

PRECIPITATION CHANGE IN A SEMI-ARID GRASSLAND:  
PLANT COMMUNITY RESPONSES AND MANAGEMENT STRATEGIES

By

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Precipitation change in a semi-arid grassland:

plant community responses and management strategies

Thesis directed by Timothy R. Seastedt

## ABSTRACT

Shifts in precipitation patterns can alter the composition and function of plant communities. My dissertation research examines the effects of changes in the amount and timing of precipitation on plant species composition in a semi-arid grassland in the foothills of Colorado, USA. I also investigated possible management strategies to promote native plant communities in the face of global change. I established a manipulative study to examine how changes in the seasonal distribution of precipitation may affect the abundance of historically dominant (native) and recently-introduced (non-native) plant species, and the resulting impacts on the function of the ecosystem. My results showed that non-native grasses, especially *Bromus tectorum*, responded positively to increases in winter precipitation. In contrast, native species were least abundant in treatments with increased winter precipitation and most abundant in treatments with reduced winter precipitation and increased summer precipitation. Plots with higher abundance of the non-native grass *B. tectorum* had lower available soil moisture and plant species diversity. Although *B. tectorum* was most successful with additional winter precipitation, *Ustilago bullata*, a pathogen that infects *B. tectorum*, was also more prevalent in treatments that received increased winter precipitation. In a separate experiment, I tested a possible management strategy to address future changes in species composition in grasslands. I used timed mowing applications designed to reduce the abundance of non-native winter-active species and increase abundance of native species. Spring and summer mowing reduced cover of non-native grasses,

but increased cover of non-native forbs. Spring mowing also increased abundance of native plant species. If yearly precipitation shifts to a more winter-wet pattern, non-native winter-active grasses could become more invasive in Colorado grasslands and reduce abundance of native plants and associated ecosystem services. However, management strategies that target the temporal niche of non-native grasses may reduce their abundance, thereby promoting more desirable grasslands in the future.

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# CHAPTER 1

## INTRODUCTION

### **1.1 How will grasslands respond to shifting precipitation patterns with a changing climate?**

Changes in the hydrological cycle may occur as a result of global climate change. There is evidence that precipitation patterns are shifting (Zhang et al. 2007), and will continue to change in the future (IPCC 2007). Examining how shifts in precipitation will affect terrestrial ecosystems is currently an active area of research. Grassland ecosystems, in particular, can be very sensitive to shifts in precipitation regimes and have been the focus of a number of experimental studies (Wu et al. 2011). Grasslands cover approximately 40% of the terrestrial surface of the Earth (World Resources Institute), and provide valuable ecosystem services, such as forage for livestock, nutrient cycling, CO<sub>2</sub> sequestration, and soil generation and conservation, among others (Sala and Paruelo 1997). Increased resource use pressures have led to the removal or overexploitation of many grassland ecosystems (Sala and Paruelo 1997, Suttie et al. 2005), so understanding how they respond to changes in climate and precipitation will be important for protection of remaining grasslands. Here, I discuss how precipitation regimes in grasslands may change in the future, how grasslands have responded to changes in precipitation in the past, and review results of manipulative experiments of precipitation change in grasslands around the world. Lastly, I'll point out some gaps in knowledge of precipitation change and grasslands, and present an outline of my dissertation research.

## **1.2 How is precipitation projected to change?**

As a result of their geographical and climatic heterogeneity, predictions of changes in precipitation vary greatly for grasslands of the world, although some overall patterns are consistent. As the Earth warms, the hydrological cycle should accelerate due to increased evaporation and thus precipitation (Del Genio et al. 1991, Loaiciga et al. 1996, Held and Soden 2006, IPCC 2007). The acceleration of the water cycle may lead to more extreme precipitation events and longer, unpredictable droughts (Easterling 2000). Recent climate records indicate that precipitation extremes are already increasing around the globe (Groisman et al 2003, Huntington 2006, Min et al. 2011), although climate oscillations may be influencing this trend, so it is difficult to say with certainty that the changes are a direct result of human-induced climate change.

Warmer mean temperatures with climate change may also increase evaporation during the growing season, reducing available soil moisture and increasing water stress during the warmest months of the year (IPCC 2007). Warmer temperatures may result in more precipitation falling as rain rather than snow at higher altitudes (Ray et al. 2008, IPCC 2007). Many climate models also predict an increase in winter precipitation at higher latitudes and altitudes. These shifts in precipitation regimes and resulting feedbacks have the potential to greatly alter water available for plants, with consequences for net primary productivity, composition of plant communities, carbon sequestration, and other biogeochemical cycles in grasslands (Knapp et al. 2002, Knapp et al. 2008, Weltzin et al 2003).

### **1.3 How have grasslands responded to precipitation change in the past?**

Past records of responses of plant communities to yearly precipitation can inform predictions of how they will respond to precipitation variation in the future (Hobbs and Mooney 1991, Debinski et al. 2010). One of the most consistent observations is greater aboveground net primary productivity (ANPP) in years with more precipitation (Hobbs and Mooney 1991, Knapp and Smith 2001, Nippert et al. 2006, Chou et al. 2008, Yang et al. 2008). In an analysis of 118 grasslands worldwide, Yang et al. (2008) observed a strong relationship between increasing precipitation and increasing ANPP. Additionally, there was a correlation between increased variability in interannual precipitation and variability in net primary production between years (Yang et al. 2008). Consistent with the findings of Knapp and Smith (2001), high interannual variability in precipitation was correlated with decreased productivity over time (Yang et al. 2008). Other factors, such as precipitation during the previous year, can affect current-year ANPP, so plant responses may be influenced by past precipitation as well (Oesterheld et al. 2001). The composition of plant species and functional groups also shifts with changes in interannual precipitation (Hobbs and Mooney 1991). In two studies, grasses responded positively to increased yearly precipitation, whereas forbs were less responsive (Hobbs and Mooney 1991, Nippert et al. 2006).

### **1.4 A review of precipitation manipulation experiments**

Future variation in precipitation patterns could be greater than those observed in the past, so previous responses may not be realistic predictors of future responses (Nippert et al. 2006, Fay et al. 2008). In addition, the uncertainty associated with modeled changes in precipitation at local scales (IPCC 2007), and the complexity of interactions in plant communities makes it

difficult to predict plant responses to changes in precipitation regimes. Manipulative experiments can be insightful because they allow observation of how changes in both intra- and interannual precipitation will impact plant species and ecosystem services at fine scales. Herbaceous communities like grasslands can be very sensitive to changes in precipitation (Knapp and Smith 2001, Knapp et al. 2008), so they are ideal for measuring responses in short-term experiments. Although there are a variety of challenges associated with correctly implementing manipulative studies (Weltzin and McPherson 2003), there are many benefits of direct comparison between ambient and altered precipitation patterns (Knapp et al. 2002, Knapp et al. 2008, Wu et al. 2011).

Manipulative experiments in grasslands commonly measure several similar response variables: net primary productivity (NPP), CO<sub>2</sub> flux, and plant species diversity, among others. Measurements of productivity, carbon flux, and diversity are important proxies for ecosystem function. They provide information about the ability of an ecosystem to store carbon and the resilience of an ecosystem to change. NPP is usually estimated by measuring aboveground or belowground biomass produced by a plant community in a given area over a year and is reported in g/m<sup>2</sup>. CO<sub>2</sub> flux is the exchange of CO<sub>2</sub> between an ecosystem and the atmosphere, and is usually measured as the rate of respiration (loss of CO<sub>2</sub>) from the soil surface (μmol/m<sup>2</sup>/s). Diversity is usually measured as an index of the number and relative abundance of different plant species in an area. For this review, I also include measurements of species richness with diversity measurements. Because most studies measure these common variables, it is easy to directly compare results. Most precipitation experiments conducted to date fall into three broad categories: simulated drought, altered timing of precipitation events, and an overall increase in

precipitation. This review will synthesize information from these three categories of studies to reveal any emergent patterns about the responses of grasslands to changing precipitation.

In most studies, drought manipulations lead to lower NPP, and reduced CO<sub>2</sub> flux, as would be expected (Table 1.1). However, in semi-arid grasslands, simulated drought often had no effect on net primary productivity (Köchy and Wilson 2004, Miranda et al 2009, Cherwin and Knapp 2012). Only large (e.g >50% reduction) simulated droughts significantly lowered NPP in these drier ecosystems. In wetter grasslands, drought reduced total NPP (Harper et al. 2005, Fay et al. 2003), but dominant plant species were relatively unresponsive to drought (Fay et al. 2003). Semi-arid grasslands may be more resilient to small reductions in precipitation in the future because species there are adapted to survive dry conditions (Lauenroth and Sala 1992). In contrast, mesic grasslands have species adapted to wetter conditions and may experience greater changes in productivity with smaller reductions in total rainfall.

Altering the timing of precipitation had contrasting effects on different grassland communities (Table 1.1). An increase in the length of dry periods between rainfall events, with larger rainfall events, significantly reduced CO<sub>2</sub> flux and NPP in mesic grasslands (Knapp et al. 2002, Fay et al. 2003, Harper et al. 2005, Fay et al. 2008). Diversity, however, increased with increasing variability in rainfall events (Knapp et al. 2002). Increased diversity could be an indirect effect of decreasing NPP and thus competition with dominant plant species (Knapp et al. 2002). These results contrast with those from a semi-arid annual grassland with a mediterranean climate, where changes in the frequency of rain events had no effect on NPP or diversity (Miranda 2009). In semi-arid shortgrass-steppe of Colorado, fewer, but larger, precipitation events actually increased NPP (Heisler-White et al. 2008). These differences may be explained by the different climates of the two grasslands. Plants in mesic grasslands such as tallgrass

prairie are adapted to consistently moist soils during the growing season, so increasing dry periods between rain events could reduce photosynthetic rates (Knapp and Smith 2001). In semi-arid ecosystems, however, the soil is only intermittently wet during the growing season, and larger precipitation events may have allowed water to percolate deeper in the soil profile before it evaporated from shallow layers, so plants had access to water for longer periods (Heisler-White et al. 2008). These results highlight how similar changes in precipitation, in this case reduced frequency and increased intensity, can have very different effects in grassland ecosystems.

Increasing precipitation resulted in increased NPP and CO<sub>2</sub> flux in most studies in grasslands (e.g. Knapp et al. 2002, Köchy and Wilson 2004, Table 1.1). Composition of plant communities and functional groups often changed dramatically following precipitation additions (Lauenroth and Dodd 1978, Suttle et al. 2007). In shortgrass-steppe, water additions virtually eliminated all succulents from plots and increased the cover of warm-season grasses and non-native forbs after five years (Lauenroth and Dodd 1978). Suttle et al. (2007) initially observed large increases in NPP in plots with additional spring precipitation, but after 5 years of manipulations there were no difference in plant biomass between water addition and control plots, and decreased species richness in spring water addition plots. The authors attributed this sharp decline in species richness to initial increases in non-native winter-annual grasses and litter and subsequent reduction in forb germination. These results show the importance of species interactions in responses of plant communities to changes in precipitation (Suttle et al. 2007).

## **1.5 Research gaps**

These studies provide a basis for hypotheses about responses of grasslands to precipitation change. Most studies of precipitation change involve manipulations of the total amount (drought or increase) or timing (variability) in yearly precipitation; however, few studies examine how intra-annual, or seasonal, changes in precipitation may impact terrestrial ecosystems (but see Bates et al. 2006, Chou et al. 2008, and Grime et al. 2000). Ecosystem processes in grasslands may be more responsive to seasonal shifts in precipitation patterns than to changes in quantity of rainfall received (Chou et al. 2008). Additionally, while several studies look at effects of precipitation change on composition of plant communities, few explicitly examine how changing abundance of plant species may affect competitive or facilitative interactions in changing precipitation scenarios (but see Suttle et al. 2007). Plant species interactions will play a strong role in determining long-term responses of grassland ecosystems to precipitation change (Suttle et al. 2007).

## **1.6 Research Outline**

My dissertation research complements existing studies of grassland responses to precipitation change. My research attempted to address some of the gaps in precipitation change research, and also look at possible management strategies for grasslands in the future. I conducted my research in a semi-arid mixed-grass prairie in the foothills of Colorado, USA. My dissertation research examined the effects of changes in the seasonality and amount of precipitation on plant species composition and primary productivity in this grassland. Chapter 2 focuses on how changes in precipitation patterns affect historically dominant (native) and recently introduced (non-native) plant species, interactions between these species groups, and

resulting effects on net primary productivity. Chapter 3 details observations of a plant pathogen found at my field site, and the effects of precipitation change on abundance of this pathogen in my experiment. Chapter 4 focuses specifically on demographic responses of the non-native grass *Bromus tectorum* to precipitation change, and how competition from other species interacts with precipitation change to influence population growth of *B. tectorum*. Finally, Chapter 5 examines responses of invaded grasslands to timed management applications aimed to reduce abundance of non-native species, and promote later-growing native plants.

**Table 1.1.** Summary of responses of grassland ecosystems to precipitation manipulations (drought, altered timing of precipitation, and increased precipitation). *notes:* ↑ indicates an increase, ↓ indicates a decrease, and ~ indicates no change. If a column is blank then that response variable was not measured in that ecosystem. Multiple symbols in a column indicate that studies found different responses to the same precipitation treatment.

Ecosystem	NPP	Diversity	Composition of functional groups	Invasive species	CO <sub>2</sub> Flux	References
<b>Drought</b>						
Patagonian steppe	↓	↓	~			Yahdjian and Sala 2006
Mesic grassland	↓		~ dominant grass ↓ C <sub>4</sub> grasses		↓	Harper et al. 2005, Fay et al. 2003, Fay et al. 2008
Semi-arid grassland	↓, ~	↓				Köchy and Wilson 2004, Miranda et al. 2009, Cherwin and Knapp 2012
Limestone grassland	↓		~			Grime et al. 2000, Grime et al. 2008
<b>Altered timing</b>						
Mesic grassland	↓, ~	↑	↑ forbs ~ grasses		↓, ~	Knapp et al. 2002, Fay et al. 2003, Harper et al. 2005, Fay et al. 2008
Semi-arid grassland	↑, ~	~				Heisler-White et al. 2008, Miranda et al. 2009, Cherwin and Knapp 2012
<b>Increased Precipitation</b>						
CA grassland	~	~, ↓, ↑	~ cool-season grasses ↓, ↑ forbs	↑	↑	Dukes et al. 2005, Suttle et al. 2007, Chou et al. 2008, Harpole et al. 2007, Silver et al. 2005, Zavaleta et al. 2003
Semi-arid grassland	↑		↑ shrub stem density ↑ warm-season grasses ↓ succulents	↑	↑	Lauenroth and Dodd 1978, Köchy and Wilson 2004, McCulley et al. 2007, Patrick, et al. 2007, Risch and Frank 2007
Mesic grassland	↑			~	↑	Fay et al. 2008, Risch and Frank 2007, Sherry et al. 2008, Siemann et al. 2007, Zhou et al. 2006
Limestone grassland	↑, ~		~			Grime et al. 2000, Grime et al. 2008

## CHAPTER 2

### PRECIPITATION CHANGE ALTERS COMMUNITY COMPOSITION OF A SEMI-ARID GRASSLAND

#### 2.1 Abstract

Shifts in precipitation patterns resulting from global climate change are expected to affect composition and functioning of vegetation communities. A relevant and largely unaddressed research question is - how will the presence of non-native species interact with precipitation change to alter ecosystem structure, function, and services? This study addressed the effects of changes in the amount and timing of precipitation on the species composition and ecosystem services of a grassland community in Colorado, USA. In spring 2010, I established a manipulative study to examine how changes in precipitation patterns may affect the abundance of historically-dominant (native) and recently-arrived (non-native) plant species, and the resulting impacts on soil moisture, nutrients, and net primary productivity. I created 3 precipitation treatments based on climate model predictions for Colorado: winter-wet/ambient-summer, winter-wet/summer-dry, and winter-wet/summer wet. In addition, a winter-dry/summer-wet treatment was added to simulate historical conditions. I monitored plant community composition and aboveground biomass in plots for four years, from 2010 – 2013. In April 2011-2013, cover of non-native winter-active grasses was greater in winter-wet treatments than in the control or winter-dry treatments. Native cool-season grasses did not respond strongly

to precipitation treatments. In August 2011-2013, cover of native warm-season grasses and forbs was greatest in the winter-dry/summer-wet treatment, and lowest in the winter-wet/summer-dry treatment. These results support the expectation that increased winter precipitation benefits non-native winter-active plants, whereas increased summer precipitation benefits later-growing native plants. However, native cool-season perennials were less affected by this climate pattern. Cover measurements revealed *Bromus tectorum* to be the most abundant winter-active species at the study site. Increased cover of *B. tectorum* correlated with decreased volumetric soil water content and species diversity per plot. These data provide evidence that greater abundance of winter-active species decrease available soil resources, and impact later-growing native plants. Peak aboveground biomass, an indicator of ecosystem productivity, was lowest in the treatment receiving reduced summer precipitation, but only in years with drier springs. Plant-available nitrogen in spring was lower in plots receiving supplemental winter precipitation, and highest in plots with reduced winter precipitation. Our results indicate that changes in seasonal precipitation patterns can alter composition, productivity, and resource availability in a semi-arid grassland. If yearly precipitation continues to shift to a more winter-wet pattern, the abundance of non-native winter-active species could increase in Colorado grasslands and reduce abundance of native plant species and associated ecosystem services.

## **2.2 Introduction**

Global climate change will cause shifts in the distribution of plant species (Neilson et al. 2005, Scholze et al. 2006, Williams et al. 2007). Several lines of evidence indicate that plant species and communities are already responding strongly to changes in climate (e.g. Walther et al. 2002, Parmesan and Yohe 2003, Kelly and Goulden 2008, Staudinger et al. 2013). Currently,

plant communities provide important ecosystem services such as erosion control, soil conservation, carbon sequestration, nutrient cycling, and maintenance of water quality, as well as provisioning services (Myers 1996, Sala and Paruelo 1997, Daily et al. 2000), and climate-induced shifts in the species compositions of these communities may alter these ecosystem services (Schröter et al. 2005, Karl et al. 2009). Grasslands are one of the most sensitive ecosystems to global climate change drivers (Seastedt and Pyšek 2011), and modification and degradation of grasslands is happening around the world (Sala and Paruelo 1997, Suttie et al. 2005). Climate change has the potential to further alter these communities and the important services they offer. Research addressing how climate change will continue to impact composition of grassland communities and associated changes in ecosystem function is necessary to inform ecosystem management options in the future.

Over the last few decades, many studies have addressed the effects of rising temperatures (e.g. Harte et al. 1995, Luo et al. 2001) and increasing CO<sub>2</sub> concentrations (e.g. Smith et al. 1987, Smith et al. 2000, Morgan et al. 2011) on plant communities. However, relatively less research has examined how changes in precipitation will affect vegetation and ecosystem services (Weltzin et al. 2003). Changes in temperature and the timing and amount of precipitation have been implicated in determining future plant distributions (Archer and Predick 2008, Bradley et al. 2009). Semi-arid ecosystems, specifically, are more likely to be affected by water than temperature (Noy Meir 1973, Sala et al. 1988), so small changes in precipitation patterns may have large effects on species composition and productivity in these communities (Knapp and Smith 2001, Huxman et al. 2004, Heisler-White et al. 2008, Byrne et al. 2013). A number of observational studies have shown the sensitivity of productivity of semi-arid grassland species to precipitation patterns, however, past responses to variation in precipitation may not

accurately predict how plant species will respond to future changes outside the historic range of variability (Nippert et al. 2006, Heisler-White et al. 2009, Cherwin and Knapp 2012). The manipulative experiment presented here examined how new shifts in precipitation patterns may impact a grassland ecosystem.

Currently, plant communities are not only responding to changes in climate, but also to changes associated with non-native species. Non-native, invasive species are often thought to benefit from changes in temperature, nitrogen deposition, and increasing CO<sub>2</sub> (Dukes and Mooney 1999, Smith et al. 2000, Rao and Allen 2010; but see Bradley et al. 2009). In many cases, invasive species not only respond favorably to environmental changes, but also act as drivers of change (Vitousek et al. 1997). These changes are often very evident in grasslands, where species can alter litter inputs, soil properties, and fire cycles (D'Antonio and Vitousek 1992, Seastedt and Pysek 2011), and possibly shift ecosystems to alternative stable states that are less diverse and dominated by non-native species (Kulmatiski 2006).

Precipitation change, as well, may benefit non-native species at the expense of natives. Climate change could shift precipitation to time periods when native species are not adapted to growing, and this fluctuation in available resources may benefit invading exotic species (Davis 2000). There are often distinct phenological differences between native and non-native species (Wolkovitch and Cleland 2011). Specifically, many exotic species in western North America are winter active, germinating in late fall and early spring and growing when native species are senesced. If precipitation shifts to a more winter-wet pattern, these species may selectively benefit from changes in precipitation.

In the foothills and montane regions of the western U.S.A, climate change has resulted in warmer temperatures and more precipitation falling as rain rather than snow (Knowles et al.

2006, Ray et al. 2008). The latest reports on climate impacts increased annual temperatures, less summer precipitation, and more winter precipitation in northern Colorado (IPCC 2007, Karl et al. 2009). Native vegetation in foothills and montane regions of Colorado are adapted to high interannual variability in precipitation. Deep-rooted shrubs and trees, and shallower-rooted annual forbs and grasses benefit from precipitation at different times of the year. Many exotic winter-active forbs and grasses have been introduced to western North America from Eurasia, and are currently extremely successful in winter-wet climates in parts of the country. For example, the invasive grass *Bromus tectorum* has spread over 200,000 km<sup>2</sup> since its introduction around 1890 (Mack 1981). This invasion is one of the most rapid and extensive recorded for a plant species (Pyšek and Hulme 2005). *Bromus tectorum* has negatively affected native ecosystems by increasing fire frequencies (Whisenant 1990, D'Antonio and Vitousek 1992) and competing with native species through early spring utilization of soil water (Melgoza et al. 1990). *Bromus tectorum*, along with other exotic winter-active species, has also become common in the foothill regions of Colorado (Bromberg et al. 2001, Bush et al. 2007). Although the establishment of *B. tectorum* in Colorado is not as widespread as in the Great Basin, invasion potential could increase as the climate changes (Bradley 2009). The predicted shift from a summer-wet to more winter-wet climate in Colorado (Karl et al. 2009) could substantially alter the species composition of foothills grasslands and montane meadows.

This study examined responses of a grassland community in Colorado, USA, to simulated changes in precipitation patterns. I created a range of manipulations based on climate model predictions, and then observed species responses and changes in resource availability over four years. I asked three questions: How will shifts in the amount and seasonal timing of precipitation affect winter-active species and historically dominant native vegetation in the

Colorado Front Range? How does the presence of non-native winter-active plants affect soil moisture and nutrients in invaded ranges under different precipitation scenarios, and how will this impact native species? How will the interaction of precipitation change and biotic change (presence of non-native winter-actives) impact ecosystem productivity?

I hypothesized that: **(1)** increases in winter precipitation would benefit winter-active species capable of exploiting either early season or late season moisture. **(2)** The consequences of early spring growth and resource use by winter active plants would suppress growth of historically dominant late spring and summer species. **(3)** Ecosystem productivity would increase as increased winter precipitation allowed for more effective use of precipitation by winter active-plants, or, alternatively **(3a)** the increase in productivity of new winter-active species would be offset by a decline in productivity of natives.

## **2.3 Methods**

### *2.3.1 Field Site*

To examine how precipitation change affects plant community dynamics, I established a precipitation manipulation experiment in a grassland along the foothills of the Colorado Front Range, USA. The field site is located in a mixed-grass prairie approximately 15 km northwest of Boulder, Colorado, USA (40° 07' N, 105° 18' W). Elevation at the site is 1,798 m, average yearly precipitation is 475 mm per year, and average yearly temperature is 10.5° C (WRCC 2012). The site has a continental climate, with most precipitation falling in spring and early summer. Soils at the field site are classified as well-drained, colluvial, sandy loams (USDA 2001).

The plant community at the field site is composed of a mix of native perennial grasses and forbs, exotic winter-annual species, and exotic, winter-active, perennial species (Knoche 2009). Common native species at the site include *Pascopyrum smithii*, *Sporobolus cryptandrus*, *Psoralidium tenuiflorum*, *Ambrosia artemisiifolia* and *Erigeron flagellaris*, among many others. Exotic species at the site include *Bromus tectorum*, *Bromus japonicus*, *Poa compressa*, *Erodium cicutatum*, *Alyssum parviflorum*, and *Sisymbrium altissimum*, among others. The field site has a history of disturbance, including heavy, seasonal grazing by cattle for perhaps 100+ years prior to being excluded from the site after the 2006 growing season. During this period the reduced amount of fine fuels during the non-growing season meant the meadow was probably not burned, although nearby fires did occur, including one in 2003 that burned the adjacent understory of a Ponderosa savanna area. The community composition of the field site is characteristic of invaded grassland ecosystems across the foothills and montane meadows of Colorado (Sims et al. 1978, Bush et al. 2007)

### 2.3.2 Experimental Design

Precipitation manipulations were based on information from global climate circulation models (GCMs) and preliminary climate analyses of historical data from climate stations along the Front Range of Colorado. GCMs disagree on how precipitation will change in northern Colorado (IPCC 2013) but most models show increases in winter precipitation, and some forecast increasing frequency of drought and decreases in summer precipitation (Weltzin et al. 2003, Ray et al. 2008, IPCC 2013). To see if any discernible changes in seasonal precipitation were occurring in the recent past along the Front Range of Colorado, I compared average winter (Oct-Mar) and summer (April-Sept.) precipitation from 1900-1970 to average winter and

summer precipitation from 1970-2010 from records of 7 climate stations along the Front Range of Colorado (WRCC 2014).

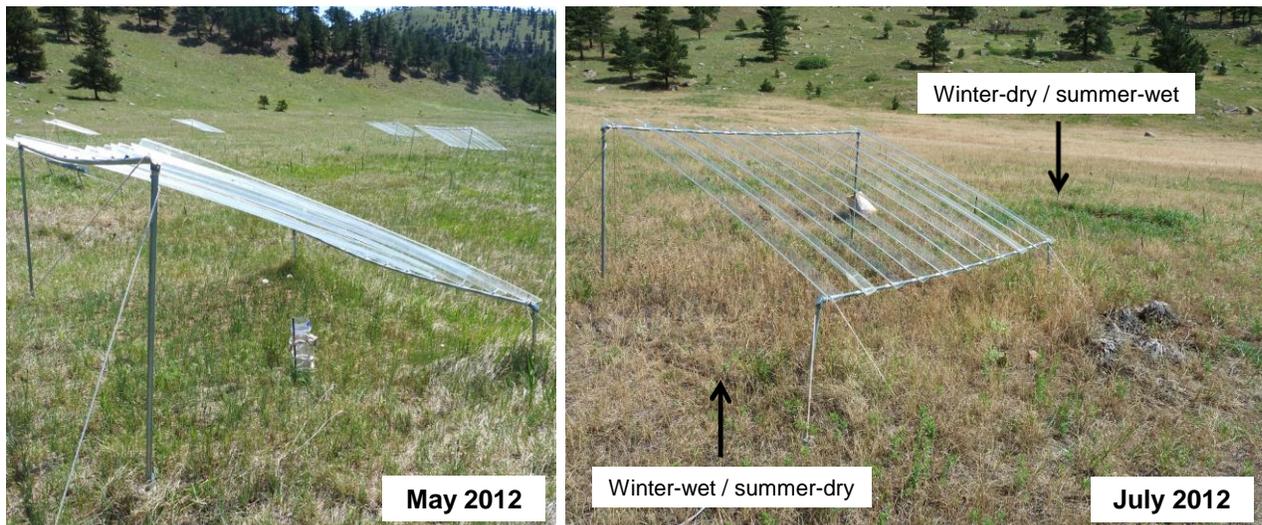
To address uncertainty in precipitation change, I established five precipitation treatments based on IPCC climate model predictions and my preliminary climate analyses: control, winter-wet/ ambient summer, winter-wet/summer-dry, winter-wet/summer-wet, and winter-dry/summer-wet (Table 2.1). The winter-wet/summer-wet treatment was created to simulate increasing frequency and intensity of precipitation in both winter and summer, and to observe how a reduction of water limitation would affect the plant community. The winter-dry/summer-wet treatment was created to simulate ‘historical’ conditions, with less precipitation falling as rain in winter, and more precipitation being received the summer, as a result of a stronger monsoon and less evapotranspiration in the past.

**Table 2.1.** Treatment manipulations for precipitation experiment. Water additions and rain-out shelters were used to either increase or decrease precipitation by ca. 50% of ambient precipitation received in summer or winter.

Treatment	Winter precipitation (Oct – March)	Summer precipitation (April – September)
Control	ambient	ambient
Winter-wet	50% increase	ambient
Winter-wet / summer-dry	50% increase	50% decrease
Winter-wet / summer-wet	50% increase	50% increase
Winter-dry / summer-wet	50% decrease	50% increase

I randomly allocated each treatment to ten 2m x 2m plots in five blocks at the study site, for 50 plots total. All study plots were located greater than 3 m away from each other within a

ca. 1 ha. area. To increase precipitation in the winter-wet and summer-wet precipitation treatments, I added water to plots in early spring and late fall, or mid-summer, respectively, using well water that is available at the study site. Precipitation additions were added using hand sprayers in relatively large events (1 – 2 cm), because precipitation events are also forecast to become more intense in the future (IPCC 2007). To decrease summer or winter precipitation in summer and winter-dry treatments, I used passive deflection rain-out shelters that blocked 50% of incoming precipitation, based on the design of Yahdjian and Sala (2002), and used in a drought experiment by Cherwin and Knapp 2012. The shelters covered 2.25 x 2.5 m areas over plots. Each shelter had eleven 11 cm wide by 2.5 m long transparent Plexiglass troughs attached to metal poles and placed at an incline above plots. Plexiglass troughs alternated with open spaces and were designed to channel ~50% of incoming precipitation off of study plots (Fig. 2.1). Rain-out shelters were designed to have minimal effects on wind speed, temperature, or incoming light (Yahdjian and Sala 2002).



**Fig. 2.1.** Photographs of rain-out shelters at the field site in May and July 2012, and a winter-dry / summer-wet plot in July 2012.

### 2.3.3 Measurements

Rain gauges were placed at the site to record ambient rainfall and reduced rainfall under shelters over the course of the experiment (Fig. 2.1). To ensure that precipitation manipulations were having the desired effects on available soil moisture, I measured volumetric water content in the top 12 cm of soil using a Hydrosense soil moisture probe (Decagon Devices, Pullman, WA) in June and August 2010, and March, June, and August 2011-2013 (Appendix 1). Soil surface temperature, temperature 10 cm above the ground, and photosynthetically active radiation in four control and four sheltered plots were recorded with HOBO temperature dataloggers over several two-week periods to measure any variation in microclimate caused by shelters.

To quantify changes in community composition in response to precipitation manipulations (**H1**), cover of living plant species was measured in each plot in June 2010 (pre-treatment), and August 2010, and then April, June, and August of 2011, 2012, and 2013. Cover of all species was estimated using the point intercept method with two 0.5 x 0.5 m quadrats with strings forming 36 intersections centered in the north and south sides of each plot. The number of intersections intercepting a plant species was divided by the total number of intersections per plot (72) for absolute cover of each plant species. For cover analysis, plant species were lumped into five functional groups: exotic grasses, exotic forbs, native cool-season grasses, native warm-season grasses, and native forbs. On June sampling dates, I also recorded all species present in plots to calculate Shannon-Weiner diversity for each plot. Species that were present in plots, but not recorded in cover surveys, were assigned cover values of  $\frac{1}{4}$  of the lowest value measured (0.35%).

To estimate effects of precipitation manipulations on plant-available nitrogen and seasonal patterns in nitrogen dynamics, I used ion-exchange resin bags placed in each plot from April-May, June-September, and October-March in 2011 and 2012, and from April-May in 2013. Resin bags were constructed similar to the methods of Binkley and Matson (1983) and Lajtha (1988). Approximately five grams of mixed-bed ion-exchange resins (Sigma Amberlite 150 mixed bed resins) were placed in nylon casing with plastic hoops to provide structure. Bags were washed in a 0.5 M HCl solution, and then rinsed with DI. Two bags were buried at 5cm depth in the center of each plot and remained in plots over the season. After removal, resin bags were extracted in 40 ml of 2 M KCl. Inorganic nitrogen was analyzed on a on a Lachat QuickChem 8500 Flow injection analyzer.

To address whether increases in exotic winter-active species reduce resources available for later-growing species under different precipitation regimes (**H2**), I compared cover of *B. tectorum*, the most common winter-active species at our site, in April to available soil moisture in early summer, plant-available nitrogen in spring and summer, and Shannon Weiner diversity on mid-June sampling dates. I also wanted to observe how precipitation treatments affected phenology of dominant winter-active species. To do this, I visually estimated the amount of *B. tectorum* that were flowering in each plot in late April/early May, and the amount that had senesced in each plot in mid-June. I estimated amounts as either 0, 1/4, 1/2, 3/4, or all *B. tectorum* in plots. I conducted visual estimations on 5/4 and 6/22/2011, 4/30 and 6/12/2012, and 4/14 and 6/15/2013.

To assess ecosystem productivity under different precipitation scenarios (**H3**), I sampled peak aboveground biomass in 0.1 m<sup>2</sup> subplots centered within each plot at the end of each

growing season in late August. Biomass was clipped at ground level, dried for three days at 60° C, and weighed.

#### 2.3.4 Statistical analysis

To discern if amounts of seasonal precipitation have changed in the recent past, I compared average winter and summer precipitation from 1900-1970 and 1970-2010 from historical climate records along the Front Range of Colorado using one-way ANOVAS. I also compared microclimate variables from control and sheltered plots using one-way ANOVAS. I analyzed cover of different functional groups, total nitrogen extracted from resin bags, phenology of *B. tectorum*, and aboveground biomass using linear mixed-effects models. Year and precipitation treatment were considered fixed effects in analyses, and individual plot and block were considered random effects. For cover analyses, data from April 2010 was analyzed separately to determine pretreatment differences in community composition. I did separate analyses for each monthly survey date (April, June, or August) over the four year study period to focus on effects of treatments over time, rather than seasonal fluctuations in plant abundance. In addition, analyses were only conducted for dates when a functional group had greater than 5% average cover over all plots, because I was not interested in dates when the focal group was not physiologically active. For example, there was high cover of exotic grasses in April and June, but most grasses were senesced by August, so only April and June dates were included in analyses. Cover values that strongly violated assumptions of homogeneity of residuals were square-root transformed before analysis. Some resin bags had anomalously high nitrogen. To remove effects of these outliers, nitrogen values that were greater than 3 standard deviations away from the mean values were removed prior to analyses. A total of nine nitrogen samples were identified as

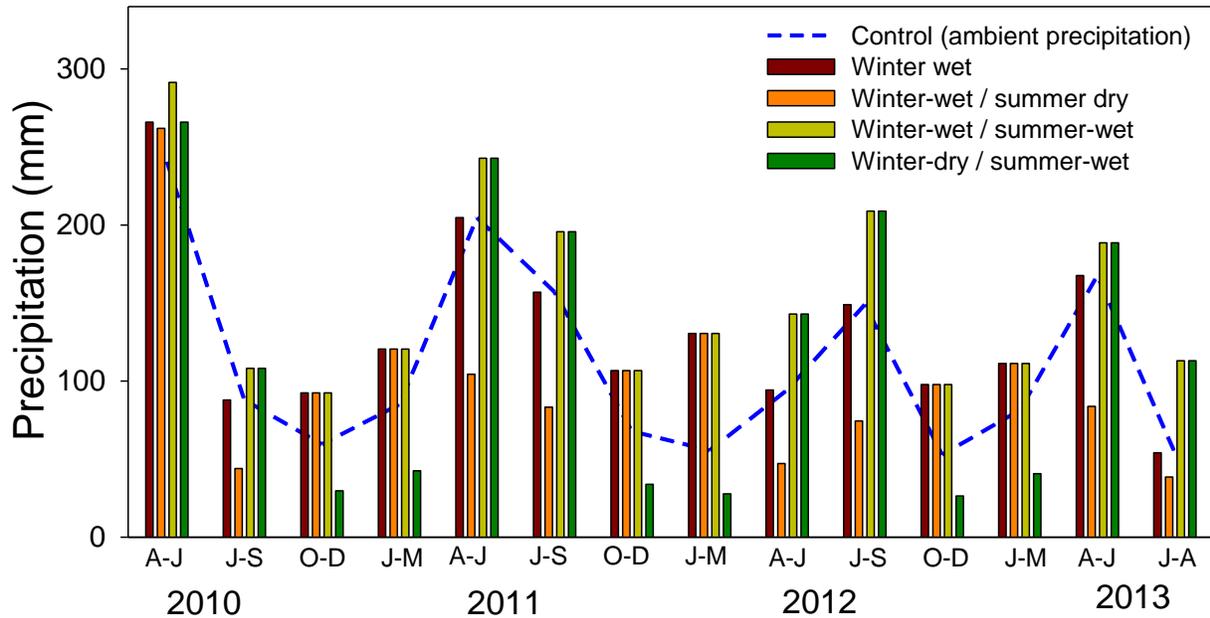
outliers and removed from analyses over all sampling periods. Total nitrogen values were log-transformed before analyses to meet assumptions of homogeneity of residuals.

I also used linear-mixed models to examine effects of *B. tectorum*, specifically, on soil moisture, total nitrogen in spring and summer, and diversity. Year and % cover of *B. tectorum* were considered fixed effects in these models, and individual plot and block were considered random effects. To obtain  $R^2$  values, all variables were also analyzed with linear models that excluded random effects of block.  $R^2$  values reported in results are from linear models, while  $p$ -values are from linear-mixed models. All statistical analyses were performed in the statistical program R (R Development Core Team 2012). Linear mixed models were conducted using the lme4 package (Bates et al. 2011), and  $p$  values for treatment differences were estimated using the p.val function from the Language R package (Baayen 2011) in R.

## 2.4 Results

Comparisons of pre-1970/post-1970 precipitation from seven weather stations along the Front Range showed a ca. 10% increase in precipitation in winter (Oct-March, Fig. A1,  $p = 0.007$ ), but no change in summer precipitation (April-Sept., Fig. A1,  $p = 0.3$ ). Temperatures at ground level and 20 cm above ground were 1.3°C greater under shelters than in un-sheltered plots (all  $p < 0.01$ ). Rainout-shelters did not significantly reduce transmittance of PAR (all  $p > 0.09$ ). In March 2011, 2012, and 2013, plots with rainout-shelters had an average of 15% less volumetric soil moisture, and plots receiving winter water additions had 35% greater soil moisture than control plots (Fig. A2). In June 2010-2013, rain-out shelters reduced soil moisture by an average of 20%, and summer water additions increased soil moisture by an average of 20% compared to control plots. On August sampling dates in 2010, 2011, and 2013, both rain-out

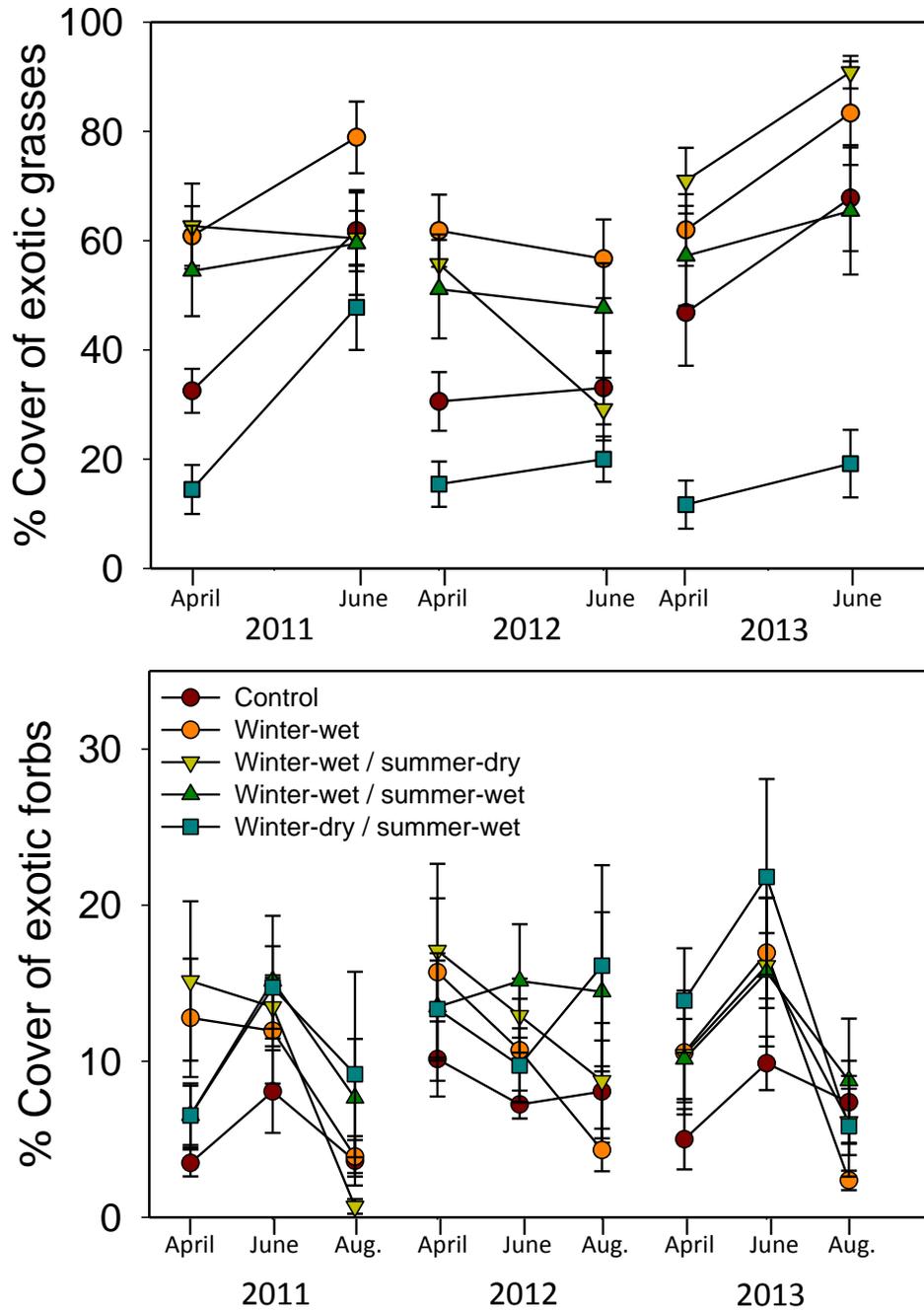
shelter and control plots had very dry soils, however, in August 2012 all soils were very wet after heavy rains (Fig. A2). Over all August sampling dates, summer water additions increased soil moisture by an average of 35% compared to controls (Fig. A2). Precipitation received by different treatments is shown in Fig. 2.2. Ambient precipitation varied over the course of the experiment. 2010 and 2011 received the highest yearly precipitation over the four year period. 2011 and 2013 had wetter-than average springs, whereas 2012 had a very dry spring, and was the driest year in the study period (Fig. 2.2). Over summer 2010, 46 mm of water was added to summer-wet plots, followed by 77 mm in summer 2011, 109 mm in summer 2012, and 80 mm in summer 2013. Rain-out shelters blocked 48 mm of precipitation from summer-dry plots in summer 2010, followed by 174 mm in summer 2011, 88 mm in summer 2012, and 99 mm through the end of the experiment in August 2013. Over winter 2010-2011, 73 mm of water was added to winter-wet plots, followed by 114 mm in winter 2011-2012, and 75 mm over winter 2012-2013. Rain-out shelters blocked 73 mm of precipitation from winter-dry plots over winter 2010-2011, followed by 62 mm over winter 2011-2012, and 67 mm over winter 2012-2013.



**Fig. 2.2.** Graph of precipitation (mm) received by treatments from April 2010 through August 2013. Precipitation values are summed over April-June, July-September, October-December, and January-March.

Absolute cover of functional groups did not differ among treatments in April 2010 (pretreatment), June 2010, or August 2010 (all  $p > 0.4$ ). In April 2011-2013, exotic grasses were more abundant in all winter-wet treatments than in the control or winter-dry/summer-wet treatment (all  $p < 0.01$ , Fig. 2.3). However, by June 2011-2013 sampling dates, cover of exotic grasses did not differ between control and winter-wet treatments (all  $p > 0.1$ , Fig. 2.3). Cover of exotic grasses was greater in the winter-wet and winter-wet/summer-wet treatments than in the winter-dry/summer-wet treatment over June 2011-2013 sampling dates (all  $p < 0.01$ ), and by June 2013, the winter-dry/summer-wet treatment had 70% less exotic grass cover than all other treatments (all  $p < 0.01$ , Fig. 2.3). Cover of exotic forbs was higher in the winter-wet and winter-wet/summer-dry treatments than in the control treatment (all  $p < 0.02$ ) over April sampling dates, and higher in the winter-dry/summer-wet treatment than in the control treatment over June

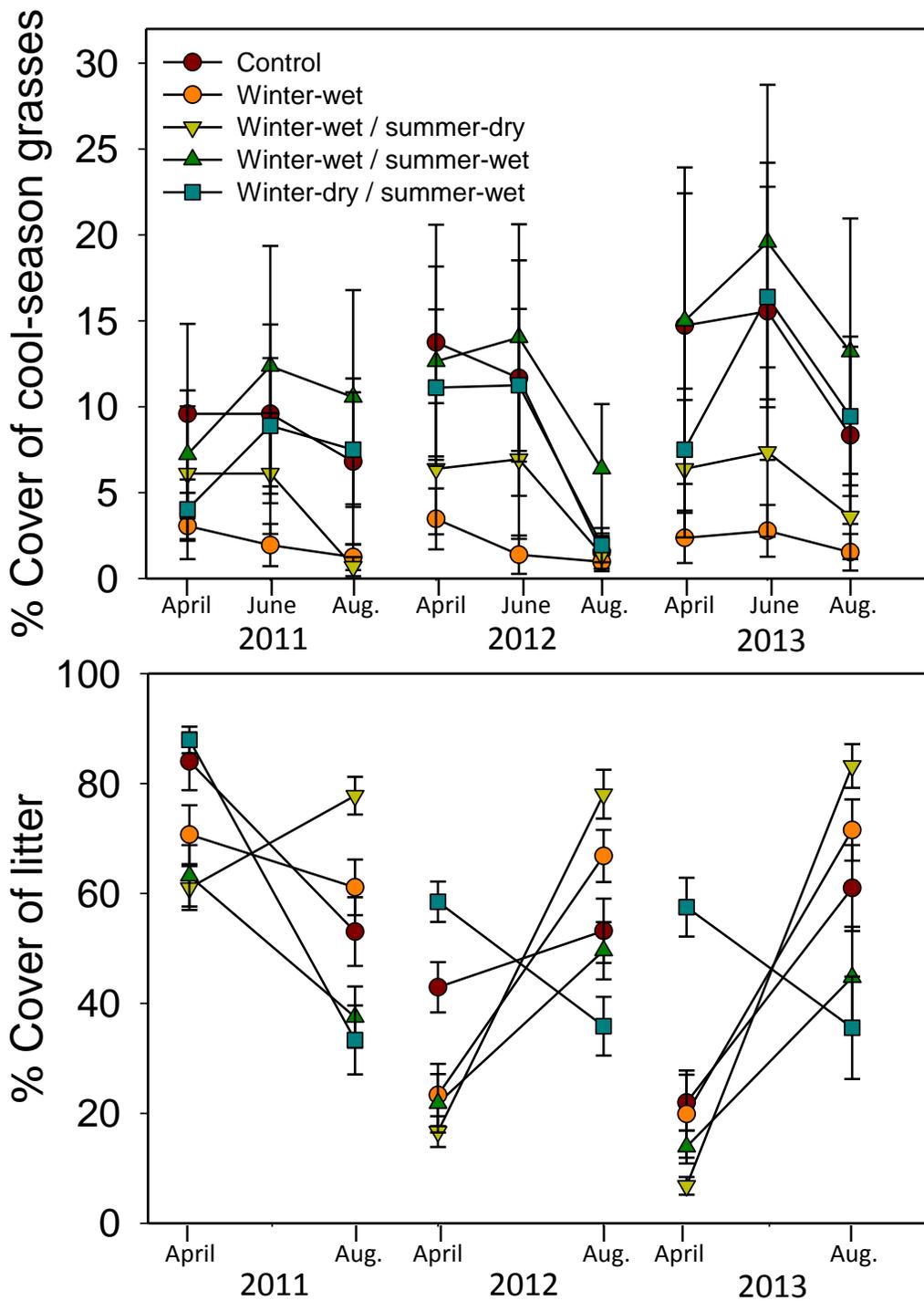
sampling dates ( $p = 0.04$ ). Cover of exotic forbs did not differ significantly between treatments on August sampling dates (all  $p > 0.2$ , Fig. 2.3).



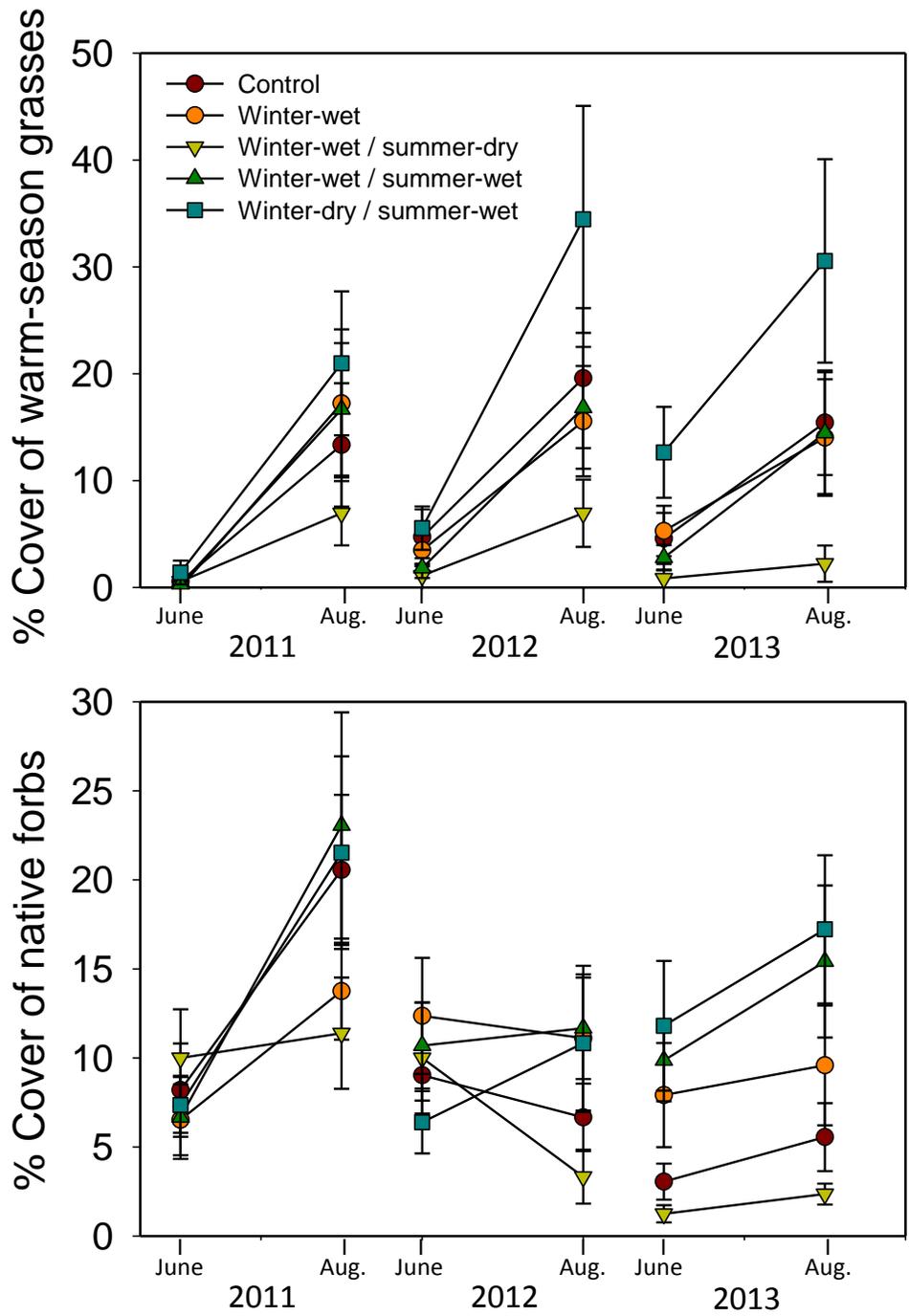
**Fig. 2.3.** Top panel shows percent cover of exotic winter-active grasses on April and June sampling dates 2011-2013 +/- standard error. Exotic grasses were most abundant in winter-wet treatments in April ( $p < 0.01$ ), and least abundant in the winter-dry treatment ( $p < 0.01$ ). Bottom panel shows % cover of exotic forbs on April, June, and August sampling dates 2011-2013.

Cover of cool-season native grasses was low compared with other cover groups, and did not differ between treatments on any sampling dates (all  $p > 0.2$ , Fig. 2.4) but was higher overall in April and June 2013 than in previous years (all  $p < 0.05$ , Fig. 2.4). Warm-season grasses did not differ between treatments on June 2011 or 2012 dates, however, by June 2013, cover of warm-season grasses was significantly higher in the winter-dry/summer-wet treatment ( $p = 0.02$ ). In August 2011- 2013, cover of warm-season grasses was higher in the winter-dry/summer-wet treatment than in the winter-wet/summer-dry treatment ( $p = 0.05$ ), and higher than all winter-wet treatments in 2012 and 2013 (all  $p < 0.006$ , Fig. 2.5). Cover of native forbs did not differ between treatments on June sampling dates (all  $p > 0.3$ ); in August 2011-2013, native forbs were more abundant in winter-dry/summer-wet and winter-wet/summer-wet treatments than in the winter-wet/summer-dry treatment (all  $p < 0.007$ , Fig. 2.5).

Changes in cover of live plant species also influenced seasonal cover of dead plant matter, or litter, in plots. Cover of litter in April 2011 and 2012 was higher in control and winter-dry/summer-wet treatments than in winter-wet treatments (all  $p < 0.05$ , Fig. 2.4). Conversely, over August sampling dates, cover of litter was lowest in winter-dry/summer-wet plots, and significantly lower than control, winter-wet, and winter-wet/summer dry treatments (all  $p < 0.008$ ). Winter-wet/summer-dry plots had the highest cover of litter in August (all  $p < 0.03$ , Fig. 2.4).  $P$ -values calculated from linear-mixed models for all treatments compared to the control treatment are presented in Table A1.

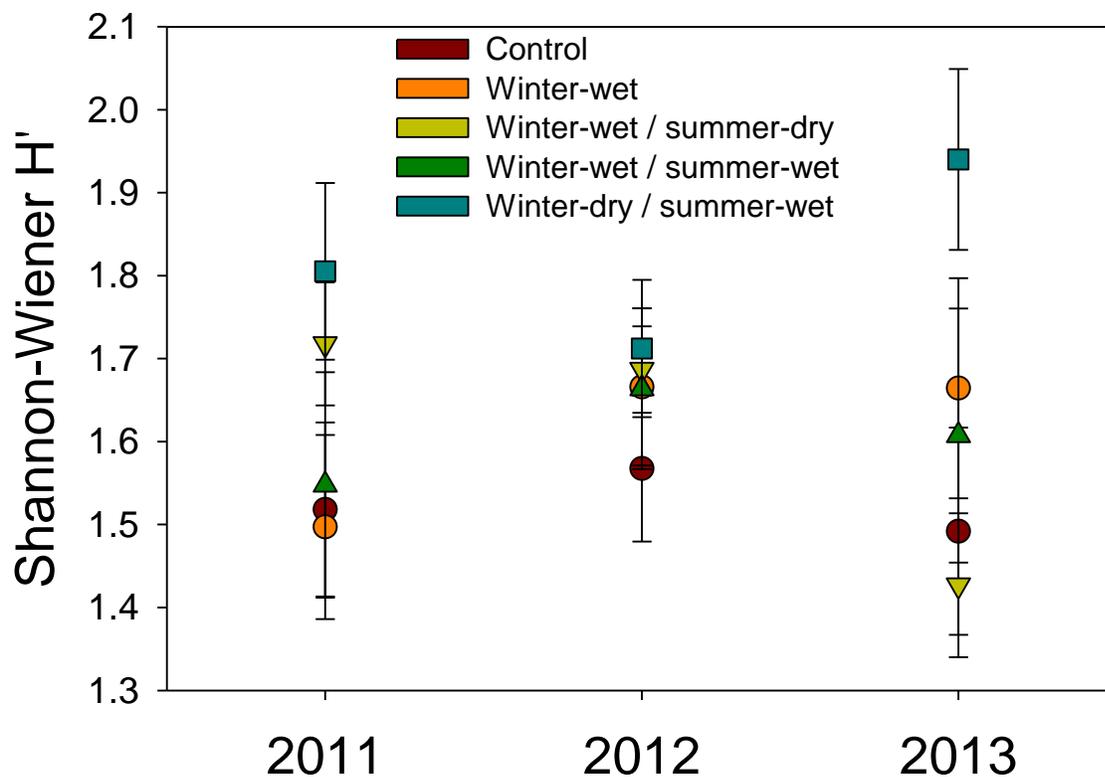


**Fig. 2.4.** Top panel shows average % cover of cool-season native grasses on April, June, and August sampling dates +/- standard error. Bottom panel shows average % cover of litter on April and August sampling dates, +/- standard error. Cover of litter was higher in winter-dry/summer-wet plots than in winter-wet plots in April ( $p < 0.02$ ). Winter-wet/summer-dry plots had the highest cover of litter in August ( $p < 0.03$ ).

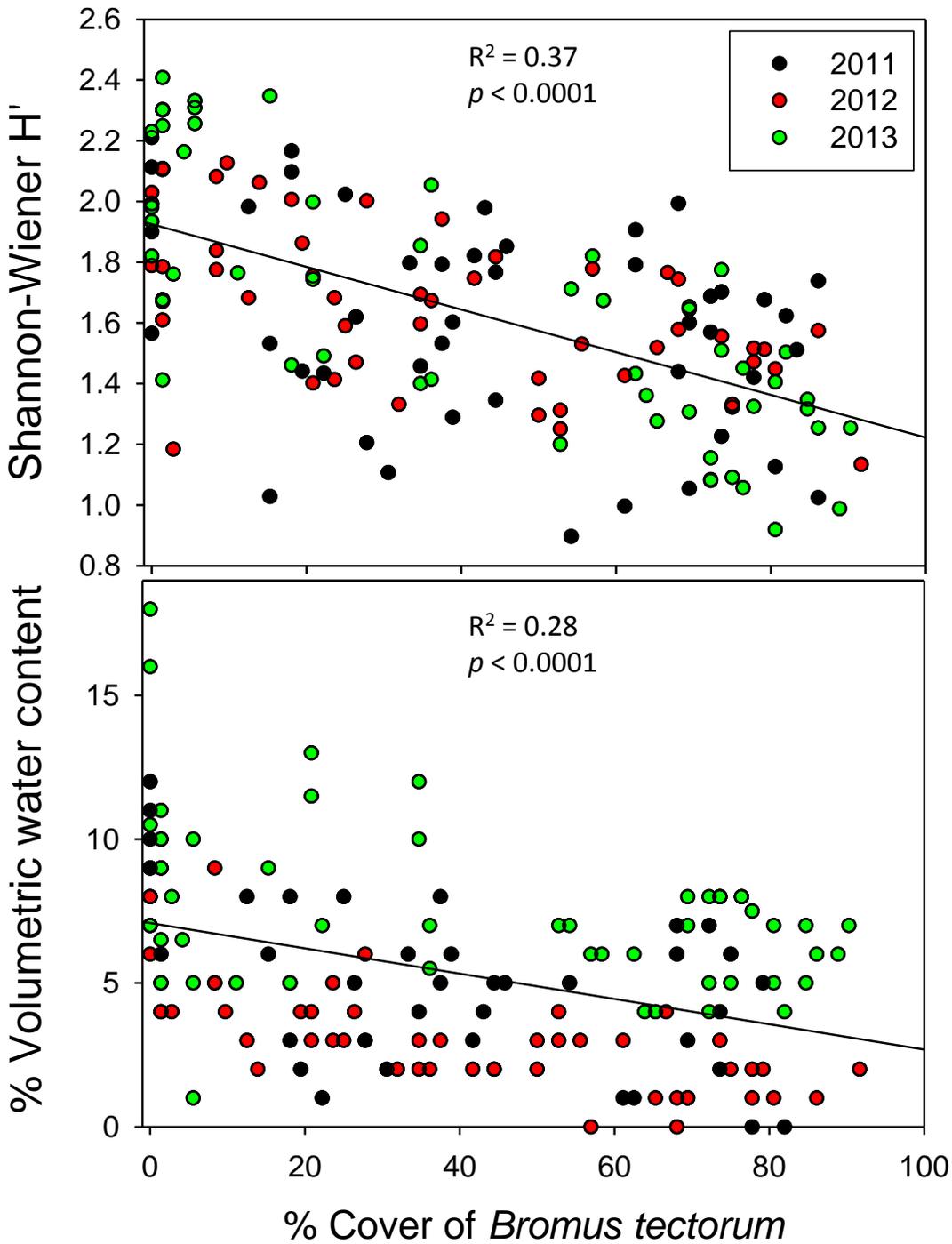


**Fig. 2.5.** Top panel shows average % cover of native warm-season grasses and bottom panel shows average % cover of native forbs on June and August sampling dates 2011-2013 +/- standard error. Native warm-season grasses were more abundant in winter-dry/summer-wet plots than in winter-wet plots in 2012 and 2013 ( $p < 0.05$ ). Native forbs were more abundant in winter-dry/summer-wet and winter-wet/summer-wet plots than summer-dry plots in August 2012 and 2013 ( $p < 0.03$ ).

Species richness was lower in 2012 than in 2011 or 2013 ( $p = 0.002$ ), but did not differ between treatments (all  $p > 0.3$ ). Diversity also did not differ between treatments in 2011 and 2012 (all  $p > 0.07$ , Fig. 2.6); however, diversity was higher in the winter-dry/summer-wet treatment than in all other treatments in 2013 (all  $p < 0.01$ , Fig. 2.6). Increased cover of *Bromus tectorum* in April correlated with reduced species richness ( $R^2 = 0.18$ ,  $p = 0.003$ ), diversity ( $R^2 = 0.37$ ,  $p < 0.0001$ ), and reduced volumetric soil water in plots in June ( $R^2 = 0.28$ ,  $p < 0.0001$ , Fig. 2.7). Cover of *B. tectorum* did not significantly correlate with spring or summer nitrogen values (all  $p > 0.09$ ).

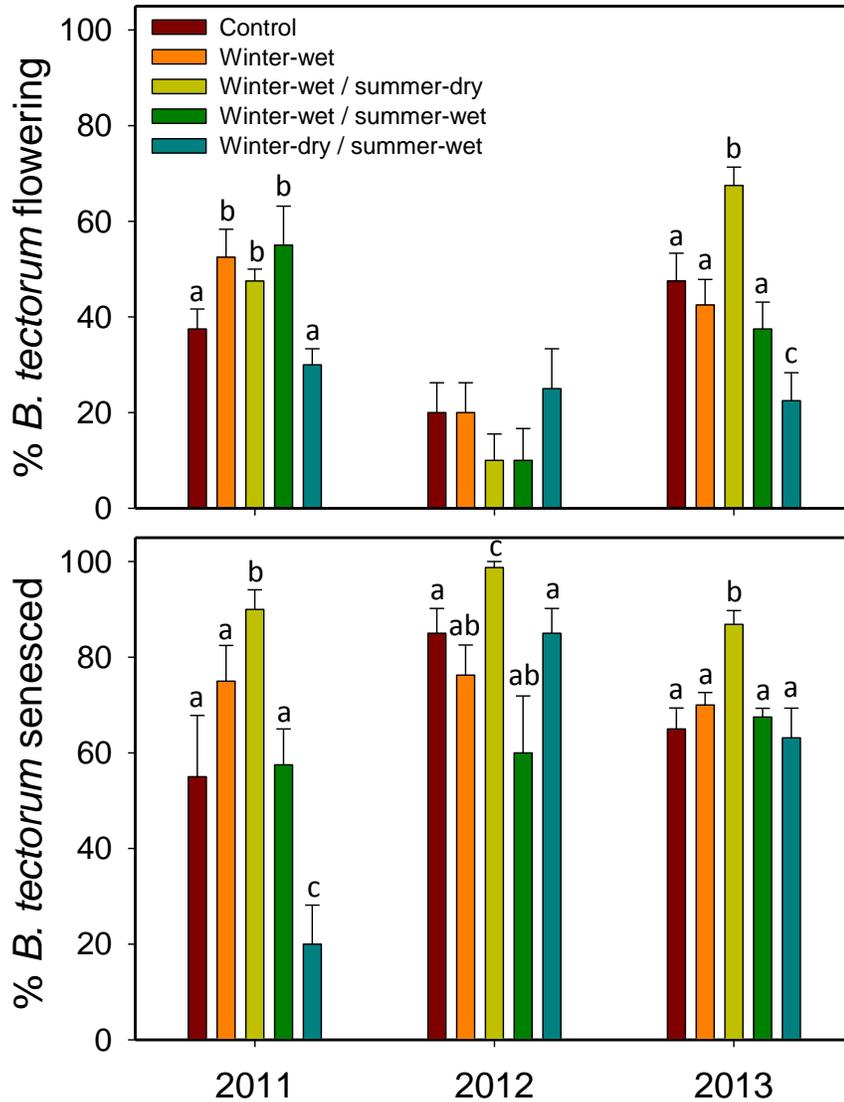


**Fig. 2.6.** Average Shannon-Weiner diversity index for treatments in 2011, 2012, and 2013 +/- standard error. Diversity was highest in winter-dry/summer-wet plots in 2013 ( $p < 0.01$ ).



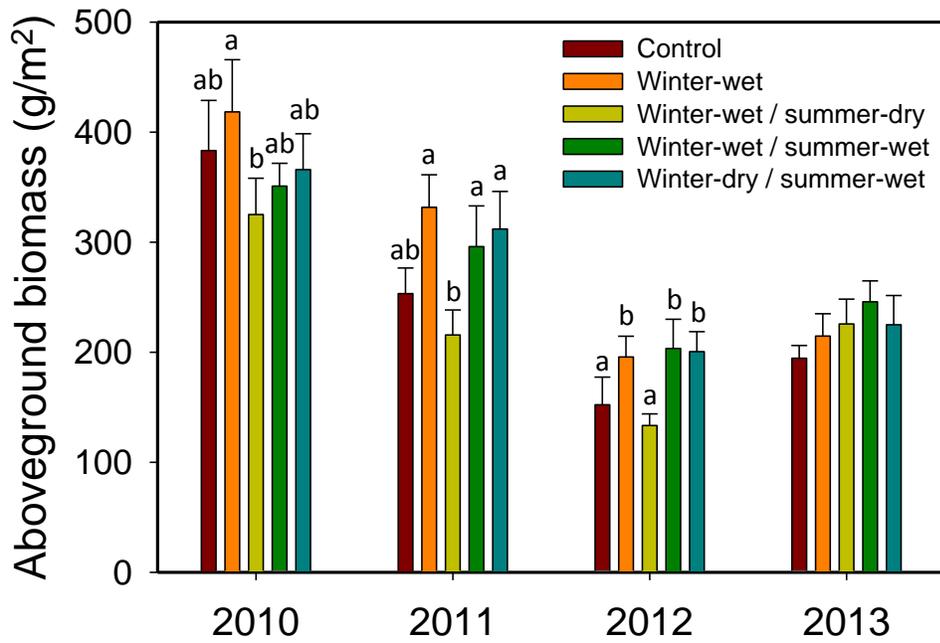
**Fig. 2.7.** Correlations between % cover of *Bromus tectorum* in April and Shannon-Weiner diversity index (top panel) and % volumetric water content (bottom panel) per plot in June 2011, 2012, and 2013.

*Bromus tectorum* flowered and senesced earlier in the winter-wet/summer-dry than in the control or winter-dry treatment in 2011 and 2013 (all  $p < 0.08$ ). However, in 2012, after a dry spring, there was no difference in the number of *B. tectorum* flowering in any treatment (Fig. 2.8). *Bromus tectorum* senesced earlier in the winter-wet/summer-dry treatment than in the control, winter-wet/summer-wet, or winter-dry/summer-wet treatments (all  $p < 0.0003$ , Fig. 2.8).

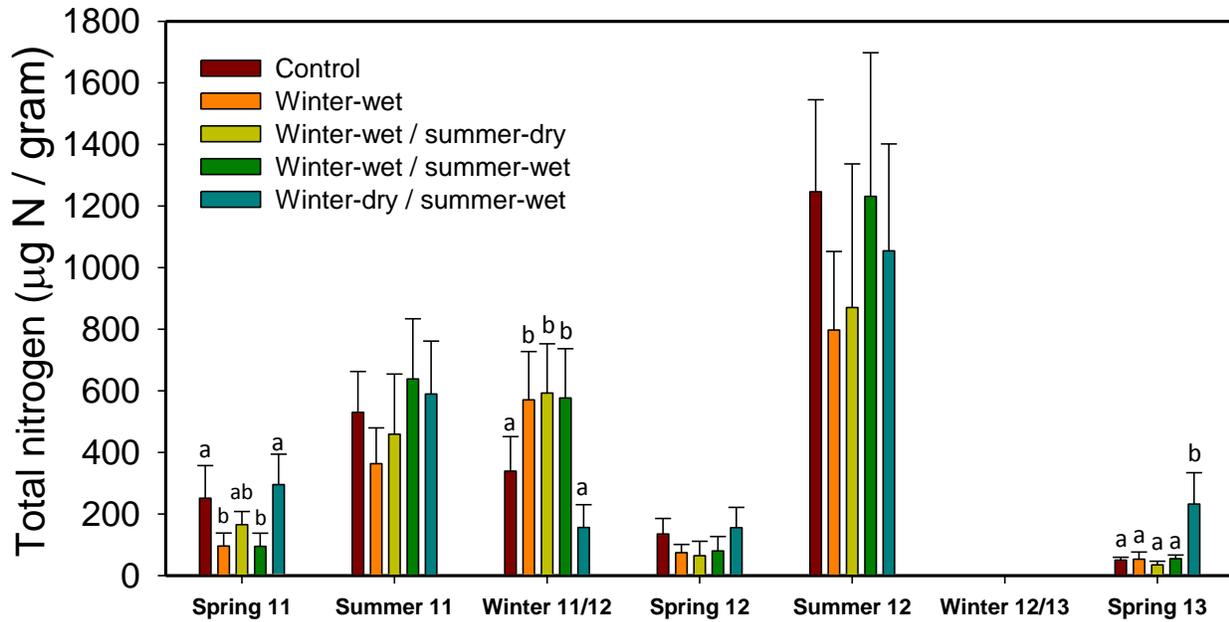


**Fig. 2.8.** Top panel shows average % of *B. tectorum* that had flowered per plot on 5/4/2011, 4/30/2012, and 4/14/2013. Bottom panel shows average % of *B. tectorum* that had senesced in each plot by 6/22/2011, 6/12/2012, and 6/15/2013, + standard error. Different letters indicate significant differences between treatments within each year at the  $p < 0.05$  level.

Aboveground biomass in all treatments differed among years (2010-2013, all  $p < 0.01$ , Fig. 2.9). In 2011 and 2012, the winter-wet/summer-dry treatment had lower aboveground biomass than the winter-wet, winter-wet/summer-wet, and winter-dry/summer-wet treatments (all  $p < 0.05$ ). Total inorganic nitrogen extracted from resin bags was higher in the winter-dry/summer-wet treatment than in winter-wet treatments during April-May 2011-2013, (all  $p < 0.01$ , Fig. 2.10). There were no significant treatment differences in total nitrogen in summers 2011-2012, however, summer 2012 had higher total nitrogen than in 2011 ( $p < 0.0001$ ). In winter 2011-2012, total nitrogen was lowest in the winter-dry/summer-wet treatment (all  $p < 0.006$ , Fig. 2.10).  $P$ -values calculated from linear-mixed models for all treatments compared to the control treatment are presented in Table A1.



**Fig. 2.9.** Average peak aboveground biomass collected from treatments in August 2011-2013, + standard error. Different letters indicate significant differences within the sampling year.



**Fig. 2.10.** Average total nitrogen extracted from resin bags placed in treatments in spring (April-May), summer (June-September) 2011-2013 and winter (Oct.-March) 2011-2012, + standard error. Different letters indicate significant differences between treatments within each season at the  $p < 0.05$  level. Nitrogen was not measured in winter 2012-2013 because of budgetary constraints.

## 2.5 Discussion

Plant communities and the ecosystem services they provide may be altered by changes in seasonal precipitation patterns resulting from climate change. Our results show that shifting the timing of precipitation can change the composition, phenology, and nutrient cycling in a grassland ecosystem, a finding one would expect from observations at regional scales (Sims et al. 1978). Increased winter precipitation benefited winter-active grass species, and increased winter precipitation coupled with decreased summer precipitation reduced abundance of native species and primary productivity.

### 2.5.1 Community composition

Increased winter precipitation led to increased cover of exotic grass species in all years, especially when accompanied by naturally wet springs, as occurred in 2011 and 2013. Similarly, in sagebrush steppe, cover of *B. tectorum* was greatest in treatments receiving 80% of yearly precipitation in winter (Bates et al. 2006). Both winter and spring precipitation are important predictors of the current distribution of the winter-annual grass *B. tectorum* (Bradley 2009). Control plots had lower cover of exotic grasses in April, but by June in most years, cover of exotic grasses increased and did not differ significantly from winter-wet plots. Rapid germination and growth in late spring allows *B. tectorum* to compensate for drier winters (Mack and Pyke 1983). If grasslands along the Colorado Front Range begin to receive a greater proportion of precipitation in winter or spring in the future, invasion potential of exotic grasses will increase.

Reducing winter precipitation by 50% drastically reduced cover of exotic grasses. By 2013, after three years of winter drought, exotic grass cover was over 70% lower in winter-dry plots than in control plots. This reduction indicates that after several years of winter drought, populations of exotic grasses may be reduced to the point where effective management could allow for reintroduction of desired species. Although climate projections indicate that winter precipitation may increase in northern Colorado in the future, they also predict an increase in the frequency of intensive droughts (IPCC 2007), and these drought periods may help control the spread of exotic grasses.

Contrary to our predictions, exotic forbs were not significantly affected by precipitation manipulations. Instead, cover of exotic forbs varied greatly among plots and over time. There may be several reasons for this observation. Many exotic forbs are tap-rooted, and although they

are active in early spring, some remain active and flower later in the year than natives. Exotic tap-rooted forbs can use water from deeper soil layers or different times of year than exotic grasses (Hill et al. 2006, Kulmatiski et al. 2006) allowing them to avoid drought and benefit from increases in either winter or summer precipitation. In observational studies, productivity of grasses usually responds strongly to variation in precipitation, however, productivity of forbs does not always correlate with precipitation (Nippert et al. 2006). Forbs may be more responsive to combinations of climate change factors. Zavaleta et al. (2003) found forbs to respond more strongly to increased precipitation in combination with increased CO<sub>2</sub> and temperature than to increased precipitation alone.

Native warm-season grasses and forbs benefited from summer precipitation additions, and were less abundant in treatments receiving additional winter precipitation. The reduction of warm-season grasses and native forbs, even in winter-wet treatments that received ambient precipitation in summer, indicates that growth of earlier growing species was likely impacting that of later growing species. Warm-season grasses were most abundant in the winter-dry/summer-wet treatment, and this treatment had the lowest cover of exotic grasses early in spring. The winter-wet/summer-wet treatment had greater cover of native forbs, indicating that if precipitation increases year-round in the future, native forbs may be able to coexist in grasslands with early growing winter-actives.

Native cool-season grasses responded differently to treatments than other native species. Cool-season grasses were not significantly less abundant in winter-wet treatments than in control treatments. While other functional groups had directional responses to treatments over the course of the study, cover of cool-season grasses remained relatively constant over three years, only increasing slightly in the winter-wet/summer-wet treatment by 2013 (Fig. 2.4). The

dominant cool-season grass at our field site, *Pascopyrum smithii*, is active earlier in the year than other native grasses and forbs (Kemp and Williams 1980), and may be able to benefit somewhat from increased winter precipitation and avoid summer drought. These traits will be beneficial if precipitation patterns shift to a more winter-wet pattern. If perennial cool-season grasses can persist through years with variable precipitation patterns, they may be able to compete with fast-growing invasive plants in drought years because they require fewer resources (Allen 1982).

### 2.5.2 Competition and phenology

Increased cover of *B. tectorum*, the most common winter-active species at the study site, correlated with reduced diversity and soil moisture in plots. *Bromus tectorum* invasions have also been associated with lower diversity in sagebrush steppe ecosystems in California and Idaho (Concilio et al 2013, Prev y et al. 2010). *Bromus tectorum* is capable of rapid use of shallow soil water (Melgoza et al. 1990), and this reduction in soil moisture may help *B. tectorum* stay dominant in ecosystems it invades. Increased winter precipitation, coupled with reduced summer precipitation, not only negatively impacts species diversity by reducing water availability, but probably also by increasing competition from winter-active species, which further reduce available resources. These results show that plant-plant interactions play an important role in determining community responses to climatic changes (Brooker 2006, Suttle et al 2007).

Precipitation changes also significantly affected phenology and senescence of the plant community. Winter-wet treatments had greater cover of vegetation and less litter in early spring; however, they had higher cover of litter in August. Conversely, the control and the winter-dry/summer-wet treatments had high litter in spring and less litter in late summer. *Bromus tectorum* senesced earlier in June in the winter-wet/summer-dry treatment than in other

treatments. The winter-wet/summer-dry treatment also had the highest cover of litter by mid-August. Studies have found that warmer mean temperatures are leading to earlier onset of the growing season in ecosystems around the world (Linderholm 2006). In alpine meadows in Colorado, herbaceous species are flowering earlier, and fewer plants are flowering by mid-summer (Aldridge et al. 2011). This shift in the timing of the growing season caused by warmer temperatures may be exacerbated by increased winter rain and summer drought, leading to earlier growing seasons and earlier senescence of plants in summer.

### *2.5.3 Productivity and nutrient availability*

Although we observed strong shifts in community composition, results for aboveground net primary productivity did not follow our hypotheses. Productivity was reduced in the summer-dry treatment in 2011-2012, when a greater proportion of ambient precipitation was received in summer; however, productivity was similar in all treatments in 2010 and 2013. Productivity of a calcareous grassland in Europe was also reduced slightly after summer drought, but was not altered significantly by increased precipitation (Grime et al. 2008). Both 2010 and 2013 experienced large precipitation events in early spring and summer, and this additional precipitation could have masked effects of water addition and drought treatments. Aboveground biomass was greatest in all treatments in 2010, the year with the highest ambient spring and summer precipitation, providing further evidence that precipitation drives productivity in many grassland ecosystems (Lauenroth and Sala 1992, Knapp and Smith 2001). It is interesting that the winter-wet/summer-wet treatment, which received 50% more precipitation than ambient conditions over both winter and summer, did not have higher overall biomass than other treatments. When water limitation is removed from this grassland, another resource, most likely

nitrogen, may be limiting productivity (Lauenroth 1978, Yahdjian et al. 2011). Several manipulative experiments have found that the greatest increases in plant productivity occur when increased precipitation is combined with increased nitrogen (Rao and Allen 2010). Precipitation addition without added nitrogen may actually increase microbial competition for nitrogen, or, if this occurs during the non-growing season, increased leaching of nitrogen from the ecosystem, further reducing availability of this limiting nutrient (Austin et al. 2004). Our results suggest that, although seasonal precipitation change may alter species composition of communities, overall effects on net primary production may be modest.

Precipitation patterns altered nitrogen availability in plots, and results differed between seasons and years. Nitrogen availability was lowest during spring, when ambient precipitation and plant competition are greatest. Treatments receiving additional winter precipitation had a higher amount of total nitrogen in resin bags in winter. However, in spring and summer, nitrogen availability was reduced in treatments receiving additional winter precipitation without additional summer precipitation. High precipitation in winter may lead to leaching of highly mobile  $\text{NO}_3$  from soil, and reduce availability for plants in summer (Reichman et al. 2013). Treatments receiving drought in winter had greater total nitrogen in spring, the season after rain-out shelters were removed. This could result from less plant growth during the winter, and thus less competition for nitrogen, leaving more nitrogen available for use the following season. Additionally, nitrifying bacteria can endure very dry conditions, and continue to nitrify and produce  $\text{NO}_3$  when water limitation prevents plants from using nitrogen (Davidson et al. 1990). Increased water and nitrogen availability and concurrent plant growth in winter could reduce nitrogen available for later growing spring plants. Thus, changing the seasonality of precipitation

may create a mismatch between the timing of water and nutrient availability and the historical growing season (Austin et al. 2004, Reichman et al. 2013).

## **2.6 Conclusion**

In semi-arid ecosystems, precipitation change associated with climate change will be one of the most influential global change factors driving plant species distributions in the future (Weltzin et al. 2003). My results illustrate the sensitivity of different plant functional groups, phenology, and resource availability to shifts in precipitation patterns in a semi-arid grassland. In addition, my results show how inter-specific competition might interact with precipitation change to affect properties of plant communities. Increased winter precipitation will increase abundance of exotic grasses, and, especially if coupled with drier summers, could detrimentally affect semi-arid grasslands by reducing availability of soil water for later growing plants, causing earlier dry-down and senescence of grasslands, and reducing diversity and ecosystem productivity. Management to reduce abundance of non-native grasses should be a priority in grassland ecosystems along the Front Range of Colorado, and native species that may benefit from increased winter precipitation, such as *Pascopyrum smithii* or other cool-season grasses, should be targeted for use in restoration efforts.

## CHAPTER 3

### RESPONSES OF THE PATHOGEN *USTILAGO BULLATA* TO PRECIPITATION CHANGE

#### 3.1 Abstract

*Ustilago bullata* is a fungal pathogen that infects grasses in western North America. *Ustilago bullata* infects the non-native invasive grass *Bromus tectorum*, sometimes at epidemic levels, and has been examined as a possible biocontrol for the plant species. I observed *U. bullata* infecting *B. tectorum* in a precipitation manipulation experiment I conducted in Colorado, USA. From 2011-2013, I monitored presence of the pathogen and infection rates in treatments receiving different amounts of winter precipitation to observe how simulated changes in seasonal precipitation might affect abundance of the naturally occurring pathogen. In 2012 and 2013, prevalence of *U. bullata* was greater than in 2011. Over all years, increased winter precipitation correlated with greater mean abundance of *U. bullata* in treatments. In 2012, infection with *U. bullata* led to a 21% decrease in seed production of *B. tectorum* in winter-wet plots. However, infection rates were not high enough to decrease population growth rates of *B. tectorum*. *Bromus tectorum* may become more successful in grasslands along the Front Range of Colorado if winter precipitation increases in the future; however, *U. bullata* may also increase in abundance. These observations have important implications: although invasive species may benefit from climate change, pathogens may also benefit, and decrease success of invasive plant populations in the future.

### 3.2 Introduction

Global climate change will affect the abundance and success of invasive plant species (Dukes and Mooney 1999, Thuiller et al. 2007, Hellmann et al. 2008), and plant pathogens (Coakley et al 1999, Chakraborty 2013). Further, biotic interactions between plants and pathogens may influence success of particular invasive species as the climate changes (Tylianakis et al. 2008). A considerable body of research has been conducted examining effects of climate change on invasive plant species (e.g. Hellman et al. 2008, Dukes et al. 2011). However, fewer studies have looked at how invasive plants may interact with pathogen pressure in a changing climate (Tylianakis et al. 2008). Interactions between plants and pathogens can greatly affect plant success (Van der Putten and Peters 1997).

Most research on plant pathogens and climate change concerns how crop pathogens will be altered in a changing climate (Coakley et al. 1999, Chakraborty et al. 2000). Another interesting, and less well-studied, impact of global change may be changes in success of pathogens on invasive species. Success of invasive plant species in new environments is often attributed to enemy release, or an escape from predators and pathogens in their home range (Klironomos 2002, Reinhart et al. 2003, Callaway et al. 2004). However, novel enemies in the new ranges can impact invasive plant abundance (Mack 1996, Parker and Gilbert 2004, Mitchell et al. 2006, Callaway et al. 2013), and abundance of both invasive species and novel enemies may change in the future (Chakraborty et al. 2000). This study examines responses of the invasive species *Bromus tectorum* (cheatgrass), and the native fungal pathogen *Ustilago bullata* (head smut) to simulated changes in seasonal precipitation patterns. Precipitation manipulations were designed to simulate changes in precipitation caused by climate change.

The native fungal pathogen, *U. bullata*, commonly infects *B. tectorum* (Stewart and Hull 1949, Mack and Pyke 1984, Gossen and Turnbull 1995). *Ustilago bullata* is native to North America, and it infects a number of cool-season grass species. *Ustilago bullata* lives in soil, and infects grasses during the seedling stage. The pathogen then grows systematically inside the host until flowering, when it entirely co-opts seed production of the plant, causing it to produce spores of the fungus instead of viable seeds (Alexopoulos et al. 1996, Meyer et al. 2008). Newly introduced species, such as *B. tectorum*, did not evolve with and may have less resistance to native pathogens such as *U. bullata*, and may be more easily infected than native species (Mack 1996, Parker and Gilbert 2004, Verhoeven et al. 2009, Callaway et al. 2013). In the past, there have been instances where this pathogen has reached epidemic proportions, wiping out entire populations of *B. tectorum* (Stewart and Hull 1949, Klemmedson and Smith 1964, Mack and Pyke 1984). Because of this, *U. bullata* has been suggested as a potential biocontrol mechanism for *B. tectorum* (Meyer et al. 2001, Meyer et al. 2008). Observing how changing precipitation patterns affect *U. bullata* will inform considerations for use of this pathogen as a possible biocontrol in the future.

Shifting precipitation patterns resulting from climate change have the potential to strongly impact plant pathogens. Soil-dwelling pathogens, such as *U. bullata*, may be particularly impacted by changes in precipitation and soil moisture availability. Plant microbial pathogens, especially fungal pathogens, often benefit from increased soil moisture (Schafer and Kotanen 2003, Wagner and Mitschunas 2008). Studies show that adequate soil moisture influences the abundance of *U. bullata* (Mack and Pyke 1984, Meyer et al. 2008), so future changes in precipitation and soil moisture availability should impact success of the pathogen.

In spring 2010, I observed *U. bullata* on seed heads of *B. tectorum* in a precipitation manipulation experiment in a grassland ecosystem. Over the next 3 years, I recorded observations of the fungal pathogen in different precipitation treatments to address two questions: How the seasonality and amount of precipitation affect abundance of *U. bullata*? Does presence of the pathogen reduce seed production and population growth of *B. tectorum* in precipitation manipulation treatments?

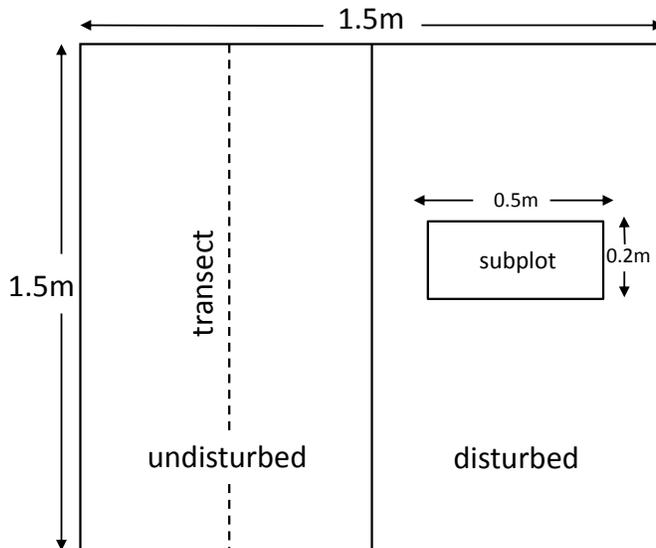
### 3.3 Methods

Observations of infection by the fungal pathogen were made in a precipitation manipulation experiment in a semi-arid grassland ecosystem near Boulder, Colorado, USA ( 40° 07' N, 105° 18' W). Elevation at the site is 1,798 m, average yearly precipitation is 475 mm per year, and average yearly temperature is 10.5° C (WRCC 2014). The site has a continental climate, with most precipitation falling in spring and early summer. A precipitation manipulation experiment was established in 2010 with five precipitation manipulations: control, winter-wet, winter-wet/summer-dry, winter-wet/summer-wet, and winter-dry/summer-wet. There were ten replicates of each treatment. All plots of the experiment were located within 1 ha of each other, on the same slope and with similar soils. More information on the experimental design of the precipitation manipulations can be found in Chapter 2.

I measured *U. bullata* presence and abundance in plots of all treatments In June 2011-2013, after all *Bromus tectorum* in plots had senesced. I visually inspected all plots for presence of the pathogen on seed heads of *B. tectorum* in each plot. In addition, I harvested six *B. tectorum* individuals per plot in June 2011-2012 and eight individuals per plot in June 2013 at evenly spaced marks 0.25 m apart along a transect running through the middle of the undisturbed

plot (Fig. 3.1). Harvested individuals were dried, weighed, and inspected for *U. bullata* infection. I counted the number of seeds produced by each *B. tectorum* individual.

In June 2012 and 2013 I also measured prevalence of *U. bullata* on *B. tectorum* growing in 0.1 m<sup>2</sup> disturbed subplots within each treatment (Fig. 3.1). Subplots were created in November 2011 to monitor demographic responses of *B. tectorum* to precipitation manipulations (Chapter 4). On November 15<sup>th</sup> 2011, 0.1 m<sup>2</sup> subplots were disturbed to remove surface vegetation. Fifty *B. tectorum* seeds were sown in each subplot. On 6/20/2012, after all *B. tectorum* in sub-plots had senesced; I harvested all aboveground biomass in subplots. Biomass of *B. tectorum* was weighed and visually inspected for infection with *U. bullata*. On October 18, 2012, I planted another 50 seeds in each subplot, and on 6/26/2013, biomass of *B. tectorum* was harvested and *U. bullata* infection was recorded. Demographic data from subplots were used to estimate the rate of population growth of *B. tectorum* in each plot (Chapter 4).



**Fig. 3.1.** Layout of sampling in plots. ‘Transect’ indicates where I sampled six *B. tectorum* in 2011 and 2012 and eight *B. tectorum* in 2013 for seed production and infection with *U. bullata*. The demography experiment was conducted in ‘subplot’.

### 3.3.1 Statistical Analyses

I employed several analyses to examine how precipitation treatments affected abundance of *U. bullata*. First, I compared presence and absence of *U. bullata* in undisturbed plots of each treatment in 2011-2013. In June 2011-2013, after all *B. tectorum* had senesced, I visually inspected all plots for presence or absence of *U. bullata* on seed heads. Because the response variable was either presence or absence, I analyzed data with generalized linear models with binomial distributions. However, presence/absence measurements could be flawed, because spatial heterogeneity in the presence of a pathogen in soil could result from factors other than precipitation treatment (Ettema and Wardle 2002). To address this, I also performed correlation analyses that only included data from plots where I observed infection by the pathogen. After removal of plots with no observed infection, I calculated the average percent of *B. tectorum* infected with *U. bullata* per treatment. This way I could look at the severity of infection in plots where I knew the pathogen was present. To examine how winter precipitation might impact infection severity, I correlated average percent of *B. tectorum* infected with *U. bullata* in each treatment in each year with the amount of winter precipitation received by that treatment in that year. I performed correlation analyses for infection severity in undisturbed plots in 2011-2013, and disturbed plots in 2012-2013.

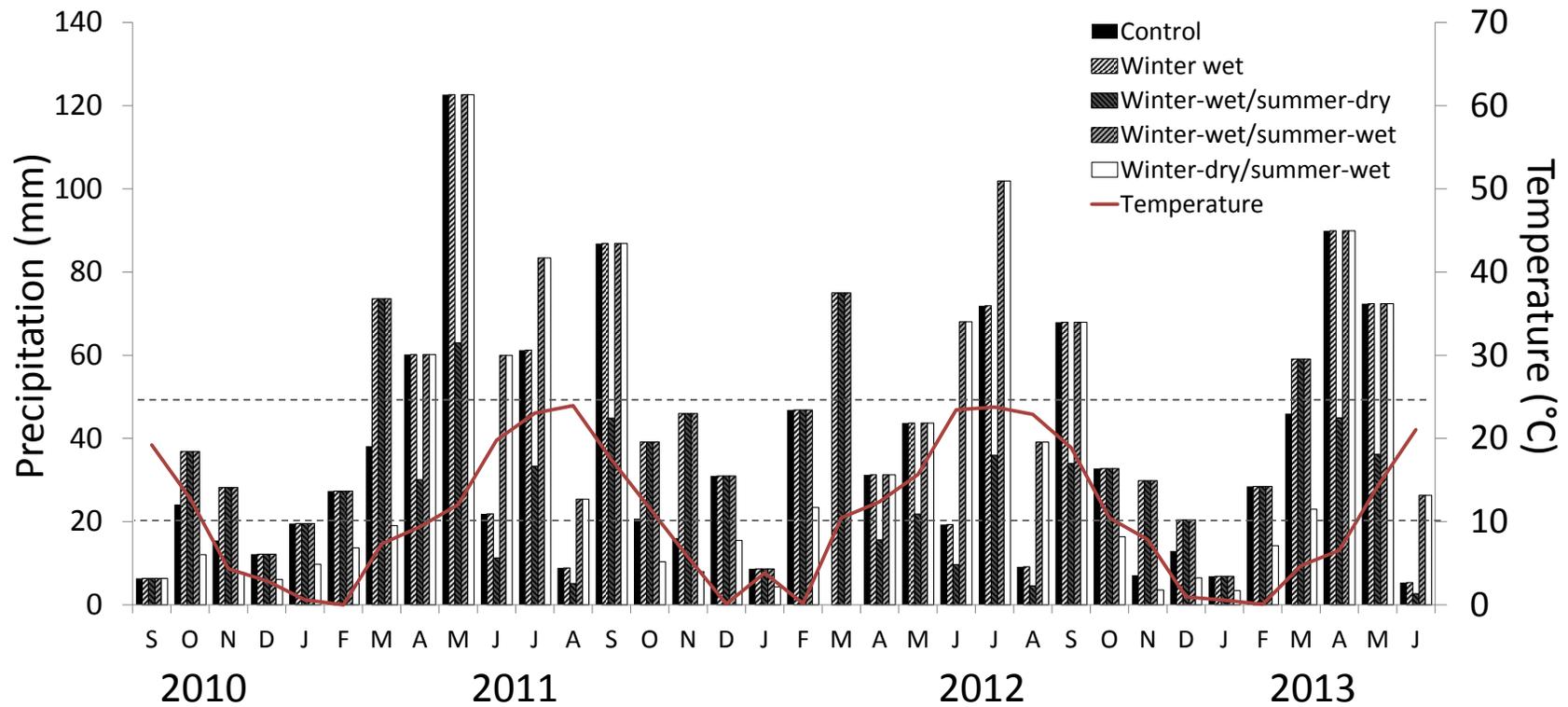
To determine if infection by *U. bullata* was negatively impacting seed production and population growth of *B. tectorum* at the field site, I examined the effects of pathogen infection on average seed production of *B. tectorum* in plots of each treatment in each year. I compared average seed production in each plot including *B. tectorum* with *U. bullata* infection (and thus no viable seeds), to average seed production excluding infected *B. tectorum*, to calculate the percent reduction in seed production of *B. tectorum* per treatment, per year. I also used linear mixed

models to examine the effects of percent of *B. tectorum* infected with *U. bullata* on estimated population growth rates of *B. tectorum*. Details on calculation of population growth rates are outlined in Chapter 4. All analyses were performed in the statistical program R (R Development Core Team 2012).

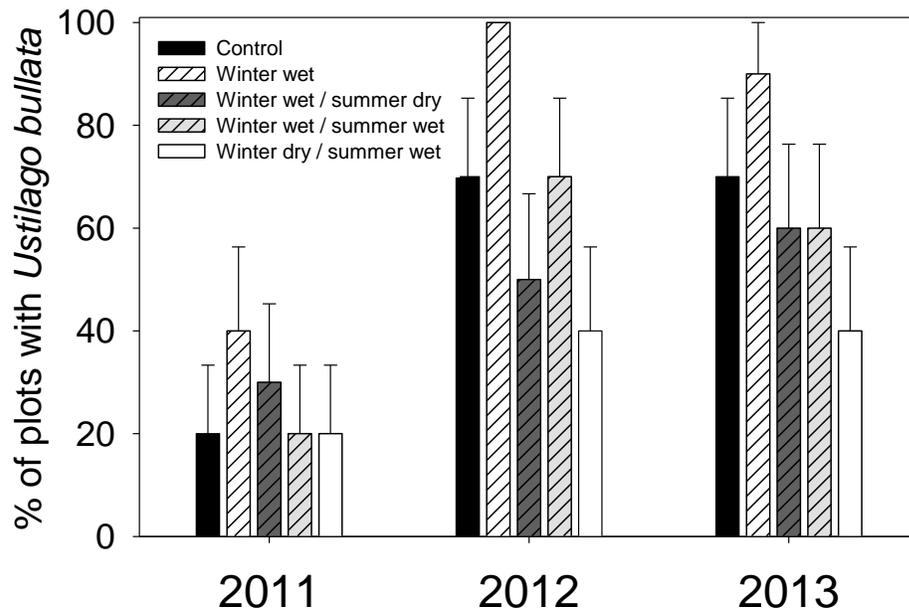
### 3.4 Results

Winter precipitation varied over the three years of the study, with drier winters in 2010-2011 and 2012-2013, and a wetter than average winter in 2011-2012. Average winter temperatures were similar over the three years, although January 2012 was unseasonably warm (Fig. 3.2). There were no significant differences in presence of *U. bullata* between treatments in any year (all  $p > 0.3$ , Fig. 3.3). Overall, *U. bullata* was present in more plots in 2012 and 2013 than in 2011 ( $p = 0.02$ , Fig. 3.3).

Correlation coefficients for infection abundance in disturbed and undisturbed plots were similar (William's t-test,  $p = 0.41$ ), so I combined all measurements from disturbed and undisturbed plots for the correlation analysis. The percent of *B. tectorum* infected with *U. bullata* positively correlated with increasing winter precipitation in undisturbed and disturbed plots over the three years ( $R^2 = 0.25$ ,  $p = 0.01$ , Fig. 3.4).

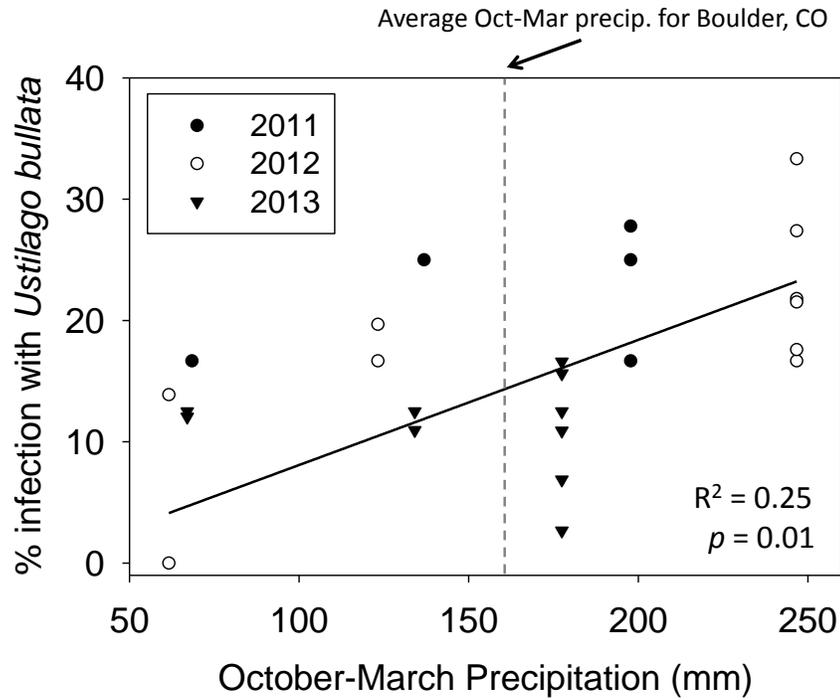


**Fig. 3.2.** Total precipitation received by each treatment in each month (bars) and average monthly temperature from September 2010-June 2013 (red line). Dotted lines indicate the temperature range within which *U. bullata* is most successful at infecting seedlings (Boguena et al. 2006).

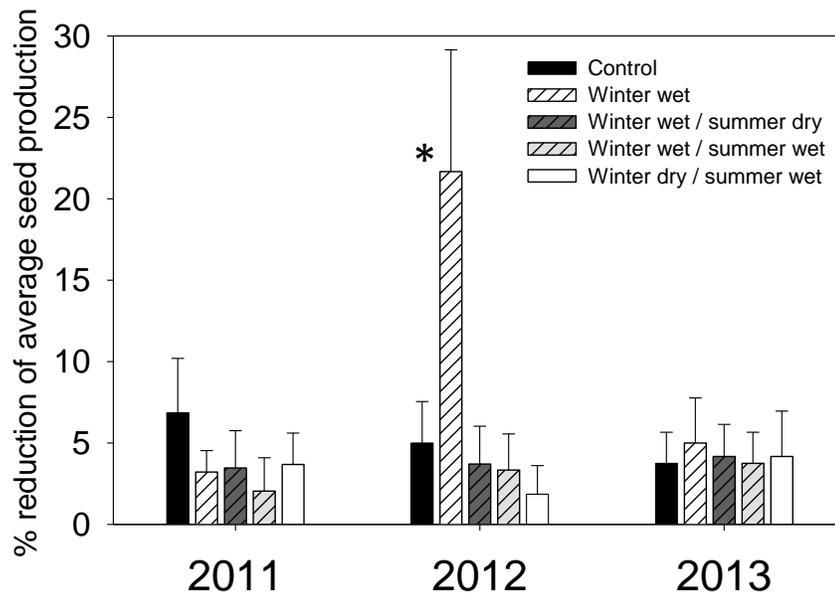


**Fig. 3.3.** Percent of plots in each treatment with *U. bullata* in 2011-2013.

Infection with *U. bullata* led to a slight reduction in seed production which was reduced by an average of 3-4% in all plots in 2012 and 2013 (Fig. 5). The largest reduction in seed production occurred in the winter-wet treatment in 2012 ( $p < 0.0001$ ), with infection by *U. bullata* leading to a 21% reduction in average seed production per plot. However, this reduction in fecundity did not significantly affect estimates of population growth rates of *Bromus tectorum* in any treatment (all  $p > 0.48$ ).



**Fig. 3.4.** Relationship between average percent of *B. tectorum* infected with *U. bullata* per treatment per year and cumulative precipitation received by that treatment from October-March. This analysis only includes plots where *U. bullata* was present.



**Fig. 3.5.** Percent reduction in seed production resulting from *U. bullata* infection in each treatment in 2011-2013.

### 3.5 Discussion

Current infection rates of *U. bullata* at the site were not high enough to significantly lower population growth rates of *B. tectorum*. However, year and precipitation treatment did affect rates of *U. bullata* infection observed in our study, and these results may have important implications for the utility of *U. bullata* as a biocontrol in future climate scenarios. Increased winter precipitation correlated with increased abundance of *U. bullata* in plots (Fig. 3.4). Notably, treatments that received above average winter precipitation had the highest rates of infection, indicating that if we receive higher than average winter precipitation in the future, these changes could benefit *U. bullata*. There are a variety of factors that could be responsible for patterns in *U. bullata* infection observed at our site. The fungal pathogen may need adequate soil moisture to survive in soil and infect emerging seedlings in late fall (Meyers et al. 2008), so treatments receiving additional winter precipitation have higher infection rates, whereas those receiving winter drought have lower rates.

Winter-wet treatments in 2012 had the highest infection abundance, and also received the most winter precipitation of all treatments in all years. In addition to a wet winter, January 2012 was also warmer than other years (Fig. 2), and warm temperatures might also benefit *U. bullata*. *Ustilago bullata* at our field site may be able to infect more seedlings during mild temperatures in fall and winter than in cold temperatures. Boguena et al. (2006) found that *U. bullata* is most successful at infecting seedlings at temperatures ranging from 20-30° C, and less successful in cold temperatures. Warmer temperatures and increased winter precipitation with climate change may benefit *U. bullata*, increasing success of this pathogen in the future.

There are many other factors that could influence abundance and success of *U. bullata* that were not examined in this study. Much more research focusing on the mechanistic reasons

for success of the pathogen in different precipitation scenarios is needed to understand how this pathogen will respond to climate change. However, our results provide preliminary evidence that increased winter precipitation could benefit the pathogen *U. bullata*. Higher infection rates of *U. bullata* in the future may decrease abundance of the invasive grass *B. tectorum*. Most climate manipulation experiments focus on responses of individual species, or trophic levels, to climate manipulations, but interactions between trophic levels will influence responses of species to climate change as well (Tylianakis et al. 2008). The observations of increased infection abundance of *U. bullata* in this climate manipulation experiment have important implications for interactions between invasive plant species and pathogens. Many invasive plants may become more successful as the climate changes; however, pathogens may also benefit, and decrease success of invasive plants in the future.

## CHAPTER 4

### EFFECTS OF PRECIPITATION CHANGE AND COMPETITION ON POPULATION DYNAMICS OF *BROMUS TECTORUM*

#### 4.1 Abstract

Shifts in precipitation patterns resulting from global climate change may influence success of invasive plant species. In the Front Range of Colorado, *Bromus tectorum* (cheatgrass) and other non-native winter annuals have invaded grassland communities and may be becoming more abundant. As the global climate warms, more precipitation may fall as rain rather than snow in winter, and this increase in rain could benefit early-growing winter annuals, such as *B. tectorum*, to the detriment of native species. This study measured responses of *B. tectorum* to simulated changes in precipitation patterns and presence of other plant species in a grassland ecosystem near Boulder, Colorado, USA. I hypothesized that *B. tectorum* would have greater population growth rates when the proportion of annual rainfall was altered to favor more winter-wet conditions. From 2011-2013, demographic data were collected to estimate population growth rates of *B. tectorum* under different precipitation scenarios and create stochastic models to predict how *B. tectorum* would respond to variable precipitation patterns over longer time periods. In addition, I collected data on neighboring plant species to examine how precipitation may interact with biotic factors to influence success of this invasive species. In 2012 and 2013, population growth rates were highest for *B. tectorum* growing in winter-wet treatments, and lowest in the winter-dry/summer-wet treatment. Survival of seedlings to flowering and seed production contributed most to population growth in all treatments. Stochastic models predicted

that populations of *B. tectorum* would increase rapidly in precipitation simulations with a higher probability of wet winters, and population sizes were predicted to be lowest in simulations with higher probabilities of dry winters. In both years, native plant biomass was positively correlated with reduced population growth rates of *B. tectorum*. This study demonstrates how interacting effects of climate change and presence of native plants can influence population growth of an invasive species. Overall, this study suggests that *B. tectorum* will become more invasive in grasslands along the Front Range of Colorado if the seasonality of precipitation shifts towards wetter winters and allows *B. tectorum* to grow when competition from native species is low.

#### **4.2. Introduction**

Climate change is expected to shift the distribution of plant species (Walther et al. 2002, Parmesan and Yohe 2003). Invasive species, in particular, may have traits that will allow them to benefit from climate change (Dukes and Mooney 1999, Thuiller et al. 2007, Hellmann et al. 2008). Accurately predicting how invasion risk will change as the climate changes is important for effective management and restoration strategies (Dukes and Mooney 1999, Bradley et al. 2009). Additionally, climate change will affect entire communities, not single species living in isolation, and research needs to address how changes in climate will affect interactions between biotic elements in an ecosystem to understand how any one species will be affected (Suttle et al. 2007, Adler et al. 2012). This study sought to examine how precipitation change associated with climate change may impact the invasive grass *Bromus tectorum*, one of the most ubiquitous non-native species in the intermountain west, using a unique combination of empirical studies examining competition from neighboring plant species and demographic analyses.

*Bromus tectorum* has invaded a large portion of rangelands in the intermountain west since its introduction to the USA from Eurasia in the late 1800's (Mack 1981). *Bromus tectorum* invasions can impact ecosystems by preempting soil resources before native plants are active, reducing plant diversity, altering nutrient cycling, and altering fire frequencies (Melgoza et al. 1991, D'Antonio and Vitousek 1992, Concilio et al. 2013). While *B. tectorum* has historically been a very successful invader in areas with winter wet climatic regimes, it is not as widespread in areas with more spring and summer precipitation (Mack 1989). However, some evidence indicates that *B. tectorum* and other winter-active non-native species are becoming more common in areas along the Front Range of Colorado (Bromberg et al. 2001, Bush et al. 2007) that historically received a majority of yearly precipitation in spring and summer.

Climatic predictions differ on exactly how precipitation will change in the future (IPCC 2007), but there is agreement that as temperatures warm, more precipitation will fall as rain rather than snow in the winter in foothills regions of the east slope of the Rockies (Knowles et al. 2006, Ray et al. 2008). Winter rain events may be more available to winter-active species, such as *B. tectorum*. In addition, warmer temperatures would increase evapotranspiration in spring and summer (IPCC 2007, Karl et al. 2009), reducing available water for later-growing native species. Bioclimatic envelope analyses and results from manipulative experiments suggest that *Bromus tectorum* may be particularly responsive to changes in precipitation (Bradley 2009, Concilio et al. 2013, Zelikova et al. 2013), so understanding how shifting precipitation patterns associated with climate change affect this species will be important for management considerations.

Other factors may influence the success of *B. tectorum* in the foothills of Colorado. Competition from resident species can affect resource availability and be a strong determinant of

invasibility of ecosystems (e.g. Tilman 1997, Naeem et al. 2000, Corbin and D'Antonio 2004). Competition from established species may limit ability of new species to invade (Kennedy et al. 2002). Alternatively, neighboring plant species may have no effect, or even facilitate establishment of new species (Bulleri et al. 2008, Griffith 2010). The outcome of interactions between species may shift under in a changing climate (Dormann 2007, Concilio et al. 2013). Competitive pressures may be affected by changes in precipitation patterns in a variety of ways. Neighboring species may be able to better take advantage of changes in precipitation and soil moisture, decreasing success of *B. tectorum*. On the other hand, competing species may not capitalize on changing precipitation patterns, and allow for an increase in unused resources available for invasive species (Davis et al. 2000). Species whose niches overlap with *B. tectorum* may experience stronger interactions with *B. tectorum* and climate change than species with strong niche differences (MacDougall et al. 2009; Adler et al. 2012).

This study examined how *B. tectorum* will respond to changes in precipitation patterns using a unique approach combining population matrix models and measures of competition to get a more informed picture of how species will respond not only to changing climatic conditions, but also changes in competition resulting from climate change. Results of this field manipulative experiment can help evaluate the predictions of bioclimatic envelope studies. Additionally, a demographic approach allows for a more detailed examination of how different life stages of *B. tectorum* will respond to changes in precipitation, and knowledge of the most vulnerable life stages of *B. tectorum* may assist management in curbing population growth of this species. The goals of this study are threefold: to understand how precipitation will affect populations of *B. tectorum* in the Front Range of Colorado, to examine how precipitation change will affect other dominant species in this ecosystem, and finally, examine how precipitation

change will interact with the plant community to affect population growth of *B. tectorum*. I used demographic parameters to estimate population growth of *B. tectorum* under different precipitation regimes, and then used these results in stochastic models to predict population growth with fluctuations in precipitation over longer timescales. I hypothesized that *B. tectorum* would have higher rates of population growth in plots receiving supplemental winter precipitation and that *B. tectorum* would be less successful in plots with more competition from other species.

## **4.3 Methods**

### *4.3.1 Field Site and Experimental Design*

The field site is in a mixed-grass prairie located approximately 15 km northwest of Boulder, Colorado, USA (40° 07' N, 105° 18' W). Elevation at the site is 1,798 m, average yearly precipitation is 475 mm per year, and average yearly temperature is 10.5° C (WRCC 2012). The site has a continental climate, with most precipitation falling in spring and early summer. Soils at the field site are classified as well drained, colluvial, sandy loams (USDA 2001). The field site has been disturbed by cattle grazing in the past, and now has a substantial invasion of *Bromus tectorum*. In June 2010, I established a precipitation manipulation experiment at the site.

Precipitation manipulations were based on information from global climate circulation models (GCMs) and preliminary climate analyses of historical data from climate stations along the Front Range of Colorado. GCMs disagree on how precipitation will change along the Colorado Front Range (IPCC 2007) but most models show increases in winter precipitation, and some show decreases in summer precipitation (Weltzin et al. 2003, IPCC 2007). To address uncertainty in precipitation change, I established five precipitation treatments based on IPCC climate model

predictions and my own preliminary climate analyses: control, winter-wet, winter-wet/summer-wet, winter-wet/summer-dry, and winter-dry/summer-wet (Table 4.1). For this study, I excluded the winter-wet/summer-wet treatment because *B. tectorum* senesces before summer precipitation additions begin, and results from the winter-wet/summer-wet treatment were similar to other winter-wet treatments (Chapter 2). I allocated each treatment to ten 2m x 2m plots at the study site for a total of 50 plots. For the winter-wet and summer-wet precipitation treatments, we added water to plots in early spring and late fall using well water that is available at the study site. To decrease summer or winter precipitation in respective treatments, I used rain-out shelters that block 50% of incoming precipitation (Yahdjian and Sala 2002). More detailed information on experimental design of the precipitation experiment is in Chapter 2.

**Table 4.1.** Treatment manipulations for precipitation experiment. Water additions and rain-out shelters were used to either increase or decrease precipitation by ~ 50% of ambient precipitation received in summer or winter.

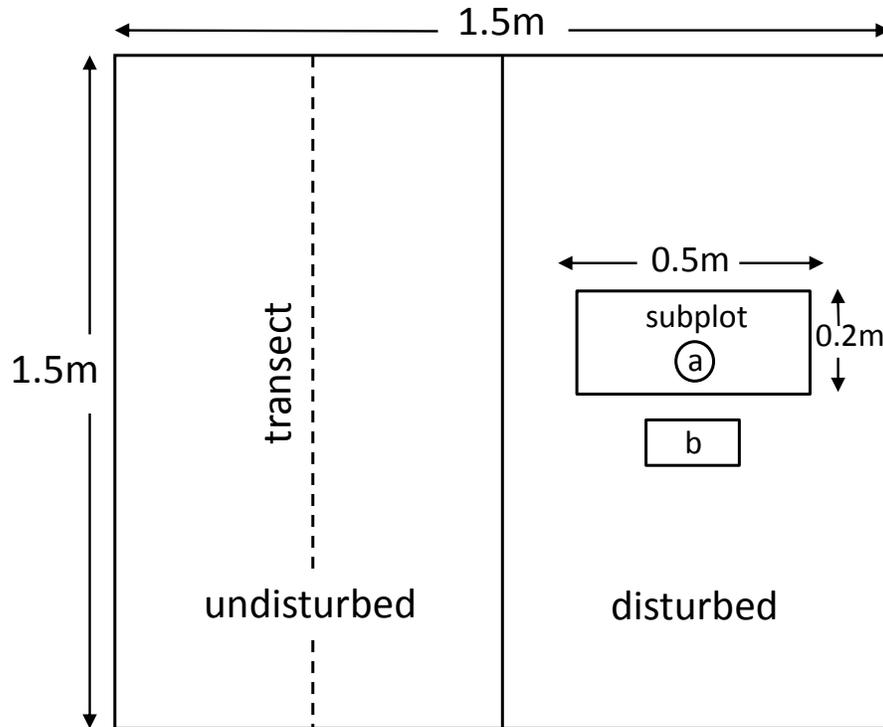
Treatment	Winter precipitation (Oct – March)	Summer precipitation (April – September)
Control	ambient	ambient
Winter-wet	50% increase	ambient
Winter-wet / summer-wet	50% increase	50% increase
Winter-wet / summer-dry	50% increase	50% decrease
Winter-dry / summer-wet	50% decrease	50% increase

#### 4.3.2 Field Measurements

I began the demographic measurements in November 2011, one year after initiation of the larger precipitation manipulation experiment. On November 15<sup>th</sup> 2011, half of each 2 m x 2 m plot was disturbed to remove surface vegetation. I monitored demography of *B. tectorum* in 0.1 m<sup>2</sup> subplots centered within disturbed sections of plots (Fig. 4.1). Removing litter and vegetation allowed for better observation of germination and survival of *B. tectorum* individuals that would otherwise be hard to see in thatch and litter layers. Fifty *B. tectorum* seeds were sown in each subplot. Prior to seed-sowings, 141.4 cm<sup>3</sup> soil samples were collected from the center of each subplot to 5 cm depth to estimate pre-existing seedbank size and viability of seeds. Soil samples were sieved to find *B. tectorum* seeds. Seeds were counted and then placed between wet filter papers in petri-dishes to test seed viability. Filter papers were kept moist over a 3 week period, and all seeds that germinated were counted and used to estimate existing seedbank size in each plot. Every two weeks after planting, from 11/25/2011 through 6/19/2011, I recorded germination and survival of all *B. tectorum* individuals growing in subplots. Each individual was classified as a new seedling (1-2 leaves, less than 1 cm tall), or a surviving seedling (3 or more leaves, > 1 cm tall, or forming a basal rosette). For censuses in fall and winter, I recorded the length of the longest leaf for the largest seedling in each subplot. In spring, I recorded the height of the tallest individual in each subplot. On 6/20/2012, after all *B. tectorum* in sub-plots had senesced, I harvested all aboveground biomass in subplots. Biomass of *B. tectorum* and all other plant species was sorted by species, dried, and weighed. Beginning in October 2012, I repeated the demographic censuses for another year. On October 18, 2013, I planted another 50 seeds in each subplot and monitored subplots every two weeks from 10/24/2012 – 6/25/2013. In addition, to test seedbank viability, I placed thirty *B. tectorum* seeds in mesh bags at 5 cm depth

below each subplot on 10/18/2012 (Fig. 4.1). The mesh bags were harvested in May 2013, after all germination had occurred. Seeds in mesh bags were classified as germinated or ungerminated. All ungerminated seeds were placed in petri dishes with moist filter paper for three weeks to test for viability. On 6/26/2013, I harvested all aboveground biomass in subplots and sorted it by species, and dried and weighed biomass. In 2012 and 2013, I also recorded infection of *B. tectorum* with the fungal pathogen *Ustilago bullata*, and those results are presented in Chapter 3.

In addition to measurements taken on *B. tectorum* in disturbed subplots, I also measured biomass and the number of seeds produced by *B. tectorum* individuals in the undisturbed side of each plot. I harvested 6 individuals per plot in June 2012 and 8 individuals per plot in June 2013 at evenly spaced marks along a transect running through the middle of the undisturbed plot (Fig. 4.1). Individuals were dried, weighed, inspected for *U. bullata* infection, and all seeds produced per individual were counted.



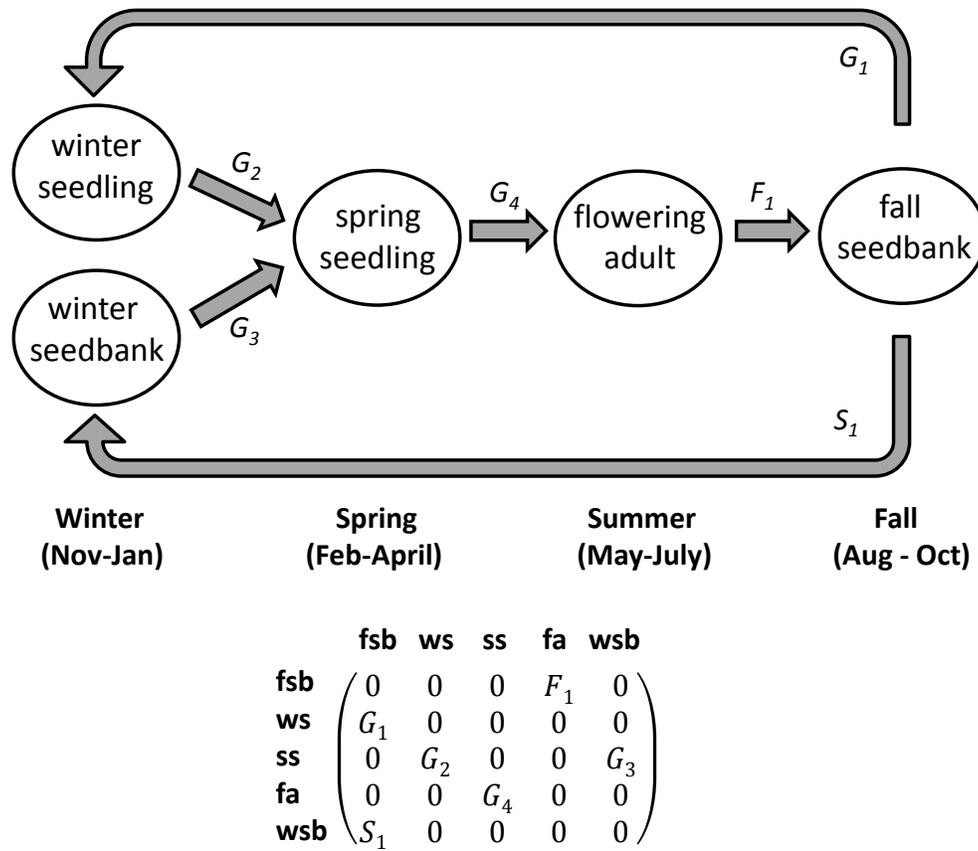
**Fig. 4.1.** Layout of sampling in plots. All demographic censuses in 2012 and 2013 occurred in ‘subplot’. The ‘a’ circle denotes seedbank soil samples, and ‘b’ shows the location where mesh seed bags were buried. ‘Transect’ indicates where six *B. tectorum* in 2012 and eight *B. tectorum* in 2013 were sampled for seed production and aboveground biomass.

#### 4.3.3 Demographic analysis and model parameterization

To determine how precipitation treatments affected population growth and importance of different life stages of *B. tectorum*, I used information from demographic censuses to create population matrix models. I utilized stage-classified matrix models with a projection interval of one season (Fig. 4.2). I established 5 life stages for *B. tectorum* (Fig. 4.2). Probabilities of transitioning between life stages (e.g.  $S_1$ ,  $G_3$ ) were calculated using information from demographic censuses from fall 2011 to summer 2012, and fall 2012 to summer 2013. Fecundity ( $F_1$ ) was calculated using the average seed production of *B. tectorum* from the undisturbed sides of each plot. I decided not to include a seedbank that persisted over more than one year based on

results from seed viability tests from mesh bags. There were no plots where I observed more than 5% of seeds in mesh bags that were ungerminated but were still viable after one year in the soil.

The dominant eigenvalue of a matrix model gives the intrinsic rate of population growth ( $\lambda$ , Caswell 2001). I calculated population growth rates separately for *B. tectorum* in each plot in each year. To examine how important transitions from different life stages were to population growth, I also performed elasticity analyses on average matrices from each treatment. All analyses were conducted using the popbio package in R (Stubben and Milligan 2007).



**Fig. 4.2.** Life cycle graph and stage-classified matrix population model for *Bromus tectorum*. The five stages in the model are winter seedbank (wsb), fall seedbank (fsb), winter seedlings (ws), spring seedlings (ss), and flowering adults (fa). Arrows between life stages indicate advancement from one life stage to the next, and labels above arrows denote the probability of transitioning from one life stage to the next. The time scale for each transition is one season.

#### 4.3.4 Stochastic models

Precipitation patterns vary greatly from year to year. Even if the climate is trending towards wetter winters and drier summers, yearly amounts of precipitation will continue to fluctuate, and this interannual variability may influence the relative abundance of *B. tectorum*. To see how fluctuations in yearly precipitation might affect *B. tectorum* over longer timescales than that of my study, I created stochastic population models. I averaged transition probabilities of the ten replicates of each treatment in each year to get eight matrix models representing responses of *B. tectorum* to the five precipitation treatments in both 2012 and 2013. To test responses of *B. tectorum* populations to variable precipitation conditions, I created three different stochastic simulations: equal probabilities of all eight precipitation scenarios over 50 years, greater probabilities of wet winters, or greater probabilities of dry winters. Table 4.2 reports the exact probabilities used in stochastic models.

Simulated population sizes of *B. tectorum* in stochastic population models were calculated for 1000 simulations for each precipitation scenario over a 50 year period using the popbio package in R (Stubben and Milligan 2007). Log stochastic growth rates and confidence intervals were also calculated using 1000 simulations of stochastic precipitation over 40 years using the popbio package in R.

**Table 4.2.** Probabilities used for stochastic population models. The second column shows the total precipitation received by each treatment manipulation from October-May of either 2011-2012 or 2012-2013. Numbers in the last three columns represent probability weights assigned to matrix models of each treatment for the three different stochastic simulations: equal probabilities of all matrices over 50 years, greater probabilities of wet winters, or greater probabilities of dry winters.

Treatment Matrix Model	Total Oct-May precipitation (mm)	Equal	More wet winters	More dry winters
2012				
Control	198.14	0.13	0.03	0.20
Winter-wet	312.14	0.13	0.35	0.01
Winter-wet/summer-dry	274.68	0.13	0.05	0.01
Winter-dry/summer-wet	136.54	0.13	0.01	0.55
2013				
Control	296.41	0.13	0.10	0.01
Winter-wet	339.76	0.13	0.35	0.01
Winter-wet/summer-dry	258.61	0.13	0.10	0.01
Winter-dry/summer-wet	229.36	0.13	0.01	0.20

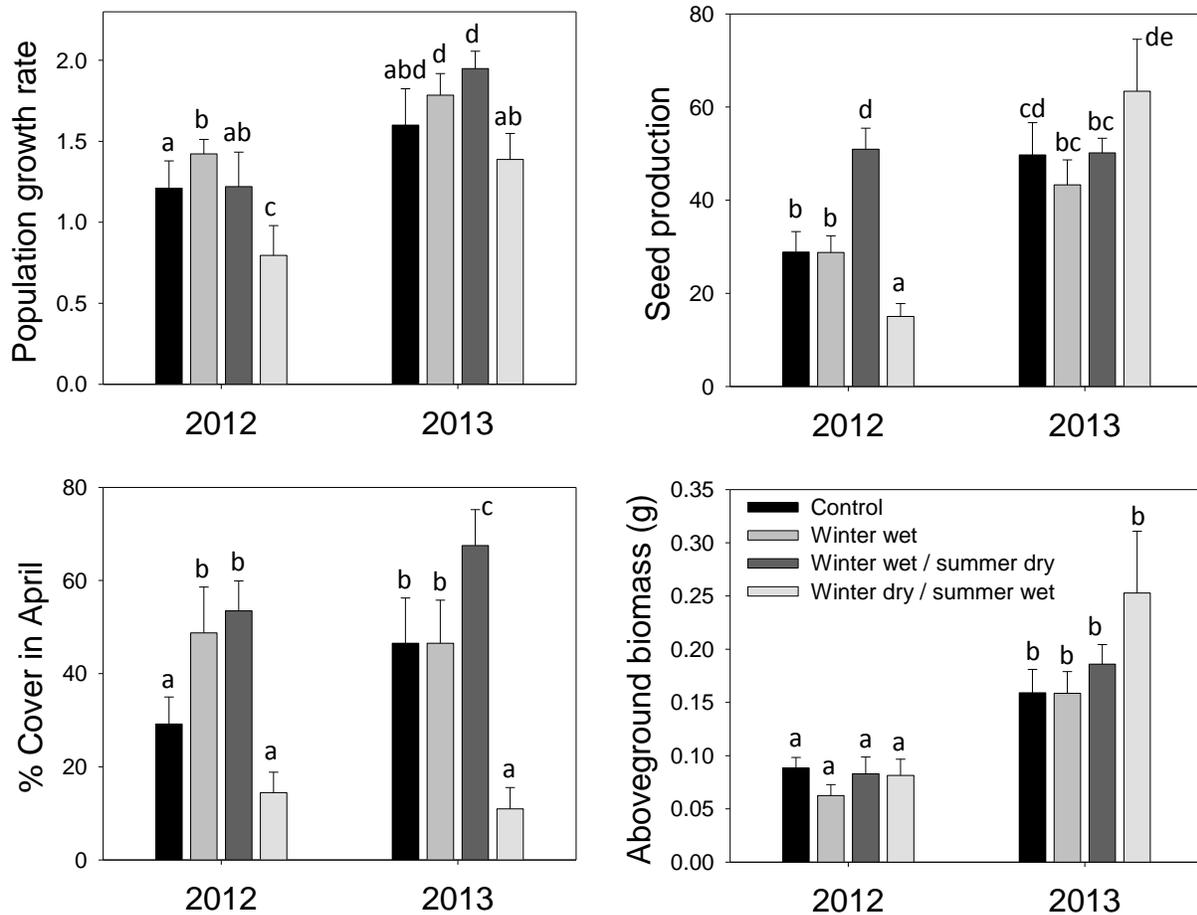
#### 4.3.5 Statistical analyses

I used linear mixed-effects models to examine the effects of year, precipitation manipulations, competition, and pathogen infection on population growth rates of *B. tectorum*. Block was considered a random effect in models. Predictor variables that did not account for significant variation in the response variable were dropped from the final model. Separate linear mixed models were conducted to specifically examine the effects of precipitation treatments on seed production, % cover in undisturbed plots, aboveground biomass, and over-winter survival of *B. tectorum*. Linear mixed models were also used to examine how precipitation treatments affected biomass of native and exotic species growing in subplots, and % of *B. tectorum* in plots infected with *U. bullata*. Pairwise-comparisons between treatments were conducted separately for 2012 and 2013. Data were analyzed using the lme4 package (Bates et al. 2011) and the p.val function from the Language R package (Baayen 2011) in the statistical program R (R Development Core Team 2012).

To examine competitive relationships in more detail, I performed Spearman's rank correlations between total competitor biomass, biomass of native species, and biomass of exotic species and population growth rates of *B. tectorum* in each plot in 2012 and 2013. Correlations were performed using the *hmst* package in R.

#### 4.4 Results

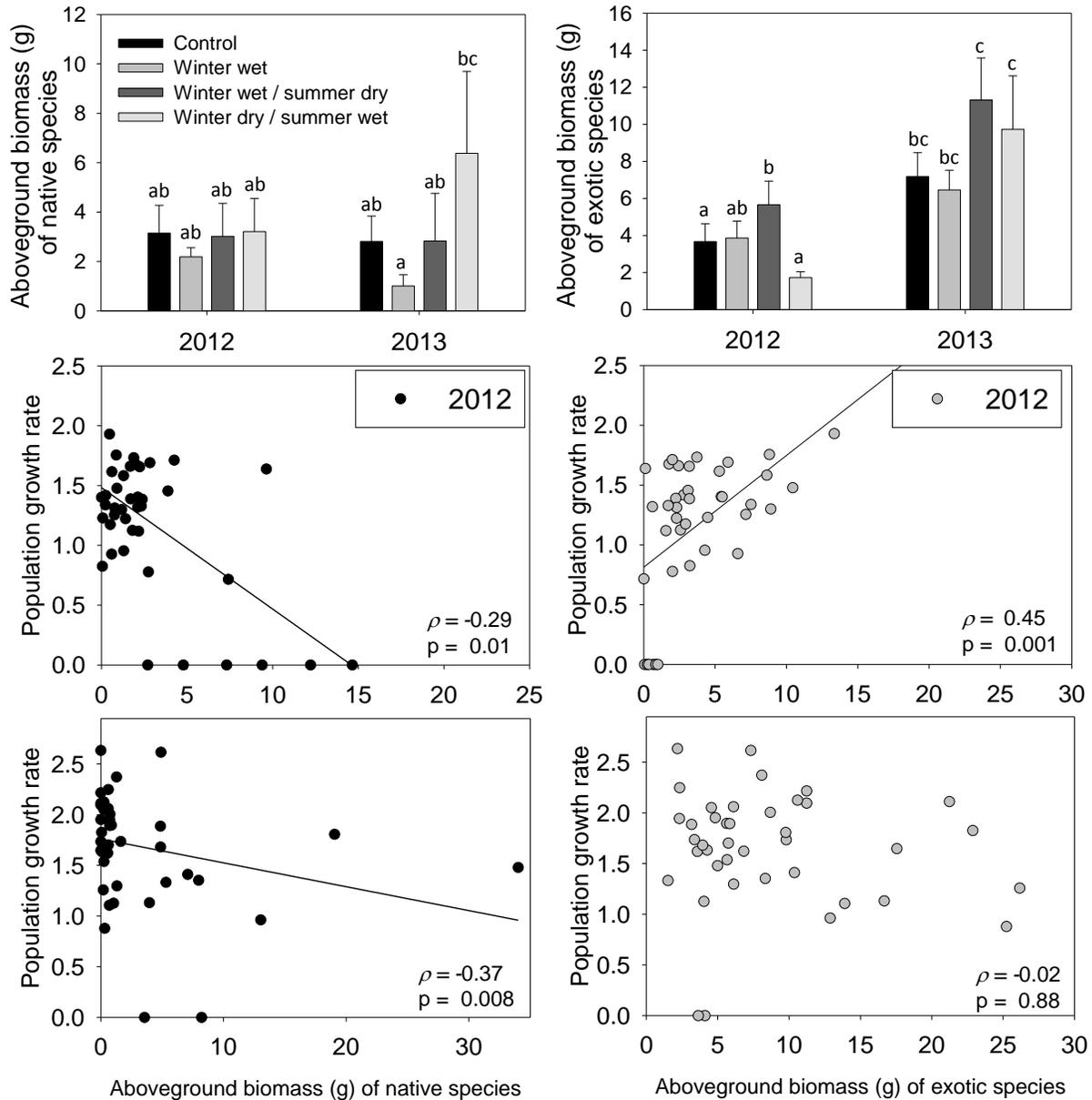
Results from linear-mixed models revealed that year, precipitation treatment, and biomass of adjacent native plants significantly affected population growth rates of *B. tectorum* over the study period (all  $p < 0.05$ , Fig. 4.3). Abundance of the pathogen *U. bullata* did not influence population growth rates in either year ( $p > 0.48$ , Chapter 3). Population growth rates of *B. tectorum* were lower overall in 2012 than in 2013 ( $p = 0.01$ ) and lowest in the winter-dry/summer-wet treatment in both years (all  $p < 0.04$ , Fig. 4.3). Native plant biomass was negatively correlated with population growth rates of *B. tectorum* in both years ( $p = 0.001$ , Fig. 4.4). Exotic plant biomass did not affect population growth rates of *B. tectorum* over either year.



**Fig. 4.3.** Average population growth rates, seed production per individual, % cover, and aboveground biomass per individual of *B. tectorum* in the four precipitation manipulations in 2012 and 2013, + standard error. Bars with different letters are significantly different from each other at the  $p < 0.05$  level.

Seed production, aboveground biomass, and cover of *B. tectorum* differed significantly between 2012 and 2013 ( $p < 0.01$ , Fig. 3). Seed production in 2012 was lowest in the winter-dry treatment, however, in 2013, seed production was highest in the winter-dry treatment ( $p = 0.02$ ). Aboveground biomass was lower in all treatments in 2012 than in 2013 ( $p < 0.001$ ). Cover of *B. tectorum* was significantly lower in the winter-dry treatment than in winter-wet treatments in both years ( $p < 0.003$ ). Native plant biomass was highest in the winter-dry treatment in 2013,

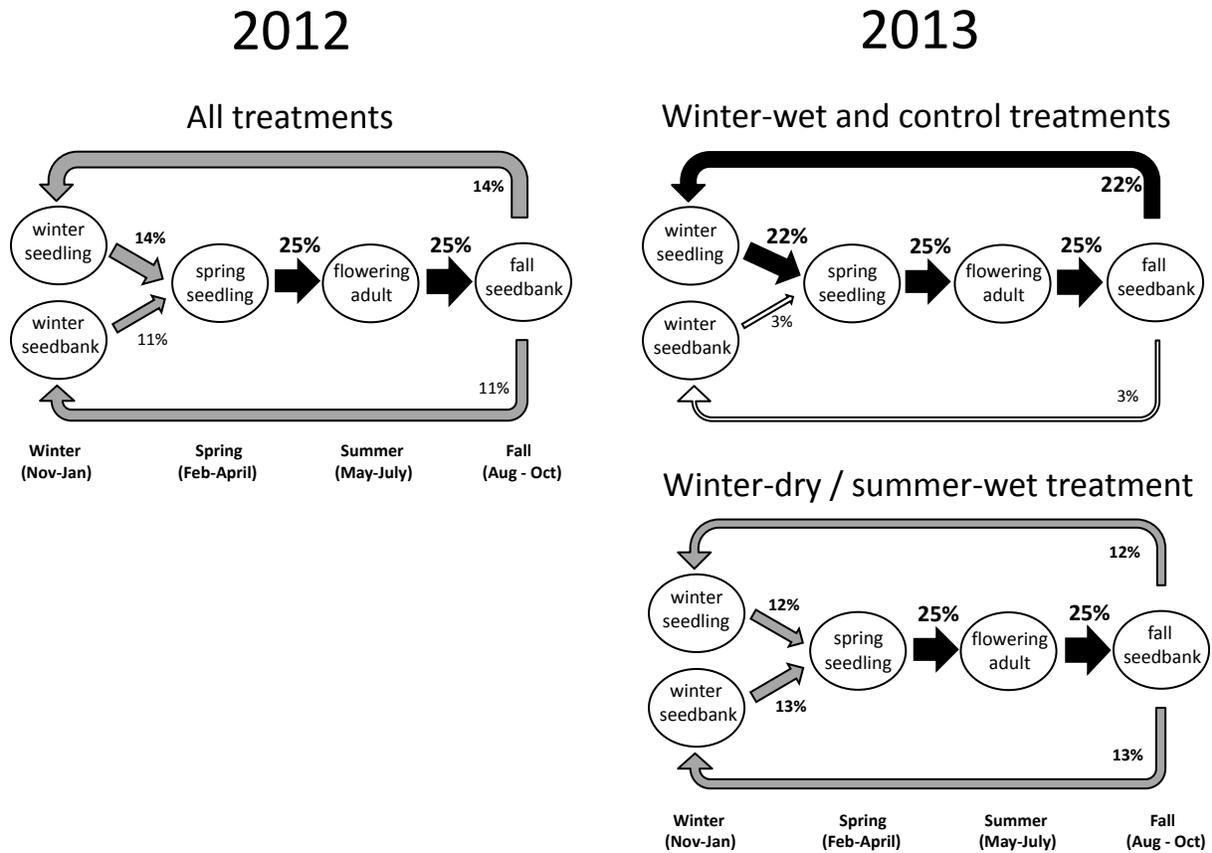
and exotic plant biomass was higher in 2013 than in 2012, however, results between treatments were not significant (Fig. 4.4).



**Fig. 4.4.** Top panels show average aboveground biomass of native and exotic plants growing in subplots in each treatment in 2012 and 2013, + standard error. Middle panels show correlations of aboveground biomass of native species and exotic species to population growth rates of *B. tectorum* in 2012. Bottom panels show correlations for 2013.

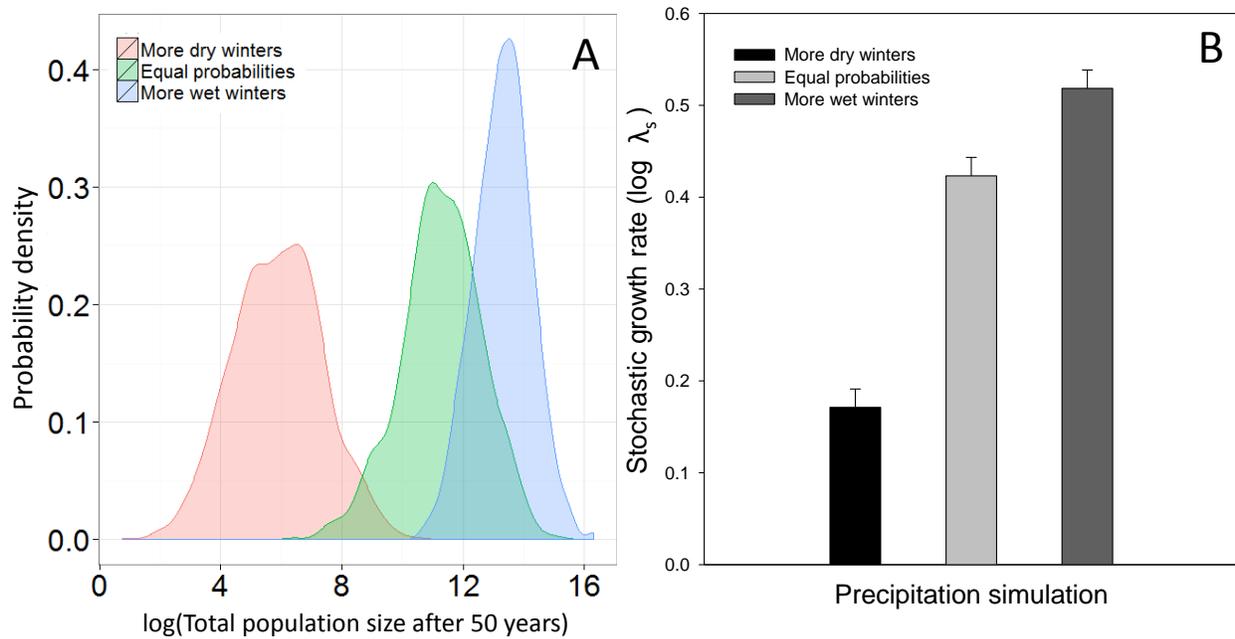
There was a negative correlation between native plant biomass and population growth rates of *B. tectorum* in 2012 and 2013 (Fig. 4.4). There was a positive correlation between exotic plant biomass and population growth rates in 2012, but no significant correlation in 2013 (Fig. 4.4). Spearman's rank correlation coefficients ( $\rho$ ) and associated  $p$  values are displayed in Fig. 4.4.

In 2012, results of elasticity analyses revealed that survival of spring seedlings to flowering and seed production contributed more to population growth than other transitions in all treatments (Fig. 4.5). In 2013, however, elasticities for the winter-dry treatment differed from the other treatments. In the winter-dry treatment, survival of spring seedlings to flowering and seed production were the most important contributors to population growth, similar to elasticities of all treatments in 2012. In the winter-wet and control treatments in 2013, the entire life history pathway for seedlings emerging in fall, surviving over winter and spring, and seed production contributed more to population growth rates than seeds overwintering in the seedbank and germinating in spring (Fig. 4.5).



**Fig. 4.5.** Elasticities of population growth rates of *B. tectorum* in 2012 and 2013. In 2012, all treatments had similar elasticities. In 2013, elasticities in the winter-dry / summer-wet treatment differed from those of the other treatments. Larger percentages and darker arrows indicate transition probabilities that contribute more to population growth than others.

Simulated population sizes from stochastic population models and log stochastic population growth rates of *B. tectorum* were greatest for simulations with more wet winters, and lowest for simulations with more dry winters. However, all model populations grew quickly over the 50 year period (Fig. 4.6).



**Fig. 4.6.** Panel A shows a histogram of log-transformed population sizes from 1000 simulations of stochastic models with either more dry winters, equal probabilities of all eight precipitation scenarios, or more wet winters over a 50 year time period. Panel B shows the stochastic growth rate ( $\log \lambda_s$ ) of *B. tectorum* under the three precipitation simulations.

#### 4.5 Discussion

Changes in precipitation patterns resulting from climate change have the potential to impact population dynamics of invasive species. My study found that increased winter precipitation benefits population growth of *B. tectorum*, especially when competition from native plants is low. Spring precipitation was also a large driver of differences in population growth rates, and population growth rates were higher for all treatments in 2013 after an unusually wet spring. Productivity, seed production, abundance, and overwinter survival all varied between treatments and years, demonstrating the sensitivity of *B. tectorum* to precipitation timing. The most important stages for population growth of *B. tectorum* were survival from seedling to flowering plant and seed production, and elasticity values also varied with precipitation pattern. Stochastic models projected that *B. tectorum* populations would increase in all precipitation

scenarios, and increase most in scenarios with higher probabilities of wet winters. Changes in precipitation can also alter the most important life transitions for *B. tectorum*.

A large body of research has been conducted on *B. tectorum* over the last half century in heavily invaded areas (e.g. Hulbert 1955, Young et al. 1969, and Mack and Pyke 1984). This species has been associated with detrimental effects to ecosystems in areas with distinct winter-wet climates. If precipitation patterns shift, so might the distribution of this species. My study suggests that *B. tectorum* may become increasingly invasive in Colorado if the climate shifts to a more winter-wet regime. Consistent with my hypotheses, population growth increased in all treatments with increased winter precipitation in both 2012 and 2013. In 2012, *B. tectorum* in the winter-dry treatment had an average population growth rate below 1, indicating that drier winters could decrease populations. However, in 2013, after an unusually wet spring, even *B. tectorum* in the winter-dry treatment had population growth rates above 1, and population growth in all treatments was higher than in 2012. This indicates that both winter and spring precipitation contribute to success of *B. tectorum*. My results agree with those from bioclimatic envelope models showing winter and spring precipitation to be strong predictors for dominance of *B. tectorum* throughout the intermountain west (Bradley 2009). Plasticity in the timing of growth allows cheatgrass to take advantage of either ample winter or spring precipitation (Harris 1967, Mack and Pyke 1983), increasing its probability of success in variable climates.

At my field site, the role of the seedbank does not seem to play a large role in population dynamics of *B. tectorum*. I found little evidence of a seedbank for *B. tectorum* that lasts more than one year. Studies in other invaded areas have found a similar lack of dormancy over multiple years in *B. tectorum* seeds (Hulbert 1955, Griffith 2010), although some studies have found viable seed that can last 2 years or more in litter layers, and maintain *B. tectorum*

populations after low seed production years (Young et al. 1969, Young and Evans 1975). In a California grassland, there is evidence that other non-native annual grasses do not form long-lived seedbanks (Faist et al. 2013). My results are promising for control measures in the Front Range of Colorado. If *B. tectorum* populations decline over a few years with dry winters and springs, it may be possible to eradicate them from an area if management applications are timed accordingly.

There was a negative correlation between native plant biomass and population growth rates of *B. tectorum*. At local scales, other studies have found similar associations between native and exotic species (Tilman 1997, Naeem et al. 2000), and several studies show that established native vegetation has the ability to limit growth of *B. tectorum* (Chambers et al. 2007, Ponzetti et al. 2007, Reisner et al. 2013, Leger et al. 2013). In 2013, native species biomass was lower in the winter-wet treatment than in 2013 in the winter-dry treatment, indicating that increased winter precipitation may lead to a reduction in native plants, which could further facilitate invasion of *B. tectorum*.

Interestingly, exotic competitor biomass did not reduce population growth of *B. tectorum*, even though biomass of other exotic species was often greater than that of native species in subplots. In 2012, exotic plant biomass was correlated with greater population growth rates of *B. tectorum*. All exotic species at my field site are winter-active annuals or perennials, and most are growing at the same time period as *B. tectorum*, so one might assume there would be greater competitive pressure because the species are occupying similar temporal niches (Adler et al. 2006). However, many of the other exotic species are tap-rooted forbs, and perhaps they are using resources from different depths in the soil than *B. tectorum*. The positive association of exotic species has been observed multiple times in more heavily invaded areas. In fallow fields

in Idaho, Piemeisel (1951) observed a succession in disturbed areas from exotic forbs to *B. tectorum*. Some of the most common exotic forbs at my site are mustards, including *Sisymbrium altissimum*, one of the species Piemeisel observed in old-field communities. Mechanisms driving these positive associations between exotic species remain unclear. Communities composed entirely of exotic species may remain in this alternative state for long periods, and prevent the re-establishment of more diverse native communities (Simberloff and Von Holle 1999, Kulmatiski 2006).

The survival of seedlings in spring to flowering plants and seed production were the two most important transitions contributing to population growth of *B. tectorum* in both years. This makes sense, as seed production of an annual plant without a substantial seedbank determines the number of individuals in the next generation (Watkinson et al. 1989). Other studies have shown that even when there is a low density of *B. tectorum* individuals, if those individuals produce a large quantity of seeds, then populations can remain viable (Hubert 1955). In 2013, overwinter survival of seedlings that germinated in fall of 2012 was also very important to population growth, but only in control and winter-wet treatments. Elasticity values in the winter-dry treatment were higher for seeds remaining viable in the seedbank until spring, and spring germination. Fall germination was low in the winter-dry treatment, with comparatively greater spring germination after wet-up in spring, making spring seedling germination a more important contributor to population growth. Altering the timing of precipitation can alter the life cycle of *B. tectorum*, and my elasticity analyses further illustrate the ability of this species to alter its phenology to match climatic conditions (Beckstead et al. 2006). Management applications aimed to reduce spring seedling survival and seed production, such as spring grazing or burning, may be effective at reducing population growth of *B. tectorum*.

Predictions of precipitation change associated with climate change are less certain than those of temperature change (IPCC 2007). Additionally, the timing and amount of precipitation varies greatly from year to year. Thus, different precipitation scenarios will impact growth of invasive species. Stochastic population models that incorporate year-to-year variation in precipitation patterns show that *B. tectorum* populations are projected to grow exponentially, especially in scenarios with greater probabilities of wet winters. However, even in scenarios with greater probabilities of dry winters, results here indicate that *B. tectorum* populations will increase. Unless there are long periods with dry winters, *B. tectorum* populations can continue to proliferate. There is a high risk of increasing invasion potential along the Colorado Front Range, even if winters are not consistently wetter in the future.

This study has important implications for management of disturbed or invaded ecosystems in a changing climate. Invasive species, such as *B. tectorum*, may be able to exploit changes in precipitation patterns that natives cannot. However, my study supports results of others showing that competition from native species may help deter invasion. Future invasibility of plant communities will not only be a function of changing climate, but of levels of disturbance, and resilience of the existing plant community to climate change (Cramer et al. 2008, Reisner et al. 2013). My study highlights the importance of considering the strong interactive effects that climate change and biotic change can have on success of invasive species.

## CHAPTER 5

# MOWING REDUCES EXOTIC GRASSES BUT INCREASES EXOTIC FORBS IN A SEMI-ARID GRASSLAND

### 5.1 Abstract

Cheatgrass (*Bromus tectorum*) and other exotic winter-active plants can be persistent invaders in native grasslands, growing earlier in the spring than native plants and preempting soil resources. Effective management strategies are needed to reduce their abundance while encouraging the re-establishment of desirable native plants. In this four year study, I investigated whether mowing and seeding with native perennial grasses could limit growth of exotic winter-actives, and benefit growth of native plants in an invaded grassland in Colorado, U.S.A. I established a split-plot experiment in October 2008 with three mowing treatments: control, spring mowed, and spring/summer mowed (spring, mid-summer, and late summer), and three within-plot seeding treatments: control, added *B. tectorum* seeds, and added native grass seeds. Cover of plant species and aboveground biomass were measured for three years. In March and June of 2010, 2011, and March of 2012, *B. tectorum* and other winter-annual grasses were half as abundant in both mowing treatments as in control plots, however, cover of non-native winter-active forbs increased two-fold in spring mowed plots and almost three-fold in spring/summer mowed plots relative to controls. Native cool-season grasses were most abundant in spring mowed plots, and least abundant in control plots, while there was a trend for higher cover of native warm-season grasses in spring/summer mowed plots. These patterns remained consistent one year after termination of treatments. The timing of management applications can have

strong effects on plant community dynamics in grasslands, and this experiment indicates that adaptive management can target the temporal niche of undesirable invasive species.

## 5.2 Introduction

Grasslands have historically been impacted by humans, but more recently, human-caused disturbance and the introduction of non-native species have increasingly led to the loss of native grassland ecosystems (Sala & Paruelo 1997; Suttie et al. 2005). In some extreme cases, native plant communities have shifted to less desirable stable states dominated by exotic species (Laycock 1991; Kulmatiski 2006; Seastedt & Pyšek 2011). Grasslands provide a host of important ecosystem services such as carbon sequestration, forage and habitat for wildlife, and soil conservation, among others (Sala & Paruelo 1997). Thus, it is of vital importance to understand how and when to intervene (Hobbs et al. 2011) in grasslands in order to maintain important ecosystem services in the face of rapid global change (Choi et al. 2008; Seastedt et al. 2008; Chapin et al. 2010).

Many of the exotic species invading grasslands of the western U.S.A. are winter-active, germinating in the late fall or early spring, growing earlier in the season than native species, and preempting soil resources that native plants could later use (Melgoza et al. 1990; Booth et al. 2003). One particularly invasive species, *Bromus tectorum*, has successfully invaded rangelands throughout the Great and Colombia Basins in the western U.S.A. (Mack 1981; Knapp 1996; Pyšek & Hulme 2005). In regions where this species has become a dominant, *B. tectorum* can alter fire frequencies (Whisenant 1990; D'Antonio & Vitousek 1992; Baker 2013) deplete soil resources (Melgoza et al. 1990), and reduce diversity and abundance of native plants (Concilio & Loik 2013).

In grasslands along the Front Range of Colorado, there has been an increase in the presence of non-native plants over time (Bush et al. 2007; Lawton 2010; Bromberg et al. 2011). In addition, *B. tectorum* and other winter-active species may become more invasive in Front Range grasslands as the climate changes (Bradley 2009; Bradley et al. 2009). In a grassland near Boulder, CO, successful control of one non-native forb with biocontrol insects was followed by an increase in abundance of two non-native grasses, rather than an increase in native species (Bush et al. 2007). Thinning Ponderosa pine trees along the Front Range has also led to an increase in *B. tectorum* and other non-native species (Miller & Seastedt 2009; Wolk & Rocca 2009). The observed increases in exotic species in response to disturbance, coupled with changing climatic conditions that may favor winter-actives, indicate a need for management strategies that not only decrease the abundance of exotic invaders, but also promote desirable native species (Brown et al. 2008; Seastedt et al. 2008).

Previous management strategies aimed to reduce these exotic species in other ecosystems have met with mixed success (e.g. Allen 1995; Humphrey & Schupp 2004). To maintain the native status of the system, novel management may be required (Seastedt et al. 2008). Clearly, management activities that can reduce the seed production of an annual species that is invading a historically perennial system can be addressed by reducing seed production. Even if such treatments harm perennial species, the regrowth and persistence of these as opposed to the potential to generate propagule limitation for the invader should favor the perennials in the subsequent composition of the system. These strategies takes advantage of phenological differences between invaders and desirable natives (Wolkovitch & Cleland 2011). Hence seasonally-timed fire, mowing, or grazing are suggested as likely management activities (Kelley et al. 2013). Here, in order to expedite a replicated experimental design within a relative small

area, mowing was chosen as the treatment of choice. In California, mowing of invaded grasslands in early spring has allowed for the suppression of exotics because it occurs when they are physiologically active (Maron & Jeffries 2001). In a relic patch of tallgrass prairie in Colorado, intensive spring grazing by cattle allowed for maintenance of native tallgrass species that usually require fire to maintain dominance (Seastedt et al. 2008). Although over-grazing of western rangelands has been associated with ecosystem degradation, especially in dry or desert grasslands (Fleischner 1994, Reisner et al. 2013), short-duration grazing or mowing applications may increase diversity and production of some grassland ecosystems (Collins et al. 1998; Jackson 1999). Additionally, seeding with native species that have similar phenologies to invaders has helped suppress exotic species in disturbed grassland ecosystems (Cleland et al. 2013). Time-sensitive management applications, in conjunction with seeding of native species, could allow for successful restoration of desirable grassland communities.

In this study, I investigated effects of seasonal mowing and seeding with native perennial grasses on growth of non-native winter-active species and native plants in an invaded grassland in Colorado. I also seeded with *B. tectorum*, to observe how mowing treatments would interact with increased invasion pressure to affect community composition. In June 2009, I established an experiment with three levels of mowing and seeding: control, spring mowing, and spring/summer mowing (spring, mid-summer, and fall), and three within-plot seeding treatments: control, added *B. tectorum* seeds, and added native grass seeds. I then examined effects on plant community composition and ecosystem processes. I hypothesized that: **1.** Native grasses would increase in plots that received early spring mowing and added native grass seed, because mowing would impact exotic species while they were active without harming the later-growing native perennials and allow for establishment of more desirable native species. **2.** Primary production

would be greatest in spring-mowed plots because early mowing would reduce cover of exotic species, allowing for increased growth and production of perennials through the growing season.

**3.** Ongoing removal of vegetation in spring/summer mowed plots would reduce primary productivity of all species. The mowing treatment would also indirectly increase nitrogen availability, because reduction of vegetation over the entire growing season would result in unused pools of soil resources.

## **5.3 Methods**

### *5.3.1 Site characteristics*

This experiment was established in a foothills mixed-grass prairie located approximately 15 km northwest of Boulder, Colorado, USA (40° 07' N, 105° 18' W). Elevation at the site is 1,798 m, with an average precipitation of 475 mm per year, and an average temperature of 10.5° C (NOAA). The site has a continental climate, with most precipitation falling in spring and early summer. Soils at the field site are classified as well drained, colluvial, sandy loams (USDA 2001). Vegetation at the site is representative of plant communities in foothills and montane meadow ecosystems across the Front Range of Colorado. The community is characterized by a mix of exotic winter annual species, exotic perennial species, and native grasses and forbs (Knochel 2009). Exotic species at the site include *Bromus tectorum*, *Bromus japonicus*, *Poa compressa*, *Erodium cicutatum*, *Alyssum parviflorum*, and *Sisymbrium altissimum*, among others. Native species include *Sporobolus cryptandrus*, *Bouteloua gracilis*, *Pascopyrum smithii*, *Psoraleidium tenuiflorum*, *Ambrosia artemisiifolia*, *Erigeron flagellaris*, and *Grindelia squarrosa*, among many others.

### 5.3.2 *Experimental design*

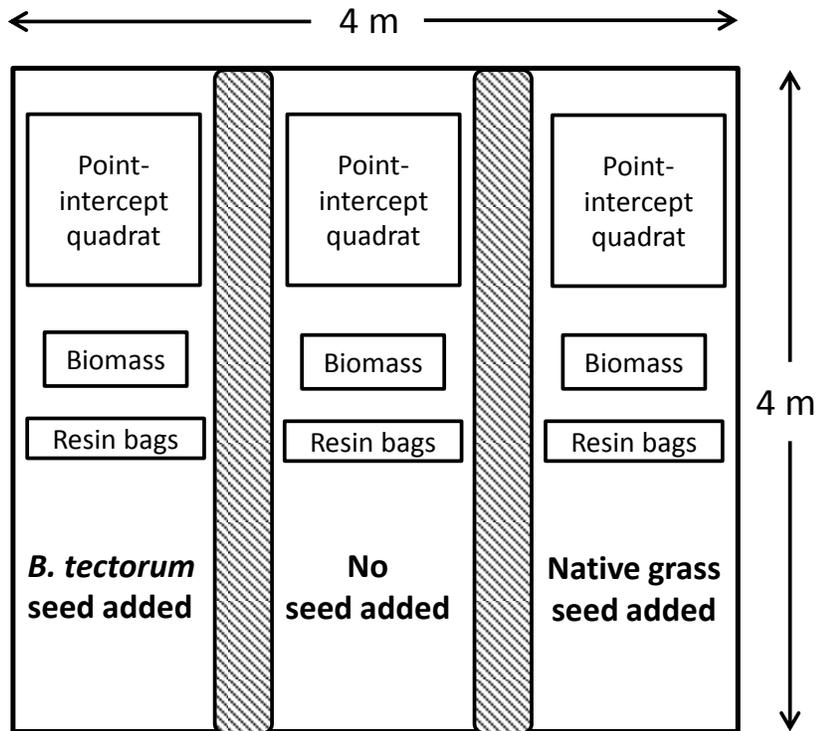
Plots were established in October, 2008, and manipulations were conducted for the following four years, from 2009-2012. Twenty-four  $4 \times 4$  m plots were established at the study site in October 2008, and randomly assigned to one of three whole plot treatments: control, spring-mowed, or spring/summer-mowed. The whole-plot mowing treatments were conducted using a mower that left cut vegetation in the plots. Cut vegetation was left in plots to reduce nutrient removal caused by the treatment. Each plot was then divided into three within-plot treatments: no added seed, added *B. tectorum* seed, and added native grass (*Pascopyrum smithii* and *Elymus trachycaulus*) seed. The within-plot treatments were  $1 \times 4$  m long strips, separated by 0.25 m buffers. Seeds were broadcast along strips at rates of over 2,000 seeds per  $m^2$ . Seeds were added on 3/25/2009, 10/18/2009, 11/3/2010, and 4/20/2011. Mowing treatments began on 6/5/2009. Spring/summer mowed plots were treated two times in 2009, and three times throughout the spring and summer during 2009 - 2012. Spring mowed plots were treated only once yearly, in late May or early June during 2009 - 2012.

### 5.3.3 *Measurements*

I measured cover of plant species using the point-intercept procedure with a  $1m^2$  quadrat in each within-plot treatment. The number of points intercepting a living plant species was divided by the total number of points sampled in the quadrat (75) to calculate % cover. Pre-treatment cover was measured in early June 2009 and was measured again in September 2009, and March, June, late July, and September of 2010 - 2012. To observe how vegetation was responding one year after treatments had stopped, cover was measured again in June 2013. To assess how mowing treatments affected net primary production, I measured aboveground

biomass on all plots in late July or early August 2009-2013 during peak biomass. Yearly-production of aboveground biomass was collected from ground level in 0.1 m<sup>2</sup> subplots from each within-plot treatment. In addition, clipped biomass was collected within a 0.1 m<sup>2</sup> subplot at 5 cm height from all mowed plots (spring and spring/summer) at each mowing event. Clipped biomass was added to August clippings to determine total biomass production of mowed plots.

After one year of treatment manipulation, I replaced ion-exchange resin-bags in plots to determine how different mowing regimes would affect plant-available inorganic nitrogen. Resin bags were constructed with Amberlite® mixed-bed ion exchange resins (Sigma-Aldrich, St. Luis, MO) following methods similar to Lajtha (1988). Two resin bags were placed in the center of each plot at 5 cm below the soil surface (Fig. 5.1). Resin bags were inserted horizontally in soil using a trowel so as not to disturb soil above resin bags. I wanted to examine spring, summer, and winter fluctuations in available nitrogen, so I placed separate sets of resin bags in plots from 4/21/2011-6/15/2011, 6/15/2011-10/12/11, 10/12/11-4/5/12, 4/5/12-6/13/2012, and 6/13/12-9/25/12. After collection from the field, resins were extracted with 2M KCl to leach inorganic nitrogen. The amount of NO<sub>3</sub> and NO<sub>2</sub> (hereafter NO<sub>3</sub>), and NH<sub>4</sub> in KCl extractions was measured on a Lachat QuickChem 8500 Flow injection analyzer.



**Fig. 5.1.** Layout and sampling design of each plot. Within-plot seeding treatments were 1 m x 4m strips separated by 0.5 m buffers. Whole-plot treatments (not shown) were control, spring mowed, and spring/summer mowed.

#### 5.3.4 Statistical Analyses

Prior to analyses, plant species were grouped into five functional groups based on phenology, growth form, and native/non-native status. The five groups were: exotic grasses, exotic forbs, native cool-season grasses, native cool-season forbs, native warm-season grasses, and native forbs.

To see if mowing treatments were significantly changing the composition of the plant community, I performed multivariate analyses (PERMANOVAs) using the vegan package in R (R Development Core Team 2012, Oksanen et al. 2012) on % cover of the five functional groups

and litter in June 2009 (pre-treatment), June 2010, June 2011, and June 2012. The  $p$ -values from pairwise comparisons were adjusted with the Bonferroni method. PERMANOVA results were graphed using non-metric multidimensional scaling (nMDS) plots.

To specifically examine how treatments affected abundance of each functional group, I analyzed % cover of individual groups over time with generalized estimating equations (GEEs) in R (Højsgaard et al. 2006). GEEs were used to account for non-independence of cover measurements made in the same plots over multiple sampling dates. Whole plot treatment, within-plot treatment, year, and sampling date were predictor variables in GEEs. Data that strongly violated assumptions of normality were square-root transformed before analysis. For each functional group, only dates that species were physiologically active were included in analyses. For instance, cover of exotic grasses declined sharply in all treatments after June sampling dates because the grasses grow early and senesce in mid-June, so only March and June dates were used in analysis of exotic grass cover.

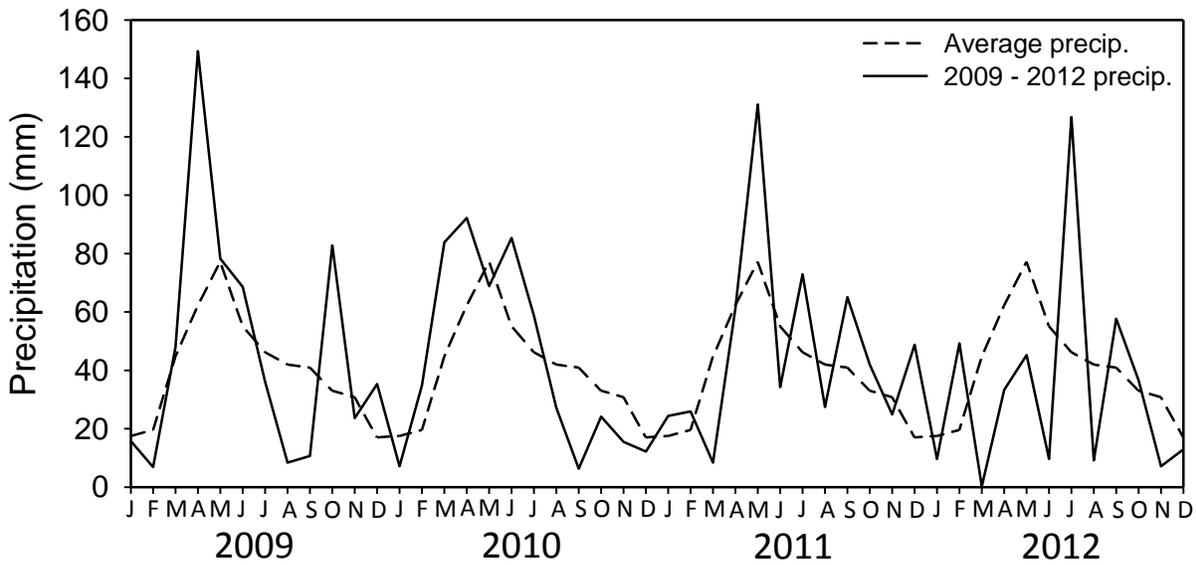
To address effects of mowing treatments on net primary productivity and nutrient cycling, I also analyzed aboveground biomass and nitrogen extracted from resin bags with GEEs. Wald chi-square statistics ( $X^2$ ),  $p$ -values from ANOVAS comparing models, and statistical contrasts (Højsgaard et al. 2012) were used to test for significant effects of predictor variables on cover, aboveground biomass, and nitrogen variables and are reported in results. In addition to examining effects of treatments on nitrogen availability, I evaluated whether plant community composition and aboveground biomass affected the amount of nitrogen collected in resin bags, a proxy for inorganic nitrogen availability. To examine the relationship between biomass production, plant species composition, and nitrogen availability, I used linear models to correlate

% cover of plant functional groups and aboveground biomass with total nitrogen per plot in spring and summer of 2011 and 2012.

## **5.4 Results**

### *5.4.1 Climate*

Monthly temperatures over the study period were near the average for Boulder, CO, and similar between years (Fig. 5.2, NOAA 2014). However, precipitation patterns varied greatly from year to year. The winter and spring of 2010 were very wet, exceeding average precipitation by ~30% over the January to July time period. 2011 had above average precipitation in January and February, but an abnormally dry March followed by an extremely wet May and July. 2012 had the most precipitation extremes. Yearly precipitation in 2012 was only 75% of average, but February and July were very wet, and received twice the average precipitation for the area (Fig. 5.2).

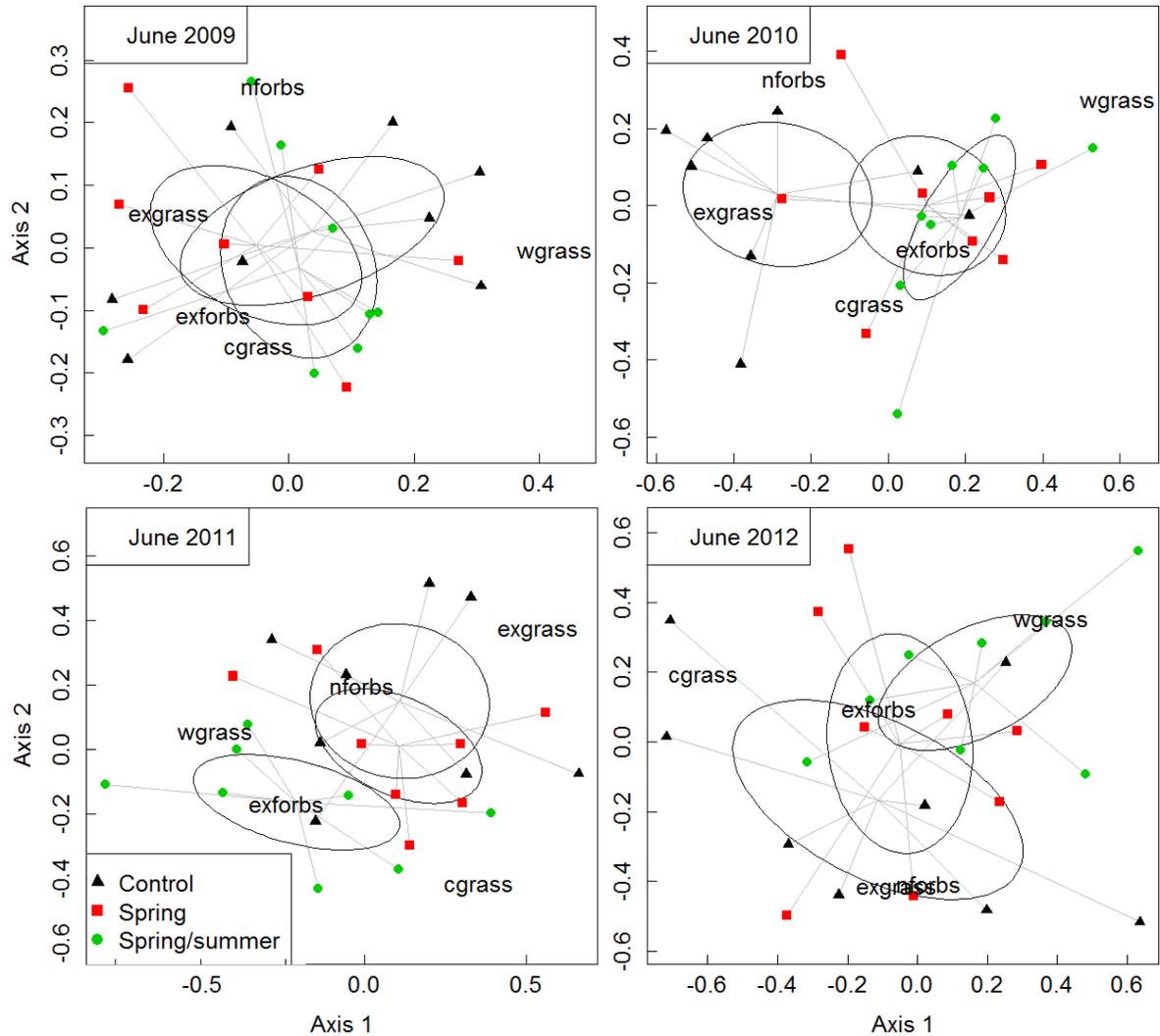


**Fig. 5.2.** Total monthly precipitation for Boulder, CO, over the four year duration of the study (solid line) compared to average monthly precipitation from 1948-2005 (dashed line). Precipitation data were collected from the Boulder weather station, located ~ 15 km from research site (NOAA 2014).

#### 5.4.2 Community composition

The within-plot seeding treatment had no effect on cover of functional groups or aboveground biomass over sampling dates (all  $p > 0.1$ ), thus, the within-plot treatment was removed from PERMANOVA and GEE models and response variables were averaged over whole-plots.

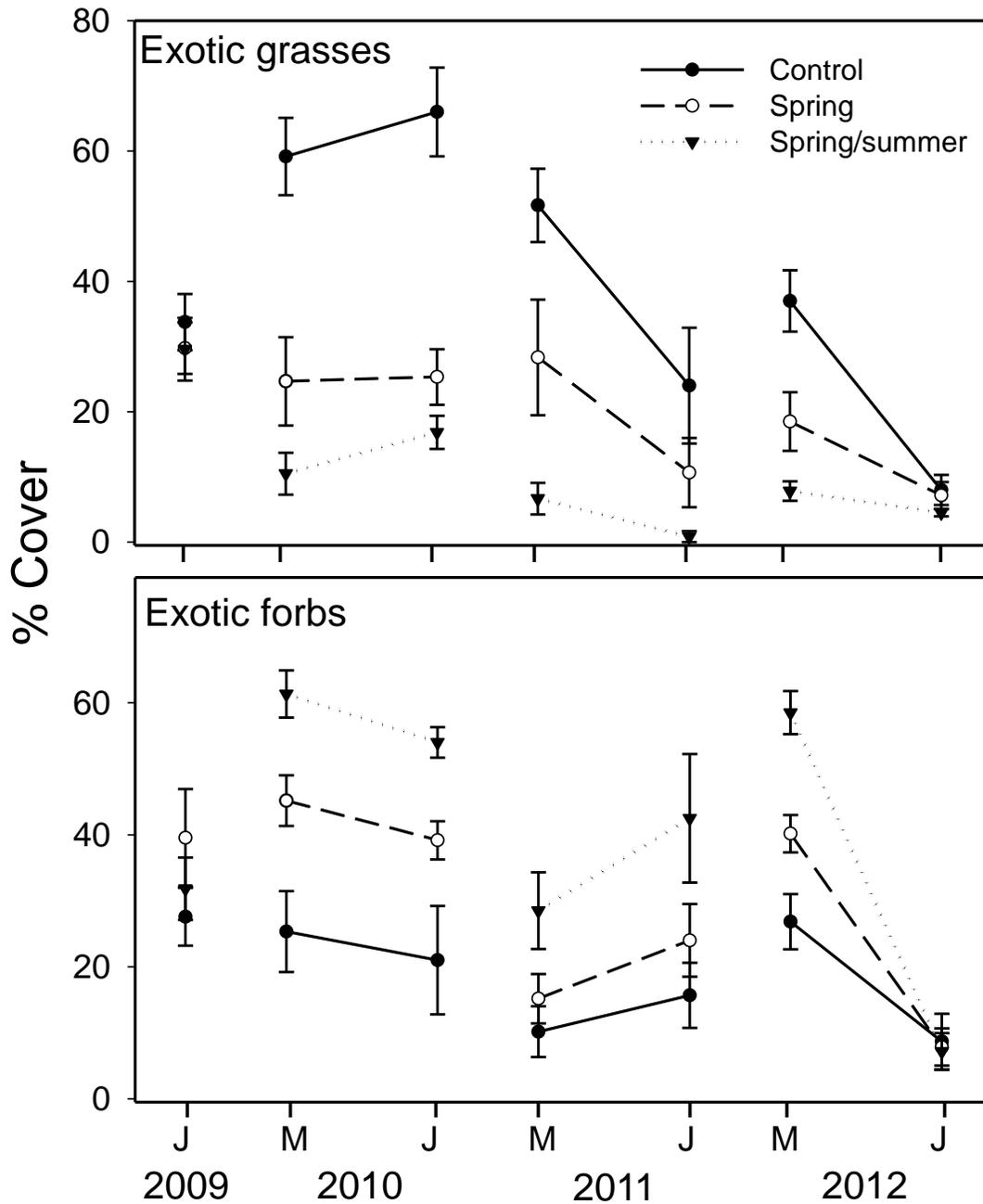
Pretreatment cover of plant species did not differ between experimental plots (PERMANOVA,  $p > 0.85$ , Fig. 5.3). In June 2010, community composition differed significantly between all whole-plot treatments ( $p < 0.04$ ). In June 2011 and 2012, community composition differed between control and spring/summer treatments ( $p < 0.05$ ), but not the spring-mowed treatment ( $p > 0.3$ ).



**Fig. 5.3.** Non-metric multidimensional scaling plots of plant community composition in control, spring mowed, and spring/summer mowed treatments in June 2009 (pre-treatment), 2010, 2011, and 2012. Words on graphs represent different groups in analysis, and points positioned closer to a cover group indicate plots that were more influenced by that cover group. Cover group codes: exgrass = exotic grasses, exforbs = exotic forbs, cgrass = cool-season grasses, wgrass = warm-season grasses, nforbs = native forbs. Circles represent 95% confidence intervals for each treatment.

Exotic grass cover significantly differed between each whole-plot treatment (Table 5.1, Fig. 5.4). Exotic grasses were over four times more abundant in control plots than in spring/summer mowed plots over all sampling dates, except June 2012 (Fig. 5.4). The most abundant exotic grass species in plots was *Bromus tectorum* (Table 5.2). Cover of exotic forbs

was diametrically opposite, with the highest cover in spring/summer mowed plots and the lowest cover in control plots (Table 5.1, Fig. 5.4). *Erodium cicutarium* and *Convolvulus arvensis* were the most abundant exotic forbs in plots (Table 5.2).



**Figure 5.4.** Percent cover of exotic grasses (top panel) and exotic forbs (bottom panel),  $\pm$  standard error. Cover measurements taken 6/5/2009 (pre-treatment), 3/31/2010, 6/15/2010, 3/31/2011, 6/20/2011, 4/1/2012, 6/11/2012, and 6/13/2013 (post-treatment).

**Table 5.1.** Mean values for absolute % cover of functional groups, litter, bare ground, aboveground biomass, and nitrogen extracted from resin bags over all analyzed sample dates,  $\pm$  standard error. Post-treatment measurements on June 2013 were not included in mean values. Wald statistics are shown for individual GEEs, and  $p$  values are shown for ANOVAs comparing GEE models for each functional group with and without the whole-plot treatment effect. Treatments with different letters across the row are significantly different (pairwise contrasts adjusted with Bonferroni corrections).

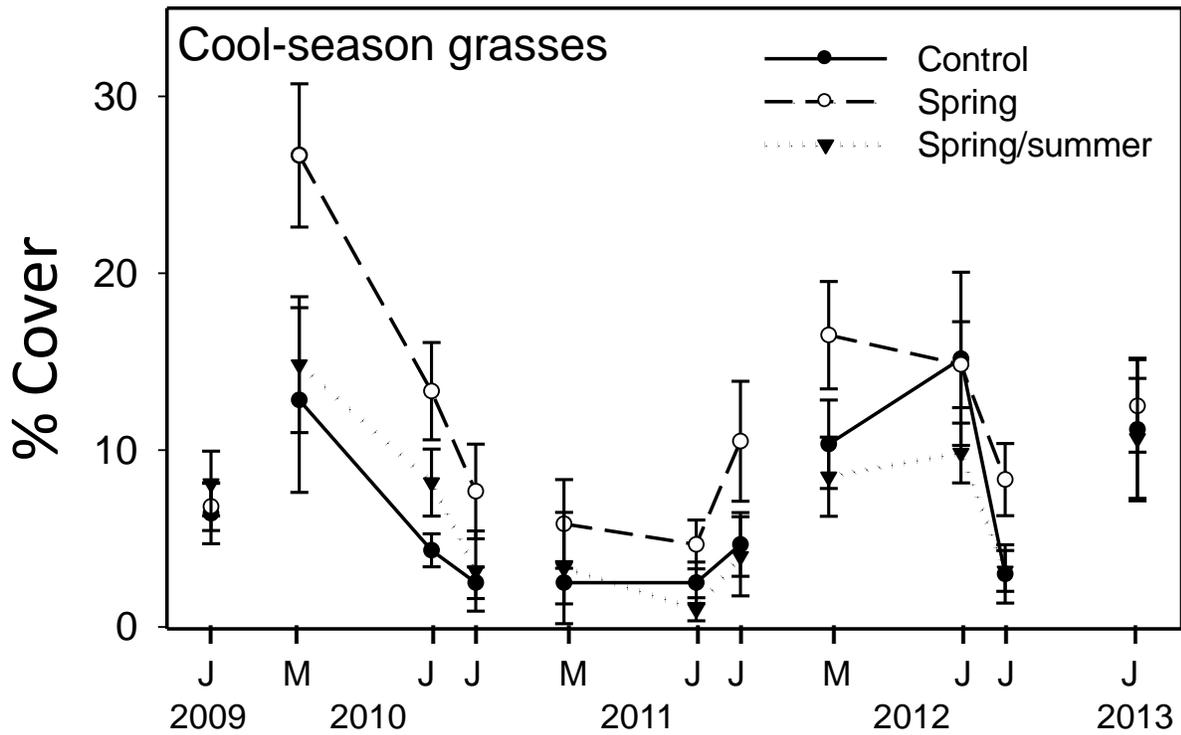
Response variable	Control	Spring-mowed	Spring/summer mowed	DF	Wald Statistic $X^2$	P
Exotic grass (%)	40.99 $\pm$ 3.76 <sup>a</sup>	19.12 $\pm$ 2.48 <sup>b</sup>	7.92 $\pm$ 1.08 <sup>c</sup>	2	102	<0.0001
Exotic forb (%)	17.95 $\pm$ 2.34 <sup>a</sup>	28.59 $\pm$ 2.48 <sup>b</sup>	42.01 $\pm$ 3.44 <sup>c</sup>	2	40.3	<0.0001
Cool-season grass (%)	6.52 $\pm$ 1.02 <sup>a</sup>	12.07 $\pm$ 1.16 <sup>b</sup>	6.32 $\pm$ 0.81 <sup>a</sup>	2	9.93	0.007
Warm-season grass (%)	25.10 $\pm$ 3.63 <sup>a</sup>	29.24 $\pm$ 3.84 <sup>a</sup>	36.54 $\pm$ 3.71 <sup>a</sup>	2	2.68	0.26
Native forb (%)	14.25 $\pm$ 1.47 <sup>a</sup>	13.52 $\pm$ 1.38 <sup>ab</sup>	8.65 $\pm$ 1.02 <sup>b</sup>	2	8.28	0.016
Litter (%)	34.2 $\pm$ 8.73 <sup>a</sup>	28.4 $\pm$ 7.24 <sup>ab</sup>	26.9 $\pm$ 7.00 <sup>b</sup>	2	0.04	0.04
Bare ground (%)	0.56 $\pm$ 0.63 <sup>a</sup>	1.67 $\pm$ 2.53 <sup>a</sup>	6.40 $\pm$ 2.49 <sup>b</sup>	2	113	<0.0001
Aboveground biomass (g/m <sup>2</sup> )	222.4 $\pm$ 19.44 <sup>a</sup>	192.3 $\pm$ 15.27 <sup>a</sup>	158.7 $\pm$ 15.72 <sup>b</sup>	2	23.5	<0.0001
NH <sub>4</sub> ( $\mu$ g/g)	49.10 $\pm$ 17.77 <sup>a</sup>	60.91 $\pm$ 37.99 <sup>a</sup>	58.30 $\pm$ 32.33 <sup>a</sup>	2	0.31	0.86
NO <sub>3</sub> ( $\mu$ g/g)	258.2 $\pm$ 95.76 <sup>a</sup>	236.1 $\pm$ 104.9 <sup>a</sup>	238.3 $\pm$ 89.75 <sup>a</sup>	2	0.16	0.92
Total nitrogen ( $\mu$ g/g)	307.3 $\pm$ 110.9 <sup>a</sup>	297.1 $\pm$ 128.9 <sup>a</sup>	296.6 $\pm$ 116.3 <sup>a</sup>	2	0.94	0.12

**Table 5.2.** The average absolute cover of the two most common plant species of each functional group in control, spring mowed, and spring/summer mowed treatments, averaged over the sampling dates.

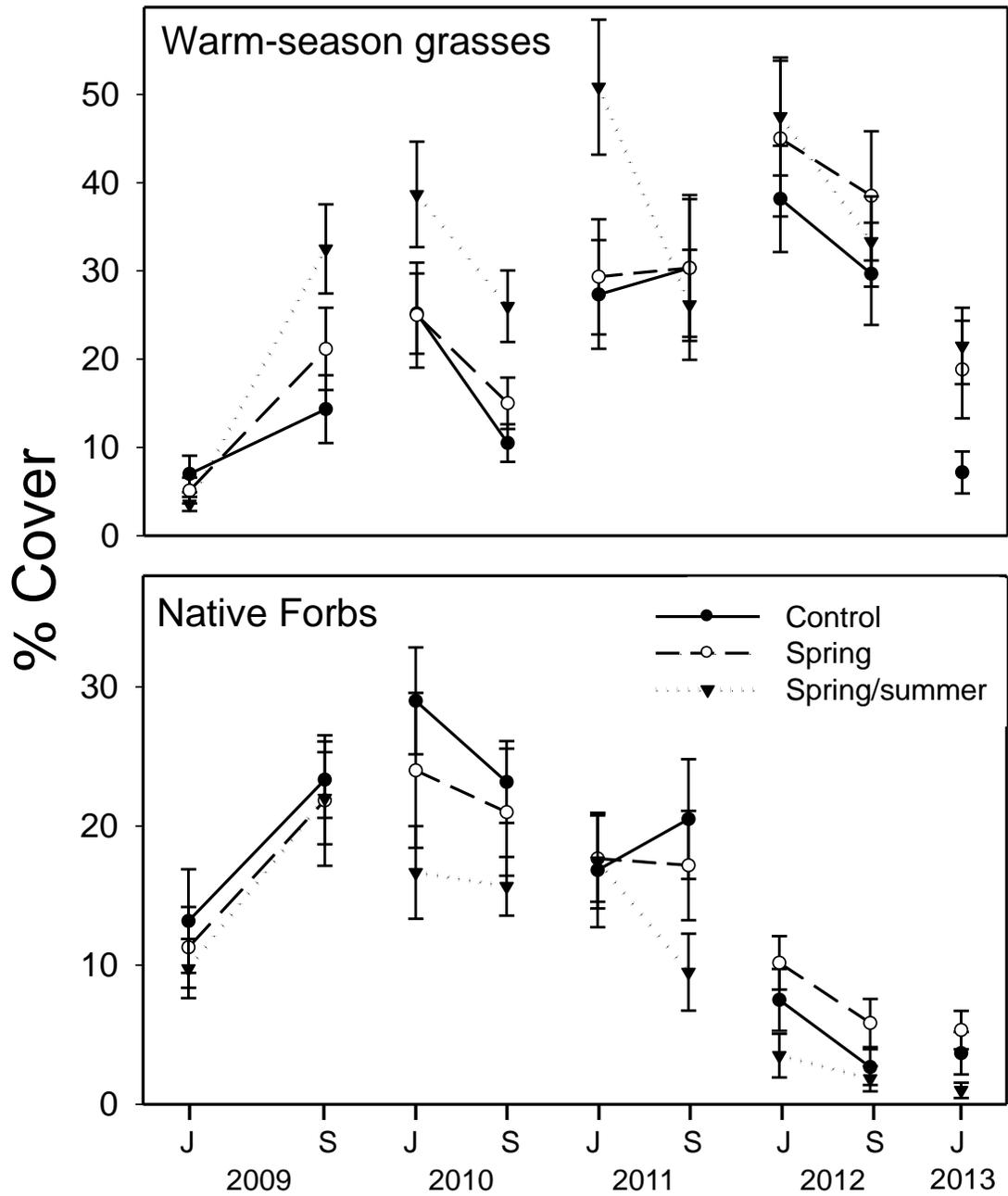
Species	Group	Control	Spring-mowed	Spring/summer mowed
<i>Bromus tectorum</i>	exotic grass	40.29	15.33	5.28
<i>Poa compressa</i>	exotic grass	0.61	4.53	3.00
<i>Erodium cicutarium</i>	exotic forb	5.31	12.17	29.39
<i>Convolvulus arvensis</i>	exotic forb	3.74	3.56	4.27
<i>Pascopyrum smithii</i>	cool-season grass	5.31	9.72	4.52
<i>Poa pratensis ssp. pratensis</i>	cool-season grass	0.87	1.32	1.70
<i>Bouteloua gracilis</i>	warm-season grass	1.67	9.25	16.28
<i>Sporobolus cryptandrus</i>	warm-season grass	22.44	20.31	21.4
<i>Ambrosia artemisiifolia</i>	native forb	14.72	13.17	10.11
<i>Psoralidium tenuiflorum</i>	native forb	1.39	1.83	0.22

Cover of cool-season grasses was almost two times greater in the spring mowed treatment than in the spring/summer mowed and control treatments over all analyzed dates (Fig. 5.5). *Pascopyrum smithii* was the most abundant cool-season grass in plots (Table 5.2). Cover of

warm-season grasses did not differ between treatments overall, although there was a trend for higher cover of warm-season grasses in the spring/summer mowed plots, particularly on July 2010 and July 2011 (Fig. 5.6). Native forbs were most abundant in control plots, and least abundant in spring/summer mowed plots (Fig. 5.6). Over all sampling dates, spring/summer mowed plots had significantly more bare soil and less litter than control plots ( $p < 0.0001, 0.04$ , Table 5.1). Cover of all functional groups significantly differed between sampling months and years (all  $p < 0.0001$ , Figs. 5.4-5.6).



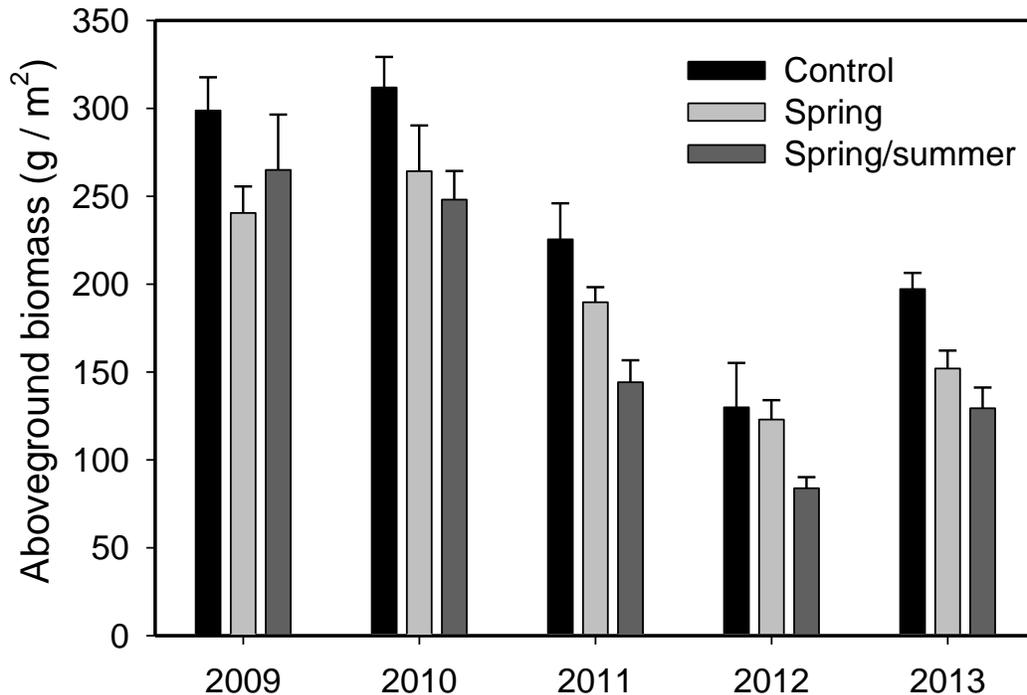
**Figure 5.5.** Percent cover of native cool-season grasses  $\pm$  standard error. Cover measurements taken 6/5/2009 (pre-treatment), 3/31/2010, 6/15/2010, 7/27/2010, 3/31/2011, 6/20/2011, 7/26/2011, 4/1/2012, 6/11/2012, 7/26/2012, and 6/13/2013 (post-treatment).



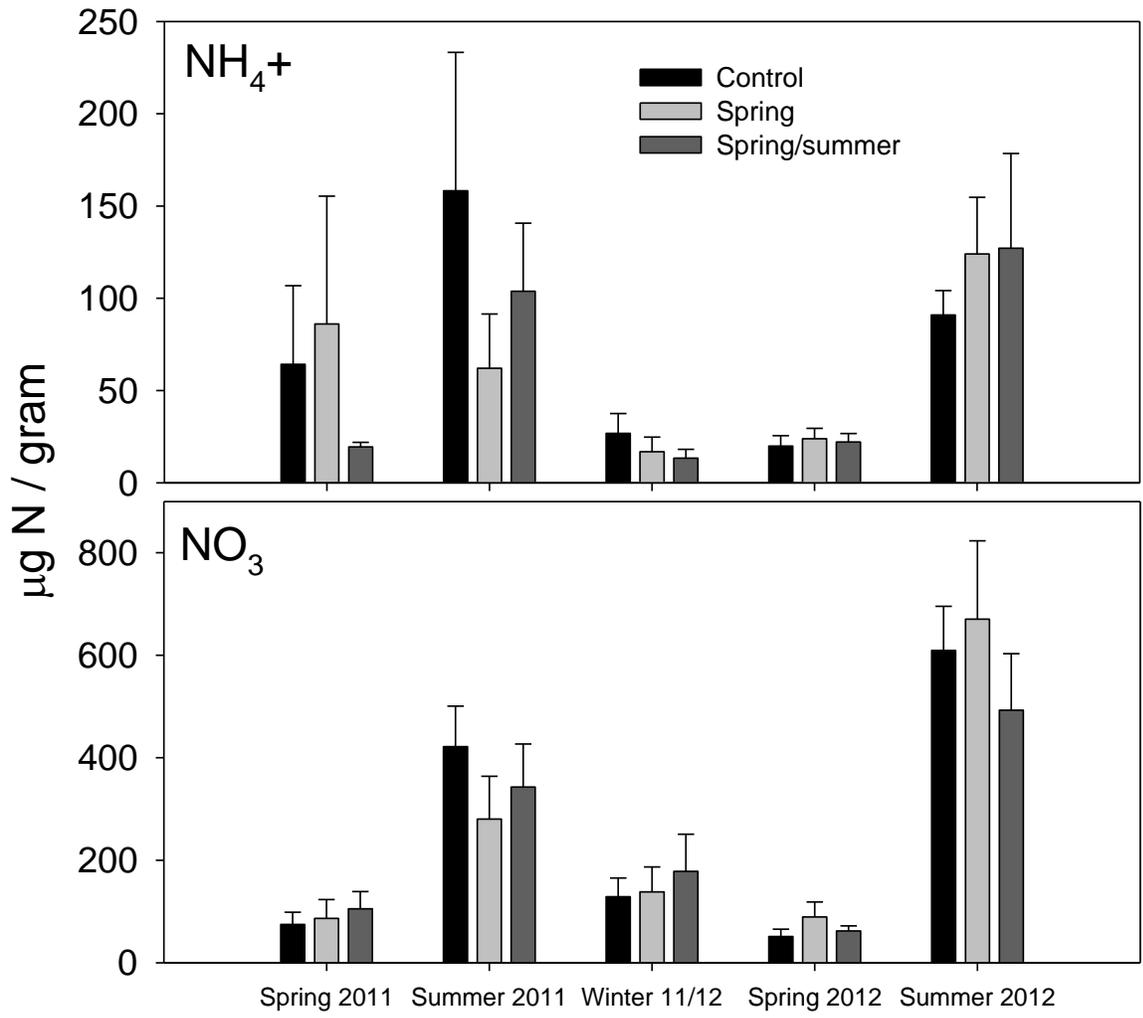
**Figure 5.6.** Percent cover of warm season grasses (top panel) and native forbs (bottom panel)  $\pm$  standard error. Cover measurements 6/5/2009 (pre-treatment), 9/16/2009, 7/27/2010, 9/13/2010, 7/26/2011, 9/14/2011, 7/26/2012, 9/10/2012, and 6/13/2013 (post-treatment).

### 5.4.3 Biomass and nitrogen

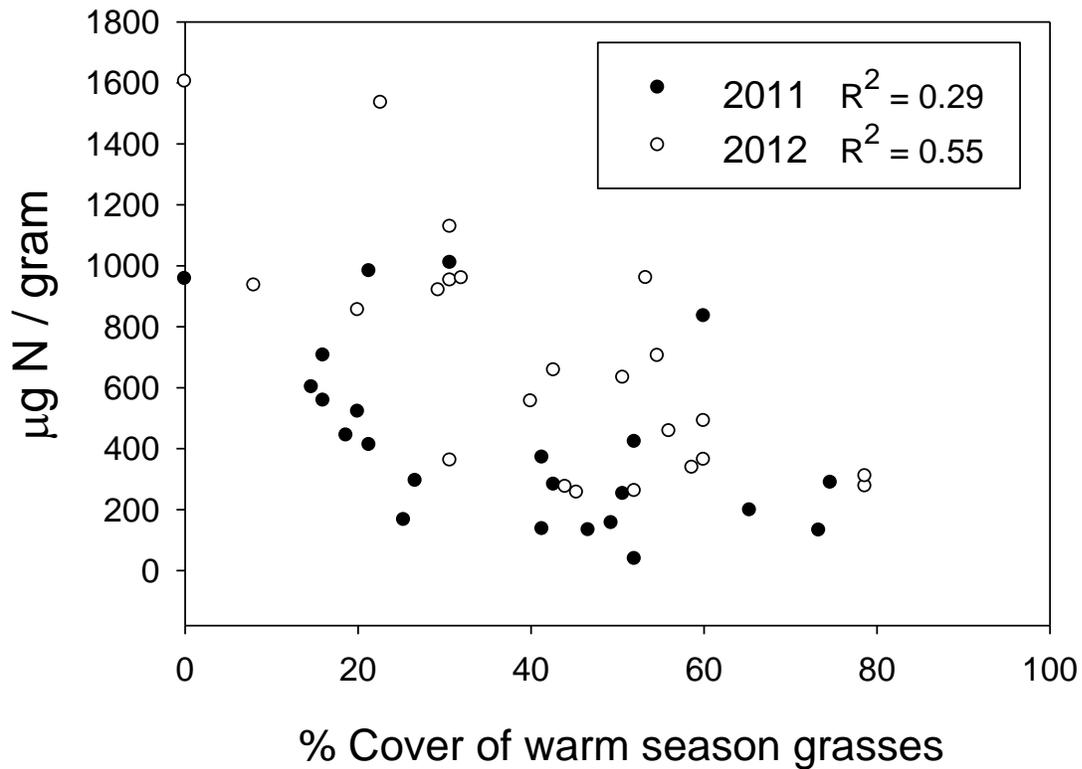
Aboveground biomass was higher in control and spring-mowed plots than in spring/summer mowed plots over all sampling dates (Table 5.1, Fig. 5.7). Available nitrogen varied greatly between individual plots and over seasons. There was no significant effect of whole-plot treatments on  $\text{NH}_4$ ,  $\text{NO}_3$ , or total inorganic nitrogen over the study period (Table 5.1, Fig. 5.8). However, there was significantly more  $\text{NH}_4$  and  $\text{NO}_3$  in plots over summer (June-Sept.) than over winter (Oct-Mar.) or spring (April-May,  $p < 0.0001$ , Fig. 5.8). There was no relationship between the amount of aboveground biomass and total nitrogen in spring or summer ( $p > 0.1$ ). However, cover of warm-season grasses in July and September 2011 and 2012 was negatively correlated to total nitrogen in summer 2011 and 2012 ( $p < 0.01$ , Fig. 5.9).



**Fig. 5.7.** Aboveground biomass from control, spring mowed, and spring/summer mowed plots collected on 8/1/2009 (pre-treatment), 7/27/2010, 8/20/2011, 8/20/2012, and 8/20/2013, + standard error.



**Fig. 5.8.**  $\text{NH}_4$  and  $\text{NO}_3$  extracted from ion-exchange resin bags in control, spring mowed, and spring/summer mowed treatments + standard error.



**Fig. 5.9.** Correlation of total nitrogen extracted from resin bags in summers 2011 and 2012 to % cover of warm-season grasses in July 2011 ( $p = 0.008$ ) and 2012 ( $p < 0.0001$ ).

## 5.5 Discussion

The mowing treatments greatly altered species composition in study plots; however, the within-plot seeding treatment did not influence species composition. As hypothesized, non-native grasses were less abundant in spring-mowed and spring/summer mowed treatments. However, contrary to my hypotheses, non-native forbs were more abundant in mowed treatments than in the control treatment. Overall, native species were most abundant in spring-mowed plots, suggesting that the reduction of non-native winter-active grasses may benefit natives. Primary production did not increase after spring mowing, and was significantly lower in spring/summer mowed plots than in controls, indicating that this ecosystem may not be resilient to extensive

mowing or grazing. However, total inorganic soil nitrogen availability, as assessed by resin bag collections, did not vary between treatments. Precipitation patterns varied between years, and the interaction between the timing of precipitation and treatment applications also affected plant species composition.

My results showed that broadcast seeding with native cool season wheatgrasses may not enhance restoration success of grasslands. The amount of seeds added to plots was over five times greater than the seeding rate suggested for restoration projects (USDA NRCS), however, I did not observe any germination of seeded species during the study period. The seeds germinated readily in the lab, so factors in the field determined the lack of germination in the experiment. Other studies have also found that broadcast seeding is not very effective (Beyers 2004; Sheley et al. 2006; Bernstein et al. 2013). This may result from seeds not being buried to a sufficient depth to germinate and survive, or seed predation by insects, rodents, and birds (Barberá et al. 2006; Orrock et al. 2009; Defalco et al. 2012). In contrast to seeding, the mowing treatments resulted in very different composition of plant species. Cover of non-native grasses, composed mostly of *B. tectorum*, declined rapidly in mowed plots after the first year of treatment applications. Mowing in late May and early June removed seed-heads of *B. tectorum* before they had after-ripened, so no new viable seed was added to plots. In June 2013, one year after termination of treatments, cover of exotic grasses was still significantly higher in control plots than mowed treatments (Fig. 4), indicating that reduction of *B. tectorum* and other exotic grasses continues beyond treatment applications. Several studies have shown that *B. tectorum* does not have a long-lived seedbank, as most seeds germinate readily after wet conditions in late fall through early spring (Hulbert 1955; Mack & Pyke 1983). Mowing or high intensity, short-

duration grazing of invaded grasslands early in spring may be a very effective means to reduce abundance of undesirable winter-active grass species.

Although early spring and spring/summer mowing decreased abundance of winter-active grasses, it also led to an increase in exotic forbs. Total reduction of exotic species was only ca. 8-9% in mowing treatments. While mowing and grazing are different in a variety of ways, the results of this mowing experiment were similar to grazing studies that differentially affected morphologically distinct groups of plant species (Hayes & Holl 2003; Stahlheber & D'Antonio 2013). Specifically, the two exotic forbs that benefited most from spring/summer mowing, *Convolvulus arvensis* and *Erodium cicutarium*, have characteristics that benefit plant species in grazed areas worldwide (Díaz et al. 2007). These two species were both prostrate annuals, and were either stoloniferous (*C. arvensis*) or rosette-forming (*E. cicutarium*). These traits give exotic forbs a distinct advantage after disturbances, like grazing or mowing, that damage tall perennial species. Studies have found *Erodium spp.* to increase after grazing in both Texas and California grasslands (Weigel et al. 1989; Kimball & Schiffman 2003). Additionally, many non-native forbs of Western U.S. grasslands originate in Eurasia, and have experienced a long evolutionary history of heavy grazing (Mack 1989). Thus, mowing or grazing may not be an adequate control to reduce abundance of this subset of exotic forb species.

Native cool-season grasses were most abundant in spring mowed plots, and *Pascopyrum smithii* was the most abundant cool-season grass. In mixed-grass prairie of Wyoming, *P. smithii* increased in areas receiving light grazing, but decreased in heavily grazed areas (Schuman et al. 1999). Unlike exotic annual grasses, this perennial grass can resprout from the base and may be stimulated by grazers. The rhizomatous root system of *P. smithii* allows it to readily re-sprout after clipping, however, it does not respond well to extensive damage. *P. smithii* performed

especially well in spring mowed plots in 2010 and 2012 (Fig. 5.5). *P. smithii* may have benefited from a lack of competition with non-native grasses in mowed treatments in those years. *Pascopyrum smithii* could be an important species for restoration of disturbed grasslands. However, this study indicates that broadcast seeding may not be an effective way to establish this grass, so drill seeding or planting starters would be necessary.

Species of warm-season grasses responded differentially to treatments. *Bouteloua gracilis* was most abundant in spring/summer mowed plots (Table 5.2). Other studies have found *B. gracilis* to increase in areas that received light to heavy grazing (LeCain et al. 2002). *Bouteloua gracilis* may be a viable option for restoration of heavily grazed grasslands. In contrast, the warm-season grass *Sporobolus cryptandrus* had similar cover in all treatments, and had particularly high cover in September 2012 after a dry early summer and wet July. *Sporobolus cryptandrus* is extremely drought tolerant (Weaver & Hansen 1939; Wan et al. 1993), and could be an important plant for restoration because of its drought tolerance and ability to grow in heavily invaded grasslands after non-native species senesce. In addition, the cover of warm season grasses in late summer was negatively correlated to nitrogen availability in the soil, indicating that these grasses may help draw down soil nutrient availability, making the nutrients less available for non-natives the following spring. However, many studies show that warm season grasses benefit under reduced soil nitrogen conditions (Paschke et al. 2000; Cherwin et al. 2008), so causality behind this pattern is complex (Seastedt et al. 1991). Planting a variety of native species with differing phenologies and drought tolerances appears effective for restoring grasslands with highly variable precipitation patterns (Cherwin et al. 2008).

Inter and intra-annual variation in precipitation can greatly impact annual species (Pitt & Heady 1978; Weigel et al. 1989; Levine & Rees 2004), and the results of this study were

influenced by the timing of treatment application and yearly precipitation patterns. In 2010 there was above-average precipitation in early spring and summer, and spring/summer mowed plots had greater overall cover of vegetation and greater warm-season grass cover in July and September. In contrast, 2012 was a very dry year, and non-native grasses in all treatments senesced before sampling dates in June. In 2012, the spring/summer mowing treatment had very low cover of all species, greater litter and bare ground, and very low primary production. Although seasonal and annual variation in precipitation produced large and significant differences in production and relative cover of plant groups, the impact of mowing treatments remained consistent over years. Hence, management applications can impact composition of plant communities with high fluctuation in precipitation.

My results indicate that grazing or mowing to target the temporal niche of annual grasses can be a successful management technique. Although mowing treatments did not reduce cover of all introduced species, the spring-mowed treatment did decrease cover of exotic grasses and increase the number of desirable species. The use of mowing or grazing for ecological restoration has been successfully applied in invaded grasslands in California (Maron & Jeffries 2001), and can be used for grasslands along the Front Range of Colorado. A meta-analysis of studies in California grasslands found grazing in early spring to be most effective in increasing cover of native species (Stahlheber & D'Antonio 2013), similar to results of this study. Strategically applied mowing or grazing treatments have positively maintained or enhanced diversity in a tallgrass prairie (Collins et al. 1998) and short-grass steppe (Hart 2001). In an age of rapid environmental change, novel approaches to ecosystem management are becoming necessary to ensure continuation of important ecosystem services. This study shows that management strategies that exploit phenological differences in exotic and native species may

allow for maintenance of resilient ecosystems that will continue to provide valuable services in the future (Chapin et al. 2009; Wolkovitch & Cleland 2011).

## CHAPTER 6

### CONCLUSION

In dry ecosystems, precipitation change associated with climate change will be one of the most influential global change factors driving plant species distributions in the future (Weltzin et al. 2003). The goal of my dissertation was to examine the effects of seasonal precipitation changes on plants in a semi-arid grassland ecosystem. In Chapter 2, I observed that non-native grasses, especially *Bromus tectorum*, increased in abundance in response to increases in winter precipitation. In Chapter 4, I found that both winter and spring precipitation increased population growth rates of *B. tectorum*, so even in years with drier winters, adequate spring moisture benefited *B. tectorum*. In contrast, native species were least abundant in treatments with increased winter precipitation and most abundant in treatments with reduced winter precipitation and increased summer precipitation. Plots with higher abundance of the non-native grass *B. tectorum* had lower available soil moisture and plant species diversity, indicating that growth by the winter-active grass may suppress later-growing native plants. Most plant functional groups in the grassland responded strongly to changes in precipitation. If climate change involves seasonal shifts in precipitation to wetter winters, the species composition in Front Range grasslands may change considerably. Increased winter precipitation will increase abundance of exotic grasses, and, especially if coupled with drier summers, could detrimentally affect semi-arid grasslands by reducing availability of soil water for later growing plants, causing earlier dry-down and senescence of grasslands, and reducing diversity and ecosystem productivity.

*Bromus tectorum* is associated with a number of detrimental effects in ecosystems where it has become a dominant species (e.g. Melgoza et. al 1991, D'Antonio and Vitousek 1992,

Concilio et. al 2103). In a study of soil characteristics at my field site, I found that soils from *B. tectorum* populations had significantly different soil properties than soils from under a native grass (O’Conner et al., *in review*). *Bromus tectorum* also grew larger in its own soils than in those of the native grass (O’Conner et al., *in review*), indicating that soil modification may further benefit *B. tectorum* and increase difficulty of eradication. Together, these results show that *B. tectorum* may become a more invasive species in Colorado as the climate changes. Currently, *B. tectorum* is on the C list of invasive species in Colorado (Colorado Dept. of Agriculture, 2003). This means that local jurisdictions can choose to manage to reduce the prevalence of *B. tectorum*, but populations of *B. tectorum* are not required to be suppressed in Colorado. I would argue that, especially in areas where populations of *B. tectorum* are still small, management should be used to reduce abundance before populations grow and negatively affect grasslands in the future.

There are a variety of management strategies that can be used to reduce abundance of winter-active grasses, such as *B. tectorum*, in grassland ecosystems along the Front Range of Colorado. In Chapter 5 of my dissertation, I used timed mowing applications that impact winter-active grasses in early spring to effectively reduce their abundance. Spring mowing resulted in an increase in cover of native plant species, however, spring and year-round mowing also led to an increase in non-native forbs. Management strategies that target the temporal niche of non-native grasses may reduce their abundance, thereby promoting more desirable grasslands in the future. Another management option involves restoration with native species that could benefit from climate change, or survive under a range of climatic conditions (Choi et al. 2008). In Chapter 2, I found that cool-season grasses were not as negatively impacted by increased winter precipitation as other native species. Thus, cool-season grasses may be ideal candidates for use in

restoration efforts. Finally, management with biocontrol may negatively impact undesirable invasive species. The use of biocontrol agents has successfully reduced populations of two invasive *Centaurea* species in grasslands along the Front Range of Colorado (Seastedt et al. 2007). To date, no biocontrol agents have been identified to be extremely successful on *B. tectorum*, but there are several native fungal pathogens that are being considered for use as biocontrols. The native fungal pathogen *Ustilago bullata* infects *B. tectorum* as a seedling and entirely co-opts seed production of the plant. Observations from Chapter 3 indicate that the pathogen *U. bullata* may become more successful at infecting *B. tectorum* with wetter winters, and this could increase its potential as a biocontrol agent.

Colorado's semi-arid grasslands, and the important services they provide, will change as the climate changes, and it will be a challenge to manage grassland ecosystems to continue to perform important functions. More research is needed on how climate change will affect composition of plant communities and interactions between plant species to get a realistic picture of how they will change. This research will help scientists and managers identify ecosystems where intervention is needed to promote desirable communities, and develop successful restoration strategies in the future.

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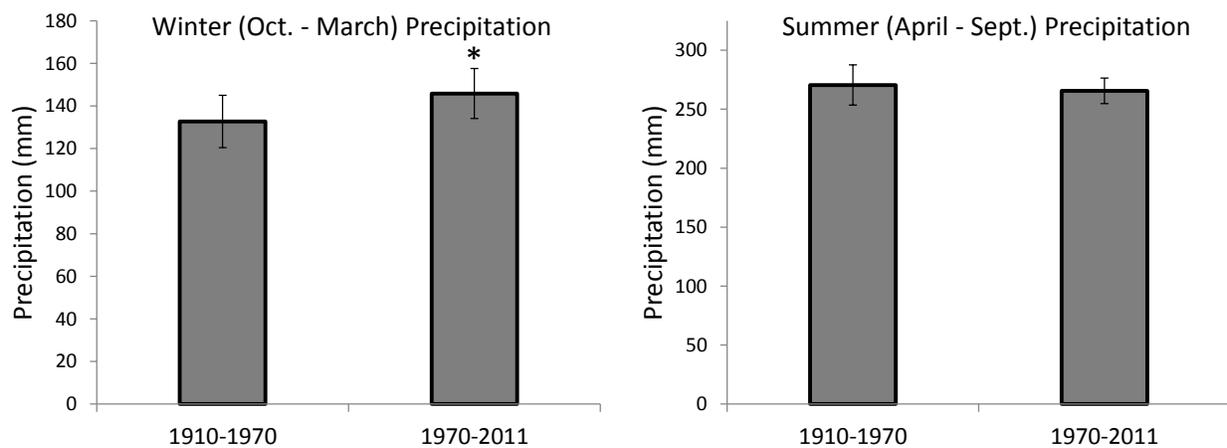
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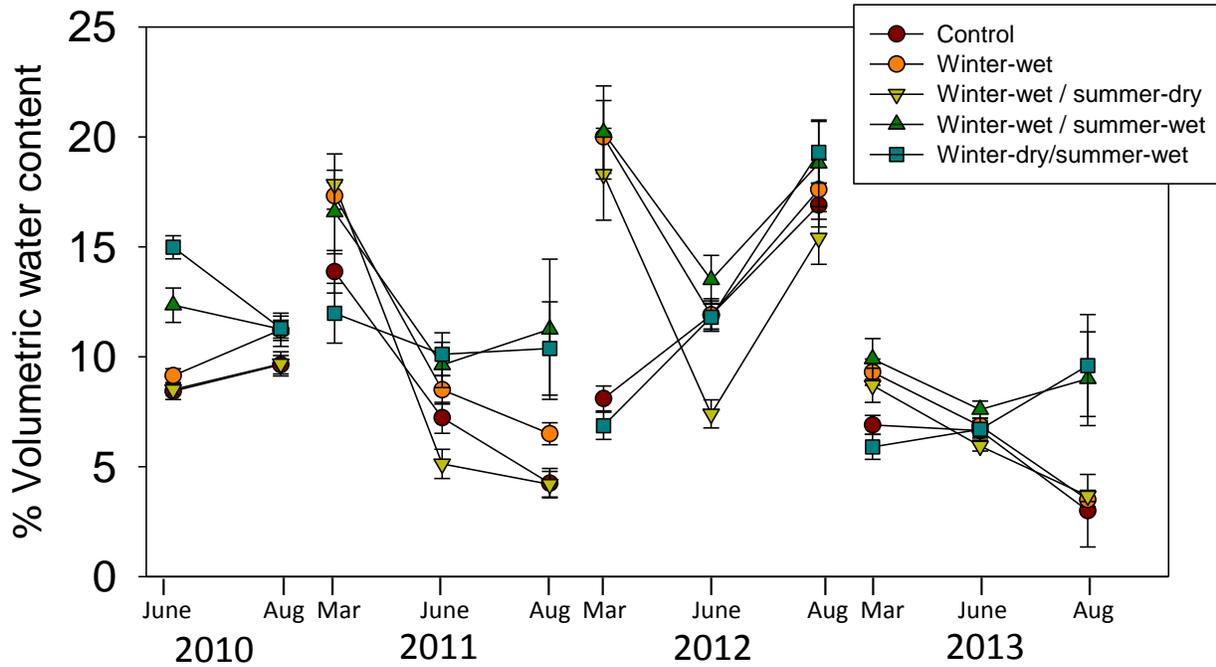
## APPENDIX 1

### Comparison of Precipitation from Boulder weather stations



**Fig. A1.** A comparison of average precipitation from seven weather stations along the Front Range of Colorado in winter (Oct- March) and summer (April – Sept.) from 1910-1970 and 1970-2011. There was a slight increase in average winter precipitation after 1970 ( $p = 0.007$ ), but no change in summer precipitation ( $p = 0.3$ ).

**Soil moisture over time in the precipitation manipulation experiment**



**Fig. A2.** Average % volumetric water content in treatments in June-August 2010, and Mar-August 2011-2013, +/- standard error. Volumetric water content was measured around the middle of each month in each plot with a Hydrosense soil moisture probe (Decagon Devices, Pullman, WA).

**Table A1.** *P*-values from Chapter 1 calculated from Markov chain Monte Carlo (MCMC) sampling of linear-mixed effects models from April 2011- August 2013 (Baayan 2011). All reported *p*-values are treatment comparisons against the control treatment. Significant differences between other treatments at the  $p < 0.05$  level are denoted by different letter subscripts above *p*-values.

Response variable	Winter-wet	Winter-wet/ summer-dry	Winter-wet/ summer-wet	Winter-dry/ summer-wet
April exotic grasses	<b>0.001<sup>a</sup></b>	<b>0.0005<sup>a</sup></b>	<b>0.01<sup>a</sup></b>	<b>0.03<sup>b</sup></b>
April exotic forbs	<b>0.01<sup>a</sup></b>	<b>0.009<sup>a</sup></b>	0.58 <sup>a</sup>	0.44 <sup>a</sup>
April native cool-season grasses	0.34 <sup>a</sup>	0.61 <sup>a</sup>	0.73 <sup>a</sup>	0.41 <sup>a</sup>
April litter	0.19 <sup>a</sup>	<b>0.02<sup>ab</sup></b>	<b>0.04<sup>ab</sup></b>	0.67 <sup>b</sup>
June exotic grasses	0.17 <sup>a</sup>	0.98 <sup>ab</sup>	0.69 <sup>ab</sup>	0.21 <sup>b</sup>
June exotic forbs	0.34 <sup>a</sup>	0.10 <sup>a</sup>	0.06 <sup>a</sup>	<b>0.04<sup>a</sup></b>
June native cool-season grasses	0.33 <sup>a</sup>	0.66 <sup>a</sup>	0.72 <sup>a</sup>	0.93 <sup>a</sup>
June native warm-season grasses	0.81 <sup>ab</sup>	0.91 <sup>a</sup>	0.99 <sup>ab</sup>	0.72 <sup>b</sup>
June native forbs	0.86	0.84	0.39	0.74
August exotic forbs	0.52 <sup>a</sup>	0.25 <sup>a</sup>	0.30 <sup>a</sup>	0.49 <sup>a</sup>
August native cool-season grasses	0.29 <sup>a</sup>	0.24 <sup>a</sup>	0.47 <sup>a</sup>	0.89 <sup>a</sup>
August native warm-season grasses	0.58 <sup>ab</sup>	0.63 <sup>a</sup>	0.36 <sup>ab</sup>	0.27 <sup>b</sup>
August native forbs	0.86 <sup>ab</sup>	0.84 <sup>a</sup>	0.39 <sup>b</sup>	0.74 <sup>b</sup>
August litter	0.27 <sup>a</sup>	<b>0.001<sup>a</sup></b>	<b>0.04<sup>c</sup></b>	<b>0.008<sup>c</sup></b>
Winter total nitrogen	0.32 <sup>a</sup>	<b>0.04<sup>a</sup></b>	0.29 <sup>a</sup>	<b>0.006<sup>b</sup></b>
Spring total nitrogen	0.15 <sup>a</sup>	0.14 <sup>a</sup>	<b>0.007<sup>a</sup></b>	0.27 <sup>c</sup>
Summer total nitrogen	0.12 <sup>a</sup>	0.16 <sup>a</sup>	0.48 <sup>a</sup>	0.46 <sup>a</sup>