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BROMUS TECTORUM INVASION AND GLOBAL CHANGE: LIKELIHOOD OF SPREAD AND FEASIBILITY OF CONTROL

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TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

BROMUS TECTORUM INVASION AND GLOBAL CHANGE: LIKELIHOOD OF SPREAD AND FEASIBILITY OF CONTROL

Amy L. Concilio

ABSTRACT

Bromus tectorum L. is an annual grass native to Eurasia that was introduced into the U.S.A. in the late 1800s and has since become dominant in large parts of the Intermountain West. At high density, it can alter the fire regime and subsequently act to displace native shrub and bunchgrass communities. In the eastern Sierra Nevada, California, *B. tectorum* exists in low-density populations and its impacts have been minimal. However, agents of global change, such as changing climate and increased anthropogenic nitrogen (N) deposition, will likely affect plant species distributions and may facilitate the spread of *B. tectorum*. In this dissertation, I examine: (1) how climate change and increased N deposition might affect *B. tectorum* spread, (2) how increased N deposition might affect species diversity and *B. tectorum* dominance, (3) the ecological effectiveness of *B. tectorum* control techniques, and (4) the feasibility of *B. tectorum* control in the eastern Sierra Nevada, CA, considering social logistical, and regulatory factors.

Through a series of *in-situ* experiments, I found that a shift from snow to rain could increase *B. tectorum* dominance in the region, depending on timing, frequency, and magnitude of rain events. Effects of increased N on *B. tectorum* were dependent on rainfall. Through a four-year study monitoring species composition, I found that *B. tectorum* dominance has increased significantly at the site at the expense of native forb species richness. In disturbed areas, *B. tectorum* cover is approaching the threshold for increased fire risk, which could result in more significant impacts for the region. Several methods of control were effective in reducing *B. tectorum* and increasing the dominance of native species, including hand pulling, soil solarization, and mulching. However, through interviews with local land managers, I identified a number of regulatory, social, and logistical obstacles to active *B. tectorum* control in the region. Future work should be focused on overcoming these barriers to prevent increased impacts of *B. tectorum* at its high elevation range margin.

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INTRODUCTION

The expansion of human transport and commerce in recent history, particularly over the last 200 years, has brought an unprecedented increase in movement of organisms across oceans and continents (Elton 1958, Mack et al. 2000, Ehrenfeld 2005). During that time, an estimated 50,000 exotic species have been introduced to the U.S.A., both deliberately (e.g., crop and livestock species) and accidentally (Pimentel et al. 2005). Among those organisms accidentally introduced, very few survive to reproduce. A small percentage of exotics become naturalized, meaning that they maintain self-sustaining populations without new introductions (Mack et al. 2000, Richardson and Pysek 2006). Many naturalized species do not cause any measurable harm to the ecosystems in which they are introduced (Williamson and Fitter 1996), but a small percentage result in substantial impacts on native flora or fauna, or on ecosystem processes, function or structure (Vitousek 1990, Vitousek et al. 1996, Mack et al. 2000, Levine et al. 2003). An introduced species is generally thought to be "invasive" when it produces large numbers of offspring with the potential of increasing rapidly over a large area if left unchecked (Richardson and Pysek 2006). Although relatively few introduced species become invasive, those that do are considered the second greatest threat to biodiversity conservation (after habitat loss; Wilcove et al. 1998) and have large economic costs to society totaling an estimated $120 billion per year in the U.S.A. (Pimentel et al. 2005).

Of those species that are considered invasive, about 10% have particularly profound impacts on ecosystems by altering resources (e.g., *Tamarix* spp.), causing shifts in fire cycles (e.g., *Bromus tectorum*), increasing or decreasing erosion (e.g., *Andropogon virginicus* and *Ammophila arenaria*), or having other process-level impacts (Mack and D'Antonio 1998, Richardson et al. 2000). These species have been termed "transformer species" (Richardson et al. 2000) and are unique in their ability to alter disturbance regimes (Mack and D'Antonio 1998). The process-changing effects that they have can be particularly difficult, and often impossible, to reverse (Levine et al. 2003) because these species "*don't merely compete with or consume native species, they change the rules of the game*" (D'Antonio and Vitousek 1992; pg 64). Some of the most widespread transformations to ecosystems have occurred as a result of the introduction of exotic grasses that alter fire regimes in a way that is detrimental to native species and advantageous to their own spread, resulting in a full scale ecosystem conversion from shrubland or forest to grassland ecosystems (D'Antonio and Vitousek 1992, D'Antonio 2000, Brooks et al. 2004). These shifts, or "invasive grass-fire cycles", have occurred throughout parts of North and South America, Oceana, and Australia in response to both deliberately introduced grasses for pasture or erosion control (most of which are from Africa and Europe) and accidental exotic grass introductions (D'Antonio 2000). Grass invasions can have impacts both locally and regionally (due to their widespread nature) including loss of native species, alteration of microclimate, loss of nutrients, decreased carbon

sequestration and regional atmospheric change (D'Antonio 2000, Brooks et al. 2004, Bradley et al. 2006, Litton et al. 2006, Prater et al. 2006).

In western North America, the most widespread invasive grass that has process-level effects on the fire cycle is *Bromus tectorum*, commonly known as cheatgrass (DiTomaso 2000). This species has come to dominate over 100 million acres of land in the Intermountain West region (Mosley et al. 1999), resulting in a full-scale conversion to the sagebrush steppe ecosystem (Figure i.1; Knapp 1996). It was introduced in the late 1800s and is thought to have reached a large part of its suitable range by the 1930s (Mack 1981), in part due to physiological limitations associated with cold winter temperatures and deep snowpack at the high elevation boundaries (e.g., the Rocky Mountains on the east and the Sierra Nevada on the west) of the region (Chambers et al. 2007, Griffith and Loik 2010). At the edge of the invasion, it exists in low-density patches without impacts on the fire regime. However, climate change and other agents of global change may provide new opportunities for expansion of invasive species, particularly in montane environments (Dukes and Mooney 1999, Bradley 2009, Pauchard et al. 2009). In this dissertation, I focus on the high elevation invasion front in the western Great Basin Desert along the eastern Sierra Nevada range of California, evaluating the impacts, likelihood of spread, and feasibility of control of *Bromus tectorum*. I begin here with a brief introduction to the history of its invasion followed by an outline of my study objectives.

History and ecology of *Bromus tectorum* invasion in the Great Basin Desert

Sagebrush steppe ecosystems of the Intermountain West have been heavily used for livestock grazing since the mid 1800s (Young and Sparks 2002). Until 1934, no grazing rules or regulations existed, and the region was an open range (Buckman 1935, Young and Allen 1997). Early settlers introduced large numbers of cattle on the range without any understanding of the damage that they could inflict (Pellant 1996, Young and Sparks 2002). The sagebrush steppe system is dominated by shrubs and perennial bunchgrasses, which did not evolve in the presence of large congregations of ungulates and were not adapted to high grazing pressure (Mack 1981). During the Great Depression, the livestock industry in the western U.S. suffered losses, like many other industries (Young and Allen 1997). Simultaneously, the west experienced a serious drought in the early 1930s (Young and Allen 1997). The combined effect of overgrazing and drought was a dramatic loss in perennial bunchgrass cover (Young and Allen 1997). Just prior to that, a price recession had spurred the abandonment of millions of acres of land that had been dry-farmed for wheat (Stewart and Hull 1949). These lands were quickly colonized by disturbance-adapted species like Russian thistle (*Salsola kali-tenuifolia* (L.) Tausch), tumbleweed (*Sisymbrium altissimum* L.), and cheatgrass (*Bromus tectorum* L) (Stewart and Hull 1949**)**.

Bromus tectorum was introduced to the Intermountain West during this period of unregulated grazing probably through ballast water of ships, and later in contaminated wheat seed and straw used for packing material (Mack 1981; Knapp

1996; Young and Allen 1997). Although primarily colonizing roadsides and abandoned cultivated lands at first, *B. tectorum* began to establish in overgrazed rangelands in the early 1900s (Stewart and Hull 1949). Its native range includes a large area from Central Asia through the Mediterranean to Spain and North Africa (Young and Allen 1997), a region where nomadic livestock husbandry dates back an estimated 10,000 years (Young and Clement 2009). Unlike grasses and shrubs native to the Intermountain West region, *B. tectorum* can withstand heavy grazing (Young and Allen 1997) and it was able to outcompete native species that had been damaged by overgrazing (Knapp 1996, Pellant 1996). Although *B. tectorum* can invade undisturbed ecosystems, it is clear that grazing has facilitated its spread (Stewart and Hull 1949, Beatley 1966, Knapp 1996). In addition to its pre-adaptation to grazing pressure, *B. tectorum* had other physiological advantages in its introduced range. It is an annual cool season grass, and as such, it fills an open niche in the sagebrush steppe ecosystem, which is dominated by perennial bunchgrasses and shrubs (Mack and Pyke 1983, Knapp 1996). It germinates earlier than native species and completes its lifecycle earlier in the season (Mack and Pyke 1983), depleting soil moisture and nutrients down to low levels unfavorable for germination and growth of native species (Stewart and Hull 1949, Klemmedson and Smith 1964, Thill et al. 1984, Upadhyaya et al. 1986).

Within a few decades of introduction and naturalization, *Bromus tectorum* had already begun to achieve dominance in shrub and bunchgrass ecosystems throughout the Intermountain West. As *B. tectorum* increases in density, the fuel surface-to-

volume ratio and horizontal fuel continuity of the system increase, which increases the risk of fire (Stewart and Hull 1949, Brooks et al. 2004, Link et al. 2006). Native perennial species are slow to recruit after fire, and *B. tectorum* can easily become dominant post-fire, resulting in full-scale alteration of the landscape (Figure i.1; Stewart and Hull 1949). Some of the first parts of the landscape to undergo conversion from sagebrush-steppe to annual grassland occurred along railroad lines, which experienced a high frequency of wildfires due to brake fires and steam locomotives (Young and Allen 1997). There are also reports of promiscuous burning to aid the expansion of *B. tectorum* as a source of forage on overgrazed, unproductive lands (Klemmedson and Smith 1964, Young and Clement 2009). However, range managers in the late 1930s began to warn that it was unwise to base grazing operations on *B. tectorum* because of its tendency toward boom and bust years (Stewart and Young 1939); during dry years, almost no *B. tectorum* grows regardless of whether it is fertilized or not (i.e., potentially resulting in mortality of livestock dependent upon it), while it increases dramatically in years of high precipitation (Kay 1966).

Bromus tectorum is currently the most dominant invasive plant species in the Intermountain West (DiTomaso 2000) and is widely thought to be highly problematic for the region (USDI-BLM 2000, Pellant et al. 2004, Chambers and Wisdom 2009). Its impacts include displacement of native shrub and bunchgrass communities (Mack 1981), reduction of biodiversity (Knapp 1996), facilitation of other plant invasions (Blaisdel 1982), reduction of the quality and quantity of livestock forage (Evans and

Young 1984, Pellant et al. 2004), and alteration of fire regimes (Ziska et al. 2005) with associated increased costs of fighting fire (USDI-BLM 2000). *B. tectorum* invasion not only increases the frequency of fire, but also the extent (Brooks et al. 2004). The 1999 fire season was particularly significant in Nevada, where *B. tectorum* had come to dominate large parts of the landscape. After two consecutive growing seasons with above average *B. tectorum* growth, fuel loads had accumulated creating conditions ripe for ignition. In July of 1999, over 100 lighting-strike fires took root across Nevada burning a total of 1-2 million acres, most of which occurred over a period of five days, with an estimated cost of suppression at $38 million (USDI-BLM 2000, Young and Sparks 2002). The increase in frequency and size of wildfires in the region has had negative consequences for ranching enterprises, increasing likelihood of bankruptcy (Brunson and Tanaka 2011). Fires have also had negative effects on native flora and associate fauna. Sagebrush-obligate species, such as the Greater Sage Grouse, are declining with the loss of sagebrush habitat (Knick and Connelly 2011), partly due to *B. tectorum* fires and the resulting conversion to annual grasslands (Johnson et al. 2011).

In response to the dramatic recent increase in wildfires and associated costs, the BLM made a commitment in 2000 to restore degraded sagebrush habitats throughout the Great Basin (USDI-BLM 2000). Several initiatives are now underway (e.g., the SageSTEP project; McIver et al. 2010), though funding restoration and land management is a chronic problem for the region (USDI-BLM 2000, Chambers and Wisdom 2009). Chambers and Wisdom (2009; pp 712-913) highlight areas of

research necessary for successful restoration of degraded Great Basin habitats. Among their suggestions are several topics addressed in this dissertation, including:

- *"Effects of changes in climate and climate variability on invasion of nonnative species"* (addressed in Chapter 1)
- *"Current status of invasions of nonnative species, rates of change, and predictions for the future"* (Chapter 1 & 2)
- *Effects of invasive species on vegetation communities... and native species"* (Chapter 2)
- *"Integrated methods for controlling priority invasive species that address the appropriate scales and stages of invasion"* (Chapter 3)
- *Methods for reestablishing native species while controlling invasive species"* (Chapter 3)
- "*Effects of efforts to control invasive species on native plant communities and species* (Chapter 3)

They also call for *"a closer alliance between research and management"* and for collaborative *"restoration experiments at management scales that serve as the basis for adaptive management."* (Chambers and Wisdom 2009; pp. 712-113), which are goals of mine in Chapters 3 and 4.

In this dissertation, I directly address several research gaps necessary for improved restoration and land management in the region. Further, my work is focused at the high elevation edge of the *B. tectorum* invasion where less research has been conducted to date (but see Chambers et al. 2007, Griffith 2010, Griffith and

Loik 2010). This is an important region of study for several reasons: (1) although historically thought to have reached its range limitation at high elevation (Mack 1981), suitable habitat for *B. tectorum* is likely to shift with climate change (Bradley 2009), (2) *B. tectorum* has not had process-level effects on the ecosystem yet at high elevation, native plants are still present, and conservation (rather than restoration) is still a possibility (Wisdom and Chambers 2009), and (3) montane ecosystems are predicted to experience shifts in species distribution faster than other areas and may be particularly susceptible to increased invasion risks (Pauchard et al. 2009). My research questions address both management and ecology of high elevation *Bromus tectorum* populations in the region.

Research Objectives

In this dissertation, I use an inter-disciplinary research approach to evaluate impacts, spread, and control of high elevation populations of *Bromus tectorum* in the eastern Sierra Nevada at the edge of the western Great Basin Desert (Figure i.2). I evaluate: (1) how agents of global change might affect *B. tectorum* spread, (2) how global change and *B. tectorum* invasion affect native herbaceous species, (3) the effectiveness and associated costs of different restoration techniques for *B. tectorum* control, and (3) social, regulatory, and logistical factors associated with the feasibility of *B. tectorum* control in the region.

Although *B. tectorum* invasion is currently limited at high elevation (Chambers et al. 2007), changing climatic and edaphic conditions may facilitate range

expansion (Bradley 2009). Changing precipitation patterns in the Sierra Nevada are predicted to occur with climate change (Miller et al. 2003, Hayhoe et al. 2004), and increased anthropogenic nitrogen (N) deposition may be expected in future years due to growth in development and agriculture across the state of California (Fenn et al. 2003b, Weiss 2006). Since the sagebrush steppe ecosystem of the eastern Sierra Nevada is water-limited and receives most of its precipitation in the form of snow, I expect that changes in snowfall patterns will affect plant community composition and could impact invasibility by *B. tectorum*. Increased anthropogenic nitrogen (N) deposition has been linked to increases in invasive grasses elsewhere (e.g., Weiss 1999, Rao and Allen 2010) and may interact with changing climate to affect *B. tectorum* spread at high elevation. In Chapter 1 of this dissertation, I explore the interactions of changing snowfall, rainfall, and nitrogen in the eastern Sierra Nevada, CA through a series of *in-situ* experimental manipulations.

Since some plants can capitalize on excess nutrients faster and/or more efficiently than others, increases in anthropogenic nitrogen deposition are likely to result in changes in community composition (Weiss 2006). These shifts are likely to lead to increased dominance of invasive species since they are often better equipped to respond to resource inputs than slow-growing natives (Dukes and Mooney 1999, Davis et al. 2000, Fenn et al. 2003a). In Chapter 2, I measure the effects of increased N deposition on plant community composition and *B. tectorum* dominance across sites with different land use history. I also explore relationships between *B. tectorum* cover and native herbaceous species diversity and cover.

Although it is difficult to control cheatgrass populations at lower elevation where it has initiated a grass-fire cycle, fewer ecological barriers to restoration should exist at higher elevation where populations are patchy (Brooks et al. 2004). It is well known that it is easier and more cost-effective to control an invasion at early stages or where infestations are relatively small in area (Moody and Mack 1988, Hobbs and Humphries 1995). In Chapter 3 of this dissertation, I present results from field trials testing different control techniques for high elevation populations of *B. tectorum* in the eastern Sierra Nevada. Specifically, I test effects of soil solarization, hand pulling, and mulching on *B. tectorum* and native species, and I calculate associated costs for each treatment. Chapter 3 concludes with recommendations for where and when each technique should be used, considering logistical, economic, and ecological factors.

Finally, even if ecological barriers to restoration of high elevation populations of *B. tectorum* are minimal, social, regulatory, logistical and/or economic barriers may exist. In Chapter 4, I present results from a series of semi-structured interviews with land managers working directly on weed control in the region and a literature review focused on legislation, agency policy, and stakeholder views on invasive species management in eastern California. I discuss factors that affect *B. tectorum* control in the region (both positively and negatively) and opportunities for improved management.

In the final section, I conclude with a summary of my main findings. Specifically, I address: (1) the likelihood of *B. tectorum* spread in future years in the

eastern Sierra Nevada (based on the main results from Chapters 1 & 2), and (3) the feasibility of *B. tectorum* control from multiple perspectives (based on the main results from Chapters 3 & 4). I provide management recommendations based on results from all four chapters.

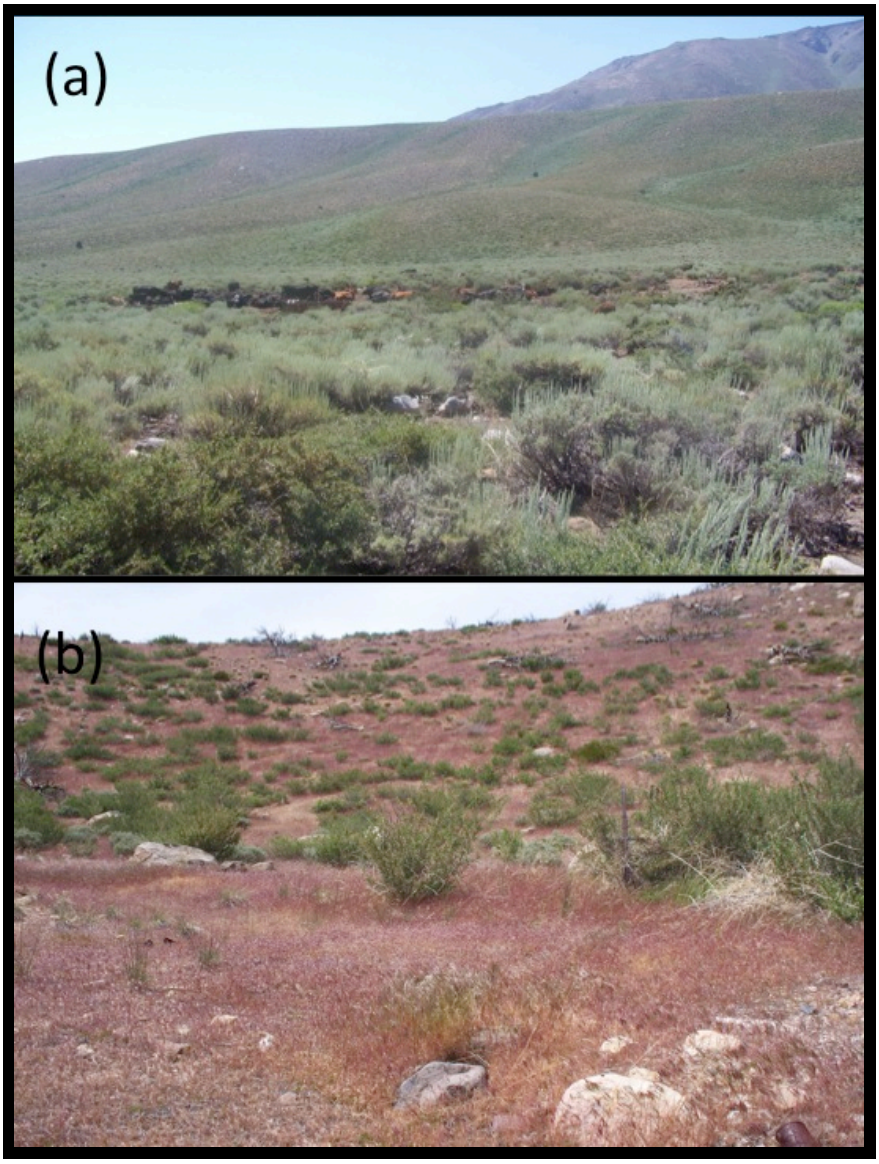

Figure i.1: Sagebrush steppe ecosystems of the western Great Basin Desert in the eastern Sierra Nevada: (a) where cheatgrass is part of the understory but has not yet changed the fire cycle (photo taken near Mammoth Lakes, CA) and native shrubs and bunchgrasses are abundant, and (b) after cheatgrass has altered the fire cycle and become dominant (taken in Nevada, near the border with CA). Cheatgrass is the small-stature red grass in the lower photo.

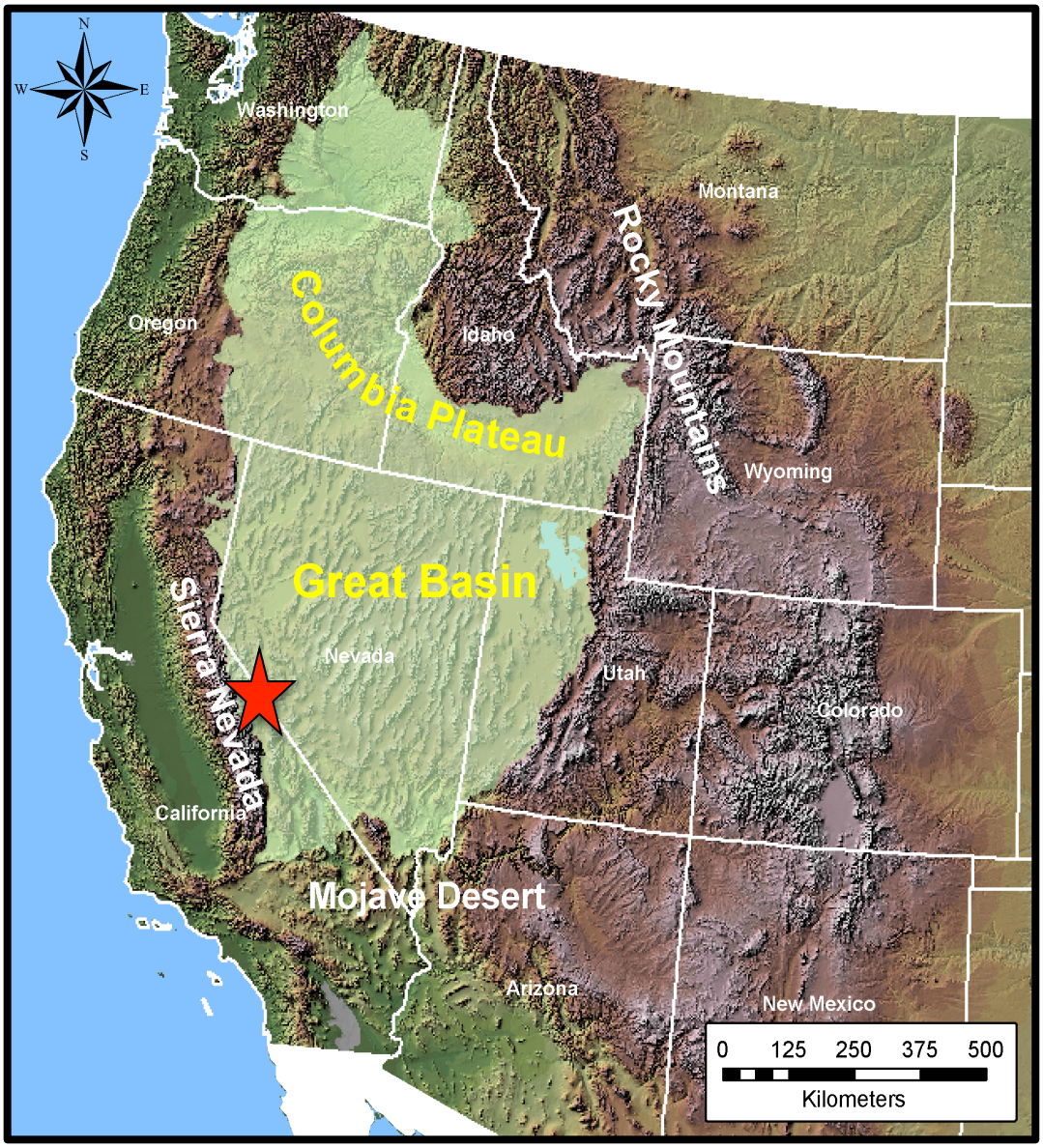

Figure i.2: Study site location (shown with the star). The Great Basin Desert lies between the Columbia Plateau to the north, the Mohave and Sonoran Deserts to the south, the Sierra Nevada range to the west and the Rocky Mountains to the east. This research took place at the high elevation western edge of the Great Basin Desert, indicated with the red star. Map Source: U.S. Geological Survey, Great Basin Information Project, http://greatbasin.wr.usgs.gov/.

CHAPTER 1

GLOBAL CHANGE EFFECTS ON *BROMUS TECTORUM* AT ITS HIGH-ELEVATION RANGE MARGIN

Introduction

There is considerable evidence that global change will affect the spread of invasive species, but much uncertainty remains about how, where, and when species will respond (Dukes and Mooney 1999, Weltzin et al. 2003a). Some widespread invasive species may already cover much of their suitable habitat in the invaded range, but changing climatic conditions could provide opportunities for range expansion or contraction (Bradley et al. 2009, Bradley and Wilcove 2009, Sandel and Dangremond 2012). Actual shifts in distribution will depend on more than just climate suitability. Edaphic conditions, biotic interactions, and disturbance history at new sites are also likely to be important, and species-specific responses will be influenced by their dispersal ability, phenotypic plasticity, and (in some cases) evolutionary responses (Dukes and Mooney 1999, Parmesan 2006). Concurrent increases in anthropogenic nitrogen (N) deposition or other disturbances may also interact with climate change to affect a species' response (Dukes and Mooney 1999). Clearly, much work is needed to accurately predict responses to climate change, and it is unlikely that a one-size-fits-all equation exists. Site-and species-specific investigations are necessary for making predictive models more robust. Here, we focus on one of the most problematic invaders of the western U.S.A. - *Bromus tectorum* L. (Poaceae,

"cheatgrass") - and use a series of *in situ* manipulations to predict how it might respond to global change drivers at the high elevation edge of its range.

Bromus tectorum is an annual grass originating in Eurasia that has been in the U.S.A. for over 150 years (Mack 1981, Knapp 1996). Within that time it has become ubiquitous in sagebrush steppe ecosystems of the Intermountain West, where it alters ecosystem function and displaces native species (Knapp 1996). The most damaging effects occur where it increases in density, alters fuel dynamics, and changes the fire cycle, resulting in more frequent fires that facilitate its expansion (Stewart and Hull 1949, D'Antonio and Vitousek 1992, Knapp 1996, Link et al. 2006). Once an invasive grass-fire cycle has been initiated, it becomes exceptionally difficult to restore the native plant community (Blaisdel et al. 1982, Pellant 1996, Brooks et al. 2004). Fortunately, *B. tectorum* does not invade all sagebrush steppe sites equally. At high elevations along the eastern escarpment of the Sierra Nevada range, *B. tectorum* exists in low-density patches likely limited by cold winter temperatures (Chambers et al. 2007, Griffith and Loik 2010). However, changing climatic and edaphic conditions may facilitate *B. tectorum* invasion in areas that are currently unaffected. Increasing temperatures, altered precipitation, land use change, and anthropogenic nitrogen (N) deposition are among the drivers most likely to affect plant species distribution, though some will be more influential than others depending on ecosystem and species of interest (Dukes and Mooney 1999, Weltzin et al. 2003a).

The sagebrush-steppe of eastern California is an arid, montane system where even small changes in precipitation may have significant effects on plant

communities. Currently, most precipitation falls in the form of snow and snowmelt is an important source of soil water for plants throughout the dry summer season (Royce and Barbour 2001). Global change models suggest more precipitation is expected to fall as rain instead of snow in the Sierra Nevada, resulting in a decrease in late season snowpack over the next century (Miller et al. 2003, Hayhoe et al. 2004). Throughout the North American Mountain West, declines in snowpack have already occurred over the last half century (Mote et al. 2005), along with trends toward earlier snow mass peak timing (Kapnick and Hall 2010) and onset of spring (Cayan et al. 2001). The effects of these anticipated changes on plant communities and ecosystem processes are largely unknown (Weltzin et al. 2003b, Loik et al. 2004). However, differences in precipitation and snowpack can have significant effects on patterns and processes such as germination and seedling establishment (Galen and Stanton 1999, Hattenschwiler and Smith 1999), decomposition (Weatherly et al. 2003), soil respiration (Concilio et al. 2009), N cycles (Bowman 1992), and plant phenology and growth (Wahren et al. 2005, Inouye 2008). Furthermore, plant community composition can be highly influenced by seasonality of precipitation in arid ecosystems (e.g., Clary 2008). Changes in frequency and magnitude of rainfall events may be just as important as changing snow depth and melt timing in driving plant responses under potential future climatic scenarios.

In recent years, N deposition has been increasing throughout the western U.S. with growth in transportation, agriculture, and industrial sectors (Fenn et al. 2003b). Because N is a limiting nutrient in many temperate ecosystems, increases in available

N are generally accompanied by increases in productivity (Vitousek et al. 1997). However, plant species' response to N may vary due to differences in co-limitations with other nutrients, plant life history, architecture, or biochemistry (Weiss 2006, Bobbink et al. 2010). Grasses tend to show large growth responses to excess N in comparison to herbs and shrubs (Fenn et al. 2003a, Fenn et al. 2010, De Schrijver et al. 2011) which can lead to shifts in plant community composition (Bowman and Steltzer 1998, Weiss 1999, Brooks 2003, Baez et al. 2007). There is evidence that exotic grass invasion has been facilitated by N deposition in parts of California (Fenn et al. 2003a, Weiss 2006, Rao et al. 2011). The eastern Sierra Nevada receives an estimated 1 - 3 kg-N ha^{-1} $yr^{-1,}$ which is relatively low compared to other parts of California (Weiss 2006, Fenn et al. 2010). However, effects on species composition may occur at rates as low as 3 - 8 kg-N ha^{-1} in low-biomass arid and semi-arid ecosystems (Fenn et al. 2010, Rao and Allen 2010, Pardo et al. 2011).

Much research has shown that *B. tectorum* responds (sometimes dramatically) to N deposition and the type, timing, and magnitude of precipitation in the Intermountain West (e.g., Stewart and Young 1939, Hull and Stewart 1948, Stewart and Hull 1949, Kay 1966, Mack and Pyke 1983, Bilbrough and Caldwell 1997, West and Yorks 2002, Bradley and Mustard 2005). However, little work has been done at higher elevations even though different factors are likely to affect its spread at various elevations (but see Chambers et al. 2007, Griffith and Loik 2010)**.** Here, we address this research gap by investigating effects of multiple agents of global change on *B. tectorum* spread at the western, high-elevation boundary of its invaded range.

Specifically, our objectives were to determine: (1) how *B. tectorum* responds to changes in snowpack depth, (2) how frequency and magnitude of spring rain events affect *B. tectorum*, (3) whether *B. tectorum* response to precipitation treatments varies by level of N applied, and (4) whether *B. tectorum* response to altered resource inputs varies across the landscape by microhabitat. We used *in-situ* experiments to address our objectives, manipulating snow depth with snow fences, spring rain with irrigation, and N deposition with N additions. We monitored *B. tectorum* germination, growth, and fecundity in response to these treatments from 2009-2011.

Methods

Study site

This research was conducted at the Valentine Eastern Sierra University of California Natural Reserve (Sierra Nevada Aquatic Research Laboratory) and in the surrounding Inyo National Forest (37º36'51"N 118º49'47"W; elevation range 2,149 to 2,169 m) on the eastern slope of the Sierra Nevada, near Mammoth Lakes, Mono County, California, U.S.A. An on-site weather station has been monitoring precipitation, air temperature, relative humidity, wind speed and direction, and solar radiation continuously since 1987. During that time, total annual precipitation was highly variable, ranging from 156 to 674 mm (mean = 313 mm, SD = 132). The climate is Mediterranean and most precipitation (~75%) falls in the winter in the form of snow between November and March (mean = 243 mm, SD = 111; Figure 1.1a). During the period of our study, all years received below-average winter precipitation (totaling

184 mm in 2008/2009, 230 mm in 2009/2010, and 191 mm in 2010/2011; Figure 1.1a,b). Springtime precipitation, between April and June, ranged from 24 mm (2011) to 47 mm (2009; mean for spring of all years =44 mm, SD = 33). Mean daily air temperature reached a minimum each year in January of -5 to -10^{o}C and a maximum in July of about 18^{o}C (Figure 1.1c), which is typical for this site. The frost-free season is short (July-August) and temperatures drop below 0^{o}C for an average of 244 days per year (Orr and Howald 2000). During our study, frost-free days ranged from 93 per year (in 2010) to 114 per year (in 2009).

Our study site is near the ecotone between Great Basin Desert sagebrush and mixed-conifer forest ecosystems. This research took place in the sagebrush zone, in areas where *Bromus tectorum* was present. The two most dominant shrub species are *Artemisia tridentata* var. *tridentata* Nutt. (Asteraceae, 'big sagebrush', ARTR) and *Purshia tridentata* (Pürsh) DC. var. *tridentata* (Rosaceae, 'antelope bitterbrush' PUTR), which make up about 20% each of the total land cover. The remaining 60% is primarily open space with <10% herbaceous cover and perennial grasses. Dominant perennial bunchgrasses include *Achnatherum hymenoides, Achnatherum nevadensis, Elymus elymoides*, and *Hesperostipa comata*. A number of native annual and perennial herbaceous species populate the site (see Orr and Howald (2000) for a complete species list). Soils at the site are derived from Holocene deposits of alluvium and stream gravels, and are composed of sandy loam and gravelly sandy loam (Orr and Howard 2000). The site has been grazed annually (<0.25 calf/cow pairs per hectare) for one month each summer over at least the last 20 years and

probably much longer (April Barron, personal communication). During the length of our study, cows were brought on site in late June; we harvested *B. tectorum* from all of our plots beforehand.

Field Methods

To address our first objective, we used snow fences to manipulate snowpack depth and thus wintertime precipitation**.** Four snow fences, each 30 m long and 1.8 m in height, were installed in 2005 (Griffith and Loik 2010) and positioned perpendicular to the prevailing wind (240^{o}) to create zones of differing snow depth, including: (1) an increased snow depth zone 3-5 m downwind of the fences (+SNOW), (2) decreased snow depth zone at about 15 m downwind of the fences (-SNOW), and (3) ambient snow depth upwind of the fences (AMBIENT). Fences were constructed with evenly spaced t-posts and plastic mesh fencing material, which was placed out every year from November to March and then removed for the length of the growing season to avoid shading and alteration of wind patterns. Before fences were constructed, Griffith and Loik (2010) reported no difference in *B. tectorum* density by snow depth zone. In 2009, there was not enough snow accumulation at the site for the snow fences to be effective, so we were not able to quantify snow depth effects. In 2010 and 2011, the fences were effective in creating a large equilibrium drift in the +SNOW zone (Figure 1.2a), but the -SNOW was insignificant (<10% reduction in snow). Thus, we present data from the +SNOW and AMBIENT snow zones in 2010 and 2011 only.

To address our second objective, we irrigated plots to simulate increased spring rain with three treatments of different magnitude and frequency (Table 1.1). Plots were set up in the AMBIENT snow zone of each fence and irrigated by hand with water from Convict Creek, the closest body of water that runs through the reserve. The +1.6 mm treatment consisted of two water additions (just after germination and 1 week later) of 0.8 mm each, totaling 1.6 mm additional springtime precipitation. The +2.4 mm treatment consisted of three water additions (just after germination, 1 week later, and 1 week after that) of 0.8 mm each, totaling 2.4 mm of additional spring rain over ambient levels. The +4.8 mm treatment consisted of three water additions of 1.6 mm each, totaling 4.8 mm of additional springtime precipitation, delivered at the same time as the +2.4 mm treatment. The +1.6 and +2.4 mm treatments were done in inter-shrub (INTR) habitats only in 2011, and the +4.8 mm treatment was done in all three microhabitats in both 2009 and 2011.

Our increased rain simulations were relatively small in magnitude compared to the total precipitation that the system receives over the course of a year. However, the simulated events were within the size range of an individual rainfall event that the system typically experiences during springtime. During the period of our study, average storm size event between April and June (when additions were made) was 1.9 mm (SD = 1.3). In comparison, our additions totaled 1.6 - 4.8 mm additional water per year, ranging from 3 - 20% of the ambient spring rainfall during the two years.

To test whether *Bromus tectorum* response to precipitation treatment varied with N addition, we used a fully replicated split-plot design with two levels of

nitrogen treatment (plus 5 g N m^{-2} yr^{-1}, and ambient levels of N) within five levels of precipitation manipulation: increased snow (+SNOW), ambient levels of snow and rain (AMBIENT), and increased rain (+1.6 mm, +2.4 mm, +4.8 mm). For each precipitation treatment, six paired plots (25 × 25 cm^2 in size; paired by N treatment) were set up within each microhabitat: under ARTR canopies, under PUTR canopies, and in INTR spaces. The exception was that the +1.6 and +2.4 mm treatments were replicated across INTR habitats only (for a total of six plots per zone per fence, 48 plots total). The remaining treatments (AMBIENT, +SNOW, +4.8 mm) were replicated across all microhabitats (18 plots per zone per fence, 216 plots total). In 2011, in addition to the 0 and +5 g N m^{-2} yr^{-1}, we also tested how +10 g N m^{-2} yr^{-1} affected *Bromus tectorum* in the INTR plots within both +1.6 mm and +4.8 mm treatments. Again, N additions were made in half of all paired plots within each rain treatment (six paired plots per precipitation treatment per fence, 48 plots total).

Nitrogen was added as ammonium nitrate (NH_4 NO_3) each year at the time of snowmelt, just after *B. tectorum* germination. We surmised that most N entering the soil through deposition at our site probably occurs during the springtime snowmelt soil water pulse. Other researchers working in montane snow-dependent systems have found that a large percentage of total annual inorganic deposited N is released in a pulse event at the time of snowmelt (Williams and Melack 1991, Bowman 1992, Williams et al. 2009). We added N to each plot mixed with water (0.8 mm per plot), and added the same amount of water (without N) to control plots at the same time. The N was mixed with water (rather than in a dry pellet form) because wind speeds

are high at the site and pellets would likely blow off the plots. The amount of water added with the N additions was small, representing only ~0.3% increase over total annual precipitation and a ~2% increase over springtime precipitation.

Each year in April, *B. tectorum* seedlings were counted in each plot before N and rain additions. From this we calculated and compared germinant density by microhabitat and by snow treatment (to measure effect), and we also compared germination by rain and N treatment to make sure there were no pre-treatment differences that would affect response. Seedlings were thinned to 15 seedlings per plot (240 ind m^{-2}) to standardize differences in propagule pressure across the landscape, and to eliminate confounding effects from intra-specific competition. Just prior to *B. tectorum* senescence (June), we counted number of plants per plot, harvested aboveground parts of all individuals, dried them (for 48 hrs at 60^{o}C), weighed them, and calculated aboveground biomass per individual for each plot. On a subsample (four plots per treatment and microhabitat, one at each fence) we counted number of tillers and spikelets on every plant, and calculated spikelet production and tiller production per individual for each plot.

Plant available nutrients were measured with resin capsules (PST-1, Unibest International Corporation, Walla Walla, WA) inserted 10 cm into the soil in a subsample of plots with the goal of capturing differences in N treatments and microhabitat. Eighteen capsules were placed per microhabitat in paired N and control plots (18 replicates x 3 microhabitats x 2 N treatments = 108 total samples). Resin capsules are designed to simulate plant roots, exchanging ions from the surrounding

soil environment, and can be used to compare the bioavailability of plant nutrients between treatments or sites (Skogley and Dobermann 1996). Resin capsules were inserted on 7 November 2008 and removed on 7 May 2009 (total 181 days). Samples were analyzed by Unibest International Corporation for plant available N, P, K, S, Ca, Mg, B, Al, Fe, Cu, Na, Mn, and Zn. We measured pH of soils collected in 2011 in AMBIENT control plots using a 1:1 mix of air dried soil and de-ionized water with a digital pH meter (model 220, Corning Science Products, Corning, NY, U.S.A.).

We used climate data from a weather station maintained by the University of California Valentine Eastern Sierra Natural Reserve, located at the Sierra Nevada Aquatic Research Station about 2 km from our plots. Hourly temperature was averaged to calculate mean daily temperature and total accumulated precipitation was summed by month for the entire study period from the winter of 2008 to summer of 2011. Snow depth was measured across the snow fences monthly from December to April each year along transects perpendicular to the fences. Depth was recorded at 1 m increments downwind (covering +SNOW and –SNOW zones) and 5 m increments upwind (AMBIENT zone) for 30 m in each direction from each fence. We measured gravimetric soil moisture to a depth of 10 cm across each of the fences monthly throughout the growing season (April - June).

Statistical analyses

Bromus tectorum invasiveness was compared across treatments and microhabitats using three main metrics: germinant density (number of seedlings m^{-2}), aboveground

growth (biomass ind^{-1}), and fecundity (spikelet production ind^{-1}). To determine how *B. tectorum* growth and fecundity responded to the effects of snow and N, we used split-plot ANOVA tests where snow fence was treated as a block, and snow zone (df = 1), microhabitat (df = 2), and N-treatment (df = 1) were treated as fixed effects within each block. Because germination occurred before N addition each year, we compared control and N plots to confirm that there was no pre-treatment density difference, which there was not ($P = 0.9028$ in 2010; $P = 0.811$ in 2011). Therefore, any differences in response between plots receiving elevated and ambient levels of N could confidently be attributed to treatment effects.

To test combined effects of increased spring rain and N, we compared *B. tectorum* biomass and fecundity between AMBIENT treatments to +4.8 mm in all three microhabitats by year (in 2009 and 2011) using the same split-plot model described above. In 2011, we focused on how changing frequency and magnitude of precipitation events might affect *B. tectorum* growth in the inter-shrub zone. Again, the same split-plot model described above was used without the effect of microhabitat. To isolate effects of magnitude of springtime rain (without frequency as a confounding factor), we compared the effects of the +4.8 mm treatment with those of the +2.4 mm treatment (+4.8 mm received twice the amount of additional water as +2.4 mm, distributed at the same frequency) using post hoc Tukey HSD tests. The response of *B. tectorum* to 0, 5, and 10 g N m^{-2} yr^{-1} within +1.6 mm and +4.8 mm treatments was compared in inter-shrub plots in 2011. Again, we used a

split -plot ANOVA with snow fence as a random blocking effect and precipitation (df = 2) and N treatment (df = 2) as fixed factors within fence.

To address our fourth objective, we compared whether response of *B. tectorum* to N treatments (0 and 5 g N m^{-2} yr^{-1}) and precipitation treatments (AMBIENT, +SNOW, and +4.8 mm) varied by microhabitat within each year using the same analyses described above but focusing on the effect of microhabitat in the model results. In addition to biomass and spikelet production, differences in tiller production ind^{-1} were also analyzed. We used post hoc Tukey HSD tests to compare means between precipitation and N treatments within each microhabitat, and treatment responses between microhabitats. Plant available nutrients were compared by microhabitat and N treatment using the same split-plot ANOVA model described above (without the effect of precipitation). To determine whether nutrients were influencing spatial distribution of *B. tectorum* growth (biomass ind^{-1}) and fecundity (spikelet production ind^{-1}) within each microhabitat, we tested significance of linear regression models with the following independent variables: N, P, Mg, and K.

All analyses were run using R software (v 2.14.1, Institute for Statistics and Mathematics, Wirtschaftsuniversität Wien, Vienna, Austria) and most variables were log transformed to meet assumptions of ANOVA. All figures were drawn with KaleidaGraph (v 4.1, Synergy Software, Reading, PA, USA) using untransformed data.

Results

Effects of snow depth

Each of the snow fences created equilibrium drifts of increased snow depth containing roughly twice as much snow with about a two-week delay in melt timing compared to ambient snow zones (Figure 1.2a). In turn, soil moisture dried down faster in the ambient plots than the +SNOW plots (Figure 1.2b). In response to increased snow depth, germination of *Bromus tectorum* was decreased under *Purshia tridentata* (PUTR) canopies by 42% in 2010 ($P = 0.025$; Figure 1.3a) and in all microhabitats in 2011 (by 40% under *Artemisia tridentata* (ARTR) canopies, $P < 0.001$; 60% under PUTR, $P < 0.001$; 36% in inter-shrub habitats (INTR), $P < 0.001$; Figure 1.3b). However, neither spikelet production nor biomass was significantly affected by snow depth in any of the three microhabitats in either year (Table 1.2).

Effects of springtime rain events

Regardless of frequency or magnitude of rain treatment (AMB versus +1.6, +2.4, or +4.8 mm), we found no difference in *B. tectorum* biomass or spikelet production in INTR in 2011 when no supplemental N was added (Table 1.2). In 2009, however, the +4.8 mm treatment resulted in increased *B. tectorum* growth and fecundity in INTR: biomass increased from 0.095 ± 0.03 to 0.33 ± 0.06 g ind^{-1} (mean ± SEM; $P < 0.0001$; Figure 1.4a) and spikelet production increased from 9.9 ± 1.2 to 27.2 ± 5.5 spikelets ind^{-1} ($P = 0.009$) in comparison to control plots (Table 1.2). We found no significant effect of the +4.8 mm treatment under either of the shrub microhabitats in

2009 (Figure 1.4a) or 2011 (Figure 1.4b), even though mean biomass was nearly doubled under PUTR canopies in 2009. Large variability at the plot level under the +4.8 mm treatment (SD was 113% of the mean) suggested that increased rain has the potential to dramatically increase growth under PUTR canopies, but other factors probably influence the response.

Combined effects of precipitation treatments and nitrogen additions

We found through resin probe analysis that our N additions were effective in increasing available N in the soil in the AMBIENT zone ($F = 50.84$, $P < 0.0001$) and had effects on other soil nutrients as well (Table 1.3). However, increased N had no effect on *B. tectorum* biomass, tiller production, or spikelet production in the AMBIENT zone in any year. Further, *B. tectorum* showed no response to the combination of +SNOW and N additions. However, the combination of supplemental rain and N did increase *B. tectorum* biomass in INTR in 2011 with +2.4 mm and +4.8 mm treatments ($P = 0.016$ and $P < 0.0001$, respectively; Figure 1.5). Tiller production and spikelet production in INTR were also increased with added N in +4.8 mm ($P = 0.0002$ and 0.052, respectively). We compared N addition plots between +2.4 mm and +4.8 mm and found that increasing the magnitude of rainwater delivered in each event, while maintaining the same frequency of events, had no additional effect on *B. tectorum* biomass, tiller production, or spikelet production. We compared the effects of an increase of 0, 5, and 10 g m^{-2} N within the +1.6 mm and +4.8 mm treatments on *B. tectorum* biomass and fecundity in INTR (Figure 1. 6).

Within the +1.6 mm treatment, mean biomass increased in the 0 to 10 g m^{-2} N comparison ($P = 0.028$), but there was no significant effect between adding 0 or 5 g m^{-2} N (Figure 1.6a). Within the +4.8 mm treatment, mean biomass doubled from 0 to 5 g m^{-2} N ($P < 0.001$) and was higher at 10 g m^{-2} N compared to the control ($P < 0.001$), but no additional increase occurred with the 10 g m^{-2} N treatment compared with the 5 g m^{-2} N treatment (Figure 1.6a). There was no significant difference in *B. tectorum* spikelet production between the N addition treatments under the +1.6 mm treatment, but within the +4.8 mm treatment adding 10 g m^{-2} of supplemental N did increase fecundity compared to control plots ($P = 0.038$), and there was a marginally significant increase with 5 g m^{-2} N ($P = 0.068$; Figure 1.6b).

Differences in treatment response by microhabitat

Bromus tectorum response to treatments varied by microhabitat. With snow additions in all microhabitats, there was a reduction in seedling density (Figure 1.3; Table 1.2). However, the magnitude of the response varied. The largest reduction in seedling density was found under PUTR canopies in both years (Figure 1.3). Response to +4.8 mm and N treatments varied between shrub and INTR habitats. There was no significant response to treatments under PUTR or ARTR canopies in either 2009 or 2011, but biomass, spikelet production and tiller growth increased with +4.8 mm in INTR microhabitats in 2009 and with +4.8 mm and N in INTR microhabitats in 2011 (as reported above).

Individuals in the inter-shrub spaces generally grew bigger and produced more

spikelets and tillers than those under the canopy of the two shrub species. Despite this fact, growing conditions appeared to be more desirable under the shrubs. Soil moisture was highest under the shrubs in the early part of the season (Figure 1.2c). Likewise, resin probe analysis showed B, Ca, K, and Mg were higher under shrubs than in INTR ($P < 0.0001$ in all cases; Table 1.3). Available N was highest under PUTR canopies ($P = 0.006$), as was P ($P = 0.0007$). In contrast, Al and Fe were higher in INTR microhabitats than under shrubs ($P = 0.003$ and 0.0004, respectively). We found that *B. tectorum* biomass was positively influenced by plant available P under ambient precipitation conditions in INTR ($R^2 = 0.37$, $P = 0.03$) and marginally significantly influenced by Mg ($R^2 = 0.27$, $P = 0.08$), but not by N or any other nutrient that we measured (Figure 1.7). Individuals growing under shrubs were not significantly influenced by any of the soil nutrients that we tested.

In response to N additions, plant available N increased dramatically in all three microhabitats (compared to non-treated plots): by 200% in INTR, 300% under ARTR canopies and 500% under PUTR canopies ($P < 0.0001$ for all comparisons). Nitrogen additions positively influenced the availability of other soil nutrients (Table 1.3). Magnesium and potassium availability increased in PUTR plots (Mg: $P = 0.002$, K: $P = 0.01$) and INTR (Mg: $P = 0.02$, K: $P= 0.001$), but not in ARTR plots. Phosphorus availability increased in INTR microhabitats by about 50% ($P = 0.005$), but not under ARTR or PUTR canopies.

Discussion

Throughout most of its range in the Intermountain West, *B. tectorum* generally germinates in the fall with sufficient precipitation, remains dormant through the winter, and then grows vigorously in the early spring (Mack and Pyke 1983, Thill et al. 1984). At the elevation of our study site, however, due to cold winter temperatures and persistent snowpack, germination takes place in the spring and the growing season is necessarily constrained to the time between snowmelt and summer drought (Mack and Pyke 1983, Griffith 2010, Griffith and Loik 2010). There is a phenological delay that accompanies a deeper, later melting snowpack measured at the same fences in previous years (Griffith & Loik 2010) and observed during our study. We also found that a deeper snowpack caused reduced germination, consistent with a prior study (Griffith & Loik 2010). Reduced germination may have been due to increased seed dormancy, seed or seedling mortality, or a combination of these or other factors. Past research has shown that *B. tectorum* can exhibit seed dormancy in response to climatic cues (e.g., Hull and Stewart 1948, Young et al. 1969, Young and Clement 2009), that repeated freeze-thaw events and seed predation can result in *B. tectorum* seed mortality (e.g., Klemmedson and Smith 1964, Savage et al. 1969), and that *B. tectorum* individuals are most vulnerable to damage or death during early development phases (Mack and Pyke 1983, Griffith and Loik 2010). Snowpack may have influenced any of these factors, but the lack of research at high elevation makes it difficult to assess the most important drivers.

Snowpack effects on germination were more pronounced in 2011 than 2010,

which could have been influenced by differences in *B. tectorum* propagule pressure. During the winter of 2008/2009, there was no persistent snowpack and no difference in germination or seed production across the fences. Subsequently, propagule pressure in 2010 would have been similar across the snow zones. However, the winter of 2010 produced fewer individuals in the increased snow zone and presumably fewer seeds relative to the ambient control (Griffith and Loik 2010). This could have led to a reduction of seed source in 2011, amplifying the snow effect on germination. The implication would be that several uninterrupted years of deep snowpack could significantly decrease *B. tectorum* populations at high elevation. However, snowpack in the Sierra Nevada is predicted to decrease in response to climate warming (Miller et al. 2003, Hayhoe et al. 2004, Cayan et al. 2008), potentially providing opportunities for increased *B. tectorum* germination and density.

Bromus tectorum growth and fecundity differed based on precipitation treatment. While increased springtime rain had a positive effect on *B. tectorum* growth and spikelet production, alone in 2009 and in combination with N in 2011, increased snow depth (delivering a much larger magnitude of supplemental water to the system) had no effect. It is well known that rain and snow can have different effects on plant communities (Weltzin et al. 2003b, Loik et al. 2004). Melt water from snow is more likely to recharge deeper soil layers, since it comes in a flush when soils are saturated and temperatures are cooler (Schwinning and Sala 2004). At our site, soils are sandy (Miles and Goudey 1997), and water infiltrates quickly to deeper layers (Loik et al. 2004, Loik 2007); melt water could infiltrate below their

rooting zone before annual plants germinate or become active. In contrast, rainwater delivered when soils are dry and temperatures are high may wet surface soil layers, and then quickly evaporate or get taken up by plants (Schwinning and Sala 2004). While native shrubs and bunchgrasses may benefit from both rain events and snowmelt recharge of deep layers (Ehleringer 1994, Loik 2007), fast growing annuals are likely to benefit more from rain events delivered during active growth. Indeed, it has been shown that rain events are most important to plants in arid environments (including *B. tectorum*) when delivered during the time that they are most phenologically active (Bilbrough and Caldwell 1997).

The importance of timing of rain inputs was further illustrated with our comparisons of *B. tectorum* response to frequency and magnitude of simulated storm events. We found no difference in response (with and without N addition) to two treatments that were delivered with the same frequency but different magnitude of event (+4.8 mm vs. +2.4 mm). Based on developmental stage, size, and density, there is a limit to how much water plants can utilize and *B. tectorum* individuals may not have been able to capitalize on the additional water that was delivered before it evaporated or infiltrated to deeper layers.

Our simulated rainfall additions were small, but it is not unusual for arid and semi-arid sites in the US West to receive a high frequency of small events with short intervals between events (Loik et al. 2004). Through analysis of weather station data from arid and semi-arid sites across western U.S., Loik *et al*. (2004) found that an average of 47% (with a range of 24 - 64%) of all precipitation events were $\leq$ 5 mm,

and that the sites that had a high percentage of small events also experienced fewer days between events. This pattern of small frequent events appears to be ideal for *B. tectorum*. Climate change predictions call for more extreme events (Hayhoe et al. 2004, IPCC 2007), which could mean higher-magnitude storms and longer intervals between precipitation events for arid regions. Our results suggest that *B. tectorum* might be less successful under this kind of climate regime and more successful under conditions of increased rainfall frequency.

With our spring rain additions, we found that *B. tectorum* was limited by water alone in 2009, but co-limited by N and water in 2011. Other studies have also found co-limitation of *B. tectorum* in response to resource additions (Link et al. 1995, Adair et al. 2008). Hooper and Johnson (1999) found through meta-analysis that N and water are tightly linked and most arid and semi-arid ecosystems appear to be co-limited. Through regression analysis, P was identified as an important influence on *B. tectorum* and growth is probably co-limited by different combinations of N, P, and water at this site both spatially (discussed further below) and temporally. Limiting resources can shift seasonally for *B. tectorum* (Miller et al. 2006) and, as we found, inter-annually. Temporal shifts are likely due to changes in biotic interactions, edaphic conditions, or climate patterns. In our study, differences in antecedent soil water levels at the time of treatments probably drove the differences in response that we saw, as has been found in other studies of arid ecosystems (e.g., Reynolds et al. 2004, Ignace et al. 2007). Although winter precipitation was similar in magnitude in 2009 and 2011, 2009 experienced little snow accumulation and fewer days below

0^{o}C. Depending on timing and delivery of precipitation, soil water availability can differ considerably (Noy-Meir 1973, Loik et al. 2004). Springtime precipitation was also different between the two years. In March and April, the site received about 56% more spring precipitation in 2011 over 2009. Consequently, soil moisture was relatively low (3 - 5%) at the time of supplemental rainwater additions in 2009 compared to 2011 (7 - 13%), and plants would have been more water-limited in 2009.

Under ambient conditions of precipitation, we saw no effect of N in any year. Other researchers have found no apparent advantage for *B. tectorum* growth with N additions in dry years (Kay and Evans 1965, Kay 1966, Ball et al. 1996). During the period of our study, total annual precipitation was below the 24-year average. It is likely that had we monitored for a longer period, we would have seen a response of *B. tectorum* to N under ambient precipitation in some years. We did not test effects of elevated N on germination, and it has been found in at least one other study (Beckstead and Augspurger 2004) that N availability can influence density of *B. tectorum* even if biomass is unaffected. We may have measured greater effects of N had we timed the additions closer to snowmelt. When we compared the effect of adding 5 versus 10 g m^{-2} N, we found an apparent threshold for N effects on *B. tectorum,* which varied based on the amount of supplemental water added. Specifically, adding more water appears to lower the threshold at which N has an effect on *B. tectorum*. With +1.6 mm, the threshold was $\geq$ 10 g m^{-2} N, while it was $\leq$ 5 g m^{-2} under the +4.8 mm scenario. It follows that under conditions of higher rainfall, lower levels of N may positively influence *B. tectorum* fecundity and

invasiveness.

The area around our study site currently experiences low N deposition rates currently estimated at 1 - 3 kg-N ha^{-1} yr^{-1} (Weiss 2006, Fenn et al. 2010). Our additions increased N input by about 15 to 30 times ambient levels, and it is unlikely that the eastern Sierra Nevada will experience such a large increase. However, under a future climate scenario that includes higher levels of spring rainfall, our results suggest the threshold for effects of N on *B. tectorum* growth is likely to be lower. Further, if the trends that we measured are generalizable to other high elevation sagebrush steppe systems, then those regions closer to cities may already be at risk of facilitated expansion of *B. tectorum* due to higher levels of N deposition, even during low rainfall years. Although average levels of N deposition are low at our site, some areas are probably receiving disproportionately more N than others, based on elevation or distance from roads, for example. Using a passive sampling approach described in Bytnerowicz et al. (2005), nitric acid (HNO_3) dry deposition data were collected in and around our research site over a 3 week period in August of 2005 (Pamela Padgett, unpublished data). Although N levels were relatively low (ranging from a mean of 0.4 to 1.7 μg N m^{-3} over the full 3 weeks), some of the highest levels were collected at the high elevation sites (in Mammoth Lakes, CA), which causes concern about the potential for upward expansion of *B. tectorum*. In another study, Padgett and Bytnerowicz (2001) found that open spaces between shrubs of the coastal sage scrub receive greater accumulation of HNO_3 on soil surfaces than shrub microhabitats. If this pattern holds true for our system, we could see enhanced

growth of *B. tectorum* in the inter-shrub spaces, which is a concern from the perspective of fuel loads for fire. Fuel continuity increases with increased density of *B. tectorum* in inter-shrub microhabitats (Link et al. 2006), which can contribute to a more rapid fire cycle (Brooks et al. 2004).

We found differences in both nutrient availability and limitations on *B. tectorum* growth by microhabitat. Available nutrients were relatively high under shrubs and did not significantly influence variation in *B. tectorum* growth. In contrast, 38% of the spatial variation in *B. tectorum* growth within the inter-shrub space could be explained by P availability and 28% by Mg availability, suggesting P-limitation and Mg also appeared to influence growth. Although P-limitation has generally been associated with highly weathered old soils occurring in tropical latitudes, its importance in other systems has increasingly been recognized (Vitousek et al. 2010, Harpole et al. 2011). Recent meta-analyses have shown that both P-limitation and N and P co-limitation occur frequently in a range of different aquatic and terrestrial ecosystems (Koerselman and Meuleman 1996, Elser et al. 2007, Harpole et al. 2011). Other researchers have found that P can be as important as N for explaining spatial patterns in *B. tectorum* growth (Bashkin et al. 2003, Gundale et al. 2008). Our N addition treatment had positive effects on P availability, which has also been found elsewhere (Treseder and Vitousek 2001). Nitrogen additions can spur increased mineralization of immobilized P by stimulating microbial production of phosphate-releasing enzymes (Olander and Vitousek 2000). The positive growth response to N-additions that we measured in the inter-shrub space may have been

due, at least in part, to increased availability of P. Stoichiometric relationships between N, P, Mg, and possibly other nutrients are likely to be important to limiting expansion of *B. tectorum* in the inter-shrub spaces.

Bromus tectorum individuals growing under shrubs did not respond to nutrient or water additions with increased growth as they did in the inter-shrub space, which provides further evidence that growth under shrubs is not limited by nutrients or water. Biotic interactions are probably more important under shrubs. As neighboring plants, shrubs can have a net positive, negative, or neutral effect on understory plant growth based on the relative importance of facilitation and competition (Callaway and Walker 1997). These effects can shift over time within one season, inter-annually, or over a longer time period; for example, through different developmental phases of a plant, in dry years versus wet years, or as an invasive species progresses through different stages from introduction, to establishment, to spread (e.g., Callaway and Walker 1997, Holzapfel and Mahall 1999). Griffith (2010) showed that the two dominant shrubs at our site ARTR and PUTR facilitate *B. tectorum* population growth under ambient edaphic and climatic conditions. Under conditions of increased soil water and nutrient input, however, the balance between facilitation and competition could shift (Brooker 2010). The stress gradient hypothesis predicts that facilitation will be particularly important under harsh environmental conditions, when neighboring plants can serve to ameliorate negative effects of intense heat or drying, for example. Much experimental evidence supports this theory, though some studies have shown mixed results (Bertness and Callaway 1994, Brooker et al. 2008 and

references therein). When resources are plentiful (e.g., in high rainfall years or at the more mesic end of an aridity gradient), plant-plant interactions can shift so that facilitation is less important (Holzapfel et al. 2006). With our increased rain treatments, *B. tectorum* may have been released from moisture stress in the inter-shrub zone and capitalized on warmer soil temperatures, higher light levels, and a lack of inter-specific competition from shrubs. Although our study was not set up to specifically test the stress gradient hypothesis, our results are consistent with what it would predict.

In conclusion, our results confirmed that changes in precipitation and N input (either directly or through a priming effect on P) could affect the spread of the invasive annual grass, *B. tectorum*, at high elevations. Antecedent edaphic and climatic conditions influenced the magnitude of responses to N and water, and type and timing of precipitation were highly influential on plant response, as has been found in arid ecosystems elsewhere. Snowpack exerted a negative effect on germinant density, while increased spring rain and N additions positively influenced *B. tectorum* growth and fecundity. Our results suggest that the predicted shift from snow to rain could facilitate *B. tectorum* expansion at high elevation, depending on timing, frequency, and magnitude of precipitation events, and likely on changes in temperature (not directly measured here). Importantly, we found that very small changes in spring rain in some years could produce rather dramatic increases in *B. tectorum* invasiveness in the inter-shrub spaces, which could lead to changes in fuel dynamics. Link *et al*. (2006) found that once *B. tectorum* cover increases to 45%,

likelihood of fire becomes imminent provided a source of ignition at the right time of year. Currently, *B. tectorum* coexists at this elevation with native shrubs, bunchgrasses and annual forbs, and has not exceeded the threshold in density to initiate process-level effects on the ecosystem. However, a wet spring season can dramatically increase the build-up of fine fuels and increase the chances of fire, as has been found in other arid systems (Turner et al. 2008). Managers should be prepared to prevent or mitigate the more serious impacts of *B. tectorum* at high elevation that might increase in likelihood with global change.

Table 1.1: Description of experimental treatments. 'Total H_2O Added' refers to the amount of additional springtime H_2O that plots received over ambient levels. All plots received at least 0.8 mm at the time of nitrogen addition (control plots received H_2O alone while increased N plots received H_2O + N), and the increased rain treatments were subject to additional simulated rain events of varying magnitude and frequency. '# Rain Events' is the number of additional springtime rain events. 'Added N' includes the nitrogen treatments that were nested within each precipitation treatment- 0 & 5 or 0 & 10 g m^{-2} was added to each paired set of plots at the time of snowmelt.

ID	Description	Total H_2O Added	# Rain Events	Added N (g m^{-2})
AMBIENT	Ambient snow	0.8 mm	1	0, 5
+SNOW	Increased snow depth, 2X more than ambient snow	0.8 mm	1	0, 5
+1.6 mm	Increased rain, 2X more supplemental water than ambient zone plots	1.6 mm	2	0, 5, 10
+2.4 mm	Increased rain, 3X more supplemental water than ambient zone plots	2.4 mm	3	0, 5
+4.8 mm	Increased rain, 6X more supplemental water than ambient zone plots	4.8 mm	3	0, 5, 10

Table 1.2: Effects of precipitation treatments on *Bromus tectorum* density, growth, and seed production in three dominant microhabitats: inter-shrub spaces (INTR), under *Artemisia tridentata* canopies, (ARTR), and under *Purshia tridentata* canopies (PUTR). P-values are reported for ANOVA comparisons of mean values and significant differences are indicated with an asterisk.

Comparison	Habitat	*B. tectorum* seedling density (ind m^{-2})		*B. tectorum* growth (biomass ind^{-1})		*B. tectorum* seed production (spikelets ind^{-1})	
		2010	**2011**	**2010**	**2011**	**2010**	**2011**
AMBIENT	**INTR**	0.405	0.0003*	0.909	0.849	0.993	0.999
versus	**ARTR**	0.127	0.0006*	0.916	0.478	0.995	1.000
+ SNOW	**PUTR**	0.025*	<0.0001*	0.783	0.979	0.374	0.999
		2009	**2011**	**2009**	**2011**	**2009**	**2011**
AMBIENT	**INTR**	-	-	<0.0001*	0.417	0.009*	0.595
versus	**ARTR**	-	-	0.433	0.999	0.998	0.991
+ 4.8 mm	**PUTR**	-	-	0.356	0.999	0.858	0.881

Table 1.3: Soil chemical characteristics: plant available nutrients (mean ± SE), measured with resin capsules in control and N-addition plots (+ 5 g N m^{-2}) in three microhabitats, and pH measured in control plots. Units are ppm extracted nutrient per 6-month period from November to May to capture nutrient exchange over the snowmelt period. Measured variables include nitrogen (NO_3-N + NH_3-N), phosphorus (P), potassium (K), and magnesium (Mg). Asterisks (* $p < 0.10$, **$p < 0.05$, ***$p < 0.001$) signify a significant increase in nutrient availability with N additions within each microhabitat group.

Treatment	n	N	P	K	Mg	pH
Under Artemisia tridentata canopy						
Control	18	6.06 ± 1.81	1.58 ± 0.49	22.1 ± 1.4	4.01 ± 1.06	5.89±0.07
+N	17	24.7 ± 4.0***	2.26 ± 0.58	28.6 ± 1.0	5.96 ± 0.96	
Under Purshia tridentata canopy						
Control	15	8.64 ± 1.1	2.11 ± 0.24	18.9 ± 0.7	5.74 ± 0.65	5.84 ±0.04
+N	16	52.0 ± 6.9***	2.74 ± 0.35	32.5 ± 0.9**	11.4 ± 1.5***	
In Inter-shrub space						
Control	17	4.0 ± 0.57	0.80 ± 0.10	2.13 ± 0.09	1.28 ± 0.17	5.70±0.04
+N	18	12.0 ± 1.02***	1.21 ± 0.10***	5.03 ± 0.18***	1.82 ± 0.14***	

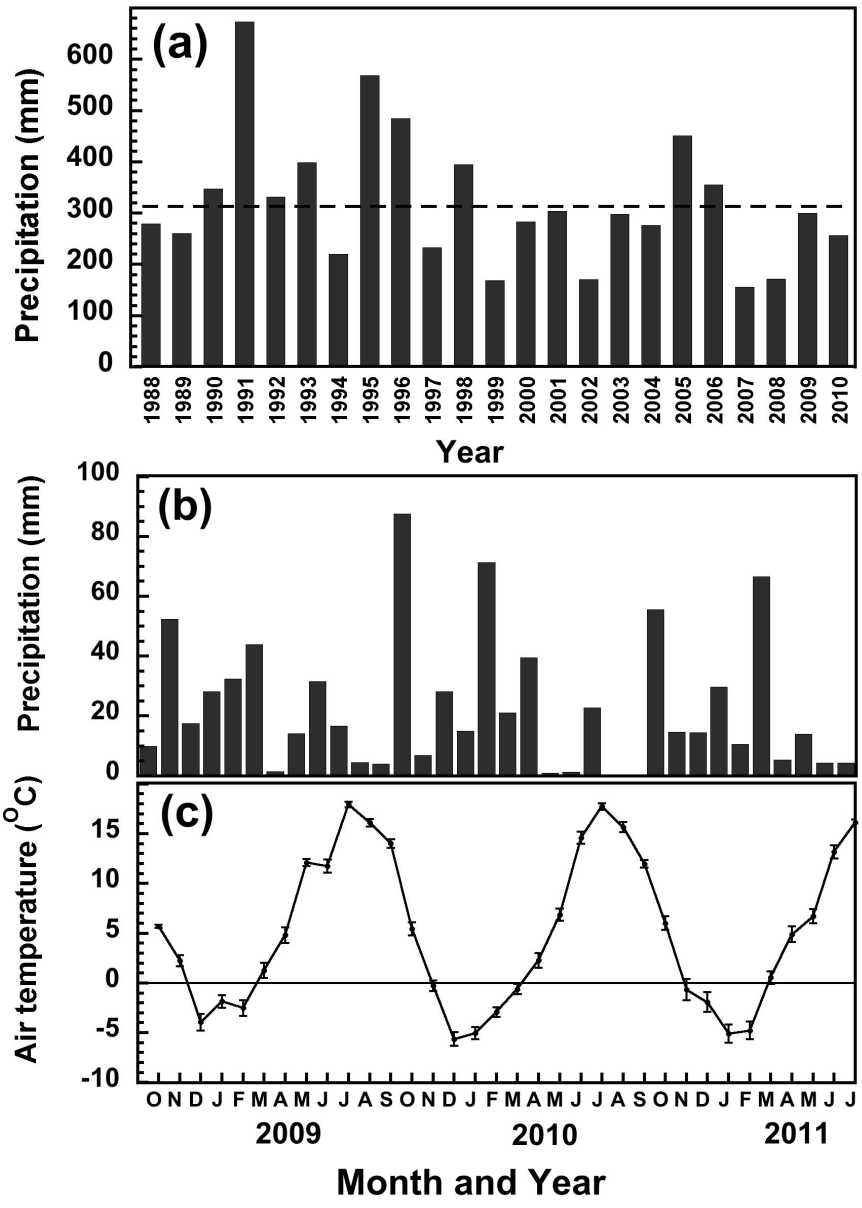

Figure 1.1: Precipitation and temperature patterns at the study site: (a) long term total annual precipitation from 1988 to 2010 (dashed line represents 24-yr average), (b) total monthly precipitation, and (c) mean monthly air temperature (bars represent one SEM) from 2008 to 2011. All data were collected at the Sierra Nevada Aquatic Research Laboratory of the Valentine Eastern Sierra University of California Natural Reserve, <2km from our study plots.

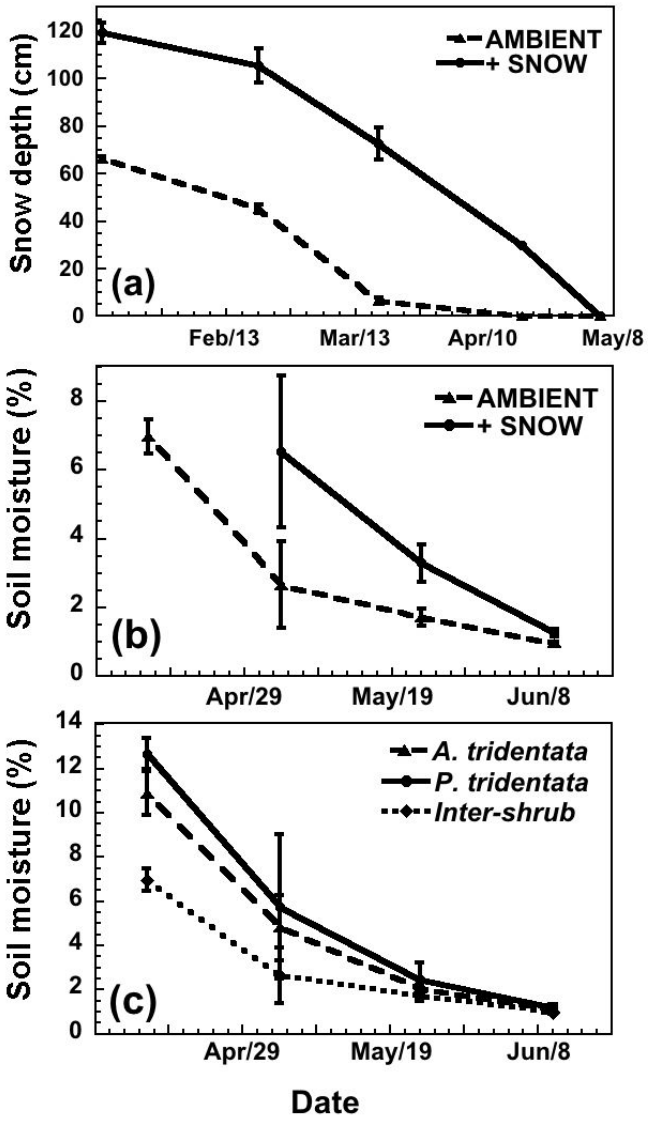

Figure 1.2: Seasonal climate data collected at study plots in 2011: (a) mean snow depth collected across the four snow fences from January to April in the ambient (dashed line) and plus snow (solid line) zones, (b) mean gravimetric soil moisture collected at inter-shrub (INTR) plots within ambient (dashed line) and plus snow (solid line) zones across the four snow fences from snowmelt to *B. tectorum* senescence (April 16-June 10), and (c) mean gravimetric soil moisture in each of 3 microhabitats (under *Artemisia tridentata* canopies (ARTR), under *Purshia tridentata* canopies (PUTR), and in inter-shrub spaces (INTR)) collected in the ambient snow zones from snowmelt to *B. tectorum* senescence (April 16-June 10). Error bars represent SEM.

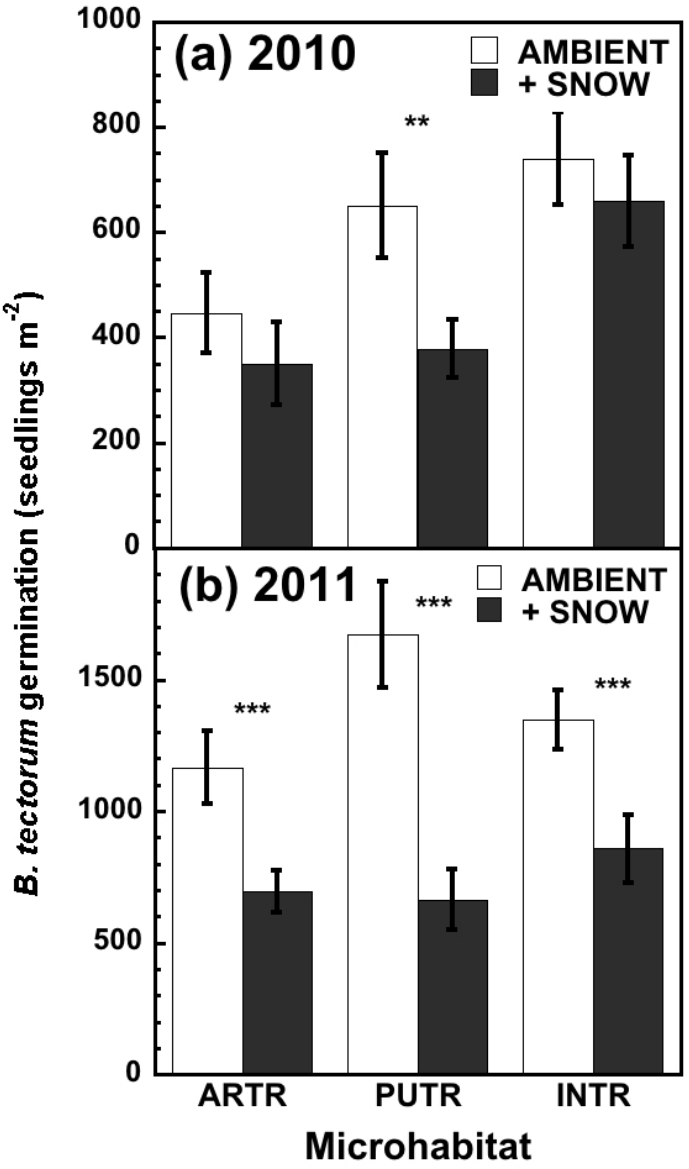

Figure 1.3: *Bromus tectorum* germination under *Artemisia tridentata* canopies (ARTR), *Purshia tridentata* canopies (PUTR), and in inter-shrub microhabitats (INTR) in ambient (AMBIENT) and increased snow zones (+ SNOW) in the spring of (a) 2010 and (b) 2011. Asterisks represent significantly different means (* $p < 0.10$, ** $p < 0.05$, *** $p < 0.001$) by precipitation treatment (AMBIENT vs. +SNOW) within each microhabitat. Error bars represent SEM.

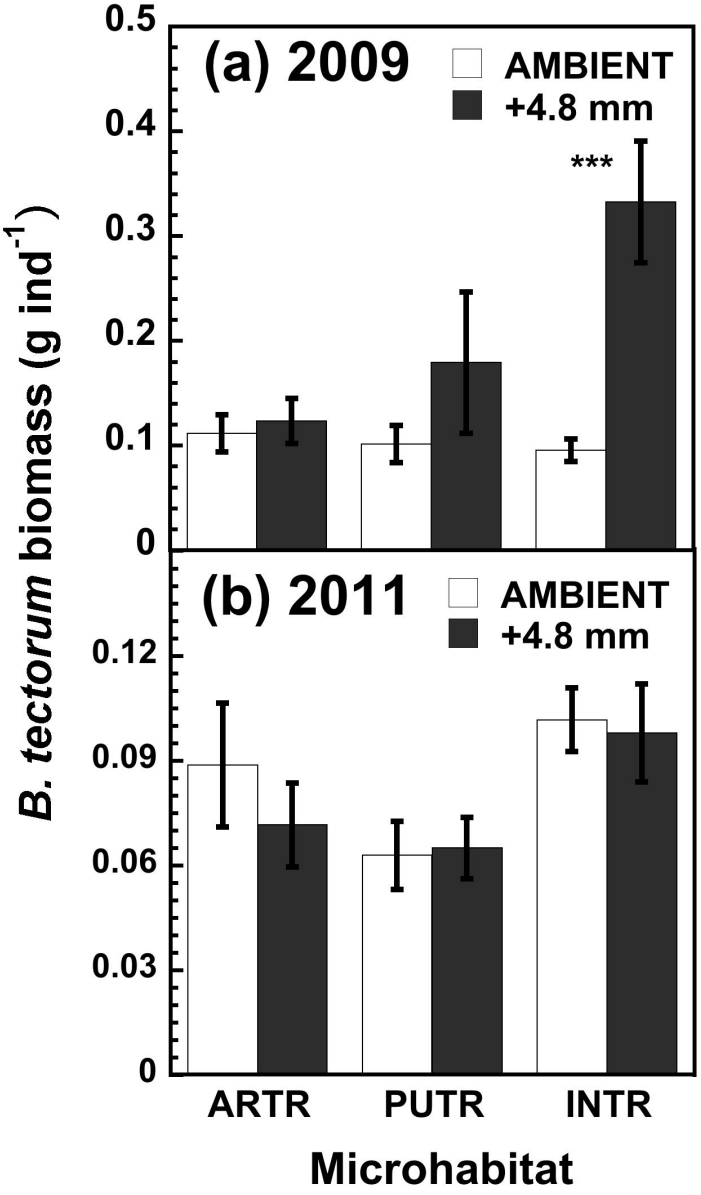

Figure 1.4: Mean *B. tectorum* biomass at the time of harvest in (a) 2010 and (b) 2011. Plants were exposed to increased springtime precipitation (+4.8 mm) compared to ambient levels (AMBIENT) in each of three different microhabitats: under *Artemisia tridentata* canopies (ARTR), *Purshia tridentata* canopies (PUTR), and in inter-shrub spaces (INTR). Asterisks represent significantly different means (* $p < 0.10$, ** $p < 0.05$, *** $p < 0.001$) by precipitation treatment within each microhabitat. Error bars represent SEM. Note the difference in scale between the two panels.

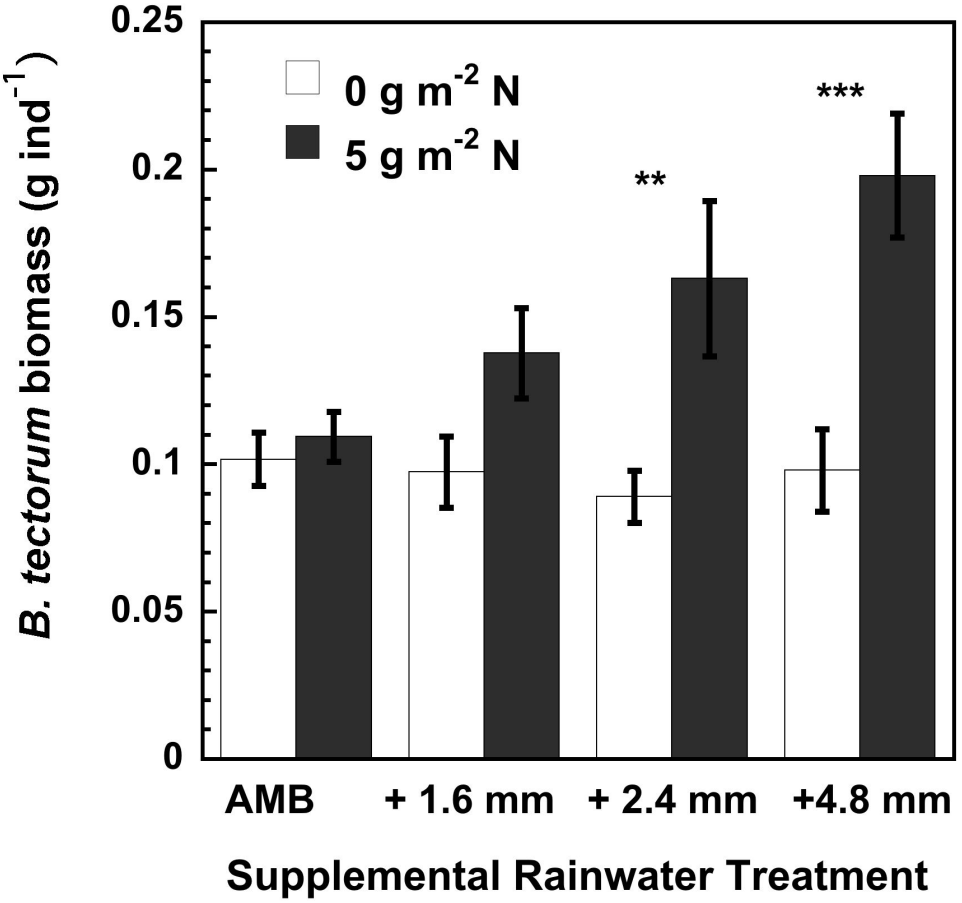

Figure 1.5: *Bromus tectorum* biomass in response to increasing supplemental water (AMB < +1.6 mm < +2.4 mm < +4.8 mm) in plots receiving no additional nitrogen (white bars) and those receiving 5 g m^{-2} N at the time of snowmelt (gray bars). Asterisks represent significantly different means (* $p < 0.10$, **$p < 0.05$, ***$p < 0.001$) between N treatments within each precipitation treatment. Error bars represent SEM.

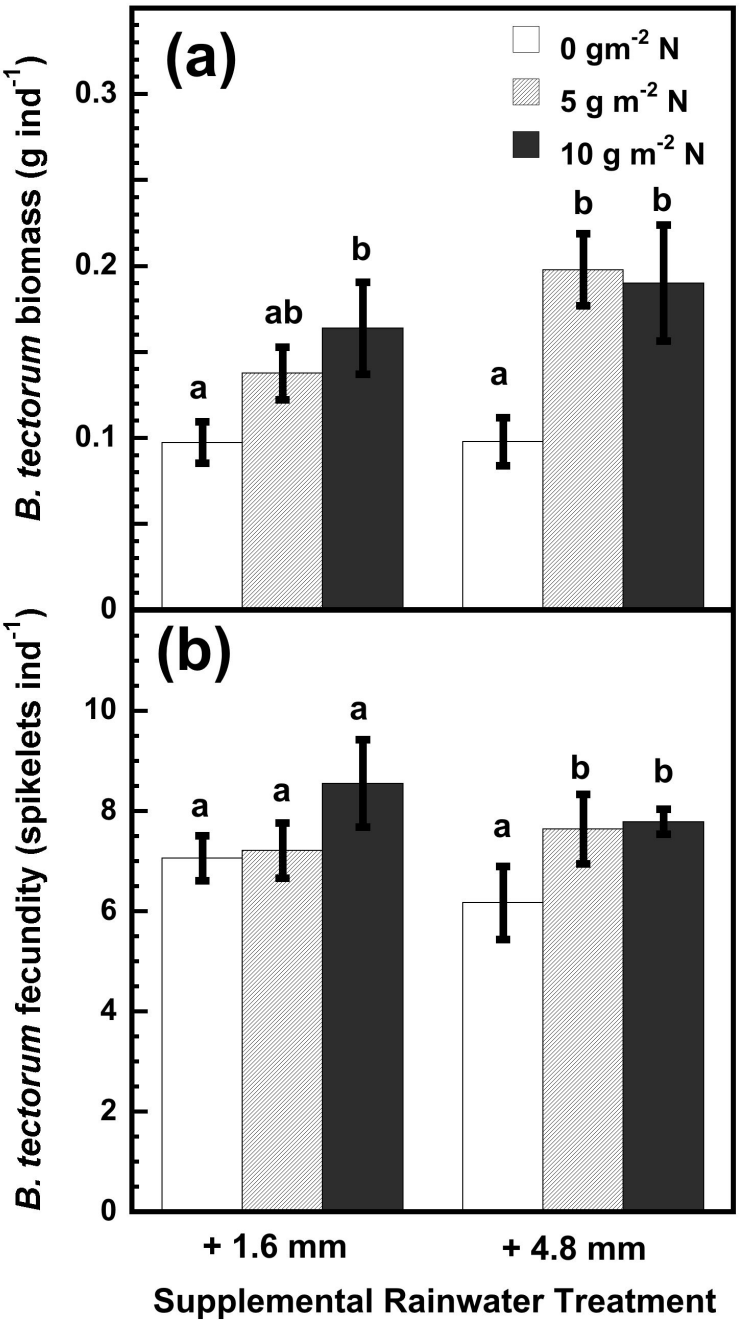

Figure 1.6: *Bromus tectorum* (a) biomass and (b) fecundity in response to nitrogen additions (+0, +5, and +10 g N m^2) under low (+1.6 mm) and high (+4.8 mm) supplemental rainwater treatments. Different letters represent significantly different means by N treatment within each rain treatment. Error bars represent SEM.

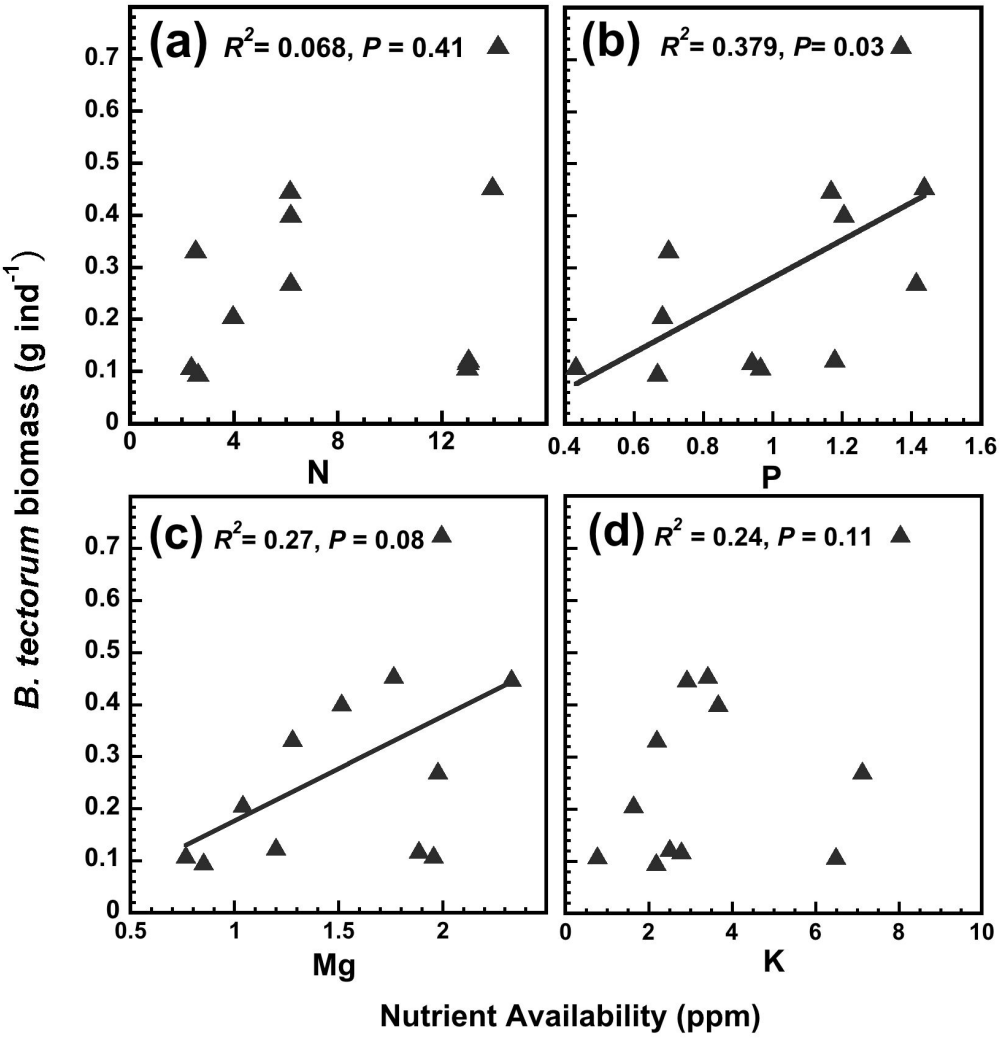

Figure 1.7: Relationships between *B. tectorum* biomass and available nutrients in ambient plots of the inter-shrub space in 2009, including (a) nitrogen, (b) phosphorus, (c) magnesium, and (c) potassium. Nutrient values are ppm extracted nutrient over 6 months from November to May.

CHAPTER 2

ELEVATED NITROGEN EFFECTS ON *BROMUS TECTORUM* DOMINANCE AND NATIVE PLANT DIVERSITY IN AN ARID, MONTANE ECOSYSTEM

Introduction

Increases in nitrogen (N) emissions and deposition have been occurring throughout the western U.S. over the last half-century as a result of industry, agriculture, and transportation (Fenn et al. 2003b) and are predicted to continue to increase on a global scale over the next few decades (Dentener et al. 2006). Plants in many terrestrial ecosystems are N-limited and can be fertilized by anthropogenic N, sometimes leading to dramatic increases in plant growth (Vitousek et al. 1997, Xia and Wan 2008). However, plant responses to N can vary by functional type or species (Duke and Caldwell 2001, Weiss 2006, Xia and Wan 2008), and increased N can consequently be associated with changes in species composition (e.g., Weiss 1999, Harpole et al. 2007, McClean et al. 2011). Fast-growing plants, including many invasive species, generally respond to exogenous N with large increases in productivity because they can more readily take advantage of excess resources (Dukes and Mooney 1999, Davis et al. 2000). Consequently, increased N deposition can facilitate the invasion of non-native plants and loss of native flora and associated fauna, particularly in low-nutrient ecosystems where natives are well-adapted to infertile soils (e.g., Weiss 1999, Brooks and Pyke 2001, Howard et al. 2004, Schwinning et al. 2005, Dong et al. 2006).

Although much research has investigated the ecological effects of N deposition on plant communities, there is a particular lack of understanding of how plant communities respond to excess N in arid and semi-arid systems (Adams 2003, Fenn et al. 2003a). Studies that have been conducted in western U.S. deserts have shown that increased N deposition can increase the dominance of invasive annual

plants (Brooks 2003, Allen et al. 2009, Rao and Allen 2010). In Joshua Tree National Park, for example, exotic grass accumulation can increase to levels that exceed the threshold for carrying fire at 3.2 – 9.3 kg-N ha^{-1} yr^{-1} in desert scrub habitats and at 3.0 - 6.3 kg-N ha^{-1} yr^{-1} in pinyon juniper habitats (Fenn et al. 2010, Rao and Allen 2010, Pardo et al. 2011). The western Great Basin Desert sagebrush steppe ecosystem receives an estimated 1 - 3 kg-N ha^{-1} yr^{-1}, which is relatively low compared to other parts of California (Weiss 2006, Fenn et al. 2010, CASTNET 2012). However, for sensitive organisms and ecosystems, effects of increased N may be detectable at levels as low as 2 - 5 kg-N ha^{-1} yr^{-1} (Baron et al. 2000, Fenn et al. 2003a, Bowman et al. 2006, Weiss 2006, Bassin et al. 2007, Pardo et al. 2011, Song et al. 2012).

Plant community composition could shift with increases in available N in the western Great Basin sagebrush steppe ecosystem. Of particular concern in the region is the spread of *Bromus tectorum* L. (also known as cheatgrass or downy brome), an invasive annual grass that has become ubiquitous throughout the Intermountain West (Mack 1981). When *B. tectorum* reaches high density, it can change the fuel dynamics of the ecosystem and trigger a more rapid fire cycle, resulting in the displacement of native flora and fauna (Stewart and Hull 1949, Inouye and Tilman 1995, Knapp 1996, Brooks et al. 2004, Link et al. 2006). At high elevation in the eastern Sierra Nevada, *B. tectorum* invasion has been limited probably by low temperatures, snowpack, or growing season length (Chambers et al. 2007, Griffith and Loik 2010), but agents of global change may facilitate its spread (Dukes and Mooney 1999). Numerous field and greenhouse studies have demonstrated that *B. tectorum* can respond to N additions with increased growth (e.g., Kay 1966, Dakheel et al. 1993, Link et al. 1995, Bilbrough and Caldwell 1997, Ball et al. 1998, Monaco et al. 2003a). However, few studies have evaluated subsequent effects on native species richness or cover in the Great Basin (but see Beckstead and Augspurger 2004) and none have been conducted at the high elevation *B. tectorum* range margin in the eastern Sierra Nevada.

We were interested in better understanding how plants in a high elevation,

arid ecosystem would respond to increased N deposition, and as a result whether *B. tectorum* dominance over native species would increase. There is evidence that ecosystem response to N is likely to vary with disturbance and land use history (Aber and Driscoll 1997, Foster et al. 2003, Mo et al. 2006, Lu et al. 2009, Pasquini and Vourlitis 2010, Lu et al. 2011), so we evaluated plant response to N in sites with different disturbance histories representative of the region (grazed, burned, and grazed-burned). Our objectives were to determine: (1) whether increases in N deposition would affect *B. tectorum* cover, herbaceous species richness or diversity, *B. tectorum* dominance over other herbaceous species, or plant community composition, (2) whether plant responses to increased N would vary on an inter-annual scale, (3) whether plant responses to increased N would vary across the landscape, and (2) whether *B. tectorum* cover was negatively related to native species diversity under ambient or increased levels of N. To address these questions, we conducted an *in-situ* experiment using paired plots that received ambient and elevated levels of N over a period of four years from 2008-2011. We hypothesized that increased N would lead to decreased biodiversity and increased dominance of *B. tectorum* in years of high rainfall, and that responses would vary across the different landscape conditions.

Methods

Study Site

This research was conducted at the Sierra Nevada Aquatic Research Laboratory (which is part of the University of California Valentine Eastern Sierra Reserve, UC VESR) and adjacent Inyo National Forest land (37º36'51"N 118º49'47"W; elevation range 2,149 to 2169 m) on the eastern slope of the Sierra Nevada, about 16 km south of Mammoth Lakes, CA. A weather station on site has been monitoring climate since 1987; during that time, annual precipitation ranged from 156 to 674 mm (mean= 313 mm; Figure 2.1a). The climate is Mediterranean and most precipitation (~75%) falls in the winter in the form of snow between November and March (Figure 2.1b). Air

temperature reaches an average minimum in January at -5 to -10^{o}C and maximum in July of about 20^{o}C.

The site is near the ecotone of Great Basin Desert sagebrush and Sierra Nevada mixed-conifer forest ecosystems. This research took place in the sagebrush zone, at the upper elevation limits of where *Bromus tectorum* has invaded. Dominant shrub species include Great Basin sagebrush (*Artemisia tridentata* Nuttall ssp. *tridentata*) and antelope bitterbrush (*Purshia tridentata* (Pursh) DC. var *tridentata*), which make up about 20- 50% of the total land cover. Other shrubs present at the site include rabbitbrush (*Ericameria nauseosa* (Pall. ex Pursh) G.L. Nesom & Baird), desert peach *(Prunus andersonii* A. Gray), and spineless horsebrush *(Tetradymia canescens* DC*)*. Open space makes up most of the land cover (~50- 75%), whereas forbs and grasses represent ~5- 30 % cover. There are no native annual grasses at the site, but a number of native perennial bunchgrasses are present, including: Indian ricegrass (*Achnatherum hymenoides* (Roem. & Schult.) Barkworth), Nevada needlegrass *(Achnatherum nevadensis* (B. Johnson) Barkworth.), bottlebrush squirreltail *(Elymus elymoides* (Raf.) Swezey ssp. *elymoides*) and needle-and-thread (*Hesperostipa comata* (Trin. & Rupr.) Barkworth ssp. Comata). A complete list of annual and perennial forbs can be found in Orr and Howald (2000).

Field Methods

In 2007, we set up fifty-four permanent 1 m × 2 m plots in three different land-use types across the landscape in grazed-unburned (GU), ungrazed-burned (UB), and burned-grazed (GB). The GU area has been grazed by cattle or sheep at least since the 1940s (in recent years at <0.25 calf/cow pairs per hectare for about a month each year) and has not burned in recent history (April Barron, personal communication). The UB area was burned on January 7, 1999 as part of a research project and rested from grazing since then with livestock exclosure fencing (Daniel Dawson, personal communication). The GB area is directly adjacent to UB and was burned in the same fire, but located outside of the exclosure. It has been grazed with the same frequency

and intensity as the GU area, both before and after the fire. Undisturbed sagebrush steppe sites (no grazing, no burning) are rare in the region, so it was not possible to fully replicate this combination. Eighteen paired plots were placed per site (half of which received ambient N and half received supplemental N; n = 54). Paired plots were located at least 0.5 m away from one another and at least 10 m from any other plot.

Because our focus was on herbaceous species, we placed plots so that they included an equal representation of the same habitat types. We identified three dominant microhabitats as distinct growing environments for herbaceous species: inter-shrub spaces (INTR), spaces under *Artemisia tridentata* shrubs (ARTR), and spaces under *Purshia tridentata* shrubs (PUTR). Inter-shrub spaces are drier, receive more sunlight, and have a shallower litter layer than under the shrubs (Griffith 2010). In contrast, under the shrubs, soil moisture is elevated, light levels are lower, and nutrient availability is higher (Griffith 2010). Nitrogen levels and plant available nitrogen are highest under *Purshia tridentata*, which forms symbioses with nitrogen-fixing actimomycetes of the genus *Frankia*, and slightly lower levels are found under *Artemisia tridentata* (Griffith 2010). Biotic interactions (including facilitation, inhibition, and competition) between herbaceous species and each of the shrubs may also differ and affect response to increased N. For these reasons, we found it important to consider microhabitat distribution when placing plots.

We aimed to place plots so that they had equal representation of the three microhabitat habitat types consistent with broader landscape patterns: ~ 25% ARTR, 25% PUTR, and 50% INTR. In reality, we were able to pair plots so that they had roughly the same distribution of habitats within each pair (e.g., both plots would have for example ~ 40% ARTR, 25% PUTR, and 35% INTR). In most cases, all three microhabitats were represented. The exception was the burned-grazed area, where *Artemisia tridentata* was sparse. In this area, many of the plots had a distribution that was closer to 10% ARTR, 40% PUTR, 50% INTR, and some had 0%

ARTR. In every case, however, plots were paired so if ARTR was missing from a plot it was also missing from its paired plot.

Each year, 5 g m^{-2} N was added to half the plots in the form of urea [$CO(NH_2)_2$]. We added N at the time of snowmelt to simulate natural patterns of nutrient delivery. In areas that experience sustained snow cover, deposited N accumulates on the snow and then infiltrates into the soil profile at the time of snowmelt (Williams and Melack 1991, Bowman 1992, Weiss 2006, Williams et al. 2009). Fertilizer applied in dry form would have likely been dispersed by wind, so we dissolved urea (equivalent to 10g N) with 6 L of water (equivalent to a 0.03 mm storm) and added it evenly across each plot, using water from Convict Creek about 1 km away. We ensured that any treatment effects were due to supplemental N rather than water by adding an equivalent amount of water to control plots at the time of N additions.

Each year in June from 2008- 2011, a quadrat was laid out over each plot and percent cover was visually estimated for all species present. Cover was categorized as: 0-1, 1-5, 5-10, 10-25, 25-50, 50-75, 75-100%. Inter-shrub space was also quantified. We measured soil nutrient status during two sampling campaigns. Before we began collecting species composition data, cation and anion plant root simulator (PRS) probes (Western Ag Innovations, Saskatoon, Saskatchewan, Canada) were inserted in the ground for one month from July to August of 2007 to estimate plant available N (Schoenau et al. 1993). Probes were 3 cm wide with a membrane area of 17.5 cm^2 and were inserted 10 cm into the soil. Samples were collected at each of the three disturbance areas (GU, UB, GB) and we made N additions to half the plots (3 replicates × 3 disturbance areas × 2 N treatments = 18 total samples). They were analyzed by Western Ag Innovations for plant available N (NO_3 & NH_4). In 2011, three samples were collected per plot in the inter-shrub space with a 2.2 cm diameter soil corer to a depth of 10 cm, sieved, dried, and analyzed for total C and N.

Data analysis

We calculated species richness (total number of species per plot) and evenness for each plot each year. Species evenness was calculated using the Shannon diversity index, Simpson's dominance index, and Simpson's evenness index. The Shannon index is most sensitive to changes in the rare species of a community, while Simpson's index is more sensitive to changes in the most abundant species (Peet 1974).

Shannon's diversity metric is calculated as:

$$H' = -\sum p_i \ln p_i$$

where p_i represents the proportion of individuals found in the *i*th species. Values for Shannon's index generally fall between 1.5 and 3.5, with higher numbers indicating more diverse communities. Data were transformed before statistical analyses by calculating $e^{H'}$ so that the values covered a wider range (Margurran 2004).

Simpson's dominance index represents the likelihood that any two organisms randomly picked from a community belong to the same species (Magurran 2004). It is calculated as:

$$D' = -\sum p_i^2$$

where p_i represents the proportion of individuals found in the *i*th species. The calculated value for *D'* increases as the dominance of some (or one) species increases over others; this metric is weighted toward the most abundant species in a sample (Peet 1974). We used Kemp's transformation, calculated as -ln(*D'*), which is a common transformation independent of sample size and recommended by Margurran(2004) and references therein.

Simpson's evenness index is calculated as:

$$E_{1/D} = (1/D')/S$$

where S is the total number of species in the sample. It ranges from 0 to 1, where a community that had perfectly even distribution of plant species would be "1".

In addition to common diversity metrics, we also calculated *B. tectorum* dominance over other herbaceous species in the community for each plot as (*B.*

tectorum cover/ total herbaceous cover)*100% where total herbaceous cover was the total cover of all non-woody species within each plot.

Statistical Analyses

We used repeated measures analysis of variance (JMP v. 9.0) to test whether the following response variables were significantly different by nitrogen treatment within each disturbance history area over the four years of the study: % cover *B. tectorum*, % cover native grasses, % cover native forbs, species richness of native grasses, species richness of native forbs, total native herbaceous species richness, *B. tectorum* dominance, and the diversity indices *H'*, -ln(*D'*), and $E_{1/D}$. We tested differences by disturbance history and by year for % *B. tectorum* using one-way Analyses of Variance. Some variables were log transformed to meet assumptions of ANOVA.

To determine whether herbaceous species composition was different by nitrogen treatment or disturbance history, we used two-way crossed analysis of similarity (ANOSIM; PRIMER 6) tests with Bray-Curtis dissimilarities. A separate analysis was run for each year from 2008 to 2011. To determine which species were most important in driving differences between sample groups, we used a similarity percentages procedure, SIMPER (Clarke 1993). When using untransformed data, the SIMPER analysis tends to highlight differences in abundant species. Transforming data can help to identify differences in rare or smaller-statured plant species by reducing the weighting of dominant species (Clarke 1993). We ran analyses using both raw data and 4^{th} root transformed data because we were interested in understanding differences in both rare and dominant species.

We used Pearson's correlation analysis to test relationships between *B. tectorum* cover and total native herbaceous species percent cover, total native herbaceous species richness, native grass percent cover, native grass species richness, native forb percent cover, and native forb species richness. We used the non-parametric equivalent, Spearman's rank-order correlation, to test relationships between *B. tectorum* percent cover and each of the diversity metrics (*H'*, -ln(*D'*), and

$E_{1/D}$) because it was clear from scatter plots that the data were heteroscedastic and that their relationships with *B. tectorum* cover were non-linear. Spearman's correlation is a rank test that describes the strength of a monotonic association (r_s) between two variables (Quinn and Keough 2002). Correlation analyses were run using data from all plots within each year, and then on subsets of data separated by disturbance area. To further explore relationships between diversity and *B. tectorum* invasion, we calculated percent change from 2008 to 2011 by plot for each diversity metric and compared them to initial *B. tectorum* cover (Pearson's correlation analyses). We then calculated percent change *B. tectorum* from 2008 to 2011 by plot and compared it to initial diversity within the plots (Pearson's correlation analyses). These analyses were designed to explore whether greater diversity conferred greater resistance to invasion, whether invasion impacted diversity, or both. We used R software for all correlation analyses (v 2.14.1, Vienna, Austria). All figures were drawn with KaleidaGraph (v 4.1, Synergy Software, Reading, PA, USA).

Results

We found that nitrogen addition treatments succeeded in increasing plant available N in soils by about 200%, and increasing total N in soils (Table 2.1). However, the increased N did not significantly impact % cover of *B. tectorum*, % cover of native species, dominance of *B. tectorum*, or species richness regardless of disturbance history or year (Table 2.2). Further, there was no difference in community composition by N treatment in any year (Table 2.3).

We identified inter-annual differences in *B. tectorum* cover ($p < 0.0001$ in UB, GU, and GB) and herbaceous species richness ($p = 0.0005$ in UB and $p < 0.0001$ in GU and GB; Figure 2.2). Species richness generally decreased and *B. tectorum* cover increased over time, particularly from 2008 to 2009 (Figures 2.2 & 2.3a, Table 2.2). Consequently, *B. tectorum* dominance over native herbaceous species increased by 170% in UB ($p = 0.02$), 330% in GU ($p = 0.0002$), and 135% in GB ($p = 0.02$) between 2008 and 2009. Within the UB plots, species richness appeared to be

declining at a greater rate in nitrogen-addition plots than controls (Figure 2.2d); however, results from the repeated measures ANOVA showed no difference by treatment ($F= 2.06$, $p=0.169$).

We found that *B. tectorum* cover varied by disturbance history ($p <0.0001$; Figure 2.3). The GB area consistently had the highest *B. tectorum* percent cover ($p \leq 0.0001$ for all years), the highest *B. tectorum* dominance over native species ($p \leq 0.0003$ for all years), and the lowest native herbaceous species richness in 2008 ($p = 0.09$) and 2011 ($p = 0.001$) but not 2009 or 2010 (Figures 2.2 & 2.3b). Analyses of similarity confirmed that there were significant differences in community composition between the disturbance areas (Table 2.3), and SIMPER analyses highlighted which species contributed to the differences (Appendix 2.1 & 2.2). Using untransformed data, *B. tectorum* was consistently the species that contributed the most to dissimilarity between communities, ranging from a contribution of 23% to 57%. Differences in all native grasses combined contributed between 21 and 37% and all forbs combined contributed between 8 and 33 % to dissimilarities. Using fourth root transformed data, a greater number of species contributed to dissimilarities (an average of 17 ± 0.3 species over all years and disturbance areas as opposed to 11 ± 0.7 with untransformed data). Notably, forbs contributed much more to the total dissimilarities (39-65%). Most forbs at the site are small stature and do not contribute much to the total biomass or vegetative cover of the system, so it was expected that their role in the community might be overlooked if we were to use raw data alone for analyses. When we totaled species cover for all years in each disturbance area, we found that some species were more abundant in the burned sites (either GB or UB) than unburned (GU), including *Pleiacanthus spinosus* and *Chenopodium album*. *Chaenactis douglasii* was present only in plots that were not grazed (UB). A number of species were found in greater abundance in the grazed alone or burned alone areas than the GB site, including *Achnathereum nevadensis*, *Elymus elymoides*, *Eriastrum wilcoxii, Gayophytum diffusum*, and *Cryptantha circumscissa*, and *Phacelia bicolor*. In contrast, *Lupinus argenteus* was more abundant in the GB plots than either GU or

UB. The combined total mean cover of all native perennial grasses was higher in UB than GB or GU in every year except 2008 (Appendix 2.1).

We found that *Bromus tectorum* cover was negatively correlated to biodiversity indices in 2009, 2010, and 2011 (we present data from 2011 as an example in Figure 2.4). The strength of these associations appeared to be driven by differences in richness of native forbs. Forb species richness was negatively correlated to *B. tectorum* % cover ($r = -0.44$, $p = 0.0008$), while grass richness was not ($p = 0.25$). Neither forb % cover nor grass % cover were related to *B. tectorum* % cover ($p = 0.17$, $p = 0.38$, respectively). Further comparisons of *B. tectorum* % cover and biodiversity were made within each land use area. In both GU and UB, initial forb species richness measured in 2008 was negatively correlated to the percent change in *B. tectorum* cover from 2008 to 2011 (Figure 2.4ac). In both GU and UB, change in *B. tectorum* cover was also related to initial $e^{H'}$ ($r = -0.53$, $p = 0.02$ and $r = -0.54$, $p = 0.02$, respectively), and $-ln(D')$ ($r = -0.46$, $p = 0.05$ and $r = -0.57$, $p = 0.01$, respectively), but not $E_{1/D}$. Conversely, initial *B. tectorum* cover measured in 2008 was negatively related to the percent change in forb species richness in GU plots (Figure 2.4d). This trend was not significant in UB plots (Figure 2.4b). Initial *B. tectorum* cover was not correlated to any of the other diversity indices in GU or UB. Percent change correlations were not significant in GB plots.

Discussion

During four years of N additions, we did not detect a difference in plant community composition or *B. tectorum* dominance in this high elevation shrub steppe ecosystem. Plants in arid environments may be less responsive to nutrient additions because they are primarily limited by water (Noy-Meir 1973). Still, studies in arid and semi-arid ecosystems have measured changes in species richness and vegetative composition with increased N deposition (Brooks 2003, Schwinning et al. 2005, Allen et al. 2009, Pasquini and Vourlitis 2010, Rao and Allen 2010, Zeng et al. 2010, Song et al. 2012). Four of these seven studies measured plant response to higher N-inputs (≥ 10 g m^{-2})

than what we used in our manipulations. It is likely that we may have measured a response by increasing the amount of N added, but not realistic for this region. Our manipulations delivered more than ten times as much N as the maximum amount that the system currently receives via deposition processes. Even low levels of N may affect the plant community in this system during years of higher precipitation. Kay (1966) found that *B. tectorum* biomass increased in response to fertilization with N at a rate of 3.4 g m^{-2} in years of high precipitation in northeastern CA. Our study site received relatively high spring precipitation during 2009 so we expected that we would see an effect of N enrichment during that year, but did not. However, total annual precipitation was below the 24-year average during all four years of our study (Figure 2.1). We might expect to see effects of N during years of higher spring precipitation. This would be consistent with past research at this same site (Chapter 1), where *B. tectorum* response to different levels of N deposition was dependent on water additions. When more water was added, *B. tectorum* responded with increased growth to lower levels of N (5 g m^{-2}) and when less water was added, *B. tectorum* only responded to higher N (10 g m^{-2}). Lastly, we may expect to see changes in the plant community with repeated N-additions over a longer time period; some longer-term studies have shown that plant community response to N can vary over time (Kay 1966, Tilman 1987, Inouye and Tilman 1995).

We measured inter-annual variation in *Bromus tectorum* cover, which was likely influenced by differences in annual precipitation and the advancing invasion of *B. tectorum*. In arid ecosystems, both wet and dry years can provide windows of opportunity for shifts in plant community composition (Holmgren and Scheffer 2001, Holmgren et al. 2001, Loeser et al. 2007, Huang and Geiger 2008). *B. tectorum* exhibits boom and bust cycles in response to annual variation in precipitation (e.g., Hull 1949; West and Yorks 2002; Bradley and Mustard 2005). In drought years, *B. tectorum* biomass can drop to close to 0%, even in highly invaded areas (Stewart and Young 1939, Kay 1966). *B. tectorum* cover was lowest in 2008, which was the driest of the four years. In 2009, the site received relatively more springtime precipitation

than other years of the study, and *B. tectorum* cover and dominance increased dramatically in all plots during that year. Link et al. (2006) found that once *B. tectorum* reaches about 45% cover, the risk of fire approaches 100%. Some plots at our site surpassed this threshold in 2009. Another year of high spring precipitation could result greater susceptibility to fire across the landscape and provide an opportunity for initiation of an invasive grass-fire cycle. In 2000, a flora of the Sierra Nevada Aquatic Research Laboratory UC Reserve, which is directly adjacent to our site, described *B. tectorum* as occurring "occasionally in disturbed areas along edge of entrance road near buildings" (Orr and Howald 2000). The increase in cover that *B. tectorum* has achieved in just nine years is alarming at this elevation and should be of concern to land managers in the region.

We found that plant community composition, species richness, and *B. tectorum* dominance varied by land use history. This is consistent with past research that found differences in species composition when comparing grazed and/or burned sagebrush steppe (Pickford 1932, Knapp 1992, West and Yorks 2002, Yeo 2005, Manier and Hobbs 2007, Davies et al. 2009). Plant community responses to disturbance may be influenced by differences in soil physical and chemical properties and herbivore pressure (Blank et al. 1994, Neary et al. 1999, Brooks and Pyke 2001, Beever et al. 2006, Scholefield et al. 2007). For example, abundance of preferred forage species (i.e., perennial grasses) was expected to be lower in grazed compared to ungrazed plots (West and Yorks 2002). Indeed, we found that the mean cover of native perennial grasses was higher in ungrazed-burned plots than grazed-unburned or grazed-burned in every year except 2011. *B. tectorum* was most abundant in the grazed-burned area compared to grazed or burned alone, which could be attributed to the increased disturbance. It is well known that disturbances facilitate plant invasions (e.g., Burke and Grime 1996, DiTomaso 2000, Keeley et al. 2003, Figueroa et al. 2004), and that grazing and fire, in particular, can promote the spread of *Bromus tectorum* (Stewart and Hull 1949, Young and Evans 1978, Mack 1981, Knapp 1996, Loeser et al. 2007). Still, Davies et al. (2009) found a pattern opposite to our results:

burning without grazing led to a large increase in *B. tectorum*, while burning with grazing did not. Likewise, while we found that species richness and diversity were consistently highest at the ungrazed site, Manier and Hobbs (2007) found that species richness was lower in ungrazed than grazed sites. Grazing exclosures at their sites were in place for much longer (42 years) than ours, which probably influenced the direction and magnitude of the response. Disturbance history and site characteristics (including, for example, the intensity of grazing, past agricultural use, dominance of invasive species, and shrub and bunchgrass cover) can have a significant influence on the response of arid and semi-arid plant communities to disturbances (Loeser et al. 2007, Davies et al. 2009).

We found strong correlations between *B. tectorum* cover and biodiversity indices every year aside from 2008. These correlations were significant within the entire dataset (thus, taking into account variation in disturbance history), but also within each disturbance area, implying that they did not simply result from disturbance. We have three hypotheses that could explain this trend: (H_1) areas of the landscape with higher diversity are more resistant to *B. tectorum* invasion, (H_2) *B. tectorum* invasion is negatively impacting native forbs through competitive displacement, and (H_3) some other driver (e.g., differences in physical or chemical properties of the soil) is influencing both *B. tectorum* cover and native species richness independent of one another. Ecological theory suggests that more diverse systems can confer increased resistance to invasion (Elton 1958) due to more complete utilization of limiting resources (MacArthur and Wilson 1967, Tilman 1997, Naeem et al. 2000, Kennedy et al. 2002). Empirical research has provided evidence to both support (Tilman 1997, Naeem et al. 2000, Anderson and Inouye 2001, Kennedy et al. 2002, Fargione et al. 2003) and refute this theory (Robinson et al. 1995, Lonsdale 1999, Stohlgren et al. 1999, Floyd et al. 2006). We did find that the initial forb species richness in each plot was correlated to the change in *B. tectorum* cover over the four years of the study in both burned and grazed sites (but not grazed-burned), which suggests that more diverse plots may be more resistant to invasion at

these sites and provides support for this hypothesis. However, this result was unexpected because many of the forb species at the site are small stature annual plants that cover an insubstantial portion of the landscape (most are <1%). In the Intermountain West, ecosystem resistance to *B. tectorum* invasion would be expected to increase with increased functional diversity (rather than total species diversity), with perennial grasses playing an especially important role (D'Antonio et al. 2009, Brooks and Chambers 2011). Some studies elsewhere in the Great Basin have found inverse relationships between perennial grass cover and *B. tectorum* cover (West and Yorks 2002, Bates et al. 2005), suggesting that established native grasses confer increased resistance to *B. tectorum* invasion (Beckstead and Augspurger 2004, James et al. 2008, D'Antonio et al. 2009). However, we did not find relationships between grass richness or cover and *B. tectorum* cover in any year.

In the burned plots, initial *B. tectorum* cover was inversely related to the change in species richness from 2008 to 2011. This suggests that *B. tectorum* invasion may contribute to declining species richness and provides support for H_2. It is well known that *B. tectorum* can replace native species after disturbance (Stewart and Hull 1949, Mack 1981, Knapp 1996), but not much evidence exists for displacement effects at the early stages of *B. tectorum* invasion. In a Sonoran Desert plant community, Olsson et al. (2012) also measured negative impacts on native species richness after invasion of an exotic grass before the grass initiated a grass-fire cycle. However, over the first 11 years of *B. tectorum* invasion into a sagebrush steppe community of eastern OR, no loss of forbs or perennial grasses was reported (Kindschy 1994). Although the time since invasion was similar, *B. tectorum* cover was relatively low (10%) at the eastern OR site compared to ours. Other studies have found effects on composition and abundance of soil biota and on nutrient cycling in response to recent *B. tectorum* invasion in perennial grass communities (Belnap and Phillips 2001, Belnap et al. 2006, Sperry et al. 2006), which could have feedback effects on native plants (Belnap et al. 2005).

Finally, some external factor may be influencing both forb richness and *B. tectorum* cover at these plots (H_3). For example, differences in nutrient availability can influence *B. tectorum* distribution across the landscape (Beckstead and Augspurger 2004, Floyd et al. 2006, Miller et al. 2006, Gundale et al. 2008) which may also influence native plants. Invasion success has also been associated with differences in soil texture, rockiness, litter layer, shrub cover, and bare ground (English et al. 2005, Miller et al. 2006, Adair et al. 2008, Gundale et al. 2008, Rao et al. 2011). Species richness did not vary by shrub cover or bare ground, but some of these other variables (which we did not measure) may have been responsible for spatial differences in community composition. The fact that we found different relationships between changing *B. tectorum* cover and species richness depending on whether plots had experienced burning and/or grazing suggests that the mechanisms causing species decline may differ by disturbance or land use history. More work is needed to adequately address this question.

In summary, we did not find evidence that increased N deposition would affect species composition or the spread of *B. tectorum* at this high elevation sagebrush steppe site. Instead, our data suggest that *B. tectorum* is already advancing and may be impacting native species richness before initiation of an invasive-grass fire cycle. During a year of high spring precipitation, *B. tectorum* surpassed the threshold in some plots for increased fire risk. Managers should monitor high elevation populations of *B. tectorum*, especially during years of high precipitation, and be prepared to initiate fuel reduction or active restoration treatments (e.g., Brooks et al. 2004, Hilty et al. 2004, Pellant et al. 2004, Diamond et al. 2009) to decrease the chances of a shift to an invasive-grass fire cycle. Our data also provide support for the ecological theory that more diverse parts of the sagebrush steppe landscape may be more resistant to invasion, which should be explored further.

Table 2.1: Chemical characteristics of soils, including total nitrogen (N; %), total carbon (C; %), C:N, plant available nitrogen (µg / 10 cm^2/ month)*, and pH for each site in control and nitrogen addition plots. Values in parentheses are SEM. Differences between nitrogen addition and control plots are indicated with p-values (ANOVA comparisons with site as a blocking factor), while NS means no significant difference.

Site	%N	%C	C:N	NO_3+NH_3	pH
Control Plots					
UNGRAZED-BURNED	0.20 (0.02)	3.06 (0.27)	15.4 (0.25)	63 (27)	5.87 (0.05)
GRAZED-UNBURNED	0.20 (0.02)	3.41 (0.32)	17.3 (0.44)	31 (3.9)	5.68 (0.07)
GRAZED-BURNED	0.19 (0.01)	2.86 (0.17)	14.7 (0.31)	50 (3.4)	5.99 (0.07)
Nitrogen Additions					
UNGRAZED-BURNED	0.23 (0.01)	2.95 (0.40)	12.7 (0.75)	97 (23)	6.60 (0.09)
GRAZED-UNBURNED	0.24 (0.02)	3.47 (0.56)	14.3 (0.37)	67 (21)	6.32 (0.08)
GRAZED-BURNED	0.24 (0.01)	3.17 (0.30)	13.5 (0.28)	98 (27)	6.53 (0.09)
Effect of Disturbance History (p-value)	NS	NS	0.0002	NS	0.0021
Effect of N (p-value)	0.046	NS	<0.0001	0.008	<0.0001

**Note: Plant available nitrogen was measured with resin probes 10 cm^2 in area buried in the soil for 3 months over the growing season, then removed and extracted for available nutrients by Western Ag. Innovations (http://www.westernag.ca/innov/).*

Table 2.2: Mean (±SEM) % cover of *B. tectorum*, % cover of all native herbaceous species combined, dominance of *B. tectorum* (*B. tectorum* cover/ total cover), and mean herbaceous species richness at the plot level over four years in control plots and N-addition plots for three disturbance histories: grazed burned (GB), grazed unburned (GU), and ungrazed burned (UB).

		% Cover *B. tectorum*		% Cover Native Herb		*B. tectorum* dominance		Species richness	
		CONTROL	NITROGEN	CONTROL	NITROGEN	CONTROL	NITROGEN	CONTROL	NITROGEN
GB	2008	7.3 (4.2)	8.9 (5.2)	9.5 (1.6)	5.1 (1.2)	42 (12)	52 (18)	9.0 (1.0)	9.0 (1.5)
	2009	30.0 (10)	29.4 (9.8)	14.1 (3.3)	13.9 (2.2)	65 (6)	62 (8)	7.2 (0.6)	8.1 (0.8)
	2010	20.8 (6.9)	19.8 (6.0)	9.5 (1.0)	7.6 (1.0)	66 (6)	72 (4)	7.7 (0.9)	8.0 (0.7)
	2011	28.1 (9.4)	29.7 (9.9)	9.7 (2.6)	9.9 (1.3)	76 (5)	74 (3)	5.3 (0.6)	6.1 (0.3)
GU	2008	1.5 (0.5)	0.9 (0.3)	11.6 (2.3)	11.4 (1.7)	13 (3)	8 (1)	10.9 (0.7)	11.0 (0.7)
	2009	8.9 (2.9)	6.7 (2.2)	14.2 (1.8)	15.6 (1.9)	39 (6)	31 (5)	7.6 (0.4)	8.0 (0.6)
	2010	9.0 (3.0)	10.7 (3.6)	8.3 (1.2)	10.1 (1.6)	48 (6)	47 (7)	10.8 (0.9)	11.5 (0.7)
	2011	12.2 (4.1)	12.1 (4.0)	5.4 (0.8)	6.8 (1.3)	68 (5)	63 (7)	6.9 (0.5)	8.0 (0.5)
UB	2008	3.3 (1.1)	5.0 (1.7)	11.5 (1.8)	13.2 (1.8)	24 (5)	26 (5)	12.0 (0.9)	11.4 (0.7)
	2009	15.3 (5.1)	14.4 (4.8)	17.9 (2.5)	21.2 (2.2)	49 (6)	40 (4)	9.2 (0.9)	8.2 (0.6)
	2010	15.5 (5.2)	14.3 (4.8)	15.9 (2.0)	17.0 (2.9)	49 (4)	44 (7)	11.9 (0.8)	10.4 (0.7)
	2011	9.3 (3.1)	13.4 (4.5)	14.3 (2.9)	14.0 (2.5)	40 (6)	45 (10)	10.3 (0.9)	7.9 (0.9)

Table 2.3: Summary of two-way analysis of similarity (ANOSIM) tests of herbaceous plant community composition by nitrogen treatment (plus N, ambient N) and disturbance history (grazed, burned, and grazed-burned) from 2008 to 2011. All data were transformed to the 4th root.

Year	Factor	R	p
2008	Nitrogen treatment	-0.035	0.760
	Disturbance history	0.236	0.002
2009	Nitrogen treatment	-0.040	0.775
	Disturbance history	0.251	0.001
2010	Nitrogen treatment	-0.080	0.985
	Disturbance history	0.211	0.001
2011	Nitrogen treatment	-0.008	0.511
	Disturbance history	0.215	0.001

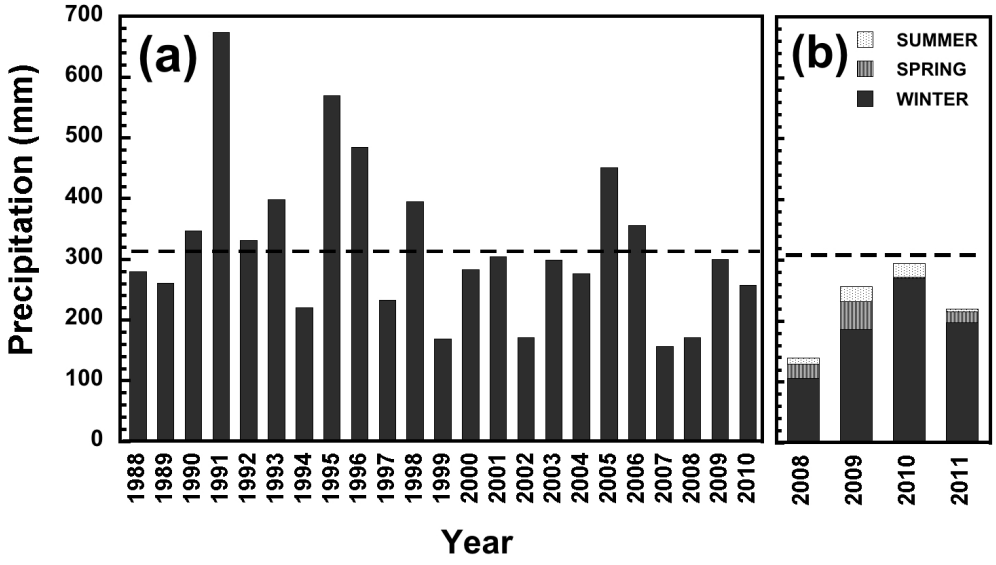

Figure 2.1: (a) Total annual precipitation measured from 1988 to 2010 (dashed line represents the 24-year average) and (b) total seasonal precipitation measured from October of the previous year to March of the year of interest (winter), April-June (spring), and July-September (summer). Data were collected at the Sierra Nevada Aquatic Research Laboratory of the Valentine Eastern Sierra University of California Natrual Reserve, < 2 km from our study plots.

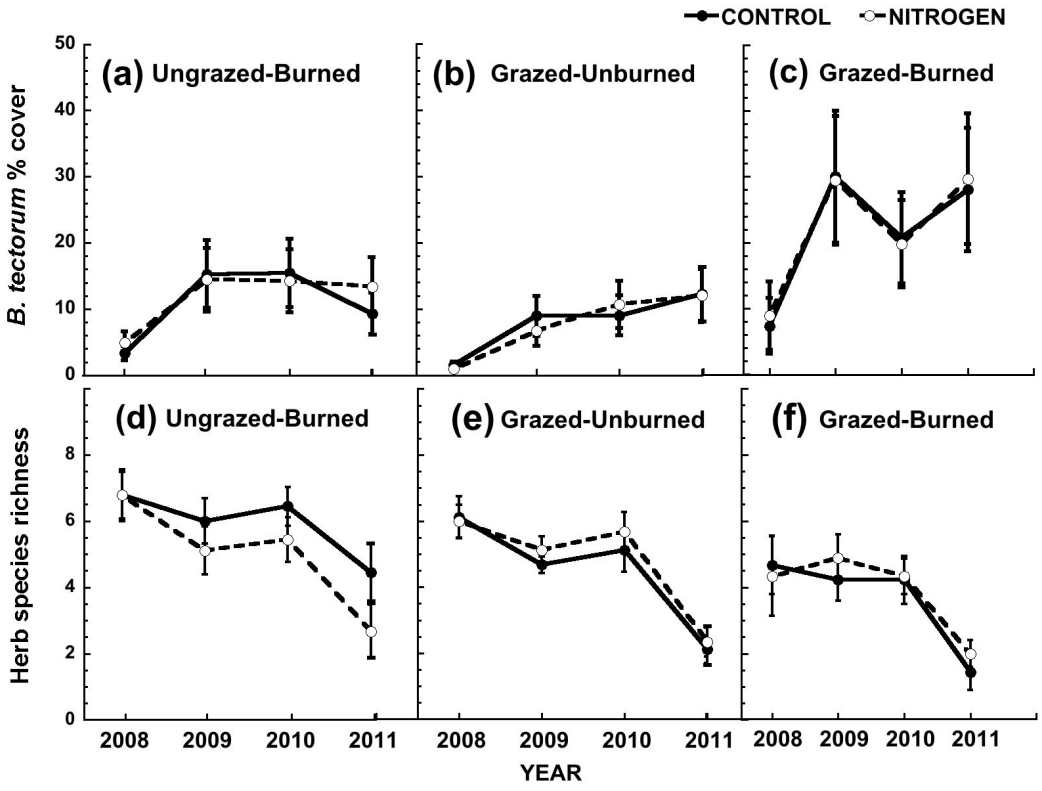

Figure 2.2: Mean *Bromus tectorum* cover (a,b,c), and herb species richness (d,e,f) measured from 2008 to 2011 in control (solid line) and N-addition (dashed line) plots in areas that were burned (a,d), grazed, (b,e), and grazed-and-burned (c,f). Bars are 1 SEM.

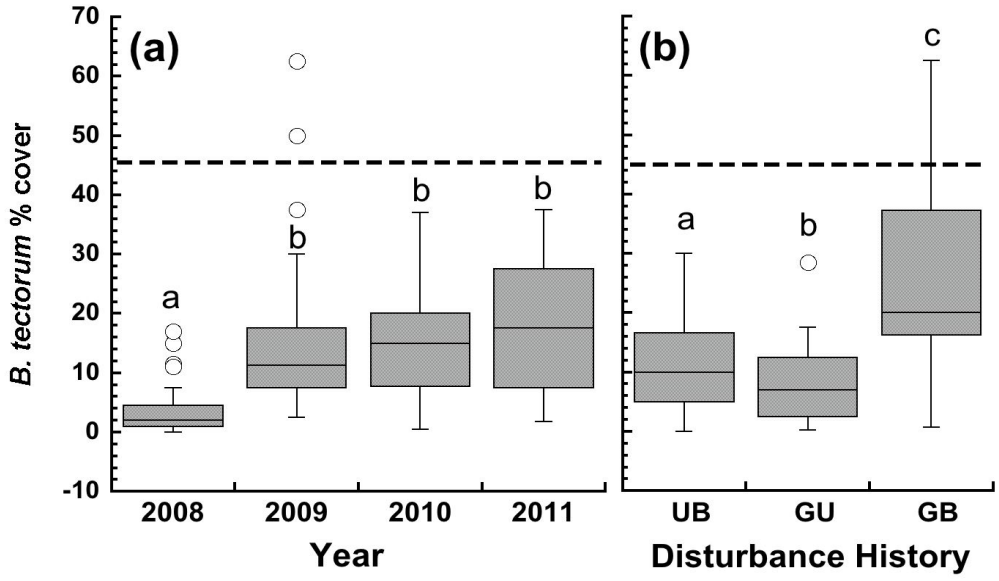

Figure 2.3: Box plots (median, 25 and 75% quartiles, minimum, maximum, and outlier values) of *B. tectorum* % cover by (a) year and (b) disturbance history including ungrazed burned (UB), grazed unburned (GU), and grazed burned (GB) plots. A dashed line is drawn at the predicted threshold in *B. tectorum* cover when fire risk approaches 100% (Link et al. 2006).

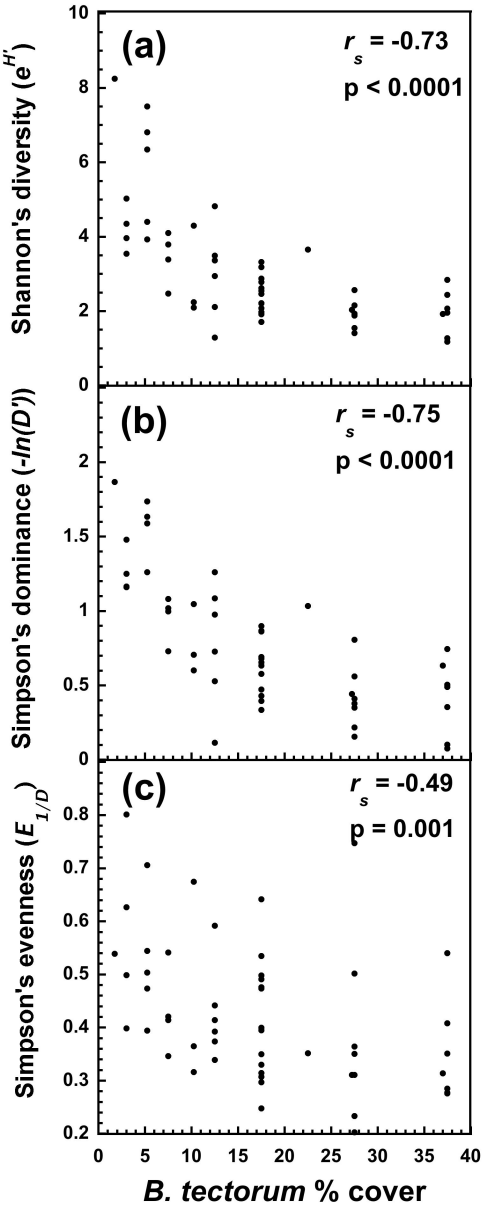

Figure 2.4: Relationships between *B. tectorum* % cover and (a) Shannon's diversity, (b) Simpson's dominance, and (c) Simpson's evenness. Spearman's rank correlation coefficient and corresponding p-value associated with each monotonic relationship appear in the upper right corner of each panel.

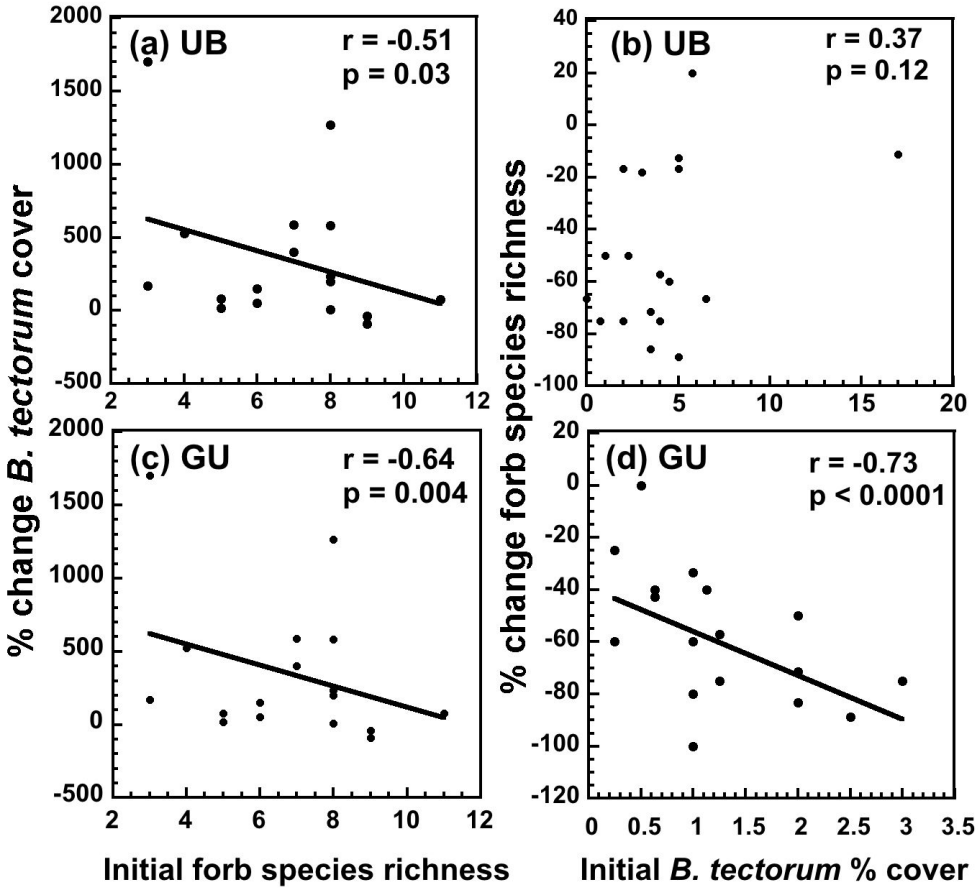

Figure 2.5: Relationships between *B. tectorum* % cover and (a) native grass cover, (b) native grass richness, (c) native forb cover, and (d) native forb richenss. Pearson's correlation coefficient and corresponding p-value associated with each linear relationship appear in the upper right corner of each panel.

CHAPTER 3

ECOLOGICAL EFFECTIVENESS AND ASSOCIATED COSTS OF *BROMUS TECTORUM* CONTROL IN THE EASTERN SIERRA NEVADA, CA

Introduction

At the edge of many plant invasions, outlier infestations can presumably facilitate spread by acting as seed sources to uninvaded sites (With 2002, Whittle et al. 2007). Targeting these patches for eradication while they are relatively small in size could significantly reduce the associated long-term costs and impacts of non-native species (Moody and Mack 1988, Mack and Foster 2009). It is well-known that invasive species control at early stages of introduction (whether it be to an entirely new landmass or to a new site within an already invaded region) is generally more cost-effective, has a higher likelihood of success, and can be accomplished using less intensive treatments than at later stages (Hobbs and Humphries 1995, McIver and Starr 2001, Theoharides and Dukes 2007, D'Antonio et al. 2009, Grice et al. 2011, Homans and Horie 2011). Targeting outlier patches for eradication has been successfully used to contain the spread of yellow starthistle (*Centaurea solstitialis*) at the leading edge of its invaded range in the western Sierra Nevada, U.S.A. (CDFA 2012c) and the hemi-parasitic witchweed (*Striga asiatica*) that attacks corn and sorghum in the Southwestern U.S.A (Mack and Foster 2009), and this strategy shows promise for being implemented more widely (Moody and Mack 1988). Here, we focus on control of a widespread invasive grass, cheatgrass (*Bromus tectorum* L.), at one of the edges of its

invaded range in the eastern Sierra Nevada, California (CA), U.S.A., where its impacts have thus far been minimal but potential future costs could be significant.

Cheatgrass is an annual grass from Eurasia, which first appeared in the U.S.A. in the mid-1800s and then spread rapidly throughout the Intermountain West (Mack 1981). It is now dominant on an estimated 20,000 km^2 in the Great Basin Desert (Bradley and Mustard 2005), with both ecological and economic impacts (Knapp 1996). At high density, it can initiate an 'invasive grass-fire cycle', creating a positive feedback loop that promotes its own persistence and spread (Stewart and Hull 1949, D'Antonio and Vitousek 1992, Brooks et al. 2004, Link et al. 2006). It germinates, completes its life cycle, and dries out earlier in the season than native perennial shrubs and bunchgrasses that dominate the system, altering fuel dynamics and instigating more frequent fires (Knapp 1996, Link et al. 2006, Baker 2011, Miller et al. 2011). Many native perennial species do not re-sprout after fire (Knapp 1996), and cheatgrass has a competitive advantage over native species at the seedling stage (Thill et al. 1984); fire thereby facilitates further invasion (Stewart and Hull 1949, D'Antonio and Vitousek 1992, Brooks et al. 2004). Once changes to the fire regime have occurred, cheatgrass control can become much more difficult and resource intensive (Brooks et al. 2004).

At elevations in the eastern Sierra Nevada, CA above ~ 2200 m, cheatgrass populations remain patchy and cheatgrass fires have not yet been documented (personal observation), probably due to physiological limitations associated with cold winter temperatures and deep snowpack (Chambers et al. 2007, Griffith and Loik 2010). However, anthropogenic climate change is likely to result in decreased snowpack and earlier snowmelt

at high elevation in the Sierra Nevada and other western US mountain ranges (Hayhoe et al. 2004, Mote et al. 2005, Cayan et al. 2008). These predicted changes could provide opportunities for cheatgrass range expansion at high elevation in the Intermountain Region (Chapter 1). Management of outlier patches at the leading edge of the invasion should be targeted for eradication to contain the invasion, conserve relatively intact native sagebrush steppe habitat, and reduce the likelihood of increased impacts on the region. Much effort has been placed on controlling cheatgrass in highly invaded areas where it has already had process-level impacts (e.g., USDI-BLM 2000, McIver et al. 2010). However, appropriate control techniques are likely to vary based on the size and impact of the infestation (Theoharides and Dukes 2007, D'Antonio et al. 2009), and less experimental work has been done testing methods that target small patches.

A combination of cheatgrass removal followed by planting native species is recommended for restoring invaded rangeland ecosystems (DiTomaso 2000, Cox and Anderson 2004, Carpenter and Murray 2009). Removal is generally necessary before revegetation because cheatgrass can create 'closed communities' that inhibit germination of native seedlings (Robertson and Pearse 1945, Rafferty and Young 2002). Combinations of herbicides, mowing, and/or burning are commonly used to remove cheatgrass with mixed results (Blaisdel et al. 1982, Mosley et al. 1999, Kaczmarski 2000, Carpenter and Murray 2009). Additional techniques that would be feasible on a small scale include hand-pulling, mulching, tarping, and soil seed bank solarization (Tu et al. 2001), each of which have long histories of use in agricultural systems (e.g., Parish 1990, Lodha and Solanki 1992, Vizantinopoulos and Katranis 1993, Elmore et al. 1997, Bond and Grundy 2001) and have

increasingly been used in wildland settings with mixed success (e.g., Banerjee et al. 2006, Hutchinson and Viers 2011, Lintz et al. 2011, Nyamai et al. 2011). After invasive species removal, revegetation with native species is often recommended to increase the likelihood that the site will be colonized by natives rather than disturbance-adapted exotic species (Masters and Sheley 2001, Carpenter and Murray 2009). If the native seed bank is intact, seeding natives may not be necessary (West and Hassan 1985).

Although herbicide use may show promise for eradicating small infestations of cheatgrass (Carpenter and Murray 2009), its logistic feasibility in eastern CA is questionable. Most of the land in the region is publically owned and administered by the USDI Bureau of Land Management (BLM) and USDA Forest Service (92% and 85% in Inyo and Mono Counties, respectively; Agricultural Commissioner's Office 2012). Cheatgrass also exists along roadsides under jurisdiction of the California Department of Transportation (Caltrans). Land managers working on weed management within these agencies are constrained by federal and state laws that restrict herbicide use. Each new weed control project is subject to an environmental analysis and public review process under the National Environmental Protection Act, and negative public opinion of herbicides can stall a weed control project for many years (K. Nelson, personal communication). In 1982, Caltrans committed to reducing its herbicide use by 80% along roadsides in CA, resulting in strict rules about how and when chemical use is permitted within the agency (R.S. Miller, personal communication). Land managers at federal agencies also have economic constraints and rely heavily on help from volunteers for weed control work (S. Weiss, personal

communication). Spraying herbicides involves human-health risks and requires training, and it would be inappropriate for volunteer groups. Consequently, we chose to test effectiveness of low-cost non-chemical methods of cheatgrass control that could be incorporated into long-term projects conducive to environmental education or work with volunteer groups.

We tested the effectiveness of three control methods aimed at removal of cheatgrass: hand pulling, mulching, and soil solarization, followed by two seeding treatments: broadcast and seedball seeding. Seedball seeding was developed in Japan to increase successful germination and establishment of agricultural species and for revegetation of arid lands (Fukuoka 1978); it involves mixing seeds with clay and humus to protect them from predation and harsh environmental conditions (Caplan et al. 1999). It has since been used in numerous restoration projects around the world with anecdotally successful results (Bones 2012), but few studies have experimentally tested the method (but see Caplan et al. 1999). We predicted that methods of cheatgrass removal targeting the seed bank (e.g., mulching, soil solarization) would be more effective than hand pulling; that seeding following cheatgrass removal would be more successful than removal alone; and that seedball seeding would be more successful than broadcast seeding in decreasing cheatgrass abundance and restoring the native plant community. We evaluated treatments based on ecological, logistical, and economic feasibility recognizing the need for more integrated approaches to weed management (Anderson et al. 2003, Chambers and Wisdom 2009).

Methods

Study Sites

This research was conducted in the eastern Sierra Nevada, CA, at the western edge of the Great Basin Desert. Research plots were set up at two main sites: on the campus of Cerro Coso Community College (Cerro Coso) in the town of Mammoth Lakes, CA, U.S.A. (37.64°N 118.97°W; elevation ~ 2400 m), and in the Inyo National Forest around the Sierra Nevada Aquatic Research Laboratory (SNARL) about 16 km south of Mammoth Lakes (37.61°N 118.82°W; elevation ~ 2150 m), referred to hereafter as Cerro Coso and SNARL. The climate is Mediterranean, with ~75% of the annual precipitation falling as snow between November and March. Cerro Coso receives more precipitation, averaging 651 ± 218 mm yr^{-1} (mean ± SD; 20-year average; collected at the Mammoth Lakes Ranger Station located ~2.5 km from the study site, Western Regional Climate Center (WRCC) 2012). SNARL receives an average of 313 ± 132 mm yr^{-1} (24-year average; measured at an on-site weather station located at SNARL < 2 km from research plots); both sites have high inter-annual variability of precipitation. At both sites, mean daily air temperature reaches a minimum in January (of -5 to -10^{o}C) and a maximum in July (between 20 to 25^{o}C).

Both sites are located within the shrub steppe ecosystem, but species composition is different. The Cerro Coso site is more disturbed by development and contains more non-native species and ornamental plantings. Dominant shrub species at the site include *Artemisia tridentata var. vaseyana* (mountain sagebrush), and *Dasiphoa fruticosa* (shrubby cinquefoil), *Ericameria nauseosa* (rabbitbrush), *Purshia*

tridentata (antelope bitterbrush), and *Arctostaphylos patula* (greenleaf manzanita). A number of native and non-native grasses and forbs are present at the site; some of the most common include *Elytrigia repens, Bromus tectorum, Leymus triticoides, Poa annua, Epilobium brachycarpum*, *Melilotus alba, Machaeranthera canescens*, and *Verbascum thapsus*.

SNARL is dominated by two widespread shrub species: *Artemisia tridentata* (mountain sagebrush) and *Purshia tridentata* (antelope bitterbrush), which make up about 20% each of the total land cover. The remaining 60% is primarily open space with < 10% herbaceous cover and perennial grasses. A number of native forbs and grasses populate the site (see Orr and Howald (2000) for a complete species list). Soils at the site are derived from Holocene deposits of alluvium and stream gravels, and are composed of sandy loam and gravelly sandy loam (Orr and Howard 2000).

Field methods

At Cerro Coso, four restoration treatments were applied between 2009 and 2011 including: control (C), mechanical removal by hand pulling with no seeding (PN), mechanical removal by hand pulling followed by seeding (PS), and sheet mulching (M). Within the PS plots, we tested two different seeding methods: broadcast and seedball. The plots were located throughout a parking area in 12 irregularly shaped island planters ranging in size from 25 to 66 m^2 that were all invaded by cheatgrass at the start of the experiment. Each treatment was replicated three times on full island

planters (the PS plots were split: half of each planter received seedballs and half received broadcast seeding).

Manual pulling treatments were applied in 2009 and 2010 in the late spring (June) when most (> 75%) of the cheatgrass had flowered but not yet set seed. For PN and PS treatments, all cheatgrass was hand pulled from plots, removed completely from the site, air dried, weighed, and then disposed. Plots that were pulled and seeded received a seeding treatment the following October. For both seeding treatments, a mix of six native bunchgrasses and perennial forbs were used at a rate of 10 kg ha^{-1} (Table 1), which is within the range of other sagebrush steppe restoration projects (Ratzlaff and Anderson 1995, Pierson et al. 2007). All seeds were obtained from stock local to the eastern Sierra Nevada and collected by Comstock Seed, Inc. (Gardnerville, Nevada). For the broadcast seeding treatment, we mixed seed with sand from the site and spread it evenly across the entire plot (excluding shrub covered areas) in late October. Seedballs were prepared by mixing three parts dry compost (Enriched Planting Compost, Supersoil, Scotts Company, LLC) to five parts dry clay (Lincoln Fire Clay, Gladding McBean Division, Pabco Clay Products, LLC) with one part seeds, adding one part water, and forming them into ~ 2.5 cm diameter balls. We dispersed seedballs in the spring of 2009 and 2010 evenly throughout the plots. The sheet mulching treatment was done at Cerro Coso in the summer of 2009. We covered plots completely (aside from space occupied by shrubs and perennial forbs and grasses) with two layers of cardboard followed by a 10-15 cm layer of wood and

bark chips from a local mill, mainly comprised of shredded Jeffrey pine (*Pinus jeffreyi*; G.C. Forest & Firewood Products, Mammoth Lakes, CA).

At SNARL, we compared soil solarization treatments with (SS) and without seeding (SN) to control (C) plots. In May 2010, we set up three groups of plots placed at least 1 km apart from one another at sites that were invaded by cheatgrass. Plots were located in open spaces between shrubs and perennial grasses. Each group contained 12 total 1 m^2 plots; six received the soil solarization treatment and six acted as controls. Soil solarization was accomplished by heating moist soil to high temperature over an extended period (Elmore *et al.* (1997) recommend at least 4-6 weeks). To prepare the plots, we used shovels and hoes to break up the ground, dug a 5 cm deep trench with 10 cm of buffer space around each plot (total area per plot and buffer = 1.44 m^2), and saturated the soil by adding 10 mm of water evenly across each plot. Clear 4-mil (0.100 mm) polyethylene plastic was then laid over the entire plot and buffer area. The corners of the plastic were nailed into the ground, the edges were secured into the trenches, and soil was tucked around the edges so that the plastic was airtight. We checked on the plastic weekly throughout the summer and repaired any rips or tears with clear tape. Plastic remained on the soil for a total of 52 days (from June 1- July 22, 2010). During that time, mean (±SD) daily air temperature was 15.9 ± 3.2°C, maximum daily air temperature averaged 26.4 ± 3.7°C, and there were 31 consecutive days from mid-June to late July when maximum air temperature exceeded 25°C. Precipitation events occurred on four days (on June 21 and July 7, 16, and 17), but the weather was generally sunny and clear.

In October, we seeded half the solarized plots (3 per group of 6; SS) with the broadcast seeding method (Table 1).

To determine effectiveness of restoration treatments, we measured cheatgrass density and % cover pre-treatment (in 2009 at Cerro Coso and 2010 at SNARL), and cheatgrass density, cheatgrass and native species % cover, and cheatgrass dominance in the seed bank post-treatment (2010 and 2011 at Cerro Coso and 2011 at SNARL). At Cerro Coso, we used a grid system to randomly identify sampling points within the plots, taking measurements at 1.5 m intervals throughout the entire plot with a 0.5 m buffer from the edge (sample sizes ranged from six to 15 per plot). At SNARL 50 × 50 cm^2 plots were sampled in the center of each 1 m^2 plot. In June of each year, we laid out a 50 × 50 cm^2 quadrat plot sectioned into 16 equal squares at each sampling point. We measured cheatgrass density by counting every individual in a 12.5 × 12.5 cm^2 subplot in the southeast corner of each plot. The only exception was that we counted individuals within the full plot in post-treatment solarized plots since density was low. In 2009 and 2011 at Cerro Coso, we collected aboveground cheatgrass biomass samples within the same subplots, dried them (48 hrs at 60^oC), weighed them, and calculated biomass m^{-2}. We visually estimated cheatgrass, native forb, and native grass cover in the same location, but within the full 50 × 50 cm^2 plot, with the following categories: 0-1%, 1-5%, 5-10%, 10-25%, 25-50%, 50-75%, 75-100% cover.

We collected samples for seed bank analysis every year in October (before seeding treatments). At Cerro Coso, we sampled along a grid system at 1 m intervals

in C, PN and PS plots (not M), with sample sizes ranging from 16-34 per plot. At SNARL, we collected three samples per plot. We collected soil inside of a 33-cm^2 cylinder (6.5 cm diameter) inserted to a depth of 10 cm. Seed bank analysis was not done on samples from mulched plots because sampling under the thick mulch and cardboard layers would have disturbed the plots and potentially decreased the effectiveness of the treatment.

We quantified species composition in the seed bank with germination tests at the UCSC Plant Growth Facility. Tests for Cerro Coso plots took place in 2010 and 2011 between January and May, and tests for SNARL plots took place in 2011 only. Each sample was placed atop 5 cm of potting soil in a 288-cm^3 pot with a surface area of 64 cm^2. Pots were watered daily with a mister at 10:00 and 14:00. Ambient light was supplemented with overhead lights each day from 5:00 to 9:00 and from 17:00 to 19:00, for a consistent 15 hours of light per day. Mean daily air temperature for the duration of the experiment was 15.6 ± 3.9^oC in 2010 and 20.0 ± 1.7^oC in 2011, reaching a maximum each day between 14:00 and 16:00 at ~ 20^oC in 2010 and 22^oC in 2011 and a minimum between 0:00 and 4:00 at ~12^oC in 2010 and 19^oC in 2011. We surveyed pots weekly, counting and identifying each seedling until no new seedling growth had occurred for at least three weeks (3.5 months total in 2010 and 4 months in 2011). Seedlings were identified to the species level when possible, and categorized as forb, shrub, grass (excluding cheatgrass), or cheatgrass.

We kept a record of person-hours spent and cost of supplies for each of our control treatments, and then calculated costs on a per area basis. Our costs for

materials were minimal because we capitalized on local, free sources of cardboard and tree bark mulch. Assuming that land managers might not have the same opportunities, we calculated costs using average online prices from the top two retailers in CA. We calculated hourly costs of labor based on USDA Forest Service base pay for a General Schedule (GS)-7 level employee, which is currently set at $16.28 per hour (OPM 2012).

Statistical Analyses

Differences in cheatgrass cover and density between treated plots were tested in pre-treatment and post-treatment years within each site. Nonparametric analyses were used because there were a large number of treated subplots with "0" cheatgrass individuals and the data could not be transformed to fit a normal distribution. We tested pre-treatment differences in cheatgrass density and % cover between C, P, and M at the Cerro Coso site in 2009 and post-treatment differences between the same groups in 2010 and 2011 using Kruskal-Wallis one-way analysis of variance tests with post-hoc Steel-Dwass comparisons (a non-parametric version of Tukey HSD based on ranks; Neuhauser and Bretz 2001). Cheatgrass cover and density were compared between C and S at the SNARL site with Mann-Whitney U tests in 2010 (pre-treatment) and 2011 (post-treatment).

Native species % cover was compared by treatment within each site in 2011 using the same analyses described above. Cheatgrass dominance was calculated as cheatgrass % cover divided by total % cover of all herbaceous species for each plot

and compared by treatment at each site (again, using Kruskal-Wallis tests with Steel-Dwass comparisons for Cerro Coso plots and Mann-Whitney U tests for SNARL).

Cheatgrass displays wide inter-annual variation (Mack and Pyke 1983) so we also used before-after within-plot comparisons of density to ensure that any treatment effects we measured were due to treatments rather than natural variation. We calculated % difference in cheatgrass density between plots at Cerro Coso from 2009 to 2010 (1 year post-treatment) and from 2009 to 2011 (2 years post-treatment) and then compared treatments (C, P, and M) using Kruskal-Wallis tests with post-hoc Steel-Dwass comparisons. For solarization treatments, we calculated % difference in cheatgrass density and cover from 2010 to 2011 within each plot and compared C and S treatments using Mann-Whitney U tests.

Cheatgrass dominance in the seed bank was calculated as the number of viable cheatgrass seeds divided by the total number of viable seeds and compared by site between C and P in 2010 and 2011 and between C and S in 2011 using Mann-Whitney U tests. We also compared PS to PN and SS to SN. However, neither the broadcast nor the seedball seeding method resulted in successful germination of seeded species, so we pooled PS and PN plots (P) and SN and SS plots (S) for most of our analyses.

All statistical analyses were run using JMP (v 9, SAS Institute, Inc., Cary, NC, USA). Means are reported with standard errors (mean ± 1 SE), and we considered differences between means to be significant when *P*-values were <0.05 ($\alpha = 0.05$).

Results

All restoration treatments resulted in a decrease in cheatgrass density compared to control plots and to pre-treatment conditions (Figure 3.1). Density was reduced by 80% ($Z= -4.71$; $P < 0.0001$) and 99% ($Z = -5.78$; $P < 0.0001$) after one year of treatments in pulled and mulched plots, respectively. After two years, density was reduced even further in pulled plots (by 94% compared to pre-treatment; $Z = -5.34$; $P < 0.0001$) and remained low in mulched plots ($Z = -5.07$; $P < 0.0001$; Figure 1a). Cheatgrass biomass decreased by 89% two years post-treatment in both pulled ($Z= -4.20$; $P < 0.0001$) and mulched ($Z= -4.20$; $P < 0.0001$) plots compared to controls (from 49 ± 14 g m^{-2} to 5.4 ± g m^{-2} after pulling and 5.5 ± g m^{-2} after mulching treatments). Soil solarization led to a large decrease in cheatgrass density compared to control plots: from an average of several thousand to 17.6 ± 3.60 individuals m^{-2} ($Z = 26.3$, $P < 0.0001$; Figure 1b).

Treatments had varying effects on herbaceous species cover and cheatgrass dominance (Figure 3.2). Pulling had no effect on native species % cover compared to control plots ($Z = -0.62$; $P = 0.81$), but cheatgrass cover was reduced ($Z = -5.12$, $P < 0.0001$) (Figure 3.2a). Cheatgrass dominance over native species consequently decreased from 54% to 22% ($Z = -4.12$; $P = 0.0001$). Both cheatgrass ($Z = -4.67$; $P < 0.0001$) and native species % cover ($Z = -2.49$; $P = 0.034$) decreased with mulching compared to the control plots. However, because the decrease in cheatgrass cover was greater than that of native species, cheatgrass dominance was reduced with

mulching treatments to 18% (compared to 54% in control plots; Z= -3.48, P = 0.0014). Native species cover did not differ between solarized plots and controls (Z= -0.09, P = 0.92), but cheatgrass % cover decreased from an average of 52.9 ± 5.53 % in the control plots to 1.0 ± 0.38 % cover in solarized plots (H =27.9, P < 0.0001) (Figure 3.2b). Dominance of cheatgrass over native species was subsequently reduced in solarized plots (43 ± 5.9%) compared to control plots (96 ± 1.7%; H = 25.6, P < 0.0001).

Our seeding treatments were unsuccessful one and two years post-treatment. We saw no evidence for germination of any seeds from seedballs or in broadcast seeded plots at Cerro Coso. At SNARL, we counted and identified all germinating seedlings in 2011 and found little difference between control and seeded plots. There were a total of 32 native individuals growing in all of the solarized plots combined, six of which were seeded species. In comparison, we counted 21 individuals in control plots, three of which were seeded species.

Although we sampled a limited number of sites, our plots represented a wide range of invasion impact (i.e., from low to high density infestations of cheatgrass). Cheatgrass density did not differ pre-treatment between C, M, or P plots at Cerro Coso (H = 2.3, P = 0.511), or between C or S plots at SNARL (Z = 0.0063, P = 0.937), but there was a lot of variability at the plot level. Density ranged from 594 ± 343 to 6821 ± 3441 ind m^{-2} at Cerro Coso, and from 1883 ± 99 to 5750 ± 651 ind m^{-2} at SNARL. Before-after comparisons within each plot confirmed that cheatgrass declined in response to the restoration treatments regardless of initial level of

infestation, while control plots showed different patterns of inter-annual variability (Figure 3.3).

Cheatgrass dominance in the soil seed bank mirrored patterns that we measured in the field (Figure 3.4). At Cerro Coso, cheatgrass seeds made up 48 ± 5.5% of the diversity in soils from the control plots. In comparison, cheatgrass was reduced to 5.1 ± 1.4% of the seed bank after two years of pulling treatments (Figure 4a). Decreased dominance of cheatgrass in the seed bank after pulling was influenced by both a reduction in cheatgrass seed density ($Z = 6.83$, $P < 0.0001$), and an increase in native seeds ($Z = -2.37$, $P = 0.018$). At SNARL, cheatgrass seeds made up 78 ± 5.2% of the total seed bank in control plots (Figure 3.4b). After soil solarization, there was a dramatic decrease in viable cheatgrass seeds ($Z = 64.32$, $P < 0.0001$). However, there was also a complete elimination of viable native grass ($Z = 4.12$, $P = 0.043$) and forb seeds ($Z = 7.41$, $P = 0.0065$).

We calculated costs associated with each treatment per m^2 (Table 3.2). The time required for hand pulling varied based on the density of the infestation. We pulled five times more cheatgrass out of plots in 2010 compared to 2009 (at a total of 35 kg dry mass in 2009 compared to 7 kg over an area of 116 m^2). Consequently, it took 32 hours in 2009 and was reduced to 20 hours in 2010 to clear the same area. All other costs were calculated for one year of treatment only. We found that labor costs were highest for soil solarization, at double the cost of two years of hand pulling. Sheet mulching cost considerably less in person-hours than other removal

treatments, but materials costs were the highest. Out of all treatments, combined costs of labor and materials were highest for soil solarization.

Discussion

We found that low-tech, non-chemical methods of control were effective at decreasing cheatgrass dominance both in the field and in the seed bank at high elevation sites in the eastern Sierra Nevada, CA. Manual pulling decreased cheatgrass density by 80% after one year and 94% after two years, and both soil solarization and sheet mulching reduced cheatgrass density by 99% after just one season of treatment. Although all methods were successful in reducing cheatgrass, they differed in their ecological impacts, logistical feasibility, and associated costs. Strengths, weaknesses, and suggested use of each method are outlined in Table 3 and discussed below.

Ecological impacts of treatments

We found that more effective cheatgrass control was accompanied by greater impacts on non-target organisms. The hand pulling treatment had a positive effect on native plants, but was less effective at reducing cheatgrass abundance than other treatments. Although cheatgrass was greatly reduced in the seed bank, it was not eliminated after two years of hand-pulling treatments. Cheatgrass seeds can remain viable in laboratory storage for at least 11.5 years (Hulbert 1955), and a large number of viable caryopses can persist from one year to the next in the field (Young et al. 1969, Mack

and Pyke 1983). Control measurements that require individuals to germinate to be effective, such as hand-pulling treatments, need to be conducted annually and resurveyed for several years to ensure that the seed-bank becomes depleted. Also of concern is the likelihood of cheatgrass seed dispersal to new sites. In reclamation areas with bare soil, Johnston (2011) reported a maximum dispersal distance 50 times higher than those that had previously been reported in intact sagebrush steppe. Even if cheatgrass cover and density is greatly reduced with hand pulling, it is unlikely to be effective at preventing spread along roadsides and other disturbed areas where dispersal is high. By contrast, sheet mulching and soil solarization were highly effective at cheatgrass control with just a single treatment, but both had negative impacts on native species.

Sheet mulching acts to physically suppress herbaceous cover in the areas where it is applied and prevents germination of viable seeds by excluding light (Teasdale and Mohler 2000, Bond and Grundy 2001). We applied mulch around the bases of perennial plants (which all survived), but most annual plants growing in the spaces between shrubs and bunchgrasses were killed. If treatments are not repeated, the cardboard and mulch additions will eventually decompose enough for soils to support annual plants. However, soil chemical and physical characteristics can change with mulching. Nitrogen (N) may be immobilized in response to the increased input of organic material (Zink and Allen 1998, Bond and Grundy 2001, Cione et al. 2002), which could have negative or positive effects on native plants. Annual plants often (but not always) respond positively to increases in N, and N

immobilization can consequently decrease their competitiveness (Zink and Allen 1998, Vinton and Goergen 2006, Blumenthal 2009). The plant community may be affected by mulching treatments long after most of the mulch has physically broken down.

Soil solarization treatments were highly effective at killing cheatgrass seeds, but also caused significant non-target impacts. The climate of the Great Basin Desert is ideal for solarization, which requires long periods of clear skies and high solar radiation to maintain high temperatures under plastic sheeting (Bond and Grundy 2001). The treatment was indiscriminate and acted to kill all native seeds in at least the top 10 cm of the soil (which is the depth we sampled for seed bank analysis), making it inappropriate for some sites. Though not measured here, solarization can also have non-target effects on soil microbial communities (Ristaino et al. 1991, Lodha and Solanki 1992, Scopa and Dumontet 2007) and nutrient cycling (Chen and Katan 1980, Arora and Yaduraju 1998, Chen et al. 2000). Positive effects on plant growth have been measured in response to solarization, at least partly due to an accompanying increase in available nutrients (Chen et al. 2000). Microbial populations are negatively affected by soil heating, but beneficial bacterial and fungal communities are thought to quickly recolonize the site (Elmore et al. 1997). There is evidence that negative effects on microbial communities can be minimized by adding organic amendments before treatments (Scopa and Dumontet 2007). However, most research on soil solarization has been done in agricultural systems (e.g., Ristaino et al. 1991, Lodha and Solanki 1992, Hartz et al. 1993, Vizantinopoulos and Katranis 1993,

Arora and Yaduraju 1998, Scopa and Dumontet 2007, Scopa et al. 2009), and microbial and plant responses to treatments is likely to be different in an arid, low-biomass system like the Great Basin Desert. Organic amendments via pre-treatment or inoculation with native micro-flora after solarization treatments in arid systems may be warranted and deserves further investigation.

We found very little evidence of successful germination or establishment with our seeding treatments. Both seed predation and dormancy can act to inhibit or delay re-vegetation attempts in arid rangeland systems (Archer and Pyke 1991, Monsen and Stevens 2004, DeFalco et al. 2012). We expected that the seedball method (which is designed to protect seeds from predation) would be more successful than broadcast seeding. The fact that germination was low in both treatments signifies that climate may have been a bigger influence than predation. Other researchers have also found poor germination with seeded native grasses and shrubs in arid rangelands due to dry conditions (Ethridge et al. 1997, Monsen 2004, Jessop and Anderson 2007, Owen et al. 2011). Desert species are known to display high variability in germination from year to year, and may require 'windows of opportunity' with optimal moisture and temperature conditions to germinate and establish (Holmgren and Scheffer 2001, Abbott and Roundy 2003, Monsen and Stevens 2004, Pugnaire et al. 2006). Tests of seed characteristics before seeding treatments showed that viability was high for most species (ranging from 43-98%), but dormancy was also high (39-98%; Comstock Seed test data). We are likely to find evidence for establishment of seeded native species at our sites in future years with more precipitation.

Seeding with different methods or species could contribute to increased success. Due in part to the difficulty of re-seeding natives, varieties of the exotic perennial crested wheatgrass (*Agropyron cristatum*) have been used somewhat indiscriminately to re-vegetate damaged or recently burned rangelands (Asay et al. 2003, Beyers 2004). However, the practice is controversial because crested wheatgrass can become weedy and form near monotypic stands that inhibit natives from establishing (Marlette and Anderson 1986, Fansler and Mangold 2011). In response, methods have been developed that increase success of native re-vegetation. For example, seed mixes containing annual species (Forbis 2011) or drought-adapted strains (Monsen and Stevens 2004) are recommended to decrease the time to germination and likelihood of establishment in arid rangelands. During Caltrans roadside re-vegetation projects in the eastern Sierra Nevada, ten different species are used in seeding mixes, including annuals and perennials, with anecdotally good success (R.S. Miller, personal communication). The disturbance-adapted shrub rabbitbrush (*Ericameria nauseosa*) and annual forbs are generally the first to colonize the site, followed by native grasses and other shrubs a few years later (R.S. Miller, personal communication). Increased germination success of native perennial grasses has been achieved with matric priming (Hardegree and Emmerich 1992, Hardegree 1994, 1996, Pill et al. 1997, Pill and Necker 2001), where seeds are partially hydrated (ideally to a point just before radicle emergence) before being broadcast (Heydecker and Coolbear 1977). This induces faster germination at lower temperatures, which increases their competitiveness with cheatgrass (Hardegree 1994). This method may

not be practical on a large scale, but would be feasible on the scale that we are interested in here. These or other seeding methods, such as seeding genetically improved cultivars of native plants (Asay et al. 2003, Monsen and Stevens 2004), using higher seeding rates (Sheley et al. 2005), or using different methods of seedbed preparation (e.g., Young et al. 1994, Ethridge et al. 1997, Gutierrez et al. 2004, Monsen and Stevens 2004, James and Svejcar 2010), might improve germination success at high elevation eastern Sierra Nevada sites.

In prioritizing sites for invasive species removal and choosing appropriate methods, it is important to consider the biotic exchange that is likely to take place after the treatment (D'Antonio and Meyerson 2002). Decisions about whether to attempt re-vegetation or use a treatment that is known to deplete the native seed bank should be made on a site-to-site basis with an understanding of likelihood of dispersal of native and exotics in the surrounding area. We found that the native seed bank was not totally depleted at our site, so re-vegetation may not be necessary after cheatgrass removal unless treatments are used that eliminate the native seed bank (such as soil solarization). Hand pulling served to decrease viable cheatgrass seeds while maintaining the native soil seed bank, increasing the ratio of native seed to cheatgrass seed. Although tedious and time-consuming, hand pulling may be the best option for cheatgrass control at many sites in the region. Sheet mulching and soil solarization should probably only be used in areas that are highly disturbed or densely populated by cheatgrass. Sheet mulching would be practical for landscaping disturbed areas adjacent to wildlands, such as roadsides, pack stations, or parking areas. Soil

solarization would be best suited to dense cheatgrass patches surrounded by native species, far from non-native seed sources, such as old sheep bedding areas.

Economic and logistical feasibility of treatments

In addition to the ecological considerations outlined above, there are economic and logistical considerations that should be evaluated in choosing an appropriate cheatgrass control method. The calculated cost estimates of our experimental treatments presented in Table 2 provide a guideline, but we expect materials costs and person-hours to vary by project, cheatgrass dominance (i.e., area covered), and other site factors. Materials costs for hand-pulling were minimal (it only includes the price of plastic bags and travel to the site), but costs of soil solarization and mulching are dependent on the price for plastic sheeting and mulching material. We located free sources of materials for sheet mulching so actual costs were much lower than the calculated costs that we presented. Purchasing mulch may be cost-prohibitive. However, a wide variety of mulching materials have been used with success in agricultural settings (Teasdale and Mohler 2000, Bond and Grundy 2001). In another restoration project, chipping and composting one invasive species was successfully used as mulching material to suppress another (Lintz et al. 2011). We would encourage the creative use of free or low-cost mulching material.

Costs for treatments may also vary based on pay rate. The pay rate we used to calculate hourly costs does not include the cost of health care or other benefits that many employees receive; actual costs may, therefore, be higher than our calculated

costs. However, all of the methods we tested require little training and have no significant safety hazards associated with them. They would all be well suited for volunteers, which could substantially reduce labor costs.

The location of an infestation can affect both labor and transport costs. The travel distance to sites would affect cost regardless of treatment method used. For sheet mulching, the distance between the site and mulching material would also be important- particularly for larger infestations that require multiple trips. The large volume of mulch needed to cover an area and effectively control weeds can make transport costs prohibitive (Bond and Grundy 2001).

The scale of the infestation is an important consideration for any invasive species control project. All of the methods that we tested here were meant to target small patches and would probably not be realistic for infestations greater than ~50 m^2. Other methods that would be more appropriate for larger-scale infestations include managed grazing, mowing, herbicide application, or prescribed fire, all of which have associated drawbacks, costs, questionable effectiveness, and potential effects on non-target species (Pellant 1996, Carpenter and Murray 2009, D'Antonio et al. 2009, Diamond et al. 2009, Mack 2011). Planting strips of fire-resistant vegetation to stop or slow the spread of wildfire appears to be a successful strategy for decreasing the impacts of cheatgrass-fires (Pellant 1996). Planting competitive native bunchgrasses around an infestation can increase ecosystem resistance to the invader and slow the spread to surrounding areas (D'Antonio et al. 2009, Davies et al. 2010). These types of treatments that act to contain the invasion would be complementary to the methods

we tested by providing a line of defense between areas of the landscape that are highly infested and areas with low-density or outlier patches. Realistically, it would be impractical and a waste of resources to eradicate outlier patches without some attempt to reduce the chances of re-introduction.

Because of the vast area of land that cheatgrass covers, the costs and time commitment to reduce its presence and impact are high. However, the costs of inaction are likely to be greater. Epanchin-Niell et al. (2010) compared long-term costs of revegetation to costs without any active intervention of fire-fighting and fire suppression on cheatgrass-infested land in the Great Basin Desert. They found that investment in restoration reduces fire management costs enough that it was a more cost-effective and efficient use of public resources over the long-term. In areas that are less impacted and restoration costs are lower, the long-term difference in costs are likely to be even greater. Considering that fire fighting and suppression costs in the Great Basin Desert were estimated at US$20 million annually in the 1990s (Knapp 1996), and large fires have increased since then (USDI-BLM 2000), cost savings due to restoration activities could be substantial.

Although the Great Basin Desert covers a vast area, intact sagebrush steppe habitat is declining rapidly due to anthropogenic development, past and present land uses, exotic annual grass invasion, altered fire regimes, and conifer encroachment (Chambers and Wisdom 2009, Davies et al. 2011). Investing in restoration and conservation of sagebrush steppe habitat has other important benefits aside from cost, such as maintaining refugia for sagebrush obligate species like the high-profile sage

grouse (*Centrocercus urophasianus*) (Holloran 2005, Meinke et al. 2009, Wisdom and Chambers 2009) and many species of songbirds that are also impacted by loss of sagebrush habitat (Ingelfinger and Anderson 2004, Gilbert and Chalfoun 2011).

Conclusions

We identified several methods that could be appropriate for eradicating or reducing cheatgrass in marginal, small, outlier patches in the eastern Sierra Nevada, CA. However, non-target effects need to be considered when applying these methods. The fact that soil solarization and mulching treatments eliminated the native seed bank reduces their suitability for many sites, especially considering that our seeding treatments were unsuccessful. These treatments should be reserved for use in disturbed locations where the native annual plant community has already been eliminated or areas where native seeds are more likely than weedy exotics to colonize the site after cheatgrass removal. Although hand pulling is time consuming and requires regular repetition, it can be more broadly applied in areas where the native seed bank is intact.

Efforts should be focused on outlier patches, stock and hiking trails, roadways, and other disturbed areas that could act as seed sources and dispersal corridors for cheatgrass range expansion. Prioritization should be on removing infestations that are most likely to result in spread based on current understanding of cheatgrass biology. For example, cheatgrass awns easily attach to cattle and horse fur, which can result in long-distance dispersal (Knapp 1996); infestations around

horse pack stations should be treated to reduce seed movement into wilderness areas. Further, cheatgrass invasion in forest ecosystems is minimal (Pierson and Mack 1990), so roadside infestations adjacent to uninvaded sagebrush steppe habitat should be prioritized over those adjacent to forests. Targeting patches of cheatgrass for removal at the leading edge of the invasion can reduce long-term costs and impacts on the ecosystem and provide an opportunity for conservation of relatively undisturbed sagebrush steppe habitat.

Table 3.1: Species and rate of seeding used for both broadcast and seedball seeding treatments.

Species	**Common Name**	**Rate (g m^{-2})**
Elymus elymoides	Squirreltail	2
Achnatherum hymenoides	Indian ricegrass	2
Hesperostipa comata	Needle-and-thread	2
Balsamorhiza sagittata	Arrowleaf balsamroot	1
Eriogonum umbellatum	Sulfur buckwheat	1
Lupinus argenteus	Silvery lupine	1
Wyethia mollis	Mules ear	1
Total		**10**

Table 3.2: Labor and materials costs associated with each cheatgrass control treatment. Labor was calculated at \$16.28 hr^{-1}. Person hours represent the actual time spent on the total area indicated. The final column represents the sum of both labor and materials costs m^{-2} for each treatment.

	Total Person-hours	Total Area (m^2)	Person-hours m^{-2}	Labor Cost m^{-2}	Materials Cost m^{-2}	Total Cost m^{-2}
Hand Pulling						
Year 1	32	116	0.28	\$4.49	\$0.27	**\$4.76**
Year 2	20	116	0.17	\$2.81	\$0.27	**\$3.08**
Sheet Mulching						
Year 1	16	109	0.15	\$2.39	\$3.74	**\$6.13**
Soil Solarization						
Year 1	16	18	0.89	\$14.47	\$0.55	**\$15.02**

Table 3.3: Strengths and weaknesses of cheatgrass control treatments and suggested appropriate uses.

Treatment	Strengths	Weaknesses	Appropriate use
Hand Pulling	* Reduced cheatgrass cover * Increased native % cover * Native seed bank maintained	* Tedious, time consuming * Needs ongoing attention * Large cheatgrass seed bank	* Wildland patches
Mulching	* Reduced cheatgrass cover * Effective after a single season	* Eliminated native annual plants * Potential high cost for materials	* Roadsides * Disturbed areas * Landscaped areas
Solarization	* Reduced cheatgrass cover * Reduced cheatgrass seed bank * Effective after a single season	* Eliminated native annual plants * Tedious, time consuming	* Disturbed areas * Landscaped areas

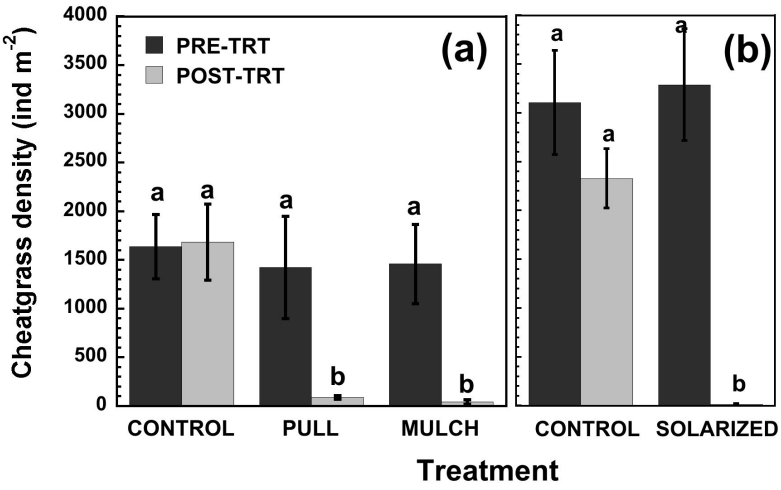

Figure 3.1: Differences in cheatgrass density pre and post-treatment in (a) control, pulled and mulched plots at Cerro Coso and (b) control and solarized plots at SNARL. Post-treatment data were from 2011 at both sites and pre-treatment data were from 2009 at Cerro Coso and 2010 at SNARL. Error bars represent 1 SEM, and different letters represent significantly different means within each panel.

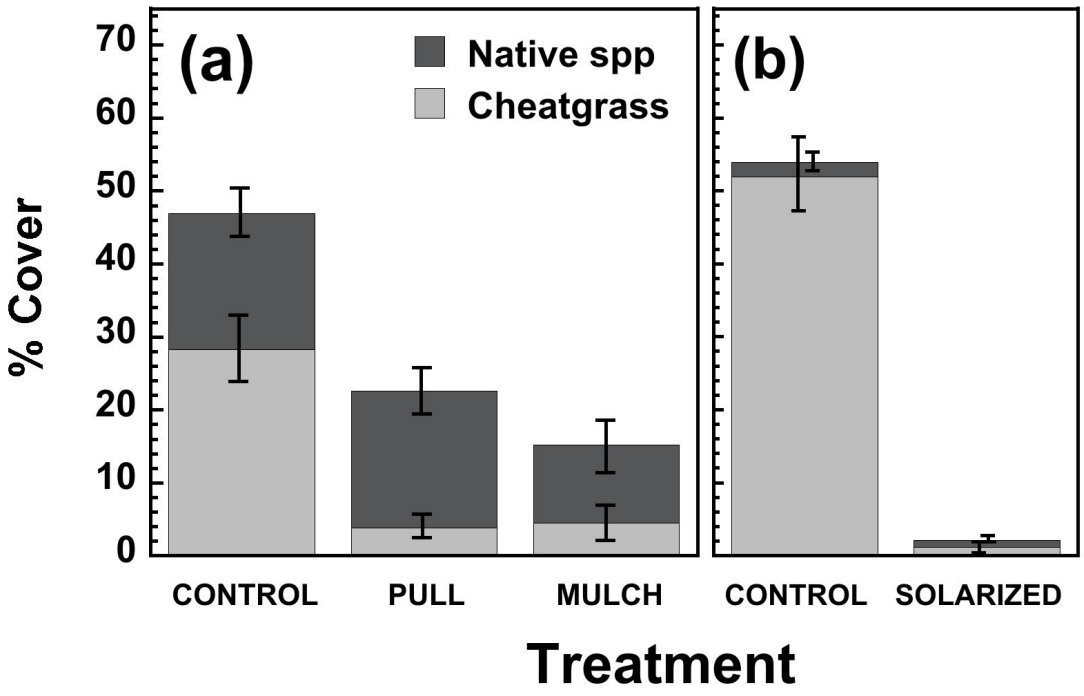

Figure 3.2: Average % cover of cheatgrass and all native herbaceous species combined in (a) control, pulled and mulched plots at Cerro Coso and (b) control and solarized plots at SNARL. Error bars represent 1 SEM.

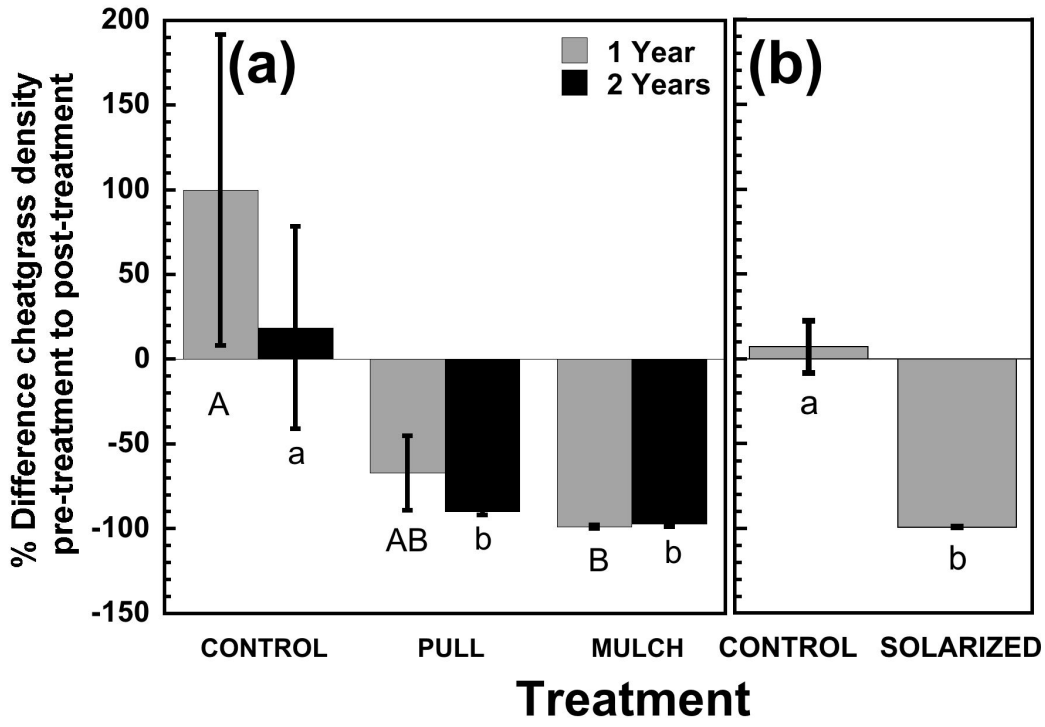

Figure 3.3: Percent difference in cheatgrass density from pre to post treatment years within each plot averaged by treatment, in (a) control, pulled, and mulched plots at Cerro Coso, and (b) control and solarized plots at SNARL. Error bars represent 1 SEM, and different letters represent significantly different means between treatments within each year (uppercase letters = 2010; lowercase letters = 2011).

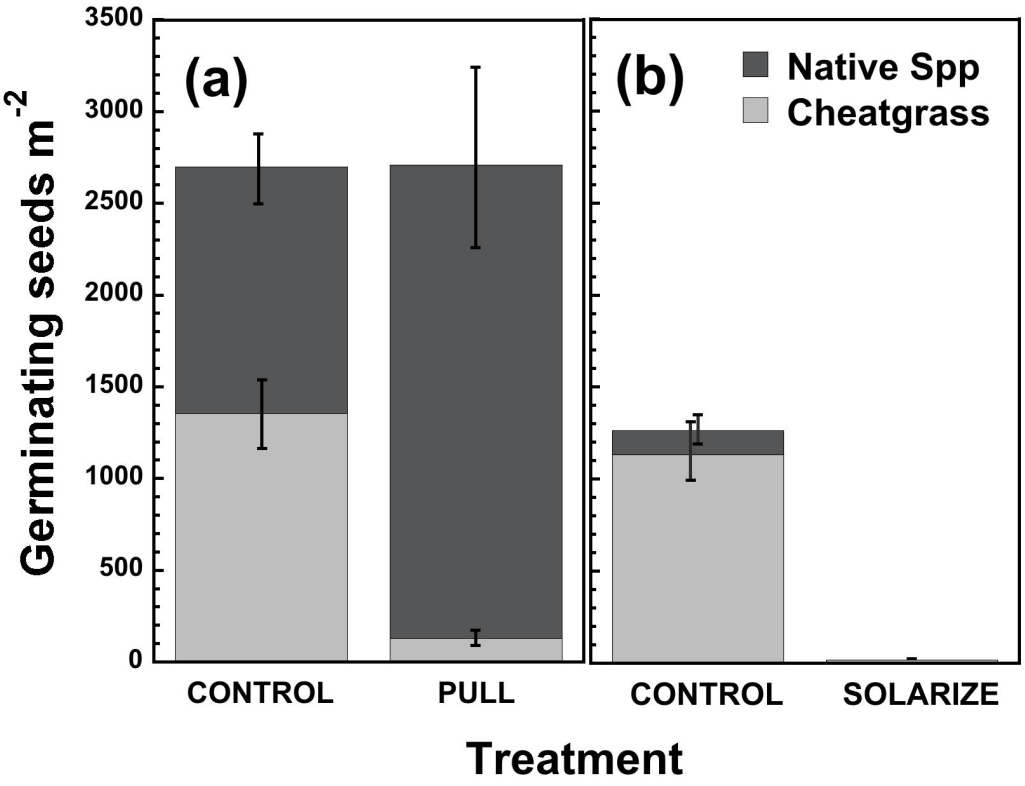

Figure 3.4: Soil seed bank composition in 2011 in (a) control and pulled plots after 2 years of treatments at Cerro Coso and (b) control and solarized plots after 1 year of treatment at SNARL. Native species seeds include germinating seeds of all species aside from cheatgrass combined. Error bars represent 1 SEM.

CHAPTER 4:

SOCIAL, LOGISTICAL, AND REGULATORY FACTORS AFFECTING FEASIBILITY OF CONTROL OF A WIDESPREAD INVASIVE SPECIES AT THE EGDE OF ITS RANGE

Introduction

Invasive plants can have varying impacts both across the landscape and as a function of time since introduction (Strayer et al. 2006, Marchante et al. 2008, Huang et al. 2010, Olsson et al. 2012). At the edge of an invasion, or the "invasion front", outlier patches often exist, which are disjunct from the main infestation and can act as seed (or propagule) sources for further spread (Moody and Mack 1988). Low-density infestations may also occur at the invasion edge with minimal impacts on native species (even for species that have profound impacts at high density; e.g., Brooks and Matchett 2006, Chambers et al. 2007, Zenni et al. 2009, Trueman et al. 2010). Reducing or eliminating infestations at the invasion front can be a strategic way to contain the impacts of an invasion, prevent further spread, and conserve areas of the landscape that are relatively pristine (Moody and Mack 1988).

Approaches to invasive species control vary based on the type of infestation. A passive approach, which would involve the removal of environmental stressors that are causing landscape degradation and facilitating invasion (e.g., grazing), may be an appropriate strategy for controlling a low-density, low-impact infestation (McIver and

Starr 2001). Once an invasive species has had severe impacts on the ecosystem, however, an active approach to restoration involving more resource inputs (e.g., removing the invasive species and revegetating with native species) is generally necessary (McIver and Starr 2001, Brooks et al. 2004). Outlier patches may be successfully eradicated using active approaches to restoration whereas these same approaches are likely to reduce, rather than eradicate, larger infestations (Moody and Mack 1988, DiTomaso 2000, Simberloff 2009). Thus, controlling an invasive plant species at the invasion front might involve passive approaches targeting low-density infestations and active approaches targeting outlier patches, and it is likely to be substantially less resource intensive, more cost-effective, and more successful than attempting to restore highly impacted areas (Moody and Mack 1988, Hobbs and Humphries 1995, Simberloff 2009).

Often, invasive species biologists think primarily about the ecological feasibility of control and the ecological impacts of the species (Anderson et al. 2003), while land managers who make decisions about weed control are likely to work with broader definitions of both feasibility and impacts (Darin 2008). Consequently, the way each group prioritizes invasive species for control can be expected to differ. From an invasion biology perspective, priority is more likely to be placed on eradicating or reducing invasive species at the invasion front – particularly when there is strong evidence that the species will spread and have increased impacts (Moody and Mack 1988, Trueman et al. 2010). Whether or not land managers are inclined to allocate resources and funding toward controlling the same infestations,

however, would likely depend on a number of additional factors such as the projected total cost of control and the agency budgets available to land managers, what kinds of impacts increased invasion might cause (e.g., economic, ecological, both), how other land managers are responding to infestations on adjacent land, legal or regulatory requirements that apply to control efforts, or how an incipient invasion ranks among other environmental problems in the region (Hall and Hastings 2007, Epanchin-Niell et al. 2010, Januchowski-Hartley et al. 2011, McDougall et al. 2011). In many montane regions where invasive species are not yet a clear ecological or economic problem, there appears to be a general lack of action toward prevention or control of small infestations at the invasion front, even when there is strong scientific evidence that future impacts are likely (McDougall et al. 2011). This inaction has been attributed in part to the difficultly of raising awareness and diverting resources toward future threats that are not yet impacting the local economy or environment (McDougall et al. 2011). Here, we examine a range of factors affecting the feasibility of cheatgrass control in California's Eastern Sierra at the western edge of the invasion.

Cheatgrass (*Bromus tectorum*) is an annual grass that has been in the U.S. for more than a century, and has had major impacts and process-level effects on the sagebrush steppe ecosystems of the Intermountain West (Mack 1981, Knapp 1996). It instigates an invasive grass/fire cycle, resulting in more frequent fires (Brooks et al. 2004) and a shift from a system dominated by perennial bunchgrasses and shrubs to an annual grassland (Stewart and Hull 1949, Knapp 1996). At the invasion front at

high elevation in the eastern Sierra Nevada (≥ 2100 m), cheatgrass exists in low-density and outlier populations (Figure 4.1a & b) and has not yet had process-level effects on the ecosystem. Ongoing observational research indicates that cheatgrass has been steadily increasing in density and coverage over the last several years (Chapter 2). The effects of climate change on cheatgrass range are currently uncertain, but range contraction or expansion will likely depend on the direction and magnitude of precipitation change (Bradley 2009, Griffith and Loik 2010).

From an ecological perspective, it appears that local eradication of outlier patches is possible at this elevation (Chapter 3), and passive approaches are likely to be successful at reducing spread and impacts of low-density infestations. But, how feasible is control from other perspectives? The rest of this chapter addresses this question, specifically focusing on the following issues: (1) what social, logistical, or regulatory barriers exist for cheatgrass control in the region, and (2) what opportunities (both realized and unrealized) are there for cheatgrass control? To answer these questions, we rely on interviews with local land managers and a review of applicable literature including state and federal legislation and agency policies for invasive and noxious weed control. We use the insights generated through combining these two types of analyses to gauge the current practical feasibility of ecologically-grounded management and control recommendations for cheatgrass.

Our discussion and analysis below is organized in five parts. First, we introduce the land managers with jurisdiction and authority for weed control in the region of study and discuss the resources available to these managers for the purposes

of weed control. Second, we look at how the responsible managers prioritize invasive species management in their jurisdictions and why. We then evaluate social, logistical, or regulatory factors that affect passive approaches to cheatgrass control. Next, we look at how these same types of factors affect active approaches to cheatgrass control. Finally, we discuss opportunities for increased effectiveness of cheatgrass control in the region. Although we focus on a single species, many of our findings are applicable to management of other widespread invasive weeds.

Approach

The geographic focus of our study encompasses California's Inyo and Mono counties in the eastern Sierra Nevada and western Great Basin Desert at the edge of cheatgrass invasion. In this region, cheatgrass infestations are low-density or relatively small in area and native species conservation would be more ecologically feasible than in other parts of the Great Basin Desert. However, significant increases in invasion can be expected to occur in the absence of management interventions (Chapters 1, 2), which would result in ecological and economic impacts on the region.

In seeking out managers who work directly on weed control efforts in the region we found that invasive species control occurs under several layers of jurisdiction. The physical jurisdiction is primarily federal (Figure 4.2). That is, much of the land is federally owned (92%) and administered by the U.S. Department of Interior Bureau of Land Management (BLM) and the U.S. Department of Agriculture Forest Service (USFS) (Agricultural Commissioner's Office 2012). The Los Angeles

Department of Water and Power (LADWP) also owns and administers 3.9% of the land, and the state of California owns 2.4%. Only 1.7% of the land is privately owned in Inyo and Mono Counties (Agricultural Commissioner's Office 2012). Cheatgrass is present in low density within sagebrush steppe ecosystems (mainly located on BLM and USFS land) and in outlier patches along roadsides, trails, access routes, and in old sheep bedding areas. The California Department of Transportation (Caltrans) has jurisdiction over roadside infestations. In addition, a number of other state and county agencies and non-governmental organizations have subject matter jurisdiction over the issue of weed control in Inyo and Mono Counties, including member groups of the Eastern Sierra Weed Management Area (ESWMA; Table 4.1).

We identified the land managers involved in weed control efforts within each of these agencies and organizations and contacted them to request involvement in the study. Semi-structured interviews were conducted with 12 respondents between 2009 and 2012 (64% of those contacted), which included representatives from 67% of the agencies or organizations that are involved with decision-making about weed control, and 100% of the agencies that regularly do on-the-ground weed control work on public rangelands. Questions addressed the following topics: (1) professional experience and history with land management, invasive species management, and fire management, (2) scientific and managerial perspectives on ecological, economic, or other impacts of cheatgrass, invasive species control, and land management, (3) funding sources for invasive weed control, particularly non-noxious species, and perception of whether funding has been sufficient for control of rangeland weeds, (4)

perspectives of inter-agency and regional collaboration working toward weed control, and (5) experience with cheatgrass control, and potential or perceived barriers or opportunities for cheatgrass control.

In addition to interviews, we review relevant environmental regulations, agency policies, and published and grey literature on the implementation of weed control policies and regulations on public lands in eastern CA. Based on the combination of interviews and policy and management review, we explain how land managers in the region prioritize weed control, highlighting when and why cheatgrass is prioritized, what factors affect specific passive and active approaches to cheatgrass control, and opportunities for improvement of invasive species management in the region.

Results and Discussion

Every land manager that we interviewed perceived cheatgrass as a potential threat to the region, even if they were not personally working in areas that were heavily infested. They cited various reasons for concern, including ecological impacts on native species and economic effects associated with altered fire regimes. Despite this trend, however, very few land managers (~25%) were actively engaged in controlling cheatgrass. We identified regulatory, social, and logistical influences on managerial action toward cheatgrass control, both positive and negative, summarized in Table 4.2 and discussed further below. First, we introduce the relevant land managers and discuss what resources are available to them. We then discuss how land managers in

the region prioritize invasive species for control and why cheatgrass is not one of the species that is prioritized. Next we present barriers and opportunities in the context of specific control methods (either passive or active). Finally, we identify opportunities for improvement of weed control in the region.

I. Who are the invasive plant managers in eastern California, and what resources are available for weed control work?

The USDA Forest Service and the USDI Bureau of Land Management are the two biggest landholders in the region, and botanists and range managers on staff at these two agencies are actively involved in weed control work. In addition, the Los Angeles Department of Water and Power (LADWP) owns approximately 310,000 acres in the Owens Valley. The primary purpose of the LADWP is to provide a reliable water source to the city of Los Angeles, but the agency also leases 80% of its land as grazing allotments, and manages the vegetation and flow rates to mediate environmental impacts of groundwater pumping and water diversion (LADWP 2012). They employ a team of 18 field technicians who work on vegetation monitoring and weed control. The Inyo/Mono Counties' Agricultural Commissioner's Office is the other main agency that regularly carries out weed control work on public land in the region, though there are several other stakeholder groups involved in the decision-making part of the process.

In the late 1990s, federal, state, and local government agencies partnered with non-governmental groups to form regionally focused 'Weed Management Area'

(WMA) groups throughout California with the goal of increasing collaboration and coordination between the various agencies and stakeholder groups working on eradication and control of noxious weeds. The Eastern Sierra Weed Management Area (ESWMA) was founded in 1999 with partners listed in Table 4.1. The local Agricultural Commissioner's Office takes a leadership role in the ESWMA, as is the case for many of the WMAs in CA. Most of the groups that are part of the ESWMA do not work directly on weed control (aside from the BLM, USFS, and LADWP), but help with decision-making and prioritization and notify the Agricultural Commissioner's Office when they spot a noxious weed infestation. The California Department of Transportation (Caltrans) does some weed control work, but it is low priority for the agency.

Perhaps unsurprisingly, almost all land managers that we spoke with cited funding and staffing shortages as a challenge to invasive weed control. Employees at the LADWP were the only managers that indicated they had sufficient funding for weed control work, with a budget of $1-2 million per year. Aside from that, funding shortages appear to be the norm in invasive species control in CA. A report issued in 2005 identified both the USFS and the County Agricultural Departments as being short on funding for invasive species management in order to meet priorities for weed control in the state (CDFA & CALIWAC 2005). The County Agricultural Departments budget was $4 million per year and they estimated they would need twice that to meet priorities on the 100 million acres of land they collectively manage. The USFS budget was $600,000 and they estimated that they would need $1.8 million

to meet priorities on the 20 million acres of Forest in CA. Caltrans was spending an estimated $1 million, the CDFA was spending $2 million, and the BLM was spending $350,000 on weed control. For these three agencies, there were no estimates about how much they would need to meet priorities, but judging from our interview results, stable funding for weed control seems to be a chronic problem for most state and federal agencies. We interviewed one BLM land manager who has successfully written grants to supplement limited funding for weed control work and to experimentally test different weed control methods, including timed grazing management for cheatgrass control. A Forest Service employee indicated that the amount of money per year allocated to weed control has gone up in recent years, but it is still low considering that they manage two million acres of land. They rely heavily on volunteer support (e.g., Friends of the Inyo) to meet their goals.

ESWMA projects are largely funded by the California Department of Food and Agriculture (CDFA), through which they are able to leverage additional funding. An official state program for regionally coordinated noxious weed control was created in 1999 to support WMA groups in California through AB 1168 (Frusetta), which designated a Noxious Weed Management Account under the CA Food and Agriculture Code (§ 7271b). Funding was added to the account through the CA legislature with bills SB 1740 (Leslie) in 2000 and AB 2479 (Villines) in 2006 but is currently awaiting renewal. Funding for WMA work is also technically available through a federal matching grants program through the Federal Noxious Weed Control and Eradication Act of 2004 (P.L. 108-412), but this is subject to the

availability of appropriations. In the last year, the CDFA budget was cut in half (this was coincident with larger state budget cuts in California over 2010-2012 (Karst 2012) and funding for the WMA program was eliminated (Dean Kelch, Cal-IPC meeting). The ESWMA is still functional and plans to maintain ongoing projects to the best of their abilities (Inyo-Mono County Agricultural Commissioner's Office, interview results). However, we conducted our interviews during a rather uncertain time period for weed managers in the region.

II. How are invasive weeds prioritized for control in the region?

Limited budgets and staff (described above) are an important driver for prioritization of invasive species control. Land managers need to consider competing mandates and responsibilities when prioritizing management activities. Since priorities could shift within agencies or budgets could increase or decrease due to changes in legislation, for example (West 2003, CDFA & CALIWAC 2005, ELI 2010), invasive weed control may receive more or less attention depending on the agency or period of time. Federal land managers with whom we spoke emphasized that invasive species control is considered an important management goal within the agencies, but at the same time, managers have jurisdiction over large land areas (~2 million acres for Inyo National Forest and 750,000 acres for BLM) and face a number of other pressing responsibilities for the management of these areas. USFS managers, for example, indicated that fire control and suppression probably receive the most attention in terms of both resources and time. For the Agricultural Commissioners office, weed

control is one of the top priorities. In contrast, invasive species control was cited as a low priority for some agencies, such as Caltrans, whose main mission is road-building and maintenance.

Even those agencies that prioritize invasive species control are still limited by time and resources, so they need to prioritize *which* species and infestations to control. Managers that we spoke with that were actively working on weed control indicated that they prioritize infestations based on three main criteria: (1) whether they are state or federally designated noxious weeds, (2) whether they are widespread in the region, and (3) whether control would be feasible with the resources and technology available. Cheatgrass is not among the invasive species that are prioritized for control because it does not meet these criteria. Although a few land managers pointed to perceived technical feasibility as a barrier to cheatgrass prioritization, by far the most common answer (given by 91% of respondents) to the question "*Why is cheatgrass not prioritized for control*" was that it is not on the state or federal noxious weed list. Noxious weed lists are compiled under federal and state statutory authorities for weed control and prevention. Below, we explore the history and protocol for listing species as noxious weeds and the implications of the listing process in terms of prioritization and management of cheatgrass.

Both the federal government and the state of California take a black listing approach to weed control; i.e. agencies are mandated to control or prevent the spread of species that are explicitly listed as noxious weeds. The federal designation for "noxious weeds" falls under the Plant Protection Act ("PPA", Pub.L. 106-224) of

2000, which superseded and consolidated the authorities of the Federal Noxious Weed Act ("FNWA", Pub.L. 93-629, 88 Stat. 2148, enacted January 3, 1975) and other plant related regulations. Under the PPA, additions to the noxious weed list could be petitioned by any "*individual, partnership, corporation, association, joint venture, or other legal entity*" (§ 403). The Secretary of Agriculture reviews petitions and has the authority to add (or remove) species to the list. Under the FNWA, the definition of a noxious weed was limited to those "*of foreign origin*" and "*new to or not widely prevalent in*" the United States (§ 2802). Its successor, the PPA has a broader definition that is not limited by origin or distribution. It includes:

> "*any plant or plant product that can directly or indirectly injure or cause damage to crops (including nursery stock or plant products), livestock, poultry, or other interests of agriculture, irrigation, navigation, the natural resources of the United States, the public health, or the environment*" (§ 403).

Although this definition is broad, the reality is that a great majority of the species listed as noxious are agricultural pests, with those threatening horticulture, forestry, and aquaculture secondary; almost all have a direct economic impact (ELI 2002).

Within the state of California, agencies are mandated to follow state weed laws in addition to federal regulations. California's state weed laws are part of the California Food and Agriculture Code (§403, 461, 5004-5434, 7201-7502). California's Pest Prevention System is coordinated by the CDFA, County Departments of Agriculture (CDA), and the US Department of Agriculture (USDA), and are aimed at protecting agricultural resources from pests (CDFA & CALIWAC

2005). Under the set of supporting laws and regulations, noxious weeds are categorized as class "A", "B", "C", or "Q". Designation as "A", "B", or "C" species are based on area coverage (i.e., "A" weeds are limited in distribution, while "C" species are the most widespread). These categories are mainly in place to provide policy guidelines and recommendations for control (i.e., different strategies are suggested for controlling an "A" species than a "C" species), though counties can use their discretion and take more stringent measures to control a species than recommended (CDFA 2012b, Range Management Advisory Committee 2012). "Q" species are those that have been flagged by the CDFA for consideration, but have not yet been classified. The process of adding or removing species from the noxious weed list is not fully transparent (Darin 2008). Biologists at the CDFA suggest exotic plants for listing based on recommendations from the counties Agricultural Commissioners and from outside experts (CDFA 2012b). The director of the CDFA then adds those species that fit the definition of noxious weeds outlined in section 5004 of the CA Food and Agriculture Code:

> *""Noxious weed" means any species of plant that is, or is liable to be, troublesome, aggressive, intrusive, detrimental, or destructive to agriculture, silviculture, or important native species, and difficult to control or eradicate, which the director, by regulation, designates to be a noxious weed. In determining whether or not a species shall be designated a noxious weed for the purposes of protecting silviculture or important native plant species, the*

director shall not make that designation if the designation will be detrimental to agriculture.

Although cheatgrass fits this description, it is not listed as a noxious weed in CA (CDFA 2012b). In fact, although it is recognized as a significant threat to native plant communities throughout the intermountain west (Mack 1981), the only state in the region that lists it as noxious is Colorado (USDA 2012). Like the federal list, most states noxious weed lists are largely made up of species that are agricultural pests rather than wildland weeds (ELI 2002).

Although not listed on the federal or state noxious weed lists, cheatgrass is listed as an invasive plant pest by the California Invasive Plant Council (Cal-IPC), a non-profit research and education group. Cal-IPC (2006) designates invasive plant species using a rating system based on 13 criteria, which fall into three categories: Ecological Impacts, Invasive Potential, and Ecological Distribution. Scores are given for each category from A (severe) to D (no impact), and U (unknown). Of the 193 plants that Cal-IPC (2006) lists as invasive, only 30% appear on the noxious weed list in CA (Table 4.3). Species on both the CA noxious weed list and the Cal-IPC list are varied in impacts, invasiveness, and distribution (Table 4.3). That is, there does not seem to be a trend in which species designated as noxious by the state are those considered to have greatest impact by Cal-IPC, nor are they those with the least widespread distribution or invasiveness. Species that appear on the Cal-IPC list, but not on the state noxious weed list, are also varied in invasiveness, impacts, and distribution. Table 4.3 lists those species that are listed as "High" by Cal-IPC but do

not appear on the state or federal noxious weed lists, which includes cheatgrass. This designation is reserved for species with severe ecological impacts, moderate to high rates of dispersal and establishment, and widespread distribution (Cal-IPC 2006). The main difference between the invasive species lists is that the noxious weed list is comprised almost entirely of agricultural pests while the Cal-IPC list focuses specifically on "invasive non-native plants that threaten wildlands" of CA (Cal-IPC 2006).

Invasive species listed by Cal-IPC that are not noxious are not as likely to be prioritized for control due to lack of funding, resources, and programs to deal with non-noxious weeds (our interview results; CDFA & CALIWAC 2005). This is not to say that they are *never* prioritized. Cal-IPC is a member of the California Interagency Noxious Weed Coordinating Committee, which is a group of state and federal agencies and stakeholder groups that works to coordinate activities and share information about weed control on public lands and on private land adjacent to public lands (CDFA 2012a). The Committee includes consideration of both the state noxious weed list and the Cal-IPC invasive species list. In practice, there are examples of non-noxious invasive species listed by Cal-IPC as 'High' (Table 4.2) that are targeted by NGOs and state agencies: *Ammophila arenaria* is targeted by the Nature Conservancy, Caltrans controls *Brassica tournafortii* along roadsides, *Spartina spp* are targeted by the California State Coastal Conservancy, and a special task force "Team Arrundo del Norte" made up of local, state, and federal organizations and agencies works toward controlling *Arundo donax*. In general,

however, because there is no regulatory agency responsible for control or prevention of non-noxious weeds, invasive species that are not listed as noxious under state or federal laws & regulations are less likely to be prioritized. This regulatory gap was cited by the CDFA and the California Invasive Weed Awareness Coalition (CALIWAC) in a 2005 action plan as a key area of CA state policy that needs improvement (CDFA & CALIWAC 2005). Since then, the budget for the terrestrial weed program in the state of California has been cut dramatically (Karst 2012) and this policy gap has yet to be addressed.

In addition to it being a non-noxious weed, some managers also cited feasibility as a barrier to prioritization of cheatgrass for control. Some of the comments that federal land managers with whom we spoke made (in reference to cheatgrass control) were:

- "*It's high on the threat list, but low on the list of things we can do anything about*",
- "*Right now, it doesn't seem feasible* [to control cheatgrass]- *not if we're just going to be throwing money away*"
- *"Well, for cheatgrass in particular, it's already relatively widespread and the effort to control it or eradicate it would have to be massive, so we feel like we have already lost the battle. Even if we controlled small populations, you have to look at the adjacent land. More seed could easily just blow in with the wind. We have Nevada next door, which is covered in cheatgrass."*

Because cheatgrass is so widespread in the Great Basin, these managers felt that targeting patches in eastern California might be futile when seeds from lower elevation populations in Nevada could continue to invade. The challenge here is not one of technical feasibility; methods for minimizing cheatgrass seed dispersal are well understood (e.g., Pellant 1996, Carpenter and Murray 2009). For control of such a widespread species with the potential for long-distance dispersal[1], coordinated efforts need to be made between adjacent landowners at local scales and larger regional scales (Epanchin-Niell et al. 2010). If land managers sense a lack of commitment or action from their neighbors, they may feel less inclined to put resources into working toward invasive species control on the land that they manage (Epanchin-Niell et al. 2010). However, the reality is that cheatgrass control is prioritized at lower elevations (e.g., USDI-BLM 2000, McIver et al. 2010), where it has caused major changes to the fire cycle. The increased costs of fighting cheatgrass-wildfires in Nevada prompted the BLM to commit to a large-scale restoration initiative in the region (USDI-BLM 2000). Increased coordination between managers in eastern CA with those in Nevada would bolster the efficacy of their respective efforts.

From an ecological perspective, it makes sense to use different strategies for management of cheatgrass at high versus low elevation that compliment one another. Where cheatgrass has already altered the fire regime and caused major impacts,

[1] Although cheatgrass seeds generally do not disperse far from parent plants in sagebrush habitat, they do disperse farther across disturbed landscapes (Johnston 2011) and they also have long awns that can attach to humans, livestock, or other animals and lead to longer-distance dispersal events (Knapp 1996).

eradication is no longer possible. In these places, the spread of fire and invasive species to adjacent land could be minimized with strategic placement of fire breaks and greenstripping (Pellant 1996). Within highly invaded areas, restoration of historic fire regimes is recommended (Brooks et al. 2004). Some mangers have also begun experimenting with maintaining a community of native plants that are fire-adapted in which cheatgrass is still present but not dominant (Figure 4.1d). In areas like eastern CA, where cheatgrass abundance is below the threshold for initiating a grass-fire cycle, it is an ideal time to be more pro-active about management and conservation of native plant communities (Brooks et al. 2004). There are cost-effective ways of maintaining *B. tectorum* at low density to minimize impacts on fuels (Carpenter and Murray 2009, Diamond et al. 2009, Mack 2011), and simple techniques that can effectively eradicate it from isolated outlier patches (Chapter 3).

Unfortunately, there are other logistical and social obstacles associated with active management in addition to the lack of prioritization of cheatgrass control. More passive approaches to cheatgrass control seem to be better supported in the eastern Sierra Nevada. We will discuss opportunities and barriers associated with different methods of cheatgrass management in more detail below.

III. What social, logistical, and regulatory factors affect passive approaches to cheatgrass control in the region?

While more active approaches to invasive species control (e.g., removing the invader and revegetating) would be necessary in areas of the landscape where cheatgrass is

dense and has already had severe impacts (such as Nevada, Figure 1c), low-density infestations may be controlled with passive approaches that require less resource input (in terms of both money and time). Passive management of invasive species include activities that remove stressors that could facilitate further spread of an invasive species (McIver and Starr 2001). In the Great Basin, cheatgrass is intimately connected to livestock grazing in almost every respect- from spread, to impacts, to feasibility of control (Stewart and Hull 1949, Knapp 1996, Diamond et al. 2009, Young and Clement 2009) - and any management program for cheatgrass control must seriously take this into consideration. Fire, too, is an important influence on cheatgrass spread in the region (Stewart and Hull 1949, Knapp 1996, Young and Clement 2009). Passive approaches to restoring cheatgrass-invaded sagebrush steppe communities involve the removal of grazing pressure or suppression of fire. Management activities that promote native shrub and bunchgrass communities could also be considered passive approaches to cheatgrass management, since there is good evidence that intact plant communities may be more resistant to invasion (Anderson and Inouye 2001, West and Yorks 2002, D'Antonio and Thomsen 2004). Here we discuss barriers and opportunities for cheatgrass control in the region focused on the passive approaches of grazing removal, fire suppression, and native species conservation.

1. Cheatgrass and grazing

When cheatgrass was first introduced to the Great Basin Desert, it was during a period of intense grazing pressure (Mack 1981). From the time of the first European settlers in the mid-1800s until the early 1900s, livestock grazing was unregulated on millions of acres of un-appropriated public lands in western states, which had become highly degraded (Young and Allen 1997, Young and Sparks 2002). Native plants had not historically experienced grazing pressure, as there were no congregating ungulates in the Great Basin for at least 2500 years prior to the arrival of cattle (Mack 1981). Cheatgrass, however, is tolerant of heavy grazing pressure and had a competitive advantage over native species with the introduction of grazing (Klemmedson and Smith 1964, Knapp 1996, Young and Allen 1997). Grazing disturbance also led to the degradation of a cryptobiotic crust layer on the soil surface, which is important for nutrient cycling and soil stability in shrubland ecosystems of the Intermountain West (Anderson et al. 1982, Brotherson et al. 1983, Knapp 1996, Belnap and Gillette 1998, Belnap 2003, Harris et al. 2003). When cheatgrass entered the Great Basin in the late 1800s, it was facilitated by these disturbances, which increased its competitive advantage over native plants and provided a window of opportunity to spread more rapidly (Mack 1981, Knapp 1996).

The Taylor Grazing Act (Pub.L. 73-482) was enacted in 1934 to prevent overgrazing and soil deterioration, stabilize the livestock industry, and bring order and improvement to the development of rangelands (Buckman 1935). In order to accomplish this, the Secretary of the Interior was granted the authority to issue

grazing permits on lands that they deemed chiefly valuable for grazing (which initially included a total of 80,000,000 acres of public land), and to make rules for the use of those lands with the intent of balancing the interests of public lands users with the ecological integrity of the land (Buckman 1937). Since then, several other grazing-related laws have been passed. The Federal Land Policy and Management Act (Pub.L. 94-579) of 1976 elevated environmental and recreation interests to legal equality with commodity driven uses and mandated that public lands be periodically inventoried. The Public Rangelands Improvement Act (P.L. 95-514) of 1978 was enacted to improve the condition of rangelands so they become as productive as possible. Most recently, in 1986, President Reagan signed into effect EO 12548, which initiated a fee system for grazing on public lands. Although the Taylor Grazing Act is specific to BLM administered land, the USDA Forest Service has adopted similar rules for grazing allotments on National Forest land. Specific to our study area, the Inyo National Forest has a Forest Land and Resources Management Plan (LRMP), which provides grazing allotment rules. In 1995, an amendment was passed regarding range utilization, which placed stricter standards on range use, requiring a site-by-site analysis of plant cover and water quality each time a grazing lease comes up for renewal (Amendment 6, LRMP).

In practice, land managers with whom we spoke at BLM and USFS do consider cheatgrass in their range utilization decisions. Each time an allotment comes up for renewal (every 10 years), land managers measure species composition and decide whether to renew the grazing permit or to rest the land from grazing. Inyo

Forest land managers whom we interviewed indicated that cheatgrass is one of the invasive species with which they are most concerned when evaluating impacts that might be associated with continued grazing. One land manager described a recent allotment assessment, where they identified a cheatgrass infestation on the land and consequently decided to rest the land from grazing. This approach to cheatgrass control could be considered a type of passive restoration (McIver and Starr 2001). Removal of grazing pressure could reduce physiological stress on native plants so that they are better able to compete with the invader, and/or reduce disturbance to soils (Olson 1999, DiTomaso 2000). However, removal or reduction of livestock alone is not always effective as a restoration strategy; it can sometimes lead to an increase in cheatgrass cover depending on site conditions and disturbance history (Green and Kauffman 1995, West and Yorks 2002, Davies et al. 2009). In these cases, more active approaches to restoration of cheatgrass-invaded sites are needed (Forbis et al. 2006, Provencher et al. 2007).

Ranchers can also play a role in decision-making about range utilization on inter-annual and seasonal time scales. Within the 10-year period that each lease is active, ranchers can decide how many head of stock to place on the land (up to the amount indicated in their agreement) and whether they want to rest the land during some years (e.g., during a dry year). Resting the land during a dry year could help maintain native plant cover. However, there is some evidence from the literature that the current system of allotments on public lands may discourage ranchers from resting land. Holechek and Hess (1995) describe a situation in which a rancher

initially voluntarily kept stocking rates low to improve the forage value of the allotment. She later requested an increase in stocking level, but the BLM denied her request on the grounds that she had underutilized her previous permit. Later, during a dry year, she kept stocking rates high out of fear that she would lose the opportunity to expand her stock on the grounds of extensive nonuse. In other words, instead of being rewarded with incentives for conservation, the rancher was penalized; in response, she shifted her strategy to one of intensive grazing. It is hard to say whether this is a real threat in the eastern Sierra Nevada. From our interviews with range managers, it appears that they (i.e., the range managers) are generally flexible about such rules. One manager that we interviewed described the process as such:

> *"Sometimes depending on the weather that year or fire or some other reason, the rancher will want to opt out on using an allotment and there's flexibility to do that. There are certain dates that are set in stone and ranchers are not allowed to graze their cattle before that date; for example, if there is a wildlife breeding season, winter habitat, bird nesting, etc. The rancher, of course, is not infinitely flexible. He/she has a certain number of cows to feed every day and herds have habits- to change them, it takes some effort. The range manager basically mediates between the agency and the rancher to find the best solutions for everyone."*

If ranchers have a close working relationship with range managers, they may be more inclined to rest the land or stock it more lightly without feeling threatened about losing rights to the allotment. Unfortunately, we were unable to conduct interviews

with the ranchers themselves, so we can only speculate about how they might make decisions that could affect cheatgrass spread. Past studies suggest that ranchers in the Intermountain West probably have mixed feelings about cheatgrass (Knapp 1996, Pellant 1996, Brunson and Tanaka 2011). It can provide early season forage for cattle, and there are examples of ranches that have successfully incorporated it into a grazing schedule (Emmerich et al. 1993, Young and Allen 1997). But cheatgrass is not a reliable source of forage due to its tendency to produce little to no biomass in dry years (Stewart and Young 1939, Kay 1966, Knapp 1996). Further, it has been associated with degradation of native perennial bunchgrasses that are essential to providing a more stable source of feed (Stewart and Young 1939, Knapp 1996). Brunson and Tanaka (2011) examined the effects of cheatgrass and fire on economic sustainability of livestock production in the Intermountain West. From their analysis, it is clear that ranchers can suffer severe economic losses due to wildfires or restoration activities that require resting grazing allotments, sometimes resulting in ranch bankruptcy. In areas where cheatgrass has initiated an invasive grass-fire cycle, effects would presumably be the worst. However, to our knowledge, no empirical studies have been conducted about ranchers' attitudes toward cheatgrass and how it might affect decisions about their range utilization. This is an area of research that deserves further investigation.

2. Cheatgrass and fire

Once cheatgrass cover passes a threshold in density (estimated at ~46% in eastern WA), fire risk approaches 100% (Link et al. 2006). The historic fire return interval in sagebrush steppe habitats of the Great Basin is estimated at 150 or more years (Baker 2011), and native plants are slow growing and do not resprout after fire (Knapp 1996). Cheatgrass can quickly dominate post-fire communities and initiate what has come to be known as an invasive grass-fire cycle (Brooks et al. 2004). Consequently, fire management of the Intermountain West is particularly important for cheatgrass control. Strategies to reduce cheatgrass dominance include fire suppression activities (Baker 2011) and post-fire seeding (Jessop and Anderson 2007, Epanchin-Niell et al. 2009).

The Federal Fire Management Policy was developed in 1995 by the USDA and USDI in response to the increasing size (and associated costs) of wildfires after nearly a century of fire suppression (USDA-USDI 1995, Stephens and Ruth 2005). The Secretaries of Agriculture and the Interior established the Wildland Fire Leadership Council (WFLC) comprised of members from various state, federal, tribal, county and municipalities to provide direction on implementation of the Federal Fire Management Policy. In 2011, the Western Regional Committee of the WFLC produced a strategy for wildland fire control on public lands, which specifically directs land managers to consider invasive species (highlighting cheatgrass) in their fire management activities. Managers are instructed to:

- *"Determine landscape vulnerability to post-fire invasive species invasions*",

- "*Work across all ownerships to develop and implement action plans for removing or preventing introduction of invasive plants that contribute to fire hazard (e.g., red brome, cheatgrass)*"
- "*Use desired and fire resistant plant species to break up large scale infestation areas*", and
- "*Prevent the spread of invasive species through movement of fire equipment; implement mitigation measures and standard operating procedures*" .

In our interviews, we found that land managers in Inyo and Mono County are, indeed, following at least some of these guidelines. For example, before a prescribed burn, botanists survey the landscape for presence of cheatgrass and they do not burn on areas where it is abundant. These guidelines also highlight how federal employees can chose to fund weed control projects (for species like cheatgrass that alter fuel properties) through fire management appropriations (GAO 2005), although our interview results suggest that land managers in the eastern Sierra are not currently taking advantage of this resource.

In large parts of the Intermountain West, reseeding is done after fire with the dual purposes of erosion control and competitive exclusion of invasive grasses, like cheatgrass (USDI-BLM 2007). However, cheatgrass response to fire differs by site probably based on pre and post-fire land use as well as cheatgrass dominance at the site pre-fire (Rew and Johnson 2010), so seeding is not always necessary or useful (e.g., Shinneman and Baker 2009). We found through interviews that managers in the eastern Sierra Nevada generally do not reseed after fire. Anecdotal evidence

suggests that post-fire rehabilitation may not be needed in the region since native plants are populating post-fire communities without artificial seeding (e.g., at June Lake and Doe Ridge, personal observation). However, it could be necessary in the future if wildland fires occur where cheatgrass exists at higher density. Managers indicated that this is an option that they would consider.

3. Management for conservation of native plant communities

Land management actions that promote conservation of native plant communities can contribute to reducing or maintaining cheatgrass at low levels (D'Antonio and Thomsen 2004). We found through interviews that there are several ways in which this is already happening in the Eastern Sierra, including (but probably not limited to): (1) enforcement of the rangeland utilization standards (2) habitat conservation measures for the Greater Sage Grouse, and (3) Caltrans revegetation projects, which use native seed and weed-free straw. We discuss each below in more detail (aside from rangeland utilization standards, which was discussed above).

The Greater Sage-Grouse (*Centrocercus urophasianus*), currently on the International Union for Conservation of Nature (IUCN 2011) red-list as near-threatened, is one of the species of greatest concern for BLM and USFS land managers in the Eastern Sierra. Sage Grouse are obligate inhabitants of sagebrush ecosystems, and their occupied range has shrunk from an estimated 45,000 km^2 to 5,000 km^2 with the decline in intact sagebrush habitat that has occurred since pre-settlement times (Knick and Connelly 2011). This decline has partly been attributed

to exotic species encroachment and cheatgrass fires (Johnson et al. 2011). Although Fish and Wildlife scientists concluded that Sage Grouse deserved inclusion on the Endangered Species list, they listed the status as "warranted but precluded" candidate species for ESA protection in order to prioritize other species that were facing more imminent threat (FR 13910 (2010-03-23)). Managers at the federal and state level have been advised to work toward conservation of Sage Grouse habitat to avoid listing the species. BLM and USFS land managers that we spoke with emphasized the importance of Sage Grouse in any decisions they make about vegetation management in the sagebrush-dominated landscapes of the region. It is likely that at least some of the actions taken to promote native plant abundance could work to inhibit cheatgrass spread.

Although Caltrans's primary goal is road building, the agency does employ a staff of environmental specialists to work on revegetation projects after roadwork is done. Execution of revegetation projects varies by district. The use of fertilizers, irrigation, and compost to grow ornamental wildflowers along roadsides is common in many districts of California. We found through our interviews, however, that the Caltrans Landscape Specialist in charge of re-vegetation in District 9 (which includes Inyo and Mono Counties) is committed to planting native species without irrigation or compost, to ensure that plants are able to endure the harsh conditions of the desert without excessive resource inputs. Certified weed-free straw is used, and a mix of 10-20 native species with ecological concepts of succession in mind. This strategy of planting is more likely to contribute toward native species conservation and,

consequently, resistance to invasive species. This is important because roadsides are highly disturbed areas that can act as vectors for weed seed dispersal including cheatgrass seeds, which disperse at far greater rates across bare disturbed ground compared to structurally intact shrubland systems (Johnston 2011).

In summary, passive approaches to cheatgrass control in the region appear to be supported. However, the fact that decisions are sometimes made on a 10-year time scale (e.g., for grazing allotments) is of concern. In Chapter 2, we showed that a cheatgrass infestation could increase significantly over a period of 10 years (from a small roadside infestation to densities that can carry fire). More frequent allotment assessments could help to ensure that infestations are caught early enough for passive restoration approaches to be successful.

IV. What social, logistical, or regulatory factors affect active approaches to cheatgrass control in the region?

Active approaches to invasive species control involve intentionally removing the pest. In the case of cheatgrass in the eastern Sierra Nevada, there are two main types of infestations: high-density small-scale outlier patches and low-density infestations covering more area (Figure 4.1a,b). Approaches to removing outlier patches of cheatgrass might include herbicides, soil solarization, mulching, or hand pulling (Chapter 3). Low-density infestations could be reduced (in terms of biomass and fuel load) with timed grazing (Diamond et al. 2009). Below, we discuss the feasibility of using these methods from a public lands management standpoint.

1. Opportunities and obstacles affecting control of outlier patches of cheatgrass

We found through interviews that active control of weeds in the eastern Sierra Nevada is primarily carried out by the USFS, BLM, and the Agricultural Commissioners Office, and to a lesser degree by the California Department of Transportation (Caltrans). Weed control projects on both federal and state land are subject to environmental impact analyses and public hearings under the National Environmental Policy Act (NEPA) and the California Environmental Quality Act (CEQA). Land managers with whom we spoke cited parts of the NEPA and CEQA processes as obstacles to active cheatgrass control. We discuss these barriers as well as some opportunities for reducing outlier populations of cheatgrass below.

The National Environmental Policy Act (NEPA, P.L. 91-190) of 1970 requires consideration of environmental impacts of proposed actions on federal lands in addition to those carried out with federal funding (Broussard and Whitaker 2009). The NEPA process has been criticized for being too costly and time consuming and diverting limited agency budgets toward planning at the expense of pro-active management and monitoring (Salk et al. 1999, West 2003). There have been suggestions of how to streamline the process by academics (e.g., Salk et al. 1999, Phillips and Randolph 2000) and within the U.S. House of Representatives (e.g., as prepared by the Task Force on Improving the National Environmental Policy Act and the Task Force on Updating the National Environmental Policy Act in 2006) .

However, there are risks that many of the suggested changes might backfire and delay the process even more or reduce the effectiveness or integrity of the process (Moriarty 2004, Hansen et al. 2007). Land managers that we spoke with did cite the NEPA process as an obstacle to efficient weed control, as described here by a USDA Forest Service manager:

> *"The NEPA process includes drawing up a proposed action, then giving the public time to scope it out and comment on it, giving potential alternatives, and coming up with a draft decision. If it's appealed, we need to wait 35 days. It takes a long time. It took about 10 years to draw up the last NEPA analysis for invasive plant species management. Issues came up for the public that we had to respond to. It is rare that there would be no conflicting priorities. It would take about 3-6 months total if that was all we were working on, but the issue is that other priorities are constantly coming up that we need to deal with.*"

The fact that the process can take 10 years could be a major impediment to effective invasive species control. A lag of years- or even months- may increase costs and likelihood of control dramatically (Hobbs and Humphries 1995). At the Forest Service, this delay appears to be driven in part by a lack of specialists on staff. Every NEPA proposal needs to be reviewed by an interdisciplinary group of specialists according to their expertise (e.g., botany, geology, archaeology). Thus, the process could be sped up by simply increasing agency staff rather than making any major

procedural changes to NEPA. However, agency budgets (and the possibility of hiring additional staff) are unlikely to increase in the current economic climate.

Another consideration is that NEPA analyses are site-specific, so a new report needs to be drawn up every time a new weed infestation is identified. Plans for weed control are based on weed occurrence when the document was drawn up, which could change dramatically by the time the plan is actually approved. We spoke with two Forest Service land managers who indicated that they were in the process of drawing up an "umbrella" Environmental Assessment using the definition of "site" more broadly to encompass similar plant communities within a region. A similar strategy has been developed and implemented in the Olympic National Forest to address new exotic species invasions with a rapid response (Desser 2007). If implemented in the Inyo National Forest, managers would be able to quickly respond to weed infestations across a broader area without having to write a new EA for each case. This would greatly increase the ability of managers to target outlier patches of cheatgrass in a timely fashion.

The final aspect of the NEPA process that was described as a barrier to efficient weed control was public aversion to herbicides. This was also cited by a Caltrans manager with respect to the California Environmental Quality Act ("CEQA", CA Public Resources Code § 21000 et seq.), a state law aimed at environmental protection with some of the same requirements for public involvement that NEPA has but with a broader scope (i.e, it includes projects that receive any kind of state permit, approval, or oversight). Negative public perception of pesticide or

herbicide use can stall or completely terminate some projects- particularly if litigation is used as a tool. A CDFA (2005) report identified litigation as a barrier to weed control on National Forest lands, confirming that it is a broader issue that affects land managers outside of Inyo and Mono Counties. Stern and Mortimer (2009) also found that the threat of litigation could be a significant influence on land managers' decisions when drawing up Environmental Impact Statements. For example, managers will sometimes spend more time adding sections that are not necessary for land management goals, but would increase the strength of the document in court. With invasive species control, managers might decide to reduce herbicide use to avoid public scrutiny, as we found was the case with Caltrans. In 1992, Caltrans committed to reduce herbicide usage on roadside projects by 50% by 2000 and by 80% by 2012 (Caltrans 1997) in response to public opposition (Shields 2001). Caltrans has since been researching and using alternative methods for vegetation control and reduced fire risk along roadsides (Shields 2001). Our interview respondent suggested that Caltrans' previous practice of spraying weeds along roadsides helped to limit the spread of noxious weeds along road corridors and the current restrictions within the agency appear to act as a barrier to weed control. Non-chemical methods of weed control may work just as effectively to reduce cheatgrass and other weeds along roadsides, but many of them are more time consuming and costly (Chapter 3). Caltrans has gotten some help with manual labor from the California Conservation Corps, county court referrals, the California Youth Authority, and the Department of Corrections (Shields 2001), though the 15,000

miles of highway and 230,000 acres of right-of-way that the agency manages (Caltrans 1997) require much attention.

When asked whether Caltrans would ever specifically target cheatgrass for removal from roadsides, the manager that we spoke with indicated that it would be extremely unlikely. For Caltrans, projects aimed at control of specific weed infestations are rare – in large part because Caltrans's primary goal is to build and maintain roadways and to make them safe. Only about 1% of the total budget goes to environmental work. Further, funding is limited even for road building projects. The result is that it often takes at least a few years (and sometimes up to 10 years or more) from the time that a project is proposed to the time that funding becomes available and work begins. Caltrans rarely initiates a project that is specifically targeting invasive species control; it only occurs when someone from a partner agency (the ESWMA, Death Valley National Park, etc.) asks for help eradicating a roadside infestation. In these cases, projects generally still take many years to complete, by which time the infestation is likely to have spread. Further, most projects with partner agencies are for eradication of noxious weeds, so a project targeting a non-noxious invasive species, like cheatgrass, would be even more rare.

In Inyo and Mono counties, the Los Angeles Department of Water and Power (LADWP) is the third largest landholder (after USFS and BLM). Because it is a private landholder, the LADWP is not subject to NEPA reviews, which may increase their ability to respond to weed infestations quickly and efficiently. The LADWP has a large budget for weed control and does not experience the same challenges that state

and federal employees do in terms of staffing and budget for weed control projects. They employ a team of 18 field technicians to monitor the property, map weed infestations, and act quickly to eradicate weeds at early stages of invasion. They indicated in interviews that cheatgrass is not dominant on their lands, but they do target it for control when it appears.

Many of the managers that we spoke felt that education was the best option for controlling a non-noxious weed like cheatgrass. Education campaigns for weed control may be beneficial for galvanizing the public to help with invasive species control efforts by participating in volunteer days or by changing behaviors, such as cleaning vehicles or shoes of weed seeds after leaving an infested area (Daab and Flint 2010, Prinbeck et al. 2011). Horse packers in the eastern Sierra Nevada regularly travel up into higher elevation wilderness areas and can be vectors for invasive species if seeds get caught in animals' fur. Forest Service managers that we interviewed indicated that they educate horse packers on problematic weed species and ask them to keep their stables clear of a specific list of weeds, which includes cheatgrass. They provide training in weed identification and a booklet with photos of the most problematic weed species. Educating the public about weed control can also reduce the threat of litigation over herbicide use for weed control projects (and subsequently reduce the time to complete the NEPA process). Studies that have been conducted on public perception of invasive species have found that environmental attitudes, education, and awareness are key to gaining public approval for weed

control projects (Bremner and Park 2007, Garcia-Llorente et al. 2011, Prinbeck et al. 2011, Sharp et al. 2011).

2. Opportunities and obstacles affecting timed grazing management

When cheatgrass increases in cover and density, it can greatly increase fire risk and instigate a change in the fire cycle (Stewart and Hull 1949, Brooks et al. 2004, Link et al. 2006), which results in a total shift in ecosystem structure and composition from one of perennial bunchgrasses and shrubs to an annual grassland. Properly timed grazing by cattle and sheep may be used as an active cheatgrass control method to decrease biomass and reduce the chances of cheatgrass-fires provided that native plants are present and cheatgrass densities are moderate (Pellant 1996, Diamond et al. 2009). Through interviews with land managers, we identified some logistical obstacles to the practical application of this method.

Most ranchers in the Eastern Sierra use a mix of LADWP, BLM, and USFS land, with commitments to each agency about when cattle or sheep need to be on and off of each allotment. Because of these commitments, it can be difficult or impossible for ranchers to participate in a cheatgrass-grazing project. One of the land mangers we spoke with described a time when this happened:

> *"Many of the ranchers have obligations throughout the season to DWP, BLM, and USFS land, and they have schedules they need to stick to. We tried to get a rancher to bring his cattle to graze cheatgrass last year, but he couldn't*

because when the cheatgrass was green, it was during the time of year that he usually grazed elsewhere."

Another concern that a BLM manager cited was that it would be more work for ranchers. To graze cheatgrass effectively, they would need to push cattle around the land. By grazing the land with sheep instead of cattle, this problem would be resolved. However, sheep are prohibited in some areas because of potential contact and disease transmission to bighorn sheep, which are federally listed as endangered (USFWS 2007).

Despite these limitations, ranchers in the region were described by federal land managers as cooperative and willing to help with conservation projects. One BLM land manager described his experience working with ranchers with this example:

"We have a good working relationship with ranchers. They are cooperative. Some are even into the mode of doing treatments on their own private lands. For example, there is one lessee managing rabbit brush. With grazing, cattle don't select rabbit brush so it becomes more dominant. He's been using mowing to keep rabbit brush back. He's also fencing off livestock on parts of the land to increase perennial grasses. He has a lot of private lands and it's advantageous for him to experiment on his land, because if it works, he can sell the project to public lands managers and see it happen on a much larger scale."

We heard similar stories from other land managers, suggesting that ranchers in this area may be receptive to helping with invasive species control projects but they probably have economic and logistic constraints that must be taken into account. Unfortunately, we were not able to interview ranchers directly. This is an area of research that deserves further investigation.

V. Summary of factors affecting cheatgrass control in the region and recommendations for improvement

We identified a number of ways in which cheatgrass is already being managed in the region and some obstacles that would need to be overcome to increase control efforts and minimize future impacts of the invasion. In general, passive approaches to restoring cheatgrass-invaded sites are better supported than active ones, but even passive approaches should be improved for optimal effectiveness of control. Below we summarize the major obstacles (listed in Table 4.2) and discuss opportunities for improvement of cheatgrass control in the region.

The most significant regulatory obstacles to active cheatgrass control that we identified appear to be: (1) a lack of sufficient regulatory mandate and authority for dealing with non-noxious weed control, (2) the National Environmental Policy Act (NEPA) procedural requirements for site-specific environmental analyses, (3) funding shortages within key agencies (USFS, BLM), which translate to inadequate specialized staff to deal with weed control over such a large area, and (4) funding instability for invasive weed control in general. These obstacles are not unique to

cheatgrass or the Eastern Sierra region, but of concern for control of invasive species in California in general (and some more broadly). Other authors have criticized the state and federal government's blacklisting approach to invasive species control as being inadequate to address wildland weed problems since the focus of the lists has clearly been on agricultural pests (ELI 2002, Miller 2004, ELI 2010). Even the state agency responsible for weed control (the California Department of Food and Agriculture) recognizes that current CA state regulations and policies are insufficient for addressing wildland weed control (CDFA & CALIWAC 2005). An official state list of wildland invasive weeds based on a transparent and science-based set of criteria (such as one based on the Cal-IPC invasive plant list) could increase prioritization of non-noxious weeds for control, and one that is backed by stable sources of funding through the legislature would be even more powerful. This would facilitate control efforts for non-noxious invasive plants in California.

The fact that NEPA assessments are site-specific has inadvertently had negative consequences for invasive species control in the eastern Sierra Nevada and beyond (e.g., Desser 2007). Methods of controlling invasive species and their likelihood of success can change dramatically over a short time as they undergo rapid expansion (Hobbs and Humphries 1995), particularly for those that affect disturbance regimes, like cheatgrass (Brooks et al. 2004). From an ecological perspective, rapid response to infestations has clear benefits in terms of likelihood of successful eradication or control (Brooks et al. 2004, Simberloff 2009). NEPA's site-specific requirement for environmental assessments reduces land managers' ability to respond

rapidly to new weed infestations, and can result in a 10-year lag from the initial infestation sighting to the time of treatment (this number is based on our interview results). Inyo Forest managers are currently working on ways to facilitate faster response to controlling plant infestations by writing an 'umbrella' environmental assessment that would cover new infestations over a wide area (see Section IV for full discussion). This approach has also been used on other National Forests for the same purpose (Desser 2007). Since this problem extends beyond the Forest level, however, it would make more sense to address it more broadly by including a mechanism within NEPA for rapid response to invasive species infestations (i.e., an exemption or special rule when it comes to time-sensitive invasive species eradication or control projects) that applies to projects on all federal land, rather than addressing it on a piecemeal basis within each National Forest. Lodge et al. (2006) recommended that NEPA should include a categorical exclusion for control of newly discovered invasive species on public land, and our results illustrate why this kind of action is needed.

Limited budgets for invasive species control have been a chronic problem at both the state and federal level (our interview results; CDFA & CALIWAC 2005, GAO 2005). In the case of federal agencies in the Eastern Sierra, this is manifested in part as a lack of specialist staff, which affects invasive species management by increasing the time to complete projects (i.e., by delaying the NEPA process). Stability of funding is also a problem at both the federal and state level. For example, although an account for funding noxious weed work in the state of CA was created in

1999 (through AB 1168), the state legislature only appropriated money for that account in some years. Invasive weed work requires consistent attention, and, therefore, stable funding (Lodge et al. 2006). In the absence of increased budgets, volunteer groups can help subsidize limited agency staff on weed control projects. The non-chemical, non-technical cheatgrass control methods tested in Chapter 3, for example, would be feasible to use with volunteer groups. However, stable government programs with adequate funding are ultimately needed for improved control of invasive weeds on federal and state lands (Lodge et al. 2006).

Although federal and state regulations (e.g., rangeland utilization standards and federal fire policy) generally support passive control of cheatgrass, they could be improved. Rangeland utilization regulations require agency personnel to survey land every time a grazing allotment comes up for renewal, which currently occurs in 10-year cycles, at which time some land managers with whom we spoke indicated that they remove grazing pressure if a cheatgrass infestation is spotted (i.e., a passive approach to restoration). A weed invasion can increase from a single small patch to a major infestation in that time period, and passive approaches to restoration only work at early stages of invasion (McIver and Starr 2001). Cheatgrass has increased dramatically at high elevation in less than 10 years (Chapter 2). If rangeland utilization standards included more frequent allotment assessments, the likelihood of success for this particular type of passive approach to cheatgrass control (e.g., grazing removal) would be improved. Currently, during the 10-year period between allotments assessments, ranchers can make decisions about levels of grazing pressure

on an inter-annual or seasonal basis that could affect native plant conservation. Policies that provide incentives to ranchers for conservation of native species could also increase passive control of cheatgrass.

Another passive approach to cheatgrass control that is currently supported by federal regulations is fire suppression. The important role that invasive species, and cheatgrass in particular, play in altering fire regimes in the Western U.S. has been given increased attention in the news (e.g., Christensen 2000, Speckman 2008, Orr 2011) and by federal agencies (Wildland Fire Leadership Council 2011), particularly after the large fire season of 1999 in Nevada, which was attributed to cheatgrass invasion (USDI-BLM 2000). New policies recommend that managers survey for fire-altering invasive species before prescribed burns, and managers in the eastern Sierra with whom we spoke indicated that do consider cheatgrass before burning (i.e., a passive approach to restoration). New policies also allow land managers to allocate money from fire appropriations to actively treat invasive species infestations that affect fuel loads (such as cheatgrass; Wildland Fire Leadership Council 2011). This resource appears to currently be under-utilized (based on our interview results), possibly because cheatgrass has not yet caused shifts to the fire regime in the region. However, cheatgrass fuel loads have been building up to high levels in recent years at higher elevations (Chapter 2), and managers would be justified in using these monies to reduce its cover. Fire appropriations could be increasingly used to support more active approaches to cheatgrass control.

The main social challenges to cheatgrass control that we identified include: (1) land managers perceptions of low overall feasibility (i.e., when considering ecological, economic, and regulatory factors) of cheatgrass control, and (2) stakeholder aversion to herbicide use on public lands. These challenges are not unique to cheatgrass control. Managers perception of whether or not adjacent landowners are working to control invasive species is likely to influence their decisions about technical feasibility of control on the land that they manage (Epanchin-Niell et al. 2010). Increased collaboration on broader scales (e.g., with Nevada WMAs) could increase perceived feasibility of control, particularly since cheatgrass control is being prioritized in Nevada (USDI-BLM 2000). Coordination is essential so that efforts to eradicate outlier patches of cheatgrass are complemented by approaches to reduce or eliminate the flow of seed sources from larger populations on adjacent land. Land managers perception of feasibility of control of widespread invasive species, in general, would also be improved with a commitment on the part of the federal government to support efforts to "slow the spread" of these species. Stable federal funding directed toward research, strategies, and implementation of programs to slow the spread of some of the most damaging of widespread invaders (e.g., zebra mussels, cheatgrass) are likely to decrease overall costs compared to scenarios where these same species are left unmanaged (Lodge et al. 2006). This would give managers on a regional scale confidence that their efforts will not be futile. It would also direct allocation of resources toward invasive species control that may not otherwise be prioritized.

We found that stakeholder views and the public comment process (part of both NEPA and CEQA) can also influence weed control on public lands. For example, if managers perceive the threat of litigation, they may not choose to use herbicides to control weed infestations (Stern and Mortimer 2009). Education campaigns targeted to inform the public about the economic and ecological costs of a plant invasion and the potential for increased problems with spread could be an effective way to garner support for invasive species work. This can include public "meet the weeds" days, volunteer weed pulling or control days, or campaigns to encourage people to minimize the transport of weed seeds into wilderness areas. Ultimately, a more informed public might also be inclined to lobby or vote for increased public funding for invasive species management programs.

We identified one main logistical challenge to using grazing management as an active approach to reducing cheatgrass cover in widespread infestations: ranchers' scheduling conflicts. Many of the ranchers in the region have commitments to multiple agencies (the USFS, BLM, and LADWP), and timelines are strict about when they should be grazing cattle on which allotment. Leasing conditions need to be more flexible for timed grazing to be effectively implemented. This may require changes to rangeland utilization rules, coordination between the agencies that administer the allotments, and flexibility on the part of the ranchers. Land managers with whom we spoke indicated good working relationships with ranchers, which could facilitate the implementation of grazing management strategies directed toward weed control. Allotment rules and regulations would also have to be modified.

Overall, much of the cheatgrass control work that is already being done in the eastern Sierra Nevada would fall into the category of a "passive approach". Given the stage and extent of the invasion, passive approaches are probably not enough to reduce future cheatgrass spread and impacts. Active approaches are likely to be much more effective at eliminating and slowing the spread of the invasion now rather than at some future time when infestations have had greater impacts on the ecosystem. In other words, ecological feasibility of successful control in this region is high with the proper resource inputs, but significant social, regulatory, and logistical barriers to restoration exist. This pattern may be common for widespread invasive weeds at their invasion fronts. There is some evidence that managers are less likely to allocate resources toward invasive species control that do not yet have direct economic impacts on a region (Pauchard et al. 2009). However, the topic is largely unexplored. Land management at invasion fronts will become increasingly in this time of rapid global change, as species range margins are shifting (Parmesan 2006, Mainka and Howard 2010). In many cases, invasive species may be ideally suited (more so than natives) to adapt to new conditions and spread in response to increases in suitable habitat, and in some cases, range contractions of invasive species may provide opportunities for restoration (Dukes and Mooney 1999, Bradley et al. 2010, Mainka and Howard 2010). Either way, it is clear that managing species based on current distribution is no longer appropriate (Mainka and Howard 2010). Land managers should be prepared to respond with flexibility to invasive species movement or increased impacts (Mainka and Howard 2010). Many of the obstacles and challenges

that we outlined here limit the flexibility and speed at which land managers respond to invasive species infestations, and finding solutions to these obstacles would benefit land management for conservation of native species in the face of climate change in general, not just cheatgrass control efforts.

In conclusion, we presented a case study of the feasibility of control of a non-noxious invasive plant, cheatgrass, at the edge of its range in eastern California. We identified regulatory, social, and logistical obstacles to specific weed control methods (including both passive and active approaches) to determine whether the actions that are being taken are those that would be recommended based on current ecological understanding of the system. Although land managers in the region view cheatgrass as problematic and appear dedicated and passionate about conservation of native species (e.g., by actively engaging in conservation activities outside of agency expectations), control efforts in their current form are probably not sufficient for minimizing future impacts of cheatgrass invasion. We identified ways of improving management that could apply more broadly to other invasive species in California and beyond. This work highlights the importance of evaluating feasibility from multiple perspectives when making recommendations for invasive plant management.

Table 4.1: Agencies and organizations involved in invasive weed control in Inyo and Mono Counties, CA. All groups listed are members of the Eastern Sierra Weed Management Area (ESWMA 2012). Asterisks appear next to groups that were represented in our interviews.

	Agency or Stakeholder Group
Federal	Bureau of Land Management Bishop Field Office (BLM) *
	Inyo National Forest (USFS) *
	Toiyabe National Forest (USFS)
State	California Department of Food and Agriculture (CDFA)
	California Department of Transportation District 9 (Caltrans) *
	California Department of Forestry
	Natural Resource Conservation Service
County	Inyo/Mono Counties' Agricultural Commissioner's Office *
	Inyo County Water Department *
	Inyo/Mono Conservation District
City of LA	Los Angeles Department of Water and Power (LADWP) *
Non-govt	Inyo/Mono Counties' Cattleman's Association

Table 4.2: Barriers and opportunities to weed control in the eastern Sierra Nevada, CA, categorized as regulatory or social/logistical. NEPA refers to the National Environmental Protection Act and CEQA refers to the California Environmental Quality Act. Each barrier and opportunity is explained further in the text.

	Barriers	Opportunities
Regulatory	No Noxious Weed Designation	Agency goals
	NEPA/ CEQA	NEPA/ CEQA
	Agency budgets (most cases)	Rangeland utilization standards and policy
		Federal Fire Management Policy
Social/ Logistical	Land managers perception of cheatgrass	Land managers perception of cheatgrass
	Ranchers- logistic considerations	Ranchers- relationship with managers
	Herbicides- stakeholder aversion	Dedicated agency employees
		Education & Volunteer programs

Table 4.3: Species listed on both the California Invasive Plant Council (Cal-IPC) invasive species list and the state noxious weed list (NOX= noxious weed rating, Cal-IPC= their rating, Imp= Impact, Inv= Invasiveness, and Dist= Distribution).

		Rating		Cal-IPC Classification			
Scientific Name	**Common Name**	**NOX**	**Cal-IPC**	**Alert**	**Imp**	**Inv**	**Dist**
Acroptilon repens	Russian knapweed	B	Moderate	No	B	B	B
Aegilops triuncialis	Barb goatgrass	B	High	No	A	A	B
Ailanthus altissima	Tree-of-heaven	A	Moderate	No	B	B	B
Alternanthera philoxeroides	Alligator weed	A	High	Alert	A	B	C
Asphodelus fistulosus	Onionweed	B	Moderate	Alert	B	A	C
Brachypodium sylvaticum	Perennial false-brome	A	Moderate	Alert	B	A	D
Cardaria draba	Hoary cress	B	Moderate	No	B	B	B
Cardaria pubescens	Hairy whitetop	B	Limited	No	C	B	C
Carduus acanthoides	Plumeless thistle	A	Limited	No	B	C	C
Carduus nutans	Musk thistle	A	Moderate	No	B	B	B
Carduus tenuiflorus	Slenderflower thistle	C	Limited	No	C	C	B
Carthamus lanatus	Woolly distaff thistle	B	Moderate	Alert	A	B	C
Centaurea calcitrapa	Purple starthistle	B	Moderate	No	B	B	B
Centaurea diffusa	Diffuse knapweed	A	Moderate	No	B	B	B
Centaurea maculosa	Spotted knapweed	A	High	No	A	B	B
Centaurea melitensis	Malta starthistle	C	Moderate	No	B	B	B
Centaurea solstitialis	Yellow starthistle	C	High	No	A	B	A
Chondrilla juncea	Rush skeletonweed	A	Moderate	No	B	B	B
Cirsium vulgare	Bull thistle	C	Moderate	No	B	B	B
Cortaderia jubata	Jubatagrass	B	High	No	A	A	A
Crupina vulgaris	Common crupina	A	Limited	No	B	C	B
Cynara cardunculus	Artichoke thistle	B	Moderate	No	B	B	B
Cynodon dactylon	Bermudagrass	C	Moderate	No	B	B	B
Cytisus scoparius	Scotch broom	C	High	No	A	B	A
Delairea odorata	Cape-ivy	B	High	No	A	A	B
Egeria densa	Brazilian egeria	C	High	No	A	A	B
Euphorbia esula	Leafy spurge	A	High	Alert	A	A	C
Euphorbia oblongata	Oblong spurge	B	Limited	No	C	C	B
Euphorbia terracina	Carnation spurge	Q	Moderate	Alert	B	B	C
Halogeton glomeratus	Halogeton	A	Moderate	No	B	A	B
Hydrilla verticillata	Hydrilla	A	High	Alert	A	B	C
Hypericum perforatum	Common St. John's wort	C	Moderate	No	B	B	B
Iris pseudacorus	Yellowflag iris	C	Limited	No	C	B	C
Isatis tinctoria	Dyer's woad	B	Moderate	No	B	B	A
Lepidium latifolium	Perennial pepperweed	B	High	No	A	A	A
Limnobium laevigatum	So Am spongeplant	Q	High	Alert	A	A	C
Linaria genistifolia s dalmatica	Dalmation toadflax	A	Moderate	No	B	B	B
Lythrum salicaria	Purple loosestrife	B	High	No	A	A	B
Ononis alopecuroides	Foxtail restharrow	Q	Limited	No	C	B	C
Onopordum acanthium	Scotch thistle	A	High	No	B	B	B
Polygonum cuspidatum	Japanese knotweed	B	Moderate	Alert	B	B	D
Polygonum sachalinense	Sakhalin knotweed	B	Moderate	Alert	B	B	D
Salsola paulsenii	Barbwire Russian-thistle	C	Limited	No	C	C	C
Salsola tragus	Russian-thistle	A	Limited	No	C	B	B
Salvia aethiopis	Mediterranean sage	B	Limited	No	C	B	B
Senecio jacobaea	Tansy ragwort	B	Limited	No	C	B	B
Sesbania punicea	Red sesbania	B	High	Alert	A	B	C
Spartina anglica	Common cordgrass	B	Moderate	Alert	B	B	D
Spartina densiflora	Dense-flr cordgrass	B	High	Alert	A	B	D
Spartina patens	Saltmeadow cord grass	B	Limited	No	C	C	D
Spartium junceum	Spanish broom	C	High	No	A	B	B
Taeniatherum caput-medusae	Medusahead	C	High	No	A	A	A
Tamarix parviflora	Smallflower tamarisk	B	High	No	A	A	B
Tamarix ramosissima	Saltceda	B	High	No	A	A	A
Ulex europaeus	Gorse	B	High	No	A	B	B
Watsonia meriana	Bulbil watsonia	B	Limited	No	C	B	C
Zostera japonica	Dwarf eelgrass	A	High	Alert	B	B	C

Table 4.4: Species listed as "High" by the California Invasive Plant Council (Cal-IPC) that do not appear on the state noxious weed list (NOX= noxious weed rating, Cal-IPC= their rating, Imp= Impact, Inv= Invasiveness, and Dist= Distribution).

Scientific Name	Common Name	Rating	Alert	Imp	Inv	Dist
Ammophila arenaria	European beachgrass	High	No	A	B	B
Arundo donax	Giant reed	High	No	A	B	A
Brassica tournefortii	Saharan mustard	High	No	A	A	B
Bromus madritensis ssp. rubens	Red brome	High	No	A	B	A
Bromus tectorum	Downy brome, cheatgrass	High	No	A	B	A
Carpobrotus edulis	Hottentot-fig, iceplant	High	No	A	B	A
Cortaderia selloana	Pampasgrass	High	No	A	A	B
Ehrharta calycina	Purple veldtgrass	High	No	A	A	B
Eichhornia crassipes	Water hyacinth	High	Alert	A	A	C
Foeniculum vulgare	Fennel	High	No	A	B	A
Genista monspessulana	French broom	High	No	A	A	B
Hedera helix, H. canariensis	English ivy, Algerian ivy	High	No	A	A	A
Ludwigia hexapetala	Uruguay water-primrose	High	Alert	A	B	C
Ludwigia peploides ssp. montevidensis	Creeping water-primrose	High	No	A	B	B
Myriophyllum aquaticum	Parrotfeather	High	Alert	A	B	C
Myriophyllum spicatum	Eurasian watermilfoil	High	No	A	A	B
Rubus armeniacus	Himalaya blackberry	High	No	A	A	A
Salvinia molesta	Giant salvinia	High	Alert	A	A	C
Spartina alterniflora (and S. alterniflora x foliosa hybrids)	Smooth cordgrass and hybrids, Atlantic cordgrass	High	Alert	A	A	C

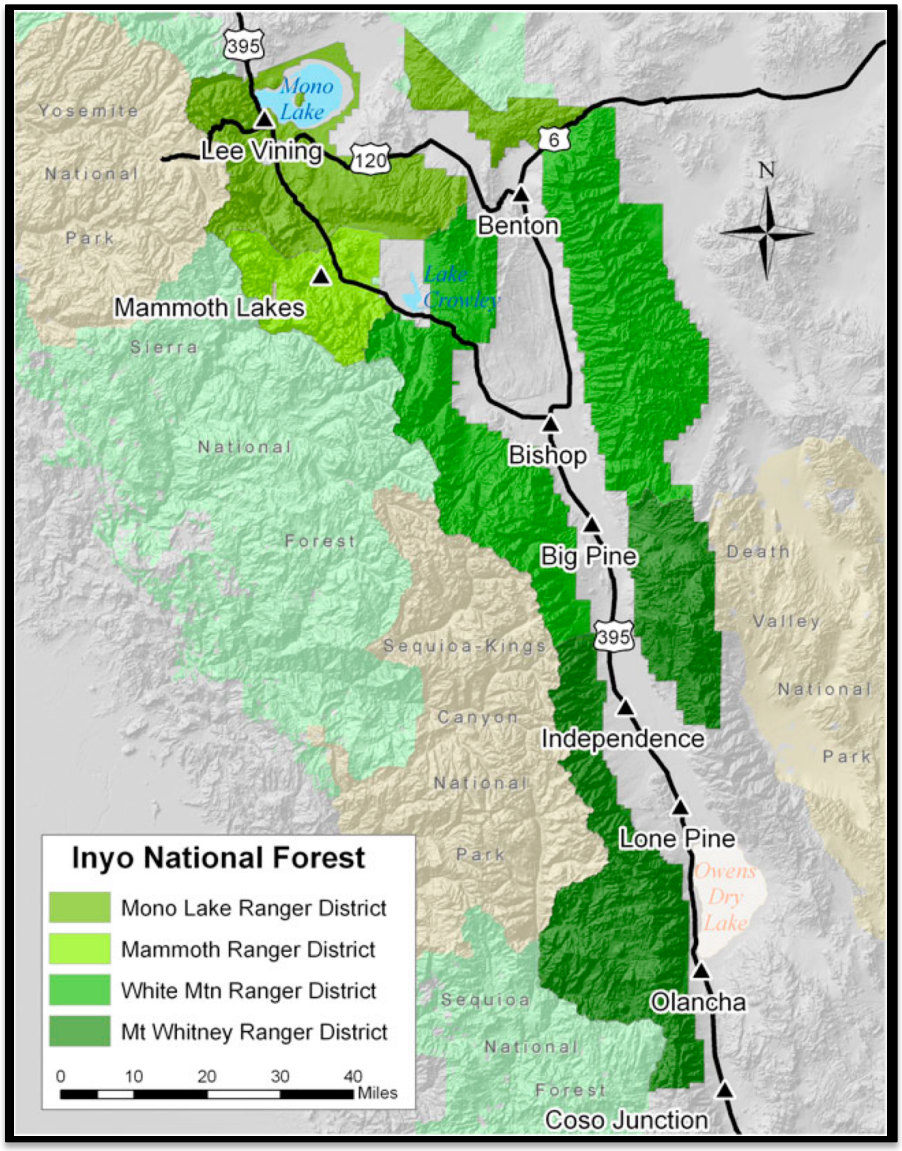

Figure 4.1: Physical jurisdiction of invasive species management in Inyo and Mono counties. Shown in dark green are Inyo National Forest lands. The grey area is a mix of Bureau of Land Management and Los Angeles Department of Water and Power land. Map source: Inyo National Forest, USDA Forest Service, http://www.fs.usda.gov/recmain/inyo/recreation

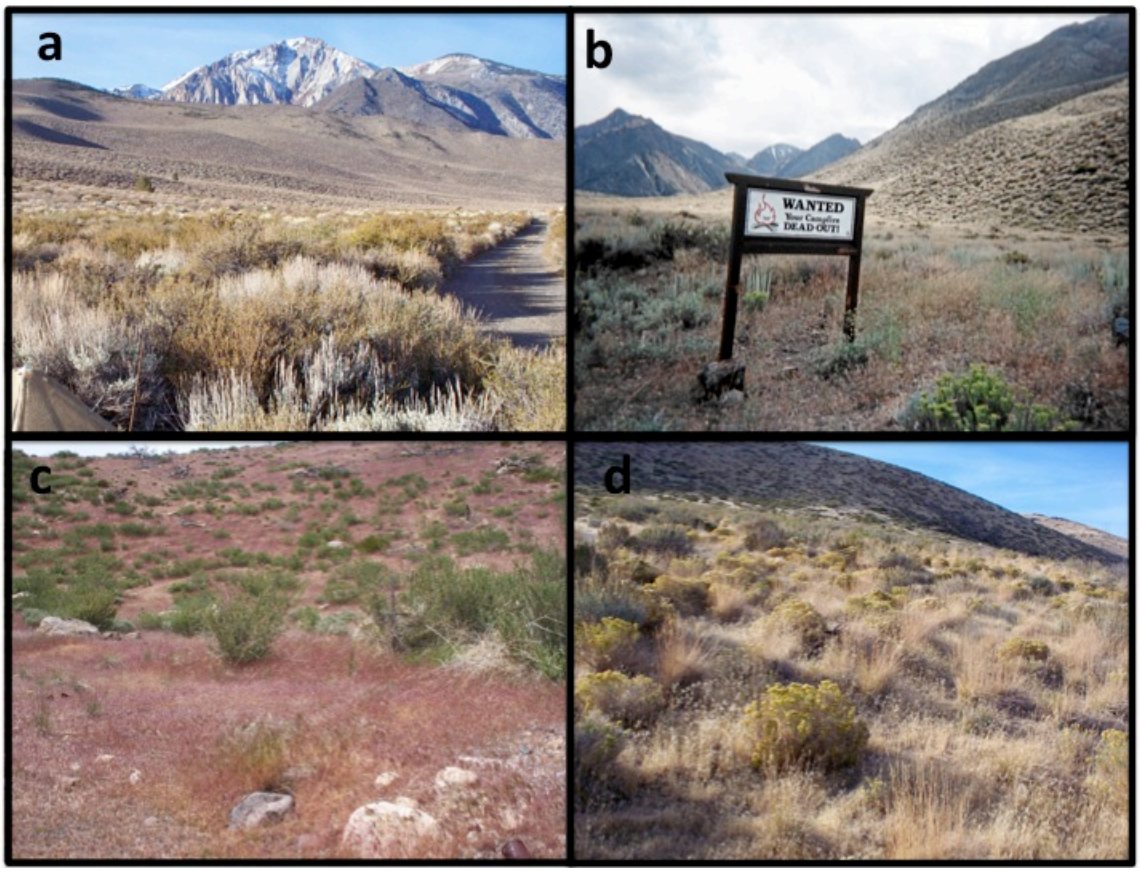

Figure 4.2: Different levels of cheatgrass invasion in the eastern Sierra Nevada landscape, including: (a) relatively undisturbed sagebrush steppe in Inyo County, CA where cheatgrass makes up a small portion of the understory but has not yet had process-level effects on the ecosystem, (b) small (< 20 m^2) roadside infestation of cheatgrass in Inyo County, CA at ~2100 m in elevation, (c) recently burned area that has been heavily invaded with cheatgrass in northern Mono County, CA, and (d) recently burned area near Carson City, NV, that was revegetated with fire-adapted native species.

CONCLUSIONS:

SUMMARY OF FINDINGS AND IMPLICATIONS FOR MANAGEMENT

In this dissertation, I took an inter-disciplinary approach to evaluating the impacts, spread, and control of high elevation populations of *Bromus tectorum* in the eastern Sierra Nevada at the edge of the western Great Basin Desert. Below, I summarize the main findings in two parts: (1) the likelihood of *Bromus tectorum* spread, and (2) the feasibility of its control. To conclude, I highlight some important implications for management of *B. tectorum*-invaded systems in the region.

Likelihood of *Bromus tectorum* spread with global change

Although uncertainty surrounds predictions of how climate (especially precipitation) might change in future years (Weltzin et al. 2003b), managing invasive species based on current occurrence and spread rates would be unrealistic (Mainka and Howard 2010). Instead, managers should be equipped with knowledge of how changing conditions might affect the spread of invasive species in their region so that they can respond quickly to a variety of different scenarios. Understanding how multiple agents of global change might interact will be crucial, since environmental stresses and disturbances often have interactive rather than additive effects on ecosystem structure and function (Savage 1994, Winner 1994, Vanheerden and Yanai 1995, Kozlowski 2000, Bielenberg et al. 2001, Felzer et al. 2004, Vinebrooke et al. 2004).

In Chapters 1 & 2 of this dissertation, I identified how agents of global change may interact to affect the spread of *B. tectorum* at its high elevation range boundary.

In Chapter 1, I found that climate change and increased anthropogenic nitrogen deposition could facilitate the spread of *B. tectorum* under certain conditions. Deep snowpack exerted a negative effect on *B. tectorum* germination and density. Predicted decreases in snowpack may alleviate physiological constraints on *B. tectorum* and allow for increased germination and subsequent increases in population growth. Increased spring rainfall events increased *B. tectorum* growth and fecundity, particularly in the inter-shrub spaces. Frequency, timing, and antecedent conditions were important influences on the magnitude of *B. tectorum* response to spring rain events. Together, my results suggest that a shift from snow to rain may increase *B. tectorum* invasiveness at this elevation, but timing and magnitude of rain events, along with growing season length (determined in part by snowpack and timing of snowmelt), will probably all interact to affect response.

In Chapter 1, I also found that effects of nitrogen on *B. tectorum* growth are tightly coupled to water availability. In 2011, *B. tectorum* seed production and biomass were co-limited by N and water. When I added increasing levels of N (at 5 g versus 10 g m^{-2}) with simulated rain events, I found that *B. tectorum* response to N was dependent on the magnitude of the rain event. The threshold for *B. tectorum* response to N was higher with less water and lower with more water. Thus, under years of high spring rainfall, *B. tectorum* spread might be facilitated by even small increases in N deposition. Under ambient precipitation conditions, *B. tectorum* did

not respond to N in any year, probably because precipitation was below average for the duration of the study.

These results combined with past research help to highlight conditions under which *B. tectorum* might be more (or less) likely to spread at high elevation. *B. tectorum* germination, growth, and seed production appear to be affected by interactive effects of snow, rainfall, temperature, and soil nutrient conditions (Figure c.1). I demonstrated that *B. tectorum* germination depends on snowpack at high elevation, which was consistent with past research (Mack and Pyke 1983, Griffith and Loik 2010); past research has also shown that rainfall events and soil temperature are important for *B. tectorum* germination (Beckstead et al. 1996, Bilbrough and Caldwell 1997, Meyer et al. 1997, Allen and Meyer 2002, Miller et al. 2006, Rawlins et al. 2012)**.** Establishment and early growth of *B. tectorum* may depend on the interaction of snowpack (and particularly the timing of snowmelt) and soil temperature (Mack and Pyke 1983, Griffith and Loik 2010), the interaction of rainfall (and its effect on soil moisture) and soil temperature (Mack and Pyke 1983), and nitrogen status of soils (Bilbrough and Caldwell 1997, Monaco et al. 2003b). My experiments confirm that depending on timing of delivery, rainfall events can be an important influence on *B. tectorum* growth and seed production, and that the previous winter's snowpack is likely to affect *B. tectorum* response to rain. *B. tectorum* response to N appears to be dependent on adequate soil moisture; above some threshold of soil moisture, rainfall and N were interactive in their effects on *B. tectorum* growth and seed production. Temperature and its influence on the number

of growing degree days can also have a significant effect on total biomass accumulation of *B. tectorum* at high elevation (Chambers et al. 2007), but not much experimental work has been done to tease out effects of temperature, snowpack, and timing of snowmelt. This is an important area for future research. Spatially, stoichiometric relationships are probably important in determining differential invasion success by *B. tectorum* across the landscape. Though my research was focused primarily on N, results suggest that *B. tectorum* growth is also influenced by phosphorus and magnesium availability. These relationships should be further explored.

Results from Chapter 2 were consistent with what I would have predicted based on findings from Chapter 1. Nitrogen was added to plots over four consecutive years at ambient precipitation levels and I found no effect on species composition or *B. tectorum* dominance. During the four years of the study, annual precipitation was below the 24-year average; in years of increased springtime precipitation, we may see expect to see a response to anthropogenic N deposition particularly in N-hotspots along roadsides. I found that *Bromus tectorum* has been increasing in cover at high elevation and potentially impacting diversity of herbaceous species, particularly native forbs. During a year of high spring precipitation, *B. tectorum* cover increased to levels above which fire risk approached 100% in some of the most disturbed parts of the landscape (that had been both burned and grazed). Land managers in the region should be prepared to use active restoration approaches that reduce *B.*

tectorum biomass (and subsequent effects on the fuel-load) during years of high rainfall to ensure that fire risk is minimized.

Feasibility of control of *B. tectorum* from multiple perspectives

Based on my results from Chapters 1 & 2, it is clear that *Bromus tectorum* is increasing at its range margin and may be further facilitated by climate change. *B. tectorum* has not yet initiated an invasive grass-fire cycle in the region, and control efforts are much more likely to be effective now when native bunchgrasses and shrubs are still abundant. In Chapters 3 & 4, I tested feasibility of *B. tectorum* control from multiple perspectives- through both ecological experiments and stakeholder interviews.

In Chapter 3, I tested approaches for active control of outlier patches of *B. tectorum* at high elevation. I found that several low-tech, non-chemical methods were effective at reducing *B. tectorum* density, cover, and dominance in the seedbank, but they had different effects on non-target organisms. Mulching and soil solarization effectively reduced *B. tectorum* by 99% after just one treatment application, but they also decreased cover of native plants. Soil solarization also resulted in a complete elimination of the native seed bank and is likely to have effects on the microbial community that I did not measure. Hand pulling was effective at reducing *B. tectorum* (by 94% after 2 consecutive years) and it had positive effects on native species, increasing native plant cover and dominance in the seedbank. Associated costs of *B. tectorum* control were highest with solarization and mulching. Although

hand pulling is time consuming and requires a multiple-year commitment, it is probably the best method for reducing outlier patches of *B. tectorum* and increasing native cover in wildland settings at high elevation where the native seedbank is still relatively intact. Mulching and solarization may be practical for use along roadsides or other disturbed areas where the main management goal is reduction of *B. tectorum* spread rather than restoration of the native plant community.

In Chapter 4, I compared my recommendations for passive and active approaches to controlling *B. tectorum* infestations (based on my results from Chapter 3 and past ecological research) with what land managers in the region are actually able to accomplish considering budgetary, regulatory, social, and logistic constraints. I found that despite the fact that land managers in the region perceived *B. tectorum* as a potential threat (both for ecological and economic reasons), very little control work is currently being done to limit its spread. Passive approaches to *B. tectorum* control (e.g., those that involve removal of stressors, such as grazing pressure and fire) are occurring in the region to some extent, but could be improved. Active *B. tectorum* control (e.g., removing infestations and working to restore native pant communities) is limited by substantial obstacles, including noxious weed laws that designate high priority invasive species for control (and do not include *B. tectorum*), staffing shortages that affect the time to complete an environmental review process, National Environmental Policy Act procedural requirements, and logistical issues with working with ranchers on public lands, among others (see Table 4.2 for complete list and section V of Chapter 4). Based on my results, I provide suggestions for improved

cheatgrass control in the region, many of which apply to the control of widespread non-noxious invasive species, in general.

Implications for Management

It is clear from my research that *Bromus tectorum* is increasing in the eastern Sierra Nevada and that agents of global change may further facilitate range expansion. Land managers should be prepared to more actively control *B. tectorum* populations to avoid future impacts. In this dissertation, I identified restoration methods that could be used to reduce the spread of *B. tectorum*, but I also identified social barriers to implementation of these techniques. Considering results from all four chapters combined, I present recommendations for management of *Bromus tectorum* populations that should be feasible considering obstacles that were identified in Chapter 4 (Table c.1). Ultimately, however, gaps in federal and state regulations and policy need to be addressed and stable sources of funding need to be allocated toward invasive species control work in order to slow or stop the spread of species like *B. tectorum* at their range margins. Results from this work highlight the importance and necessity of inter-disciplinary approaches to environmental problem solving. My hope is that this dissertation will directly result in increased conservation of native species in the eastern Sierra Nevada sagebrush steppe ecosystem.

Table c.1.: Recommendations for cheatgrass (*Bromus tectorum*) control at high elevation in the eastern Sierra Nevada, CA, based on ecological feasibility alone ("Optimal Strategy") and based on the integration of ecological knowledge and the awareness of social barriers ("Recommended Strategy").

TYPE OF INFESTATION	OPTIMAL STRATEGY	BARRIERS	RECOMMENDED STRATEGY
Roadside Infestations	Use mulch or herbicides	Mulch is costly; Chemical herbicides restricted on Caltrans projects	Prioritize infestations that are adjacent to sagebrush habitat of high conservation value; Experiment with the use of organic herbicides
Outlier infestations in wildland settings	Hand pull annually	Staff shortages	Encourage volunteer groups or environmental education groups to "adopt an infestation"; Organize volunteer weed control days
Outlier infestations in disturbed locations	Mulch or use solarization to eliminate cheatgrass, and plant native plugs	Costly	Use funding from fuels reduction programs and/or pair with other fuels reduction work (e.g., use woodchips from tree removal projects to mulch invasive species patches); Encourage environmental educators in the region to use this strategy
Widespread low-density infestations	Monitor annually for increases in biomass; Use livestock to reduce biomass in years of high precipitation	Logistical feasibility associated with using livestock	Use passive approaches to restoration (e.g., reduction of grazing pressure, fire suppression) until logistical barriers to timed grazing management are overcome

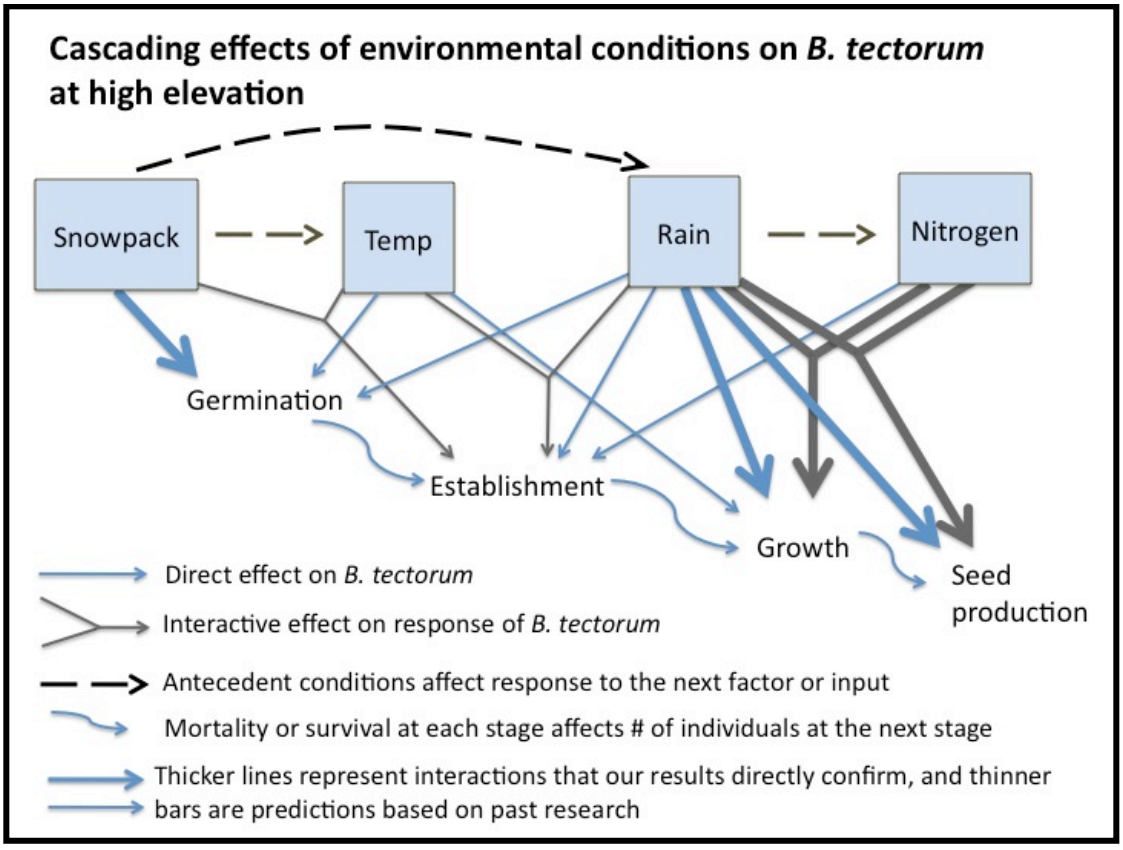

Figure c.1: Conceptual diagram representing direct, indirect, and interactive effects of climate and soil nutrient status on *Bromus tectorum* germination, establishment, growth, and seed production at high elevation in the eastern Sierra Nevada, CA. Predictions are based on results from Chapter 1 of this dissertation and past research.

Supplemental Material

Appendix 1: Summary of one-way SIMPER comparisons of herbaceous community composition by disturbance history in 2008, 2009, 2010, and 2011. Dissimilarity values refer to the average calculated dissimilarity between species cover at the two sites being compared (Table 1: GB vs UB, Table 2: GB vs GU, and Table 3: UB vs GU). Average abundance, average dissimilarity, and the standard deviation of dissimilarity are listed for each species. Individual contributions of each species toward the dissimilarity between groups are listed in the "Contribution" column. The final column includes the cumulative contribution to the total dissimilarity as species are added. At the bottom of each set of data, we list the cumulative contribution of native grasses and forbs to the difference. All data were transformed to the 4th root.

Table 1: Comparisons of plant community composition between grazed burned (GB) and ungrazed-burned (UB) from 2008 to 2011 (4^{th} root transformed data).

Species	Average abundance GB group	Average abundance UB group	Average dissimilarity	Dissimilarity/ SD	Contribution (%)	Cumulative Contr (%)
A). 2008. Average dissimilarity = 50.08						
Pleiacanthus spinosus	1.06	0.69	4.88	1.25	9.74	9.74
Phacelia bicolor	0.65	1.20	4.19	1.43	8.37	18.12
Achnatherum hymenoides	0.61	0.93	3.98	1.20	7.94	26.06
Gayophytum diffusum	0.77	1.16	3.60	1.26	7.18	33.24
Hesperostipa comata	0.31	0.57	3.16	1.01	6.31	39.55
Bromus tectorum	1.89	1.55	3.08	1.04	6.15	45.71
Eriastrum wilcoxii	0.24	0.77	3.08	1.37	6.15	51.86
Gilia brecaarum	0.30	0.50	2.89	0.87	5.77	57.62
Viola purpurea	0.47	0.34	2.56	1.06	5.11	62.73
Elymus elymoides	1.07	0.95	2.48	1.14	4.95	67.68
Eriogonum spergulinum	0.26	0.64	2.44	1.33	4.88	72.56
Chenopodium album	0.00	0.44	2.09	0.91	4.18	76.74
Cryptantha cicumscissa	0.12	0.43	1.99	1.06	3.97	80.71
Monardella linoides	0.29	0.08	1.75	0.50	3.49	84.19
Unknown herbaceous	0.12	0.31	1.71	0.85	3.41	87.60
Cryptantha simulans	0.26	0.16	1.56	0.83	3.11	90.71
CUM NATIVE GRASSES	***1.99***	***2.45***			***19.20***	
CUM NATIVE FORBS	***4.54***	***6.72***			***65.36***	

Table 1 continued

Species	Average abundance GB group	Average abundance UB group	Average dissimilarity	Dissimilarity/ SD	Contribution (%)	Cumulative Contr (%)
B). 2009. Average dissimilarity = 53.29						
Achnatherum hymenoides	0.67	1.03	4.15	1.28	7.78	7.78
Gayphytum diffusum	0.21	0.91	3.92	1.45	7.36	15.15
Hesperostipa comata	0.35	0.72	3.88	1.02	7.28	22.43
Achnatherum nevadensis	0.78	0.68	3.28	1.32	6.16	28.58
Pleiacanthus spinosus	0.34	0.46	3.23	0.76	6.07	34.65
Elymus elymoides	0.54	0.37	3.02	1.02	5.67	40.33
Cryptantha cicumscissa	0.15	0.65	3.01	1.36	5.65	45.97
Eriastrum wilcoxii	0.15	0.59	2.79	1.15	5.24	51.22
Lupinus argentus	0.49	0.05	2.62	0.78	4.92	56.14
Gilia brecaarum	0.66	0.85	2.60	1.08	4.89	61.02
Eriogonum spergulinum	0.62	0.58	2.55	1.08	4.79	65.81
Phacelia bicolor	0.38	0.36	2.51	0.97	4.71	70.53
Viola purpurea	0.17	0.44	2.44	0.82	4.58	75.10
Bromus tectorum	2.24	1.92	2.37	1.46	4.45	79.55
Chenopodium album	0.37	0.22	2.20	0.83	4.13	83.68
Carex spp	0.23	0.24	1.88	0.75	3.53	87.21
Stephanomeria pauciflora	0.34	0.07	1.86	0.57	3.50	90.71
CUM NATIVE GRASSES	***2.57***	***3.04***			***30.42***	
CUM NATIVE FORBS	***3.88***	***5.18***			***55.84***	
C). 2010. Average dissimilarity = 52.01						
Pleiacanthus spinosus	0.36	0.66	4.28	0.90	8.23	8.23
Hesperostipa comata	0.56	0.71	4.08	1.05	7.84	16.07
Achnatherum hymenoides	0.33	0.90	3.97	1.41	7.63	23.70
Achnatherum nevadensis	0.74	0.85	3.85	1.14	7.41	31.11
Elymus elymoides	0.61	0.70	3.66	1.12	7.05	38.15
Eriastrum wilcoxii	0.20	0.82	3.61	1.58	6.94	45.09
Gayphytum diffusum	0.38	0.86	3.19	1.24	6.14	51.23
Cryptantha cicumscissa	0.12	0.59	2.78	1.47	5.34	56.57
Phacelia bicolor	0.27	0.63	2.74	1.35	5.27	61.84
Gilia brecaarum	0.56	0.28	2.41	1.15	4.63	66.47
Eriogonum baileyi	0.24	0.48	2.32	1.11	4.46	70.93
Carex spp	0.37	0.00	2.15	0.55	4.13	75.06
Bromus tectorum	2.12	1.89	1.90	1.27	3.65	78.71
Eriogonum spergulinum	0.16	0.31	1.89	0.89	3.63	82.35
Viola purpurea	0.13	0.29	1.81	0.74	3.48	85.83
Lupinus argentus	0.29	0.00	1.57	0.68	3.03	88.85
Chorizanthe brevicornu	0.00	0.24	1.25	0.70	2.40	91.25
CUM NATIVE GRASSES	***2.61***	***3.16***			***34.06***	
CUM NATIVE FORBS	***2.71***	***5.16***			***53.55***	

Table 1 continued

Species	**Average abundance GB group**	**Average abundance UB group**	**Average dissimilarity**	**Dissimilarity/ SD**	**Contribution (%)**	**Cumulative Contr (%)**
D). 2011. Average dissimilarity = 53.48						
Pleiacanthus spinosus	0.44	0.73	5.81	0.92	10.86	10.86
Achnatherum hymenoides	0.38	1.00	5.46	1.29	10.21	21.07
Achnatherum nevadensis	0.56	1.03	5.22	1.21	9.76	30.83
Hesperostipa comata	0.70	0.65	5.03	1.10	9.41	40.24
Elymus elymoides	0.71	0.62	4.59	1.10	8.59	48.82
Bromus tectorum	2.30	1.74	3.86	1.59	7.22	56.05
Viola purpurea	0.20	0.41	2.98	1.02	5.58	61.62
Cryptantha cicumscissa	0.00	0.39	2.57	0.95	4.80	66.42
Eriastrum wilcoxii	0.00	0.38	2.40	0.85	4.49	70.91
Lupinus argentus	0.26	0.08	2.11	0.60	3.95	74.86
Gayphytum diffusum	0.00	0.32	1.98	0.76	3.69	78.56
Carex spp	0.23	0.00	1.69	0.41	3.16	81.72
Gilia brecaarum	0.20	0.04	1.42	0.64	2.66	84.38
Eriogonum spergulinum	0.00	0.20	1.23	0.61	2.30	86.68
Eriogonum baileyi	0.00	0.18	1.10	0.52	2.06	88.74
Aster spp	0.04	0.13	0.95	0.43	1.78	90.52
CUM NATIVE GRASSES	***2.58***	***3.30***			***41.13***	
CUM NATIVE FORBS	***1.14***	***2.86***			***42.17***	

Table 2: Comparisons of plant community composition between grazed-burned (GB) and grazed-unburned (GU) from 2008 to 2011 (4^{th} root transformed data).

Species	Average abundance GB group	Average abundance GU group	Average dissimilarity	Dissimilarity/ SD	Contribution (%)	Cumulative Contr (%)
A). 2008. Average dissimilarity = 56.13						
Pleiacanthus spinosus	1.06	0.17	5.49	1.30	9.78	9.78
Phacelia bicolor	0.65	1.15	4.54	1.26	8.09	17.87
Gayophytum diffusum	0.77	1.34	4.13	1.29	7.36	25.23
Bromus tectorum	1.89	1.21	3.98	1.56	7.09	32.32
Achnatherum hymenoides	0.61	0.42	3.45	1.07	6.15	38.47
Unknown herbaceous	0.12	0.73	3.40	1.32	6.05	44.52
Eriastrum wilcoxii	0.24	0.73	3.30	1.24	5.89	50.41
Viola purpurea	0.47	0.32	2.82	1.08	5.02	55.43
Elymus elymoides	1.07	1.00	2.65	1.12	4.72	60.15
Hesperostipa comata	0.31	0.39	2.64	0.93	4.71	64.86
Cryptantha simulans	0.26	0.45	2.55	1.02	4.55	69.41
Unknown herbaceous	0.12	0.44	2.25	1.06	4.00	73.41
Gilia brecaarum	0.30	0.27	2.09	0.90	3.73	77.14
Achnatherum nevadensis	0.00	0.42	2.00	0.69	3.57	80.71
Cryptantha cicumscissa	0.12	0.36	1.85	0.92	3.29	84.00
Calochortus bruneaunis	0.26	0.23	1.80	0.87	3.20	87.20
Monardella linoides	0.29	0.00	1.43	0.44	2.54	89.74
Eriogonum spergulinum	0.26	0.00	1.35	0.69	2.40	92.14
CUM NATIVE GRASSES	***1.99***	***2.23***			***19.15***	
CUM NATIVE FORBS	***4.92***	***6.19***			***65.90***	
B). 2009. Average dissimilarity = 56.02						
Gayphytum diffusum	0.21	0.86	4.05	1.47	7.23	7.23
Achnatherum hymenoides	0.67	0.72	4.01	1.17	7.16	14.38
Elymus elymoides	0.54	0.80	3.75	1.07	6.69	21.07
Achnatherum nevadensis	0.78	0.99	3.69	1.39	6.59	27.66
Bromus tectorum	2.24	1.63	3.49	1.52	6.22	33.88
Cryptantha simulans	0.31	0.60	3.31	1.05	5.91	39.80
Eriogonum spergulinum	0.62	0.06	3.27	1.30	5.84	45.63
Phacelia bicolor	0.38	0.49	3.02	1.02	5.39	51.02
Gilia brecaarum	0.66	0.86	2.97	1.16	5.31	56.33
Lupinus argentus	0.49	0.07	2.85	0.79	5.09	61.42
Cryptantha cicumscissa	0.15	0.53	2.75	1.08	4.92	66.34
Eriastrum wilcoxii	0.15	0.43	2.37	0.93	4.24	70.57
Viola purpurea	0.17	0.36	2.32	0.74	4.14	74.72
Chenopodium album	0.37	0.20	2.27	0.83	4.05	78.77
Pleiacanthus spinosus	0.34	0.12	2.19	0.63	3.92	82.69
Hesperostipa comata	0.35	0.00	2.00	0.60	3.57	86.26
Stephanomeria pauciflora	0.34	0.00	1.76	0.52	3.15	89.40
Unknown herbaceous	0.14	0.20	1.40	0.67	2.49	91.90
CUM NATIVE GRASSES	***2.34***	***2.51***			***24.01***	
CUM NATIVE FORBS	***4.33***	***4.78***			***61.68***	

Table 2 continued

Species	**Average abundance GB group**	**Average abundance GU group**	**Average dissimilarity**	**Dissimilarity/ SD**	**Contribution (%)**	**Cumulative Contr (%)**
C). 2010. Average dissimilarity = 54.09						
Achnatherum hymenoides	0.33	0.87	4.31	1.36	7.96	7.96
Elymus elymoides	0.61	0.80	3.82	1.13	7.06	15.02
Achnatherum nevadensis	0.74	0.68	3.79	1.12	7.02	22.04
Hesperostipa comata	0.56	0.32	3.61	0.97	6.67	28.71
Chorizanthe brevicornu	0.00	0.56	3.24	1.29	5.98	34.69
Bromus tectorum	2.12	1.69	3.08	1.22	5.69	40.38
Phacelia bicolor	0.27	0.54	3.03	1.13	5.60	45.98
Cryptantha simulans	0.16	0.53	2.94	1.15	5.43	51.40
Eriastrum wilcoxii	0.20	0.56	2.92	1.21	5.40	56.80
Gayphytum diffusum	0.38	0.52	2.45	1.08	4.53	61.33
Carex spp	0.37	0.00	2.37	0.55	4.38	65.71
Pleiacanthus spinosus	0.36	0.06	2.36	0.63	4.37	70.08
Gilia brecaarum	0.56	0.44	2.25	1.00	4.15	74.23
Viola purpurea	0.13	0.29	2.16	0.73	3.99	78.22
Lupinus argentus	0.29	0.08	2.08	0.70	3.85	82.07
Cryptantha cicumscissa	0.12	0.29	1.82	0.84	3.36	85.43
Eriogonum spergulinum	0.16	0.20	1.68	0.77	3.10	88.53
Eriogonum baileyi	0.24	0.00	1.43	0.70	2.64	91.17
CUM NATIVE GRASSES	***2.61***	***2.67***			***33.09***	
CUM NATIVE FORBS	***2.87***	***4.07***			***52.40***	
D). 2011. Average dissimilarity = 51.43						
Elymus elymoides	0.71	0.96	5.64	1.12	10.97	10.97
Hesperostipa comata	0.70	0.46	5.55	1.07	10.80	21.77
Achnatherum hymenoides	0.38	0.64	5.07	1.15	9.86	31.63
Achnatherum nevadensis	0.56	0.34	4.79	1.01	9.32	40.95
Bromus tectorum	2.30	1.83	3.76	1.76	7.32	48.26
Pleiacanthus spinosus	0.44	0.07	3.41	0.66	6.63	54.89
Cryptantha simulans	0.04	0.37	2.92	0.87	5.67	60.56
Viola purpurea	0.20	0.24	2.82	0.77	5.49	66.04
Lupinus argentus	0.26	0.06	2.46	0.57	4.78	70.82
Carex spp	0.23	0.00	1.98	0.41	3.85	74.67
Phacelia bicolor	0.08	0.16	1.73	0.62	3.36	78.03
Gilia brecaarum	0.20	0.00	1.47	0.61	2.85	80.89
Leptodactylon pungens	0.08	0.15	1.38	0.42	2.67	83.56
Cryptantha cicumscissa	0.00	0.16	1.28	0.52	2.48	86.05
Eriastrum wilcoxii	0.00	0.13	1.00	0.44	1.95	88.00
Eriogonum baileyi	0.00	0.12	0.95	0.44	1.85	89.85
Chorizanthe brevicornu	0.00	0.13	0.89	0.44	1.73	91.57
CUM NATIVE GRASSES	***2.58***	***2.40***			***44.80***	
CUM NATIVE FORBS	***1.30***	***1.59***			***39.46***	

Table 3: Comparisons of plant community composition between grazed-burned (GB) and grazed-unburned (GU) from 2008 to 2011 (4^{th} root transformed data).

Species	Average abundance UB group	Average abundance GU group	Average dissimilarity	Dissimilarity/ SD	Contribution (%)	Cumulative Contr (%)
A). 2008. Average dissimilarity = 50.67						
Achnatherum hymenoides	0.93	0.42	3.88	1.21	7.65	7.65
Pleiacanthus spinosus	0.69	0.17	3.39	0.85	6.70	14.35
Hesperostipa comata	0.57	0.39	3.09	0.96	6.10	20.45
Gayophytum diffusum	1.16	1.34	2.98	1.17	5.88	26.33
Elymus elymoides	0.95	1.00	2.94	1.14	5.80	32.14
Eriogonum spergulinum	0.64	0.00	2.92	2.06	5.77	37.90
Unknown herbaceous	0.25	0.73	2.82	1.25	5.57	43.47
Phacelia bicolor	1.20	1.15	2.74	1.11	5.41	48.87
Eriastrum wilcoxii	0.77	0.73	2.68	1.19	5.29	54.16
Gilia brecaarum	0.50	0.27	2.57	0.83	5.08	59.24
Bromus tectorum	1.55	1.21	2.45	1.30	4.84	64.08
Cryptantha simulans	0.16	0.45	2.22	0.95	4.37	68.45
Viola purpurea	0.34	0.32	2.12	0.88	4.19	72.65
Unknown herbaceous2	0.31	0.44	2.05	1.08	4.05	76.70
Chenopodium album	0.44	0.13	2.00	0.96	3.96	80.65
Cryptantha cicumscissa	0.43	0.36	1.95	1.06	3.84	84.50
Achnatherum nevadensis	0.00	0.42	1.80	0.69	3.55	88.05
Phlox stansburyi	0.16	0.23	1.33	0.77	2.63	90.67
CUM NATIVE GRASSES	***2.45***	***2.23***			***23.10***	
CUM NATIVE FORBS	***7.05***	***6.32***			***62.74***	
B). 2009. Average dissimilarity = 49.53						
Achnatherum hymenoides	1.03	0.72	3.93	1.21	7.93	7.93
Achnatherum nevadensis	0.68	0.99	3.85	1.21	7.77	15.69
Hesperostipa comata	0.72	0.00	3.80	0.91	7.67	23.36
Elymus elymoides	0.37	0.80	3.76	1.19	7.59	30.95
Cryptantha simulans	0.07	0.60	3.11	0.96	6.28	37.23
Viola purpurea	0.44	0.36	2.93	0.93	5.91	43.14
Phacelia bicolor	0.36	0.49	2.90	1.00	5.85	49.00
Eriogonum spergulinum	0.58	0.06	2.87	1.20	5.79	54.79
Eriastrum wilcoxii	0.59	0.43	2.72	1.14	5.50	60.29
Pleiacanthus spinosus	0.46	0.12	2.71	0.66	5.47	65.76
Gayphytum diffusum	0.91	0.86	2.62	1.06	5.28	71.04
Cryptantha cicumscissa	0.65	0.53	2.48	1.09	5.00	76.05
Gilia brecaarum	0.85	0.86	2.40	1.07	4.85	80.89
Bromus tectorum	1.92	1.63	1.79	1.35	3.62	84.51
Chenopodium album	0.22	0.20	1.66	0.73	3.35	87.86
Chorizanthe brevicornu	0.09	0.20	1.26	0.63	2.54	90.40
CUM NATIVE GRASSES	***2.80***	***2.51***			***30.96***	
CUM NATIVE FORBS	***5.22***	***4.71***			***55.82***	

Table 3 continued

Species	Average abundance UB group	Average abundance GU group	Average dissimilarity	Dissimilarity/ SD	Contribution (%)	Cumulative Contr (%)
C). 2010. Average dissimilarity = 47.10						
Hesperostipa comata	0.71	0.32	3.79	1.01	8.05	8.05
Pleiacanthus spinosus	0.66	0.06	3.73	0.77	7.92	15.97
Achnatherum nevadensis	0.85	0.68	3.71	1.22	7.87	23.84
Elymus elymoides	0.70	0.80	3.68	1.16	7.81	31.65
Achnatherum hymenoides	0.90	0.87	3.12	1.09	6.63	38.27
Cryptantha simulans	0.09	0.53	2.65	1.16	5.63	43.90
Gayphytum diffusum	0.86	0.52	2.59	1.08	5.50	49.41
Chorizanthe brevicornu	0.24	0.56	2.52	1.15	5.34	54.75
Eriogonum baileyi	0.48	0.00	2.43	1.20	5.15	59.90
Eriastrum wilcoxii	0.82	0.56	2.37	1.05	5.04	64.94
Cryptantha cicumscissa	0.59	0.29	2.31	1.19	4.91	69.85
Phacelia bicolor	0.63	0.54	2.30	1.17	4.88	74.73
Viola purpurea	0.29	0.29	2.25	0.82	4.79	79.52
Gilia brecaarum	0.28	0.44	2.03	1.06	4.31	83.82
Bromus tectorum	1.89	1.69	2.03	1.10	4.30	88.12
Eriogonum spergulinum	0.31	0.20	1.85	0.92	3.92	92.05
CUM NATIVE GRASSES	***3.16***	***2.67***			***30.36***	
CUM NATIVE FORBS	***5.25***	***3.99***			***57.39***	
D). 2011. Average dissimilarity = 52.43						
Achnatherum nevadensis	1.03	0.34	6.24	1.37	11.90	11.90
Pleiacanthus spinosus	0.73	0.07	5.53	0.82	10.55	22.44
Achnatherum hymenoides	1.00	0.64	4.97	1.23	9.48	31.92
Hesperostipa comata	0.65	0.46	4.84	1.03	9.24	41.16
Elymus elymoides	0.62	0.96	4.84	1.10	9.23	50.39
Viola purpurea	0.41	0.24	3.11	1.01	5.93	56.32
Cryptantha cicumscissa	0.39	0.16	2.74	0.99	5.22	61.54
Eriastrum wilcoxii	0.38	0.13	2.65	0.92	5.05	66.59
Cryptantha simulans	0.12	0.37	2.64	0.90	5.03	71.62
Bromus tectorum	1.74	1.83	2.36	1.35	4.50	76.12
Gayphytum diffusum	0.32	0.08	2.19	0.81	4.17	80.29
Eriogonum baileyi	0.18	0.12	1.64	0.67	3.14	83.43
Eriogonum spergulinum	0.20	0.00	1.26	0.61	2.40	85.83
Phacelia bicolor	0.00	0.16	1.18	0.53	2.24	88.07
Phacelia distans	0.09	0.09	1.11	0.48	2.12	90.20
CUM NATIVE GRASSES	***3.30***	***2.40***			***39.85***	
CUM NATIVE FORBS	***2.82***	***1.42***			***45.85***	

Appendix 2: Summary of one-way SIMPER comparisons of herbaceous community composition by disturbance history in 2008, 2009, 2010, and 2011. Dissimilarity values refer to the average calculated dissimilarity between species cover at the two sites being compared (Table 1: GB vs UB, Table 2: GB vs GU, and Table 3: UB vs GU). Average abundance, average dissimilarity, and the standard deviation of dissimilarity are listed for each species. Individual contributions of each species toward the dissimilarity between groups are listed in the "Contribution" column. The final column includes the cumulative contribution to the total dissimilarity as species are added. At the bottom of each set of data, we list the cumulative contribution of native grasses and forbs to the difference. All data are untransformed.

Table 1: Comparisons of plant community composition between grazed burned (GB) and ungrazed-burned (UB) from 2008 to 2011 (untransformed data).

Species	Average abundance GB group	Average abundance UB group	Average dissimilarity	Dissimilarity/ SD	Contribution (%)	Cumulative Contr (%)
A). 2008. Average dissimilarity = 65.22						
Bromus tectorum	16.25	8.31	19.12	1.59	29.32	29.32
Pleiacanthus spinosus	4.92	4.14	10.23	0.96	15.68	45
Phacelia bicolor	2	4	6.56	0.92	10.06	55.05
Gayophytum diffusum	1.58	4.06	5.79	0.94	8.87	63.93
Achnatherum hymenoides	1.33	3.47	5.63	0.94	8.63	72.56
Elymus elymoides	1.75	2.36	3.76	0.99	5.76	78.32
Gilia brecaarum	0.29	1.53	2.9	0.32	4.45	82.77
Hesperostipa comata	0.25	1.69	2.87	0.58	4.4	87.17
Monardella linoides	1.5	0.24	2.69	0.49	4.13	91.3
CUM NATIVE GRASSES	**3.33**	**7.52**			**18.79**	
CUM NATIVE FORBS	**10.29**	**13.97**			**43.19**	

Table 1 continued

Species	Average abundance GB group	Average abundance UB group	Average dissimilarity	Dissimilarity/ SD	Contribution (%)	Cumulative Contr (%)
B). 2009. Average dissimilarity = 58.34						
Bromus tectorum	29.72	14.86	22.79	1.47	39.05	39.05
Achnatherum hymenoides	2.14	3.42	5.04	0.88	8.64	47.69
Pleiacanthus spinosus	1.25	2.64	4.45	0.62	7.62	55.31
Hesperostipa comata	0.92	3.11	4.31	0.61	7.38	62.69
Gayphytum diffusum	0.19	2.19	2.64	0.57	4.52	67.21
Achnatherum nevadensis	1	1.53	2.33	0.9	4	71.21
Stephanomeria pauciflora	1.53	0.14	1.89	0.4	3.23	74.44
Lupinus argentus	1.36	0.03	1.82	0.56	3.12	77.57
Viola purpurea	0.22	1.36	1.79	0.38	3.07	80.63
Elymus elymoides	1.06	0.67	1.79	0.83	3.06	83.69
Gilia brecaarum	0.78	1.11	1.44	0.96	2.47	86.16
Carex spp.	0.61	0.17	1.13	0.51	1.94	88.1
Eriogonum spergulinum	0.67	0.58	1.13	0.62	1.93	90.03
CUM NATIVE GRASSES	5.73	8.9			25.02	
CUM NATIVE FORBS	6	8.05			25.96	
C). 2010. Average dissimilarity = 50.52						
Bromus tectorum	21.69	14.33	18.66	1.47	36.93	36.93
Pleiacanthus spinosus	1.06	3.99	6.6	0.78	13.07	50
Hesperostipa comata	1.25	2.63	4.77	0.84	9.45	59.45
Achnatherum nevadensis	1.43	2.39	3.69	1.14	7.3	66.74
Elymus elymoides	0.9	2.04	3.5	0.62	6.92	73.67
Achnatherum hymenoides	0.25	1.75	3.08	0.99	6.1	79.76
Carex spp.	1.57	0	2.33	0.44	4.62	84.38
Gayphytum diffusum	0.17	1.17	1.98	0.72	3.92	88.3
Eriastrum wilcoxii	0.08	0.88	1.55	0.77	3.07	91.37
CUM NATIVE GRASSES	5.4	8.81			34.39	
CUM NATIVE FORBS	1.31	6.04			20.06	
D). 2011. Average dissimilarity = 50.96						
Bromus tectorum	28.86	12.15	29.03	1.88	56.96	56.96
Elymus elymoides	1.85	1.96	3.72	1.15	7.29	64.26
Hesperostipa comata	1.83	0.79	3.57	0.79	7.01	71.27
Pleiacanthus spinosus	2.01	0.17	3.3	0.57	6.47	77.73
Achnatherum hymenoides	0.58	1.06	2.15	0.91	4.22	81.95
Carex spp.	1.08	0	2.04	0.35	4.01	85.96
Achnatherum nevadensis	0.83	0.71	2.01	0.88	3.95	89.91
Lupinus argentus	0.56	0.08	1.15	0.42	2.27	92.18
CUM NATIVE GRASSES	**6.17**	**4.52**			**26.48**	
CUM NATIVE FORBS	**2.57**	**0.25**			**8.74**	

Table 2: Comparisons of plant community composition between grazed-burned (GB) and grazed-unburned (GU) from 2008 to 2011 (untransformed data).

Species	Average abundance GB group	Average abundance UB group	Average dissimilarity	Dissimilarity/ SD	Contribution (%)	Cumulative Contr (%)
A). 2008. Average dissimilarity = 76.88						
Bromus tectorum	16.25	2.49	23.84	1.51	31.01	31.01
Gayophytum diffusum	1.58	6.64	9.74	0.91	12.67	43.68
Pleiacanthus spinosus	4.92	0.78	9.11	1.02	11.84	55.53
Phacelia bicolor	2	3.88	8.17	0.89	10.63	66.16
Elymus elymoides	1.75	2.42	4.01	1.24	5.22	71.38
Achnatherum hymenoides	1.33	1.06	3.43	0.85	4.46	75.84
Monardella linoides	1.5	0	2.71	0.44	3.52	79.36
Eriastrum wilcoxii	0.08	1.35	2.5	0.62	3.25	82.62
Unknown herbaceous	0.04	1.51	2.27	0.58	2.96	85.57
Hesperostipa comata	0.25	0.97	1.75	0.52	2.28	87.85
Leptodactylon pungens	0	0.89	1.63	0.29	2.12	89.98
Achnatherum nevadensis	0	0.94	1.43	0.6	1.87	91.84
CUM NATIVE GRASSES	**3.33**	**5.39**			**13.83**	
CUM NATIVE FORBS	**10.12**	**15.05**			**46.99**	
B). 2009. Average dissimilarity = 66.39						
Bromus tectorum	29.72	7.83	30.1	1.55	45.34	45.34
Achnatherum nevadensis	1	3	4.39	1.17	6.62	51.96
Achnatherum hymenoides	2.14	1.89	4.3	0.96	6.48	58.43
Elymus elymoides	1.06	1.83	2.78	0.96	4.18	62.62
Lupinus argentus	1.36	0.14	2.23	0.59	3.35	65.97
Cryptantha simulans	0.31	1.28	2.15	0.74	3.24	69.21
Gilia brecaarum	0.78	1.36	2.05	1.02	3.09	72.3
Pleiacanthus spinosus	1.53	0	2.03	0.38	3.06	75.36
Gayphytum diffusum	0.19	1.25	1.98	0.85	2.99	78.35
Stephanomeria spinosa	1.25	0.17	1.9	0.57	2.87	81.21
Viola purpurea	0.22	0.97	1.73	0.49	2.6	83.81
Phacelia bicolor	0.42	0.81	1.54	0.85	2.32	86.13
Hesperostipa comata	0.92	0	1.51	0.52	2.27	88.4
Carex spp.	0.61	0	1.18	0.41	1.78	90.18
CUM NATIVE GRASSES	**5.73**	**6.72**			**21.33**	
CUM NATIVE FORBS	**6.06**	**5.98**			**23.52**	

Table 2 continued

Species	**Average abundance GB group**	**Average abundance UB group**	**Average dissimilarity**	**Dissimilarity/ SD**	**Contribution (%)**	**Cumulative Contr (%)**
C). 2010. Average dissimilarity = 56.33						
Bromus tectorum	21.69	9.85	28.07	1.61	49.82	49.82
Achnatherum hymenoides	0.25	1.85	3.42	0.94	6.08	55.9
Hesperostipa comata	1.25	0.57	3.38	0.74	5.99	61.9
Elymus elymoides	0.9	1.6	3.22	1.03	5.71	67.6
Achnatherum nevadensis	1.43	1.14	3.17	1.08	5.63	73.24
Carex spp.	1.57	0	2.83	0.44	5.03	78.27
Pleiacanthus spinosus	1.06	0.1	2.48	0.53	4.4	82.67
Leptodactylon pungens	0.1	0.63	1.56	0.4	2.78	85.45
Phacelia bicolor	0.17	0.5	1.17	0.76	2.07	87.52
Lupinus argentus	0.26	0.29	1.11	0.43	1.97	89.49
Viola purpurea	0.06	0.44	0.94	0.49	1.67	91.15
CUM NATIVE GRASSES	5.4	5.16			28.44	
CUM NATIVE FORBS	1.65	1.96			12.89	
D). 2011. Average dissimilarity = 57.62						
Bromus tectorum	28.86	11.35	28.7	1.77	49.81	49.81
Pleiacanthus spinosus	2.01	4.43	7.47	0.86	12.96	62.78
Achnatherum nevadensis	0.83	3.1	4.3	1	7.46	70.23
Hesperostipa comata	1.83	1.58	3.72	0.92	6.45	76.69
Achnatherum hymenoides	0.58	2.32	3.37	1.11	5.85	82.54
Elymus elymoides	1.85	0.97	2.85	0.85	4.94	87.48
Carex spp.	1.08	0	1.82	0.35	3.15	90.63
CUM NATIVE GRASSES	**6.17**	**7.97**			**27.85**	
CUM NATIVE FORBS	**2.01**	**4.43**			**12.96**	

Table 3: Comparisons of plant community composition between grazed-burned (GB) and grazed-unburned (GU) from 2008 to 2011 (untransformed data).

Species	Average abundance GB group	Average abundance UB group	Average dissimilarity	Dissimilarity/ SD	Contribution (%)	Cumulative Contr (%)
A). 2008. Average dissimilarity = 69.96						
Gayophytum diffusum	4.06	6.64	10.47	1.04	14.96	14.96
Bromus tectorum	8.31	2.49	10.44	1.19	14.93	29.89
Phacelia bicolor	4	3.88	8.35	0.94	11.94	41.83
Pleiacanthus spinosus	4.14	0.78	7.41	0.59	10.6	52.42
Achnatherum hymenoides	3.47	1.06	6.33	0.93	9.05	61.47
Elymus elymoides	2.36	2.42	4.57	1.24	6.53	68
Hesperostipa comata	1.69	0.97	3.8	0.69	5.42	73.42
Eriastrum wilcoxii	1.32	1.35	3.15	0.85	4.51	77.93
Gilia brecaarum	1.53	0.18	3.04	0.31	4.35	82.28
Unknown herbaceous	0.11	1.51	2.16	0.58	3.09	85.37
Leptodactylon pungens	0.06	0.89	1.65	0.31	2.35	87.72
Achnatherum nevadensis	0	0.94	1.39	0.61	1.98	89.7
CUM NATIVE GRASSES	**7.52**	**5.39**			**22.98**	
CUM NATIVE FORBS	**15.22**	**15.23**			**51.8**	
B). 2009. Average dissimilarity = 59.25						
Bromus tectorum	14.86	7.83	14.06	1.32	23.73	23.73
Achnatherum hymenoides	3.42	1.89	6.17	0.86	10.41	34.14
Hesperostipa comata	3.11	0	5.01	0.55	8.46	42.6
Achnatherum nevadensis	1.53	3	5	1.23	8.45	51.05
Pleiacanthus spinosus	2.64	0.17	4.8	0.52	8.09	59.14
Gayphytum diffusum	2.19	1.25	3.79	0.72	6.4	65.54
Viola purpurea	1.36	0.97	3.4	0.56	5.73	71.27
Elymus elymoides	0.67	1.83	3.36	1.12	5.68	76.95
Cryptantha simulans	0.14	1.28	2.36	0.73	3.98	80.93
Gilia brecaarum	1.11	1.36	2.22	1.09	3.75	84.67
Phacelia bicolor	0.56	0.81	1.84	0.84	3.11	87.78
Leptodactylon pungens	0.14	0.72	1.38	0.43	2.33	90.11
CUM NATIVE GRASSES	8.73	6.72			33	
CUM NATIVE FORBS	8.14	6.56			33.39	

Table 3 continued

Species	**Average abundance GB group**	**Average abundance UB group**	**Average dissimilarity**	**Dissimilarity/ SD**	**Contribution (%)**	**Cumulative Contr (%)**
C). 2010. Average dissimilarity = 55.74						
Bromus tectorum	14.33	9.85	17.08	1.31	30.63	30.63
Pleiacanthus spinosus	3.99	0.1	6.86	0.65	12.3	42.93
Hesperostipa comata	2.63	0.57	5.05	0.68	9.05	51.99
Achnatherum nevadensis	2.39	1.14	4.97	1.13	8.91	60.9
Elymus elymoides	2.04	1.6	4.84	0.75	8.68	69.58
Achnatherum hymenoides	1.75	1.85	4.19	1.06	7.51	77.09
Gayphytum diffusum	1.17	0.25	2.34	0.72	4.2	81.29
Eriastrum wilcoxii	0.88	0.36	1.76	0.71	3.16	84.45
Viola purpurea	0.35	0.44	1.32	0.67	2.36	86.82
Leptodactylon pungens	0	0.63	1.22	0.32	2.19	89.01
Phacelia bicolor	0.29	0.5	1.12	0.85	2.01	91.02
CUM NATIVE GRASSES	**8.81**	**5.16**			**34.15**	
CUM NATIVE FORBS	**6.68**	**2.28**			**26.22**	
D). 2011. Average dissimilarity = 53.46						
Bromus tectorum	12.15	11.35	17.51	1.38	32.75	32.75
Pleiacanthus spinosus	0.17	4.43	9.03	0.73	16.9	49.65
Achnatherum nevadensis	0.71	3.1	6.74	1.05	12.6	62.25
Achnatherum hymenoides	1.06	2.32	5.06	1.12	9.46	71.71
Elymus elymoides	1.96	0.97	3.94	1.12	7.38	79.09
Hesperostipa comata	0.79	1.58	3.78	0.99	7.08	86.17
Viola purpurea	0.35	0.28	1.33	0.51	2.49	88.66
Eriastrum wilcoxii	0.06	0.43	1.22	0.37	2.28	90.95
CUM NATIVE GRASSES	**4.52**	**7.97**			**36.52**	
CUM NATIVE FORBS	**0.58**	**5.14**			**21.67**	

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