Title

Climate Change, Bromus tectorum (Cheatgrass) Invasion, and Wildfire Risk Management in the Eastern Sierra Nevada, California

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CLIMATE CHANGE, *BROMUS TECTORUM* (CHEATGRASS) INVASION, AND WILDFIRE RISK MANAGEMENT IN THE EASTERN SIERRA NEVADA, CALIFORNIA

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by

Catherine E. Wade

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TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

ABSTRACT

CLIMATE CHANGE, *BROMUS TECTORUM* (CHEATGRASS) INVASION, AND WILDFIRE RISK MANAGEMENT IN THE EASTERN SIERRA NEVADA, CALIFORNIA

Catherine E. Wade

Bromus tectorum L. (Poaceae, 'cheatgrass') is a flammable, non-native, annual grass from Eurasia that has spread throughout the western United States, exerting serious impacts on ecosystems by fueling frequent fires and displacing native vegetation. Over the last decade, *B. tectorum* has begun expanding into higher elevations, where it currently coexists with native vegetation and has not yet altered fire regimes. In this dissertation, I examine the impacts of climate change and management activities on high-elevation *B. tectorum* populations in the eastern Sierra Nevada, California. In Chapter 1, I explore the impacts of changing patterns of snow and rain on *B. tectorum* as compared to native species. I found that *B. tectorum* responses to precipitation change (snow and rain) were of greater magnitude than the responses of native species at the University of California Valentine Eastern Sierra Reserve. *Bromus tectorum* density followed the declining trend in winter snowpack over three years, and within-year snowpack reductions advanced the timing of *B. tectorum* phenology. Species-specific responses to spring rainfall showed some variation in different years of the study, highlighting the importance of both winter and spring precipitation and suggesting that inter-annual variability will generate different impacts on different species depending on specific conditions. Chapter 2 presents a greenhouse experiment to study the impacts and interactions of temperature, competition, and facilitation on native species and *B. tectorum*. Higher temperatures in the greenhouse dramatically decreased *B. tectorum* reproductive allocation and increased vegetative biomass. *Bromus tectorum* tended to have negative impacts on neighboring species by reducing their biomass, reproductive allocation, stomatal conductance, and photosynthetic rates (suggesting possible competition), while a native nitrogen-fixing forb tended to have positive impacts on these variables for *B. tectorum* and other native species (suggesting possible facilitation). Chapter 3 is an applied research project conducted at Devils Postpile National Monument to assess the impacts of extreme disturbance events and fuels management activities on fuel loads and *B. tectorum* invasion. An extreme windstorm substantially elevated fuel loads, which were reduced in areas that were treated for hazardous fuel reduction. Anthropogenic disturbance from fuel reduction projects was not creating establishment sites for *B. tectorum*, but areas that were subjected to a high-severity wildfire burn about twenty years ago provided loci of *B. tectorum* invasion. Prioritizing monitoring efforts in high-severity burned areas, especially when they coincide with high levels of disturbance from recreational activities, such as along hiking trails and near pack stations, would strengthen active management of *B. tectorum* infestations at Devils Postpile National Monument. Overall, this dissertation shows that various climatic changes and anthropogenic impacts could influence mechanisms for future high-elevation *B. tectorum* expansion in different ways.

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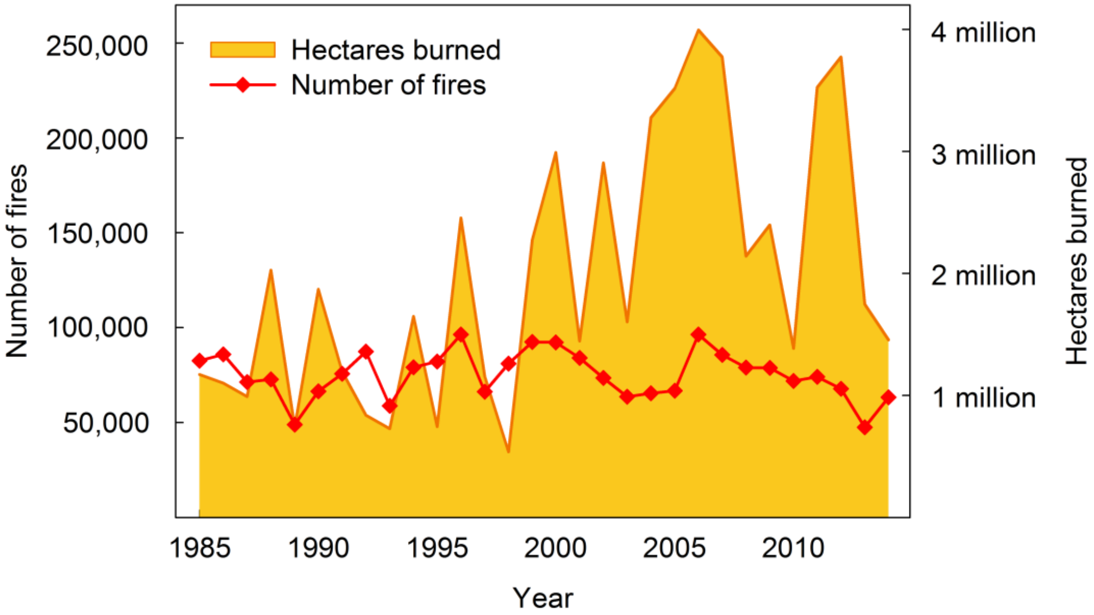
INTRODUCTION

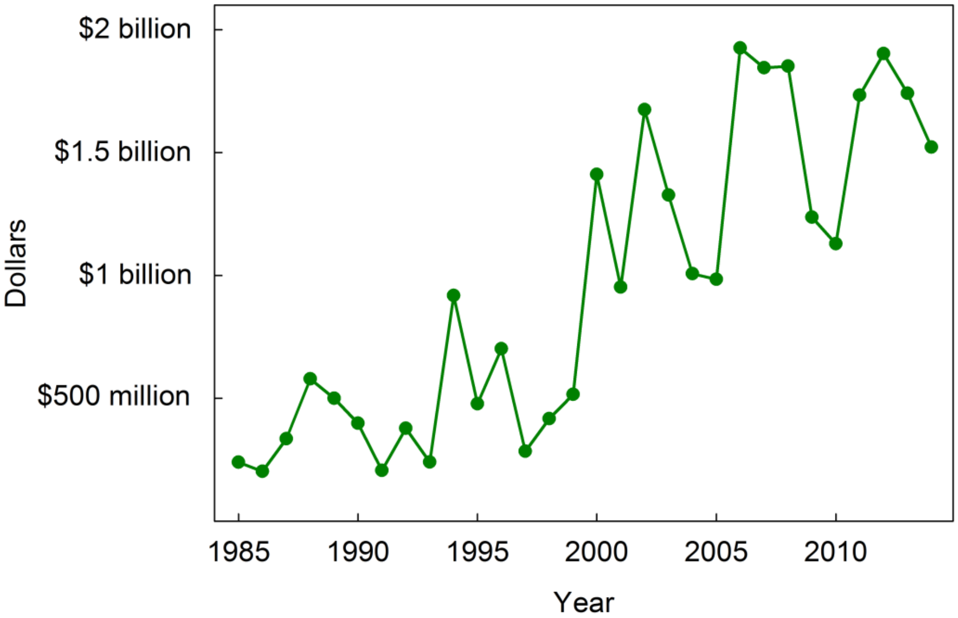
> *Ecological stowaways began to arrive with the earliest settlements.... and found thousands of square miles of ready-made seedbed prepared by the trampling hoofs of range livestock. In such cases the spread was often so rapid as to escape recording; one simply woke up one fine spring to find the range dominated by a new weed. A notable instance was the invasion of the intermountain and northwestern foothills by....cheat grass (*Bromus tectorum*).*
>
> —Aldo Leopold, *A Sand County Almanac* (1949); pp. 164-165

Wildfire is integral to many ecosystems, especially in the semiarid western United States. Each year, the total area burned by wildfires fluctuates due to inter-annual variation in climate. However, since the mid-1980s, despite the total number of fires remaining relatively constant, annual area burned has been increasing (Figure i-1). Not surprisingly, federal fire suppression costs (Figure i-2) have mirrored the upward trend in area burned. Wildfire damage potential and the demand for fire protection are also escalating due to the rapid expansion of human communities into wildlands. Growth of the natural-amenity-rich wildland-urban interface (WUI) has been outpacing that of other land-use types for decades (McGranahan 1999, Brown et al. 2005, Radeloff et al. 2005, Hammer et al. 2009). Despite the important ecological role of wildfire, recent incidences of uncharacteristically severe fires pose numerous ecological, economic, and social challenges. These include a loss of biodiversity, wildlife habitat, and ecosystem carbon; decreased quality of forage for livestock; increased firefighting costs; and higher risks of losses of human lives and property.



Data source: National Interagency Fire Center (NIFC) 2015

Figure i-1. Annual number of wildfires and area burned in the United States, 1960-2014.



Data source: National Interagency Fire Center (NIFC) 2015

Figure i-2. Federal fire suppression costs, 1985-2014.

Three key anthropogenic factors have been attributed to recent increases in area burned: (1) warmer temperatures and earlier snowmelt in high-elevation regions associated with climate change are leading to longer, drier fire seasons (Westerling et al. 2006); (2) the spread of flammable non-native species (of which, *Bromus tectorum* L. [Poaceae, ‘cheatgrass’] is the most notorious) is increasing fine fuel loads and fire frequencies (Brooks et al. 2004, Balch et al. 2013); and (3) a legacy of fire suppression policy inadvertently promoted the accumulation of hazardous densities of vegetation to serve as fuel (Dombeck et al. 2004, Johnson et al. 2009). Climate change is expected to amplify many of these impacts, and potential interactions among these factors further complicate the issue. The relative importance of each of these drivers of wildfire depends on the specific ecosystem.

Invasion by *Bromus tectorum*

In sagebrush steppe ecosystems of the Great Basin Desert, the non-native annual grass *B. tectorum* has substantially altered fire regimes. In its pristine (i.e., uninvaded) state, sagebrush steppe ecosystem structure typically does not carry fire very effectively. Vegetation is patchy and native shrubs and bunchgrasses are separated by bare ground; hence, fire is limited by the availability of continuous fuel (Westerling and Bryant 2008, Littell et al. 2009). *Bromus tectorum* increases fuel continuity by colonizing bare ground amid native vegetation, completes its life cycle before native species, and becomes highly combustible by early summer (Brooks et al. 2004). The resulting frequent fires do not provide adequate recovery time for native species, while *B. tectorum* thrives and displaces native vegetation, ultimately transforming ecosystems from native perennial shrublands to invasive annual grasslands (Smith et al. 1997). As such, *B. tectorum* engineers a positive feedback cycle with fire that perpetuates its own dominance, often called the “grass-fire cycle.” Figure i-3 shows the transition from a native sagebrush steppe ecosystem to a near-monoculture of *B. tectorum*. In addition to altering wildfire regimes, *B. tectorum* reduces forage quantity and quality, species diversity, and wildlife habitat (Knapp 1996). Once *B. tectorum* has altered natural fire cycles, ecosystem restoration to pre-invasion conditions is extremely difficult, if not impossible (Brooks et al. 2004).

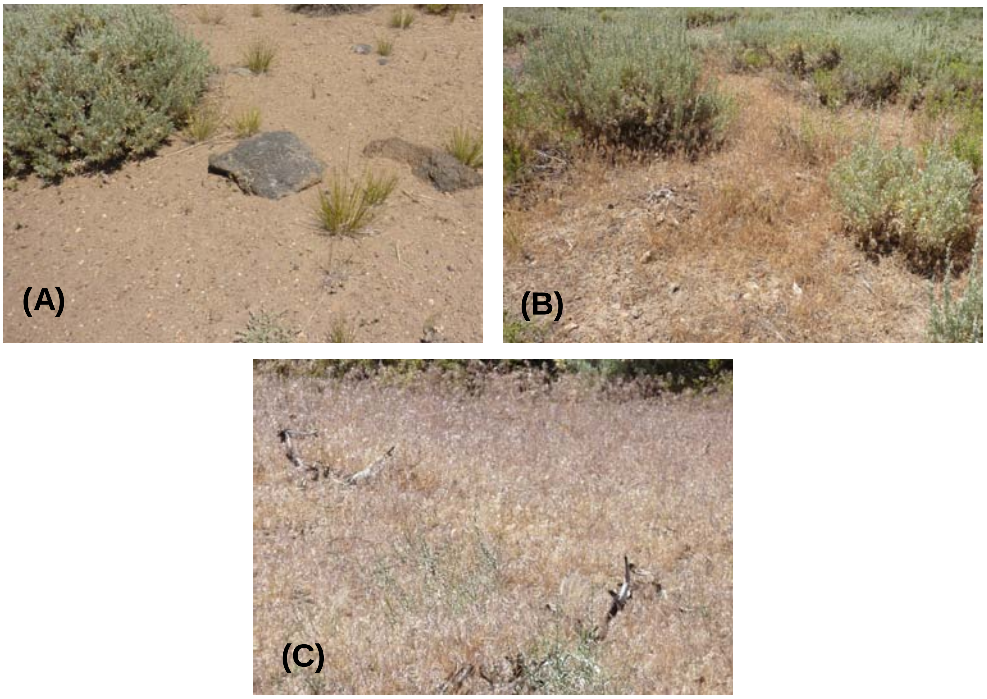
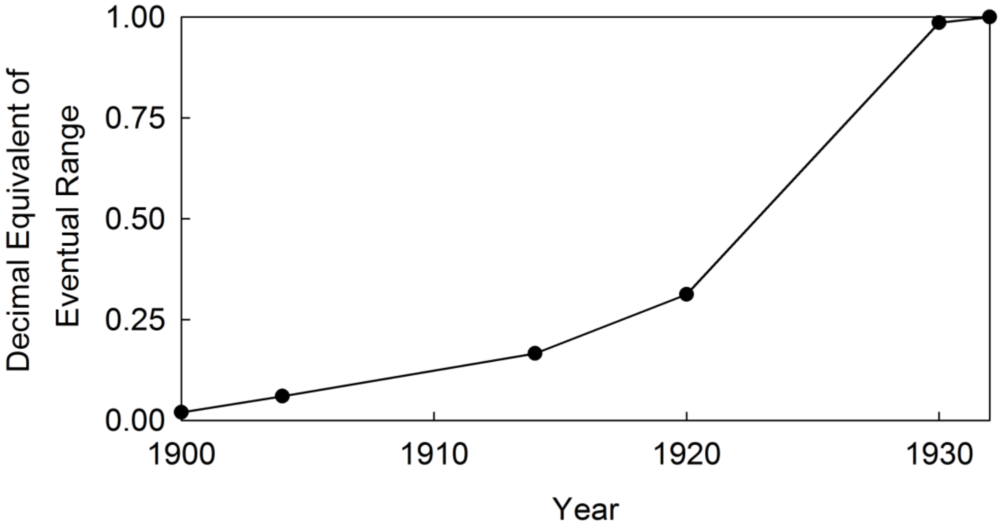


Figure i-3. Transition from an intact sagebrush steppe ecosystem to a *Bromus tectorum* monoculture. (A) Native sagebrush steppe vegetation community; (B) *Bromus tectorum* coexisting with sagebrush steppe vegetation; (C) *Bromus tectorum* monoculture following fire (note burned shrub skeletons).

History and Distribution of Bromus tectorum

Bromus tectorum is native to arid regions of western and central Europe, southwestern Asia, and northern Africa (Novak and Mack 2001) and was accidentally introduced to North America in the late 1800s through at least seven independent events, often via contaminated grain seed, packing material, and ship ballasts (Mack 1981, Novak and Mack 2001). Genetic analyses indicate that source populations from North America were drawn exclusively from Europe (Novak and Mack 2001). Early infestations primarily occurred near wheat fields (wheat seeds were often contaminated with *B. tectorum* seeds) and along railroads (straw contaminated with *B. tectorum* was used as packing material for goods transported by rail). *Bromus tectorum* was also occasionally intentionally sold and planted as forage for deteriorated rangelands (Mack 1981). Its spread pattern closely aligns with European human immigration and emigration (Novak and Mack 2001).

Once *B. tectorum* had been introduced, a combination of factors facilitated its rapid spread throughout the West, where it became locally abundant within three decades, largely reaching its current extent by the 1930s (Figure i-4; Mack 1981). Because its native range has a climate regime similar to that of the semiarid western United States, *B. tectorum* was pre-adapted to the region's wet, cold winters and hot, dry summers (Mack 1981). *Bromus tectorum* introduction coincided with rampant livestock overgrazing that degraded western rangelands and increased their susceptibility to invasion by reducing native herbaceous vegetation cover, creating widespread soil disturbance, and aiding *B. tectorum* seed dispersal (Mack 1981, Knapp 1996). Disturbances to native vegetation coupled with the lack of dominant native annual flora in the Great Basin provided an unoccupied ecological niche for *B. tectorum* to exploit (Knapp 1996, Smith et al. 1997). *Bromus tectorum* also proved to be a strong competitor with native vegetation due to its relatively high rates of acquisition of water and other resources (Harris 1967, Melgoza et al. 1990, Melgoza and Nowak 1991). Finally, the initiation of the grass-fire cycle eliminated fire-sensitive native species, allowing *B. tectorum* to rapidly exploit post-fire increases in resources and become increasingly dominant (Smith et al. 1997). *Bromus tectorum* has decreased fire return intervals in many invaded sagebrush steppe communities from approximately 30-110 years to less than 10 years, hindering the re-establishment of native species with longer disturbance recovery times (Knapp 1995, West and Yorks 2002, Mazzola et al. 2011).



Adapted from Mack (1981)

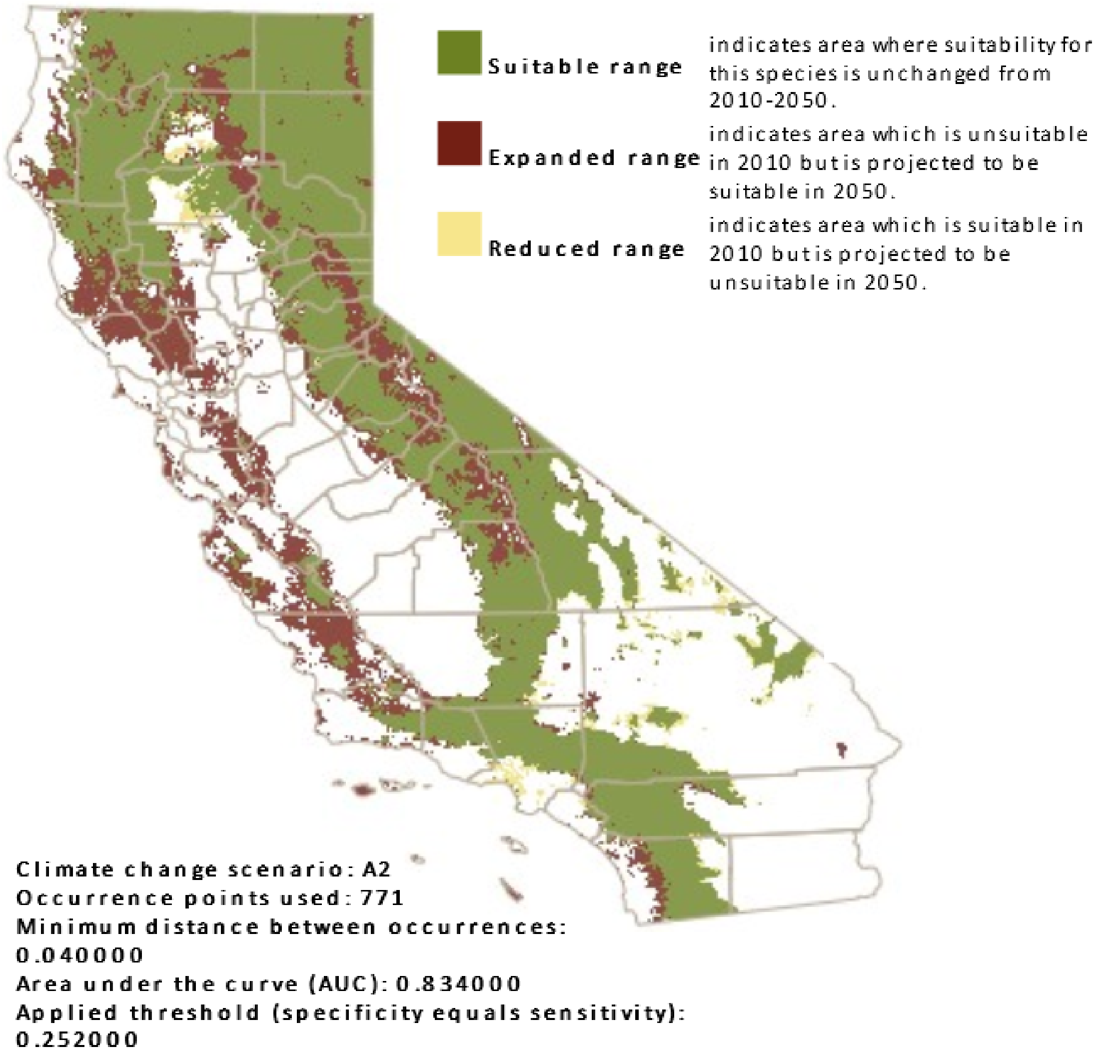
Figure i-4. *Bromus tectorum* area occupied versus time based on percentage of eventual range occupied.

Climate Change

Bromus tectorum is now the most ubiquitous invasive plant species in the western United States (Weltz et al. 2011), dominating over 40 million hectares (ha) in the Great Basin (Whisenant 1990) and approximately 20% of sagebrush steppe (Knapp 1996). Across the Great Basin, *B. tectorum* land cover has served as a primary ignition source, consistently burned more frequently (~2-4×) than native land cover types, and was a disproportionate fuel source in 78% of the 50 largest fires from 2000-2009 (Balch et al. 2013). Climatic controls on wildfire activity include both direct, short-term and indirect, long-term effects by influencing fire weather conditions and the distribution and amount of flammable vegetation, respectively (Krawchuk et al. 2009). In the historic record, years of widespread fire have been linked to both higher-than-normal antecedent precipitation and lower-than-normal precipitation concurrent with the fire season (Littell et al. 2009). The specific relationships of precipitation and wildfire activity vary by ecosystem type. For example, forests contain abundant fuels but fire is typically limited by flammability, thus forest fires correlate with current-year drought (Littell et al. 2009). Consensus among climate models regarding future temperature increases make predictions for future forest fire activity relatively straightforward (Westerling and Bryant 2008). Conversely, shrublands contain more sparse fuels and fire is limited by fuel continuity, thus shrubland fires correlate with high antecedent precipitation (i.e., exhibiting a lagged relationship) that promotes the growth of fuels that subsequently cure in the hot, dry summer months (Westerling and Bryant 2008, Littell et al. 2009).

Fire frequency and size for *B. tectorum* are strongly correlated with the preceding year's precipitation (Balch et al. 2013). Thus, for shrubland ecosystems—especially those invaded by *B. tectorum*, changes in precipitation are likely to be more important to fire activity than changes in temperature (Westerling and Bryant 2008). The variability in both spatial and seasonal precipitation projections from climate models represents greater uncertainty for how fire risk in these ecosystems may respond to climate change (Westerling and Bryant 2008, Littell et al. 2009). Considerable inter-annual variation in precipitation leads to considerable inter-annual variation in *B. tectorum* biomass (Griffith and Loik 2010) and *B. tectorum* fires (Balch et al. 2013). Future precipitation projections suggest greater inter-annual variability (Abatzoglou and Kolden 2011), which is likely to have strong impacts on *B. tectorum* fires, either resulting in increases or decreases depending on the amount of antecedent precipitation.

In recent decades, *B. tectorum* has spread from the Great Basin Desert into higher elevations of the surrounding mountain ranges of the Sierra Nevada and Rocky Mountains (Brown and Rowe 2004, Pauchard et al. 2009, Griffith and Loik 2010, Banks and Baker 2011). *Bromus tectorum* now occurs at elevations >2,700 m (pers. obs.), though its impacts at high elevations are limited (i.e., its presence has not yet initiated changes to fire cycles). Climate change is expected to expand the range of suitable *B. tectorum* habitat (Figure i-5), which may exacerbate the invasion of *B. tectorum* into higher elevations.



Climate change scenario: A2
Occurrence points used: 771
Minimum distance between occurrences: 0.040000
Area under the curve (AUC): 0.834000
Applied threshold (specificity equals sensitivity): 0.252000

Report generated on April 1, 2014 using calweedmapper.calflora.org

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Figure i-5. Change in *Bromus tectorum* suitable range, 2010-2050.

Most research on invasive species, including *B. tectorum*, has focused on lower elevations where impacts have been extensive (Pauchard et al. 2009), while comparatively less research has explored outlier *B. tectorum* infestations near its high-elevation range margin (but see Chambers et al. 2007, Griffith and Loik 2010, Concilio and Loik 2013, Concilio et al. 2013). However, montane ecosystems are likely to be especially sensitive to climate change (Dunne et al. 2003), and the combination of climate change and increased human use of these areas, due to rapid WUI growth and increased tourism, is expected to escalate high-elevation plant invasions (Radeloff et al. 2005, Pauchard et al. 2009). More research urgently needs to address *B. tectorum* invasions at high elevations before the ecosystem transformations experienced at lower elevations occur there.

Dissertation Outline

This dissertation addresses this research gap by exploring potential climate change and management impacts on *B. tectorum* invasion at the western Great Basin/eastern Sierra Nevada ecotone near Mammoth Lakes, Mono County, California (Figure i-6), near the high-elevation edge of *B. tectorum*'s invaded range. Here, despite the incipient invasion at relatively higher elevations, *B. tectorum* has not yet altered fire regimes, thus the window of opportunity for conservation, rather than restoration, still exists (Tzankova and Concilio 2015). *Bromus tectorum* in the eastern Sierra Nevada is present in lower densities among relatively intact native communities (Figure i-7), likely constrained by snow-free periods under current climatic conditions (Chambers et al. 2007, Griffith 2010, Griffith and Loik 2010) and lower propagule pressure (Pauchard et al. 2009).

Data source: Level III Ecoregions of the Continental United States,
U.S. Environmental Protection Agency

Figure i-6. Map of the study region location (red star) at the western Great Basin/eastern Sierra Nevada ecotone.

Figure i-7. *Bromus tectorum* invasion characteristics typical of the study region, whereby *B. tectorum* has colonized shrub interspaces and coexists with native vegetation.

The town of Mammoth Lakes exemplifies many characteristics of the WUI nationwide, including rapid population growth, an amenity-dependent economy, and significant population fluctuations resulting from tourism and seasonal occupation of homes (McGranahan 1999, Everett and Fuller 2011). The permanent resident population of 8,234 grew by 16.1% between 2000-2010, considerably higher than the statewide average of 10.0% (U.S. Census Bureau 2012). Tourism drives the town's economy and results in economic and employment fluctuation (Town of Mammoth Lakes 2007). Diverse winter and summer recreational opportunities can increase the population to >40,000 during peak weekends and holidays (Mammoth Lakes Fire Protection District 2012). The region is home to the Mammoth Mountain Ski Area, Yosemite National Park, Devils Postpile National Monument, Sequoia and Kings

Canyon National Parks, and the Inyo National Forest. Elevation ranges from approximately 2,130 to over 3,350 m (Mammoth Lakes Fire Protection District 2012). Of the 9,626 housing units, over half (51.7%) are occupied only for seasonal, recreational, or occasional use (U.S. Census Bureau 2010). Maintaining its aesthetic character as a small mountain community is a high priority for Mammoth Lakes; the town describes itself as a "village in the trees" (Town of Mammoth Lakes 2007). The City of Los Angeles also relies on snowpack from the eastern Sierra Nevada as its primary water source; as such, the Los Angeles Department of Water and Power (LADWP) owns property throughout the Owens Valley and diverts a substantial amount of surface water from the region to the City of Los Angeles.

In this dissertation, I investigate three potential mechanisms for expansion of high-elevation *B. tectorum* populations: (1) changing precipitation patterns, (2) increasing temperatures and interactions with native vegetation, and (3) large-scale natural and small-scale anthropogenic disturbance events. Imminent anthropogenic climate change impacts (e.g., rising temperatures, reductions in snowpack and earlier melt timing, changes in precipitation regimes) may exacerbate the impacts of high-elevation *B. tectorum* populations by expanding its climatically suitable range, increasing the duration of the fire season, and creating conditions that favor invasive annual species over longer-lived native perennials (Smith et al. 1997, Griffith and Loik 2010, Abatzoglou and Kolden 2011, Concilio et al. 2013).

Precipitation in semiarid regions exhibits considerable seasonal and inter-annual variability and seasonal soil water deficits strongly limit plant growth during the dry growing season (Weltzin et al. 2003, Loik et al. 2004). The amount, type, and timing of precipitation exert a strong influence on ecosystem structure and function and, consequently, resistance to invasion and resilience to fire (Austin et al. 2004, Bates et al. 2006, Abatzoglou and Kolden 2011, Brooks and Chambers 2011). In sagebrush steppe, snowfall comprises the dominant form of precipitation and snowpack serves as an essential reservoir of water and nutrients for plant uptake during the growing season, delivered during snowmelt as a large, predictable spring resource pulse that replenishes water throughout the soil profile (Bowman 1992, Bilbrough and Caldwell 1997). Deep-rooted shrubs and herbaceous perennials access soil moisture at depth from cold-season precipitation to maintain their water status throughout the growing season (Schlaepfer et al. 2012). Smaller rainfall events during spring and summer typically evaporate before infiltrating to deeper soil layers and thus do not result in long-term soil moisture storage (Bilbrough and Caldwell 1997, Smith et al. 1997, Weltzin et al. 2003). These stochastic and ephemeral increases in soil water availability elicit rapid responses from plants through mechanisms such as rapid fine root growth and/or changes in root uptake capacity (Bilbrough and Caldwell 1997, Bowman and Bilbrough 2001, Loik 2007, Peek and Forseth 2009). Water-limited ecosystems are especially sensitive to changes in precipitation because of its effects on soil moisture (Weltzin et al. 2003, Loik et al. 2004). Chapter 1 examines the effects of future precipitation (snow and rain) change scenarios on *B. tectorum* and coexisting native sagebrush steppe vegetation. This study uses *in situ* snowpack manipulations and rainfall simulations to assess impacts on intrinsic (e.g., photosynthetic rates) and extrinsic (e.g., arrangement on the landscape) fuel properties.

Interactions between individual plants (i.e., competition and facilitation) play an important role in regulating community composition by scaling up to influence the relative abundance of species in ecosystems (Brooker 2006). Environmental conditions mediate the nature and outcome of interactions (Daehler 2003). The stress-gradient hypothesis predicts that competition should be more common when stress is low and facilitation should be more common when stress is high (Bertness and Callaway 1994). Rapid rates of anthropogenic global change portend changing levels of resources and stress, with implications for plant-plant interactions and, hence, community structure. As such, climate change will have direct effects on species by altering resource availability and environmental stress, as well as indirect effects mediated by species interactions. The role of species interactions in influencing plant community responses to climate change is uncertain (Adler et al. 2012). In Chapter 2, I evaluate the roles of competition and facilitation among individual *B. tectorum* and native plants on vegetation community structure under different temperatures.

The widespread success of fire suppression policies that dominated forest management in the United States for more than a century predisposed some ecosystems to uncharacteristically severe fires fueled by dense, homogeneous vegetation structure (Dombeck et al. 2004). As such, fuel reduction projects are now a widespread land management strategy throughout the country to reduce fire hazards and restore historic ecosystem structure (Agee and Skinner 2005). However, some research suggests that the ongoing vegetation disturbances associated with the creation and maintenance of fuel breaks could facilitate invasive species expansion (Keeley 2006, Merriam et al. 2006, Kane et al. 2010), potentially altering fuel dynamics to replace the fire hazard posed by overgrown vegetation with the fire hazard posed by flammable invasive grasses. This could undermine extensive fuel reduction efforts. Chapter 3 monitors effects from an uncharacteristically severe wildfire, an extreme windstorm, and hazardous fuel reduction activities to assess whether these disturbances are contributing to *B. tectorum* spread.

I conclude with a summary of my main findings from each chapter and synthesize the information from these three studies within the context of *B. tectorum* spread and control at high elevation. The results of these three studies advance ecological understanding of the study system in the context of climate change. Based on my findings, I also provide insights into potential management strategies for the region and offer a discussion of specific management efforts that are underway in the region. This dissertation research has broad applications to climate change science, invasion biology, rangeland ecology, arid ecosystem ecology, and natural resource management.

CHAPTER 1

IMPACTS OF PRECIPITATION CHANGE ON *BROMUS TECTORUM* AND NATIVE SPECIES IN A SAGEBRUSH STEPPE ECOSYSTEM

> *While the sportsmen and stockmen wrangle over who should move first in easing the burden on the winter range, cheat grass is leaving less and less winter range to wrangle about.*
>
> —Aldo Leopold, *A Sand County Almanac* (1949); pp. 166-167

Abstract

The flammable invasive grass *Bromus tectorum* L. (Poaceae, ‘cheatgrass’) has had serious impacts on sagebrush steppe ecosystems throughout the western United States by fueling frequent fires and displacing native species. Over the last decade, *B. tectorum* has expanded its invaded range from the Great Basin into higher elevations of the eastern Sierra Nevada, where it coexists with native vegetation and has not yet altered fire regimes. I tested the effects of snowpack manipulations (increased, decreased, and ambient depth) over three drought years (2012-2014) and springtime water additions (+10 mm H_2O) over two drought years (2013-2014) to compare potential responses to precipitation change of *B. tectorum* with the native perennials *Achnatherum hymenoides* (Roem. & Schult.) Barkworth (Poaceae, ‘Indian ricegrass’), *Elymus elymoides* (Raf.) Swezey (Poaceae, ‘squirreltail’), and *Lupinus argenteus* Pursh (Fabaceae, ‘silvery lupine’) at ~2,175 m elevation. Decreased snow depth resulted in earlier flowering for *B. tectorum*. Although within-year snowpack manipulations did not affect *B. tectorum* density, inter-annual declines in snowpack over three years resulted in reduced *B. tectorum* density in 2014. Experimental watering resulted in a 26% increase in leaf water potential (Ψ_{leaf}) for *B. tectorum* and a 28% increase for *E. elymoides*, but no increase in Ψ_{leaf} for *A. hymenoides* and *L. argenteus*, possibly due to interspecific differences in rooting patterns. *Bromus tectorum* had the greatest increase of the four study species in stomatal conductance (g_s) in response to watering in 2013 (27%), but g_s for *B. tectorum* did not increase in 2014; watering increased g_s for *A. hymenoides* to the greatest degree in 2014 (32%). Experimental watering increased overall CO_2 assimilation (A) for *B. tectorum* by 78% and 71% in 2013 and 2014, respectively, relative to 17% and 28% for *A. hymenoides*, 2% and 9% for *E. elymoides*, and 29% and 13% for *L. argenteus*. Climate change impacts on precipitation patterns in both winter and spring—as well as inter-annual variation—are likely to affect the spread of *B. tectorum* at the edge of its high-elevation range.

Key words: cheatgrass, climate change, Great Basin Desert, invasive species, photosynthesis, soil water, stomatal conductance, water potential

Introduction

Sagebrush steppe is one of the most widespread semiarid shrubland ecosystem types in the western United States, yet also one of the most threatened (Noss et al. 1995) due to a positive feedback loop between invasions by the non-native annual grass *Bromus tectorum* L. (Poaceae, ‘cheatgrass’) and fire. The most ubiquitous invasive plant species in the Intermountain West (Weltz et al. 2011), *B. tectorum* densely colonizes bare ground between native vegetation, matures before native species, and becomes extremely flammable upon senescence, thus creating serious fire risk. *Bromus tectorum* is twice as likely to ignite as native vegetation (Balch et al. 2013), increasing fire frequency, fire spread rate, and fire season length for invaded ecosystems (Brooks et al. 2004). Native perennials are slow to recover following frequent fires, whereas *B. tectorum* has a disproportionately large seed bank and rapidly exploits post-fire increases in resources, becoming increasingly dominant and eventually displacing native species (Knapp 1996).

Since its accidental introduction as a grain contaminant from Eurasia in the late 1800s, *B. tectorum* has transformed fire regimes and ecosystem structure on over 40 million hectares (ha) in the Intermountain West (Whisenant 1990), which comprises approximately 6% of the Great Basin (Balch et al. 2013) and approximately 20% of the sagebrush steppe vegetation zone (Knapp 1996). Over the last 10-15 years, *B. tectorum* has been expanding into higher elevations (Brown and Rowe 2004, Bromberg et al. 2011, Weltz et al. 2011, Concilio et al. 2013), threatening to displace over 40% of the current area of sagebrush steppe in the next 30 years (Chambers et al. 2007). Climate change is likely to exacerbate the trend of *B. tectorum* expansion into higher elevations by increasing the range of suitable *B. tectorum* habitat and potentially creating climatic conditions that favor *B. tectorum* over native species.

Sagebrush steppe is highly sensitive to climate change—particularly altered ecosystem water balance. The amount, type (i.e., rain or snow), and timing (i.e., winter or spring) of precipitation exert strong influences on sagebrush steppe ecosystem structure and function (Austin et al. 2004, Bates et al. 2006, Abatzoglou and Kolden 2011, Brooks and Chambers 2011, Loik et al. 2015). Snowfall comprises the dominant form of precipitation and snowpack can persist for six months or more at upper elevations (Smith et al. 1997, Loik et al. 2004).

Seasonal and daily temperatures are rising, leading to earlier snowmelt timing and increased proportions of rainfall rather than snowfall across the western United States (Cayan et al. 2001, Knowles et al. 2006). Snowmelt initiates the onset of the growing season, thus earlier melt timing results in earlier spring plant growth (Cayan et al. 2001), which accelerates soil water depletion (White et al. 2009) and vegetation dry-down (Loik et al. 2004), leading to a longer, drier growing season (Westerling et al. 2006). Impending climate change impacts are expected to magnify these trends. Climate model precipitation scenarios are variable and have not reached a consensus on whether precipitation in the western United States will increase or decrease. Some scenarios include increased winter precipitation and drier spring and summer conditions across the Great Basin, an earlier termination of cool-season precipitation, further precipitation phase shifts from snow to rain, greater inter-annual variability, and increasing numbers and magnitude of extreme events (Weltzin et al. 2003, Hayhoe et al. 2004, Knowles et al. 2006, Cayan et al. 2008, Westerling and Bryant 2008, Abatzoglou and Kolden 2011, Pavelsky et al. 2012).

Most research on *B. tectorum* has focused on invasions at lower elevations, where impacts are extensive, but some recent work has explored responses of *B. tectorum* population dynamics to precipitation near its high-elevation range boundary in the southwestern Great Basin Desert in eastern California, where infestations are patchy and have not yet altered fire cycles (e.g., Griffith and Loik 2010, Concilio and Loik 2013, Concilio et al. 2013). Throughout most of the Intermountain West, *B. tectorum* germinates in the fall (Mack and Pyke 1983). At high elevations, deep winter snow cover typically prevents germination until spring, thus the growing season for *B. tectorum* in such locations is constrained entirely to the time between snowmelt and summer drought and individuals tend to be smaller than their lower elevation counterparts (Griffith and Loik 2010). Snowmelt recharges water throughout the soil profile (Bates et al. 2006) and is the primary source of water and nutrients for plant uptake during the growing season (Bowman 1992), thus changes in snow depth and/or melt timing are likely to have consequences for water availability in upper soil layers where it can be obtained by the roots of *B. tectorum*. Moreover, an increase in the frequency and/or magnitude of spring rain events—during the relatively brief window of opportunity for *B. tectorum* growth—could facilitate *B. tectorum* expansion (Concilio et al. 2013).

This study investigates effects of precipitation change scenarios on *B. tectorum* and coexisting native vegetation. Study objectives were to determine (1) how snow depth and snowmelt timing influence patterns of phenology, species composition, and vegetation (i.e., fuel) density, and (2) whether *B. tectorum* and native species have different responses to spring rainfall. I used snow fences to manipulate winter snowpack (increased, decreased, and ambient snow depth) and water additions in the spring to simulate an increase in the frequency and magnitude of spring rainfall. I hypothesized that (H_1) experimentally increased and decreased snowpack would delay and advance plant (i.e., fire fuel) phenology, respectively, due to differences in snowmelt timing; (H_2) species composition would vary according to snow depth; (H_3) decreased snow depth would result in lower soil moisture, leaf area index, and *B. tectorum* density, while increased snow depth will have opposite effects; (H_4) water additions during the growing season would increase plant water potential and photosynthetic rates relative to unwatered controls; and (H_5) because of a suite of traits that favor rapid springtime growth, *B. tectorum* responses to the water additions would be greater than those of native perennial bunchgrass and forb species among which *B. tectorum* occurs.

Methods

Study System

I conducted this study in a high-elevation sagebrush steppe ecosystem adjacent to the Sierra Nevada Aquatic Research Laboratory of the Valentine Eastern Sierra Reserve, part of the University of California Natural Reserve System, on Inyo National Forest land on the eastern slope of the Sierra Nevada near Mammoth Lakes, Mono County, California (37°36'51"N / 118°49'47"W, ~2,175 m elevation). Co-dominant shrub species are *Artemisia tridentata* Nutt. (Asteraceae, 'big sagebrush') and *Purshia tridentata* (Pursh) DC. (Rosaceae, ‘antelope bitterbrush’) with other less common shrubs also present. Several native bunchgrasses and forbs also populate the site, including *Achnatherum hymenoides* (Roem. & Schult.) Barkworth (Poaceae, ‘Indian ricegrass’), *Elymus elymoides* (Raf.) Swezey (Poaceae, ‘squirreltail’), and *Lupinus argenteus* Pursh (Fabaceae, ‘silvery lupine’). *Bromus tectorum* coexists with native vegetation here (i.e., has not yet altered fire cycles) but has been increasing in density over the last decade, while native herbaceous species richness has simultaneously declined (Concilio and Loik 2013). Soils are sandy at the surface with gravel and larger rocks beneath and are derived from Holocene deposits of alluvium and stream gravels (Orr and Howald 2000). The site has been grazed annually (<0.25 calf/cow pairs per ha) for one month each summer for at least the last 20 years (Concilio et al. 2013).

Meteorology

An on-site weather station (<2 km from the study site) has continuously monitored precipitation, air temperature, and relative humidity since 1987. Total water-year precipitation is highly variable (Figure 1-1), ranging from 130 mm in 2007 to 557 mm in 1991 (mean ± 1 SD = 304 ± 130 mm). The climate is Mediterranean and most precipitation (~70%) falls as snow in the winter (November-March). January and July are usually the coldest and warmest months of the year, respectively (Orr and Howald 2000). Between 1988-2013, mean minimum air temperature was approximately -19°C in January and mean maximum air temperature was

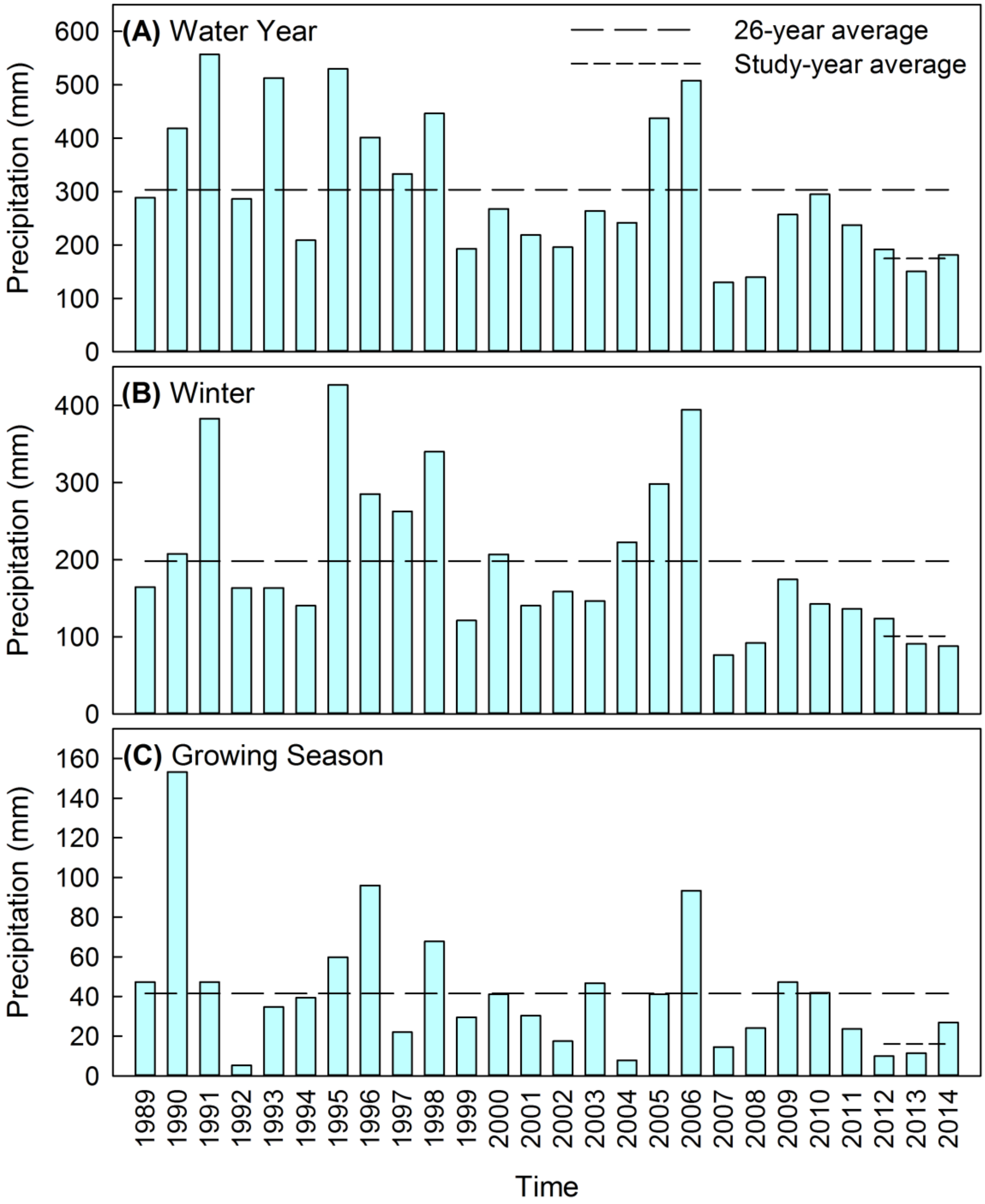

Figure 1-1. Precipitation patterns at the study site from 1989 to 2014 for (A) the water year (October 1 to September 30), (B) the winter period (November 1 to March 31), and (C) the growing season (April 1 to June 30). The years on the abscissa correspond to the calendar year in which the period ends. All data were collected at the Sierra Nevada Aquatic Research Laboratory of the Valentine Eastern Sierra Reserve, <2 km from the study site.

approximately 30°C in July. Typically, July and August are the only frost-free months and frost-free days average 121 per year (derived from Orr and Howald 2000).

During the study period (2012-2014), the mean maximum air temperature of 30°C in July was typical of the site, while the mean minimum temperature was -13°C in December, warmer than the 26-year average and occurring earlier than usual. Frost-free days during the study ranged from 102 per year (in 2012) and 132 per year (in 2013). Winter (November-March) precipitation was below the 26-year average (Figure 1-1) of 198 mm (SD = 100) during the study, totaling 124 mm in 2011/2012, 91 mm in 2012/2013, and 88 mm in 2013/2014. Similarly, growing season (April-June) precipitation during the study was also below the 26-year average (Figure 1-1) of 42 mm (SD = 33), totaling 10 mm in 2012, 11 mm in 2013, and 27 mm in 2014.

Study Species

To compare with *B. tectorum*, I focused on three native perennial species as much as possible: *A. hymenoides*, a widespread and highly drought-tolerant bunchgrass in sagebrush steppe ecosystems (Ogle et al. 2013); *E. elymoides*, a bunchgrass with phenological similarities and reported competitive abilities with *B. tectorum* (Booth et al. 2003, Humphrey and Schupp 2004); and *L. argenteus*, one of the most common N_2-fixing legumes in high-elevation sagebrush steppe, which has potential to facilitate other vegetation by providing microhabitats with higher soil N, soil water, and shade (Goergen and Chambers 2012).

Winter Snowpack Manipulations

To manipulate snowpack (and, hence, snowmelt timing), four snow fences (30 m long and 1.8 m tall) were constructed at the study site in 2004 and 2005 (see Griffith and Loik 2010) consisting of T-posts and green plastic mesh that is removed during the snow-free season (roughly April-October) to avoid unwanted effects of shading and wind disruption. The fences are oriented perpendicular to the prevailing winter wind direction (240°) and produce zones of increased snow accumulation 3-5 m downwind of each fence ("+snow") and reduced snow accumulation ~15 m downwind ("-snow") by reducing wind speed and creating a large equilibrium drift. An additional snow depth zone ("ambient snow") was established 15 m upwind of each fence where snow depth is unaffected by the fences (Figure 1-2). At each fence, all data were collected along parallel transects in each snow zone spanning the lengths of each fence.

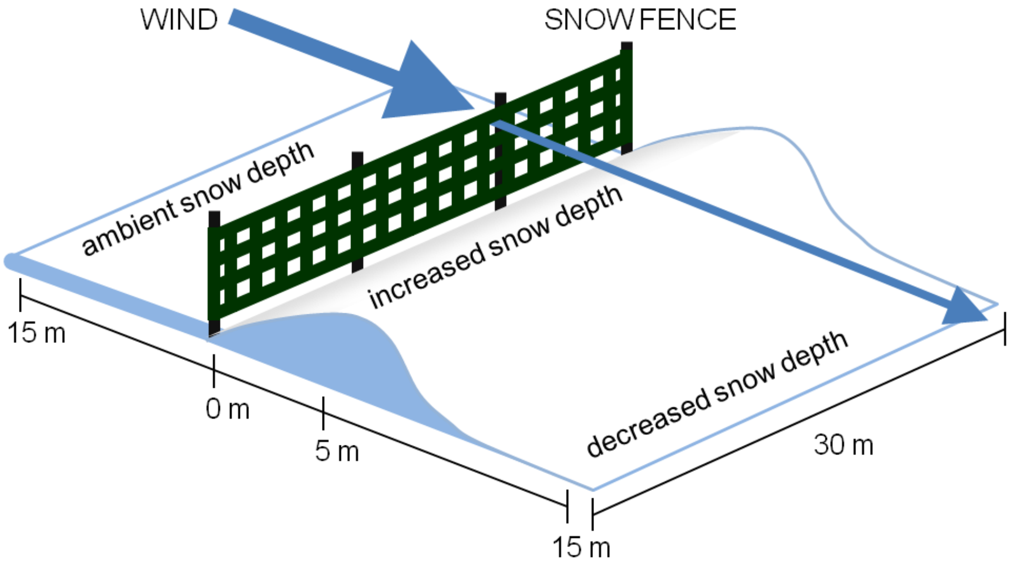

Figure 1-2. Snow fence design and function. (Not to scale.)

To test H_1, phenological status monitoring of 60 individuals each (five per snow zone per fence) of the invasive *B. tectorum* and native bunchgrasses *E. elymoides* and *A. hymenoides* (too few *L. argenteus* individuals were located in the snow zones to effectively monitor that species) occurred from mid-April 2013 and continued until early June 2013 using species-specific guidelines established by the USA National Phenology Network (https://www.usanpn.org). These guidelines establish different protocols for documenting specific phenophases of species, both the presence/absence and magnitude of the phase. Sampling occurred roughly once per week, and *B. tectorum* sample size was doubled during the sampling period in May 2013 to increase the accuracy of results (this was not possible for native species because the snow zones contained fewer numbers of individual native plants).

To test H_2, I recorded species composition each year along the entire length of each transect using a line-intercept method. Species were divided into functional groups (percent cover of *B. tectorum*, bunchgrasses, forbs, shrubs, and bare ground) for analyses to avoid confusion in identification of some plants (primarily native grasses and forbs) that were either difficult to identify due to grazing or phenotypic similarities.

To test H_3, I collected five soil samples (to 7.62 cm depth) per snow zone per fence in April and May 2013 and four samples per snow zone per fence in May 2014, recorded wet and oven-dry (105°C for ~48 h) weights to calculate soil gravimetric water content (GWC; water weight divided by oven-dry weight). Leaf area index

(LAI; i.e., fuel canopy biomass) was measured at regular intervals along each transect using a PAR-LAI ceptometer (AccuPAR LP-80, Decagon Devices, Pullman, WA) and values were subsequently averaged for each fence/snow zone combination. *Bromus tectorum* density was also recorded each year from 2012-2014 in a 0.25 × 0.25 m quadrat placed along the transect at 5-m intervals.

Spring Rainfall Simulations

To test the effects of increased frequency and magnitude of spring rainfall events on study species, I watered plants (+10 mm H_2O) in May 2013 and May 2014. This amount is larger than the most common rainfall event size class across arid and semiarid regions of the western United States—47% of all precipitation events are ≤ 5 mm (Loik et al. 2004)—and was intended to overcome effects of a multi-year drought as well as simulate a large rainfall event. I haphazardly selected 10 individuals each (N = 40) of *B. tectorum*, *E. elymoides*, *A. hymenoides*, and *L. argenteus* within a grazing exclosure (fenced since 1999; Daniel Dawson, pers. comm.). Plants were randomly assigned to either the "control" (five of each species for a total n = 20) or "+H_2O" (five of each species for a total n = 20) treatment. In 2014, I included an additional 10 plants of each species in the study for destructive sampling of leaf water potential (Ψ_{leaf}). Water was applied to individual plants within a 0.5 × 0.5 m quadrat centered around each plant using a watering can held above the plant canopy. Water was added slowly to allow maximal infiltration and minimal runoff of plots.

I collected soil samples within the 0.5 × 0.5 m plot around study plants and recorded wet and oven-dry (105°C for ~48 h) weights to calculate soil GWC. In 2013, I collected soil samples before and after watering on the day that water was applied to plots. In 2014, I collected soil samples one day after watering and twice more throughout the study period (~2 weeks) to examine the response of soil GWC to a water pulse over time.

I measured mid-day Ψ_{leaf} in 2014 using a WP4 Dewpoint PotentiaMeter (Decagon Devices, Pullman, WA). I collected leaf samples on three dates throughout the course of the experiment (~2 weeks) to observe trends over time, immediately placed them into sample cups and sealed them with masking tape, and processed all samples the same day that they were collected.

I measured stomatal conductance to water vapor (g_s), instantaneous rates of CO_2 assimilation (A), and plant growth (height before and after the experiment) in both years, and quantum yield of Photosystem II (Φ_{PSII}) and electron transport rate (ETR) in 2013 using an open-mode portable photosynthesis system (LI-6400, Li-Cor Biosciences, Lincoln, NE) for several days after watering (seven sampling dates each year over a period of ~2 weeks). Vapor pressure deficit within the chamber was maintained at pre-measurement ambient levels. The CO_2 concentration within the leaf measurement chamber was maintained at a constant level (400 μmol mol^{-1}) by scrubbing the incoming airstream with soda lime, and the subsequent addition of a precise amount of CO_2 via injection from an external cartridge. Photosynthetically

Active Radiation (PAR; 400-700 nm) within the chamber was maintained at 1500 μmol m^{-2} s^{-1} using Li-Cor red-blue LEDs. Mature leaves were inserted into the cuvette (for grass species, leaves were aligned adjacent to one another without overlapping to fill the chamber; for *L. argenteus*, leaves were inserted to fill the chamber at their natural branch orientation), and photosynthetic measurements were recorded when all stability criteria were met and the coefficient of variation for A and g_s combined was below 0.5%. I recorded three measurements per leaf and subsequently averaged the values.

Statistical Analyses

I analyzed all results using JMP Pro (v. 11.0.0; SAS Institute, Cary, NC). I used analysis of variance (ANOVA) and *post hoc* Tukey's honestly significant difference tests (HSD) to analyze differences between treatment groups. I used repeated-measures ANOVAs to analyze phenology and plant physiological responses to treatments, as well as repeated-measures effects (i.e., within-subjects effects) of time and interactions between time and treatments. To analyze relationships between continuous dependent variables (i.e., g_s and A), I tested for homogeneity of slopes. For all analyses, I considered differences at $P \leq 0.05$ to be significant and differences between $P = 0.10$ and $P > 0.05$ to be marginally significant to account for high variation typical of field data.

Results

Meteorology

Throughout the study period, water-year precipitation was below average (Figure 1-1). In fact, the three study years had the third (2013), fourth (2014), and fifth (2012) lowest water-year precipitation of the 26-year record, respectively (behind 2007 and 2008). Moreover, winter 2013-2014 had the second lowest winter precipitation of the record (behind winter 2006-2007), winter 2012-2013 had the third lowest winter precipitation, and winter 2011-2012 had the sixth lowest winter precipitation. Spring 2012 and 2013 had the third and fourth lowest spring precipitation, respectively (behind 1992 and 2004). Hence, extreme drought conditions persisted throughout the study period. Figure 1-3 shows monthly precipitation and temperature patterns at the study site during the study period (November 2011-June 2014).

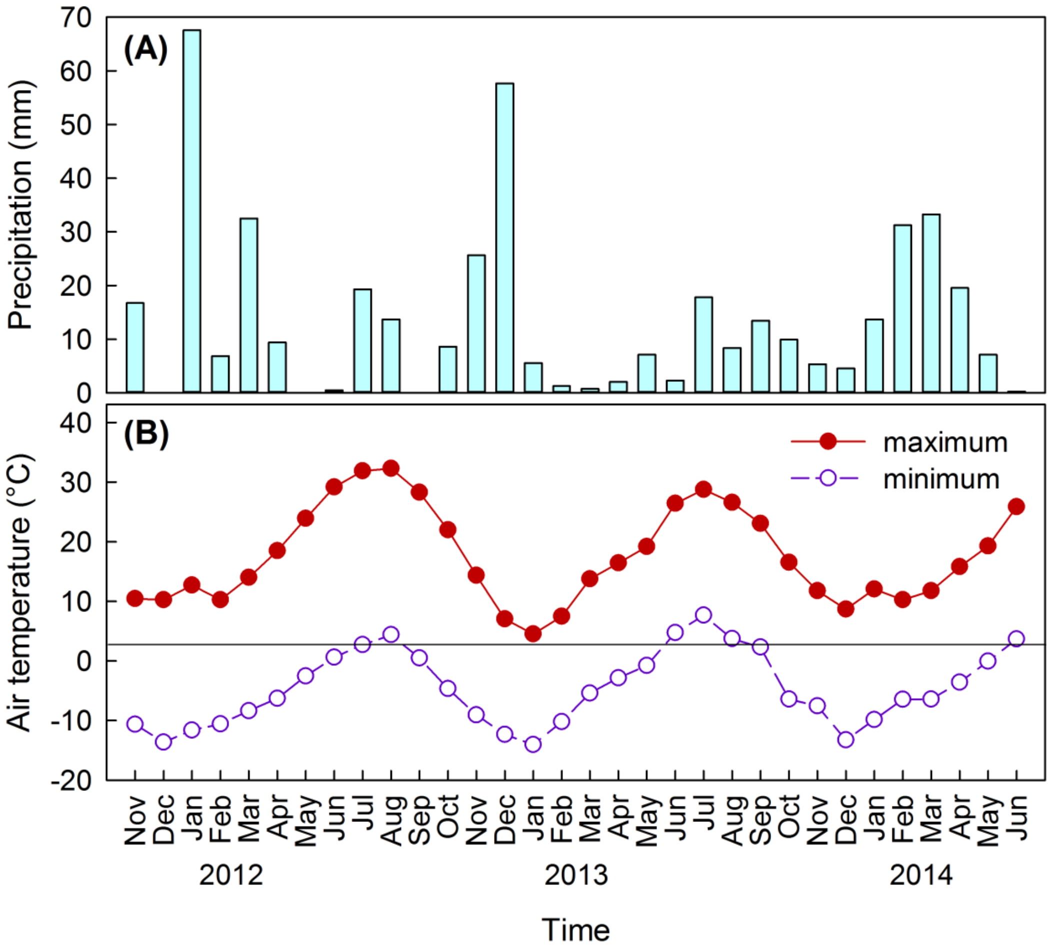

Figure 1-3. Precipitation and temperature patterns during the study period (November 2011 to June 2014). (A) Total monthly precipitation and (B) mean monthly maximum and minimum air temperatures at the study site. All data were collected at the Sierra Nevada Aquatic Research Laboratory of the Valentine Eastern Sierra Reserve, <2 km from the study site.

Snowpack Manipulations

Snowpack manipulations did not significantly affect soil moisture (Table 1-1), though early spring (April) soil GWC in snow zones followed the trend that +snow > ambient snow > -snow. Soil GWC had declined to <1% by May in both the 2013 and 2014 growing seasons.

Table 1-1. Soil gravimetric water content (GWC) in snow depth treatment zones at 7.62 cm depth during the 2013 and 2014 growing seasons.

Month and year	GWC (%)[1]		
	-Snow	Ambient snow	+Snow
April 2013	1.23^{a} (0.99, 1.47)	1.89^{a} (1.27, 2.50)	2.26^{a} (1.15, 3.38)
May 2013	0.456^{b} (0.403, 0.510)	0.468^{b} (0.353, 0.582)	0.482^{b} (0.471, 0.494)
May 2014	0.710^{b} (0.494, 0.926)	0.589^{b} (0.382, 0.797)	0.592^{b} (0.507, 0.677)

[1] Data are means (± 1 SD). Superscript letters indicate significant differences ($P < 0.05$) among snow depth treatment levels as revealed by Tukey's HSD test; values that do not share a common letter are significantly different.

Leaf area index did not significantly differ by snow zone in any year of the study (Table 1-2). I could not assess trends in LAI across years as measurements occurred during different seasons (i.e., early to late spring, mid-summer) in different years of the study, which confounded comparisons.

Table 1-2. Mean leaf area index (LAI) by snow zone.

Month and year	LAI[1]		
	-Snow	Ambient snow	+Snow
July 2012	0.84 (0.69, 0.99)	0.54 (0.32, 0.75)	1.32 (1.02, 1.62)
April 2013	1.23 (0.78, 1.67)	1.14 (0.84, 1.44)	1.46 (1.17, 1.74)
May 2013	1.45 (0.93, 1.97)	1.19 (0.99, 1.40)	1.48 (0.96, 2.00)
May 2014	0.86 (0.73, 1.00)	1.24 (0.98, 1.51)	1.14 (0.86, 1.39)

[1] Data are means (± 1 SD).

Species richness did not significantly differ by snow zone in any year of the study. Mean number of species in each snow zone increased over the years, though this may have been due to my enhanced ability to differentiate among species with time and experience (Table 1-3).

Table 1-3. Mean species richness by snow zone.

Year	Mean number of species[1]		
	-Snow	Ambient snow	+Snow
2012	10 (7, 13)	9 (7, 11)	11 (8, 14)
2013	13 (10, 16)	13 (11, 15)	13 (10, 16)
2014	17 (14, 20)	15 (12, 18)	16 (13, 19)

[1] Data are means (± 1 SD).

A preliminary survey in 2010 (data not shown) showed a significant decrease in *B. tectorum* percent cover in the +snow zone, with a mean percent cover of 8.6%, relative to the -snow zone, with a mean percent cover of 17.8% ($F_{2,6}$ = 5.4063, P = 0.0455); however, this trend was not observed in subsequent years. In 2013, percent cover of "other shrubs" (i.e., shrubs other than the co-dominant *A. tridentata* and *P. tridentata* such as *Ericameria nauseosa* [Pall. ex Pursh] G.L. Nesom & Baird [Asteraceae, 'rubber rabbitbrush'] and *Prunus andersonii* A. Gray [Rosaceae, 'desert peach']) was higher in the +snow zone than the other zones ($F_{2,7}$ = 38.7005, P = 0.0002; Figure 1-4). However, this trend was not observed in 2012 or 2014.

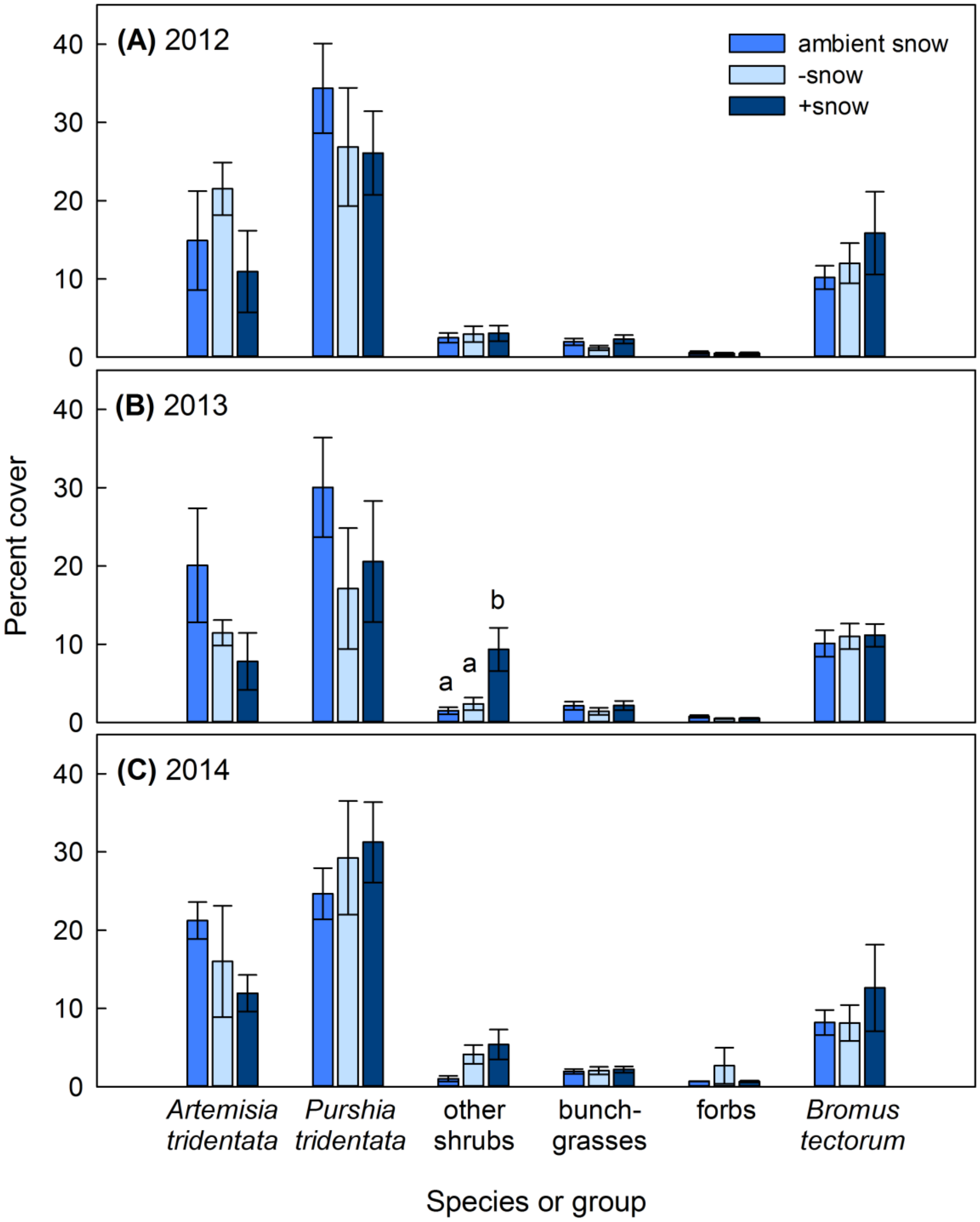

Figure 1-4. Species composition in (A) 2012, (B) 2013, and (C) 2014 divided into functional groups by snow zone. Error bars are ± 1 SE.

Phenological monitoring demonstrated the overall early phenology of *B. tectorum* relative to native species ($F_{2,72}$ = 163.2755, P < 0.0001; Figure 1-5).

Bromus tectorum began producing spikelets approximately 1-2 weeks before *Elymus elymoides*. By the end of May, *B. tectorum* had reached peak flowering (i.e., 100% of *B. tectorum* plants sampled were flowering), whereas, by the final sampling date on June 6, *E. elymoides* inflorescence production still had yet to reach 100%. Peak flowering for *A. hymenoides* was further delayed than that for *E. elymoides.*

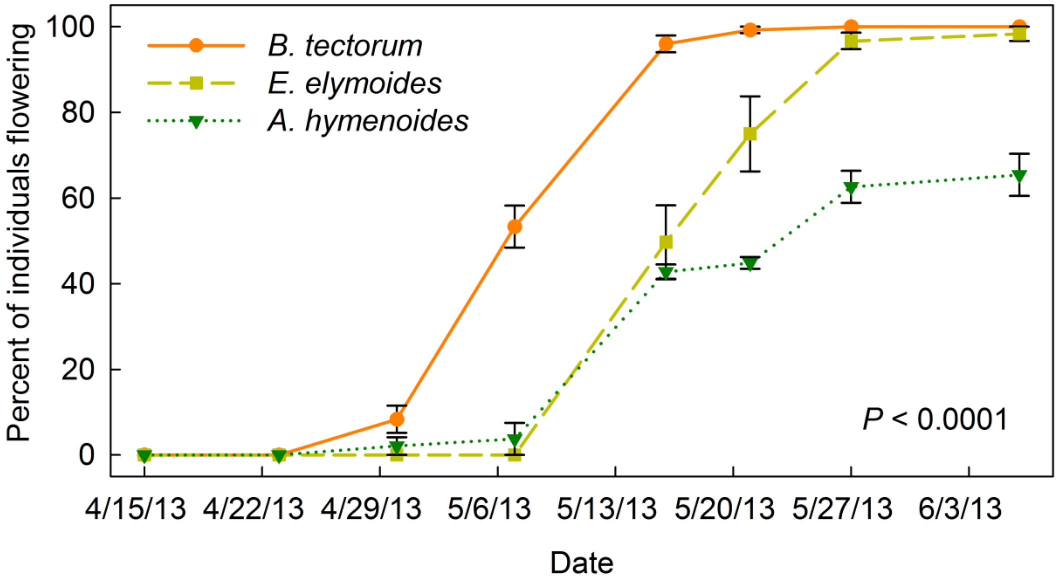

Figure 1-5. Phenological timing by species: *Bromus tectorum*, *Elymus elymoides*, and *Achnatherum hymenoides* inflorescence production by date for all snow zones combined. Error bars are ± 1 SE.

Phenological responses to different snow zones varied according to species (Figure 1-6). *Bromus tectorum* showed a significant phenological advance in the -snow zone (i.e., plants in the -snow zone began flowering earlier; $F_{2,72} = 6.5249$, $P = 0.0025$). *Achnatherum hymenoides* plants showed similar patterns in each snow zone until later in the season (late May), when a greater number of plants in the

+snow zone were flowering than in the other snow zones ($F_{2,72}$ = 8.7637, P = 0.0004). *Elymus elymoides* phenology did not differ among snow zones.

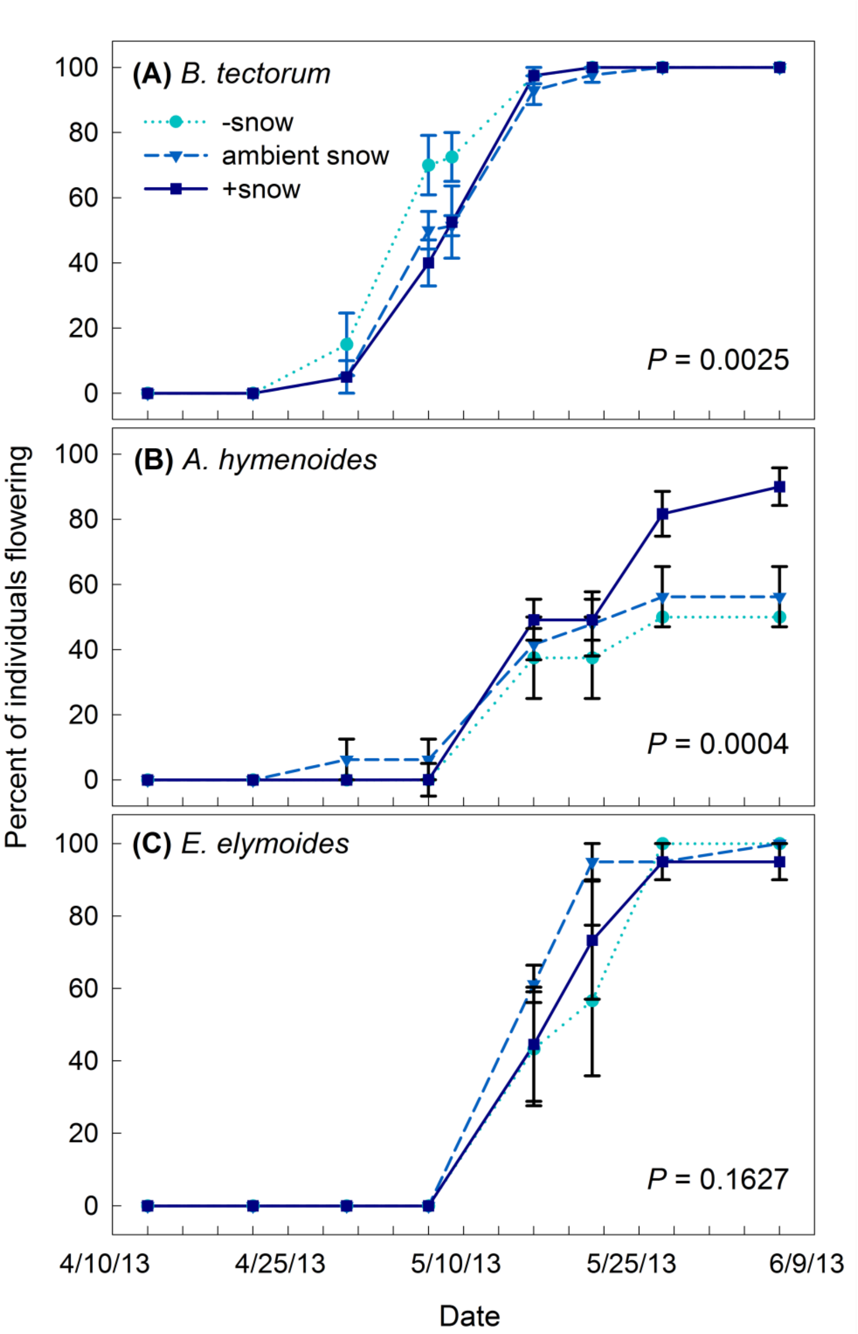

Figure 1-6. Phenological trends by date in each snow zone for (A) *B. tectorum*, (B) *A. hymenoides*, and (C) *E. elymoides*. Error bars are ± 1 SE.

Bromus tectorum density did not significantly differ between snow depth zones within any year of the study, but inter-annual overall *B. tectorum* density declined over the three study years and was dramatically reduced in 2014 ($F_{2,33} = 8.4174$, $P = 0.0011$; Figure 1-7) following several drought years and the year with the lowest winter snowpack.

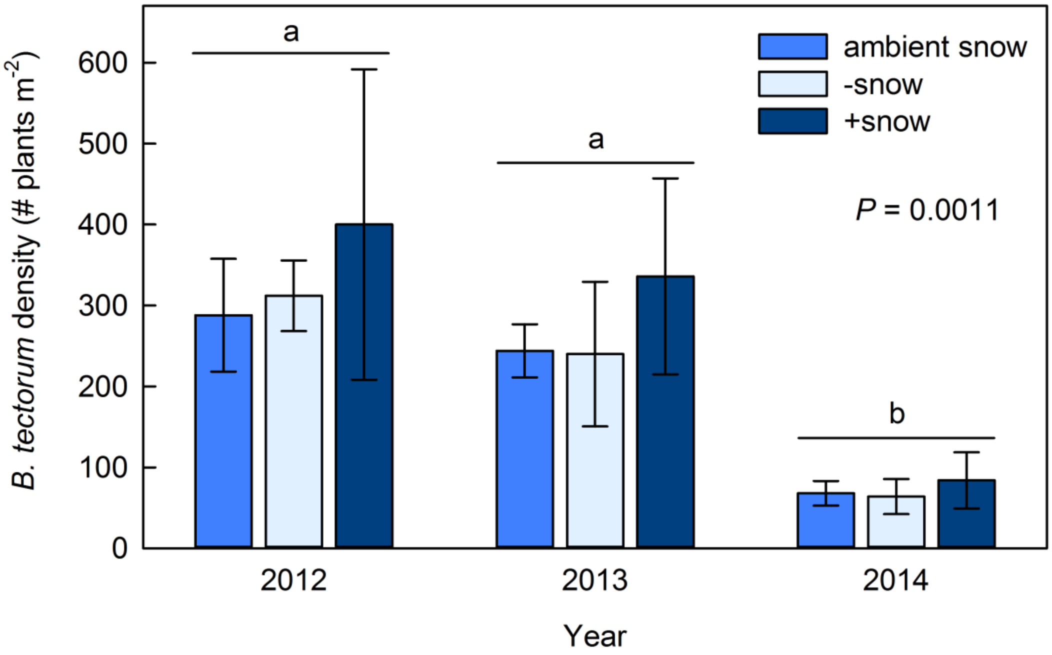

Figure 1-7. *Bromus tectorum* density over three years. Error bars are ± 1 SE.

Rainfall Simulations

The 10-mm water additions significantly increased soil moisture levels for all plots (Table 1-4), which dried rapidly in subsequent days. In 2013, mean soil GWC for control and +H_2O plots on the water addition day was <1% and 10.1%, respectively ($F_{1,38} = 114.5332$, $P < 0.0001$). In 2014, mean soil GWC was <1% for control plots and 2.63% for +H_2O plots one day after watering ($F_{1,38} = 39.3661$,

$P < 0.0001$; Figure 3). Between May 20-22, 2014, the study site received ~7 mm of precipitation (both in the form of rain and snow), which increased mean soil moisture to >5% for all plots on the May 22 sampling date regardless of treatment. Soil moisture had decreased to <1% by one week later, on May 29.

Table 1-4. Mean soil gravimetric water content (GWC) in control and watered plots of each species after the 10-mm springtime rainfall event simulation.

Species	GWC (%)^{A}			
	2013		2014	
	Control	$+H_2O^{B}$	Control	$+H_2O^{C}$
Achnatherum hymenoides	$0.59^{a,a}$ (0.46, 0.71)	$10.45^{c,c}$ (6.02, 14.88)	$0.78^{a,a}$ (0.63, 0.92)	$2.23^{b,a}$ (1.34, 3.12)
Bromus tectorum	$0.81^{a,ab}$ (0.60, 1.01)	$11.22^{c,c}$ (7.88, 14.56)	$0.73^{a,a}$ (0.61, 0.85)	$3.72^{b,a}$ (1.80, 5.63)
Elymus elymoides	$0.97^{a,ab}$ (0.66, 1.29)	$12.14^{c,c}$ (8.81, 15.47)	$0.79^{a,a}$ (0.51, 1.07)	$2.29^{b,a}$ (1.66, 2.92)
Lupinus argenteus	$1.17^{a,b}$ (0.73, 1.61)	$6.64^{c,c}$ (4.14, 9.13)	$0.78^{a,a}$ (0.51, 1.04)	$2.29^{b,a}$ (1.11, 3.47)
Mean	$0.88^{a,a}$ (0.53, 1.23)	$10.11^{c,c}$ (6.27, 13.95)	$0.77^{a,a}$ (0.57, 0.97)	$2.63^{b,a}$ (1.32, 3.95)

[A] Data are means (± 1 SD). Superscript letters indicate within-year significant differences ($P < 0.05$) among treatments as revealed by Tukey's HSD test; values that do not share a common letter are significantly different. The first letter corresponds to differences across the row; the second letter corresponds to differences down the column.

[B] Samples were collected the day of watering.

[C] Samples were collected one day after watering.

I measured mid-day Ψ_{leaf} one, nine, and 15 days after watering in 2014 (on May 16, 24, and 30). Water additions did not significantly affect Ψ_{leaf} (Figure 1-8) for *A. hymenoides* or *L. argenteus*, but had a marginally significant impact on *B. tectorum* Ψ_{leaf} ($F_{1,24}$ = 3.4811, P = 0.0743) and a significant impact on Ψ_{leaf} for *E. elymoides* ($F_{1,24}$ = 4.7177, P = 0.0400). Interestingly, *B. tectorum* controls were the only group that increased Ψ_{leaf} following the natural precipitation event that occurred during the experiment.

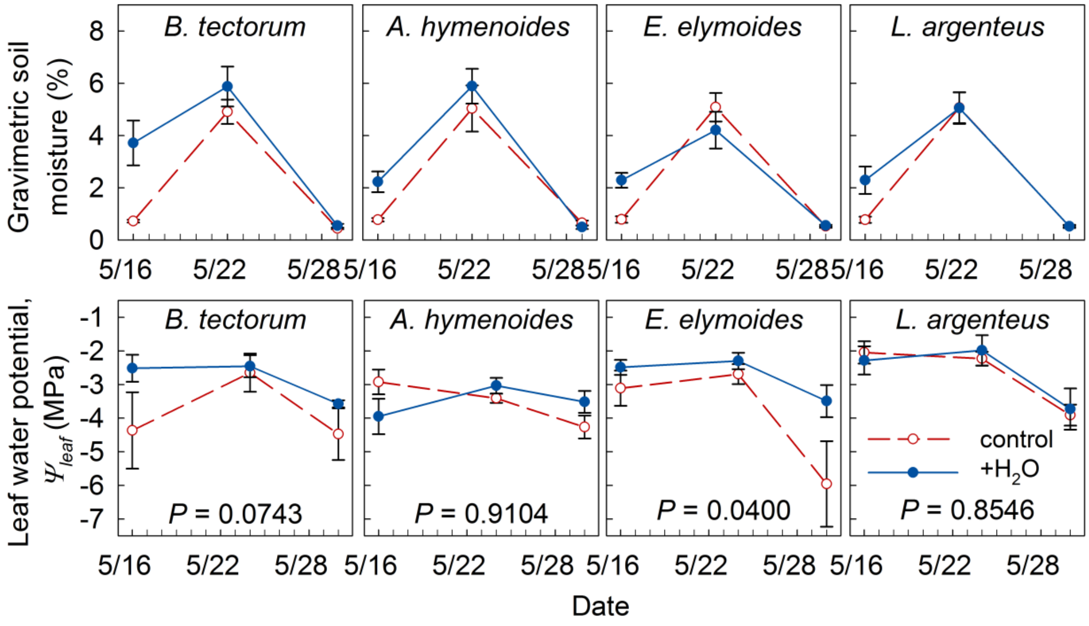

Figure 1-8. Gravimetric soil moisture (top row) and leaf water potential (bottom row) of control and watered plants in 2014. Water additions occurred on May 15, 2014. Data are means ± 1 SE for n = 5 plants per treatment for each species.

Intrinsic rates of g_s and A varied by species, with *B. tectorum* having the lowest rates and *L. argenteus* the highest. In both study years, *B. tectorum* controls had the lowest mean (± 1 SE) g_s values (2013: 0.117 ± 0.00858 mol H_2O m^{-2} s^{-1}; 2014: 0.197 ± 0.0433 mol H_2O m^{-2} s^{-1}) and *L. argenteus* controls had the highest mean (± 1 SE) g_s (2013: 0.226 ± 0.0284 mol H_2O m^{-2} s^{-1}; 2014: 0.406 ± 0.0256 mol

$H_2O\ m^{-2}\ s^{-1}$), with *A. hymenoides* and *E. elymoides* having intermediate values. Patterns for g_s in response to watering differed across species and by year (Figure 1-9). In 2013, *B. tectorum* ($F_{1,56} = 17.0$, $P = 0.0001$) and *E. elymoides* ($F_{1,56} = 17.7$, $P < 0.0001$) had significant responses of g_s to added water, whereas responses of g_s for *A. hymenoides* ($F_{1,56} = 3.2253$, $P = 0.0779$) and *L. argenteus* ($F_{1,56} = 3.9546$, $P = 0.0516$) were marginal. By contrast, in 2014, *B. tectorum* did not increase g_s in response to watering, while all three native species did (*A. hymenoides*: $F_{1,56} = 24.2642$, $P < 0.0001$; *E. elymoides*: $F_{1,56} = 4.2236$, $P = 0.0445$; *L. argenteus*: $F_{1,56} = 5.6508$, $P = 0.0209$). In 2013, watering increased overall g_s (i.e., averaged over the ~2-week study period) for *B. tectorum* by 27%, *E. elymoides* by 22%, *L. argenteus* by 19%, and *A. hymenoides* by 17%. The pattern was different in 2014, with a 32% increase in g_s for *A. hymenoides*, 24% increase for *L. argenteus*, 4% decrease for *B. tectorum*, and 14% decrease for *E. elymoides*.

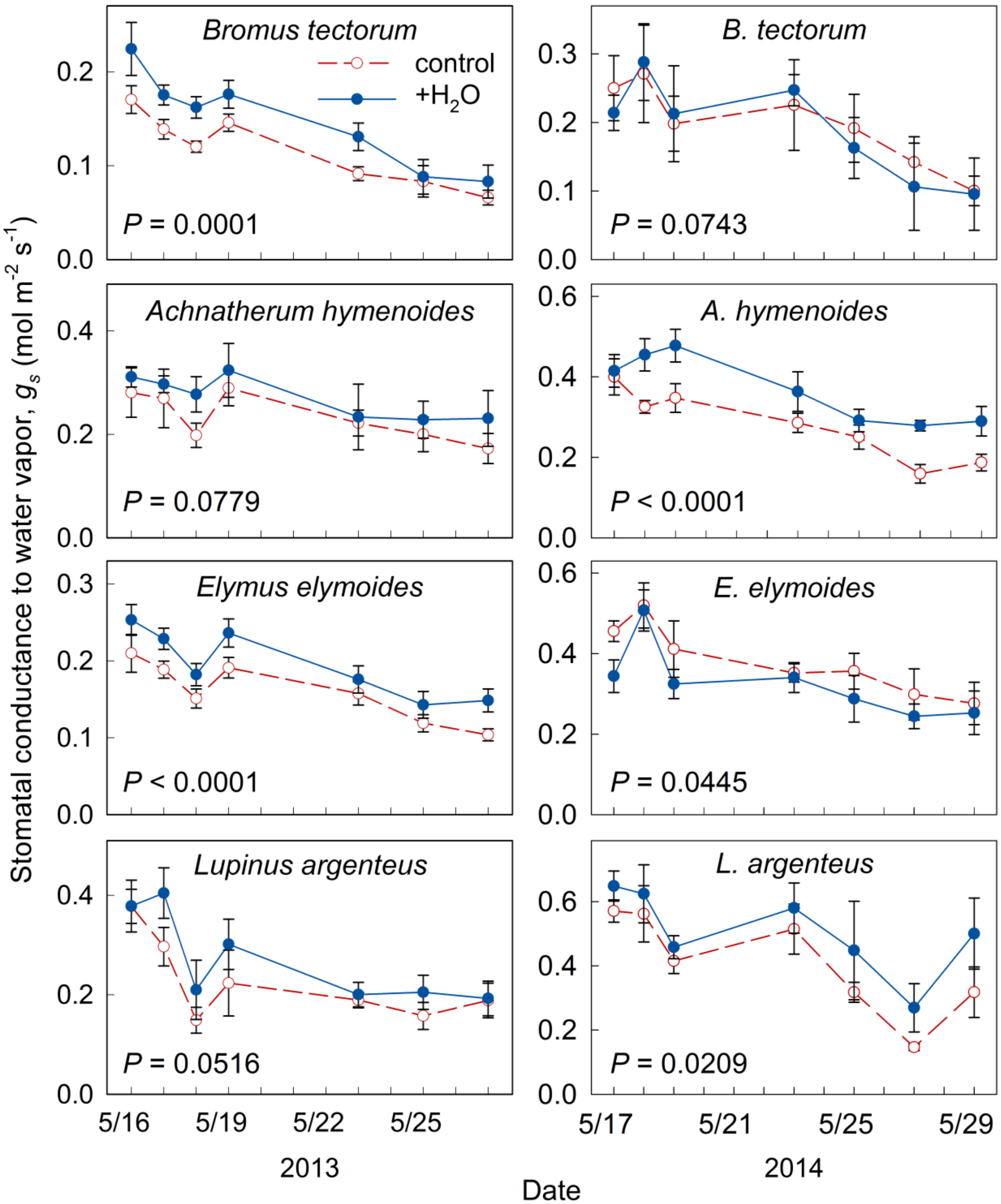

Figure 1-9. Stomatal conductance to water vapor (g_s) for control and watered plants in 2013 (left column) and 2014 (right column). Note that the scales of the ordinate differ by species and year. Water additions occurred on May 14, 2013 and May 15, 2014. Data are means ± 1 SE for n = 5 plants per treatment for each species.

The N_2-fixing *L. argenteus* had the overall highest mean (± 1 SE) rate of A across years (2013: 14.2 ± 1.69 μmol CO_2 m^{-2} s^{-1}; 2014: 24.8 ± 1.25 μmol CO_2 m^{-2} s^{-1}) and *B. tectorum* had the lowest (2013: 4.99 ± 0.0770 μmol CO_2 m^{-2} s^{-1}; 2014: mean = 2.71 ± 1.10 μmol CO_2 m^{-2} s^{-1}). Over the course of the experiment in 2013, watering resulted in significantly higher rates of A (Figure 1-10) for *B. tectorum* ($F_{1,56} = 39.3776$, $P < 0.0001$) and *L. argenteus* ($F_{1,56} = 8.3866$, $P = 0.0054$) and a marginally significantly higher rate of A for *Achnatherum hymenoides* ($F_{1,56} = 3.3401$, $P = 0.0729$). By contrast, *E. elymoides* did not have a response of A to watering. In 2014, I observed a similar pattern, with *B. tectorum* ($F_{1,56} = 5.7301$, $P = 0.0201$), *A. hymenoides* ($F_{1,56} = 7.1266$, $P = 0.0099$) and *L. argenteus* ($F_{1,56} = 5.5977$, $P = 0.0215$) all significantly increasing A in response to water additions, while A for *E. elymoides* did not respond to watering. In 2013, watering increased overall A for *B. tectorum* by 78%, *L. argenteus* by 29%, *A. hymenoides* by 17%, and *E. elymoides* by 2%. In 2014, watering increased overall A for *B. tectorum* by 71%, *A. hymenoides* by 28%, *L. argenteus* by 13%, and *E. elymoides* by 9%.

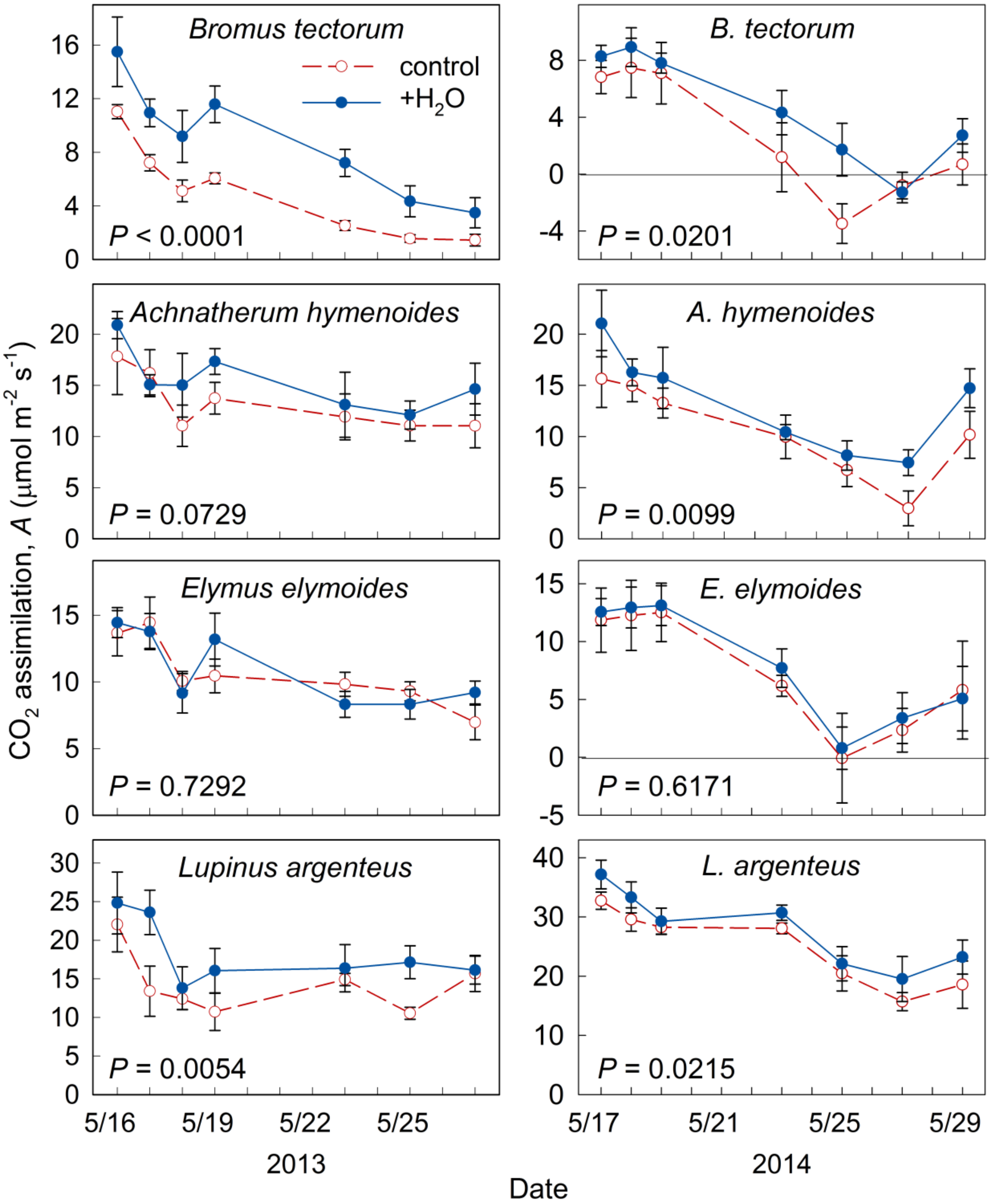

Figure 1-10. Leaf-level CO_2 assimilation (A) for control and watered plants in 2013 (left column) and 2014 (right column). Note that the scales of the ordinate differ by species and year. Water additions occurred on May 14, 2013 and May 15, 2014. Data are means ± 1 SE for n = 5 plants per treatment for each species.

Carbon dioxide assimilation had a strong positive relationship with g_s for all species (Figure 1-11). The slopes of the regression lines, which indicate water-use efficiency (WUE), did not significantly differ between the control and +H_2O treatment within any species in either year. Comparing between species in 2013, the regression for *B. tectorum* had a significantly steeper slope ($m = 78.32$) than that for the three native species ($F_{3,272} = 6.6322$, $P = 0.0002$; *A. hymenoides*: $m = 47.21$, *E. elymoides*: $m = 49.40$, *L. argenteus*: $m = 43.49$). In 2014, the slopes of the regression lines for the four species did not significantly differ ($F_{3,272} = 1.0054$, $P = 0.3908$; *A. hymenoides*: $m = 37.22$, *B. tectorum*: $m = 27.66$, *E. elymoides*: $m = 34.37$, *L. argenteus*: $m = 28.75$). Between years, the slopes of the regression

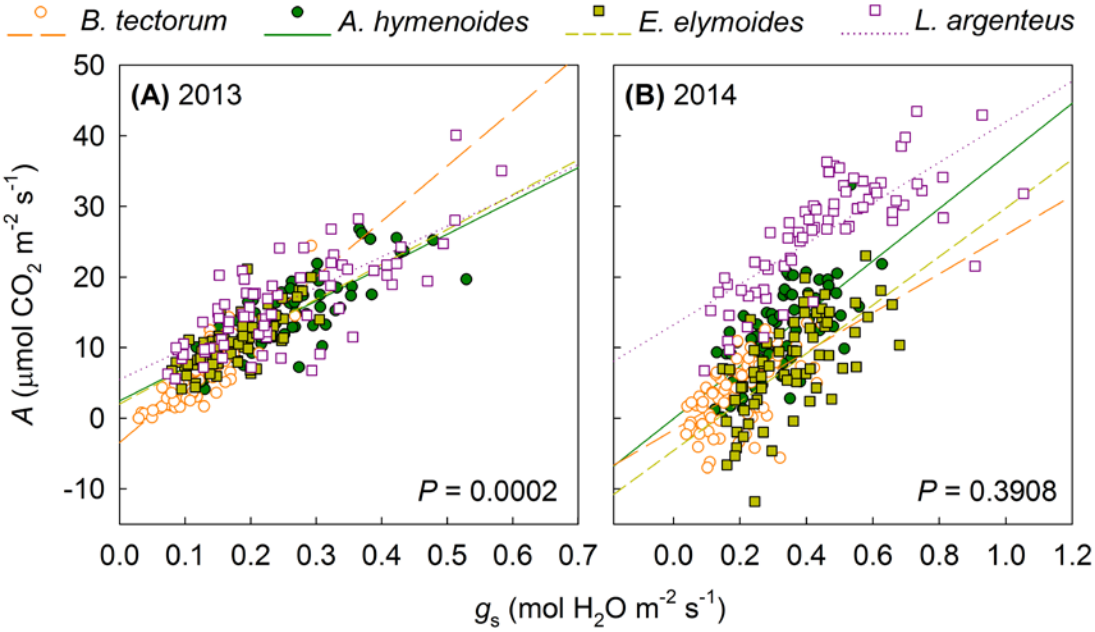

Figure 1-11. Correlations between leaf-level CO_2 assimilation (*A*) and stomatal conductance to water vapor (g_s) for the four study species in (A) 2013 and (B) 2014. Note that the scales of the abscissa differ by year. Water additions occurred on May 14, 2013 and May 15, 2014.

lines for *B. tectorum* (t_{139} = 5.99, P = < 0.0001) and *L. argenteus* (t_{139} = 2.62, P = 0.0099) significantly decreased in 2014, while those for *A. hymenoides* and *E. elymoides* were not significantly different.

Watering affected the quantum yield of Photosystem II (Φ_{PSII}) for some, but not all, species (Figure 1-12). It was significantly higher for watered *B. tectorum* ($F_{1,56}$ = 31.1316, P < 0.0001) and *A. hymenoides* ($F_{1,56}$ = 7.1172, P = 0.0100) compared to controls (Figure 6). Conversely, Φ_{PSII} in *E. elymoides* and *L. argenteus* did not respond to watering. Electron transport rate (ETR) mirrored the trends in Φ_{PSII}, with *B. tectorum* ($F_{1,56}$ = 33.8929, P < 0.0001) and *A. hymenoides* ($F_{1,56}$ = 6.7579, P = 0.0119) having significant responses to watering, whereas *E. elymoides* and *L. argenteus* did not. Despite that watering generally increased photosynthetic measurements, I did not detect a significant increase in plant growth in response to watering.

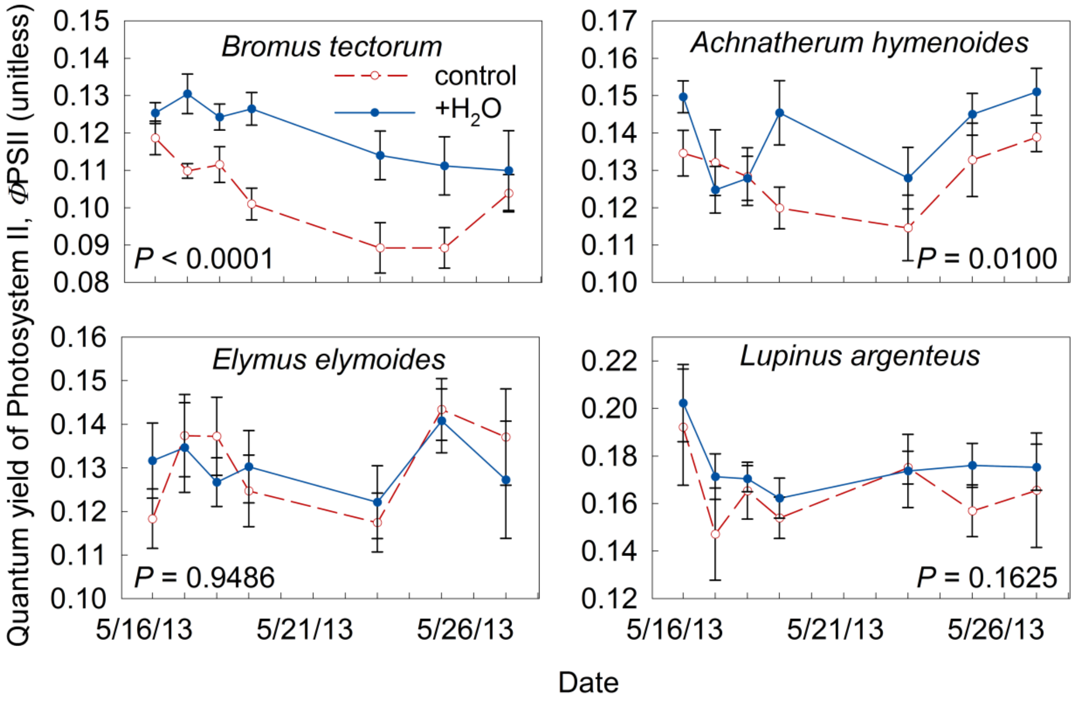

Figure 1-12. Quantum yield of Photosystem II (Φ_{PSII}) for control and watered plants in 2013. Water additions occurred on May 14, 2013. Data are means ± 1 SE for n = 5 plants per treatment for each species.

Discussion

Altered precipitation regimes as a result of climate change will likely affect future species distributions, depending on the amount, type, and timing of precipitation. While increased summer precipitation may confer an advantage for native perennial species by increasing water availability after the highly problematic Great Basin invasive grass species *B. tectorum* has senesced (Loik 2007), increased spring precipitation could facilitate *B. tectorum* expansion by increasing water resources during its short growing season (Bradley 2009, Concilio et al. 2013).

Decreased snowpack (~7% less relative to the ambient snow zone) advanced the timing of *B. tectorum* phenology, consistent with H_1, while effects on native species were mixed (i.e., a ~20% increase in snow depth in the +snow zone resulted in more flowering for *A. hymenoides*, and *E. elymoides* phenology did not respond to snow zone). Species composition varied minimally, if at all, by snow zone, thus I found limited support for H_2. In 2013, I found a greater percent cover of “other shrubs” in the +snow zone, a trend that appears to have been driven by *Ericameria nauseosus*. However, I found the opposite pattern for *E. nauseosus* in 2012, and no pattern in 2010 or 2014, highlighting the importance of inter-annual variation on effects of snow depth on different species.

Effects of the snowpack manipulations on soil moisture were relatively minimal due to the drought conditions that persisted throughout the study; as such, I found few within-year differences between snow depth zones. Snow depth treatments did not have significant effects on soil GWC, LAI, or *B. tectorum* density within any year of the study, contrary to H_3. However, inter-annual differences in *B. tectorum* density followed a trend in declining winter snowpack. In 2014, following the winter with the lowest snowpack of the three study years, *B. tectorum* density was dramatically reduced. Vegetation can show a time lag in responding to precipitation, whereby antecedent precipitation can affect community composition in subsequent years (Lauenroth and Sala 1992). Multiple consecutive years of below-average precipitation may have had lagged effects that contributed to the reduction in *B. tectorum* density in 2014.

I found that both native perennial species and *B. tectorum* generally responded to water added in May to simulate spring rainfall, consistent with though the magnitude of responses was not always statistically significant. In most cases, watered plants tended to have higher values of Ψ_{leaf}, g_s, A, Φ_{PSII}, and ETR relative to control plants. These results also reveal that *B. tectorum* had more pronounced responses to added springtime water than native species, consistent with H_5. Watering nearly doubled overall A for *B. tectorum*. Watering also increased A for the native species *A. hymenoides* and *L. argenteus* (though to a smaller degree), but had negligible impacts on A for *E. elymoides*.

Species responses to watering were not always uniform across the two study years. For instance, g_s for *B. tectorum* responded to watering in 2013 (increasing by 27%) but not 2014. By contrast, g_s for the native bunchgrass *A. hymenoides* and the native N_2-fixing forb *L. argenteus* had stronger responses to watering in 2014 than 2013 (going from marginal to significant). Stomatal conductance for the native bunchgrass *E. elymoides* significantly responded to springtime water additions in both years, though in different directions: watering increased g_s in 2013 and decreased g_s in 2014. Stomata respond rapidly to changing environmental conditions, so warmer temperatures and increased natural spring precipitation in 2014 may have obscured effects of watering on g_s. During the measurement period, 2014 daily mean, maximum, and minimum temperatures were on average 1.9°C, 1.6°C, and 2.7°C warmer, respectively, than in 2013. Similarly, daily mean, maximum, and minimum relative humidity was about 1.4% lower, 5.4% lower, and 2.5% higher, respectively.

Also, there was some natural rain and snow during the study period in 2014, which may have affected the impact of antecedent soil water conditions on the response of g_s (Loik 2007, Ogle et al. 2015).

Comparing across years, A for *B. tectorum* was about half in 2014 what it was in 2013, A for *L. argenteus* increased in 2014 relative to 2013, and A for *A. hymenoides* and *E. elymoides* was similar in both years. Inter-annual variation in uncontrolled field conditions can drive differences in results for experiments conducted in multiple years, especially in systems where inter-annual variability is high and in experiments that are investigating annual phenomena (Vaughn and Young 2010). Loik *et al.* (2015) found that inter-annual differences in snow depth yielded significant effects on Ψ_{stem}, g_s, and A for the shrubs *Artemisia tridentata* and *Purshia tridentata*. Such "year effects" can result in conditions that favor grass species in some years and forb species in others. From 2013 to 2014, within-species differences in overall A may have been due to inter-annual differences in precipitation patterns; 2013 had more snow and less spring rain, while 2014 had less snow and more spring rain. As a result, 2014 was a favorable year for forbs relative to grasses at the study site (pers. obs.), consistent with the increase in A for *L. argenteus* and decrease in A for *B. tectorum* in 2014 relative to 2013. Moreover, *B. tectorum* can exhibit dramatic "boom and bust" cycles in response to inter-annual variation in precipitation, with drought years negatively impacting *B. tectorum* biomass (Griffith and Loik 2010, Concilio and Loik 2013). *Lupinus argenteus* sustained the highest A of the three study species in both years, possibly due to its N_2 fixation. These results highlight the importance of species traits and inter-annual variation in driving responses of plant communities to altered patterns of springtime rainfall.

While the watering treatment did not significantly influence WUE for any species, I did observe interspecific differences in WUE. Relative to native species, *B. tectorum* had higher WUE in 2013, demonstrating less constraint of photosynthesis by water limitation. Water-use efficiency decreased in 2014 relative to 2013 for *B. tectorum* and *L. argenteus*, but not for *A. hymenoides* and *E. elymoides*. Watered plants generally had higher photosynthetic capacities relative to controls. In 2013, aside from *E. elymoides* which had a similar range of values of A and g_s between treatments, watered plants were able to achieve higher maximum A and g_s values than control plants. In 2014, watered *L. argenteus* plants maintained this extended range, while the three grass species did not show as much of a benefit from watering.

Relative to the three grass species, *L. argenteus* had a greater range of values for Φ_{PSII} and ETR, revealing greater plasticity of photochemical efficiency. Plants have two pathways for dissipating excess light energy: photochemical (i.e., photosynthesis) and non-photochemical (i.e., fluorescence and heat), the rates of which are affected by environmental stresses (Demmig-Adams and Adams 2006). Non-photochemical processes are activated by stressors such as high temperatures, high irradiance, and drought (Zhu et al. 2009). Relative to *L. argenteus*, a lower range of values of Φ_{PSII} and ETR for the grass species shows that they were dissipating more energy through non-photochemical processes, indicating that the grass species either have less stress resistance or were under more drought stress. Non-photochemical pathways also played a larger role in control plants (i.e., plants under drought stress) than watered plants. Photosynthesis of *L. argenteus* was more tolerant to drought stress by contrast to the other species, as evidenced by its comparatively higher range of values for Φ_{PSII} and ETR.

All four study species exhibited low Ψ_{leaf} values, with the mean for controls of grass species ranging from approximately -3.5 to -4 MPa and *L. argenteus* being approximately -3 MPa. Exceptionally low Ψ_{leaf} values are not surprising given that the combination of low precipitation and high temperatures since 2012 have created a record-setting, multi-year drought in California (Diffenbaugh et al. 2015). I observed species-specific responses to added water for Ψ_{leaf}. The temporary increase in soil moisture from water additions led to a sustained ~2-week Ψ_{leaf} effect for *B. tectorum* and *E. elymoides* (Figure 3), yet *A. hymenoides* and *L. argenteus* did not respond to watering. I hypothesize that these results reflect interspecific differences in rooting patterns. *Achnatherum hymenoides* is drought tolerant and has extensive, fibrous, deep roots (Ogle et al. 2013). *Lupinus* spp. also have deep root systems and grow a thick, long taproot (Beuthin 2012, St. John and Tilley 2012). The lack of a Ψ_{leaf} response for *A. hymenoides* and *L. argenteus* suggests that the deep roots of these species may have had access to sufficient soil moisture or water additions may not have infiltrated soils to the depth of their rooting zones. *Elymus elymoides* and *B. tectorum* are both known to produce roots with considerable lateral spread, with *E. elymoides* rooting to depths of at least 100 cm and *B. tectorum* having fine, diffusely branched roots that are primarily concentrated in the top 30 cm of soil (Harris 1967, Reynolds and Fraley 1989). With shallower, lateral roots, *E. elymoides* and *B. tectorum* may have been better able to capitalize on the ephemeral pulse of soil moisture from experimental watering. Moreover, *B. tectorum* control plants increased Ψ_{leaf} (from <-4 to >-3 MPa) following a natural precipitation event (a response that I did not observe for watered *B. tectorum* or native species), evidence of *B. tectorum*'s rapid exploitation of increases in soil moisture.

Bromus tectorum was more responsive to supplemental springtime water than native species, regardless of inter-annual and seasonal differences in natural precipitation patterns, revealing its highly opportunistic exploitation of ephemeral increases in soil moisture. Native species varied in their degree of responsiveness to added water, with *A. hymenoides* and *L. argenteus* responding similarly to water additions, while *E. elymoides* was the least responsive. Notorious for its fire impacts, ecosystem transformations, rapid spread, and difficulty to eradicate, *B. tectorum* invasion already poses enormous threats to ecosystem integrity, which may intensify as climate change impacts progress. This is especially important in high-elevation areas where *B. tectorum* impacts so far have been relatively minimal (i.e., invasion is occurring but has not yet reached density thresholds sufficient to alter fire cycles). These results demonstrate that an increase in spring precipitation would likely benefit *B. tectorum* to a greater extent than native species. As this study coincided with several drought years, it would be interesting to determine whether results differ in years with average or above-average winter and/or spring precipitation. The combination of winter and spring precipitation and inter-annual variability are likely to yield significant impacts on sagebrush steppe vegetation. Regardless of specific precipitation patterns, *B. tectorum* has rapid and highly plastic responses to increases in water resources, which may enable this ecologically detrimental invasive species to increase the extent of its invasion at high elevations in years with increased precipitation. Uncertainty about future precipitation patterns and the small window of opportunity to manage invasions necessitate close monitoring of high-elevation areas at risk of *B. tectorum* encroachment. Management efforts should consider variations in inter-annual conditions to capitalize on years in which *B. tectorum* biomass is naturally reduced and native vegetation is at an advantage to target infestations for control.

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CHAPTER 2

IMPACTS OF TEMPERATURE ON THE PERFORMANCE OF AND INTERACTIONS BETWEEN *BROMUS TECTORUM* AND NATIVE SPECIES

> *Today the honey-colored hills that flank the northwestern mountains*
> *derive their hue not from the rich and useful bunchgrass and*
> *wheatgrass which once covered them, but from the inferior cheat*
> *which has replaced these native grasses.*
>
> —Aldo Leopold, *A Sand County Almanac* (1949); p. 165

Abstract

In ecosystems, coexisting plants interact with one another, exerting both negative (i.e., competitive) and positive (i.e., facilitative) impacts on one another—the degree of which depends on factors such as resource availability and environmental conditions. Species interactions scale up to structure ecosystems and their role in influencing ecosystem responses to climate change is uncertain. This study use a controlled greenhouse experiment to test the effects of high (day/night: 27°C/4°C) and low (day/night: 16°C/1°C) temperature regimes on the relative performance of, as well as interactions between, the invasive annual *Bromus tectorum* L. (Poaceae, 'cheatgrass') and the native perennials *Elymus elymoides* (Raf.) Swezey (Poaceae, 'squirreltail') and *Lupinus argenteus* Pursh (Fabaceae, 'silvery lupine')—common sagebrush steppe plant species in the western United States. Temperature had a stronger impact on *B. tectorum* than native species, whereby high temperatures dramatically reduced *B. tectorum* reproductive allocation (inflorescence production and reproductive biomass) but increased vegetative biomass, though temperature did not affect total aboveground biomass (reproductive and vegetative) for *B. tectorum*. Under high temperatures, native species also generally developed greater vegetative biomass. *Bromus tectorum* typically exerted negative impacts on neighboring plant photosynthetic physiology and biomass accumulation (of both conspecifics and native species), while the N_2-fixing *L. argenteus* generally enhanced physiology and biomass of its neighbors. These results suggest that strong interspecific and intraspecific competition from *B. tectorum* and potential facilitation of other plants by *L. argenteus* will play a role in the responses of sagebrush steppe ecosystems to climate change, and that temperature may mediate the effects of competition and facilitation under a future climate.

Key words: biomass, cheatgrass, climate change, competition, *Elymus elymoides*, *Lupinus argenteus*, photosynthesis, plant growth, reproduction

Introduction

Invasive species are widely reputed to possess traits that make them superior competitors with native species, such as a high degree of plasticity, high fecundity, high rates of resource acquisition, and rapid growth rates (Abatzoglou and Kolden 2011). However, interactions between native and invasive species are dynamic and their relative performance is context dependent. Changes in abiotic environmental conditions and resource availability can alter the relative competitive abilities of different species (Daehler 2003), and interactions between individual plants ultimately scale up to structure ecosystems (Brooker 2006).

Negative (i.e., competitive) interactions have been the predominant focus of studies considering interactions between native and invasive species, but the role of positive (i.e., facilitative) interactions of native species on invaders has garnered increasing recognition in the literature (Brooker et al. 2008). Compared to bare soil patches, microclimates created by native vegetation can provide "islands of fertility" that can facilitate other plant species and seedlings by ameliorating abiotic and biotic stressors. The canopies of native vegetation can provide protection from herbivory; higher levels of soil nutrients from N_2 fixation, litterfall, and/or root exudates; and increased soil moisture from the effects of shading on temperature and evaporation and/or hydraulic lift by roots (Schlesinger et al. 1996, Holzapfel and Mahall 1999, Loik 2007, Griffith 2010). The stress-gradient hypothesis predicts that competition should be more common when environmental stress is low and facilitation should be more common when stress is high (Bertness and Callaway 1994). Facilitation of invasive species by native species has the potential to exacerbate invasions by permitting non-native plants to persist under environmental conditions that would otherwise be too stressful (Holzapfel and Mahall 1999, Brooker 2006, Griffith 2010). The role of species interactions is one of the greatest sources of uncertainty in predicting how plant communities will respond to climate change (Adler et al. 2012).

The Great Basin sagebrush steppe is one of the most heavily invaded ecosystems in the western United States. The invasive Eurasian annual grass *Bromus tectorum* L. (Poaceae, 'cheatgrass') has proven to be a strong competitor with many native perennial species, as evidenced by its rapid expansion since the late 1800s and current dominance on roughly 200,000 km^2 in the Intermountain West (Bradley and Mustard 2005). *Bromus tectorum* grows more quickly than native species and rapidly depletes water and nutrients from shallow soil layers, which can reduce the root systems of neighboring native species, depressing their water status and productivity for prolonged time periods (Harris 1967, Melgoza et al. 1990, Melgoza and Nowak 1991, Knapp 1995, 1996, Booth et al. 2003, Chambers et al. 2007). Native perennial species can also be effective competitors with *B. tectorum*, though this depends on the particular species considered, its life history strategy, and its life stage. High cover of established perennial bunchgrasses confers resistance to *B. tectorum* invasion and post-fire expansion. Chambers et al. (2007) reported dramatic increases in *B. tectorum* biomass following removal of perennial vegetation (2-3×), burning (2-6×), and removal and burning (10-30×). Booth et al. (2003) found an inverse relationship between *B. tectorum* and *Elymus elymoides* (Raf.) Swezey (Poaceae, ‘squirreltail’) cover, with near complete suppression of *B. tectorum* when *E. elymoides* cover approached 20%. Similarly, Concilio and Loik (2013) reported an inverse relationship between *B. tectorum* cover and native forb species richness. Mature perennials with more extensive root systems likely gain a competitive advantage over annual grasses by accessing soil moisture from greater depths than annuals can, thereby altering moisture availability (Booth et al. 2003, Humphrey and Schupp 2004, McGlone et al. 2012). Conversely, native perennial seedlings are generally poor competitors with *B. tectorum* (Humphrey and Schupp 2004), possibly because the disparity in root biomass between perennials and annuals is not as pronounced at the seedling stage (McGlone et al. 2012). Facilitation of *B. tectorum* has been reported for various perennial grasses, forbs, and shrubs (Belnap and Sherrod 2009 and references therein). At a location near its high-elevation range margin, *B. tectorum* capitalizes on favorable shrub understory microhabitats of *Artemisia tridentata* Nutt. (Asteraceae, ‘big sagebrush’) and *Purshia tridentata* (Pursh) DC. (Rosaceae, ‘antelope bitterbrush’), potentially promoting its high-elevation persistence and spread (Griffith 2010).

Thus, while *B. tectorum* invasion and subsequent dominance is largely driven by disturbance (i.e., grazing and fire), it can also invade relatively undisturbed communities where it coexists with—and sometimes incurs benefits from—native species. Due to its extremely high fecundity, even low densities of *B. tectorum* create the risk of rapid population expansion following severe disturbance to the native perennial community (McGlone et al. 2012, Concilio 2013) or following resource increases, e.g., years of above-average precipitation (Concilio et al. 2013). Currently, cold winter temperatures and a brief growing season restrict the widespread expansion of *B. tectorum* at its high-elevation range margin (Chambers et al. 2007, Griffith and Loik 2010). However, ongoing anthropogenic impacts are altering environmental conditions and resource availability in ways that are thought to favor the performance of invasive species over natives (Daehler 2003). Research has demonstrated that *B. tectorum* has highly plastic responses to increased resource availability and temperature. Relative to native perennial species, *Bromus* spp. exhibit greater growth under high levels of N (Claassen and Marler 1998) and enhanced rates of N acquisition under elevated temperatures (Leffler et al. 2011). Higher temperatures, greater water stress, and altered precipitation patterns are all expected to occur with continued climate change (Schwinning and Sala 2004) and have the potential to alter species interaction outcomes, possibly in ways that further benefit *B. tectorum*. In the case of *B. tectorum* and other fire-altering invasive species, restoring the native plant community is exceptionally difficult and costly once the invasive grass/fire cycle has been initiated (Brooks et al. 2004). This highlights the importance of preventative management to increase resistance of sagebrush steppe ecosystems still dominated by natives (Noss et al. 1995, Chambers et al. 2007).

In invaded communities, plant-plant interactions can positively affect ecosystem structure when one native increases the abundance of another native or when natives are effective competitors with invasive species. By contrast, facilitation of invasive species by natives could exacerbate invasions. This study tested species performance (i.e., photosynthesis and growth) and interactions (i.e., interspecific competition, intraspecific competition, and facilitation) among *B. tectorum*, the native perennial bunchgrass *E. elymoides*, and the native perennial forb *Lupinus argenteus* Pursh (Fabaceae, ‘silvery lupine’). *Elymus elymoides* is thought to be one of the most promising competitors with *B. tectorum* due to its fire tolerance and similar phenology and resource use characteristics to annual species (Booth et al. 2003, Humphrey and Schupp 2004). *Lupinus argenteus* is a native N_2-fixing legume that has been shown to facilitate the growth and survival of an *Elymus* spp. in the field, while having both positive (increased biomass and reproduction) and negative (decreased emergence and survival) effects on *B. tectorum* (Goergen and Chambers 2012).

The objectives of this study were to improve understanding of (1) the relative strength of direct effects of temperature vs. indirect effects mediated by species interactions on plant physiological performance, growth, and reproduction and (2) what conditions favor native perennials vs. the invasive annual *B. tectorum*. I hypothesized that (H_1) *E. elymoides* would have overall negative effects on *B. tectorum* because of its relatively strong competitive abilities which would be more pronounced under low abiotic stress (low temperatures); (H_2) *L. argenteus* would have overall positive effects on *E. elymoides* and *B. tectorum* due to its N_2 fixation which would be more pronounced under high abiotic stress (high temperatures); and (H_3) High temperatures would negatively impact the performance and growth of native species due to greater stress, but *B. tectorum* would be resistant to negative effects of high temperatures due to its high degree of plasticity.

Methods

This research was performed in the greenhouse facilities at the University of California, Santa Cruz between October 2013 and August 2014. The three study species were grown in pairs (i.e., two plants per container) in species monocultures and mixtures: *B. tectorum* monoculture, *E. elymoides* monoculture, *L. argenteus* monoculture, *B. tectorum*/*E. elymoides* mixture, *B. tectorum*/*L. argenteus* mixture, and *E. elymoides*/*L. argenteus* mixture. All seeds were collected from a single study site in the eastern Sierra Nevada, Mono County, California, between June 2012 and July 2013.

Seeds of each species were germinated in Petri dishes on Whatman filter paper on a 12-hour day/night cycle (9 am to 9 pm) with a day/night temperature regime of 22°C/12°C. *Lupinus argenteus* seeds were pre-treated by soaking them for approximately 24 hours in hot water to encourage the seeds to imbibe. (*Bromus tectorum* and *E. elymoides* did not require any special pre-treatment to germinate.) Upon germination, seedlings of roughly the same age were paired and planted into 656-mL containers (D40H Deepot Cells, Stuewe & Sons, Tangent, OR; 6.4 cm diameter and 25.4 cm depth). Seedlings were planted in high-porosity soil containing a mix of 65-75% peat moss and 25-35% Perlite (Pro-Mix HP, Premier Tech Horticulture, Quakertown, PA). *Lupinus argenteus* seedlings were inoculated upon planting by coating the radicle with a peat-based lupine inoculant (N-DURE, INTX Microbials, Kentland, IN) containing 200 million *Bradyrhizobium* spp. per gram to ensure nodulation as well as adding inoculant directly to the soil with the seedling. After planting, seedlings were well watered and grown under ambient greenhouse temperatures until plants were established in their containers (~4 weeks). Table 2-1 shows the number of replicates for each container.

Table 2-1. Replicates of each species combination.

Species combination	Number of replicates
Bromus tectorum monoculture	20
Elymus elymoides monoculture	20
Lupinus argenteus monoculture	18[1]
B. tectorum/*E. elymoides* mixture	20
B. tectorum/*L. argenteus* mixture	16[1]
E. elymoides/*L. argenteus* mixture	20
Total containers	114

[1] Due to difficulties with germination rates, the final number of *L. argenteus* seedlings fell short relative to the other species.

After the establishment period, containers were randomly assigned to either a high (day/night: 27°C/4°C) or low (day/night: 16°C/1°C) temperature regime (Figure 2-1) that simulated July and April temperature regimes, respectively, at the seed collection site. Continual soil water delivery into the bottom of the containers was achieved through the use of floral foam (Capri, Floral Supply Syndicate, San Jose, CA) following the methods of Lambrecht et al. (2007) to maintain consistent soil moisture levels regardless of plant size. Foam blocks were placed in 2.2-L polypropylene bins and wetted to induce capillary action. Within each bin, two containers were randomly selected and placed into the floral foam. Plants were fertilized twice during the experiment, each time using 100 ppm N solution (Peters Professional 20-20-20 general purpose water soluble fertilizer, the Scotts Company, Marysville, OH).

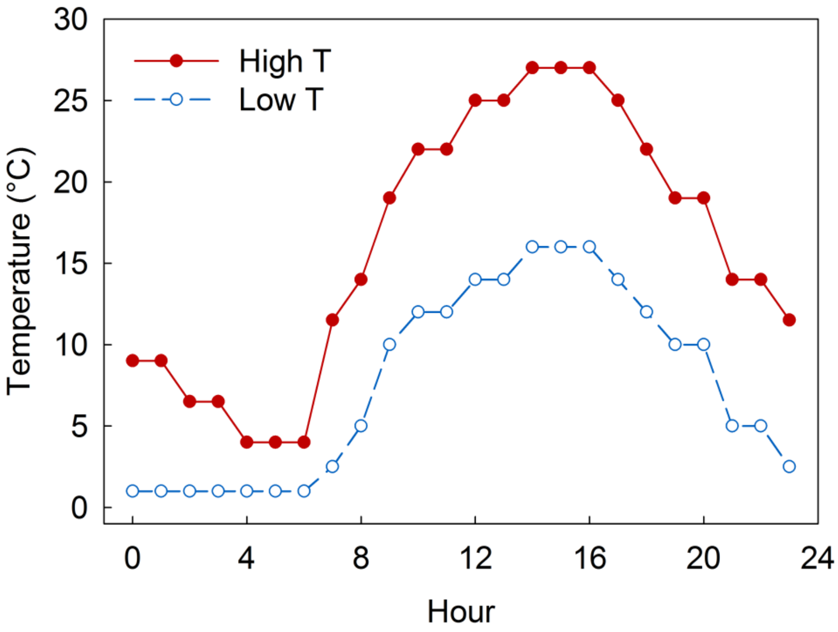

Figure 2-1. Growth chamber temperature regimes. Note that the minimum temperatures for the cold temperature treatment were limited by the growth chamber's inability to operate at negative temperatures.

I monitored plant height and leaf production to measure growth rates while plants were in the chambers (data not shown). Using an open-mode portable photosynthesis system (model LI-6400, Li-Cor Biosciences, Lincoln, NE), I measured instantaneous rates of stomatal conductance to water vapor (g_s), CO_2 assimilation (A), quantum yield of Photosystem II (Φ_{PSII}), and electron transport rate (ETR) after ~2-3 weeks of acclimation to conditions in the growth chambers. Upon *B. tectorum* seed set (after ~8 months in the growth chambers), I harvested plants, separated them into aboveground (reproductive and vegetative biomass) and belowground (combined root and soil mass, due to difficulty in separating heavily entangled plant roots) components, and weighed samples before and after ovendrying at 40°C for 3 days to compute gravimetric moisture content, dry reproductive and vegetative biomass, and dry mass of roots and soil.

Statistical Analyses

I used factorial analyses of variance (ANOVAs) to test for main and interaction effects of neighboring species and temperature and used *post hoc* Tukey's HSD tests when the effect of neighboring species was significant to differentiate between the three species. All data analyses were conducted using JMP Pro (v. 11.0.0; SAS Institute, Cary, NC).

Results

Photosynthetic Measurements

Stomatal conductance (Figure 2-2) for *E. elymoides* was not affected by temperature nor neighboring species. Conductance for *B. tectorum* was significantly higher in the low temperature treatment than the high temperature treatment for plants grown with a conspecific ($F_{1,38} = 8.4084$, $P = 0.0062$). In the high temperature treatment, g_s for *B. tectorum* grown with a conspecific was significantly lower than when grown with either of the two native species ($F_{2,35} = 10.3070$, $P = 0.0003$). *Lupinus argenteus* consistently had significantly higher g_s in the high temperature treatment than the low temperature treatment across all species combinations (with *B. tectorum*: $F_{1,14} = 4.8411$, $P = 0.0451$; with *E. elymoides*: $F_{1,17} = 10.1013$, $P = 0.0055$; with *L. argenteus*: $F_{1,32} = 8.6149$, $P = 0.0061$). Within the high

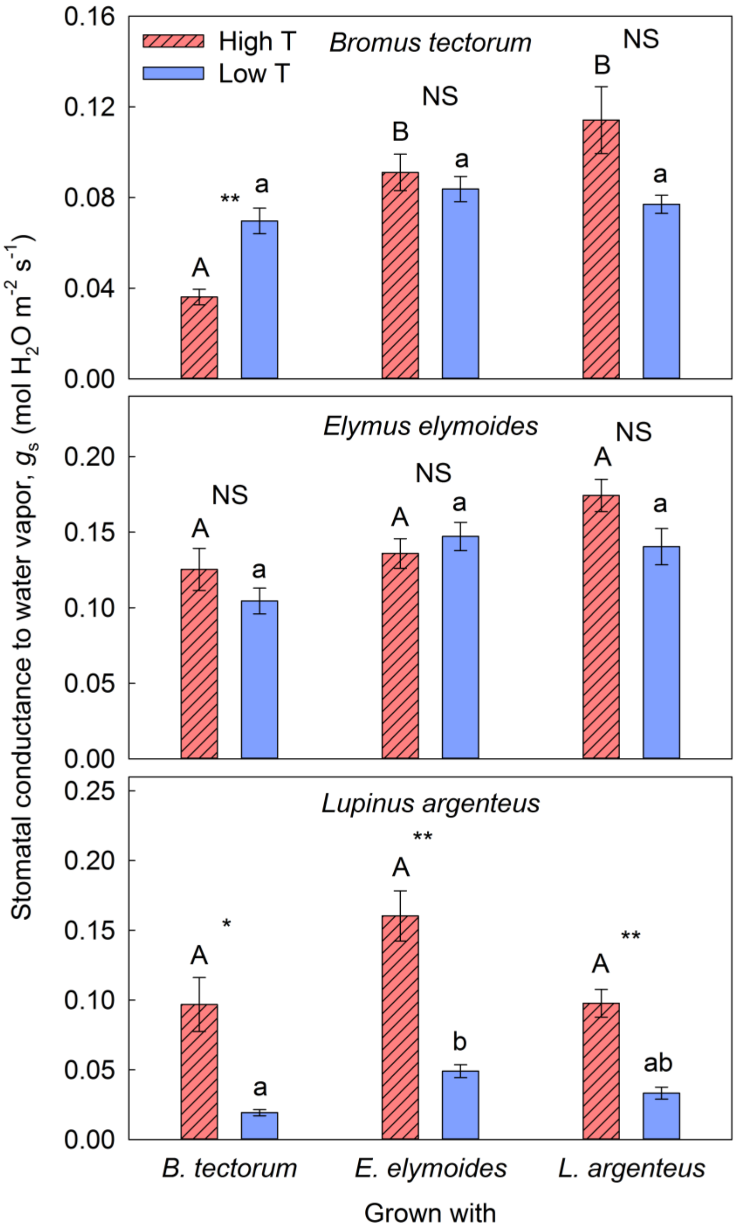

Figure 2-2. Stomatal conductance (g_s) for each species combination. Capital letters represent Tukey's HSD tests for different species combinations within the high temperature regime and lowercase letters represent Tukey's HSD tests for different species combinations within the low temperature regime. Asterisks show differences (ANOVA) for the two temperature treatments within a species combination (NS = not significant, † = $P \leq 0.1$, * = $P \leq 0.05$, ** = $P \leq 0.01$, *** = $P \leq 0.001$, **** = $P \leq 0.0001$).

temperature treatment, neighboring species did not affect g_s for *L. argenteus* but, within the low temperature treatment, g_s was highest when grown with *E. elymoides*, lowest with *B. tectorum*, and intermediate with another *L. argenteus* ($F_{2,28} = 3.2743$, $P = 0.0527$).

CO_2 assimilation (Figure 2-3) for *B. tectorum* was higher in the low temperature treatment, while native species tended to have higher A in the high temperature treatment. For *B. tectorum*, high temperatures significantly reduced A relative to low temperatures only when the neighboring plant species was a conspecific ($F_{1,38} = 10.4620$, $P = 0.0025$). The neighboring plant species did not affect A for *B. tectorum* in the low temperature treatment but, in the high temperature treatment, *B. tectorum* grown with *L. argenteus* had higher A than *B. tectorum* grown with a conspecific, with *B. tectorum* grown with *E. elymoides* having intermediate A values ($F_{2,35} = 9.5822$, $P = 0.0005$). CO_2 assimilation for *E. elymoides* did not have any significant responses to either temperature or neighboring plant species. The neighboring plant species did not affect A for *L. argenteus* in either temperature regime, but A was significantly higher in the high temperature treatment than the low temperature treatment when grown with a conspecific ($F_{1,32} = 8.2019$, $P = 0.0073$) and marginally higher when grown with *B. tectorum* ($F_{1,14} = 3.7510$, $P = 0.0732$). In the low temperature treatment, *L. argenteus* grown with *E. elymoides* had higher A than when grown with the other two species, but this trend was not significantly different.

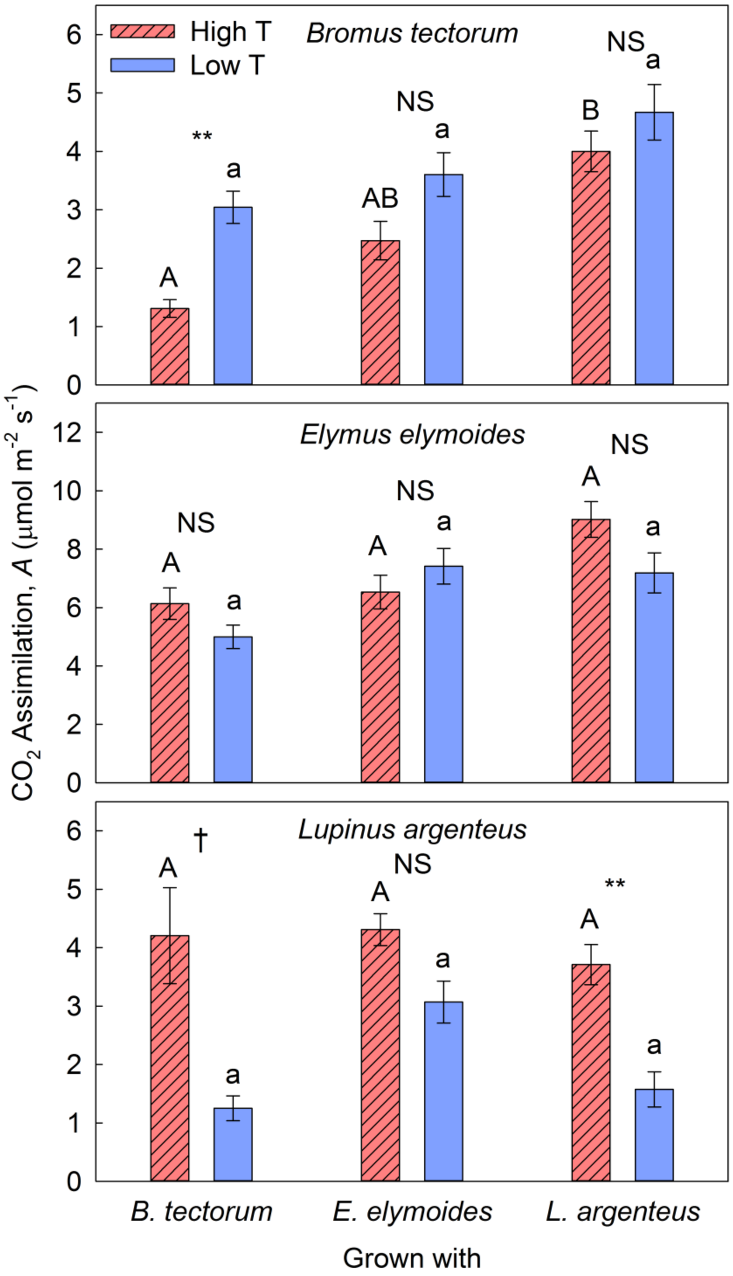

Figure 2-3. CO_2 assimilation (*A*) for each species combination. Capital letters represent Tukey's HSD tests for different species combinations within the high temperature regime and lowercase letters represent Tukey's HSD tests for different species combinations within the low temperature regime. Asterisks show differences (ANOVA) for the two temperature treatments within a species combination (NS = not significant, † = $P \leq 0.1$, * = $P \leq 0.05$, ** = $P \leq 0.01$, *** = $P \leq 0.001$, **** = $P \leq 0.0001$).

The quantum efficiency of Photosystem II electron transport (Figure 2-4) was significantly higher in the low temperature treatment than the high temperature treatment for *B. tectorum* across all species combinations (with *B. tectorum*: $F_{1,38} = 17.5132$, $P = 0.0002$; with *E. elymoides*: $F_{1,18} = 4.6605$, $P = 0.0446$; with *L. argenteus*: $F_{1,14} = 7.4923$, $P = 0.0160$). For *E. elymoides*, Φ_{PSII} was significantly higher in the low than high temperature treatment only when grown with *L. argenteus* ($F_{1,18} = 5.5309$, $P = 0.0303$), with no effect of temperature when grown with *B. tectorum* or *E. elymoides*. In the high temperature treatment, *E. elymoides* had a lower Φ_{PSII} when grown with *B. tectorum* than with the two native species ($F_{2,36} = 4.7635$, $P = 0.0146$). *Lupinus argenteus* had marginally higher Φ_{PSII} in the high temperature than low temperature treatment only when grown with another *L. argenteus* ($F_{1,32} = 2.9932$, $P = 0.0933$), with no effect of temperature on Φ_{PSII} for the other species combinations and no effect of neighboring species on Φ_{PSII} under either temperature treatment.

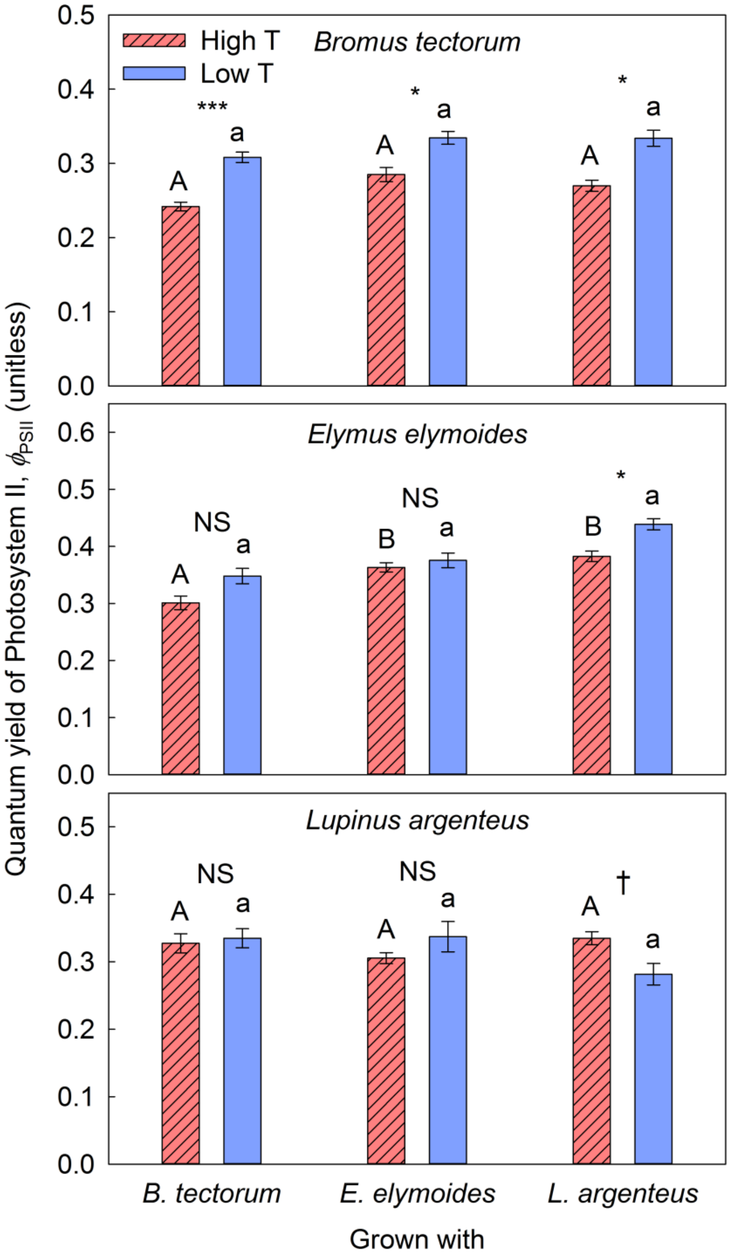

Figure 2-4. Quantum yield of Photosystem II (Φ_{PSII}) for each species combination. Capital letters represent Tukey's HSD tests for different species combinations within the high temperature regime and lowercase letters represent Tukey's HSD tests for different species combinations within the low temperature regime. Asterisks show differences (ANOVA) for the two temperature treatments within a species combination (NS = not significant, † = $P \leq 0.1$, * = $P \leq 0.05$, ** = $P \leq 0.01$, *** = $P \leq 0.001$, **** = $P \leq 0.0001$).

Like Φ_{PSII}, ETR (Figure 2-5) was significantly higher for *B. tectorum* in the low temperature treatment across all planting combinations (with *B. tectorum*: $F_{1,38} = 16.2683$, $P = 0.0003$; with *E. elymoides*: $F_{1,18} = 4.5218$, $P = 0.0476$; with *L. argenteus*: $F_{1,14} = 7.4682$, $P = 0.0162$). The identity of the neighboring species had no effect on ETR for *B. tectorum*. *Elymus elymoides* had higher ETR in the low temperature treatment than in the high temperature treatment only when grown with *L. argenteus* ($F_{1,18} = 5.5523$, $P = 0.0300$). In the high temperature treatment, ETR was significantly lower for *E. elymoides* grown with *B. tectorum* than with the two natives ($F_{2,36} = 4.8331$, $P = 0.0138$). In the low temperature treatment, ETR for *E. elymoides* was lowest when grown with *B. tectorum*, highest when grown with *L. argenteus*, and intermediate with a conspecific ($F_{2,37} = 3.2989$, $P = 0.0480$). *Lupinus argenteus* had marginally lower ETR in the low temperature treatment than high temperature treatment only when grown with another *L. argenteus* ($F_{1,32} = 3.3015$, $P = 0.0786$), with no effect of temperature on ETR for the other species combinations and no effect of neighboring species on ETR under either temperature treatment.

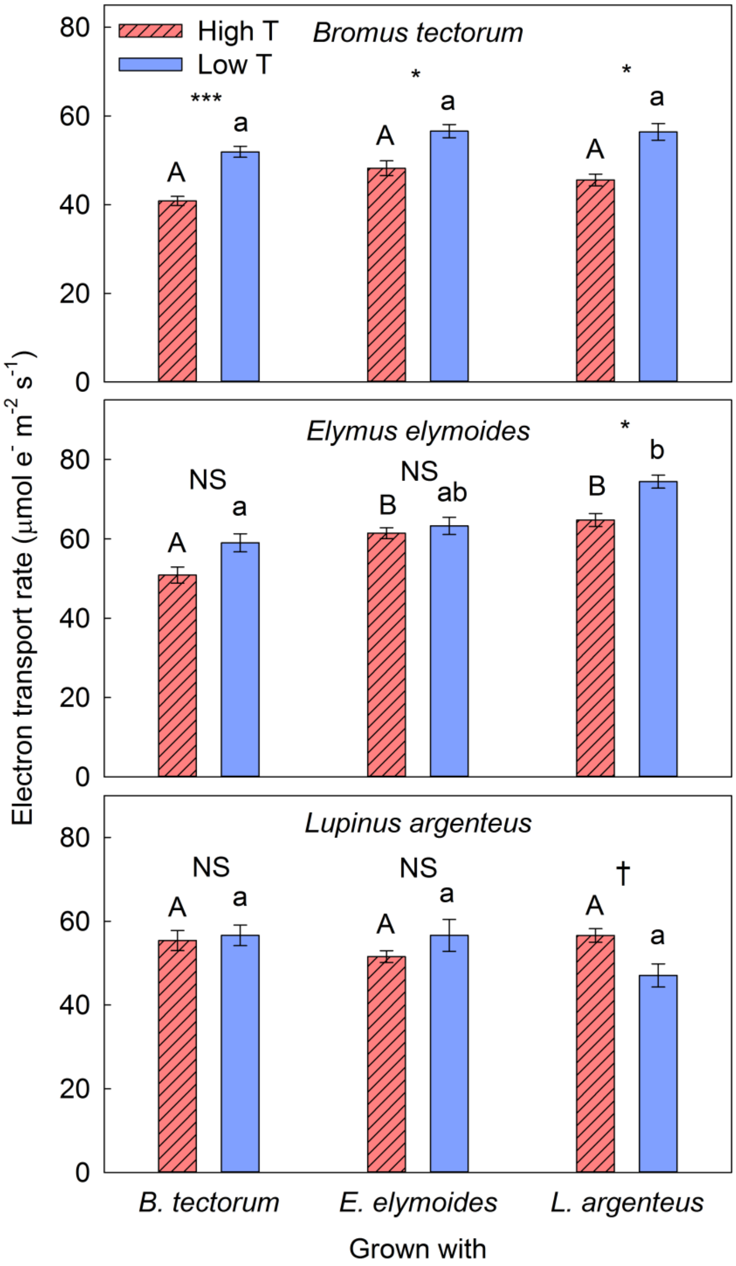

Figure 2-5. Electron transport rate (ETR) for each species combination. Capital letters represent Tukey's HSD tests for different species combinations within the high temperature regime and lowercase letters represent Tukey's HSD tests for different species combinations within the low temperature regime. Asterisks show differences (ANOVA) for the two temperature treatments within a species combination (NS = not significant, † = $P \leq 0.1$, * = $P \leq 0.05$, ** = $P \leq 0.01$, *** = $P \leq 0.001$, **** = $P \leq 0.0001$).

Roots and Soil

The weight of roots and soil (Figure 2-6) in the *B. tectorum* monoculture was significantly higher in the low temperature treatment ($F_{1,18} = 7.3536$, $P = 0.0143$), and that for the *L. argenteus* monoculture was significantly higher in the high temperature treatment ($F_{1,16} = 4.5415$, $P = 0.0489$).

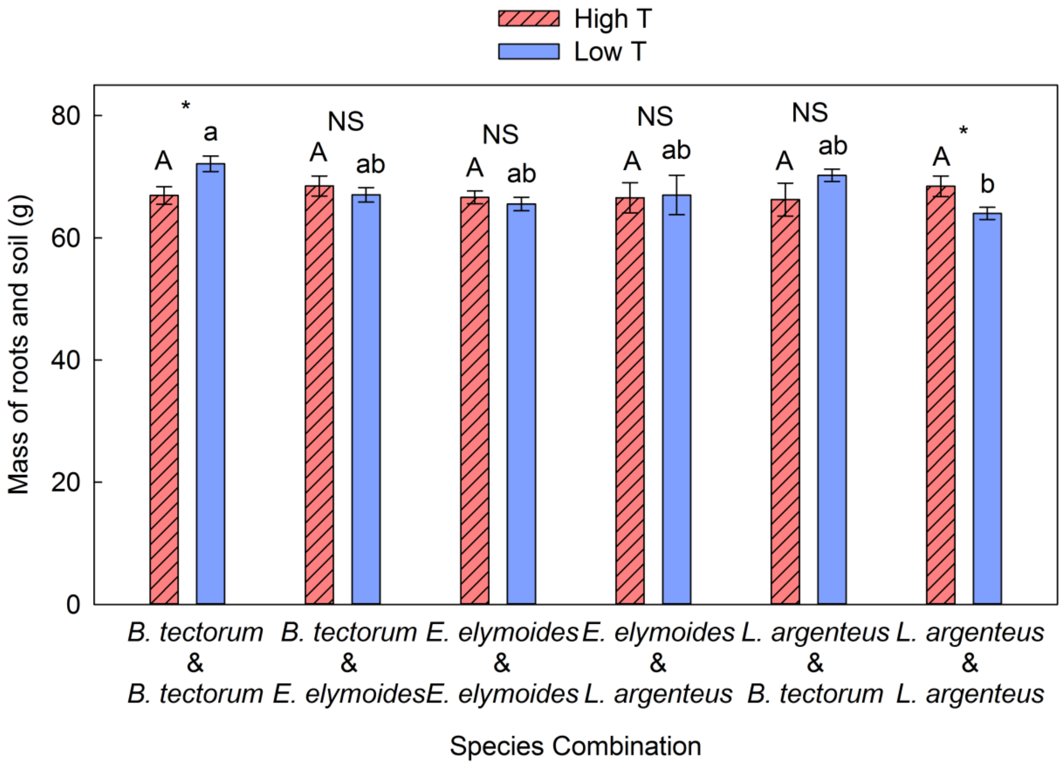

Figure 2-6. Dry belowground root biomass combined with soils for each species combination. Capital letters represent Tukey's HSD tests for different species combinations within the high temperature regime and lowercase letters represent Tukey's HSD tests for different species combinations within the low temperature regime. Asterisks show differences (ANOVA) for the two temperature treatments within a species combination (NS = not significant, † = $P \leq 0.1$, * = $P \leq 0.05$, ** = $P \leq 0.01$, *** = $P \leq 0.001$, **** = $P \leq 0.0001$).

Aboveground Biomass

Bromus tectorum was the only species that achieved a significant amount of flowering, hence, aboveground biomass for the native species was nearly all vegetative. Total aboveground biomass (i.e., reproductive and vegetative) did not differ by temperature regime for *B. tectorum*, nor by the neighboring plant species (data not shown). However, differences for *B. tectorum* were readily apparent when aboveground biomass was separated into reproductive and vegetative components, discussed further below.

Vegetative Biomass

Bromus tectorum significantly suppressed vegetative biomass (Figure 2-7) regardless of temperature for conspecifics (high temperature: $F_{2,35} = 7.5778$, $P = 0.0018$; low temperature: $F_{2,35} = 10.6310$, $P = 0.0002$). Vegetative biomass of *B. tectorum* was lower in low temperatures than in high temperatures for all planting combinations (significantly for plants grown with *B. tectorum* [$F_{1,38} = 9.5433$, $P = 0.0037$] and *L. argenteus* [$F_{1,14} = 5.1304$, $P = 0.0399$] and marginally for plants grown with *E. elymoides* [$F_{1,18} = 3.7423$, $P = 0.0689$]).

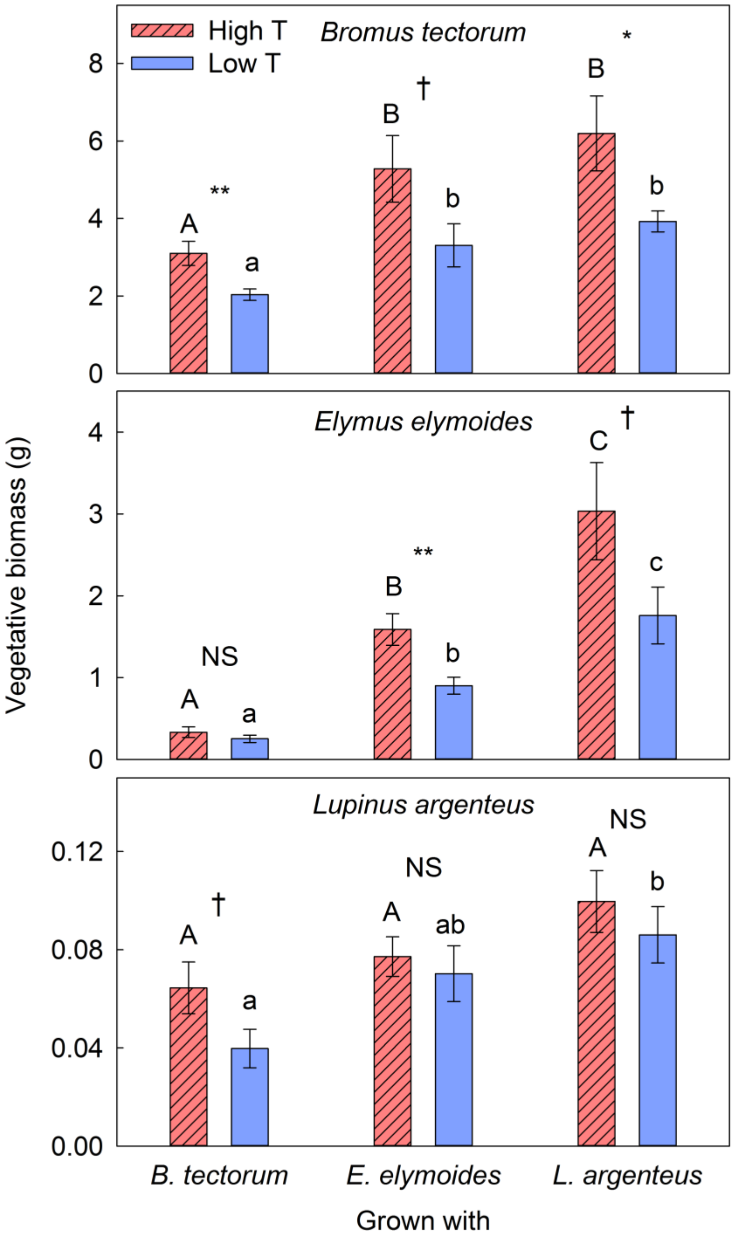

Figure 2-7. Dry aboveground vegetative biomass for each species combination. Capital letters represent Tukey's HSD tests for different species combinations within the high temperature regime and lowercase letters represent Tukey's HSD tests for different species combinations within the low temperature regime. Asterisks show differences (ANOVA) for the two temperature treatments within a species combination (NS = not significant, † = $P \leq 0.1$, * = $P \leq 0.05$, ** = $P \leq 0.01$, *** = $P \leq 0.001$, **** = $P \leq 0.0001$).

Elymus elymoides vegetative biomass was suppressed by *B. tectorum*, enhanced by *L. argenteus*, and intermediate with another *E. elymoides* under both temperature treatments (high temperature: $F_{2,37} = 14.5815$, $P < 0.0001$; low temperature: $F_{2,37} = 14.0326$, $P < 0.0001$). Temperature significantly affected biomass for *E. elymoides* grown with another *E. elymoides*, with higher biomass under high temperatures ($F_{1,38} = 9.7159$, $P = 0.0035$), and marginally affected biomass for *L. argenteus*, with higher biomass under high temperatures ($F_{1,18} = 3.4486$, $P = 0.0797$).

The neighboring plant species did not affect biomass of *L. argenteus* under high temperatures. Under low temperatures, *B. tectorum* significantly suppressed *L. argenteus* biomass relative to those grown with a conspecific, and *L. argenteus* grown with *E. elymoides* had intermediate biomass ($F_{2,31} = 3.8058$, $P = 0.0333$). *Lupinus argenteus* grown with *B. tectorum* had marginally higher vegetative biomass under high temperatures than low temperatures ($F_{1,14} = 3.5361$, $P = 0.0810$).

Reproductive Biomass

Both temperature and the neighboring plant species had significant impacts on the number of inflorescences produced by *B. tectorum* (Figure 2-8). Plants grown under the high temperature regime produced significantly fewer inflorescences than those grown under the low temperature regime (with *B. tectorum*: $F_{1,38} = 115.5808$, $P < 0.0001$; with *E. elymoides*: $F_{1,18} = 15.4449$, $P = 0.0010$; with *L. argenteus*: $F_{1,14} = 42.7746$, $P < 0.0001$). Under high temperatures, the neighboring plant species did not influence the number of inflorescences. However, under low temperatures, the number of inflorescences produced by *B. tectorum* was lowest when grown with another *B. tectorum*, intermediate when grown with *E. elymoides*, and highest when grown with *L. argenteus* ($F_{2,35} = 4.1577$, $P = 0.0240$).

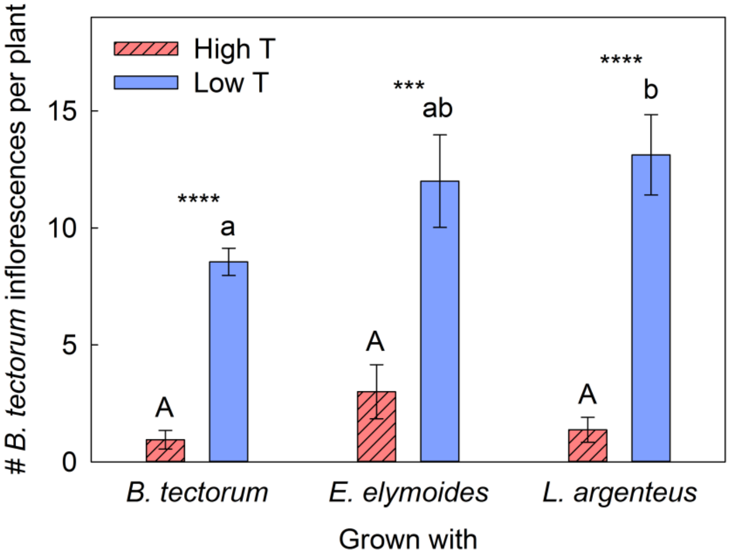

Figure 2-8. Number of inflorescences produced by *B. tectorum* for each species combination. Capital letters represent Tukey's HSD tests for different species combinations within the high temperature regime and lowercase letters represent Tukey's HSD tests for different species combinations within the low temperature regime. Asterisks show differences (ANOVA) for the two temperature treatments within a species combination (NS = not significant, † = $P \leq 0.1$, * = $P \leq 0.05$, ** = $P \leq 0.01$, *** = $P \leq 0.001$, **** = $P \leq 0.0001$).

The neighboring plant species did not significantly affect the dry weight of reproductive biomass for *B. tectorum* under either temperature regime (Figure 2-9), despite the difference in the number of inflorescences by neighboring plant species under the low temperature regime. As *B. tectorum* produced more inflorescences under the low temperature regime, it follows that reproductive biomass was also significantly higher under the low temperature regime than the high temperature regime (with *B. tectorum*: $F_{1,38} = 45.6925$, $P < 0.0001$; with *E. elymoides*: $F_{1,18} = 30.2391$, $P < 0.0001$; with *L. argenteus*: $F_{1,14} = 12.4542$, $P = 0.0033$).

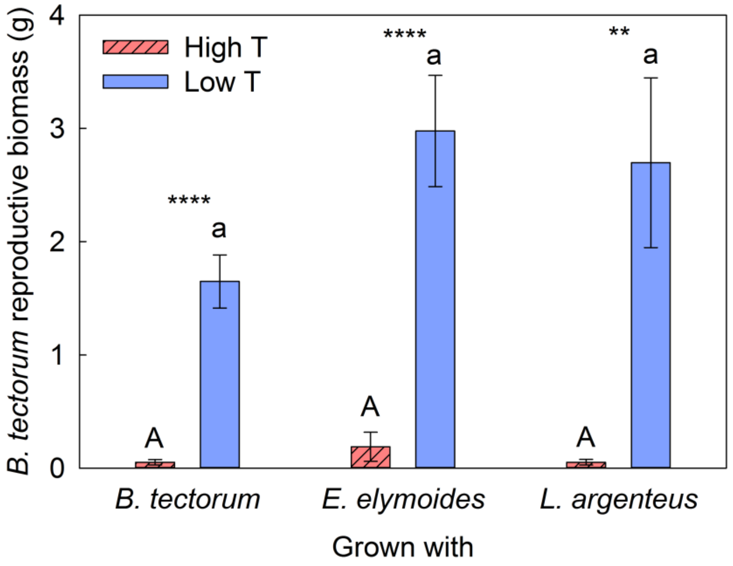

Figure 2-9. Dry aboveground *B. tectorum* reproductive biomass for each species combination. Capital letters represent Tukey's HSD tests for different species combinations within the high temperature regime and lowercase letters represent Tukey's HSD tests for different species combinations within the low temperature regime. Asterisks show differences (ANOVA) for the two temperature treatments within a species combination (NS = not significant, † = $P \leq 0.1$, * = $P \leq 0.05$, ** = $P \leq 0.01$, *** = $P \leq 0.001$, **** = $P \leq 0.0001$).

Similar to reproductive biomass, the ratio of *B. tectorum* reproductive to vegetative biomass did not significantly differ by neighboring plant species, but did significantly differ by temperature regime (Figure 2-10), with the low temperature treatment having a significantly larger ratio across all species combinations (with

B. tectorum: $F_{1,38} = 70.6905$, $P < 0.0001$; with *E. elymoides*: $F_{1,18} = 43.0321$, $P < 0.0001$; with *L. argenteus*: $F_{1,14} = 17.3530$, $P = 0.0010$).

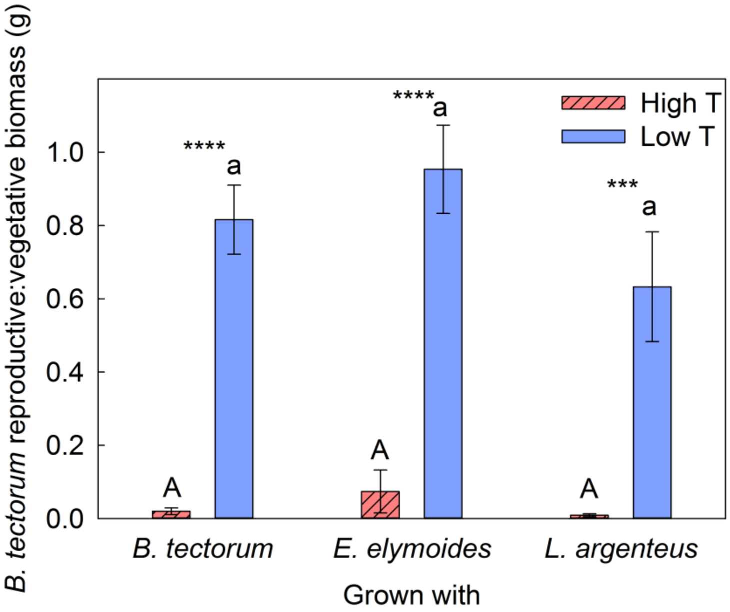

Figure 2-10. Ratio of reproductive to vegetative *B. tectorum* biomass for each species combination. Capital letters represent Tukey's HSD tests for different species combinations within the high temperature regime and lowercase letters represent Tukey's HSD tests for different species combinations within the low temperature regime. Asterisks show differences (ANOVA) for the two temperature treatments within a species combination (NS = not significant, † = $P \leq 0.1$, * = $P \leq 0.05$, ** = $P \leq 0.01$, *** = $P \leq 0.001$, **** = $P \leq 0.0001$).

Discussion

Temperature, interspecific and intraspecific competition, and facilitation influenced different performance variables for the non-native *B. tectorum* and the natives *E. elymoides* and *L. argenteus* in different ways. High temperatures generally resulted in greater vegetative biomass for all species. Temperature had a stronger effect on *B. tectorum* than native species, most notably in that *B. tectorum* allocation to reproduction was dramatically increased under low temperatures relative to high temperatures. *Bromus tectorum* and other invasive species are known to have greater plasticity in resource acquisition and tissue production than native species (Leffler et al. 2011, Griffith et al. 2014), consistent with this observation. Root respiration is positively correlated with temperature (Burton et al. 2002), so it is possible that high temperatures caused more respiration by roots, making them a stronger sink for photosynthates, and reducing the amount available to allocate to inflorescences.

Temperature mediated the effects of competition and facilitation for some measured variables, and not for others. Interspecific competition was most pronounced for *B. tectorum* and not very apparent in native species. For *B. tectorum,* interspecific competition resulted in decreased g_s and A under high temperatures, but not under low temperatures. Interspecific competition reduced *B. tectorum* vegetative biomass under both temperature treatments, and reduced the number of *B. tectorum* inflorescences under low temperatures, but not high temperatures.

Plants have both photochemical (i.e., CO_2 assimilation) and non-photochemical (i.e., fluorescence and heat) pathways for dissipating excess light energy, the rates of which are affected by environmental stresses (Demmig-Adams and Adams 2006). Stressful environmental conditions (e.g., high temperatures) activate non-photochemical processes (Zhu et al. 2009). While g_s and A were generally not affected by temperature for *B. tectorum* (except when grown with a conspecific, when both variables were higher under low temperatures), both Φ_{PSII} and ETR were reduced for *B. tectorum* under high temperatures, revealing that high temperatures amplified the dissipation of excess light energy through non-photochemical pathways for *B. tectorum*. In other words, *B. tectorum* was using more of the incoming light energy for photochemistry under the low temperature regime.

While interspecific competition was evident for *B. tectorum*, *B. tectorum* also showed strong intraspecific competition with the native species, evidenced by negative effects of *B. tectorum* on native species. *Bromus tectorum* reduced Φ_{PSII} and ETR for *E. elymoides* under high temperatures, and also suppressed *E. elymoides* ETR under low temperatures, though to a lesser degree. Previous research has shown that *B. tectorum* competition reduced first-year biomass for *E. elymoides* (Humphrey and Schupp 2004), which is consistent with my observation that *B. tectorum* dramatically suppressed *E. elymoides* biomass regardless of temperature.

Conversely, native species generally did not have negative impacts on *B. tectorum*. *Elymus elymoides* was not nearly as competitive with *B. tectorum* despite that mature native perennials generally are more resistant to effects of intraspecific competition with *B. tectorum* and better competitors with *B. tectorum* (Claassen and Marler 1998, Humphrey and Schupp 2004, McGlone et al. 2012). *Elymus elymoides* may have suppressed *A* for *B. tectorum* under high temperatures to a small degree. Given the imbalance in initial growth rates and resource acquisition for native and invasive species, it is not surprising that native seedlings in this study exerted minimal competitive impacts on *B. tectorum*.

Lupinus argenteus generally had positive impacts on neighboring species, evidence that facilitation may be occurring. Under both high and low temperatures, *L. argenteus* enhanced vegetative biomass for *E. elymoides*, but not for *B. tectorum*. A positive impact of one native species on other native—and not on invasive—species would increase ecosystem functional stability and potentially reduce the magnitude of invasions. *L. argenteus* also may have facilitated ETR for *E. elymoides*, though this positive influence of *L. argenteus* was less pronounced than that for *E. elymoides* biomass. However, *L. argenteus* did appear to facilitate *B. tectorum* in that it enhanced inflorescence production for the invasive under low temperatures—though it did not affect inflorescence biomass. Consistent with this study, Goergen and Chambers (2012) also found that *L. argenteus* positively impacted an *Elymus* spp. but had mixed effects on *B. tectorum*.

Limitations of this study include the difficulty of simulating realistic field conditions in a greenhouse setting. Growing plants in containers with constrained volume can impede plant growth by reducing resource availability, photosynthetic rates, and both shoot and root biomass (Poorter et al. 2012). Also, because experiments were done with seedlings in containers with limited space to grow, the apparent effects of competition and facilitation could be confounded by intraspecific differences in growth rates. As an annual species, *B. tectorum* exhibits rapid growth rates (Knapp 1996) relative to native perennial seedlings. In this experiment, after *B. tectorum*, *E. elymoides* had an intermediate growth rate, while *L. argenteus* grew the slowest, so observed differences could be the result of *B. tectorum* growing fastest to fill the containers. Despite this caveat, the results of this study are consistent with trends found in other studies on interactions between native and invasive species (Booth et al. 2003, Chambers et al. 2007, Belnap and Sherrod 2009, Goergen and Chambers 2012).

Bromus tectorum invasion into sagebrush steppe communities leads to increasingly difficult and costly management challenges as the stages of invasion progress (Brooks et al. 2004). Moreover, climate change portends even greater management challenges by potentially enhancing the performance and competitive abilities of *B. tectorum* relative to native species. The ability of native species to aid in suppressing *B. tectorum* spread may be a useful tool for both suppressing *B. tectorum* and increasing the functional stability of native communities if it is not counteracted by facilitation of *B. tectorum* by certain other native species. While eliminating *B. tectorum* from invaded sagebrush steppe communities is not likely feasible, suppressing *B. tectorum* populations through the use of native species is a more realistic goal for land managers. The findings of this study suggest, however, that native seedlings have minimal competitive impacts on *B. tectorum* photosynthesis, growth, and reproduction. This reinforces the importance that managers make every effort to preserve sagebrush steppe ecosystems with intact, mature native perennial communities to limit *B. tectorum* expansion.

Acknowledgements

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CHAPTER 3

EFFECTS OF EXTREME DISTURBANCE EVENTS AND FUELS MANAGEMENT ON FUEL LOADS AND *BROMUS TECTORUM* INVASION

> *It is impossible fully to protect cheat country from fire.*
>
> —Aldo Leopold, *A Sand County Almanac* (1949); p. 166

Abstract

Invasive species are often the first to colonize disturbed areas, which have lower biotic resistance to invasion due to removal of native species. The flammable non-native grass, *Bromus tectorum* L. (Poaceae, ‘cheatgrass’) forms a positive feedback with wildfire disturbances that enables it to dominate ecosystems. In Devils Postpile National Monument near Mammoth Lakes, California, an extreme windstorm in December 2011 exacerbated fuel loads that were already high after over a century of fire suppression. In response to this large-scale disturbance, land managers are treating sites to reduce hazardous fuels, raising concerns that disturbance associated with vegetation clearing activities could promote the spread of *B. tectorum,* which occurs throughout Devils Postpile in low-density, dispersed patches. Devils Postpile also experienced an uncharacteristically severe wildfire in 1992. This study monitored effects of the wildfire, windstorm, and fuel reduction activities to assess how fuel loads have been affected and whether these disturbances were contributing to *B. tectorum* spread. Fuel treatments were not creating establishment sites for *B. tectorum*. The windstorm primarily affected areas that had not been burned in the wildfire; these sites also did not contain *B. tectorum*. At

Devils Postpile, *B. tectorum* was only present in areas that had been burned in the wildfire; these areas were characterized by low canopy cover and low soil moisture, high species richness, and a low amount of fine woody fuels. Results suggest that the windstorm did substantially increase downed woody fuel loads, but that fuel reduction treatments are reducing associated fire hazards. At Devils Postpile, the areas that are most at risk for *B. tectorum* encroachment are those that burned in the Rainbow Fire, therefore, vigilant monitoring of burned areas is a prudent management strategy.

Key words: cheatgrass, Devils Postpile National Monument, eastern Sierra Nevada, wildfire, windstorm

Introduction

Disturbance is an important component of ecosystems and exerts dramatic influences on ecosystem structure, composition, and function. However, climate change is contributing to departures from natural disturbance regimes in many ecosystems by influencing the timing, frequency, duration, and intensity of disturbances (Dale et al. 2001), in some cases leading to an increase in the frequency and magnitude of extreme events (Jentsch and Beierkuhnlein 2008, Smith 2011). Extreme weather and climatic events are generally expected to increase in the future, though attributing causality of specific extreme events to climate change versus weather anomalies is not possible (Cowie 2013). Extreme events in some cases can cause abrupt and long-lasting changes in ecosystems despite their relatively short duration, and these can have stronger direct effects on ecosystems over the long term than do trends in temperature and precipitation (Jentsch and Beierkuhnlein 2008). Similarly, human-induced alterations to natural disturbance regimes through management activities can exert a powerful influence on ecosystems. One prime example of this is the fire suppression policy that dominated forest management in the United States for over a century and led to the unintended build-up of hazardous fuel densities.

Excluding fires from the landscape allowed hazardous densities of vegetation to accumulate that ironically predisposed some ecosystems to uncharacteristically severe fires that have burned extensive areas, depleted suppression resources, and claimed numerous human lives and structures (Dombeck et al. 2004, Agee and Skinner 2005, Johnson et al. 2009, Kane et al. 2010, Adams 2013, Stephens et al. 2014). Moreover, extreme weather, rising temperatures, and droughts attributed to climate change have also contributed to worsening wildfire seasons in recent decades (Westerling et al. 2006). Annual area burned by wildfire has followed a rising trajectory for the last three decades, at least in parts of western North America, a trend that scientists have attributed to both the legacy of fire suppression and a changing climate (Westerling et al. 2006, Nijhuis 2012). Federal fire suppression costs have mirrored the rising trend in area burned as increasing numbers of people living in high-risk wildland-urban interface (WUI) communities require firefighting resources (Radeloff et al. 2005, Hammer et al. 2009). Consequently, reducing hazardous fuel loads has become a high priority for land managers to mitigate wildfire threats to WUI communities, reduce potential burn size and severity, and restore fire-dependent ecosystems as directed by the National Fire Plan (2000) and the Healthy Forests Restoration Act (HFRA; 2003). As such, fuel reduction projects are now being implemented at a scale unprecedented in U.S. history (Agee and Skinner 2005).

Like fire suppression, fuel reduction may also have unintended consequences. Invasive species are known to readily establish in disturbed areas. Growing evidence has shown that disturbances associated with vegetation removal and periodic maintenance for fuel reduction may inadvertently promote undesirable changes in community composition by providing establishment sites for problematic invasive species (Keeley 2006, Merriam et al. 2006, Potts and Stephens 2009, Kane et al. 2010, Syphard et al. 2011b, a, Ross et al. 2012). Clearing vegetation to reduce fuels eliminates plant competitors, increases light levels, and exposes bare ground (Keeley 2006), increases opportunities for accidental non-native species introductions through seed dispersal via vehicles, equipment, and gear (Dombeck et al. 2004, Merriam et al. 2006), and may even create corridors for invasion into surrounding wildlands (Gelbard and Belnap 2003, Keeley 2006). This could undermine management goals and lead to yet another contradiction in fire risk management.

Some recent research has discovered that, relative to adjacent unmanaged areas, fuel breaks had a higher abundance and richness of non-native plants, as well as an increase in non-native cover over time due to periodic maintenance (Merriam et al. 2006, Kane et al. 2010). In those studies, *Bromus tectorum* L. (Poaceae, 'cheatgrass') was the most common invasive species found on fuel breaks. *B. tectorum* is an invasive annual grass that is widespread in the western United States and notorious for its fire-altering properties (Weltz et al. 2011). Three of its characteristics have made it a very successful invader. Compared to native vegetation, *B. tectorum* has both earlier phenology and superior competitive abilities, which allow it to better exploit limiting resources. However, it exerts its most dramatic impacts on ecosystems by increasing fire frequencies and engineering a disturbance regime that perpetuates its own dominance. *Bromus tectorum* becomes extremely flammable upon completing its early phenological cycle and forms a continuous fuel bed across the landscape, increasing fire season length, ignition probability, and fire spread rate, then thrives in the post-fire environment to the detriment of native vegetation (Brooks et al. 2004). Thus, *B. tectorum* infestations threaten not only the ecological integrity of invaded ecosystems, but also the many WUI communities situated among them (Schoennagel et al. 2009).

At high elevations, harsh environmental conditions and/or low propagule pressure (i.e., directional ecological filtering) can limit invasive species richness (Pauchard et al. 2009, Alexander et al. 2011). However, climatic variables that historically limited *B. tectorum* spread, such as cold temperatures, deep winter snowpack, and a short snow-free season, are changing (Chambers et al. 2007, Griffith 2010, Griffith and Loik 2010). *Bromus tectorum* populations have been expanding into higher elevations over the last ~15 years and are likely to experience further increases under a changing climate due to high fecundity and dispersal ability into newly suitable habitats (Brown and Rowe 2004, Griffith and Loik 2010, Bromberg et al. 2011).

The combined impacts of climate change, altered disturbance regimes, and invasive species are likely to affect ecosystems in ways that are not yet clearly understood (Richardson et al. 2000, Nijhuis 2012). This highlights the need to study interactions between these variables and their effects on *B. tectorum* and fire risk to better predict future *B. tectorum* abundance and areas at risk of invasion, and incorporate invasive species management into fire management activities. This chapter explores these effects on *B. tectorum* invasion at Devils Postpile National Monument and assesses feasible *B. tectorum* management approaches there.

This study monitored effects of several recent disturbance events (i.e., extreme windstorm, severe wildfire, and fuels management) in Devils Postpile National Monument in the eastern Sierra Nevada near the WUI town of Mammoth Lakes, California, with the goal of understanding how these various disturbances have affected fuel loads and *B. tectorum* invasion. Climate change and management activities have the potential to exacerbate expansion of *B. tectorum* at high elevations; the severity of *B. tectorum* impacts and difficulty of control warrant studies of factors that may promote its spread near its high-elevation range margin before the occurrence of fire regime transformations like those experienced at lower elevations.

Several different federal agencies manage National Monuments in the United States, including (but not limited to) the National Park Service (NPS), Forest Service (USFS), Fish and Wildlife Service (USFWS), and the Bureau of Land Management (BLM). The NPS is the managing agency for Devils Postpile, established in 1911 and comprising 323 ha (>300 of which are located in Ansel Adams Wilderness). Located on the western slope of the Sierra Nevada range between 2,200-2,500 m elevation, Devils Postpile's vegetation is a montane forest dominated by *Abies magnifica* A. Murray bis (Pinaceae, 'red fir') and *Pinus contorta* Douglas ex Loudon (Pinaceae, 'lodgepole pine'), but contains diverse biological communities due to its proximity to both west and east sides of the Sierra Nevada. Devils Postpile National Monument has 8 miles of trails and over 100,000 annual visitors and is surrounded by Inyo National Forest land.

Two extreme events have affected Devils Postpile over the last few decades: the 1992 Rainbow Fire and the 2011 Devils Windstorm, both of which had extensive local impacts on ecosystem structure and fuel loading. The study region is now contending with over-accumulated fuels, drought conditions, and a high risk of a severe wildfire. As such, land managers in this area urgently need information to address multiple complicated fuels management challenges.

In the past, heavy fuel loads and drought conditions contributed to an uncharacteristically severe wildfire. In 1992, after more than a century of fire exclusion and six years of drought, lightning ignited the Rainbow Fire in the Inyo

National Forest. Aided by dense conifer stands and high winds, the Rainbow Fire was a significant departure from the predominant surface fire regime of the pre-settlement era (Caprio et al. 2006), spreading to >3,500 hectares (ha), including 82% (265 ha) of Devils Postpile, burning large areas with high severity, starting several spot fires in Mammoth Lakes due to firebrands, and taking nearly a month to contain. This highlighted the region's hazardous fuel conditions and portends future challenges; 10 years post fire in burned areas, total fuel loads had reached similar levels to those in unburned areas (Caprio et al. 2006) and the eventual occurrence of another severe fire is likely.

In unburned portions of Devils Postpile, heavy fuel loads were recently exacerbated by the most extensive wind event on record for the Sierra Nevada (Hilimire et al. 2013). From November 30-December 1, 2011, a large-scale wind disturbance occurred in the region and was unusual in its long duration, atypical direction, and high intensity. Extreme wind speeds lasted for 12 h and exceeded 145 km h^{-1}, with gusts of at least 240 km h^{-1}. The winds had a particularly strong impact in the Upper Middle Fork of the San Joaquin River drainage, where channeling and acceleration led to extensive blowdown of approximately 118.5 trees km^{-1} (Hilimire et al. 2013), creating abrupt increases in fuel loads and long-lasting changes in forest structure (Figure 3-1).

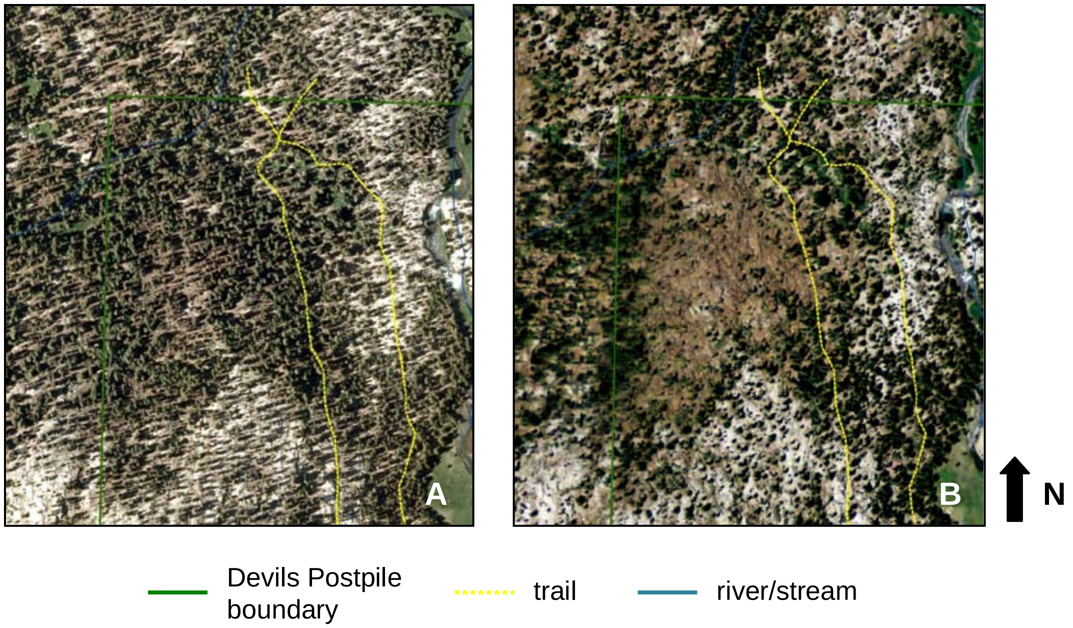

Figure 3-1. Satellite imagery of Devils Postpile National Monument before (A; in 2010) and after (B; in 2012) the 2011 Devils Windstorm. (A) Before the windstorm, the northwest corner of Devils Postpile contains dense tree cover. (B) After the windstorm, tree cover has been reduced. Images courtesy of Deanna Dulen, National Park Service.

Fuels management projects are underway in both Devils Postpile and surrounding Inyo National Forest lands through an ongoing vegetation management program and in response to the wind event. Another large fire in this region might threaten the Mammoth Lakes community and as many as 2,000 visitors to the Devils Postpile area on peak-use days. An added hazard is the lack of escape routes, in that vehicle access is limited to one single-lane road with steep slopes. The Inyo National Forest Mammoth Ranger District is actively treating fuels on ~90 ha with severe tree damage under authority of the HFRA. Approximately 50 ha of this area lies within the WUI defense zone (¼-mile buffer around developed sites) and the remaining

~40 ha is within the WUI threat zone (1¼-mile buffer beyond the defense zone). Concerns remain that high levels of soil disturbance and heavy equipment traffic from clearing activities may inadvertently promote expansion of nearby invasive plant colonies. Isolated *B. tectorum* populations infest roadsides, stock trails, facilities, and recreation areas and are potentially poised to colonize nearby disturbed areas.

This study evaluated the effectiveness of current fuels management practices at mitigating fire risk and helped predict future abundance of *B. tectorum* and areas at risk for invasion. Study objectives were to (1) characterize differences in fuel loads between areas subjected to different disturbances and management practices, and (2) identify associations between abiotic variables (e.g., bare ground exposure, soil moisture, canopy cover) and *B. tectorum* infestations.

I selected study sites within four different treatments: unburned, treated unburned, burned, and treated burned. Unburned areas typically contained high levels of wind-fallen trees from the Devils Windstorm, while burned areas experienced less severe impacts from the windstorm, especially in areas of high burn severity where few trees remained after the Rainbow Fire. Fuel reduction projects occurred in both unburned and burned areas; fuel treatments consisted of piling and burning slash onsite.

I hypothesized that: (H_1) overall fuel loads would follow the pattern: unburned > treated unburned > burned > treated burned due to greater numbers of wind-thrown trees in unburned plots than burned plots; (H_2) species composition would differ among different treatments due to differences in abiotic factors, (H_3) *B. tectorum* would be positively associated with lower canopy cover and the amount of bare ground exposed and negatively associated with physical and ecological barriers provided by dense vegetation, litter layers, and canopy shading.

Methods

This study sampled a total of 32 plots (n = 8 for each treatment; 50 × 20 m each) from June to July 2014. Twenty-three of the study sites were selected by randomly generating Universal Transverse Mercator (UTM) coordinates. Ten plots used in a prior study and ongoing monitoring efforts (Caprio et al. 2006) were re-sampled by the authors for fuel loading in 2012; those sites were also used in this study and the 2012 fuel data were used in the analyses here. I visited those nine sites in summer 2014 to supplement fuel load data with data on species composition, soil moisture, and canopy cover. *Bromus tectorum* was not present in the 32 random plots, so four non-random plots containing *B. tectorum* (hereafter '*B. tectorum* hotspots') of 25 documented infestation sites at Devils Postpile were subsequently added to the study to facilitate comparisons with the other treatments, all of which were located in high-severity burned areas. Documented *B. tectorum* infestations range in size from just a few individual plants to a patch area of ~300 m^2. Devils Postpile staff treat *B. tectorum* infestations by hand pulling plants; in this study, I only surveyed areas where *B. tectorum* infestations had not yet been treated. Study sites ranged in elevation from 2,223 to 2,243 m (see Table 3-1 for a complete plot list).

Table 3-1. Plot elevations and locations. UTM coordinates are for Zone 11 and Datum NAD83. Asterisks denote plots used in prior monitoring studies by Caprio et al.

Treatment	Replicate	Elevation (m)	UTM E	UTM N
unburned	1*	2,334	315703	4167001
	2*	2,420	315307	4166919
	3	2,306	315855	4166737
	4	2,325	315793	4166955
	5	2,315	315866	4166367
	6	2,393	315545	4166911
	7	2,353	315793	4166282
	8	2,335	315685	4167057
treated unburned	1*	2,316	316205	4166879
	2	2,361	316182	4166508
	3	2,315	316190	4166807
	4	2,317	316180	4166920
	5	2,323	316085	4167016
	6	2,313	316029	4166444
	7	2,329	316208	4167019
	8*	2,343	316253	4166734

Table 3-1. Plot elevations and locations. UTM coordinates are for Zone 11 and Datum NAD83. Asterisks denote plots used in prior monitoring studies by Caprio et al.

Treatment	Replicate	Elevation (m)	UTM E	UTM N
burned	1*	2,356	315753	4165978
	2*	2,422	315565	4165633
	3*	2,316	316137	4165845
	4*	2,418	315545	4165714
	5*	2,223	315857	4163278
	6*	2,264	316122	4164313
	7	2,420	315561	4165332
	8	2,387	315375	4164796
treated burned	1	2,348	316062	4166340
	2	2,373	316149	4166321
	3	2,374	316138	4166273
	4	2,349	316078	4166355
	5	2,374	316159	4166345
	6	2,380	316179	4166380
	7	2,362	316098	4166289
	8	2,385	316190	4166202
B. tectorum hotspot	1	2,355	315503	4164368
	2	2,328	315601	4164243
	3	2,295	316586	4163975
	4	2,261	316083	4163287

At each site, a 50-m main transect was established along a randomly selected azimuth through the center of each plot. At 10 m intervals along the entire length of the transect (i.e., 0, 10, 20, 30, 40, and 50 m), I recorded species composition, soil moisture, and canopy cover. To measure species composition, I recorded all species present in a 0.5 × 0.5-m quadrat divided into 25 equal sections and visually estimated the percent cover of each. Species were categorized into functional groups (e.g., grass, forb, shrub) and identified to the species level when possible. Soil moisture was recorded to 12 cm depth using a soil moisture meter (FieldScout TDR 100, Spectrum Technologies, Aurora, IL). Overstory canopy cover was measured by averaging four readings (N, S, E, and W) taken with a concave spherical densiometer (Model-C, Robert E. Lemmon Forest Densiometers, Bartlesville, OK). Consistent with sampling protocol in a prior study by Caprio et al. (2006), I conducted four 25-ft fuel transects at 10, 20, 30, and 40 m along the main transect at random azimuths using Brown's planar intercept method (Brown 1974).

Statistical Analyses

The ecological monitoring tool, FEAT/FIREMON Integrated (FFI), was used to process fuel load data and data on canopy, soil moisture, species richness, and fuels were analyzed using analyses of variance and post-hoc Tukey's honestly significant difference (HSD) tests in JMP Pro (v. 11.0.0; SAS Institute, Cary, NC). Soil moisture data were translated (+1) then log transformed because the raw data contained many zero values and, hence, did not have a normal distribution. For species composition, I used multivariate discriminant analysis to examine within- and between-type variability and differentiate among treatments using functional groups (bare ground, conifer, forb, grass, litter/duff, rock, shrub, wood) as predictor variables.

Results

Canopy

Canopy cover (Figure 3-2) was higher in unburned plots (mean ± 1 SE: unburned = 43.1 ± 8.58%, treated unburned = 51.7 ± 3.35%), generally lower in burned plots (mean ± 1 SE: burned = 14 ± 5.95%, treated burned = 34.9 ± 6.57%), and <1% (± 0.293%) in *B. tectorum* hotspots ($F_{4,31} = 9.0865$, $P < 0.0001$).

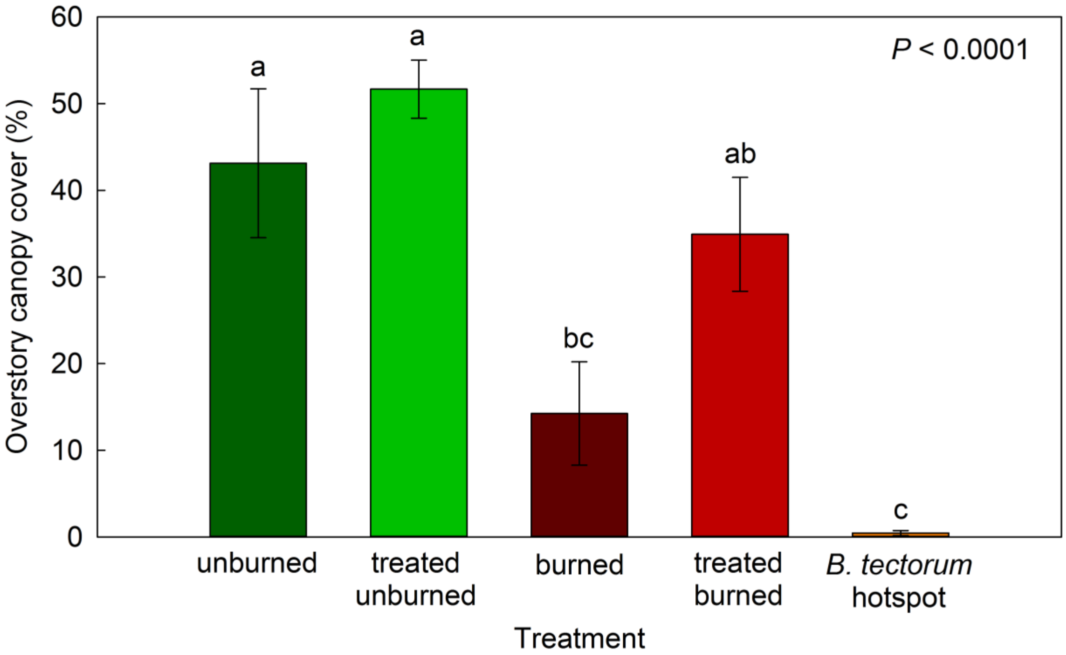

Figure 3-2. Mean canopy cover (%) in study plots. Error bars are ± 1 SE.

Soil Moisture

Soil volumetric water content to 12 cm depth was low overall (Figure 3-3) and was higher in unburned plots (mean ± 1 SE: unburned = 1.91 ± 0.773%, treated unburned = 0.832 ± 0.323%) and lower in burned plots (mean ± 1 SE: burned = 0.159 ± 0.0811%, treated burned = 0.075 ± 0.050%). In *B. tectorum* hotspots, all soil moisture readings were 0% ($F_{4,31}$ = 6.4362, P = 0.0007).

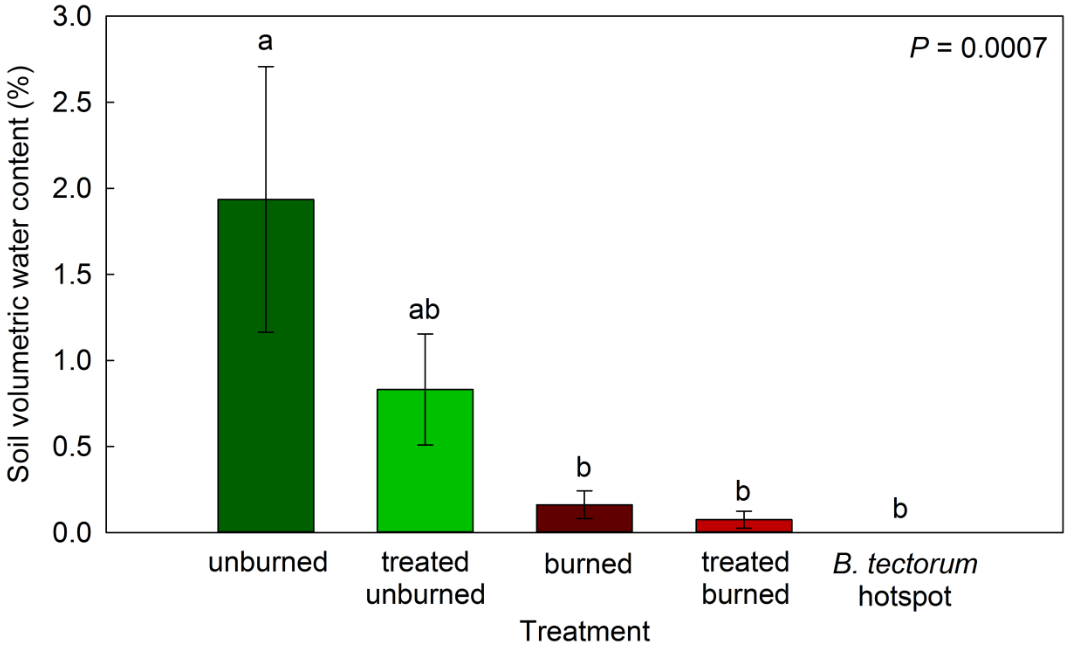

Figure 3-3. Mean soil volumetric water content (%) to 12 cm depth in study plots. Error bars are ± 1 SE.

Species Composition

The discriminant function accounted for 63.9% of between-group variability. The percentage of cases correctly classified for specific groups were as follows: treated unburned and burned = 75%, unburned = 62.5%, treated burned and

B. tectorum hotspots = 50%. *Bromus tectorum* hotspots were a smaller group, which may explain its poorer classification rate. The relative positions of the 95% confidence ellipses (Figure 3-4) provides a visual representation of between-group variability, with large differences between groups being indicated by greater separation of confidence ellipses. Treated burned and unburned groups had the greatest overlap, evidence that the distinction between them was the most arbitrary. Unburned and treated unburned groups also had considerable overlap. Overlap between the remaining groups was minimal or nonexistent. The position of the confidence ellipses also reveals a continuum of burn severity: unburned, treated unburned, and treated burned (all low severity); burned (mixture of burn severity); and *B. tectorum* hotspots (all high severity).

The tightness of the clusters of points for each group indicates within-group variability. The unburned group formed the tightest cluster, while *B. tectorum* hotspots formed the loosest cluster (which may be in part due to a lower sample size). Treated burned, treated unburned, and burned clusters were of intermediate tightness, with treated burned being the tightest of the three.

Relative to the other sites, *B. tectorum* hotspots were characterized by higher percent cover of shrubs, rocks, and bare ground, and a lower percent cover of litter/duff, wood, and conifers. Stepwise discriminant function analysis showed that the three most correlated predictors of the treatment groups, in order of correlation strength, were shrub, litter/duff, and rock cover.

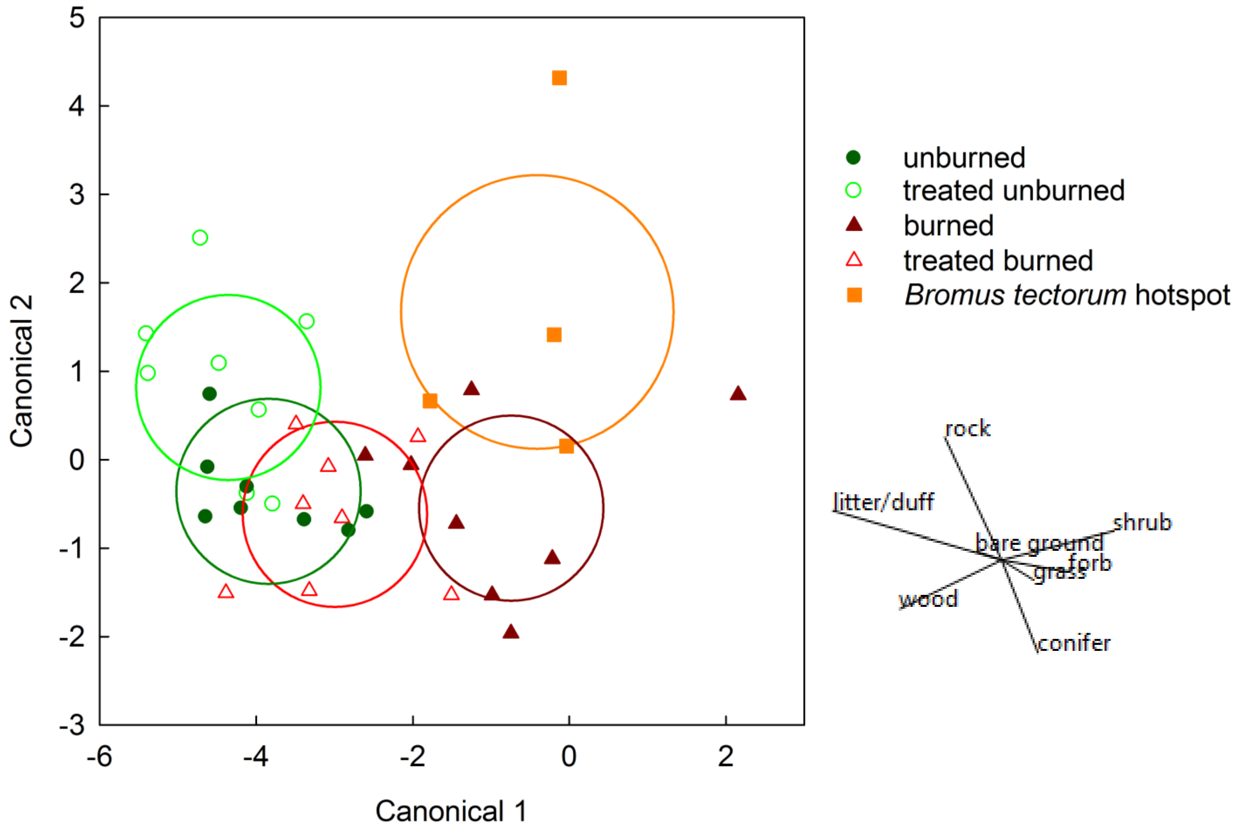

Figure 3-4. Functional group assemblages in study plots plotted in relation to the first two discriminant axes with 95% confidence ellipses. Each point represents one 50 × 20-m plot. Biplot rays are showing the coordinate directions in canonical space.

Species Richness

Species richness (Figure 3-5) was roughly twice as high on burned (mean ± 1 SE = 7.75 ± 0.701 species) than unburned (mean ± 1 SE = 4.25 ± 0.901 species) plots, with *B. tectorum* hotspots (mean ± 1 SE = 8 ± 0.707 species) having the highest mean species richness and treated unburned (mean ± 1 SE = 3.13 ± 0.639 species) plots having the lowest ($F_{4,31}$ = 7.4251, P = 0.0003).

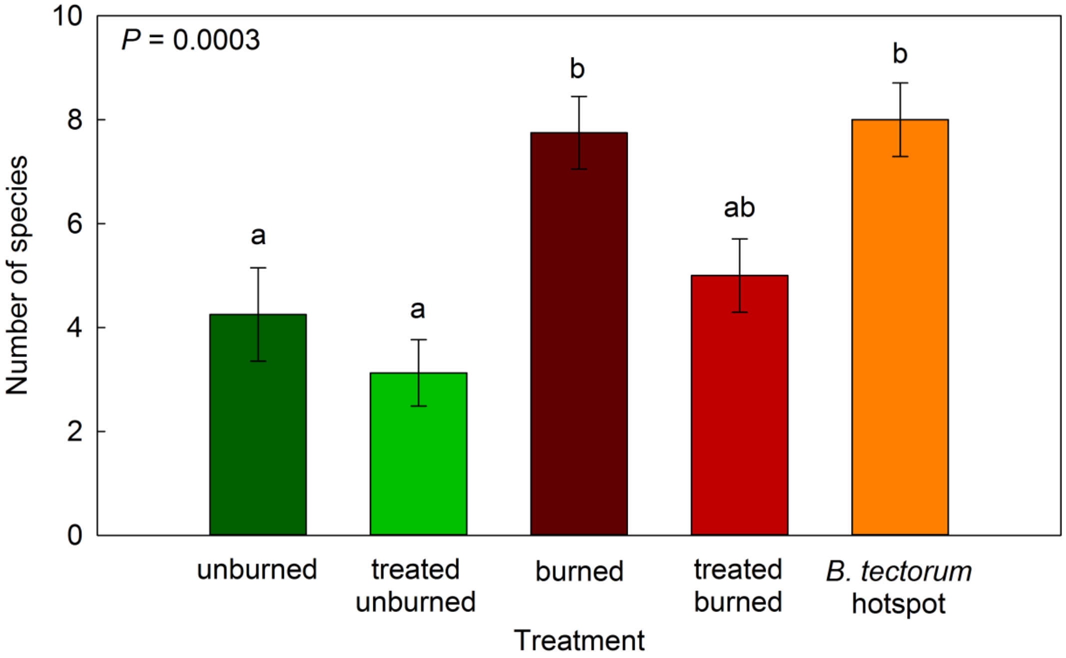

Figure 3-5. Mean species richness in study plots. Error bars are ± 1 SE.

Fuel Loading

Total fuel loads (Figure 3-6) were reduced in plots that were treated for fuel reduction relative to their untreated counterparts, and fuel loads in *B. tectorum* hotspots were similar to those in the treated plots ($F_{4,31}$ = 27403, P = 0.0463). Mean (± 1 SE) total fuel load was 29.3 ± 7.00 kg m^2 in unburned plots, 10.5 ± 2.67 kg m^2 in treated unburned plots, 20.4 ± 4.71 kg m^2 in burned plots, 13.1 ± 2.81 kg m^2 in treated burned plots, and 12.7 ± 5.03 kg m^2 in *B. tectorum* hotspots (which were also only located in burned areas).

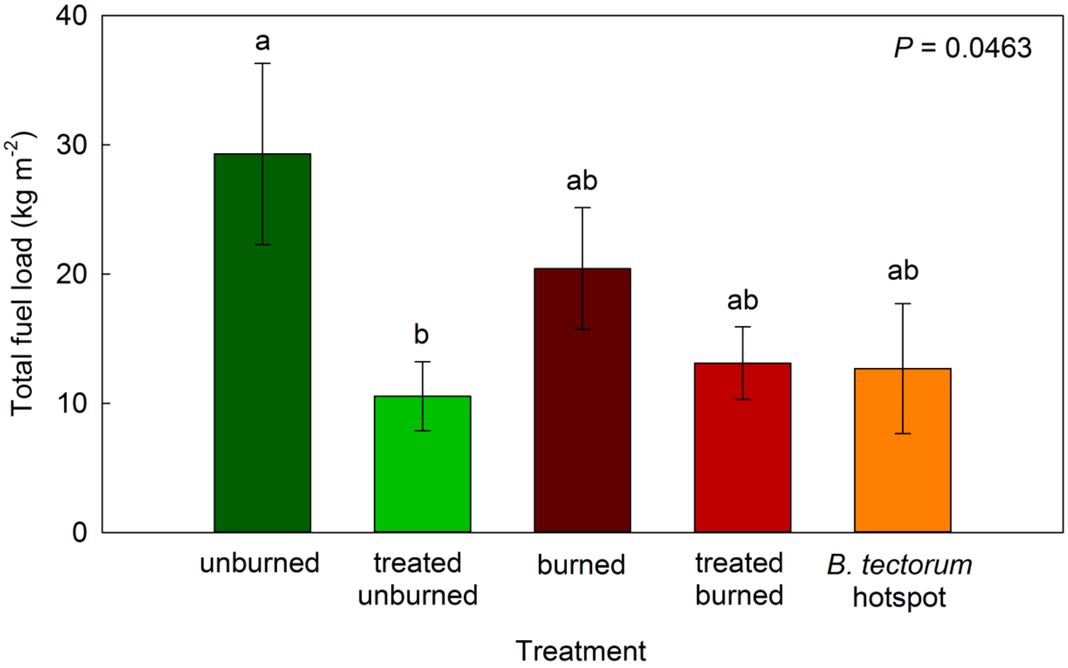

Figure 3-6. Total downed woody fuel load (kg m^{-2}) in study plots. Error bars are ± 1 SE.

However, fine woody fuels (i.e., 1-100-hr fuels, which take from 1-100 hours for fuel moisture to respond to changes in environmental conditions and include any woody debris under 3 inches in diameter; Figure 3-7), were much lower in *B. tectorum* hotspots than other plots ($F_{4,31} = 3.4994$, $P = 0.0181$).

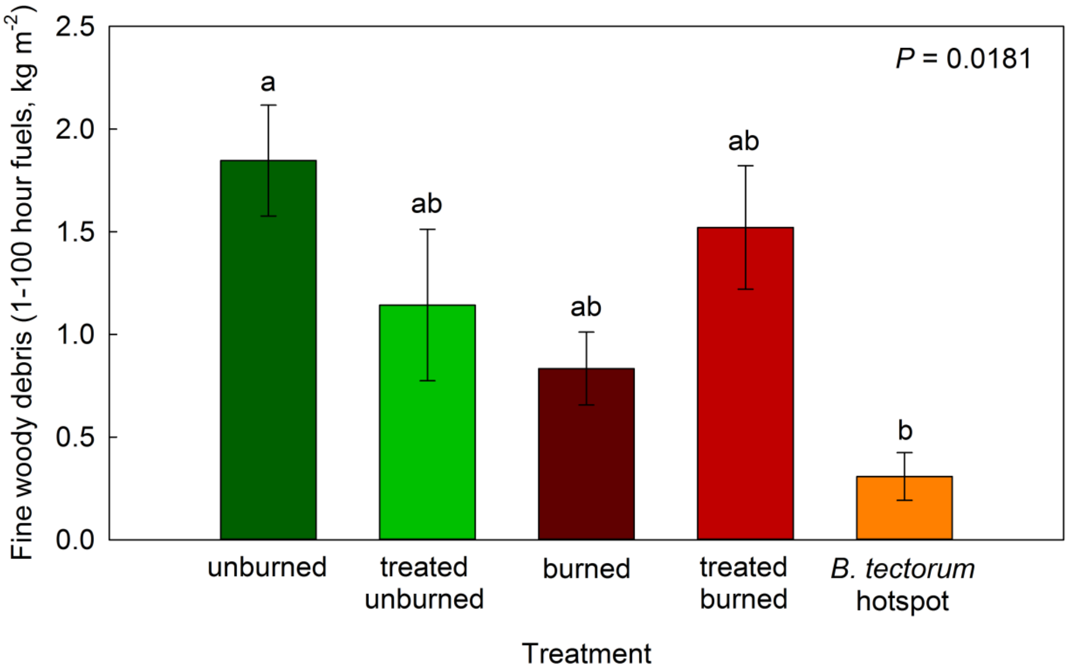

Figure 3-7. Mean fine woody fuel (<3 in diameter) loading (kg m^{-2}) in study plots. Error bars are ± 1 SE.

Discussion

Consistent with H_1, unburned plots had the highest fuel loading, and fuel loads in treated plots were generally reduced relative to those in untreated plots (though this trend was not significant for untreated and treated burned plots). An earlier monitoring study (Caprio et al. 2006) reported total fuel loads of ~15 kg m^{-2} in both unburned and burned plots at Devils Postpile in 2002 (10 years after the Rainbow Fire). A 2012 resurvey (20 years post-fire, but <1 year after the Devils Windstorm) found total fuel loads in unburned and burned plots to be ~42 kg m^{-2} and ~19 kg m^{-2}, respectively (Caprio et al., unpublished data), suggesting that the windstorm disproportionately increased fuel loading in unburned plots relative to burned plots—

an intuitive result given that unburned areas would have contained many more standing live trees than burned areas at the time of the windstorm.

In this study, I found that mean total fuel load in unburned plots was ~29 kg m^{-2} (lower than the most recent survey) and in burned plots was ~20 kg m^{-2} (comparable to the most recent survey). A decrease in fuel load for unburned plots in this study compared with the most recent survey may be the result of sampling inconsistencies. The mean total fuel load in treated unburned plots was ~ 2/3× lower than that in untreated unburned plots, and the mean total fuel load in treated burned plots was ~1/4× lower than that in untreated burned plots; therefore, I conclude that fuels management at Devils Postpile is reducing fuel loading and, thus, fire hazards. A greater proportion of fuel reduction in treated unburned relative to treated burned plots likely reflects the greater fuel load in unburned relative to burned plots. Consistent with H_2, species functional group assemblages differed among the different treatments, which represented a continuum of burn severity. Fuel reduction activities at Devils Postpile are not creating establishment sites for *B. tectorum*, as none of the treated plots surveyed in this study contained *B. tectorum*. I speculate that this may be because treated areas at Devils Postpile possess habitat characteristics that are unsuitable for *B. tectorum* (e.g., higher levels of canopy shading, greater litter/duff cover, and low-severity burn impacts).

Bromus tectorum invasion at Devils Postpile is not widespread, indicating that invasion is either in its early stages or that ecosystems there are resistant to invasion.

However, *B. tectorum* infestations may have expanded over the last decade at Devils Postpile. Devils Postpile officially began documenting *B. tectorum* invasion in 2001 and, in 2010, staff found *B. tectorum* infestations at several new locations (Travaglini 2011). Known *B. tectorum* infestations at Devils Postpile occur near horse corrals and other stock use areas, hiking trails, and other recreation areas (e.g., at the foot of the popular rock climbing area, Bear Crag), but also far from trails in wilderness areas, where potential dispersal vectors (e.g., humans, horses and other pack stock, domestic dogs), are limited, atop rocky ridges and bluffs. In this study, two of the *B. tectorum* hotspots surveyed were along pack trails towards the popular Rainbow Falls visitor area and two were atop rocky ridges and bluffs in an area of Devils Postpile known as the Buttresses.

Of the 25 documented *B. tectorum* infestations in and around Devils Postpile, all are located in areas that had been burned in the Rainbow Fire. In this study, *B. tectorum* hotspots were located only in high-severity burned areas (i.e., areas that had experienced >90% vegetation mortality in the Rainbow Fire). Relative to the other experimental sites (unburned, treated unburned, burned, treated burned), *B. tectorum* hotspots were characterized by extremely low canopy cover and soil moisture, high species richness, and low fine woody fuel loads. Low soil moisture in burned plots was likely due to high radiation load and evaporative losses associated with lower canopy cover. *Bromus tectorum*, which rapidly removes water from shallow soil layers early in the spring (Melgoza et al. 1990), may have also depleted soil moisture in plots during its active growth period.

In other contexts, *Bromus tectorum* has been associated with lower species richness attributed to its impacts on coexisting vegetation communities; it rapidly depletes limited resources (e.g., soil water) relative to native species (Melgoza et al. 1990) and ultimately forms *B. tectorum* monocultures after altering fire cycles (Brooks et al. 2004, Concilio and Loik 2013). Hence, it was surprising to find that *B. tectorum* hotspots actually contained the highest number of species of the treatments. Successional trends following disturbances may explain this finding. After a disturbance event—in this case, fire—soil resources generally increase in the short term due a decline in uptake associated with lower biomass (Romanya et al. 2001, Wan et al. 2001, Knops et al. 2002), which could promote higher species richness. At Devils Postpile, *B. tectorum* infestations have not reached densities sufficient to elicit the increase in fire frequency that has promoted *B. tectorum* dominance elsewhere.

The low amount of fine woody fuels in *B. tectorum* hotspots may represent residual effects of the Rainbow Fire; since hotspots were only in high-severity burned areas, fine woody fuels were likely consumed in the burn. Vegetation functional groups (e.g., shrubs) and abiotic site characteristics (e.g., low canopy and, hence, high light levels) that were associated with *B. tectorum* are factors that are typical of burned and open habitats in which *B. tectorum* is known to thrive. Where *B. tectorum* was present, percent cover of shrubs, rocks, and bare ground was high, and percent cover of litter/duff, wood, and conifers was low, consistent with H_3. These results suggest that land managers may want to prioritize areas for *B. tectorum* monitoring and control efforts by focusing on 1) high-severity burned areas where canopy has been eliminated, 2) rocky outcrops with a high level of exposed bare ground, where competition with native species may be reduced, and 3) in areas that receive high levels of anthropogenic disturbance (i.e., more potential dispersal vectors), such as along hiking trails, near stock use areas, and at popular recreation spots.

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CONCLUSION

> *I experienced a minor irritation myself when I arrived at a 'port of entry' on the northern California border, where my car and baggage were searched by a quarantine officer. He explained politely that California welcomes tourists, but that she must make sure their baggage harbors no plant or animal pests. I asked him what pests. He recited a long list of prospective garden and orchard afflictions, but he did not mention the yellow blanket of cheat, which already extended from his feet to the far hills in every direction.*
>
> —Aldo Leopold, *A Sand County Almanac* (1949); p. 167

In this dissertation, I assessed effects of future climate change scenarios, species interactions, ecological disturbances, and land management activities on the highly problematic invasive annual grass *Bromus tectorum* L. (Poaceae, 'cheatgrass') near its high-elevation range boundary in the western Great Basin/eastern Sierra Nevada. *Bromus tectorum* is extremely flammable and has increased fire frequencies and sizes across the Great Basin. Colloquially, *B. tectorum* has been compared to "growing gasoline" (NAPS 2015) and described as "nature's kindling" (BLM and UNCE 2015). The eastern Sierra Nevada is currently experiencing invasion of *B. tectorum* into dispersed patches of disturbed areas and in low densities coexisting with native vegetation. Despite that this region has not yet experienced the process-level impacts on fire cycles that have made *B. tectorum* a notorious weed species across the Great Basin, low-density invasions are not innocuous; just a few plants can produce hundreds of viable seeds (Concilio 2013). It may just be a matter of time and conditions before *B. tectorum* alters the fire cycle in this region. In the eastern Sierra Nevada, a limited window of opportunity exists to contain infestations before impacts become severe. Here, I outline the main findings from the chapters of this dissertation and discuss applications of my results to land management under a changing climate.

Chapter 1 explored potential consequences of precipitation change on *B. tectorum* and native species. *Bromus tectorum* was more responsive than native species to a simulated large spring rain event, nearly doubling its photosynthetic rates in response to experimental watering. This suggests that *B. tectorum* is better at exploiting ephemeral increases in soil water availability from spring precipitation than native species. I also observed a dramatic decline in *B. tectorum* density following multiple drought years in which winter snowpack was notably low. This finding is consistent with *B. tectorum* "boom" and "bust" cycles described by other studies (e.g., Griffith and Loik 2010, Balch et al. 2013) in response to inter-annual variation in precipitation patterns. Therefore, natural climate variability between years may provide both management challenges and opportunities. Targeting *B. tectorum* populations for eradication or reduction in years when *B. tectorum* density is naturally reduced by low antecedent precipitation may facilitate control of *B. tectorum* infestations. In years with high antecedent precipitation, land managers may anticipate large *B. tectorum* populations and higher fire risk during the following growing season and take precautions to limit seed dispersal, e.g., by altering the timing of grazing, or reduce the risk of fire, e.g., by restricting burning.

Chapter 2 studied potential effects of competition and facilitation under high and low temperature regimes through a greenhouse experiment. *Bromus tectorum* allocated more aboveground biomass to vegetative structures under high temperatures and to reproductive structures under low temperatures, a pattern that warrants further study due to difficulties in simulating realistic conditions in a greenhouse setting. Seedlings of the native bunchgrass *Elymus elymoides* (Raf.) Swezey (Poaceae, 'squirreltail'), reported to be one of the best native competitors with *B. tectorum*, did little to reduce *B. tectorum* photosynthetic performance, growth, or reproduction. While seedlings typically are not effective competitors with *B. tectorum*, mature perennials are known to have stronger competitive impacts on *B. tectorum* (Booth et al. 2003, Humphrey and Schupp 2004, McGlone et al. 2012). Conversely, *B. tectorum* seedlings were strong competitors with seedlings of native species, exhibiting more rapid growth and reproductive effort. The native N_2-fixing legume, and *Lupinus argenteus* Pursh (Fabaceae, 'silvery lupine'), tended to have positive effects on *B. tectorum* photosynthesis, growth, and reproduction, suggesting a facilitative effect. In fact, some native species, like *L. argenteus* and the shrubs *Artemisia tridentata* Nutt. (Asteraceae, 'big sagebrush') and *Purshia tridentata* (Pursh) DC. (Rosaceae, 'antelope bitterbrush') may facilitate *B. tectorum* invasion, helping it to persist under conditions that would otherwise be too stressful (Griffith 2010). Despite the potential for facilitation of *B. tectorum* by some native species, *B. tectorum* is less likely to invade areas with established, competitive native perennials (Bradley 2009). Land managers should focus on maintaining mature native species in areas where their populations remain intact to confer resistance to *B. tectorum* invasion. If re-seeding with native species is part of a plan to restore an area previously infested with *B. tectorum*, monitoring and removal of *B. tectorum* seedlings would help native species avoid negative effects of competition with *B. tectorum* and enhance their establishment success.

Chapter 3 monitored effects of natural and anthropogenic disturbances on fuel loads and *B. tectorum* invasion at Devils Postpile National Monument. The Devils Windstorm increased downed woody fuel loads in late 2011. The management response to this extreme event to clear hazardous densities of vegetation and wind-fallen trees has not promoted further expansion of *B. tectorum* populations in Devils Postpile National Monument, nor has the windstorm itself. This may be due to the ecosystem characteristics in areas most strongly affected by the windstorm, including dominance of conifer species, high levels of canopy shading, deep litter and duff layers, and minimal exposed bare ground, which are not favorable conditions for the establishment of *B. tectorum*. In some areas burned by the 1992 Rainbow Fire, *B. tectorum* invasion is occurring. These areas experienced substantial vegetation mortality in the fire and in subsequent years have been colonized and dominated by shrubs, with little conifer regeneration (Caprio et al. 2006). They are also characterized by low canopy cover, low soil moisture, low litter and duff cover, low fine woody fuel loads, and high levels of exposed bare ground. While *B. tectorum* populations are currently dispersed and patchy, the risk of rapid expansion into adjacent native communities in years with favorable conditions is high due to

B. tectorum's extremely high fecundity and dispersal ability. This suggests that vigilant monitoring of burned areas in Devils Postpile is important to detect invasions in their early stages, and documented populations causing incipient invasions should be eradicated.

***Bromus tectorum* Management in the Eastern Sierra Nevada**

Bromus tectorum management in the United States has been widely studied, yet *B. tectorum* continues to be a highly problematic invasive species in the Intermountain West. Because of its vast extent and severe fire impacts, *B. tectorum* management is a daunting task—in fact, in many areas, land managers deem it futile (Davidson and Belnap 1997). Control of *B. tectorum* is not mandated in many states, including California; *B. tectorum* is not a federally listed noxious weed and is only a state-listed noxious weed in Colorado and Connecticut—absent from noxious weed lists in states that have experienced its most extensive impacts. This is often a barrier to active management of *B. tectorum*, as managers must prioritize listed noxious weed species and have limited budgets and resources to control plant invasions (Tzankova and Concilio 2015). At each successive phase of *B. tectorum* invasion, the cost of management interventions exponentially rises while the probability of their success exponentially declines (Brooks et al. 2004). Meanwhile, land managers often ignore invasive species management until later stages of invasion (Mack et al. 2000), at which point the scale of the invasion can overwhelm management interventions. Moreover, managers are often unable to consult scientific literature to inform management strategies due to limited accessibility of peer-reviewed articles and mismatches in the spatial and temporal scales of research vs. management (Matzek et al. 2014).

The most cost-effective and successful way to prevent long-term costs and loss of ecosystem services resulting from the spread of invasive species is to use a strategy of early detection and rapid response (EDRR; Brooks et al. 2004). Options for managing *B. tectorum* include passive techniques, which indirectly target the invader by seeking to rectify bad land management practices that may be facilitating invasion (e.g., reducing grazing pressure, re-vegetating native species, and avoiding burning), and active approaches, which directly target the invader for removal (e.g., manual removal, herbicide applications, and timed grazing; Tzankova and Concilio 2015). While both passive and active management strategies can make valuable contributions toward controlling *B. tectorum*, active approaches are more effective because of their direct impacts on *B. tectorum* populations (Tzankova and Concilio 2015).

While eradication of widely established invasive plants like *B. tectorum* (Figure c-1) is unlikely given currently available control options, containing outlier infestations at the invasion front—which characterizes the current nature of *B. tectorum* invasion in the eastern Sierra Nevada—is a good strategy for preventing further spread into pristine areas and avoiding associated ecological and economic impacts (Moody and Mack 1988, Mack et al. 2000, Brooks et al. 2004, Tzankova and

Concilio 2015). For these smaller, localized infestations, low-technology, non-chemical, active control methods are effective at reducing *B. tectorum* density and dominance in the seed bank (Concilio 2013). However, the majority of land managers in the eastern Sierra Nevada region are not actively managing *B. tectorum* infestations due to multiple institutional and policy barriers; rather, they tend to use passive management approaches (Tzankova and Concilio 2015).

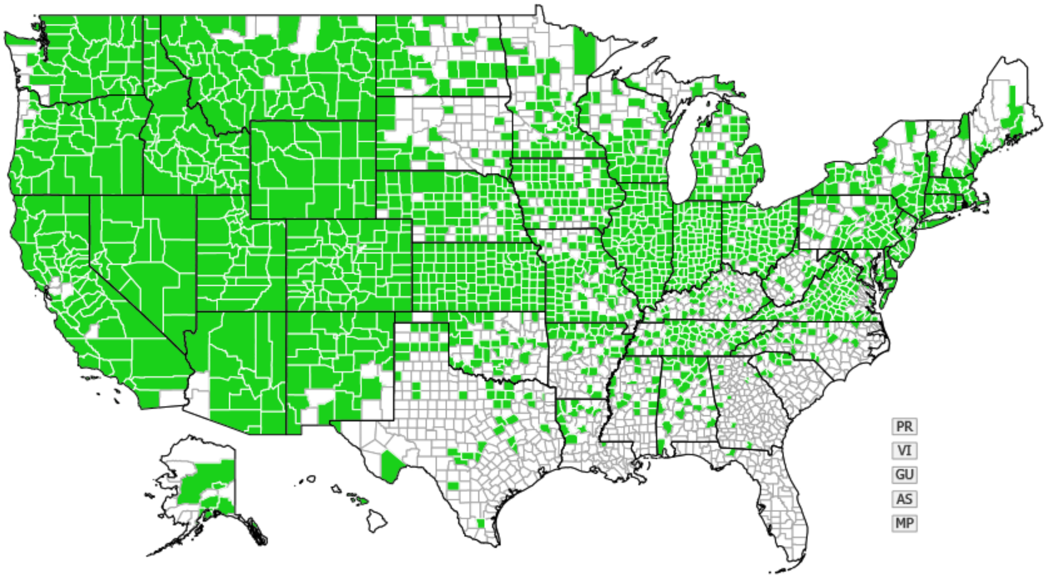

Image from University of Georgia Center for Invasive Species and Ecosystem Health Early Detection and Distribution Mapping System (EDDMapS) 2014

Figure c-1. *Bromus tectorum* distribution by county in the United States.

Conversely, Devils Postpile (NPS) is engaged in active *B. tectorum* management. The monument's 5-year (2012-2016) Invasive Plant Management Plan (IPMP), which designates *B. tectorum* as the highest priority invasive plant in Devils Postpile, details procedures for directly targeting invasive plant populations throughout Devils Postpile as well as on surrounding Inyo National Forest land. Staff and volunteers at Devils Postpile began documenting and controlling invasive plants in 2001, employing the proactive EDRR strategy, as most invasive plant populations at Devils Postpile are relatively small and diffusely dispersed. Staff and volunteers at Devils Postpile survey and map populations of invasive species (including, but not limited to, *B. tectorum*) throughout Devils Postpile and use manual control techniques to eradicate or contain the highest priority species. The IPMP also includes directives for interagency cooperation, community education, and managing potential seed dispersal vectors into Devils Postpile.

Manual control is the only active management option available to Devils Postpile because most of the monument is federally designated wilderness and the use of chemicals or mechanical equipment would trigger additional review to comply with the National Environmental Policy Act (NEPA) regulations. General weed removal activities are categorically excluded under NEPA. Regulatory compliance aside, manual removal (more specifically, hand-pulling) is suitable for many of Devils Postpile’s relatively small, patchy, and remote *B. tectorum* infestations. Pulled plants are bagged and either burned in a campfire near the ranger housing area or sent to the Mono County landfill. For some of the larger patches of *B. tectorum* (~300 m^2), cutting plants may be more feasible than hand pulling, however, cut plants can produce new spikelets so treatments would need to be repeated.

While hand-pulling is not practical over a large area, the majority of infestations at Devils Postpile are conducive to this approach. *Bromus tectorum* at Devils Postpile coexists with a rich array of native species. This makes hand-pulling an excellent candidate tool for management of satellite and outlier populations within Devils Postpile because re-seeding efforts, which are necessary in conjunction with control methods that have non-target impacts, are difficult and often unsuccessful (Concilio 2013). Hand-pulling has a positive effect on native herbaceous species, while achieving further reductions in *B. tectorum* density with each year of treatment (Concilio 2013). Treatments need to be repeated annually until *B. tectorum* has been eliminated from the seed bank (approximately three years), as just a few plants can produce hundreds of viable seeds (Concilio 2013). The first targeted manual removal treatments for *B. tectorum* at Devils Postpile began in 2002. From 2002-2011, records indicate three years (2004, 2006, 2007) in which *B. tectorum* may not have been treated. Records do not indicate consistent annual treatments at the same sites. Ensuring that treatments are repeated annually, monitored in following years, and properly documented would strengthen *B. tectorum* management efforts.

Timing is an important consideration in hand-pulling control methods; treatments are most effective when implemented at a specific phenophase—just before seed set. Pulling plants too late undermines the efficacy of the method, as copious numbers of ripe seeds readily drop from plants and enter the seed bank. Devils Postpile faces a temporal management challenge in that the field season for controlling invasive plants is extremely short (approximately two months). The

ISMP schedules *B. tectorum* hand-pulling in June and July but, at Devils Postpile, flowering occurs in the spring and seed set occurs by mid-July. A one-month shift in the window for hand-pulling efforts (May and June), would likely overcome this barrier. However, Devils Postpile has considerable inter-annual variation in snowpack and is only accessible by one road that is typically closed until June, which complicates a rigid hand-pulling schedule. If possible, employing a flexible schedule for hand-pulling, in which efforts are concentrated as soon as areas are accessible (after snowmelt, but not immediately as hand-pulling first requires plants to germinate) would maximize treatment effectiveness. Hand-pulling after seed set should still contribute to reductions in the *B. tectorum* population, but would require Devils Postpile field crews to continue with hand-pulling efforts over a longer time period.

In addition to active management by directly targeting *B. tectorum* infestations with manual removal, Devils Postpile has adopted several passive management practices focused on preventive measures and other practices that indirectly address problems of invasions. These include public education, limiting the presence of seed dispersal vectors, and supporting applied research projects. As many of the *B. tectorum* infestations at Devils Postpile occur in areas that are frequented by recreational visitors, the Devils Postpile Superintendent released a public news bulletin to increase awareness among rock climbers that they could unintentionally disperse seeds on their shoes and climbing gear and suggest precautions. Devils Postpile also limits vehicle traffic into the monument, requiring most visitors to take shuttle buses, which dramatically reduces the number of vehicles entering the monument that could potentially serve as vectors for dispersing invasive seeds. Devils Postpile also requires construction materials and feed for pack stock to be certified weed free. Finally, Devils Postpile is helping to close the "knowing-doing gap" highlighted in other studies (e.g., Esler et al. 2010, Matzek et al. 2014), which have found that much scientific research fails to inform management, by collaborating on research projects in Devils Postpile that generate results that are directly applicable to management, like this study. Devils Postpile National Monument is surrounded by USFS land; as such, Devils Postpile engages in interagency cooperation with the USFS to also treat *B. tectorum* infestations on surrounding Inyo National Forest lands.

In summary, Devils Postpile has adopted many effective practices in managing *B. tectorum* infestations, and is one of the few land management jurisdictions in the eastern Sierra Nevada engaged in active, rather than passive, management. Through interagency cooperation between the NPS and USFS, public education efforts, policies to limit unintended vectors for seed dispersal, and collaborations with researchers, Devils Postpile has developed a suite of activities and practices that will help limit further spread of *B. tectorum*. When updating the IPMP in summer 2016, two considerations could help make *B. tectorum* management efforts even stronger: (1) ensuring that treatments are repeated annually until *B. tectorum* has been eliminated from the seed bank, and (2) completing all hand pulling treatments before seeds have ripened.

Concluding Remarks

Aldo Leopold documented the take-over of *B. tectorum* and the difficulty of its control in his 1949 environmental classic, *A Sand County Almanac*:

> I listened carefully for clues whether the West has accepted cheat as a necessary evil, to be lived with until kingdom come, or whether it regards cheat as a challenge to rectify its past errors in land-use. I found the hopeless attitude almost universal (pp. 167-168).

More than six decades later, this pessimistic viewpoint endures among many land managers and researchers alike, and *B. tectorum* invasion continues to escalate. As climate change and exurban population growth continue to alter mountain ecosystems and influence the spread of *B. tectorum*, managers will need to be increasingly vigilant at monitoring and controlling populations. Novel research must explore possible future control options, e.g., the potential for biological control of *B. tectorum* through fungal pathogens (Boguena et al. 2007, Meyer et al. 2007) such as *Ustilago bullata* Berk. (Ustilaginaceae, 'head smut') or *Pyrenophora semeniperda* (Brittleb. & D. B. Adam) Shoemaker (Pleosporaceae, 'black fingers of death'). Most likely, a combination of treatments and land management strategies will be necessary to control *B. tectorum* spread and ameliorate invasions on a local scale. It is my sincere hope that this dissertation improves understanding of how *B. tectorum* invasion and associated increases in fire risk may progress in light of climate change and provides a scientific basis for management strategies that will render the hopeless attitude that Leopold describes obsolete.

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