation is 341 and 583 mm for the shortgrass steppe and mixed grass prairie, respectively. Mean annual temperature differs as well (8.2°C at the shortgrass steppe and 12.1°C

at the mixed grass prairie). Despite these differences, the grasslands are often lumped together in climate change modeling.

The semiarid shortgrass steppe site is located at the Central Plains Experimental Range (CPER), 60 km northeast of Fort Collins, Colorado (40° 49' N, 104° 46' W). The CPER is administered by the USDA Agriculture Research Service and is also a National Science Foundation Long Term Ecological Research site. The plant community is dominated by the short-stature C₄ grasses blue grama (*Bouteloua gracilis* Willd. ex Kunth Lag. ex Griffiths) and patches of bare ground are prevalent. The soils are Aridic Argiustolls. The second site is located in the subhumid mixed grass prairie, at the Fort Hays State University College Farm, in west-central Kansas, 3 km west of Hays (38° 52' N, 99° 23' W). The plant community includes a mixture of tall- mid- and short- stature grasses, predominantly C₄ species. The soils are relatively shallow Typic Argiustolls, with underlying limestone bedrock. Cattle grazing is excluded at both study sites. Species nomenclature follows USDA Plants Database (USDA 2011).

Experimental Protocol

Shortgrass steppe

In May, 2008, I selected 30 plot locations with similar abundances of the dominant species, *B. gracilis*, and associated subdominant species. I randomly assigned a treatment (drought or ambient) to each 1.0 m² plot. I imposed drought by creating 15 1.8 m long x 1.6 m wide rainfall shelters designed to decrease incoming ambient rainfall by 60% (Yahdjian and Sala 2002). The roofs had a 15° inclination with the short side of the shelters oriented west; the dominant direction of incoming rainstorms. The shorter side of the shelters were 0.6 m tall, while the taller sides were 1.1 m tall, thus the shelter was always at least ~0.5 m above maximum vegetation height. The roofs were made of 15 cm wide strips of corrugated polycarbonate which

transmit >90% PAR (Dynaglass brand). The corrugated strips channel rainfall into gutters that lead water away from the plots. Shelter extended an additional 0.2 m beyond the plot in each direction to help reduce the amount of rain flowing horizontally into the plots from outside, and shelter sides were open to maximize air movement and minimize potential temperature and relative humidity artifacts. To examine the effects of altered growing season precipitation, drought shelters were present on plots during the May – September growing season, and were taken down during the dormant period. I removed any dust or bird droppings from the shelters before reassembling them each May.

In May 2009, I selected 15 additional plots with similar species composition to the existing plots and began a water addition treatment. Throughout the growing season (May - September) I calculated the weekly long term average rainfall for the site, and added the difference between the observed rainfall and double the weekly long term average rainfall once weekly by hand using watering cans. During the 2009 growing season this amounted to an additional 92 mm of water added, and 179 mm in 2010, which is an average increase in precipitation of 71% over mean annual precipitation.

Mixed grass prairie

In late March, 2008, my collaborators selected two blocks of nine plots, each block separated by 0.5 km. They randomly assigned each plot to one of three precipitation treatments: drought, ambient, and water addition. Each plot is 2.0 m x 8.0 m; long sides oriented with the slope. The shortest shelter height was ~ 1.5 m above ground level. They constructed six 4.0 m x 10.0 m rainfall shelters that are designed to intercept 50% of incoming ambient rainfall. Similar to the shortgrass steppe site, a pitched roof of 15 cm wide strips of corrugated polycarbonate (Dynaglass brand) channeled rainfall into gutters and removed water from the plots. Each shelter

extended 1.0 m beyond the plots in each direction to help reduce the amount of rain flowing horizontally into the plots from outside, and like the shelters at the shortgrass steppe, shelter sides at this site were open. Drought shelters were permanent and left up year-round. While it is possible that the differences in experimental set up between sites (growing season rainfall shelters at the shortgrass steppe and year-round rainfall shelters at the mixed grass prairie) may have influenced my results, the sites both receive the majority of annual precipitation during the summer growing season, when shelters were up at both sites.

Water was applied with a pump system from a 5,680 liter holding tank connected to a network of drip lines. Once a week throughout the growing season (April - September) the long-term average weekly precipitation was applied to the plots, regardless of the actual rainfall received during the week, totaling an addition of 380 mm of water during the growing season each year, which is an average increase in precipitation of 61% over mean annual precipitation. This approach ensured a wetter than normal treatment, even if ambient precipitation was below average.

Soil Water

Decagon Devices EC-5 soil water probes were installed in March 2008 at the mixed grass prairie site at a depth of 5 cm in a subset of plots for each treatment (n=2 for control, n=5 for drought, n=6 for water addition; Decagon Devices Inc., Pullman, WA, USA). In June 2009, I installed ECH2O soil water probes at the shortgrass steppe site at a depth of 10 cm in a subset of plots for each treatment (n=5 for control, drought, and water addition treatments; Decagon Devices Inc., Pullman, WA, USA). All probes were installed perpendicular to the soil surface and remained in place for the duration of the experiment at each site. Soil water probes measured volumetric soil water content (θ_v) every 4 hours at each site.

I sampled soil in all plots and found that textural differences between treatments at each site were small (data not shown), so I used the mean absolute difference in soil θ_v to quantify how my treatments altered soil θ_v during the growing season at each site. I determined these values using daily soil θ_v in the control (n=5 at shortgrass steppe and n=2 at mixed grass prairie), drought (n=5 at shortgrass steppe and n=5 at mixed grass prairie), and water addition (n=5 at shortgrass steppe and n=6 at mixed grass prairie) treatments.

Aboveground Net Primary Production

I estimated ANPP nondestructively at both sites to minimize plot disturbance. I used methods that have been proven to be effective in semiarid and subhumid grasslands (Byrne et al. 2011; Frank and McNaughton 1990; Paruelo et al. 2000; Przeszlowska et al. 2009). I estimated ANPP nondestructively on the shortgrass steppe in 2008 using green cover estimates derived from a digital camera (Byrne et al. 2011). This method produced variable results ($r^2=0.23$, $p<0.05$), however, my 2008 estimates were well within the range of clipped ANPP estimates recorded in 2008 at nearby sites (SGS LTER, unpublished data). In 2009 and 2010, I estimated ANPP on the shortgrass steppe using both a point-frame and a radiometer technique (Byrne et al. 2011). The point-frame technique has been shown to better predict ANPP on the shortgrass steppe, yet I also used the radiometer technique since this was the method used to estimate ANPP from 2008-2010 at the mixed grass prairie site. For the radiometer technique at the mixed grass prairie, I took reflectance measurements at eight randomly selected locations within each treatment plot and averaged these measurements to calculate plot-level ANPP estimates, while at the shortgrass steppe I took one reflectance measurement within each treatment plot.

I performed each nondestructive method on every treatment plot (one location per plot on the shortgrass steppe; six locations per plot on the mixed grass prairie) at peak biomass (late July

in the mixed grass prairie; early August on the shortgrass steppe). I selected 15 separate calibration plots in which I performed the nondestructive techniques, then clipped green and recent dead material of grasses and forbs and current year's green production (excluding woody tissue) for dwarf-shrubs. I clipped biomass at the soil surface, separated by functional group, and placed in paper bags. I dried samples for at least 48 h at 55 °C then weighed them. We used total biomass data as an estimate of ANPP (Lauenroth et al. 1986; Lauenroth et al. 2006). Each year I fit a regression relating the nondestructive methods to our estimate of ANPP (see Byrne et al. 2011).

Belowground Net Primary Production

I obtained estimates of BNPP using a modified root ingrowth technique (Vogt et al. 1998; McCulley et al., 2005; Milchunas 2009). In early May of each year, I excavated 5 cm diameter cores to a depth of 15 cm at the shortgrass steppe and 12 cm at the mixed grass prairie (due to a thick limestone layer beginning at 12 cm). I note that this method is not perfect, as roots certainly extend beneath the top 12 or 15 cm of the soil profile, and I missed any changes in BNPP that possibly occurred at depths below our measurements. However, previous work in the shortgrass steppe has shown that over 35% of roots occur in the top 0-10 cm (compared to 10-40 cm) (Milchunas et al. 2005b), and Frank et al. (2010) reported an exponential decline in root biomass with increasing depth. Worldwide, grasses have an average of 44% of total standing root biomass in the top 10 cm (Jackson et al. 1996). While my method is an underestimate of total belowground production, it captures a large proportion of total root production. One core was excavated in each plot on the shortgrass steppe and five cores were excavated in each plot at the mixed grass prairie. I placed a mesh cylinder of the same dimensions with 1.0 mm square openings within the excavated core, as 1.0 mm mesh allows the largest diameter roots to pass

through (Milchunas et al. 2005a; LeCain et al. 2006). Excavated cores were refilled with twice sieved root free soil from the site. In October of each year, ingrowth cores were removed by driving an 8 cm diameter soil corer into the soil surrounding the ingrowth core. Roots and soil on the outside of the mesh cylinders were brushed away, and cores were placed in paper bags and air-dried to minimize decomposition before processing. Once root cores dried, I manually separated out the largest roots (>2 cm), and used a hydropneumatic elutriation system to separate fine roots from the soil. The hydropneumatic elutriator uses a combination of pressurized air and water to gently separate roots from soil, then allows water to wash over the roots and clean them. Once all root samples were cleaned and separated, I dried roots for 48 hours at 55° C and weighed samples. I then combusted each sample in a muffle furnace at 500° C for 5 hours to determine ash content. I calculated BNPP from the values obtained from the total root sample weight and report BNPP in $\text{g m}^{-2} \text{y}^{-1}$ on an ash free basis.

Data analysis

I performed a residual analysis on each year's estimated ANPP and BNPP for each plot in each treatment and removed any data points that fell more than three SD from the mean (no more than one point was removed each year). To assess if my treatments had a different effect on ANPP and BNPP at each site between years, I used a mixed model analysis of variance in the Statistical Analysis System (v 9.2, Cary, NC, USA). The fixed effects in the model were year, treatment, and the interaction between those two terms. I included year as a fixed effect to account for any differences between treatments not accounted for by treatment. I included plot (and block for the mixed grass prairie site) as a random effect. In cases where the treatment effect was significant, I tested for differences among treatments using a Tukey adjustment for multiple comparisons.

To assess if there was a linear relationship between estimated precipitation (mm) received in each treatment and each response variable (ANPP, BNPP, and NPP), I replaced the categorical variable “treatment” from my mixed model analysis of variance above with the continuous variable, estimated precipitation received in each treatment (henceforth “treatment precipitation”). At each site and for each response variable (ANPP, BNPP, and NPP) I created models using the fixed effects that were significant for each site and response variable. The year* treatment precipitation interaction term was only significant for BNPP and NPP at the shortgrass steppe, so the interaction term was only included in the final model for those variables. Values presented are means \pm 1 SE and the level of significance for all statistical tests are $P < 0.05$, unless otherwise noted.

RESULTS

Temperature and Precipitation

The 50-year (1959 – 2009) mean annual temperature at the shortgrass steppe is 8.2° C, and annual temperature ranged from 7.5 - 8.3° C during the 3-year experiment. The 50-year mean annual temperature at the mixed grass prairie is 12.1° C, and annual temperature ranged from 11.7 – 12.9 ° C during the 3-year experiment. Annual precipitation, growing season precipitation, and monthly precipitation were much more variable than temperature throughout the experiment at both sites. Annual precipitation ranged from 330 – 436 mm at the shortgrass steppe, while the long term mean precipitation is 341 mm. Long term mean growing season precipitation (May – September) is 251 mm and ranged from 176 – 282 mm during the experiment (Fig. 3.1a). At the mixed grass prairie site, the long term mean annual precipitation is 582 mm. During the experiment, annual precipitation ranged from 552 – 727 mm. Long term

mean growing season (April – September) precipitation is 431 mm, and ranged from 441 – 495 mm during the experiment (Fig. 3.1b).

Soil Water (θ_v)

Shortgrass steppe

The drought and water addition treatments strongly influenced growing season soil water content. Treatment differences were smallest at the beginning of the growing season, but increased in July and August as soils dried in the drought and control treatments while soil water was replenished by weekly water addition in the water addition treatment (Fig. 3.2). During the 2009 growing season (soil water probes were not installed until 16 June 2009) in the upper 10 cm of the soil profile, the drought treatment reduced mean soil water content by 24% while the water addition treatment increased mean soil water content by 15%. Over the 2010 growing season (1 May – 30 Sept.), the drought treatment reduced mean soil water content by 17% while the water addition treatment increased mean soil water content by 13.5%.

Mixed grass prairie

Like the shortgrass steppe site, the imposed water manipulation treatments influenced growing season soil water content, and the largest treatment differences occurred during the months of June – August, while the smallest treatment differences occurred towards the beginning and end of the growing season, when temperatures were relatively cooler (Fig. 3.3). During the 2008 growing season (1 April – 30 Sept), the drought treatment reduced mean soil water content by 37% and the water addition treatment increased mean soil water content by 49%. Over the 2009 growing season, the drought treatment reduced mean soil water content by 18% and the water addition treatment increased mean soil water content by 82%. Over the 2010

growing season, the drought treatment reduced mean soil water content by 13% and the water addition treatment increased mean soil water content by 88%.

Shortgrass steppe

ANPP

Year, but not treatment, was a factor for ANPP at the shortgrass steppe site (Appendix Table 3.1). Within each treatment, ANPP was higher in 2009 and 2010 than in 2008, but ANPP was similar between 2009 and 2010, except for the irrigation treatment, which had lower ANPP in 2010 than in 2009 (Fig. 3.4a). However, within years, ANPP was similar among treatments. Only in 2010 was there a difference between treatments, and here the drought treatment had higher ANPP than both the control and water addition treatments. There was not a significant linear relationship between treatment precipitation and ANPP (Table 3.1).

BNPP

BNPP at the shortgrass steppe was affected by treatment, year, and the year*treatment interaction (Appendix Table 3.1). In the control and drought treatments, BNPP was higher in 2009 than in 2008 or 2010, but there was no difference in BNPP for the water addition treatment between years. There was no consistent trend in BNPP differences between treatments within years (Fig 3.4a). In the first treatment year (2008), the drought and control treatments had very similar values for BNPP. In 2009 both the drought and control treatments had higher BNPP than the water addition treatment. In contrast, in 2010 the drought treatment had lower BNPP than the water addition treatment, and the drought treatment had slightly less BNPP than the control treatment ($p=0.106$). There was not a significant linear relationship between treatment precipitation and BNPP (Table 3.1).

NPP

Total NPP at the shortgrass steppe was affected by treatment, year, and the year*treatment interaction (Appendix Table 3.1). Within each treatment, there was a difference in NPP between years for the drought and control treatments for all 3 years, but no difference in NPP for the water addition treatment. NPP for the drought and control treatments was remarkably similar throughout the experiment (Fig 3.4a). The water addition treatment had lower NPP than both the drought and control treatments in 2009, but in 2010 there were no differences in NPP between treatments. Although there was a linear relationship between treatment precipitation and NPP, the slope was very low (Table 3.1).

Mixed grass prairie

ANPP

Treatment and year were factors for ANPP at the mixed grass prairie site (Appendix Table 3.1). All three treatments had higher ANPP in 2009 and 2010 than in 2008, but only in the water addition treatment was there a difference in ANPP between 2009 and 2010 (Fig. 3.4b). Throughout the experiment, there was a trend towards reduced ANPP in the drought treatment and increased ANPP in the water addition treatment, with the control treatment falling in the middle. The difference was significant between the drought and water addition treatments for all 3 years, but the difference was never significant between the drought and control treatments. There was a positive linear relationship between treatment precipitation and ANPP (Table 3.1).

BNPP

Treatment and year were factors for BNPP at the mixed grass prairie site (Appendix Table 3.1). There was no difference in BNPP among years for any treatment, except for the control, which had higher BNPP in 2010 than in 2009 (Fig. 3.4b). Likewise, the only differences

between treatments occurred in the final treatment year (2010). Here, the control had higher BNPP than both the drought and water addition treatments (Fig 3.4b). There was not a significant linear relationship between treatment precipitation and BNPP (Table 3.1).

NPP

Similar to above and belowground production, treatment and year were factors for NPP at the mixed grass prairie site (Appendix Table 3.1). There was no difference in NPP among years for the drought treatment. The control treatment had higher NPP in 2009 and 2010 than in 2008, and the water addition treatment had higher NPP in 2009 than in 2008 (Fig 3.4b). The differences within years among treatments were similar to the results for ANPP. In 2008 and 2009 the water addition treatment had higher NPP than both the control and drought treatments. In 2010 both the control and water addition treatments had higher NPP than the drought treatment, but the NPP values for the control and water addition treatments were similar (Fig. 3.4b). There was a significant linear relationship between treatment precipitation and NPP (Table 3.1).

DISCUSSION

Climate models forecast warming and changes in precipitation in the central grassland region of North America during the twenty-first century (Christensen et al. 2007; CCSP 2008). Such predictions represent novel conditions for the region and the effects of these changes remain largely unknown. My results show that the two grasslands were differentially sensitive to changes in soil water, and that above and belowground responses to our experimental manipulation were contrasting.

1. Sensitivity of Net Primary Production to changes in soil water across sites -ANPP

Previous studies have established a tight link between precipitation and ANPP in grassland regions (Sala et al. 1988; Knapp and Smith, 2001). My ANPP results from the shortgrass steppe were not consistent with this previous research. I found that NPP was not sensitive to changes in treatment precipitation, and ANPP only showed a minimal ($P < 0.1$) treatment response in the drought treatment in the final treatment year (2010). While BNPP was responsive to changes in treatment precipitation, the direction of the response was variable among years. (Fig. 3.4a, Table 3.1). In contrast to the shortgrass steppe, my NPP results from the mixed grass prairie were congruent with previous research. I found a strong linear relationship between estimated treatment precipitation and both ANPP and NPP, but not BNPP (Table 3.1, Fig. 3.4b).

An examination of the ecohydrology of the region can partially explain the lack of observable response in NPP at the shortgrass steppe. Potential evapotranspiration (PET) exceeds precipitation by a factor of 3 during the growing season, and the most common state of the top 45 cm of the soil is dry (Lauenroth and Bradford 2006). Dry soil during the growing season is the result of pulse precipitation followed by rapid drying (Sala and Lauenroth 1982). The rapid cycling of soil water conditions between wet and dry is not conducive to plant production. Noy-Meir (1973) suggested that “an effective rain event” is one that activates biological processes (in particular, production and reproduction). Apparently, my water additions in the shortgrass steppe were not large enough to change soil water content long enough to stimulate production. This explanation is consistent with the results of Lauenroth et al. (1978) and Heisler-White et al. (2008). Both reported an increase in ANPP in response to increased soil water. Yet Lauenroth et al. (1978) added much more water than we did: an average of 228 mm of water per growing

season while I added roughly half as much, an average of 135 mm per growing season. While Heisler-White et al. (2008) did not increase growing season precipitation *per se*, they increased soil water by manipulating rainfall event size and frequency. These two studies demonstrate that if enough water is added during the growing season, the shortgrass steppe is responsive, yet the amount required to illicit a response in ANPP exceeds current predictions by general circulation models of climate change.

While my study focused on changes in soil water during the growing season, perhaps future efforts would be better focused on predicted changes in soil water during the dormant period when PET is low at the shortgrass steppe. In an analysis of long term production at the CPER, Milchunas et al. (1994) found that production was very sensitive to changes in cool season (Oct-April) precipitation, but only slightly sensitive to changes in growing season precipitation. Another recent study of net ecosystem production at the CPER concluded that additional precipitation during the July – Oct period would have much less of an impact on net ecosystem production than additional precipitation received during the April – June time period (Parton et al. 2011). Additionally, a rainfall manipulation experiment in the northern mixed grass prairie found that severe spring drought (May – June) reduced ANPP, while water addition in the summer (July – August) did not significantly increase ANPP compared to a control treatment (Heitschmidt and Vermeire 2006).

In contrast to the semiarid shortgrass steppe, subhumid grasslands experience relatively high soil water availability for a large portion of the growing season, and growing season rainfall events are more likely to maintain ecosystem processes such as photosynthesis in an unstressed state (Knapp et al. 1993). Indeed, studies have shown that soil water is typically not the most limiting resource in the tallgrass prairie (Briggs and Knapp 1995). While the mixed grass prairie

does not receive as much precipitation as the tallgrass prairie, we can estimate the atmospheric demand for water (MAPET) and the ratio of MAP/MAPET as an indication of the adequacy of the water supply to meet the atmospheric demand for each site using the formula from Lauenroth and Burke (1995);

$$MAPET = 94 + 5 \times MAT (r^2 = 0.71),$$

where MAPET and MAP are measured in cm and MAT is measured in °C. A value at or above 1 indicates that the water supply does adequately meet the atmospheric demand for water. The estimated value at the shortgrass steppe is 0.25, while the value at the mixed grass prairie is 50% higher; 0.38. Although precipitation at the mixed grass prairie does not completely satisfy the atmospheric demand for water, less additional water is needed to ameliorate water stress and result in an “effective rainfall event” (Noy-Meir 1973). My irrigation treatment clearly was able to stimulate production at this more mesic site.

The differing sensitivities of ANPP to changes in soil water at our two sites may also be partly explained by vegetational constraints. The shortgrass steppe is dominated by drought resistant species, especially the dominant grass species, *B. gracilis* (Hyder 1975; Mueller and Weaver 1942). *Bouteloua gracilis* is adapted to persist below ground in extended periods of low soil water, although the plant’s aboveground leaves may wither and die. The bunchgrass’s lack of rhizomes and stolons make it difficult for individual genets or tillers to respond quickly to favorable water conditions (Mueller 1941). It is likely that *B. gracilis* and other species had limited responses to the surplus or decrease of soil water in the treatments during our 3-year experiment. A longer study may be needed to see consistent ecosystem responses. Indeed, another study on the shortgrass steppe found that there were no significant changes in total cover in a 50% drought treatment for the first 4 years of a drought manipulation (Evans et al. 2011),

and other studies in semiarid grasslands have found little reduction in ANPP due to drought (Heitschmidt et al. 1999; Cipriotti et al. 2008).

In contrast, the vegetation at the mixed grass prairie is dominated by grass species with a range of traits. These species can adjust total cover or leaf area index faster than the drought tolerant shortgrasses and were therefore able to respond faster to changes in soil water. Previous research by Weaver (1954) during and after the great drought of the 1930s confirms these findings: he recorded much greater changes in the plant communities of the tall and mixed grass prairies as compared to the shortgrass steppe.

2. Sensitivity of Net Primary Production to changes in soil water across sites -BNPP

My trends in ANPP were consistent with previous soil water manipulation research (Lauenroth et al. 1978; Heisler-White et al. 2008; Heisler-White et al. 2009) and predictions regarding the sensitivity of the central grassland region to variability in precipitation (Paruelo et al. 1999; Knapp and Smith 2001), but trends in BNPP were not. Although the between-year patterns were variable for the shortgrass steppe, BNPP responded significantly to soil water manipulation in the second and third treatment years (Fig. 3.4a). In contrast, BNPP at the mixed grass prairie was insensitive to changes in soil water except for the third treatment year, although there was a trend towards reduced BNPP in the drought treatment and increased BNPP in the water addition treatment (Fig. 3.4b).

A few other studies have examined the effect of soil water manipulation on BNPP in grassland ecosystems. In a European grassland experiment, Fiala et al. (2009) found that BNPP was reduced with drought and increased with water addition. Two rainfall experiments in Inner Mongolia also reported an increase in BNPP due to water addition, but the studies had no corresponding drought manipulation (Bai et al. 2010; Gao et al. 2011). In a study spanning the

central grassland region, McCulley et al. (2005) found that BNPP was virtually identical at the shortgrass steppe in 2 different rainfall years, while BNPP at the mixed grass prairie was greater in the year with higher growing season rainfall. While I couldn't determine a pattern in BNPP response to soil water manipulation at the shortgrass steppe, it is clear that BNPP did exhibit sensitivity to changes in soil water. This result corresponds with previous soil water manipulation studies, while my BNPP results at the mixed grass prairie were in contrast to experiments reporting rapid and significant belowground responses to altered precipitation (Fiala et al. 2009; Bai et al. 2010; Gao et al. 2011). This discrepancy points to the need for additional long term manipulations to gain a better understanding of both above and belowground plant production responses to predicted changes in climate and soil water.

3. Are ANPP and BNPP responses similar within and across sites?

To my knowledge, this is the first multiple-year study that examines the response of both ANPP and BNPP in grasslands to both an increase and decrease in soil water across multiple sites. At the shortgrass steppe, I generally found that BNPP, but not ANPP, was sensitive to changes in soil water (Fig. 3.4a). The opposite was true at the more mesic mixed grass prairie, where ANPP and total NPP were sensitive to changes in soil water, while BNPP generally was not (Table 3.1, Fig. 3.4b). The results of my study indicate that we cannot assume that belowground production will mirror aboveground production in response to predicted climate changes, and highlights the importance of including measurements of belowground net primary production and total net primary production in future climate change experiments and models. Considering the importance of BNPP in contributing to total plant carbon inputs in grassland ecosystems, ignoring grassland BNPP may lead to erroneous predictions if our assumptions about belowground responses to changes in precipitation are incorrect. Additional experimental

studies across multiple sites are required to broaden our understanding of the controls of BNPP in grassland ecosystems.

4. Implications

My results have several important implications for future climate change research and for predicting the magnitude of temperate grassland responses to these expected climate changes. First, it is clear that we must be careful when we employ previous assumptions about net primary production in our efforts to predict responses to future predicted changes in soil water. I found that two similar ecosystems within the grassland biome showed different above and belowground production responses to soil water manipulations. Second, my results indicate that there may be differences in the periods of ecosystem sensitivity among ecosystems within the same biome. The shortgrass steppe was relatively insensitive, while the mixed grass prairie was clearly sensitive to changes in growing season precipitation. Given the agricultural importance of grasslands within this region and worldwide, the complexity of both within site and across biome NPP responses to predicted climate changes warrant future experiments to improve our understanding of ecosystem dynamics within the grassland biome.

TABLES

Table 3.1. Slope of relationship between treatment precipitation and aboveground (ANPP), belowground (BNPP), and total net primary production (NPP) at the shortgrass steppe and mixed grass prairie in mixed models analysis of variance.

Site response variable	Slope ($\text{g m}^{-2} \text{mm}^{-1}$)	F value	P>F
Shortgrass steppe ANPP	-0.05	2.2	0.15
Shortgrass steppe BNPP	0.11	3.8	0.06
Shortgrass steppe NPP	0.03	4.5	0.04
Mixed grass prairie ANPP	0.31	25.7	<0.0001
Mixed grass prairie BNPP	0.04	1.8	0.19
Mixed grass prairie NPP	0.28	12.0	0.001

FIGURES

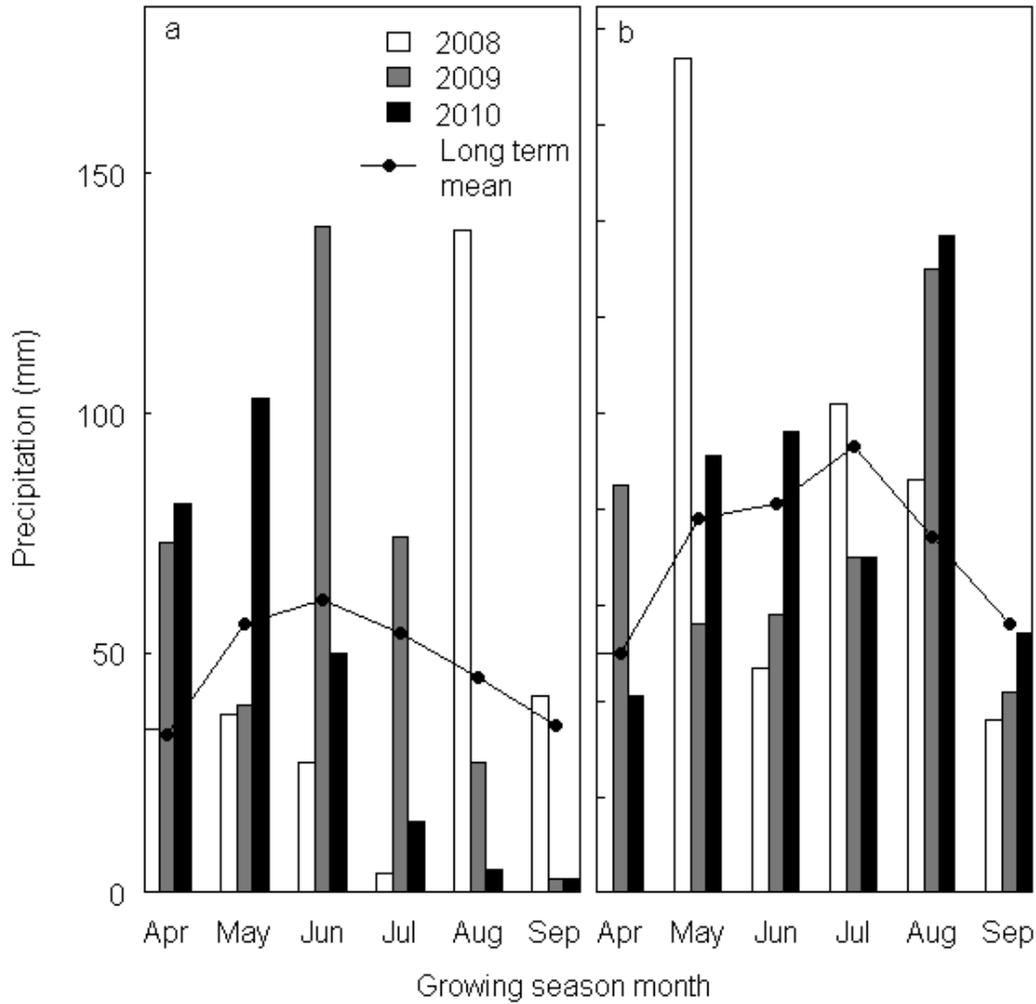


Figure 3.1. (a) April and growing season (May – September) precipitation received at the shortgrass steppe, and (b) growing season (April – September) precipitation received at the mixed grass prairie, during the experiment years (2008 – 2010) and long term monthly growing season precipitation.

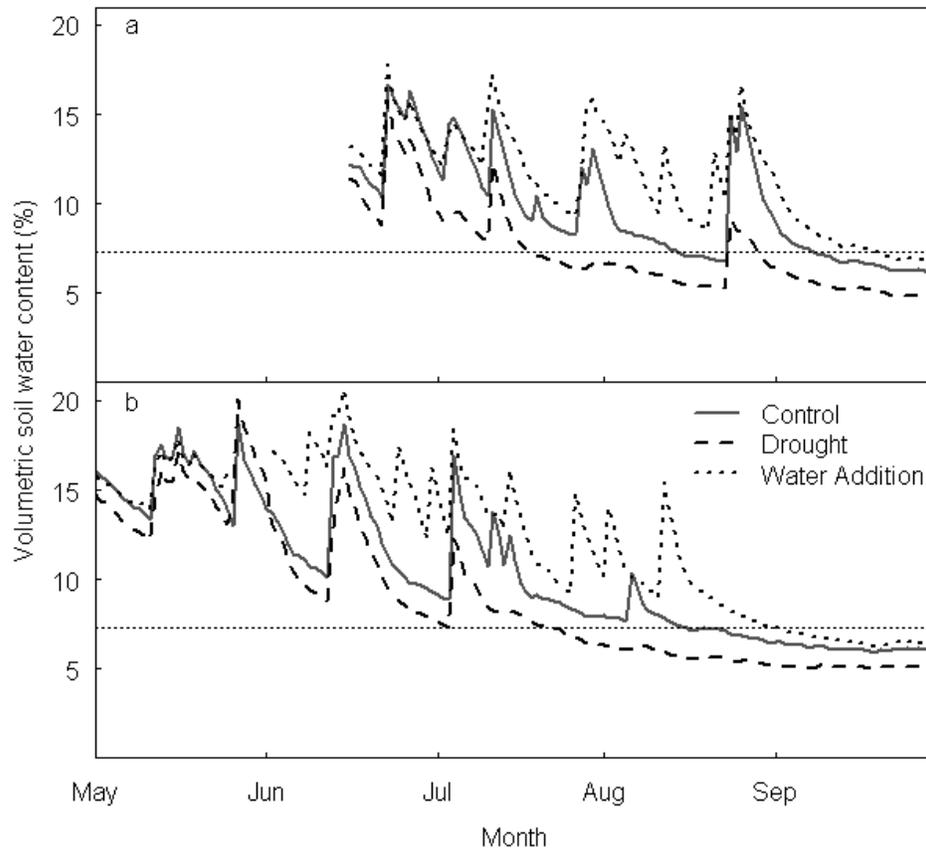


Figure 3.2. Daily volumetric soil water content (θ_v) in **(a)** 2009 and **(b)** 2010 at the shortgrass steppe. Lines are means for each treatment ($n=5$) integrated over 0-10 cm. Error bars were removed for clarity. Dashed line represents wilting point; -1.5 MPa.

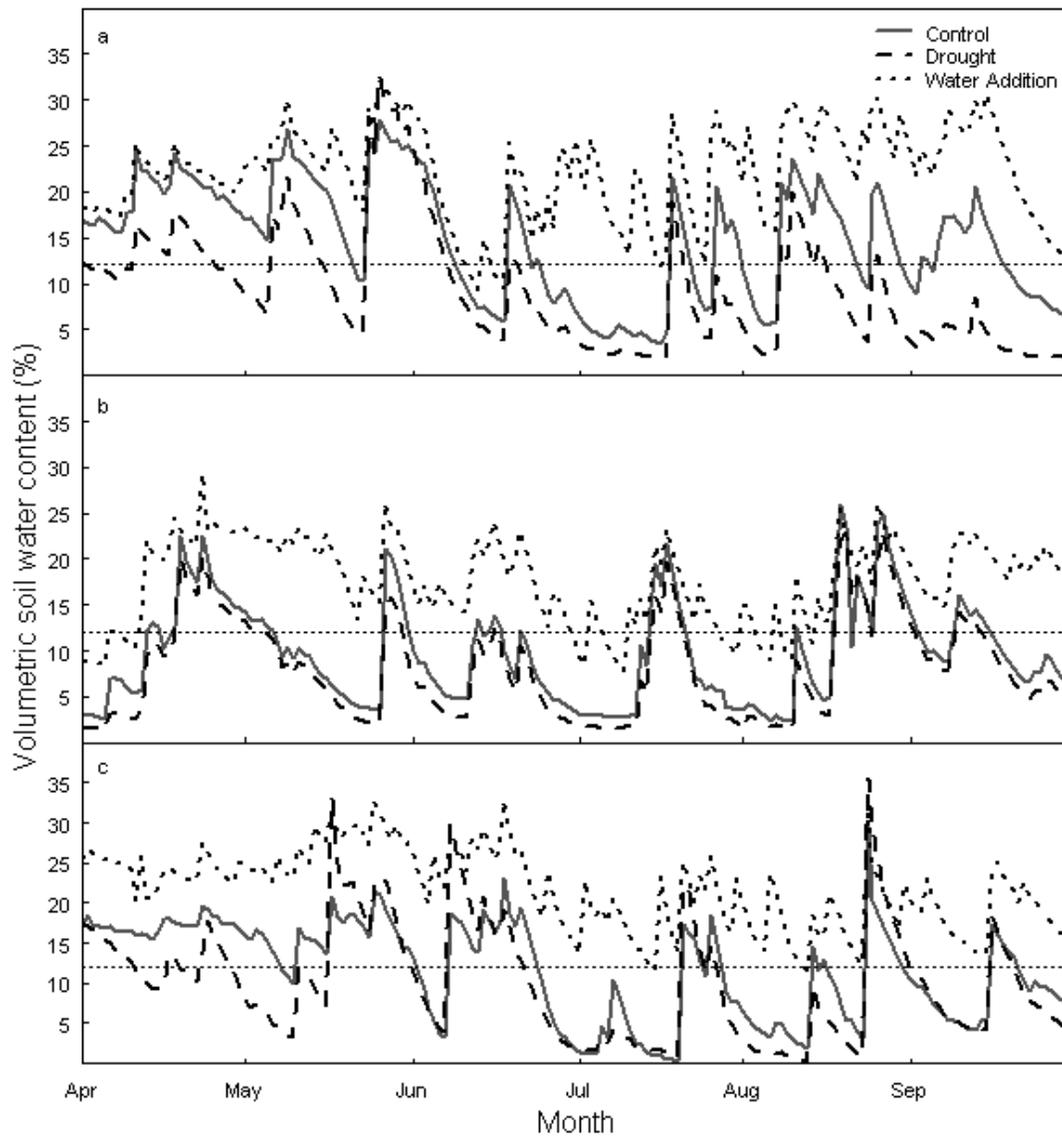


Figure 3.3. Daily soil water content (θ_v) in (a) 2008, (b) 2009, and (c) 2010 at the mixed grass prairie. Lines are means for each treatment (n=5 for drought, n=6 for water addition, and n=2 for control) integrated over 0-5 cm. Error bars were removed for clarity. Dashed line represents wilting point; -1.5 MPa.

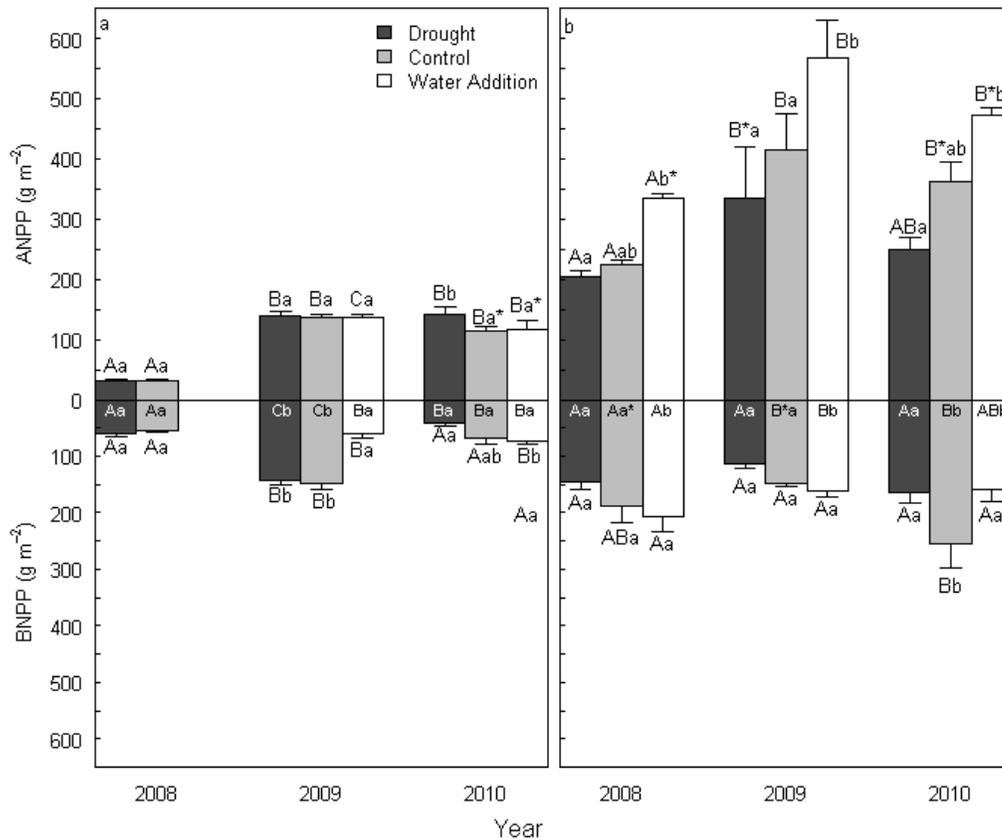


Figure 3.4. (a) Shortgrass steppe NPP, and (b) mixed grass prairie NPP, in drought, control, and water addition treatments. Uppercase letters represent differences within a given treatment between years, and lowercase letters represent differences between treatments within a given year. Differences significant at $P < 0.05$, but * indicates significance at $P < 0.10$. Bars represent standard error. Differences in ANPP are shown above the NPP bars, differences in BNPP are shown below the NPP bars, and differences in NPP are shown within the NPP bars.

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APPENDIX

Table A.3.1. The effect of treatment and year on Aboveground (ANPP), Belowground (BNPP) and total Net Primary Production (NPP) at the shortgrass steppe (SGS) and mixed grass prairie (MGP). * represents P<0.10, ** represents P<0.05, and *** represents P<0.001.

Effects	Df	SGS ANPP		SGS BNPP		SGS NPP		MGP ANPP		MGP BNPP		MGP NPP	
		F		F		F		F		F		F	
Treatment (T)	2	1.4	12.2	8.5	14.1	4.3	16.4	16.4	*	14.1	***	16.4	***
Year (Y)	2	134.	52.7	147.	14.4	4.2	7.2	7.2	*	14.4	***	7.2	***
		2		9									
TxY	3 (SGS) or 4 (MGP)	1.4	19.4	8.3	0.5	1.9	0.8	0.8	NS	0.5	NS	0.8	NS

Chapter Four: Plant community response to climate change is mediated by biotic interactions among species in semiarid and subhumid grasslands

SUMMARY

Changes in climate, including an increase in temperature and alterations to precipitation patterns, are occurring in grasslands worldwide, modifying soil water dynamics. As grasslands are primarily water limited, these predicted changes in climate will likely have dramatic impacts on ecosystem function and community structure, yet the magnitude of change and the types of species favored may differ among ecosystems. I measured changes in species composition, density, diversity, evenness, and cover by plant functional groups across four years (2008-2011) to understand how changes in soil water content will affect species composition and community structure at two sites within the central grassland region of North America. My water manipulation treatments resulted in different compositional changes at each site, which were largely driven by the response of the dominant grass species. The differing sensitivities of the dominant species and functional groups to similar induced changes in soil water at two sites demonstrates that both abiotic (soil water availability) and biotic (interspecific interactions) factors play important roles in regulating plant community structure and composition responses to climate change in grasslands.

INTRODUCTION

Abiotic factors including temperature and water availability play a strong role in controlling the functioning of terrestrial ecosystems by affecting plant growth, nutrient cycling and net primary production (Rosenzweig 1968, Webb et al. 1983). Yet recent predictions of an increase in mean global temperature and changes in precipitation timing and quantity (Christensen et al. 2007) have the potential to alter terrestrial communities in novel ways by

changing both the strength of abiotic controls on ecosystem processes as well as changing biotic interactions such as competition in plant communities (Ives 1995, Suttle et al. 2007, Tylianakis et al. 2008). Specifically, climate change will directly affect the dominant species by changing the quantity and timing of resources, while the response of subdominant species will depend on both the direct effects of climate change and the indirect effects of altered competitive interactions with the dominant species.

Water is a key control on ecosystem processes in grasslands (Noy-Meir 1973), giving us reason to believe that they will be particularly sensitive to predicted changes in climate (Knapp and Smith 2001, Huxman et al. 2004). Additionally, grasslands represent the potential natural vegetation cover of over 40% of the Earth's terrestrial surface; including many productive agricultural and rangeland areas worldwide (White et al. 2000). The potential sensitivity of grasslands to climate change, combined with the global ecological and agricultural importance of the biome, make it crucial that we are able to predict future implications of climate change.

The central grassland region of North America is an ideal ecosystem for studying the effects of global change on grassland communities. Both temperature and precipitation vary along the north-south and east-west gradients of the region, and this range of climates within the region allows for comparisons with grasslands worldwide. Climate models predict that the central grassland region will warm substantially (3 – 4.4 °C) during the twenty-first century (Christensen et al. 2007; CCSP 2008). Associated predictions of precipitation changes are less certain and range from small increases to small decreases. These changes in precipitation could either exacerbate or ameliorate water limitation in grasslands. However, previous research suggests that any changes in precipitation will likely have profound effects on ecosystem dynamics, whether climate change increases or decreases soil water (Weltzin et al. 2003).

While many studies have found a consistent response of grassland production to experimentally manipulated precipitation (Fay et al. 2003, Yahdjian and Sala 2006, Sherry et al. 2008), plant community composition and diversity respond inconsistently in such experiments. In an observational study, plant species richness was positively related to precipitation across the central grassland region of North America (Adler and Levine 2007), but the relationship was much weaker through time at an individual site. Some precipitation manipulation experiments have found a positive relationship between increased precipitation and species richness and diversity (Sternberg et al. 1999, Zavaleta et al. 2003, Stevens et al. 2006, Yang et al. 2011a), while other studies found a negative effect of increased precipitation on species richness (Suttle et al. 2007, Engel et al. 2009). One study found that drought decreased species diversity, but water addition had no effect on diversity (Grime et al. 2008), and still another study found that drought had no effect on species richness or diversity (Knapp et al. 2002). Most of these studies occurred at a single site and are therefore not ideally suited to test if the community response is similar across a biome. As species composition and diversity are known to affect ecosystem structure and function (Wardle et al. 2000, Hooper et al. 2005, Isbell et al. 2011), it is imperative that we improve our understanding of how plant community composition will respond to predicted changes in climate both within an individual ecosystem and across biomes.

Here, I report the influence of soil water on plant community composition and structure at two grassland sites across the driest portion of the central grassland region of North America. To my knowledge, this is the first longer term, multi-site, water manipulation experiment in native grasslands that examines the effects of altered soil water dynamics on species composition and diversity. My four year study explored the response of individual species, functional groups, and community diversity to both increased and decreased soil water at two study sites spanning

the driest portion of the central grassland region. Specifically, I was interested in the following questions: (1) How do changes in soil water affect plant community structure and composition in semiarid and subhumid grasslands; (2) Do the dominant species and functional groups at the two sites display similar responses to changes in soil water; and; (3) Does water addition or drought cause a larger change in important plant community characteristics at each site?

METHODS

Study sites

I conducted this study at two grassland sites in the driest portion of the central grassland region, spanning a 550 km transect from eastern Colorado to central Kansas. The region is characterized by a continental climate, and the majority of precipitation falls during the summer growing season at each site. The two grasslands are similar in that each is dominated by native perennial C₄ grasses and soils are characterized as Argiustolls, yet there are some important differences between them as well. Mean annual precipitation increases from west to east across the central grassland region, and each site occurs at different locations along this gradient. Mean annual precipitation is 341 and 583 mm for the shortgrass steppe and mixed grass prairie, respectively. Mean annual temperature differs as well (8.2 °C at the shortgrass steppe and 12.1 °C at the mixed grass prairie). Despite these differences, the grasslands are often lumped together in climate change modeling.

The semiarid shortgrass steppe site is located at the Central Plains Experimental Range (CPER), 60 km northeast of Fort Collins, Colorado (40° 49' N, 104° 46' W). The CPER is administered by the USDA Agriculture Research Service and is also a National Science Foundation Long Term Ecological Research site. The plant community is dominated by the short-stature C₄ grass blue grama (*Bouteloua gracilis* Willd. ex Kunth Lag. ex Griffiths), which

typically accounts for 80-90% of plant cover in this ecosystem (Milchunas et al. 1989). Common subdominant species include the perennial forb scarlet globemallow (*Sphaeralcea coccinea* (Nutt.) Rydb.), and the dwarf-shrubs prairie sagewort (*Artemisia frigida* Willd.), spreading buckwheat (*Eriogonum effusum* Nutt.), and broom snakeweed (*Gutierrezia sarothrae* (Pursh) Britton & Rusby). The soils are Aridic Argiustolls and patches of bare ground are prevalent.

The second site is located in the subhumid mixed grass prairie, at the Fort Hays State University College Farm, in west-central Kansas, 3 km west of Hays (38° 52' N, 99° 23' W). The plant community includes a mixture of tall- mid- and short- stature C₄ grasses, but the clear dominant species at the study site is the tall-stature grass little bluestem (*Schizachyrium scoparium* (Michx.) Nash.). Big bluestem (*Andropogon gerardii* Vitman), also a tall-stature grass, is a common subdominant species, while sideoats grama (*Bouteloua curtipendula* (Michx.) Torr.) and hairy grama (*B. hirsuta* Lag.) play a less important role. Forbs are quite diverse at the site, and the dwarf-shrub broom snakeweed is also prevalent. The soils are relatively shallow Typic Argiustolls, with underlying limestone bedrock. Cattle grazing is excluded at both study sites. Species nomenclature follows USDA Plants Database (USDA 2012).

Experimental design

Shortgrass steppe

In May, 2008, I selected 30 plot locations with similar abundances of the dominant species, *B. gracilis*, and associated subdominant species. I randomly assigned a treatment (drought or ambient) to each 1.0 m² plot. I imposed drought by creating 15 1.8 m long x 1.6 m wide rainfall shelters designed to decrease incoming ambient rainfall by 60% (Yahdjian and Sala 2002). The roofs had a 15° inclination with the short side of the shelters oriented west; the dominant direction of incoming rainstorms. The shorter side of the shelters were 0.6 m tall, while

the taller sides were 1.1 m tall, thus the shelter was always at least ~0.5 m above maximum vegetation height. The roofs were made of 15 cm wide strips of corrugated polycarbonate which transmit >90% PAR (Dynaglass brand). The corrugated strips channel rainfall into gutters that lead water away from the plots. Shelter extended an additional 0.2 m beyond the plot in each direction to help reduce the amount of rain flowing horizontally into the plots from outside, and shelter sides were open to maximize air movement and minimize potential temperature and relative humidity artifacts. To examine the effects of altered growing season precipitation, drought shelters were present on plots during the May – September growing season, and were taken down during the dormant period. I removed any dust or bird droppings from the shelters before reassembling them each May.

In May 2009, I selected 15 additional plots with similar species composition to the existing plots and began a water addition treatment. Throughout the growing season (May - September) I calculated the weekly long term average rainfall for the site, and added the difference between the observed rainfall and double the weekly long term average rainfall once weekly by hand using watering cans. During the 2009 growing season this amounted to an additional 92 mm of water added, 179 mm in 2010, and 148 mm in 2011, which is an average increase in precipitation of 71% over mean annual precipitation.

Mixed grass prairie

In late March, 2008, my colleagues selected two blocks of nine plots, each block separated by 0.5 km. They randomly assigned each plot to one of three precipitation treatments: drought, ambient, and water addition. Each plot is 2.0 m x 8.0 m; long sides oriented with the slope. The shortest shelter height was ~ 1.5 m above ground level. They constructed six 4.0 m x 10.0 m rainfall shelters that are designed to intercept 50% of incoming ambient rainfall. Similar

to the shortgrass steppe site, a pitched roof of 15 cm wide strips of corrugated polycarbonate (Dynaglass brand) channeled rainfall into gutters and removed water from the plots. Each shelter extended 1.0 m beyond the plots in each direction to help reduce the amount of rain flowing horizontally into the plots from outside, and like the shelters at the shortgrass steppe, shelter sides at this site were open. Drought shelters were permanent and left up year-round. While it is possible that the differences in experimental set up between sites (growing season rainfall shelters at the shortgrass steppe and year-round rainfall shelters at the mixed grass prairie) may have influenced our results, the sites both receive the majority of annual precipitation during the summer growing season, when shelters were up at both sites.

Water was applied to plots with a pump system from a 5,680 liter holding tank connected to a network of drip lines. Once a week throughout the growing season (April - September) the long-term average weekly precipitation was added, regardless of the actual rainfall received during the week, totaling an addition of 380 mm of water during the growing season each year, which is an average increase in precipitation of 61% over mean annual precipitation. This approach ensured a wetter than normal treatment, even if ambient precipitation was below average.

Soil water

Decagon Devices EC-5 soil water probes were installed in March 2008 at the mixed grass prairie site at a depth of 5 cm in a subset of plots for each treatment (n=2 for control, n=5 for drought, n=6 for water addition for 2008-2010, and n=2 for each treatment in 2011; Decagon Devices Inc., Pullman, WA, USA). In June 2009, I installed ECH2O soil water probes at the shortgrass steppe site at a depth of 10 cm in a subset of plots for each treatment (n=5 for control, drought, and water addition treatments; Decagon Devices Inc., Pullman, WA, USA). All probes

were installed perpendicular to the soil surface and remained in place for the duration of the experiment at each site. Soil water probes measured volumetric soil water content (θ_v) every 4 hours at each site. I sampled soil in all plots and found no significant textural differences between treatments at each site (data not shown), so I used the mean absolute difference in soil θ_v to quantify how our treatments altered soil θ_v during the growing season at each site. I determined these values using daily soil θ_v in each treatment.

Data Collection

Shortgrass steppe

I measured aboveground plant species composition at peak biomass (first week in August) by visually estimating canopy cover of each species in four 0.25 m² subplots within each 1.0 m² plot. I recorded species density by surveying each plot completely twice each growing season; once in early May to capture the cool season species, and again in early August to capture the warm season species, and I report mean species density in each treatment at a 1.0 m² sampling area.

Mixed grass prairie

In 2008-2010, I measured aboveground plant species composition by visually estimating canopy cover in ten 0.1 m² subplots within each 16.0 m² plot. In 2011, I estimated canopy cover in five 0.1 m² subplots within each 16.0 m² plot. I surveyed each plot completely in early May and late July to capture cool and warm season species, but I calculated species density per plot as the sum of species present in five 0.1 m² subplots in each year so that I could compare species density across years.

I defined dominant species as those that make up the majority of cover in the plant communities, and subdominant species as those species that are common across treatments and

contribute to at least 2 % of total cover. I divided plants into different functional groups on the basis of growth form: graminoids, forbs, and dwarf-shrubs. I also grouped ruderal species together to assess if water manipulation affected invasion in the plant communities. I defined ruderals as species that quickly respond to disturbances (Grime 2001). This includes short-lived, fast-growing native and non-native species often considered undesirable by range managers (see Appendix for full list of species considered ruderal at each site). Finally, I grouped cool season (C_3) and warm season (C_4) species together to examine if our rainfall manipulation experiments differentially affected the two plant types. I used the USDA NRCS Plants Database as our naming authority, and for native and non-native status. In addition to dominant species and different functional groups, I described patterns of community structure using species richness (number of species per 1.0 m² or 0.5 m² for the shortgrass steppe and mixed grass prairie, respectively), Shannon-Weiner diversity index (H), and Pielou evenness index (E), using $H = -\sum P_i \ln P_i$, and $E = (-\sum P_i \ln P_i) / \ln S$, where P_i is the relative cover of species i and S is species richness.

Statistical analysis

For each site, I conducted a mixed model analysis of variance (ANOVA) with a repeated measure design to test the effects of year, treatment, and their interactions on vegetation variables. I compared AIC values (Akaike information criterion; Burnham and Anderson 2002) of models with several autoregressive error terms and chose the model with the lowest AIC value for each site. For the shortgrass steppe site, I conducted t tests for vegetation variables in the first treatment year, 2008, between the drought and control treatments, but conducted an analysis of variance for the remaining years (2009-2011) when all three treatments were present. The fixed effects in the model were treatment, year, and their interaction, while the random effects were

plot and the plot by treatment interaction. The model with the lowest AIC value included a heterogeneous autoregressive process in the error term.

For the mixed grass prairie, the fixed effects in the model were block, treatment, the block by treatment interaction, year, and the year by treatment interaction. I included plot and the plot by year interaction as random effects. The model with the lowest AIC value did not include an autoregressive process in the error term. When treatment effects were significant, I made specific comparisons between treatments using the LSMEANS statement. The level of significance for all statistical tests is $P < 0.05$.

RESULTS

Temperature and Precipitation

The 50-year (1959 – 2009) mean annual temperature at the shortgrass steppe is 8.2° C, and annual temperature ranged from 7.5 - 8.3° C during my 3-year experiment. The 50-year mean annual temperature at the mixed grass prairie is 12.1° C, and annual temperature ranged from 11.7 – 12.9 ° C during my 4-year experiment. Annual precipitation, growing season precipitation, and monthly precipitation were much more variable than temperature throughout my experiment at both sites (Fig. 4.1). Annual precipitation ranged from 330 – 436 mm at the shortgrass steppe, while long term mean annual precipitation is 341 mm. Long term mean growing season precipitation (May – September) is 251 mm and ranged from 176 – 282 mm during my experiment (Fig. 4.1a). At the mixed grass prairie site, the long term mean annual precipitation is 582 mm. During my experiment, annual precipitation ranged from 474 – 727 mm. Long term mean growing season (April – September) precipitation is 432 mm, and ranged from 306 – 495 mm during my experiment (Fig. 4.1b).

Soil Water (θ_v)

Shortgrass steppe

The drought and water addition treatments strongly influenced growing season soil water content. Treatment differences were smallest at the beginning of the growing season, but increased in July and August as soils dried in the drought and control treatments while soil water was replenished by weekly water addition in the water addition treatment (Table 4.1). Between 2009 -2011 when soil water was measured, the drought treatment decreased mean growing season soil water by 20% and the water addition treatment increased mean growing season soil water by 24%. During the 2009 growing season (soil water probes were not installed until 16 June 2009), the drought treatment reduced mean soil water content by 24% while the water addition treatment increased mean soil water content by 15%. Over the 2010 growing season (1 May – 30 Sept.), the drought treatment reduced mean soil water content by 17% while the water addition treatment increased mean soil water content by 22%. Over the 2011 growing season, the drought treatment reduced mean soil water content by 20% while the water addition treatment increased mean soil water content by 35%.

Mixed grass prairie

Similar to the shortgrass steppe site, the imposed water manipulation treatments influenced growing season soil water content, and the largest treatment differences occurred during the months of June – August, while the smallest treatment differences occurred towards the beginning and end of the growing season, when temperatures were relatively cooler (Table 4.2). Over the course of the experiment (2008 -2011), the drought treatment reduced mean growing season soil water by 23% and the water addition treatment increased mean growing season soil water by 80%. During the 2008 growing season (1 April – 30 Sept), the drought

treatment reduced mean soil water content by 37% and the water addition treatment increased mean soil water content by 49%. Over the 2009 growing season, the drought treatment reduced mean soil water content by 18% and the water addition treatment increased mean soil water content by 82%. Over the 2010 growing season, the drought treatment reduced mean soil water content by 13% and the water addition treatment increased mean soil water content by 88%. Over the 2011 growing season, the drought treatment reduced mean soil water content by 23% and the water addition treatment increased mean soil water content by 102%.

Shortgrass steppe

Species diversity, evenness, and density

Species density varied between years, with lowest values in 2008 (7 1.0 m⁻², 0.3 SE) and highest values in 2009 (12 1.0 m⁻², 0.5 SE), but was not significantly affected by treatment (Table 4.3, Fig. 4.2). In contrast, species diversity and evenness were significantly different among years, treatments, and the interaction was significant as well (Table 4.3, Fig 4.2). Evenness was 18 % lower in the drought treatment than the control treatment in 2008, and in 2011 evenness in the water addition treatment was 22% higher than the control treatment. In the remaining years, there were no significant differences in evenness among treatments. Diversity in the two treatments was significantly different from the control in 2011, but no other years. In 2011, diversity was 11% lower in the drought treatment than the control, and 21% higher in the water addition treatment than in the control.

Total canopy cover and cover by functional groups

Total cover and cover by graminoids and forbs fluctuated significantly across the 4 years (Table 4.4; Fig. 4.3). For each group, 2008 was the year with the lowest cover values (17% for total cover, 12% for graminoids, and 1 % for forbs). Highest cover values occurred in 2009 for

total cover and forb cover (59% and 14%, respectively), while highest cover occurred in 2010 for graminoids (35%). There were only significant treatment differences between the treatments and the control in 2011. Total percentage cover was 12% higher in the water addition treatment than in the control in 2011. Graminoid cover was 7% lower in the drought treatment than the control in 2011, and was 10% greater in the water addition than the control in the same year. Forb cover was slightly (4% greater), but significantly higher in the water addition treatment than the control in 2011 as well.

Cover of dominant species, subdominant species, and ruderal species

As was the case for cover by functional groups, there was significant interannual variation in the cover of the dominant species, *B. gracilis*, subdominant species *C. eleocharis*, and ruderal species across the 4 years (Table 4.3; Fig 4.4). In 2008 each group had the lowest percentage cover (7%, 3%, and 2%, for *B. gracilis*, *C. eleocharis*, and ruderal species).

Bouteloua gracilis had the highest percentage cover in 2010 (24%) and *C. eleocharis* had the highest percentage cover in 2011 (8%), while ruderal species had the highest percentage cover in 2009 (14%). Cover of *B. gracilis* and ruderal species were both significantly higher in the water addition treatment than the control in 2011 (12% and 6% increases for *B. gracilis* and ruderal species, respectively; Fig. 4.4). Year significantly interacted with treatment to influence *C. eleocharis* and ruderal species cover.

Mixed grass prairie

Species diversity, evenness, and richness

Species density and species diversity were significantly different between years (Table 4.5). The highest mean species density occurred in 2008 (16 0.5 m⁻², 0.8 SE) and the highest mean species diversity occurred in 2009 (2 0.5 m⁻², 0.1 SE), while the lowest occurred in 2011

for both ($11 \text{ } 0.5 \text{ m}^{-2}$, 1 SE; and $1 \text{ } 0.5 \text{ m}^{-2}$, 0.1 SE for density and diversity, respectively; Fig 4.2). Species diversity, evenness, and density were all affected by the rainfall treatments (Fig. 4.2); and the interaction was significant for species evenness and species density. Species diversity was higher (by 45%) in the drought treatment than in the control throughout the experiment (Fig 4.2), and was lower in the water addition treatment than the control in 2010 only (by 29%). Species evenness was higher in the drought treatment than the control in 2009 and 2011 (by 57%), although the trend of greater species evenness in the drought treatment existed throughout the experiment (Fig. 4.2). Species evenness in the water addition treatment was similar to that of the control except in 2009, when the evenness was almost twice as large in the water addition treatment (Fig. 4.2). In contrast to diversity and evenness, where the bulk of the differences occurred between the drought and control, the differences occurred between the water addition treatment and the control for species density. In 2010 and 2011, the water addition treatment had on average, 7 fewer species (0.5 m^{-2}) than the control. The drought treatment had a different species density than the control only in 2010, when the drought treatment had 3 more species (0.5 m^{-2}) than the control.

Total canopy cover and cover by functional groups

Total cover and cover by graminoids, forbs, and shrubs fluctuated significantly over the 4 years (Table 4.6). Lowest total cover and cover by graminoids occurred in 2008 (48% and 37% for total and graminoid cover, respectively), while lowest forb and shrub cover occurred in 2011 (5% and 0.3% for forbs and shrubs, respectively). Highest average total cover and cover by forbs occurred in 2010 (71 % and 9% for total and forb cover, respectively), while highest graminoid cover occurred in 2011 (61 %), and highest shrub cover occurred in 2008 (4%; Fig. 4.5).

From 2009 – 2011, the drought treatment decreased total percentage cover by an average absolute difference of 25% across the three years, while the water addition treatment increased total percentage cover by an average absolute difference of 18% across the three years (Fig. 4.5a). The pattern for graminoid cover was similar: the drought and water addition treatments altered percentage cover by graminoids from 2009 -2011; causing an average decrease in percentage cover of 28% across the three years in the drought treatment, and an average increase in percentage cover of 19% in the water addition treatment (Fig. 4.5b). The drought and water additions did not affect forb cover, and only affected shrub cover in 2008; where percentage cover in the drought treatment and water addition treatment was 3% and 2% higher than in the control, respectively (Table 4.6 and Fig. 4.5).

Cover of dominant species, subdominant species, and ruderal species

Cover by the dominant species, *S. scoparium* and subdominant species, *A. gerardii* varied significantly over the four years, while cover by ruderal species was not affected by year (Table 4.5, Fig. 4.6). Cover of *S. scoparium* and *A. gerardii* was lowest in 2008 (26% and 7% for *S. scoparium* and *A. gerardii*, respectively), while cover of *S. scoparium* was greatest in 2011 (41%) and cover of *A. gerardii* was greatest in 2010 (18%). The rainfall treatments also affected cover by the dominant and subdominant species. The drought treatment decreased the absolute percentage cover of *S. scoparium* by 19% over the four year experiment, and the difference was significant in 2009-2011 (23% decrease), while the water addition treatment increased percentage cover of *S. scoparium* by 5% over the experiment, although the difference was only significant in 2009 (13% increase). There was a significant year by treatment interaction only for *A. gerardii*.

DISCUSSION

Climate models forecast warming and changes in precipitation in the central grassland region of North America during the twenty-first century (Christensen et al. 2007; CCSP 2008). These changes in abiotic conditions will combine with biotic interactions among species to create novel conditions for the region. I found that two grasslands sites responded differently to changes in soil water, and that the community responses were largely determined by the response of the dominant species. However, interspecific interactions also played an important role in mediating plant community response to changes in abiotic conditions, which highlights the importance of conducting experiments in natural communities so that we can realistically predict community response to climate change.

Interannual variability in plant community structure and composition

Water availability is the key limiting factor for plant growth and ecosystem production in semiarid grasslands (Noy-Meir 1973), and much of the variability in measured vegetation variables among years can likely be ascribed to interannual fluctuations in the timing and quantity of precipitation. Indeed, growing season precipitation strongly varied between years at each site over the experiment (Fig 4.1). At the shortgrass steppe site, for example, the 2008 growing season received precipitation much below the long term average in May – July (Fig 4.1a), causing low cover of individual species and functional groups that year (Figs 4.3 - 4.4). In fact, the low vegetation cover in the first year of the experiment at the shortgrass steppe exceeded any treatment-induced difference over the course of our 4 year experiment. Likewise, precipitation in April and June 2009 was more than double the long term average (Fig 4.1a), leading to the highest vegetation cover over the experiment.

Other inherent dynamics of the plant communities may have contributed to the interannual variability in plant community response. Grazing is known to have little effect on diversity and community structure in the shortgrass steppe ecosystem (Milchunas et al. 1988, Milchunas et al. 1989), but enhances species richness and diversity in the tallgrass prairie (Milchunas et al. 1988, Collins et al. 1998). Light to moderate cattle grazing occurred during the spring and summer at the mixed grass prairie site since the 1930's until an electric fence was constructed to exclude cattle in 2007. While there is clearly a treatment effect for many of the vegetation variables, it appears that time since grazing also affects some response variables; perhaps even more so than interannual variability in growing season precipitation. For example, April – July precipitation was highest in 2008, more than 70 mm above the long term mean, yet total cover, cover by graminoids, and cover of the dominant species in the control was lowest this year, and tended to be highest in the final treatment year, although growing season precipitation was 189 mm lower than in 2008 (Fig 4.1b). The increase in cover over time is likely due to release and recovery from grazing pressure over the course of the experiment. Nonetheless, the effects of my imposed water manipulation treatments were strong enough to determine the plant community response to soil water availability through the response of the plant community to release from grazing or interannual variation in growing season precipitation. Thus, I will discuss treatment differences, rather than yearly differences, for the remainder of this manuscript, and I argue that long term research is essential to fully understand community responses to future climate change scenarios through the noise of variation in annual and growing season precipitation and successional processes.

Effects of manipulated soil water on species diversity, evenness, and density

My treatments had very different effects on species diversity, evenness, and density between sites. At the shortgrass steppe site, species density, diversity, and evenness varied by year, but the plant community structure was relatively insensitive to my soil water treatments (Table 4.3, Fig. 4.2). Only in the final year was evenness higher in the water addition treatment, and both the drought and water addition treatments altered species diversity in 2011. There were never differences in species density between treatments (Fig. 4.2a). While the lack of response at the shortgrass steppe was somewhat surprising, previous research in semiarid grasslands has obtained similar results. An 11 year drought experiment at the shortgrass steppe found that species density decreased during the first 4 years of drought treatment, yet the difference was only significant in the more extreme (75% rainfall reduction) treatment in the fourth year and beyond (Evans et al. 2011). Likewise, neither species richness, diversity, nor evenness were significantly altered after two years of imposed drought in the semiarid Patagonian steppe, except in the most extreme (80% rainfall reduction) treatment (Yahdjian and Sala 2006). Finally, in the mesic tallgrass prairie of North America, Knapp et al. (2002) found that a 30% reduction in rainfall did not significantly alter species diversity, even after 4 years of rainfall manipulation. The shortgrass steppe is dominated by slow growing, drought tolerant species, and it appears that a 50% reduction or 50% increase in growing season precipitation is not enough to greatly alter community structure and stability, at least in the timescale of my experiment. A longer term drought and water addition study would be useful to test the limits of resilience in this ecosystem.

In contrast, the mixed grass prairie site experienced strong treatment effects throughout the experiment. Notably, my water addition treatment drastically reduced species density by the

end of the experiment; from an average of 15 species 0.5m^{-2} in 2008, to 5 species 0.5m^{-2} in 2011 (Fig 4.2a). This decrease in species density can likely be attributed to the increased cover of *S. scoparium* and *A. gerardii*. The increase in cover by the dominant and subdominant grass species over the experiment corresponded with a decrease in forb species density (from 9 to 2 forb species 0.5m^{-2} from 2008 – 2011); although percentage cover by forbs was not affected (Table 4.6, Fig 4.5c). I hypothesize that the increase in grass cover created low light conditions unsuitable for many short stature forbs, as has been observed in the tallgrass prairie (Turner and Knapp 1996).

While species density decreased in the water addition treatment at the mixed grass prairie, species diversity and evenness tended to be more sensitive to drought than to water addition. Diversity was higher in the drought treatment than in the control for all 4 years of the experiment; and species evenness was higher in the drought treatment than in the control in 2009 and 2011 (Fig 4.2). These differences can also be attributed to changes in cover of the dominant grass species. *Schizachyrium scoparium* had much lower cover in the drought treatment than in the control; while cover by forbs and shrubs (the bulk of the species contributing to species richness in the ecosystem) were not affected. The decrease in graminoid cover, combined with no other changes in species density, would lead to higher diversity and evenness in the drought treatment.

A rapid community response has been observed in several other rainfall manipulation experiments, especially in ecosystems with many annual species. An old field experiment found that diversity, evenness, and richness were greater in the drought treatment than in the water addition treatment by the second treatment year (Engel et al. 2009). Although the opposite response was seen in my study, a naturally occurring year of extreme drought in another old field

caused a reduction in species richness of 37 % (Tilman and Haddi 1992). Two water addition studies also found results not congruent with our own. Increased precipitation stimulated species richness, but did not affect evenness or diversity in the semiarid steppe of Inner Mongolia (Yang et al. 2011b). Likewise, elevated precipitation increased diversity progressively over a 3 year study in an annual grassland (Zavaleta et al. 2003). The contingency in the response of both grasslands in my study, along with the varying responses of grassland community structure to water addition and drought across experiments other experiments, demonstrates that we must consider both abiotic (climatic) and biotic factors when predicting community response to climate change. While the dominance of slow growing, drought tolerant species at my drier site led to few changes in community structure, the subhumid mixed grass prairie experienced large changes in species density, diversity, and evenness, which are likely attributable to competitive interactions with the dominant species, *S. scoparium*.

Effects of manipulated soil water on total cover and cover by functional groups

My functional group classifications were useful in determining the response of different plant types to changes in soil water. At the shortgrass steppe site, total cover and cover by individual functional groups were fairly insensitive to the rainfall manipulation treatments. Total cover, cover by graminoids, and cover by forbs all increased with water addition, but only in the fourth treatment year (Fig. 4.3a-c). The only functional group that responded to drought was the graminoids; also only in the fourth treatment year (Fig 4.3b). These results were not entirely unexpected, as a long term (11 year) drought experiment at the shortgrass steppe found that total cover did not decrease until the fifth treatment year (Evans et al. 2011). Likewise, in a European grassland precipitation manipulation experiment that lasted almost a decade, the authors found

that vegetation cover in the drought plots did not diverge from the control for the first 4 years of the experiment (Morecroft et al. 2004).

In the few cases where there was a treatment response, the response tended to be an increase in cover due to water addition; in accordance with a previous water addition experiment at the shortgrass steppe. In a study that measured functional group biomass production, an ecosystem property that is closely related to vegetation cover, biomass production by warm season grasses increased by a factor of 3 over the 5 year water addition experiment (Lauenroth et al. 1978). The smaller response (a relative increase of 27%, 33%, and 65% for total cover, cover by graminoids, and cover by forbs) seen in my experiment as compared to Lauenroth et al. (1978) is likely due to the difference in the amount of water added: they added an average of 228 mm of water per growing season while I added roughly half as much, an average of 140 mm per growing season. Similarly, water addition stimulated total cover and cover by graminoids over a 5 year water addition experiment in a semiarid steppe in China (Yang et al. 2011b), and supplemental summer rainfall increased total cover in a long term European grassland experiment (Morecroft et al. 2004).

Unlike the shortgrass steppe, which had slow responses to soil water manipulation, the mixed grass prairie site responded rapidly to both water addition and drought. There were differences between both treatments and the control beginning in the second year of the experiment and continuing through 2011 for both total and graminoid cover (Fig. 4.5a-b). Both the drought and water addition treatments had greater dwarf-shrub cover in the first treatment year, yet this difference appears to be transitory as there was no difference between treatments in subsequent years.

The differing sensitivities of total cover and cover by graminoids to changes in soil water at my two sites may be partly explained by vegetational constraints (Paruelo et al. 1999). The shortgrass steppe is dominated by drought resistant species, especially the dominant grass species, *B. gracilis* (Mueller and Weaver 1942, Hyder 1975). The bunchgrass's lack of rhizomes and stolons make it difficult for individual genets or tillers to respond quickly to favorable water conditions (Mueller 1941). The slowness in response time is demonstrated by the lack of significant treatment differences in graminoid and total cover during the first 3 treatment years (Fig. 4.3a-b). In contrast, the vegetation at the mixed grass prairie is dominated by grass species with a range of traits. These species can adjust total cover or leaf area index faster than the drought tolerant shortgrasses and were therefore able to respond faster to changes in soil water. Previous research by Weaver (1954) during and after the great drought of the 1930s supports these findings: he recorded much greater changes in the plant communities of the tall and mixed grass prairies than in the shortgrass steppe.

Effect of manipulated soil water on cover by dominant and subdominant species

Changes in total and graminoid cover were largely driven by the response of the dominant grass species at each site. The shortgrass steppe ecosystem is unique among Great Plains grasslands in that it is dominated by a single species. *Bouteloua gracilis* consistently makes up 80% or more of total net primary production in the ecosystem (Milchunas et al. 1989), and previous research has shown that it plays an important role in maintaining community structure (Milchunas et al. 1990) and stability (Sasaki and Lauenroth 2011). I found that my drought manipulation did not perturb this drought-tolerant species. The sustained predominance of *B. gracilis* maintained species richness, evenness, and net primary production (Byrne et al., submitted) over the 4 year experiment. *Bouteloua gracilis* was affected by the water addition

treatment, however, and I observed a concomitant increase in ruderal species, species diversity, and species evenness along with the increase in the dominant species (Fig. 4.2b-c, Fig. 4.4). This provides further evidence of the role *B. gracilis* plays in controlling ecosystem structure and processes.

At the mixed grass prairie site, the dominant species *S. scoparium* and the subdominant species *A. gerardii* were both important drivers of changes in community dynamics. Percentage cover by *S. scoparium* was significantly lower in the drought treatment than in the control in all but the first treatment year, and although not significant, *A. gerardii* cover in the drought treatment tended to be lower than in the control in 2009 - 2011 (Fig. 4.6). When grazing was removed from our research site in the end of the growing season in 2007, it appears that *S. scoparium* exhibited a positive linear response to grazing removal in the control treatment by increasing in cover over time (Fig. 4.6).

Although not as dramatic, *A. gerardii* exhibited a positive grazing removal response as well. During the first 3 years of the experiment, there is a linear increase in percentage cover of *A. gerardii* in the control treatment. Yet in 2011, percentage cover drops. It is likely that soil water conditions contributed to this difference in response observed between *S. scoparium* and *A. gerardii* in 2011. *Andropogon gerardii* has greater moisture requirements than *S. scoparium* (Weaver 1954), and 2011 was a dry year at the site, particularly in April – July (Fig. 4.1b). During the drought of the 1930's, observational studies in the tallgrass prairie reported that *A. gerardii* suffered much larger decreases in abundance than the co-dominant species *S. scoparium* (Weaver and Albertson 1943). Furthermore, plant physiology measurements taken in 2009 in my experiment showed that *A. gerardii* was less drought tolerant than *S. scoparium*; experiencing higher limitations on photosynthesis and a less of an ability to lower its water potential (Maricle

and Adler 2011). The decrease in *A. gerardii* cover in 2011 in the control treatment was likely due to lack of sufficient soil water, while *S. scoparium*, a more drought tolerant species, did not experience a drop in cover.

Although several studies have investigated the response of tallgrass species to herbivory and fire (Pfeiffer and Hartnett 1995, Towne et al. 2005, Limb et al. 2011), to my knowledge, there are no studies that explicitly track the recovery of *S. scoparium* and *A. gerardii* to grazing removal. The grazing removal responses observed in my study were an interesting additional ecosystem response that I did not anticipate, and highlights the importance of conducting climate change experiments in natural ecosystems that do not exclude important higher trophic levels, as they may influence the plant community response to climate change manipulations. Interestingly, at the mixed grass prairie site, it appears that grazing pressure exerted a similar level of control on the dominant and subdominant species as did my imposed 50% drought; given the relatively stable cover of *S. scoparium* and *A. gerardii* in the drought treatment through time.

While there is a clear grazing removal response of *S. scoparium* in the control, the response of *S. scoparium* in the water addition treatment was less straightforward. Initially, there was a rapid increase in percentage cover of *S. scoparium* in the water addition treatment, as evidenced by the 15% increase in cover between 2008 and 2009 (Fig. 4.6). After this initial increase in percentage cover, however, the cover values level off and by 2011, *S. scoparium* cover in the water addition treatment is lower than in the control, although the difference is not significant (Fig. 4.6). The plateau in cover of *S. scoparium* to around 48% was accompanied by a concomitant increase in percentage cover of the subdominant species, *A. gerardii* to around 31% in the water addition treatment (Fig. 4.6). I hypothesize that this change in community structure is driven by competitive interactions between *A. gerardii* and *S. scoparium*. Unlike the mixed

grass prairie, where *S. scoparium* is the dominant species, the greater soil water availability of the tallgrass prairie allows *A. gerardii* to flourish, and *A. gerardii* makes up just under 40% of total cover (Silletti and Knapp 2001) in this more mesic grassland. Apparently my water addition treatment added enough additional water to make *A. gerardii* a better competitor with *S. scoparium*. These results indicate that in times of long term above average soil water availability, the structure of the mixed grass prairie may change significantly.

A number of studies have reported increased success of exotic and ruderal species in water addition treatments in grasslands (Milchunas and Lauenroth 1995, Davis and Pelsor 2001, Miller et al. 2006, Blumenthal et al. 2008). Yet cover by ruderal species at the mixed grass prairie site stayed very low in all treatments over my 4 year experiment; averaging under 3% cover across treatments and years (Fig. 4.6). This gives us reason to believe that, under current management and disturbance regimes, the mixed grass prairie site may resist invasion by exotic species, even in times of extended drought or above-average precipitation. Yet the mixed grass prairie is certainly not immune to species invasion, as previous studies have demonstrated (Larson 2003, Blumenthal et al. 2008). However, the lack of response by ruderal species in my 4 year experiment does indicate that the ecosystem may resist invasion for some period of time under fairly dry or wet conditions during the growing season.

Conclusions and Implications

My results have two important implications for future climate change research and for predicting the magnitude of temperate grassland responses to these expected climate changes. First, I found that our two sites, located within the same biome, had different responses to manipulated soil water content. The shortgrass steppe site was relatively insensitive to changes in growing season soil water, and responded more to water addition than to drought, but only in the

final treatment year. The mixed grass prairie, in contrast, had a rapid response to both water addition and drought, and there was not a clear pattern among vegetation variables as to whether the community responded more to increased or decreased water availability. The differences in community responses between my two sites highlight the importance of multi-site studies to refine our knowledge of the mechanisms and generalities of community response to climate change at the biome level. Second, my study suggests that both soil water availability and interspecific interactions play important roles in regulating plant community response to climate change. Although not explicitly tested here, it appears that at the mixed grass prairie site, both interspecific competition between plant species and between plants and herbivores interacted to affect plant community structure and response to soil water manipulation. If we are to accurately predict biodiversity and ecosystem response to global change, we must improve our understanding of both the abiotic and biotic interactions in natural ecosystems and apply these interactions in ecological forecasting models. Given the importance of grassland and savanna ecosystems worldwide, the complexity of both within site and across biome community responses to predicted climate changes warrants future experiments to improve our understanding of community and ecosystem dynamics within the grassland biome.

TABLES

Table 4.1. Mean monthly volumetric soil water content at the shortgrass steppe during the 2009 – 2011 growing seasons. Standard error of treatment means shown in parentheses.

	Month					
2009	4	5	6	7	8	9
Drought	-	-	11.7 (0.7)	8.1 (0.6)	6.4 (0.4)	5.4 (0.3)
Control	-	-	13.5 (1.4)	11.3 (1.2)	9.1 (1.0)	6.9 (0.8)
Water Addition	-	-	14.0 (0.9)	12.8 (1.2)	12.0 (1.0)	7.9 (0.7)
2010						
Drought	13.0 (0.9)	14.5 (1.0)	11.0 (0.8)	8.2 (0.6)	5.8 (0.4)	5.1 (0.4)
Control	14.3 (1.4)	15.7 (1.6)	12.7 (1.1)	10.4 (0.9)	7.6 (0.6)	6.2 (0.6)
Water Addition	14.2 (0.8)	16.3 (0.8)	15.8 (0.6)	12.7 (1.1)	9.9 (0.8)	6.6 (0.7)
2011						
Drought	11.3 (0.7)	12.5 (0.9)	10.1 (0.6)	8.6 (0.6)	5.8 (0.4)	8.8 (1.1)
Control	12.9 (1.1)	14.5 (1.2)	12.3 (0.8)	10.9 (0.5)	7.4 (0.2)	11.7 (0.7)
Water Addition	12.1 (1.0)	14.1 (0.9)	13.7 (1.1)	12.0 (1.1)	8.7 (0.7)	11.5 (1.0)

Table 4.2. Mean monthly volumetric soil water content at the mixed grass prairie during the 2008 – 2011 growing seasons. Standard error of treatment means shown in parentheses.

	Month					
	4	5	6	7	8	9
2008						
Drought	13.1 (1.2)	15.8 (0.9)	9.7 (0.8)	5.8 (1.0)	8.9 (0.9)	4.1 (1.1)
Control	19.5 (2.3)	20.4 (2.1)	12.9 (2.1)	8.8 (2.5)	15.1 (1.4)	12.2 (1.9)
Water	21.0 (1.0)	25.4 (1.6)	18.2 (1.2)	20.2 (0.8)	25.3 (0.7)	22.5 (1.1)
2009						
Drought	9.8 (1.0)	8.0 (0.9)	6.2 (0.9)	6.0 (0.9)	9.9 (1.0)	8.7 (0.7)
Control	11.6 (1.3)	9.8 (0.9)	8.0 (1.1)	7.6 (-)	11.1(1.4)	10.3 (0.4)
Water	17.9 (1.2)	20.6 (2.4)	17.4 (2.9)	13.9 (2.3)	16.8 (2.2)	19.3 (2.8)
2010						
Drought	13.1 (0.6)	13.8 (0.9)	12.5 (0.8)	5.8 (0.6)	7.7 (0.5)	8.1 (0.7)
Control	17.2 (0.7)	16.1 (1.2)	12.5 (1.2)	6.3 (1.5)	8.9 (2.1)	8.9 (1.3)
Water	24.2 (3.3)	27.2 (2.2)	24.3 (1.8)	18.6 (1.3)	18.1 (1.3)	18.8 (1.5)
2011						
Drought	11.1 (3.3)	9.2 (1.8)	9.0 (1.0)	4.3 (1.3)	7.6 (2.4)	1.9 (1.2)
Control	15.6 (4.0)	12.6 (3.5)	11.1 (3.8)	7.1 (3.2)	6.7 (2.1)	3.2 (0.7)
Water	21.3 (3.4)	24.6 (2.9)	22.8 (1.8)	15.6 (1.1)	15.7 (0.7)	11.6 (0.9)

Table 4.3. Results (F statistic) of ANOVA on the effects of year (Y), treatment (T), and their interactions on the percentage total cover and cover of graminoids (G), forbs (F), and shrubs (S) at the shortgrass steppe site. ***=P<0.001, **=P<0.01, *=P<0.05, ns=P>0.05.

Source of variation	df	Total Cover	Graminoid Cover	Forb Cover	Dwarf-shrub cover
Treatment (T)	2,82	0.15 ^{ns}	1.05 ^{ns}	2.94 ^{ns}	1.74 ^{ns}
Y	2,82	10.51 ^{***}	3.95 [*]	124.91 ^{***}	1.20 ^{ns}
T x Y	4,82	6.17 ^{***}	4.94 ^{**}	2.79 [*]	0.88 ^{ns}

Table 4.4. Results (F statistics) of ANOVA on the effects of year (Y), treatment (T), and their interactions on evenness, diversity and richness of graminoids at the shortgrass steppe site. ***=P<0.001, **=P<0.01, *=P<0.05, ns=P>0.05.

Source of variation	df	<i>B. gracilis</i>	<i>C. eleocharis</i>	Ruderal	Species density	Evenness	Diversity
Treatment (T)	2,82	3.54 [*]	1.45 ^{ns}	1.90 ^{ns}	0.44 ^{ns}	3.33 [*]	3.78 [*]
Y	2,82	6.60 ^{**}	10.94 ^{***}	39.09 ^{***}	18.84 ^{***}	3.77 [*]	20.10 ^{***}
T x Y	4,82	2.22 ^{ns}	4.35 ^{**}	4.01 ^{**}	1.55 ^{ns}	4.28 ^{**}	7.82 ^{***}

Table 4.5. Results (F statistic) of ANOVA on the effects of year (Y), treatment (T), and their interactions on the percentage total cover and cover of graminoids (G), forbs (F), and shrubs (S) at the mixed grass prairie site. ***=P<0.001, **=P<0.01, *=P<0.05, ns=P>0.05.

Source of variation	df	Total Cover	Graminoid cover	Forb cover	Dwarf-shrub cover
Block (B)	1,587	0 ^{ns}	0.04 ^{ns}	5.42 [*]	24.39 ^{***}
Treatment (T)	2,587	67.71 ^{***}	46.49 ^{***}	1.03 ^{ns}	3.27 [*]
Y	3,45	30.52 ^{***}	40.69 ^{***}	5.25 ^{**}	19.89 ^{***}
B x T	2,587	0.85 ^{ns}	0.86 ^{ns}	0.48 ^{ns}	2.46 ^{ns}
T x Y	6,587	6.85 ^{***}	8.73 ^{***}	0.82 ^{ns}	1.33 ^{ns}

Table 4.6. Results (F statistic) of ANOVA on the effects of year (Y), treatment (T), Block (B), and their interactions on the percentage cover of the dominant, subdominant, and ruderal species at the mixed grass prairie site. ***=P<0.001, **=P<0.01, *=P<0.05, ns=P>0.05.

Source of variation	df	<i>S. scoparium</i>	<i>A. gerardii</i>	ruderal	H	J	Species density
Block (B)	1,587	3.81 ^{ns}	3.94 [*]	2.84 ^{ns}	1.59 ^{ns}	1.54 ^{ns}	3.33 ^{ns}
Treatment (T)	2,587	27.75 ^{***}	10.79 ^{***}	0.57 ^{ns}	25.01 ^{***}	7.57 ^{**}	35.79 ^{***}
Y	3,45	5.18 ^{**}	9.67 ^{***}	1.81 ^{ns}	8.15 ^{***}	0.60 ^{ns}	17.25 ^{***}
B x T	2,587	1.64 ^{ns}	3.02 [*]	1.28 ^{ns}	2.05 ^{ns}	2.36 ^{ns}	0.64 ^{ns}
T x Y	6,587	1.59 ^{ns}	4.98 ^{***}	1.44 ^{ns}	1.24 ^{ns}	4.53 ^{**}	7.07 ^{***}

FIGURES

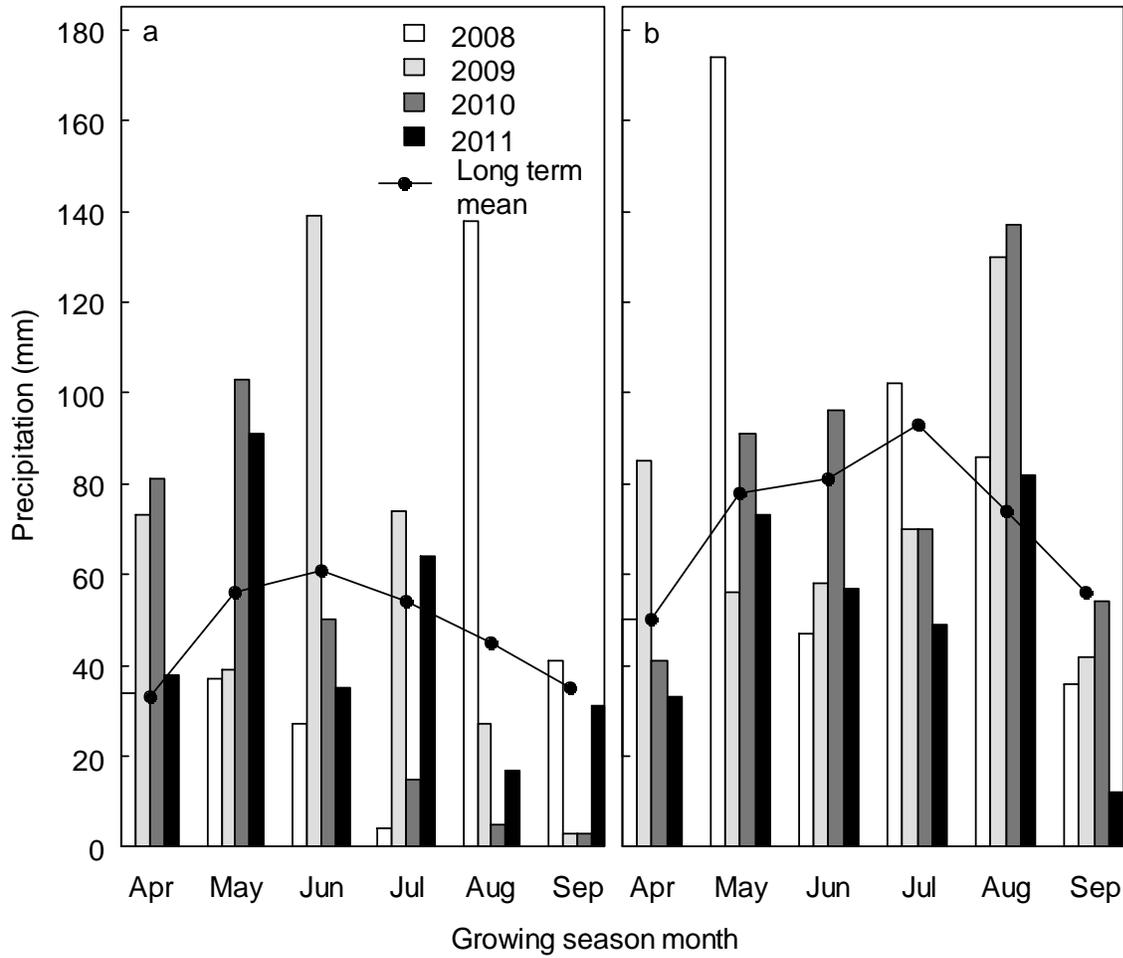


Figure 4.1. (a) April and growing season (May – September) precipitation received at the shortgrass steppe, and (b) growing season (April – September) precipitation received at the mixed grass prairie, during the experiment years (2008 – 2011) and long term monthly growing season precipitation.

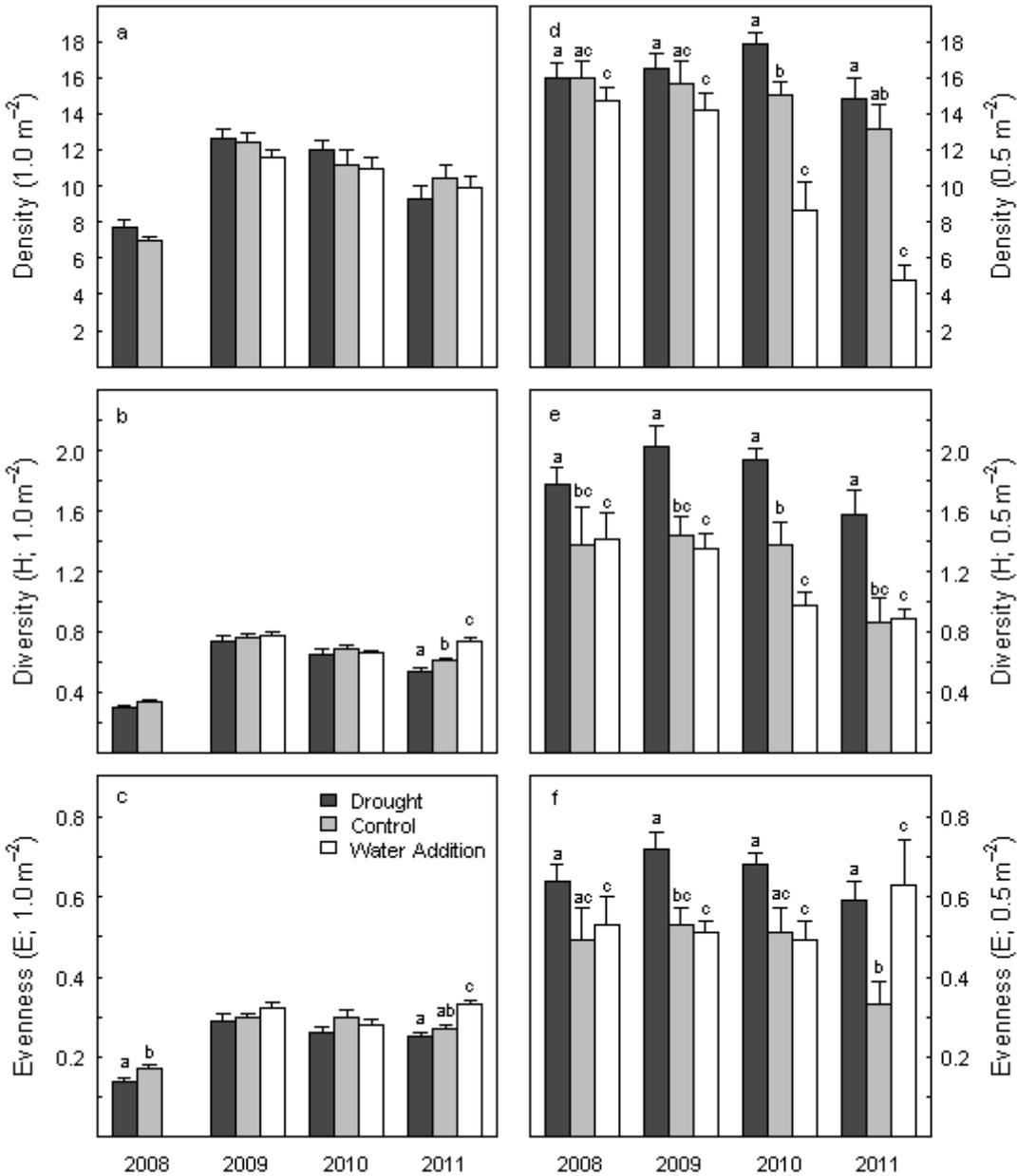


Figure 4.2. Species richness (a), Shannon-Wiener index (b), and Pielou evenness index (c) within 1.0 m² for drought, control, and water addition treatments at the shortgrass steppe, and species richness (d), Shannon-Wiener index (e), and Pielou evenness index (f) within 0.5 m² for drought, control, and water addition treatments at the mixed grass prairie. Bars represent standard error. Letters indicate significant treatment differences.

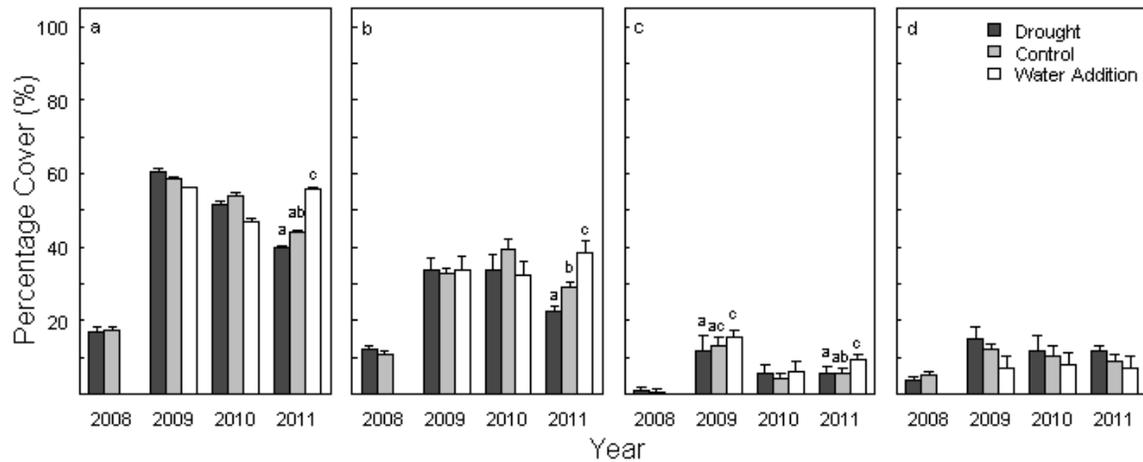


Figure 4.3. Percentage total cover (a), cover by graminoids (b), cover by forbs (c), and cover by dwarf-shrubs (d), in the drought, control, and water addition treatments at the shortgrass steppe. Bars represent standard error. Letters indicate significant treatment differences.

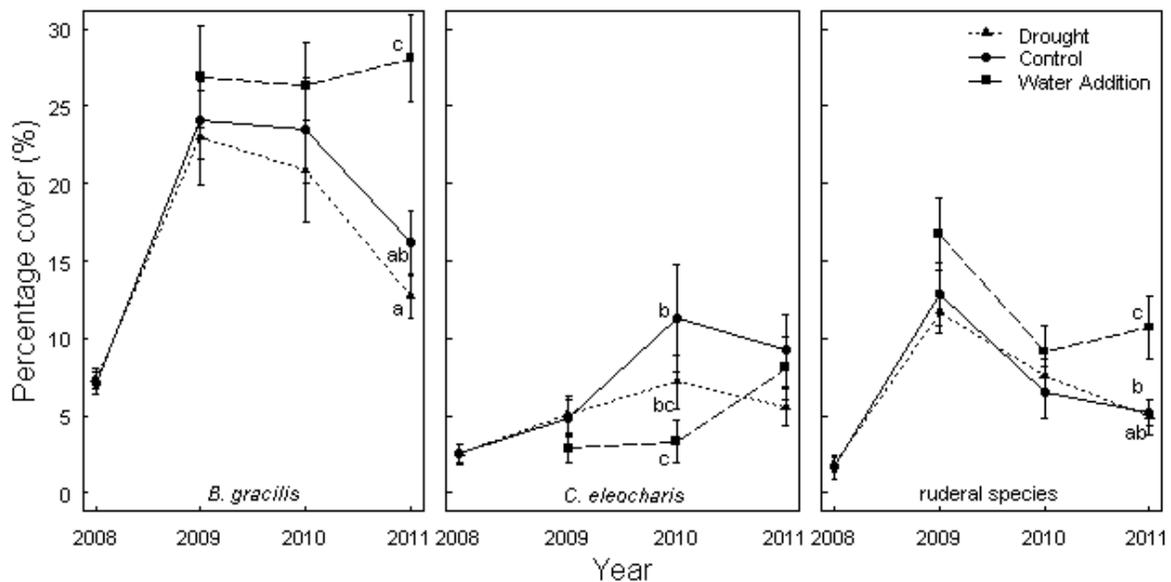


Figure 4.4. Percentage cover of dominant species (*Bouteloua gracilis*), subdominant species (*Carex eleocharis*), and ruderal species in drought, control, and water addition treatments at the shortgrass steppe site. Bars represent standard error. Letters indicate significant treatment differences.

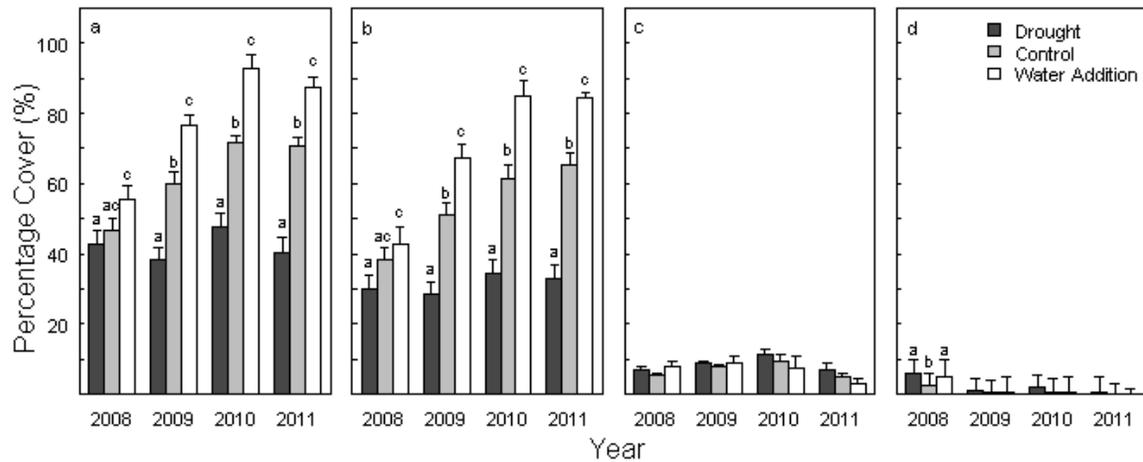


Figure 4.5. Percentage total cover (a), cover by graminoids (b), cover by forbs (c), and cover by dwarf-shrubs (d) in drought, control, and water addition treatments at the mixed grass prairie. Bars represent standard error. Letters indicate significant treatment differences.

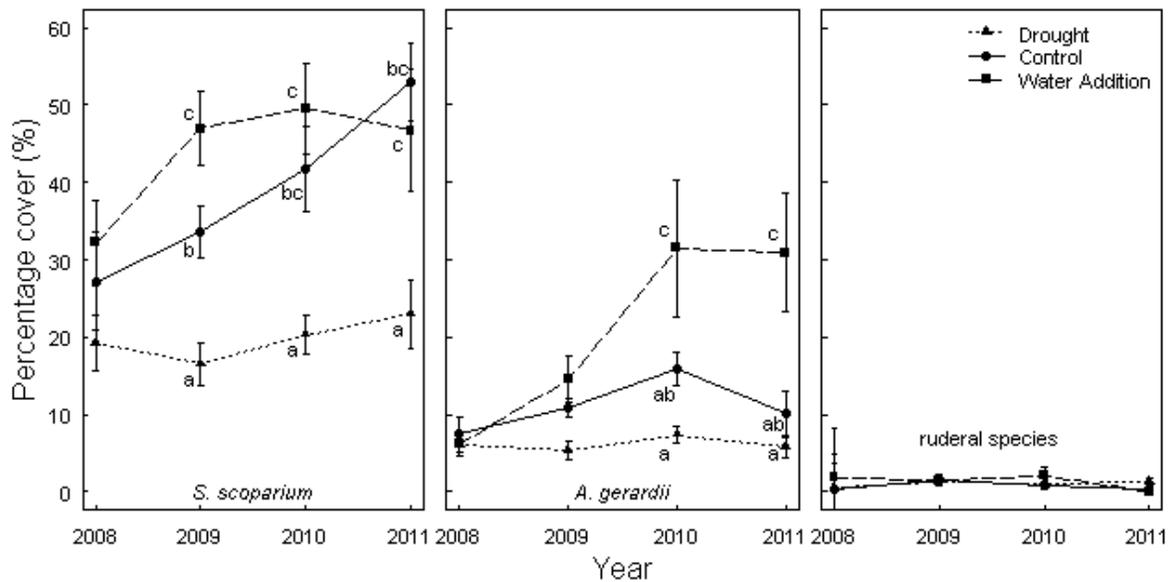


Figure 4.6. Percentage cover of dominant species (*S. scoparium*), subdominant species (*A. gerardii*), and ruderal species in drought, control, and water addition treatments at the mixed grass prairie. Bars represent standard error. Letters indicate significant treatment differences.

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APPENDIX

Table A.4.1. Cover of species considered ruderal at the shortgrass steppe site across all years.

Species name	Percentage cover (%)	Growth form	Native or non-native
<i>Aristida purpurea</i> Nutt. var. <i>purpurea</i>	0.18	PG	Native
<i>Artemisia frigida</i> Willd.	1.59	PS	Native
<i>Chenopodium album</i> L.	0.07	AF	Non-native
<i>Chenopodium incanum</i> (S. Watson) A. Heller	0.08	AF	Native
<i>Chenopodium leptophyllum</i> (Moq.) Nutt. ex S. Watson	0.26	AF	Native
<i>Chrysopsis villosa</i> (Pursh) Nutt. ex DC.	0.04	PF	Native
<i>Conyza canadensis</i> (L.) Cronquist	0.06	AF	Native
<i>Cryptantha minima</i> Rydb.	0.01	AF	Native
<i>Bassia scoparia</i> (L.) A.J. Scott	0.00	AF	Non-native
<i>Lactuca serriola</i> L.	0.01	AF	Non-native
<i>Lepidium densiflorum</i> Schrad.	1.85	AF	Native
<i>Oenothera albicaulis</i> Pursh	0.15	AF	Native
<i>Oenothera coronopifolia</i> Torr. & A. Gray	0.57	PF	Native
<i>Plantago patagonica</i> Jacq.	0.47	AF	Native
<i>Salsola tragus</i> L.	0.47	AF	Non-native
<i>Sisymbrium altissimum</i> L.	0.01	AF	Non-native
<i>Solanum triflorum</i> Nutt.	0.00	AF	Native
<i>Sporobolus cryptandrus</i> (Torr.) A. Gray	1.33	PG	Native
<i>Chamaesyce glyptosperma</i> (Engelm.) Small	0.50	AF	Native
<i>Tragopogon dubius</i> Scop.	0.03	PF	Non-native
<i>Vulpia octoflora</i> (Walter) Rydb.	0.29	AG	Native

Table A.4.2. Cover of species considered ruderal at the mixed grass prairie site across all years.

Species name	Percentage cover (%)	Growth form	Native or non-native
<i>Ambrosia psilostachya</i> DC.	0.24	PF	Native
<i>Aristida purpurea</i> Nutt. var. <i>purpurea</i>	0.10	PG	Native
<i>Bromus japonicus</i> Thunb.	0.15	AG	Non-native
<i>Cirsium undulatum</i> (Nutt.) Spreng.	0.26	PF	Native
<i>Croton capitatus</i> Michx.	0.03	AF	Native
<i>Helianthus annuus</i> L.	0.12	AF	Native
<i>Melilotus officinalis</i>	0.14	AF	Non-native
<i>Plantago patagonica</i> Jacq.	0.02	AF	Native
<i>Portulaca oleracea</i> L.	0.04	AF	Non-native
<i>Salsola tragus</i> L.	0.03	AF	Non-native

Chapter 5: Summary and Conclusions

As water-limited systems, the structure and function of grasslands worldwide are largely determined by the timing and quantity of available soil water. Precipitation, often used as a surrogate for soil water, is tightly linked to important ecosystem properties in arid-semiarid regions including aboveground net primary production (Rosenzweig 1968, Webb et al. 1983, Sala et al. 1988), species richness (Tilman and Haddi 1992, Givnish 1999, Adler and Levine 2007), nitrogen availability (Burke et al. 1997), and carbon storage (Parton et al. 1987). Yet recent predictions of an increase in mean global temperature and changes in precipitation timing and quantity (Christensen et al. 2007) have the potential to alter terrestrial communities in novel ways by changing both the strength of abiotic controls on ecosystem processes as well as changing biotic interactions such as competition. The results from my dissertation research show how predicted changes in temperature and precipitation will affect plant available soil water, net primary production, and species composition at two sites spanning the driest portion of the central grassland region of North America.

While the IPCC predicts that my study sites at the shortgrass steppe and mixed grass prairie will experience similar percentage changes in annual precipitation and temperature, the consequences of these changes on the spatial and temporal dynamics of soil water were different between sites. Spatial differences in available water between simulated current conditions and GCM predicted dynamics were small at the shortgrass steppe, and tended to be greatest during the non-growing season. Likewise, there were very small changes in the temporal distribution of available water. Differences were greatest in wet years, when there was a small decrease in available soil water during the growing season in the surface and deeper soil layers in the climate change scenarios. Changes in the spatial dynamics of available water at the mixed grass prairie

were smaller, but temporal changes were quite large. The greatest decrease in the percentage of days with available water in the 0 – 30 cm layer in climate change scenarios occurred during the summer season. Soil water decreased in the 30 -120 cm layer as well, although the seasonality of the decrease differed among year types. Many experimental manipulations have examined the short term consequences of changes in precipitation and temperature predicted by the IPCC, but our simulation study is unique in that it provides a long term perspective on daily soil water dynamics throughout the soil profile and over a range of annual conditions (dry, average, and wet years). At the shortgrass steppe site, we found that we can gain a reasonable understanding of the spatial and temporal dynamics of soil water under future predicted climate change scenarios by examining the surface layers. However, at the mixed grass prairie site, the most important changes in soil water occurred deeper in the soil, from 30 -120 cm. The predicted changes in soil water availability throughout the soil profile will likely affect ecosystem dynamics in these grasslands, and our results suggest that the more mesic mixed grass prairie may experience greater changes in community structure and function than the more xeric shortgrass steppe site, even though predicted changes in precipitation and temperature are similar between the sites.

My rainfall manipulation experiment confirmed some of the predictions I made about potential changes in NPP based on my soil water simulation study, although the experiment lasted only 3 years. I constructed rainout shelters, water addition plots, and control plots (n=15 and 6, for the shortgrass steppe and mixed grass prairie, respectively) and estimated ANPP, BNPP, and NPP in each treatment for 3 consecutive growing seasons (2008 - 2010). The rainfall manipulation experiment successfully altered soil water content in my treatments, but these changes resulted in different, but significant responses in ANPP and BNPP at our two sites. At

the shortgrass steppe, neither NPP nor ANPP were sensitive to treatment precipitation, and while BNPP was sensitive to changes in treatment precipitation, the direction of the response varied between years. In contrast, ANPP was very sensitive to treatment precipitation at the mixed grass prairie, while BNPP was insensitive. My findings that two grassland ecosystems showed dramatically different above and belowground production responses to soil water manipulations suggests that we cannot assume that predicted changes in climate will cause similar above and below ground production responses, and demonstrates that sites within the same region may differ markedly in the sensitivity of NPP to changes in growing season precipitation.

The changes in species composition and diversity that I observed in my rainfall manipulation experiment also confirmed some of my predictions from the soil water simulation. I measured changes in species composition, density, diversity, evenness, and cover by plant functional groups across four years (2008-2011) in the rainfall manipulation experiment outlined above. My soil water manipulation treatments resulted in different compositional changes at each site, which were largely driven by the response of the dominant grass species. Percentage cover of *Bouteloua gracilis*, the dominant species at the shortgrass steppe, increased in the water addition treatment, but only in the final treatment year (2011). There was a concomitant increase in percentage total, graminoid, forbs, and ruderal species cover. The drought treatment did not alter percentage cover for any group except graminoids, which had a 6.6 % reduction in percentage cover in the final treatment year. In contrast, the treatments resulted in rapid changes in species density, diversity, and evenness, total cover and cover by graminoids, and cover of the dominant and subdominant species, *Schizachyrium scoparium* and *Andropogon gerardii*. The differing sensitivities of the dominant species and functional groups to similar induced changes in soil water at two sites demonstrates that both abiotic (soil water availability) and biotic

(interspecific interactions) factors play important roles in regulating plant community structure and composition responses to climate change in grasslands.

The results of my dissertation research have several important implications for future climate change research and for predicting the magnitude of temperate grassland responses to these expected climate changes. First and foremost, I found that two grasslands that are often lumped together for modeling purposes responded very differently to predicted changes in precipitation and temperature. From the perspective of soil water availability, similar percentage changes in precipitation led to quite different changes in the spatial and temporal availability of soil water. My rainfall manipulation experiment corroborated these results for both NPP and species composition. The differences in community responses between my two sites highlight the importance of multi-site studies to refine our knowledge of the mechanisms and generalities of community response to climate change at the biome level. Second, my work suggests that both soil water availability and interspecific interactions play important roles in regulating plant community response to climate change. There is still much uncertainty in climate change predictions, particularly regarding changes in the timing and quantity of precipitation. As GCMs improve, it will be important for additional simulation and experimental studies to improve our understanding of both the abiotic and biotic interactions in natural ecosystems and apply these interactions to improve our ability to forecast the impacts of global change on ecosystems worldwide.

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