UNDERSTANDING ECOLOGICAL INTERACTIONS TO IMPROVE

MANAGEMENT OF *BROMUS TECTORUM* IN RANGELAND AND

CROPLAND ECOSYSTEMS

by

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ABSTRACT

Bromus tectorum L. (downy brome or cheatgrass) has been called the most dominant invasive plant species in the western United States. It is a barrier to restoration efforts in degraded lands and a serious weed problem for small grain growers. Investigating ecological interactions that play a mechanistic role in its success is a necessary step towards developing effective ecologically-based management strategies for *B. tectorum*. We investigated how biotic and abiotic factors impact interactions between *B. tectorum* and desired vegetation, with implications for restoration of lands dominated by *B. tectorum* and management of *B. tectorum* in small-grain cropping systems. Our research objectives were; 1) appraise the impact of relative size and soil nitrogen (N) availability on interactions between *B. tectorum* and *Pseudoroegneria spicata* (Pursh) A. Löve (bluebunch wheatgrass), a species important in rangeland revegetation, and, 2) determine the impacts of *Wheat streak mosaic virus* (WSMV), resource availability, and neighborhood characteristics on *B. tectorum* performance in a winter wheat (*Triticum aestivum* L.) system.

Objective 1 was carried out in a greenhouse experiment with two trials, following an addition series factorial design with four density treatments for each species, three *P. spicata* size cohort treatments, and two N treatments. Regression analysis indicated that giving *P. spicata* an initial size advantage over *B. tectorum* increased its ability to both suppress and avoid suppression by *B. tectorum*. We also observed that while N availability increased productivity of both species, it did not change their competitive relationship.

Objective 2 was explored in two trials of a field experiment using a split-plot design with N availability assigned to main plots, WSMV inoculation assigned to subplots, *B. tectorum* proximity to the nearest wheat row as a predictor, and neighborhood characteristics as covariates. Regression analysis indicated that in low and high N environments (compared to the recommended N rate), distance from row influenced individual *B. tectorum* biomass only in disease-free environments, suggesting that healthy wheat suppressed *B. tectorum* that was closest to the row. Wheat inoculated with WSMV did not suppress *B. tectorum*. In an intermediate N environment, increased distance from row increased *B. tectorum* performance only with WSMV inoculation.

CHAPTER ONE

PROJECT BACKGROUND AND OBJECTIVES

Introduction

Traditional approaches to weed management focus on short-term solutions such as herbicides or tillage to reduce the spread and impact of undesired species. It is increasingly being recognized that to attain long-lasting weed control that meets both land management and societal objectives, a more integrated, ecologically-based approach is necessary (Di Tomaso 2000, Sheley and Krueger-Mangold 2003, Shennan 2008). Understanding ecological processes and interactions could provide a useful basis for formulating integrated ecologically-based weed management systems that are economically viable and environmentally sound (Liebman 2001, Booth et al. 2003, Radosevich et al. 2007). To gain this understanding, it is important to assess how weeds interact with biotic (e.g. herbivores, other plants, and soil biota) and abiotic (e.g. disturbance regimes, soil characteristics, and moisture availability) factors in their environment (Booth et al. 2003). This knowledge could help explain patterns of invasion as well as mechanisms of competition between desired plants and weeds, enabling the prediction of impacts of weeds and the outcomes of integrated management (Radosevich and Rouch 1990).

Bromus tectorum L. (downy brome or cheatgrass) is an exotic annual grass that is troublesome in rangelands and croplands in the western United States, Canada, and Mexico (Zimdahl 2007, Mack 2011). Since it was first introduced to the U.S. in the late

1890's (Mack 1981), the area infested by *B. tectorum* has expanded to an estimated 23 million hectares in 17 Western states (Duncan et al. 2004). According to Mack (2011), *B. tectorum* is the most dominant invasive plant species in the Intermountain West, and it has also been identified as a major barrier to restoration efforts in degraded lands (Allen 1995). In cropping systems, *B. tectorum* seeds were first found as a grain contaminant in 1916, and it has since become a serious weed problem for small grain growers in the western U.S. (Morrow and Stahlman 1984).

The main goal of this project is to increase our understanding of *B. tectorum* ecology, a necessary step for developing ecologically-based management strategies to effectively reduce its spread and impacts in both rangeland and cropland systems. Specifically, this project focused on two aspects of *B. tectorum* ecology and management. First, the competitive relationship between *B. tectorum* and *Pseudoroegneria spicata* (Pursh) A. Löve (bluebunch wheatgrass) was assessed, with the intent of understanding how seedling establishment could be improved in rangeland revegetation projects. Second, the relationship between *Wheat streak mosaic virus* (WSMV) and *B. tectorum* was explored. In winter wheat (*Triticum aestivum* L) systems, *B. tectorum* co-occurs with WSMV, a generalist grass pathogen that decreases crop yield, and knowledge of this interaction could provide insights into the joint management of these two pests. In this chapter, I review literature relevant to this project, starting with *B. tectorum* biology. Next, I discuss how biotic and abiotic factors change competitive interactions between *B. tectorum* and desired vegetation in rangeland and cropland ecosystems.

Literature Review

Bromus tectorum Biology

Assessing the biology of *B. tectorum* provides a basis for understanding the underlying processes that contribute to its success in both rangelands and croplands. *Bromus tectorum* is a ruderal species that can quickly colonize disturbed areas such as overgrazed rangelands, burned areas, and crop and fallow fields through high seed production and rapid germination (Rydrych 1974, Morrow and Stahlman 1984). In favorable conditions, plant height can reach 40 cm, though plants as short as 2.5 cm can produce viable seed in conditions of severe moisture stress (Stewart and Hull 1949).

Most *B. tectorum* plants follow a winter annual life history; in regions that experience dry summers, they germinate and emerge in late summer or fall with resumption of rainfall (Harris 1967, Mack and Pyke 1983). However, like many annuals dependent on recruitment from seed, they exhibit varied life history traits that mitigate risk to the population as a whole (Crawley 1997). Seedlings are capable of emerging through the winter and into spring, provided enough moisture and little snow cover (Mack and Pyke 1983), and can initiate root growth at temperatures of five degrees C (Aguirre and Johnson 1991). It has been suggested that *B. tectorum* persists in variable, unpredictable environments through continuous emergence from August to May (Mack and Pyke 1983, Mack 2011). By producing multiple cohorts, *B. tectorum* can avoid excessive seedling mortality due to desiccation (Mack and Pyke 1983, Mack 2011).

Rangelands and Natural Areas

Bromus tectorum Impacts and Management. *Bromus tectorum* invasion has been

associated with widespread biotic impoverishment of arid and semi-arid rangelands in the

western U.S. (Mack 2011). This species can become dominant on rangelands following a

disturbance and can form near monocultures that may be an alternate stable state for the

plant community, preventing recruitment and recolonization of native species (Harris

1967, Humphrey and Schupp 2004, Chambers et al. 2007, Norton et al. 2007, Mack

2011). Dominance of *B. tectorum* has been associated with loss of sagebrush-steppe

habitat, altered fire regimes and nutrient cycling patterns (D'Antonio and Vitousek 1992,

Knapp 1996, Mack 2011), species shifts in plants and soil biota, and decreases in species

richness (Belnap et al. 2005).

Bromus tectorum is also detrimental to livestock producers. Though this species

can be used as nutritious spring forage, it is less reliable than the perennial grass species

it replaces (Morrow and Stahlman 1984). Not only does *B. tectorum* senesce and become

unsuitable forage earlier in the summer than perennial grasses, biomass yield of *B.*

tectorum can also vary up to 1000% annually based on precipitation patterns, making

reliance on this species impractical (Hull and Stewart 1948, Hull 1949). Further,

livestock can be harmed by *B. tectorum* as injury from its sharp awns can contribute to

infections of the eyes and mouth (Knapp 1996).

Rangeland management should aim to improve degraded lands and decrease their

susceptibility to weed invasion and spread (Di Tomaso 2000). Chemical control is the

most common method of invasive plant management in rangeland systems, and is

sometimes effective in managing *B. tectorum* (Di Tomaso 2000, Morris et al. 2009). Carefully timed prescribed burning and grazing also can be used to decrease seed production. However, usually a single approach to weed control is ineffective in the long term (Di Tomaso 2000), and an integrated approach is critical, particularly when *B. tectorum* has dominated a site for a long time period. Native perennial species may be lost through seed bank impoverishment and decreased recruitment due to *B. tectorum* competition (Humphrey and Schupp 2001, 2004, Mack 2011) and simply controlling *B. tectorum* may not be sufficient to restore native plant communities. Thus, *B. tectorum* control efforts should be integrated with revegetation as long-term strategies to suppress this invasive species and provide desirable forage (Di Tomaso 2000). However, reseeding desired species is often difficult on *B. tectorum* - dominated lands (Allen 1995, Di Tomaso 2000). Revegetation of lands dominated by *B. tectorum* using competitive native and introduced perennial species been the focus of much research (Hull and Stewart 1948, Cox and Anderson 2004, Davies et al. 2010). Due to mixed success of revegetation efforts, additional research is needed about meeting perennial species establishment requirements in revegetation projects (Call and Roundy 1991).

Resource Mediated Competition in Rangelands. Arid and semi-arid rangeland systems in the western U.S. have relatively low levels of soil nitrogen (N), with estimated annual net mineralization ranging from 1.5 to 10.5 g m^{-2} (Burke et al. 1997). Soil fertility in these rangelands has impacts on species composition (Elberse and Berendse 1993), and increased resource availability could favor weedy annual species over desirable perennial grasses (Wilson et al. 1966, Paschke et al. 2000), facilitating ecosystem invasion (Davis

et al. 2000). Soil fertility can be impacted by disturbance (e.g. fire, grazing, and herbicide application), which can increase nutrient availability in rangeland soils through decreased plant uptake, increased decomposition due to plant death, or increased mineralization rates due to higher light availability (Blank et al. 2007, Chambers et al. 2007).

Increased N may lead to increased competitive ability of *B. tectorum* and other problematic plants compared to desired perennial species (Davis et al. 2000, Chambers et al. 2007). Several competition experiments between invasive and desired plants over a range of soil N availability have been conducted. Paschke et al. (2000) determined that adding N to an old-field system increased the relative abundance of annual weedy plants, while experimentally decreasing N increased the abundance of perennial species. Studies have also focused on the relationship between exotic annual and native perennial grasses. Wilson et al. (1966) showed that heavy fertilization of mixed *B. tectorum* and *P. spicata* communities increased *B. tectorum* yields by 400-600%, while decreasing *P. spicata* yields by 50%, and that N fertilization facilitated *B. tectorum* invasion into perennial grass stands. Increasing soil N was also shown to increase the competitive ability of *B. tectorum* relative to native grasses in greenhouse experiments (Monaco et al. 2003, Vasquez et al. 2008a, Mangla et al. 2011). Further, Abraham et al. (2009) found that for two native perennial grasses, increased soil N led to decreased growth when sown with the exotic annual grass *Bromus diandrus* Roth (ripgut brome) compared to monoculture, suggesting that the relative competitive ability of *B. diandrus* increased with N enrichment.

Intrinsic differences in nutrient use between plant species may help explain competitive interactions (Berendse and Elberse 1990). Plant species differ in their response to increased N; some are able to increase uptake resulting in higher growth rates and seed production, while others have a more fixed rate of nutrient uptake (Chapin 1980). It is hypothesized that species native to nutrient limited environments, such as rangelands in the Rocky Mountains and Northern Great Plains, absorb nutrients at a relatively low rate even when more nutrients become available (Chapin 1980, Berendse and Elberse 1990). Problematic exotic plants such as *B. tectorum* are often shown to be more effective at quickly utilizing available nutrients than native plants, perhaps because they are adapted to higher nutrient environments and have more plasticity in nutrient absorption rates (Daehler 2003). Greenhouse experiments have shown that species native to nutrient rich habitats absorbed more N and grew faster than species from nutrient poor environments (Elberse and Berendse 1993).

Life-history strategy can also impact how competing plants respond to soil resources. Fast growing annual species such as *B. tectorum* may be able to increase uptake resulting in higher growth rates and seed production, while slower growing perennials generally have a less responsive rate of nutrient uptake (Chapin 1980, Crawley 1997). Nutrient acquisition patterns associated with these differing life histories have been described as conservative for perennial species and acquisitive for annual species, and traits associated with these patterns can help explain relative competitive ability (Grime 1977, Roumet et al. 2006). For example, higher specific leaf area and specific root length are traits often associated with annual species, and are related to greater

nutrient foraging and photosynthetic capacity (Roumet et al. 2006). Specifically, high leaf

N productivity (increase in plant dry mass per unit plant N per unit time) contributes to

faster uptake and growth of exotic annual grasses *B. tectorum* and *Taeniatherum caput-*

medusae (medusahead) compared to native perennial grasses *P. spicata* and *Elymus*

elymoides (Raf.) Swezy (bottlebrush squirreltail) (James 2008a). These traits allow

annual grasses to outperform perennial grasses in early stages of growth in both high and

low N settings (James 2008a).

Restoration of *Bromus tectorum-* Dominated Rangeland. The importance of

revegetating *B. tectorum* infested rangelands with desired perennial species has long been

recognized (e.g. Hull and Stewart 1948, Allen 1995, Whitson and Koch 1998, Davies et

al. 2010). Early and continued attempts to reseed perennial species have focused on

establishing competitive introduced grasses such as *Agropyron cristatum* L. (crested

wheatgrass), which has been useful in reclaiming sites from *B. tectorum* and providing

more reliable forage for livestock (Hull 1949, D'Antonio and Meyerson 2002, Davies et

al. 2010). It is widely recognized that competitive introduced species can form monotypic

stands than prevent recolonization of native species and promote low species diversity,

and that reestablishing native species has value for preservation and restoration of

ecosystem services including wildlife habitat and conservation of genetic diversity (Allen

1995, Richards et al. 1998, Norton et al. 2007, Mack 2011). Unfortunately, native

perennial species are often more difficult to establish on *B. tectorum*-dominated lands

than competitive introduced species (Hull and Stewart 1948, Davies et al. 2010).

The most vulnerable life history stages for seeded perennial species are germination, emergence, and establishment (Allen 1995, James and Svejcar 2010). Survival in these early stages of plant growth depends on the availability of suitable microsites that provide adequate conditions for survival such as sufficient light, moisture, and nutrients (Crawley 1997, Davis 2009). Though many factors (e.g. precipitation amount and timing, soil properties, and choice of plant materials) influence success of seeded perennial species, competition from invasive species may be a key factor in the failure of some revegetation projects. Competition from neighboring plants can impact seedling establishment by altering the microsite environment (Allen 1995). However, research on the effects of *B. tectorum* presence on seedling establishment in revegetation projects has had mixed results. For example, high *B. tectorum* densities have been shown to decrease seedling establishment in field experiments (Hull and Stewart 1948, Harris 1967), but James and Svejcar (2010) found that low densities (< 12 plants m^{-2}) of *B. tectorum* had no impact on seeded species establishment.

One important aspect impacting seedling establishment in restoration of *B. tectorum*-infested rangelands may be the difference in emergence times between neighboring seedlings. Through size asymmetries, these intrinsic differences could drive competitive interactions and impact seedling establishment. The relative emergence time of different plants in a mixture can impact outcomes of competition; earlier-emerging plants may preempt available space and suppress later-emerging plants (Ross and Harper 1972, Firbank and Watkinson 1990, Stevens and Fehmi 2009, Firn et al. 2010). As a result, early size discrepancies between plants cause reduced growth rates for the smaller

competitor (Connolly and Wayne 1996), and may allow the larger species to remove a disproportionate amount of resources (Freckleton and Watkinson 2001).

Life history differences between *B. tectorum* and native perennial grasses may cause early size disparities that reduce seeded species establishment. *Bromus tectorum* seedlings can gain a size advantage over perennial seedlings through earlier emergence and rapid growth rates. Because *B. tectorum* is a facultative winter annual species, most individuals germinate and emerge in late summer or fall with resumption of rainfall (Harris 1967, Mack and Pyke 1983). As a result, these plants have an established root system by spring. In addition, previous research has shown that *B. tectorum* initiates growth earlier in the spring than native grass seedlings (Harris and Wilson 1970, Aguirre and Johnson 1991), and has a higher relative growth rate (Arredondo et al. 1998, Mangla et al. 2010). Typical revegetation efforts include a fall herbicide application to control *B. tectorum*, followed by a fall-dormant seeding of cool-season species such as *P. spicata* (e.g. Sheley et al. 2001). This approach can lead to *P. spicata* seedlings emerging in the spring competing against established *B. tectorum* plants that emerged in late fall or early spring despite herbicide application. Seeded species that emerge in the spring after neighboring *B. tectorum* is actively growing have an initial size disadvantage, which may lead to decreased establishment due to asymmetric competition for resources.

Management practices that allow perennial seedlings to attain an initial size advantage over exotic annual grass competitors may lead to better establishment in revegetation projects (Abraham et al. 2009, Stevens and Fehmi 2009). In a greenhouse experiment, delayed emergence of exotic annual grass, *B. diandrus*, caused an increase in

biomass of perennial grasses *Nassella pulchra* A. Hitchcock (purple needlegrass) and *Festuca rubra* L. (red fescue) compared to concurrent species emergence (Abraham et al. 2009). In a field experiment conducted in California, the importance of initial size was again demonstrated. Three-month-old transplants of established perennial grasses *Agrostis oregonensis* Vasey (Oregon bentgrass), *F. rubra* and *N. pulchra* survived their first season and effectively suppressed exotic annual grasses *B. diandrus*, *Vulpia myuros* L. (rat-tail fescue), and *Avena barbata* Link. (slender wild oat) over the next three years (Corbin and D'Antonio 2004).

Small Grain Cropping Systems

Bromus tectorum Impacts and Management. *Bromus tectorum* is an increasingly problematic winter annual grassy weed in winter wheat cropping systems due to similar life histories, increased adoption of conservation tillage techniques, and reliance on broadcast nitrogen fertilizer (Morrow and Stahlman 1984, Radosevich and Rouch 1990, Blackshaw 1994, Zimdahl 2007). As in many crop-weed associations, the life forms of the two species are similar (Radosevich and Rouch 1990), allowing *B. tectorum* to compete effectively for resources (Zimdahl 2007). Indeed, in two studies, *B. tectorum* reduced winter wheat yields about 5% for every 10 *B. tectorum* plants m^{-2} (Rydrych and Muzik 1968, Cochran et al. 1990). Another study reported that densities of 24, 40, and 65 *B. tectorum* plants m^{-2} caused 10, 15, and 20% reductions in wheat yield, respectively (Stahlman and Miller 1990).

Similar to rangeland systems, chemical control is commonly used to manage *B. tectorum* in reduced tillage winter wheat-fallow systems (Morrow and Stahlman 1984,

Blackshaw 1991). In the past, chemical control of this species in small grain systems was difficult due to risk of crop injury (Morrow and Stahlman 1984). Though products for selective control of *B. tectorum* are now available (Menalled et al. 2008), excessive reliance on herbicides has resulted in unintended economic and environmental impacts including the proliferation of difficult to control weeds, decreased crop yields due to carryover effects, and surface and groundwater contamination (Pimentel et al. 1992, Liebman 2001, Ball et al. 2007, Zimdahl 2007). Further, herbicide resistant *B. tectorum* populations have been identified in one state in the United States, as well as in France and Spain (e.g. Menendez et al. 2006, Ball et al. 2007).

Cultural methods can also be used to control *B. tectorum*. Manipulation of fertilizer strategies represents a useful tool for weed management, particularly in crop-weed associations where increased fertility benefits the weed more than the crop (Di Tomaso 1995). For example, careful timing and placement (banded versus broadcast application) of fertilizer can increase crop competitive ability and reduce the effects of *B. tectorum* (Rasmussen 1995, Blackshaw 2004). Crop rotation and the use of more competitive cultivars of winter wheat are further possibilities to minimize the impact of *B. tectorum* on yield and quality (Blackshaw 1994).

Wheat Streak Mosaic Virus Biology, Impacts, and Management. *Wheat streak mosaic virus*, a viral disease vectored by the wheat curl mite (*Aceria tosichella* Keifer), is a common disease in the central plains of the United States. Both vector and virus occur on a diverse set of grass species, including crops as well as native and weedy species including wheat and *B. tectorum* (Duffus 1971, Christian and Willis 1993, Ito 2011). The

virus requires living plant tissue to survive and reproduce, and depends on the wheat curl mite to transmit it before host plant senescence (Wegulo et al. 2008). The mites are also dependent on green plant tissue for survival (Slykhuis 1955). As the host plant senesces, the mites move to the top of the plant to be dispersed by wind to a new host where mites and virus overwinter (Wegulo et al. 2008). In wheat-fallow agricultural systems, the wheat curl mite and WSMV both require alternate hosts to persist during periods when the crop is not present in the field. It has long been understood that volunteer wheat present in the fallow period contributes to the spread of WSMV by providing suitable habitat for both the virus and its vector (Connin 1956, Wegulo et al. 2008). It is suspected that winter annual grassy weeds like *B. tectorum* may play a similar role as an inoculum reservoir in infected fields (Duffus 1971, Wisler and Norris 2005).

Symptoms of WSMV include plant stunting, rosetting, and yellowing of leaves, and it also causes reductions in wheat kernel size, number, and weight (Atkinson and Grant 1967). *Wheat streak mosaic virus* interferes with chloroplast development in systemic infections (Brakke et al. 1988), and it also inhibits root development, leading to a reduction in water uptake (Price et al. 2010). Yield reductions from this disease can approach 100% in extreme cases (Atkinson and Grant 1967), though less severe reductions in yield are more common in infected fields. *Wheat streak mosaic virus* is managed primarily by preventative cultural methods, the goal being to eliminate alternate hosts for the wheat curl mite after fall wheat harvest (Wegulo et al. 2008). This can be accomplished by avoiding early wheat plantings in the fall, controlling volunteer wheat and grassy weeds, and planting WSMV- tolerant wheat cultivars (Wegulo et al. 2008).

Resource Mediated Competition in Croplands. Competitive interactions between crop and weed species may be impacted when growth of each species responds differently to environmental conditions, including soil resource availability (Liebman 2001, Blackshaw et al. 2003, Blackshaw and Brandt 2008). In cropping systems, N fertilizer is the most common input used to increase crop yield, but it also impacts weed-crop competitive interactions (Blackshaw et al. 2003, Zimdahl 2004). Fertilization can have unintended consequences if weeds are more responsive than crop species to N enrichment, making them more competitive under elevated N conditions (Di Tomaso 1995, Liebman and Mohler 2001, Zimdahl 2004, Blackshaw and Brandt 2008). In some cases, N enrichment decreases crop yield due to increased weed competitive ability (Di Tomaso 1995, Liebman and Davis 2000). Weed population dynamics can also be impacted, as increased soil resources can lead to higher weed germination rates and seed production (Liebman and Davis 2000).

Ecologically-based weed management hinges on shifting competitive relationships in favor of crops over weed species (Committee on Twenty-First Century Systems Agriculture; National Research Council 2010). In this context, understanding how fertilizer use impacts interactions between *B. tectorum* and winter wheat is critical to design effective management for this species. In field studies, increased N has been shown to increase *B. tectorum* performance, including seedling survival, culm production, and growth (Rasmussen 1995). Further, *B. tectorum* growth has been found to be more responsive than wheat to N enrichment under greenhouse conditions (Blackshaw et al. 2003), which may lead to increased impact on wheat yield (Blackshaw

and Brandt 2008). Because broadcast synthetic N fertilizer appears to increase the competitive ability of *B. tectorum* relative to winter wheat, fertilizer placement has been investigated as an integrated weed management approach (Rasmussen 1995, Beres et al. 2010). The form of added N is also important; in a field study comparing granular ammonium sulfate to manure, the *B. tectorum* seedbank was greatest in the manure treatment after four years (Blackshaw et al. 2005). The authors concluded that the slower release of nutrients from the manure benefitted *B. tectorum* more than winter wheat.

Understanding and Managing Multiple Pests in Agroecosystems. Pests such as *B. tectorum* and WSMV should not be studied and managed in isolation; instead we need to understand the interactions between them and how management practices may influence these interactions (Schroeder et al. 2005). As primary producers, weeds can potentially impact all other trophic levels in an agroecosystem, including other pests such as pathogens; some of these multi-pest interactions have the potential to impact crop yield (Norris 2005). Unfortunately, in croplands both research and integrated pest management recommendations are usually designed to target pests in one category (e.g. weeds, arthropods, or pathogens) at a time (Norris 2005, Schroeder et al. 2005, Wisler and Norris 2005). Consequently, although *B. tectorum* and WSMV co-occur in winter wheat systems, their joint impact, if any, is unknown.

Disease Impact on Plant Performance and Competition. Understanding multi-trophic pest interactions is critical to both define ecologically-based pest management recommendations and to predict the joint impact of pests on agricultural systems (Committee on Twenty-First Century Systems Agriculture; National Research Council

2010).While knowledge exists on the impact of infections on crop vigor, the response of weed species performance to plant disease is rarely considered (Schroeder et al. 2005). Yet, knowledge of pathogen impact on weed fitness and competitive ability is crucial to understanding crop-weed interactions (Schroeder et al. 2005).

Exposure to a pathogen can impact individual plant performance in different ways. A susceptible plant is a suitable host for the pathogen, and infection can severely reduce its growth or cause mortality because resources must be allocated to defense at the expense of growth and/or reproduction (Louda et al. 1990, Schroeder et al. 2005). For susceptible plants, infection modifies individual characteristics such as growth, fecundity, and ability to acquire resources (Louda et al. 1990). For example, in a recent study, increasing irrigation did not increase yield in wheat plants infected with WSMV, while it did increase yield for non-infected plants (Price et al. 2010). The mechanism identified in the study was a reduction in root weight and resulting lower water uptake caused by WSMV, suggesting that resource acquisition may be detrimentally impacted by WSMV infection in wheat.

Interspecific competition between desired species and weeds may be altered in the presence of a shared pathogen if infection has differential impacts on the performance of competing species (Louda et al. 1990, Alexander and Holt 1998, Schroeder et al. 2005). Because *B. tectorum* is less susceptible to WSMV infection than winter wheat (Ito 2011), the disease could change competitive interactions between the two species. Generally, attack by a pathogen decreases crop vigor and makes the crop less resistant to weed infestation (Schroeder et al. 2005), and may decrease the ability of the crop to acquire

limited resources (Louda et al. 1990). Weed populations that are tolerant or resistant to infection are the biggest concern for agroecosystem managers because weed populations that are less impacted by or immune to a disease will be more competitive for resources, which may lead to further decreases in crop yield (Louda et al. 1990, Alexander and Holt 1998, Schroeder et al. 2005). To our knowledge, the relative importance of these relationships in interactions between winter wheat and *B. tectorum* is largely unknown.

<u>Project Justification and Objectives</u>

Developing ecologically-based management strategies is critical for more effective weed management in both rangeland and cropland systems (Di Tomaso 2000, Liebman 2001, Sheley and Krueger-Mangold 2003, Shennan 2008, Committee on Twenty-First Century Systems Agriculture; National Research Council 2010). This project explored the extent to which biological and environmental factors modify competitive interactions between desired plants and *B. tectorum,* with the hope that this information will provide first principles for designing better management techniques. The first experiment assessed the competitive relationship between *B. tectorum* and a native perennial grass with the aim of improving rangeland revegetation practices. In the second experiment, the interaction between *B. tectorum*, resource availability, and WSMV was evaluated with the intent of understanding how the two pests can be better managed simultaneously in a cropland setting.

Objectives

1. Appraise the impact of relative size and soil nitrogen availability on interactions between *B. tectorum* and *P. spicata*.

2. Determine the impact of WSMV, resource availability, and neighborhood characteristics on *B. tectorum* performance in a winter wheat system.

CHAPTER TWO

IMPACT OF RELATIVE SIZE, RESOURCE AVAILABILITY, AND STAND

DENSITY ON THE COMPETITIVE RELATIONSHIP BETWEEN AN EXOTIC

ANNUAL AND NATIVE PERENNIAL GRASS

Introduction

Bromus tectorum L. (cheatgrass or downy brome) invasion across arid and semi-arid rangelands of the western United States has been associated with loss of sagebrush-steppe habitat, altered fire regimes, species shifts, and widespread biotic impoverishment (D'Antonio and Vitousek 1992, Knapp 1996, Mack 2011). This species can become dominant on rangelands following a disturbance, sometimes forming near monocultures that may be an alternate stable state for the plant community, preventing recolonization by native species (Humphrey and Schupp 2004, Chambers et al. 2007, Mack 2011). The importance of revegetating rangelands dominated by *B. tectorum* with perennial species as an approach to restore desired plant communities has long been recognized (Hull and Stewart 1948, Allen 1995, Whitson and Koch 1998, Davies et al. 2010), though these efforts are often unsuccessful (Mack 2011). Competition between established *B. tectorum* plants and perennial species seedlings could lead to revegetation failure (Hull and Stewart 1948, Harris 1967, but see James and Svejcar 2010), though established perennial grasses may be more competitive and resistant to invasion by annual grasses over the long term (Corbin and D'Antonio 2004, McGlone et al. 2011).

Early size discrepancies between plants cause reduced growth rates for the smaller competitor (Connolly and Wayne 1996), and may allow the larger individuals to remove a disproportionate amount of resources (Firbank and Watkinson 1990, Freckleton and Watkinson 2001). Life history differences between *B. tectorum* and native perennial grasses could cause these size disparities that may hinder the success of revegetation programs, with *B. tectorum* seedlings gaining a size advantage over perennial seedlings through their earlier emergence and higher growth rates (Harris 1967, Harris and Wilson 1970). Most *B. tectorum* plants follow a winter annual life history, meaning they germinate and emerge in late summer or fall with resumption of rainfall (Harris 1967, Mack and Pyke 1983). As a result, these *B. tectorum* plants have an established root system by spring that allows them to initiate growth earlier than native grass seedlings (Harris and Wilson 1970, Aguirre and Johnson 1991). This initial advantage is further compounded by the higher relative growth rate of *B. tectorum* in comparison with that of perennial grasses (Arredondo et al. 1998, Mangla et al. 2010). Species seeded during the fall that emerge in the spring after neighboring *B. tectorum* seedlings are actively growing may be at an initial size disadvantage, leading to decreased establishment.

Competitive ability of a species also varies with resource availability (Berendse and Elberse 1990, Firn et al. 2010). Fast growing annual species such as *B. tectorum* are able to increase resource uptake relatively quickly, resulting in higher growth rates and seed production, while slower growing perennials generally have a more fixed rate of nutrient uptake (Chapin 1980, Crawley 1997). Nutrient acquisition patterns associated with these differing life histories have been described as conservative for perennial

species and acquisitive for annual species, and traits associated with these patterns can help explain relative competitive ability (Grime 1977, Roumet et al. 2006). For example, high leaf N productivity (increase in plant dry mass per unit plant N per unit time) contributes to faster uptake and growth of exotic annual grasses *B. tectorum* and *Taeniatherum caput-medusae* (medusahead) compared to native perennial grasses *Pseudoroegneria spicata* (Pursh) A. Löve (bluebunch wheatgrass) and *E. elymoides* (James 2008b). In addition, species that are adapted to higher nutrient environments also tend to have more plasticity in nutrient absorption rates than plants native to low nutrient environments (Elberse and Berendse 1993, Daehler 2003). In accordance, *B. tectorum* may be more effective at quickly utilizing available nutrients than native perennial grasses (Wilson et al. 1966, Monaco et al. 2003, Vasquez et al. 2008a).

Though the importance of relative emergence time in the competitive relationship between *B. tectorum* and perennial seedlings has been identified (Harris and Wilson 1970, Aguirre and Johnson 1991), the utility of giving desired plants an initial size advantage has not been fully explored. For example, little is known about the relative importance of time of emergence, stand density, and resource availability in determining the outcome of *B. tectorum* and perennial seedlings competitive relationship. To fill this knowledge gap, we conducted a greenhouse study to investigate the impact of relative size, plant density, and soil nitrogen (N) availability on interactions between *B. tectorum* and *P. spicata* with the intent of improving rangeland revegetation practices. *Pseudoroegneria spicata* was chosen for this study because it is one of the most widely distributed native bunchgrasses on rangeland in the northern Rocky Mountain region, and

it is valuable forage for livestock and wildlife (Zlatnik 1999). We predicted that giving *P. spicata* an initial size advantage over *B. tectorum* would increase its relative competitive ability (i.e. ability to suppress *B. tectorum* and to avoid suppression *by B. tectorum*). We further predicted that N enrichment would reduce the ability of *P. spicata* to outcompete *B. tectorum*.

Materials and Methods

Experimental Design

The study was conducted in a light and temperature controlled greenhouse (average 28°C day, 17°C night) at the Plant Growth Center, Montana State University (MSU), Bozeman, Montana, U.S.A. Supplemental light was applied as needed to achieve 16- hour days. The study was conducted twice with trial one completed between August and November 2009, and trial two conducted from March to June 2010. Each trial followed an addition series factorial design with four density treatments for each species, three *P. spicata* size cohort treatments, and two N treatments. Each of the resulting 96 treatment combinations were replicated four times in a randomized complete block arrangement for a total 384 pots (experimental units). Densities of *P. spicata* were 0, 2, 6, 12 plants pot^{-1} and densities of *B. tectorum* were 0, 5, 10, 20 plants pot^{-1}. Cohort treatments were applied by introducing *B. tectorum* seeds into the pots with three different cohorts of *P. spicata*; both species were planted together as seeds (0L cohort), or *B. tectorum* seeds were planted when most plants in *P. spicata* cohorts had two leaves (2L cohort) or four leaves (4L cohort). Nitrogen treatment levels were low (1 mg NO_3^- kg^{-1}) or high (31.5 mg NO_3^- kg^{-1}). To complement the addition series experiment,

individual plants of both species (24 in Trial 1, 48 in Trial 2) were grown to determine response of both species to N treatments (Trials 1 and 2), and *P. spicata* cohort response to N treatments (Trial 2) in the absence of competition.

Pseudoroegneria spicata ssp. *Spicata* Goldar variety seed was obtained from the USDA- NRCS Aberdeen Plant Materials Center in Aberdeen, Idaho, U.S.A., and *B. tectorum* seed was hand collected in 2008 at the MSU Red Bluff Research Ranch near Norris, Montana. *Bromus tectorum* densities used in the experiment were based on observed densities at Buffalo Jump State Park approximately 37 km west of Bozeman, Montana. *Pseudoroegneria spicata* densities were based on recommendations for rangeland drill seeding rates (USDA 2000).

A steam-sterilized soil mixture (50% washed concrete sand, 25% mineral soil, 25% sphagnum peat moss) was placed in 7.9 L pots (15.2 cm diameter x 43.2 cm depth). Nitrate was leached from the soil by adding 28.5 L of water to each pot. After leaching, soil samples were analyzed for nitrate (composite from ten pots, one sample per replicate, AgVise Laboratories, Northwood, North Dakota), and average nitrate was 1 mg kg^{-1}. The nitrogen addition treatment was applied 7 days after planting the 0L *P. spicata* cohort and *B. tectorum*. Ammonium sulfate prills (21-0-0; 0.3 g) were dissolved in 1.5 L of water and applied to each high N pot. At the same time, 1.5 L of water was applied to each low N pot to control for the effect of additional water. No supplemental nutrients were added to low N pots. The N treatment was repeated three times at 21 - day intervals for a total N application rate of 31.5 mg kg^{-1} over the course of the experiment. This value falls within the range of average annual net N mineralization in the Great Plains (Burke et al. 1997),

and is also comparable to rates used in other competition experiments (e.g. Paschke et al. 2000, Lowe et al. 2002, Monaco et al. 2003, Abraham et al. 2009).

Pseudoroegneria spicata 2L and 4L cohort treatments were planted two and four weeks, respectively, before planting 0L *P. spicata* and *B. tectorum* density treatments. Seeds of both species were sprinkled evenly on the soil surface and covered with 0.5 cm soil. Seedlings of both species were thinned or transplanted at the one leaf stage as needed to approximate target densities. Water was applied with an automated drip irrigation system. To allow each cohort to establish, pots were watered 0.5 L pot^{-1} daily for 35 days to keep the soil near field capacity. For the remaining 67 days of the experiment, plants were watered twice a week at a rate of 0.5 L pot^{-1}. The plants grew for 74 days after *B. tectorum* and 0L *P. spicata* were planted. At that time, aboveground biomass of both species was harvested from each pot to 5 mm above the soil surface. Final density for both species was recorded at the time of harvest. Additionally, belowground biomass of single plant pots was obtained by washing roots. All biomass was dried to constant mass and weighed.

Statistical Analysis

Analyses were conducted using R software including the nlme and gmodels packages (Warnes et al. 2007, R Development Core Team 2008, Pinheiro et al. 2011). To determine differences in how *B. tectorum* and *P. spicata* responded to N enrichment in the absence of competition (single plant pots), we calculated the proportional change in single plant shoot and root biomass in response to N using natural log transformed response ratios (lnRR = ln(biomass$_{\text{high N}}$/biomass$_{\text{low N}}$) (Hedges et al. 1999, James 2008a).

Higher positive lnRR values indicate more growth in the high N compared to low N treatments. Pots were randomly paired by N (*P. spicata* and *B. tectorum*) and cohort (*P. spicata* only) and the lnRR for shoot and root biomass was calculated for each pair. To determine if *P. spicata* cohorts differed in their response to N, we performed an analysis of variance (ANOVA) with lnRR of *P. spicata* shoot and root mass as the response variables and cohort as the predictor variable (23 pairs). When differences occurred, we performed Tukey's Honestly Significant Difference (HSD) post-hoc tests to compare treatment means. To investigate if *B. tectorum* was more responsive to N than *P. spicata*, we performed Welch's two-sample t-tests with shoot and root lnRR as the response variables and species as the predictor (20 pairs).

To assess the impact of relative size, intra- and interspecific competition, and N availability on *P. spicata* and *B. tectorum* growth, per capita biomass of each species was modeled using linear mixed effects models following Pinheiro and Bates (2000) and Crawley (2007). Fixed effects for both models were *P. spicata* cohort, N availability, and *P. spicata* and *B. tectorum* final densities. Trial was included as a random variable to allow generalization over the two trials (Crawley 2007). Prior to the analysis, we performed a natural log transformation of per capita biomass. In addition to normalizing the distribution, this transformation reflected the log-linear nature of the data, where small changes in density were associated with relatively large changes in per capita biomass. In addition, due to a non-linear trend in per capita *B. tectorum* biomass in response to *P. spicata* density, we performed a square root transformation of *P. spicata* density. Our initial models included all three way interactions. We then simplified the

models by removing individual parameters based on *p*-values ($\alpha = 0.05$) generated with

ANOVA and re-fitting them based on restricted maximum likelihood estimation (Zuur et

al. 2009). We utilized diagnostic plots to check for equal variance among and within

groups (Pinheiro and Bates 2000). The *P. spicata* model was adequate; however, the *B.*

tectorum model had a pattern of increasing variance with increasing fitted values within

N treatments, and results should be interpreted cautiously.

In our analysis, the intraspecific competition coefficient was estimated by the

regression coefficient associated with the density of one species on itself, while the

interspecific competition coefficient was estimated by the regression coefficient

associated with the density of one species on the other (Goldberg and Landa 1991). In

both the *P. spicata* and *B. tectorum* models, the competition coefficients can be

interpreted as the percent decrease in per capita biomass for each plant in the pots as

modified by N availability and *P. spicata* cohort. To determine if *P. spicata* cohort

changed intra- and interspecific competitive interactions, we tested for interactions

between the cohort treatment and both competition coefficients in our models. Similarly,

to determine if N enrichment modified intra- and interspecific competition, we tested for

interactions between our N treatment and competition coefficients for each species. We

also tested for three way interactions between N, cohort, and competition coefficients for

each species to determine if N modified the impact of cohort on intra- and interspecific

competition. When interactions occurred, we performed contrasts to determine if the

differences between competition coefficients were equal to zero ($\alpha = 0.05$) among

relevant levels of factors N and cohort (Warnes et al. 2007).

<div align="center">Results</div>

Impacts of Resource Availability and Cohort
on Non–Competing Individuals of Each Species

Results of ANOVA indicated that *P. spicata* shoot biomass response to N, as estimated by lnRR values, differed by cohort ($p = 0.046$, Table 2.1a). Specifically, *P. spicata* shoot growth in the 2L cohort was about five times more responsive to N enrichment than the 4L cohort ($p = 0.050$ from Tukey's HSD test, Table 2.2a). No differences were detected between the 0L and the two remaining cohorts according to post-hoc tests. We failed to detect a difference in lnRR values for root biomass between the three *P. spicata* cohorts ($p = 0.217$, Table 2.1b).

Because *P. spicata* cohorts differed in their response to N, we compared only the lnRR of the 0L *P. spicata* cohort with *B. tectorum* because they were planted at the same time. Two-sample t-test results indicated that there were no differences in the shoot or root biomass production between these two species ($p = 0.700$ and 0.987, respectively). *Pseudoroegneria spicata* and *B. tectorum* plants increased their growth under high N compared to low N, as shown by positive mean lnRR root and shoot biomass values (Table 2.2b). *Pseudoroegneria spicata* and *B. tectorum* plants in the high N treatment were 1.5 ± 0.52 and 1.2 ± 0.42 times larger than plants in the low N treatment (Table 2.2b).

Impact of Resource Availability, Cohort,
and Competition on *Pseudoroegneria spicata*

As predicted, the effect of interspecific competition on *P. spicata* biomass decreased as cohort size increased, reflected by the less pronounced effect of increasing *B. tectorum* density observed in later cohorts compared to concurrent sowing (Fig. 2.1). Further, N enrichment increased the effect of the intraspecific competition coefficient for any given cohort, shown in Fig. 2.1 as increases in biomass are driven more by *P. spicata* than *B. tectorum* density (lines more vertical) in the high N compared to low N treatment. However, contrary to the prediction that N enrichment would modify the effect of interspecific competition on *P. spicata*, the lack of a *B. tectorum* density × N interaction indicated that N availability did not modify interspecific competition.

The relative time of *P. spicata* and *B. tectorum* emergence modified the interspecific competition coefficient as shown by a *B. tectorum* density × cohort interaction ($p < 0.001$, Table 2.3). A comparison of the interspecific competition coefficients among cohort treatments indicated that when both species were planted concurrently (0L cohort), each *B. tectorum* plant decreased *P. spicata* per capita biomass by $6.6\% \pm 0.7\%$ ($p < 0.001$, Table 2.4) regardless of N availability. The interspecific competition coefficient decreased when *P. spicata* had an initial size advantage. In the 2L and 4L treatments each *B. tectorum* plant decreased *P. spicata* per capita biomass by 3.1% ($p < 0.001$) and 1.7% ($p = 0.008$), respectively (Table 2.4), regardless of N availability. There was no statistical difference between interspecific competition coefficients for the 2L and 4L cohorts ($p = 0.138$, Table 2.5), suggesting that *P. spicata* with a two- or four-leaf initial size advantage equally avoided suppression by *B.*

tectorum. However, interspecific competition was not modified by N enrichment; indicated by the failure to detect a significant *B. tectorum* density × N interaction.

Pseudoroegneria spicata initial size and N availability also modified the intraspecific competition coefficient as shown by the *P. spicata* density × cohort interaction ($p < 0.001$, Table 2.3) and the *P. spicata* density × N interaction ($p < 0.001$, Table 2.3). Larger *P. spicata* consistently had the greatest impact on per capita *P. spicata* biomass. For example, each 4L *P. spicata* plant had an 8.1% ± 1.6% larger impact on per capita biomass than in the 0L cohort ($p < 0.001$, Table 2.5), and a 3.9% ± 1.5% larger impact compared to the 2L cohort ($p = 0.011$, Table 2.5). Further, the effect of the intraspecific competition coefficient was 4.7% ± 1.3% larger in the high N treatment compared to the low N treatment ($p < 0.001$, Table 2.5), indicating that the impact that *P. spicata* had on its own biomass increased with N availability.

Impact of Resource Availability, Cohort,
and Competition on *Bromus tectorum*

As predicted, when *P. spicata* had an initial size advantage, *B. tectorum* competitive ability decreased. When *B. tectorum* was grown with established *P. spicata* plants, the interspecific competition coefficient increased, as shown by a larger impact of increasing *P. spicata* density as cohort size increased (Fig. 2.2). The intraspecific competition coefficient decreased as cohort increased, as shown by the smaller impact of *B. tectorum* density in larger cohorts (Fig. 2.2). The relative importance of intra- and interspecific competition can be observed in Figure 2.2, where more vertical lines indicate an increase in the effect of *P. spicata* density compared to *B. tectorum* density as cohort size increased. Contrary to our prediction that N enrichment would modify the

effects of the density and cohort treatments, N availability did not change the effect of intra- or interspecific competition or relative emergence time on *B. tectorum* biomass. However, N enrichment did cause *B. tectorum* to accumulate more biomass over all treatments, as shown by larger biomass values for the high N compared to low N treatment for any given cohort (Fig. 2.2).

Relative time of emergence modified the interspecific competition coefficient as reflected by the *P. spicata* density × cohort interaction ($p < 0.001$, Table 2.6). Further, the effect of increasing *P. spicata* density on *B. tectorum* per capita biomass was non-linear, and was modeled with a square-root transformation (Fig. 2.2) ($p < 0.001$, Table 2.6). There were relatively larger changes in interspecific competition at low densities of *P. spicata* compared to high densities. In addition, the effect of interspecific competition increased as *P. spicata* cohort increased from 0L to 4L (Table 2.7).

Pseudoroegneria spicata cohort modified the effect of intraspecific competition on per capita *B. tectorum* biomass, as shown by the *B. tectorum* density × cohort interaction ($p = 0.020$, Table 2.6). *Bromus tectorum* had the most impact on its own biomass when grown with the 0L *P. spicata* cohort; with each additional *B. tectorum* plant in the pots, per capita biomass decreased by 7.7% ± 0.8% ($p < 0.001$, Table 2.7). The impact of intraspecific competition on *B. tectorum* biomass decreased with increasing *P. spicata* cohort, as *B. tectorum* density reduced per capita biomass by 4.7% ± 0.9 and 5.0% ± 1.0% in the 2L and 4L cohorts, respectively ($p < 0.001$, Table 2.7).

Nitrogen enrichment enhanced *B. tectorum* per capita biomass ($p < 0.001$, Table 2.6). At any given density or cohort, N enrichment increased per capita *B. tectorum*

biomass fivefold (Fig. 2.2). However, there were no significant interactions between N

and competition coefficients or N and cohort treatments. The lack of a significant

interaction between N and any other variables indicates that N did not modify the effect

of relative size or density of either species on *B. tectorum* per capita biomass.

Discussion

In this study, relative time of emergence and stand density played a role in

determining the competitive interactions between *P. spicata* and *B. tectorum*. Relative

initial size of competing plants can have long-lasting impacts in a plant community with

larger individuals extracting a disproportionate amount of resources and suppressing

smaller neighbors (Ross and Harper 1972, Connolly and Wayne 1996, Freckleton and

Watkinson 2001). This asymmetric pattern of plant-plant competition could hinder

revegetation with perennial species on rangeland dominated by *B. tectorum*. Because *B.*

tectorum emerges in the fall and is established by spring, perennial seedlings that emerge

in the spring must compete with larger *B. tectorum* plants (Harris 1967, Harris and

Wilson 1970). In accordance with our first prediction, we found that giving *P. spicata* an

initial size advantage over *B. tectorum* increased its ability to both suppress and avoid

suppression by *B. tectorum*. However, contrary to our second prediction, we also

observed that while N availability increased productivity of both species, it did not

change their competitive relationship.

Effect of Relative Initial Size

Pseudoroegneria spicata established prior to *B. tectorum* emergence effectively

suppressed it, with its competitive effect increasing with cohort age. In accordance, Firn

et al. (2010) determined that native Australian perennial grasses *Bothriochloa decipiens*

(pitted bluegrass) and *Themeda triandra* (kangaroo grass) more effectively suppressed

Eragrostis curvula (African lovegrass), an exotic perennial grass, when the native grasses

were sown 21 days prior to the exotic one. We also observed that increasing *P. spicata*

initial size allowed it to avoid suppression by *B. tectorum* more effectively. This result is

consistent with Abraham et al. (2009), where perennial grasses *Nassella pulchra* A.

Hitchcock (purple needlegrass) and *Festuca rubra* L. (red fescue) productivity strongly

increased if they emerged 14 days before *Bromus diandrus* Roth (ripgut brome), an

exotic winter annual grass. Further, Stevens and Fehmi (2011) observed that native

perennial grass *Digitaria californica* (Benth.) Henr. (Arizona cottontop) that had a 21-

day advantage in emergence time over exotic perennial grass *Pennisetum ciliare* (L.)

Link (buffelgrass) had a strong increase in biomass compared to concurrent sowing.

There is strong evidence that first principles about relative time of emergence

gained from greenhouse studies (Abraham et al. 2009, Firn et al. 2010, Stevens and

Fehmi 2011) could be extended to a field setting with the aim of improving seeded

species establishment. In a field experiment conducted in California, the long-term

importance of initial size was demonstrated with three-month-old transplants of

established perennial grasses *Agrostis oregonensis* Vasey (Oregon bentgrass), *F. rubra*

and *N. pulchra* surviving their first season and effectively suppressing exotic annual

grasses *B. diandrus*, *Vulpia myuros* L. (rat-tail fescue), and *Avena barbata* Link. (slender wild oat) over the next three years (Corbin and D'Antonio 2004). Consequently, future studies could test the results from our greenhouse study on lands dominated by *B. tectorum*.

Effect of Resource Availability

It is often argued that competitive relationships between plants are modified by soil nutrient availability, with fast-growing ruderal species such as *B. tectorum* having increased relative competitive ability in higher nutrient environments than slower-growing perennial species such as *P. spicata* (Chapin 1980, Crawley 1997). We did not find evidence to support this argument. Though N enrichment increased productivity of both species in our study, this increase in productivity did not differ between the two species. Further, the ability of *B. tectorum* to suppress *P. spicata* growth did not change with N availability. Our findings were consistent with James (2008a), where nutrient stress did not result in a reduction in *B. tectorum* growth compared to native perennial bunchgrasses *P. spicata* and *Elymus elymoides* (Raf.) Swezy (bottlebrush squirreltail). In contrast, Abraham et al. (2009) found that for native perennial grasses *N. pulchra* and *F. rubra*, increased soil N, in rates similar to the ones used in our study, led to decreased growth when sown with exotic annual grass *B. diandrus* compared to a monoculture. This disparity between our results and those of Abraham et al. (2009) can be accounted for by the fact that changes in plant performance and relative competitive ability in response to environmental conditions are species-specific (Daehler 2003). Unfortunately, the

inconsistency between our results and previous findings points to the difficulty in making generalizations across species, even within the same functional group.

Also in contrast to our observations, Wilson (1966) found that heavy fertilization (90 kg N ha^{-1} for four successive years) of mixed *B. tectorum* and *P. spicata* communities increased *B. tectorum* yield by 400-600%, while decreasing *P. spicata* yield by 50%. This discrepancy with our results can be explained by the fact that our N enrichment treatment was much lower than Wilson's (1966) as we attempted to mimic N availability in rangeland settings. Therefore, it is possible that where N availability is relatively low, small increases in N may not change the relative competitive ability of *B. tectorum* and *P. spicata* enough to impact plant interactions. However, in situations where N enrichment is more pronounced, such as former agricultural sites (conservation reserve program (CRP) lands, for example), or in areas with substantial agricultural runoff, the relative competitive ability of these two species may be altered.

Conclusions and Management Implications

Biotic and abiotic factors can impact interactions between plants with implications for restoration of lands dominated by invasive species (Call and Roundy 1991, Allen 1995). While modifying environmental factors (i.e. soil N availability) to better suit desired species may be one way to shift competitive relationships and increase seeded species establishment (Daehler 2003, Vasquez et al. 2008b, Firn et al. 2010), we did not find support for the use of this technique. In accordance with previous research (Corbin and D'Antonio 2004, Abraham et al. 2009, Firn et al. 2010, Stevens and Fehmi

2011), our results suggest that relative time of emergence for seeded species versus invasive species is an important aspect of revegetation planning.

It has been suggested that site preparation techniques designed to decrease available soil resources in rangeland systems may be a strategy to decrease competitive ability of invasive species and increase perennial species establishment (Vasquez et al. 2008b, Firn et al. 2010, Perry et al. 2010). These measures could include soil amendments such as sucrose or sowing a nurse crop to sequester N (Mangold and Sheley 2008, Perry et al. 2010). It has also been argued that the effects of these treatments are species-specific and may not be useful in some cases (Lowe et al. 2002). Similar to results observed by James (2008a) and Abraham (2009), our results suggest that in early stages of growth, reducing soil N may not decrease exotic annual grass impact on seeded perennial grasses. However, based on research conducted in higher N environments (Wilson et al. 1966), revegetation of CRP or former agricultural land dominated by *B. tectorum* may benefit from measures designed to decrease N availability.

Our results complement growing evidence that developing management practices that allow perennial species to emerge first and attain a size advantage over exotic annual grasses may improve seedling establishment in rangeland revegetation projects. Typical revegetation efforts include a fall herbicide application to control weeds, followed by a fall-dormant seeding of cool-season species such as *P. spicata* (e.g. Sheley et al. 2001). This approach can lead to *P. spicata* seedlings emerging in the spring and competing against established *B. tectorum* plants that emerged in late fall or early spring. To establish an initial size difference that favors seeded species, managers could modify the

standard timing of revegetation practices to ensure that perennial species receive a

sufficient head start. For example, perennial species that do not require cold stratification,

such as *P. spicata*, could be sown in the spring. The *B. tectorum* population could be

controlled with herbicide the previous fall, with a follow-up application used at the time

of spring seeding as necessary. This approach may allow perennial species to attain

sufficient size to compete effectively before the next *B. tectorum* cohort emerged the

following fall, and would also allow for control of *B. tectorum* that emerged over the

winter or early spring. Another way to promote an initial size difference would be using

transplants or plugs to restore critical sites.

Tables and Figures

Table 2.1: Results from ANOVA conducted to assess the effect of
Pseudoroegneria spicata cohort treatment on its mean response ratio for
a) shoot biomass and b) root biomass.

a) *P. spicata* lnRR shoot biomass

	Df	Sum Sq	Mean Sq	*F* value	*p* value
Cohort	2	9.524	4.762	3.598	0.046
Residuals	20	26.47	1.324		

b) *P. spicata* lnRR root biomass

	Df	Sum Sq	Mean Sq	*F* value	*p* value
Cohort	2	4.884	2.442	1.651	0.217
Residuals	20	29.59	1.480		

Response ratios were calculated using the natural log response ratio
(lnRR), where lnRR = ln (biomass$_{highN}$/biomass$_{low N}$). Cohort refers to *P.
spicata* cohort treatment; where the two species were seeded
concurrently, or *B. tectorum* seeds were planted into pots with two- or
four-leaf cohorts of *P. spicata.*

Table 2.2: Mean response ratios of *Pseudoroegneria spicata* and *Bromus tectorum* shoot and root biomass for single plants grown in the absence of competition when nitrate was increased from 1 mg kg^{-1} to 31.5 mg kg^{-1} (lnRR ± SE).

a) *Pseudoroegneria spicata* shoot and root mean lnRR by cohort

Initial size	Shoot lnRR (SE)	Root lnRR (SE)
0 Leaf	1.5 (0.52)[ab]	1.1 (0.57)
2 Leaf	1.9 (0.50)[a]	1.3 (0.48)
4 Leaf	0.35 (0.13)[b]	0.23 (0.16)

b) Shoot and root mean lnRR by species

Species	Shoot lnRR (SE)	Root lnRR (SE)
P. spicata	1.5 (0.52)	1.1 (0.57)
Bromus tectorum	1.2 (0.42)	1.1 (0.52)

Response ratios were calculated using the natural log response ratio (lnRR), where lnRR = ln (biomass$_{highN}$/biomass$_{low N}$). Higher lnRR values indicate a greater response to nitrate addition. Superscript letters for shoot lnRR indicate differences in treatment means determined by Tukey's HSD post-hoc tests. Cohort refers to *P. spicata* cohort treatment; where the two species were seeded concurrently, or *B. tectorum* seeds were planted into pots with two- or four-leaf cohorts of *P. spicata.*

Table 2.3. Results from ANOVA conducted to assess the effect of plant density, N availability, and cohort (fixed effects) on *Pseudoroegneria spicata* per capita biomass in the most parsimonious linear mixed effects model.

Parameter	Df	Sum Sq	Mean Sq	*F* value	*p* value
P. spicata density	1	62.21	62.21	141.2	**< 0.001**
B. tectorum density	1	62.57	62.57	142.0	**< 0.001**
N	1	184.9	184.9	419.6	**< 0.001**
Cohort	2	508.1	254.1	576.7	**< 0.001**
P. spicata density × N	1	5.422	5.422	12.31	**< 0.001**
P. spicata density × Cohort	2	9.030	4.511	10.25	**< 0.001**
B. tectorum density × Cohort	2	12.49	6.252	14.18	**< 0.001**
N × Cohort	2	25.54	12.77	28.98	**< 0.001**
Residuals	630	277.6	0.443		

B. tectorum refers to *Bromus tectorum*. N refers to nitrogen availability treatment (1 mg kg^{-1} or 31.5 mg kg^{-1}). Cohort refers to *P. spicata* cohort treatment; where the two species were seeded concurrently, or *B. tectorum* seeds were planted into pots with two- or four-leaf cohorts of *P. spicata.*

Table 2.4. Coefficients from linear mixed effects model conducted to assess the effect of intra- and interspecific competition, N availability, and cohort on *Pseudoroegneria spicata* per capita biomass.

N × *P. spicata* cohort combination	Parameter description	Estimate (standard error)	*p* value
Low N × 0 Leaf	Intercept	-3.1 (0.11)	**< 0.001**
	Intraspecific competition	-0.009 (0.013)	0.489
	Interspecific competition	-0.066 (0.007)	**< 0.001**
Low N × 2 Leaf	Intercept	-1.5 (0.11)	**< 0.001**
	Intraspecific competition	-0.033 (0.013)	**0.009**
	Interspecific competition	-0.031 (0.007)	**< 0.001**
Low N × 4 Leaf	Intercept	-0.29 (0.099)	**0.004**
	Intraspecific competition	-0.072 (0.012)	**< 0.001**
	Interspecific competition	-0.017 (0.007)	**0.008**
High N × 0 Leaf	Intercept	-1.2 (0.11)	**< 0.001**
	Intraspecific competition	-0.038 (0.013)	**0.003**
	Interspecific competition	-0.066 (0.007)	**< 0.001**
High N × 2 Leaf	Intercept	-0.18 (0.11)	0.116
	Intraspecific competition	-0.080 (0.013)	**< 0.001**
	Interspecific competition	-0.031 (0.007)	**< 0.001**
High N × 4 Leaf	Intercept	0.61 (0.099)	**< 0.001**
	Intraspecific competition	-0.12 (0.012)	**< 0.001**
	Interspecific competition	-0.017 (0.007)	**0.008**

Intra- and interspecific competition refer to the regression coefficients associated with increasing *P. spicata* and *Bromus tectorum* density, respectively. Low N is 1 mg kg^{-1} N, High N is 31.5 mg kg^{-1} N. 0 Leaf is concurrent sowing of *P. spicata* and *B. tectorum*, 2 Leaf and 4 Leaf is *B. tectorum* planted into pots with two- and four-leaf *P. spicata* cohorts. DF for all estimates = 608. *P* values are for the null hypothesis that the estimate equals zero. Estimates are presented in the natural log scale.

Table 2.5. Treatment contrasts from linear mixed effects model conducted to assess the effect of intra- and interspecific competition, N availability, and cohort on *Pseudoroegneria spicata* per capita biomass.

	Estimate (Std Error)	t value	Pr(>|t|)
Intraspecific contrasts			
Low N vs High N	-0.047 (0.013)	-3.748	**< 0.001**
0 Leaf vs 2 Leaf	-0.042 (0.016)	-2.681	**0.007**
0 Leaf vs 4 Leaf	-0.081 (0.016)	-5.231	**< 0.001**
2 Leaf vs 4 Leaf	0.039 (0.015)	2.550	**0.011**
Interspecific contrasts			
0 Leaf vs 2 Leaf	0.035 (0.010)	3.628	**< 0.001**
0 Leaf vs 4 Leaf	0.049 (0.010)	5.105	**< 0.001**
2 Leaf vs 4 Leaf	-0.014 (0.009)	-1.485	0.138

Degrees of freedom for all contrasts is 630. Intra- and interspecific contrasts are the differences in competition coefficients associated with treatment contrasts for *P. spicata* and *Bromus tectorum* density, respectively. Low N is 1 mg kg^{-1} N, High N is 31.5 mg kg^{-1} N. 0 Leaf is concurrent sowing of *P. spicata* and *B. tectorum*, 2 Leaf and 4 Leaf is *B. tectorum* planted into pots with two- and four-leaf *P. spicata* cohorts. *P* values are for the null hypothesis that the differences between coefficients equals zero. Estimates are presented in the natural log scale.

Table 2.6. Results from ANOVA conducted to assess the significance of plant density, N availability, and cohort (fixed effects) on *Bromus tectorum* per capita biomass in the most parsimonious linear mixed effects model.

Parameter	Df	Sum Sq	Mean Sq	*F* value	*p* value
√*P. spicata* density	1	137.1	137.1	243.5	**< 0.001**
B. tectorum density	1	95.15	95.15	169.1	**< 0.001**
N	1	424.9	424.9	755.1	**< 0.001**
Cohort	2	82.63	41.31	73.41	**< 0.001**
√*P. spicata* density × Cohort	2	28.96	14.48	25.73	**< 0.001**
B. tectorum density × Cohort	2	4.431	2.223	3.940	**0.020**
Residuals	608	342.2		0.560	

P. spicata refers to *Pseudoroegneria spicata.* N refers to nitrogen availability treatment (1 mg kg^{-1} or 31.5 mg kg^{-1}). Cohort refers to *P. spicata* cohort treatment; where the two species were seeded concurrently, or *B. tectorum* seeds were planted into pots with two- or four-leaf cohorts of *P. spicata.*

Table 2.7. Coefficients from linear mixed effects model conducted to assess the effect of intra-
and interspecific competition, N availability, and cohort on *Bromus tectorum* per capita
biomass.

P. spicata Cohort	Parameter	Estimate ± SE	*p* Value
0 Leaf	Low N intercept	-1.9 ± 0.16	**< 0.001**
	High N intercept	-0.22 ± 0.19	0.168
	Intraspecific competition	-0.077 ± 0.008	**< 0.001**
	Interspecific competition	-0.11 ± 0.040	**0.004**
2 Leaf	Low N intercept	-2.4 ± 0.19	**< 0.001**
	High N intercept	-0.71 ± 0.19	**< 0.001**
	Intraspecific competition	-0.047 ± 0.009	**< 0.001**
	Interspecific competition	-0.35 ± 0.046	**< 0.001**
4 Leaf	Low N intercept	-2.3 ± 0.19	**< 0.001**
	High N intercept	-0.69 ± 0.19	**< 0.001**
	Intraspecific competition	-0.050 ± 0.010	**< 0.001**
	Interspecific competition	-0.58 ± 0.048	**< 0.001**

Intra- and interspecific competition refer to the regression coefficients associated with *B.
tectorum* and $\sqrt{Pseudoroegneria\ spicata}$ density, respectively. Low N is 1 mg kg^{-1} N, High N is
31.5 mg kg^{-1} N. 0 Leaf is concurrent sowing of *P. spicata* and *B. tectorum*, 2 Leaf and 4 Leaf is
B. tectorum planted into pots with two- and four-leaf *P. spicata* cohorts. Degrees of freedom
for all estimates = 608. P values are for the null hypothesis that the estimate equals zero.
Estimates are presented in the natural log scale.

Table 2.8. Treatment contrasts from linear mixed effects model conducted
to assess the effect of intra- and interspecific competition, N availability,
and cohort on *Bromus tectorum* per capita biomass.

	Estimate (SE)	t value	p value
Intraspecific contrasts			
0 Leaf vs 2 Leaf	0.031 (0.012)	2.515	**0.012**
0 Leaf vs 4 Leaf	0.027 (0.012)	2.184	**0.029**
2 Leaf vs 4 Leaf	0.004 (0.013)	0.2680	0.789
Interspecific contrasts			
0 Leaf vs 2 Leaf	-0.24 (0.061)	-3.902	**< 0.001**
0 Leaf vs 4 Leaf	-0.47 (0.062)	-7.463	**< 0.001**
2 Leaf vs 4 Leaf	0.23 (0.067)	3.421	**< 0.001**

Degrees of freedom for all contrasts is 608. Intra- and interspecific
contrasts are the differences in competition coefficients associated with
treatment contrasts for *B. tectorum* and *Pseudoroegneria spicata* density,
respectively. *P* values are for the null hypothesis that the differences
between slopes equals zero. Estimates are presented in the natural log
scale.
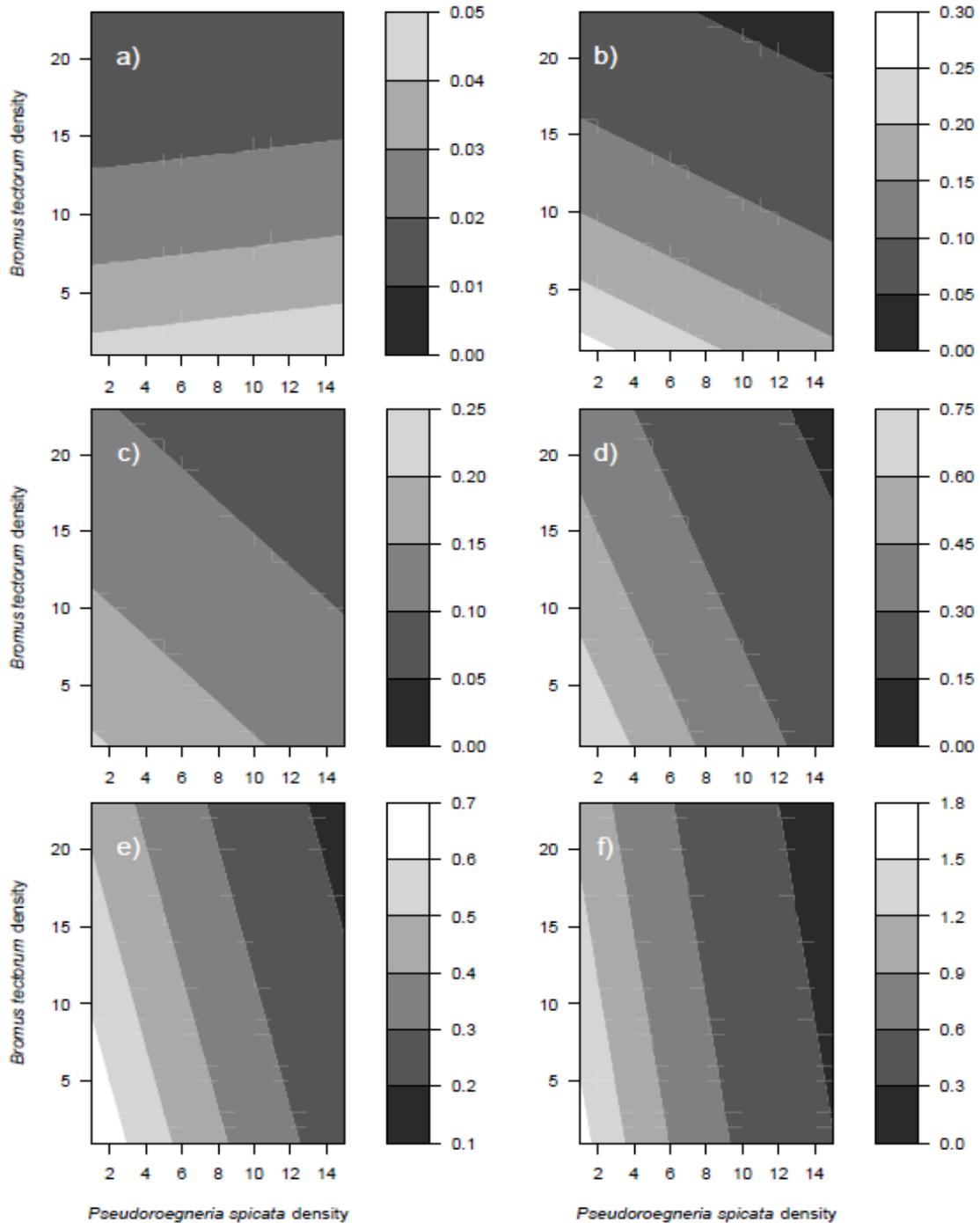
Figure 2.1. Predicted response of per capita *Pseudoroegneria spicata* biomass (g) to *P. spicata* and *Bromus tectorum* density under a) Low N 0L, b) High N 0L, c) Low N 2L, d) High N 2L, e) Low N 4L, f) High N 4L. Low N is 1 mg kg^{-1} N, High N is 31.5 mg kg^{-1} N. 0L is concurrent sowing of *P. spicata* and *B. tectorum*, 2L is *B. tectorum* planted into *P. spicata* cohort at 2-leaf stage, 4L is *B. tectorum* planted into *P. spicata* cohort at 4-leaf stage. Grayscale represents per capita biomass (g) of *P. spicata*. Scale varies among treatment combinations.
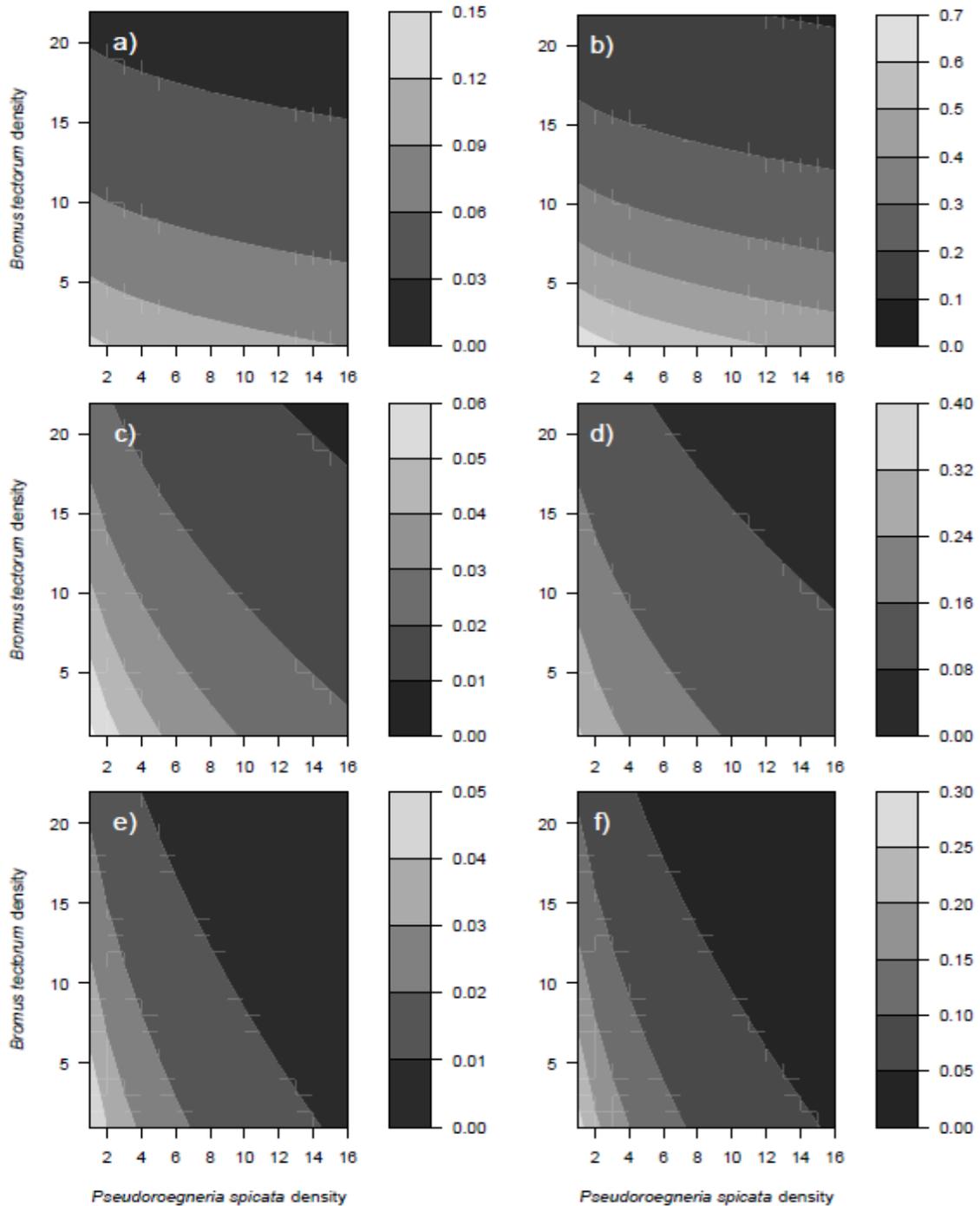
Figure 2.2. Predicted response of per capita *Bromus tectorum* biomass (g) to *Pseudoroegneria spicata* and *B. tectorum* density under a) Low N 0L, b) High N 0L, c) Low N 2L, d) High N 2L, e) Low N 4L, f) High N 4L. Low N is 1 mg kg^{-1} N, High N is 31.5 mg kg^{-1} N. 0L is concurrent sowing of *P. spicata* and *B. tectorum*, 2L is *B. tectorum* planted into *P. spicata* cohort at 2-leaf stage, 4L is *B. tectorum* planted into *P. spicata* cohort at 4-leaf stage. Grayscale represents per capita biomass (g) of *P. spicata*. Scale varies among treatment combinations.

CHAPTER THREE

JOINT IMPACT OF BIOLOGICAL AND ENVIRONMENTAL STRESSORS ON

BROMUS TECTORUM PERFORMANCE

Introduction

Traditional approaches to weed management focus on short-term solutions such as herbicides or tillage to reduce the spread and impact of undesired species. It is increasingly being recognized that to attain long-lasting weed control that meets societal and land management objectives, it is necessary to adopt an ecologically-based approach (DiTomaso 2000, Sheley and Krueger-Mangold 2003, Shennan 2008). In agricultural settings, a main principle of ecologically-based weed management is to increase the competitive effect of the crop on weeds to secure yields and minimize weed seed inputs into the seedbank (Radosevich et al. 2007, Committee on Twenty-First Century Systems Agriculture; National Research Council 2010). Unfortunately, many times it is difficult to achieve this goal as crops face multiple environmental and biological stressors that can impact their performance and competitive ability. In addition, pest management recommendations are usually designed to target one type of pest at a time (i.e. weeds, pathogens, or arthropods) and could result in conflicting and unintended results (Norris 2005, Schroeder et al. 2005, Wisler and Norris 2005).

Assessing multitrophic pest interactions and understanding the role of environmental constraints in determining their impact on weed performance is required for the development of ecologically-based pest management programs (Louda et al. 1990,

Committee on Twenty-First Century Systems Agriculture; National Research Council 2010). For example, competition between crops and weeds may be altered in the presence of a shared pathogen if infection has differential impacts on the competing species (Louda et al. 1990, Alexander and Holt 1998, Schroeder et al. 2005). While knowledge exists on the impact of infections on crop vigor, the response of weed species to plant diseases is rarely considered (Schroeder et al. 2005). Yet, knowledge of pathogen impact on weed fitness and competitive ability is crucial to understanding crop-weed interactions (Schroeder et al. 2005). Weed species that are less susceptible to crop pathogens are the biggest concern for agroecosystem managers as they are less impacted by infections than the crop, possibly leading to additional decreases in crop yield (Louda et al. 1990, Alexander and Holt 1998, Schroeder et al. 2005).

Bromus tectorum L. (downy brome or cheatgrass) and *Wheat streak mosaic virus* (WSMV) are two co-occurring pests of winter wheat (*Triticum aestivum* L.). *Bromus tectorum* is an increasingly problematic winter annual grassy weed in winter wheat due to similar life histories, increased adoption of conservation tillage techniques, and reliance on broadcast nitrogen fertilizer (Morrow and Stahlman 1984, Radosevich and Rouch 1990, Blackshaw 1994, Zimdahl 2007). Several studies have concluded that *B. tectorum* substantially decreases winter wheat yield. For example, in two studies, *B. tectorum* reduced winter wheat yields about 5% for every ten plants m^{-2} (Rydrych and Muzik 1968, Cochran et al. 1990). Another study reported that densities of 24, 40, and 65 *B. tectorum* plants m^{-2} caused 10, 15, and 20% reductions in wheat yield, respectively (Stahlman and Miller 1990).

In cropping systems, nitrogen (N) fertilizer is the most common input used to increase crop yield, but it also impacts weed-crop competitive interactions (Blackshaw et al. 2003, Zimdahl 2004). Fertilization can have unintended consequences if weeds are more responsive than crop species to N enrichment, making them more competitive under elevated N conditions (Di Tomaso 1995, Liebman and Mohler 2001, Zimdahl 2004, Blackshaw and Brandt 2008). Understanding how soil fertility impacts interactions between *B. tectorum* and winter wheat is critical to design effective management techniques for this weed. In field studies, increased N has been shown to increase *B. tectorum* performance, including seedling survival, culm production, and growth (Rasmussen 1995). Further, *B. tectorum* growth has been found to be more responsive than wheat to N enrichment under greenhouse conditions (Blackshaw et al. 2003), which may increase its impact on wheat yield (Blackshaw and Brandt 2008).

Wheat streak mosaic virus, a viral disease vectored by the wheat curl mite (*Aceria tosichella* Keifer), is a common disease in the central plains of the United States. Both vector and virus occur on a diverse set of grass species, including crops as well as native and weedy species including wheat and *B. tectorum* (Duffus 1971, Christian and Willis 1993, Ito 2011). *Wheat streak mosaic virus* interferes with chloroplast development (Brakke et al. 1988) and inhibits root growth, leading to a reduction in water uptake (Price et al. 2010). In a recent survey of symptomatic wheat in the Great Plains, WSMV was found in 47% of samples (Burrows et al. 2009). In infected fields, yield loss due to WSMV can approach 100% in extreme cases (Atkinson and Grant 1967). Because *B.*

tectorum is less susceptible to WSMV infection than winter wheat (Ito 2011), the disease could modify competitive interactions between the two species.

The effect of disease on plant performance and competitive interactions may have important implications for crop yield and weed management (Committee on Twenty-First Century Systems Agriculture; National Research Council 2010), and can change along environmental gradients (Louda et al. 1990). However, to our knowledge, the joint impact of WSMV and resource availability on *B. tectorum* performance in small grain fields has not been investigated. This field study evaluated the extent to which biological and environmental stressors modify *B. tectorum* biomass production. Specifically, we evaluated the combined impact of WSMV, wheat competition, and N availability on *B. tectorum* biomass.

Materials and Methods

Experimental Design

This study was conducted during the 2009 and 2010 growing seasons at the Montana State University Post Research Farm, Bozeman, MT, U.S.A (45º 40'29" N, 111º09'14"W, 1423 m elevation). Long term average annual precipitation (1966 – 2010) at the Post Research Farm is 416 mm, and total precipitation in 2009 and 2010 was 441 mm and 454 mm, respectively (WRCC 2008). Soil in the area is classified as an Amsterdam-Quagle Silt Loam (NRCS 2008). The entire site had been fallow for at least two years prior to the start of this research, and weeds had been managed using a disc cultivator as needed.

We conducted a randomized split-plot field study with four blocks to investigate the extent to which biological and environmental stressors modify weed performance. Nitrogen treatments were randomly assigned to main plots (5.0 m x 2.4 m) and WSMV inoculation treatments were randomly assigned to subplots (5.0 m x 1.2 m). On 8 October 2008 and 6 October 2009 the entire site was planted with winter wheat (var. Neely) at 67 kg ha^{-1} and 25 cm row spacing utilizing a no-till drill.

To estimate nitrogen availability prior to planting, soil cores (three per block) were obtained on 29 August 2008 to a depth of 91 cm and sent to a lab for analysis of nitrate level (N) (AgVise laboratories, Northwood, North Dakota). Based on the results, urea fertilizer was applied to the main plots using a handheld broadcast spreader in September 2008 to reach two target N levels [95 kg ha^{-1} (ambient, no fertilizer added) and 291 kg ha^{-1} (high)]. The high N level corresponded to recommended rates for the region (Jacobson et al. 2005). To assess N during the growing season, soil cores were taken to a depth of 45 cm on 9 June 2009 (one per subplot). These samples revealed that due to pre-existing N, nitrate levels ranged between 11 kg ha^{-1} and 207 kg ha^{-1}. Finally, we obtained 45 cm soil cores to evaluate post harvest N on 17 September 2009. Based on these values, urea fertilizer was applied to the main plots in September 2009. However, to obtain results over a range of N availability, four target N levels (17 kg ha^{-1} (ambient), 122 kg ha^{-1}, 244 kg ha^{-1} and 366 kg ha^{-1}) were randomly assigned to the main plots for the 2010 trial. Soil tests for N were taken again during the second growing season on 9 June 2010 (five per subplot) to a depth of 45 cm.

Locally collected *B. tectorum* seeds were hand-broadcast in all subplots on 16

September 2008 at a density of 2500 seeds m^{-2}. The majority of *B. tectorum* seed from

the first growing season was not harvested, and provided the seed for the second year. To

minimize the impact of the observed relationship between N available in 2009 and seed

inputs on *B. tecto*rum abundance, we added 3100 seeds m^{-2} on 18 September 2009 to

subplots that had less than 34 kg ha^{-1} N in the summer 2009 sampling.

On 21 May 2009 and 19 May 2010, half the subplots were inoculated with

WSMV using procedures similar to Ito (2011). Flats of susceptible spring wheat (var.

Choteau) were grown in the greenhouse and inoculated twice with WSMV (strain

Conrad-I). Infected wheat tissue from the greenhouse was macerated in a blender with 1X

phosphate buffered saline (PBS, pH 7.2) (1:10 tissue to buffer) to make inoculum for the

field study. The inoculum was mixed with 0.5% carborundum and applied in the field at

80 psi at a rate of 3 L per subplot using siphon feed spray guns (HDS75000AV Home

Depot, Inc., Atlanta, GA) attached to an air compressor (B335B-335TV, CompAir,

Sidney, OH). In total, in 2009 we implemented two target N treatments and two WSMV

treatments replicated 12 times for a total of 48 subplots. In 2010, we had four target N

treatments and two WSMV treatments replicated five times for a total of 40 subplots.

Detection of WSMV

Incidence of WSMV was estimated by sampling at the subplot level using

methods outlined below. We used incidence information to verify that our inoculation

treatment was successful, and that wheat had higher incidence than *B. tectorum* as

expected based on previous research (Ito 2011).Wheat and *B. tectorum* were evaluated

for WSMV infection when wheat in treated subplots began to show symptoms of systemic infection (i.e. chlorosis and streaking). Target *B. tectorum* individuals were not evaluated for infection because it would have required destructive sampling of small individuals. Instead, ten wheat leaves were randomly collected from outside sampling rings in inoculated subplots, and one leaf was collected from non-inoculated subplots (controls). *Bromus tectorum* leaves from outside sampling rings in inoculated subplots were collected (three and ten leaf samples per subplot in 2009 and 2010, respectively), and one leaf sample from non-inoculated subplots was also collected (controls). Samples were tested for WSMV using a double-antibody sandwich enzyme-linked immunosorbant assay (ELISA).

Two hundred μl of 1X carbonate buffer (0.05M sodium carbonate, pH 9.6) was loaded in each well of 96-well microtiter plates (Fisher Scientific, Pittsburgh, PA) and incubated for 1 h. Leaf tissue (0.10 g) and a corresponding amount of 1X PBS were combined to make a 1:10 dilution (wt/vol), and the samples were macerated to extract sap. One hundred μl of extracted sap was placed in each well of the plates, and two replicates of each plate were prepared. Plates were incubated overnight at 4°C, followed by seven cycles of rinsing with 5 sec soaks with 200 μL of 1X PBST (1X PBS with 0.5% Tween 20, Agdia, Elkhart, IN) using a 96-well PW™ microplate washer (Tecan, Durham, NC). *Wheat streak mosaic virus* antiserum (American Type Culture Collection (ATCC), Manassas, VA) at a 1:3200 dilution in ECI buffer (Agdia) was added and plates were incubated for 2 h in a sealed plastic bag at room temperature. Plates were washed as described above and 100 μl of goat anti-rabbit IgG alkaline phophatase conjugate (Sigma,

St. Louis, MO) at a 1:30,000 dilution in ECI buffer was added to each well. After a 2 h

incubation and a final wash, 100 µL of p-nitrophenol (PNP) substrate (Agdia) was added

to the wells. The plate was incubated for 1 h in the dark, and absorbance (A_{405}) was

quantified using a microplate reader (SpectraMax Plus, Molecular Devices, Sunnywyle,

CA).

Bromus tectorum Performance

Within each subplot, we randomly placed three (2009) or five (2010) 0.1 m^2 rings

to define competitive neighborhoods. Ring size was selected following Pollnac et al.

(2009). On 28 May 2009 and 15 July 2010, wheat and *B. tectorum* densities were

determined by counting the number of plants of each species within rings (Table 3.1). In

the center of each ring, up to three *B. tectorum* individuals were harvested when all seeds

were mature and prior to seed shatter. In 2009 *B. tectorum* matured simultaneously in all

treatments, so biomass was collected at the same time (14 July). In 2010 plants matured

more quickly in the two lowest N treatments. Accordingly, we harvested all *B. tectorum*

at the same phenological stage but at different times (16 July for the two lowest N

treatments, and 28 July for the two highest N treatments). Distance of each harvested *B.*

tectorum individual to the closest wheat row was measured at the time of harvest. In total,

we harvested 370 and 409 *B. tectorum* plants in 2009 and 2010, respectively. These

plants were dried to constant biomass in a 60° C oven and weighed to the nearest 0.01 g.

Statistical Analysis

To determine incidence of WSMV infection at the subplot level in both wheat and

B. tectorum, the absorbance of non-inoculated plants was used to create a cutoff value for

infected individuals. We calculated a 99% confidence interval around the mean absorbance of six negative controls on each plate. Inoculated samples with absorbance values above the upper boundary of the confidence interval were considered infected. Differences in incidence of infection were investigated using ANOVA with incidence of infection as the response variable and year and N level as predictors. Differences in means between years and N levels were further investigated using Tukey's HSD (Honestly Significant Difference) post-hoc tests.

To investigate the impact of environmental (i.e. N) and biological stressors (i.e. presence of a virus) on weed performance, *B. tectorum* biomass was modeled using a linear mixed effects regression model following Pinheiro and Bates (2000) and Crawley (2007). The analysis was conducted using R software including the nlme and gmodels packages (Warnes et al. 2007, R Development Core Team 2008, Pinheiro et al. 2011). Fixed effects were N availability and WSMV inoculation as categorical variables, distance from crop row as a continuous variable, and wheat and *B. tectorum* densities as covariates. The random component of the model included year, N within year (whole plots), WSMV within N (subplots), and ring within subplot (sub-subplot). This random structure allowed generalization over the two years, and also accounted for the split-plot design (Crawley 2007).

We performed a natural log transformation of individual *B. tectorum* biomass to normalize the distribution of the response variable. Further, because of high variation in N availability found in 2009 soil tests we did not use the N levels from the experimental design for data analysis. Instead, we used results from soil tests taken during the growing

season to create categorical variables for N. These categorical variables were determined

by reviewing partial residual plots for N which suggested that the response of ln (*B.

tectorum* biomass) to N was asymptotic (results not shown). To model this relationship,

we split N into four categories (1 = 10-21 kg ha^{-1}, 2 = 22-38 kg ha^{-1}, 3 = 42-84 kg ha^{-1}, 4

= 100-207 kg ha^{-1}) that were used for data analysis. In our analysis, the slope of the

relationship between distance from row and *B. tectorum* individual biomass is interpreted

as the percent decrease in weed biomass for each cm it occurred from the wheat row. We

expected the relationship between distance from row and *B. tectorum* biomass to change

if crop competitive ability was modified by the N and WSMV treatments we imposed.

Thus, we tested for a three-way interaction between distance from row, N, and WSMV to

determine if N and WSMV changed the relationship between distance from row and *B.

tectorum* performance. To obtain a parsimonious model, we then simplified it by

removing individual parameters based on *p*-values ($\alpha \geq 0.05$) generated in ANOVA and

re-fitting based on restricted maximum likelihood estimation (Zuur et al. 2009). We

viewed diagnostic plots to check for equal variance among and within groups (Pinheiro

and Bates 2000) and found no evidence of unequal variance.

Results

Wheat and *B. tectorum* densities differed between the two years (Table 3.1).

Incidence of WSMV infection of inoculated *B. tectorum* was low ($3\% \pm 4\%$, mean $\pm$

standard deviation), regardless of year or N level. However, incidence of infection for

wheat differed between years and among N levels. Incidence of WSMV in wheat was

higher by about 20% in 2009 compared to 2010 for each N level ($p < 0.001$, Table 3.2).

Additionally, wheat grown in N levels 3 and 4 had higher incidence of infection than wheat in N levels 1 and 2 in both years (Table 3.2).

Biomass of individual *B. tectorum* plants was modified by a three-way interaction between distance from wheat row, N level, and WSMV inoculation ($p = 0.042$, Table 3.3). This interaction suggested that the relationship between distance from row and *B. tectorum* biomass depended on specific combinations of resource availability and disease status. We examined the regression coefficients associated with distance from row for each N × WSMV combination, and determined that there was a statistically significant relationship between distance from row and biomass only in certain N × WSMV treatment combinations (Table 3.4).

Distance from row influenced individual *B. tectorum* biomass in non-inoculated subplots in N levels 1 and 4 ($p = 0.005$ and 0.047, respectively, Table 3.4), and marginally influenced it in the N2 level ($p = 0.094$) (Table 3.4, Fig 3.1). In non-inoculated subplots individual *B. tectorum* biomass increased 8.3% ± 3.0% per cm from wheat row (estimated mean biomass = 0.12 g and 0.33 g at 0 and 12 cm from row) in N level 1, while in N level 4 individual *B. tectorum* biomass increased 6.9% ± 3.4% per cm from the wheat row (estimated mean biomass = 0.62 g and 1.4 g at 0 and 12 cm from row). N level 2 within non-inoculated subplots had a similar trend, with an increase in *B. tectorum* biomass of 4.9% ± 2.9% per cm from the wheat row (estimated mean biomass = 0.38 g and 0.67 g 0 and 12 cm from row). We failed to detect an effect of distance from row on *B. tectorum* biomass for inoculated subplots in N levels 1, 2, and 4 ($p = 0.256$, 0,206, and 0.191, respectively, Table 3.4).

The pattern detected in N levels 1, 2, and 4 was reversed in N level 3, where we observed a relationship between distance from row and *B. tectorum* biomass in inoculated subplots, and no relationship in non-inoculated subplots. In N level 3, there was a significant relationship between distance from row and *B. tectorum* biomass in inoculated subplots, but not in non-inoculated subplots. In inoculated environments, *B. tectorum* had an estimated 12% ± 4.4% increase in individual biomass per cm from the row ($p = 0.005$, Table 3.4), which represents the largest distance from row effect of the study. Thus, a *B. tectorum* plant growing in the wheat row (distance = 0 cm) had an estimated mean biomass of 0.27 g, while a plant located 12 cm (maximum distance) from the wheat row had an estimated mean biomass of 1.1 g (Fig. 3.1). In contrast, there was no relationship between distance from row and *B. tectorum* biomass in non-inoculated subplots for N level 3 ($p = 0.950$, Table 3.4). A *B. tectorum* plant in this treatment combination had estimated mean biomass of 0.84 g, regardless of proximity to the wheat row (Fig. 3.1).

Discussion

The relative response of two species to disease often changes over an environmental gradient (Louda et al. 1990, Alexander and Holt 1998, Schroeder et al. 2005). Our results provide further evidence for this observation and provide insights on its ecological significance. In this study, the relationship between proximity to wheat and *B. tectorum* performance changed with disease and N availability. Identifying the suite of environmental and biological conditions under which weeds are most competitive represents a useful step to formulate ecologically-based management recommendations (Crawley 1997, Freckleton and Watkinson 2001, Pollnac et al. 2009). Targeting

management at the most competitive individuals rather than treating the entire field may

be a strategy for designing effective weed management techniques that reduce herbicide

use or tillage. Further, this knowledge may allow managers to avoid conditions that favor

weedy species and reduce crop competitive ability (Committee on Twenty-First Century

Systems Agriculture; National Research Council 2010, Sciegienka et al. 2011).

Previous research conducted in a controlled environment with no variation in

resource availability showed that *B. tectorum* size increased proportionally to its distance

from winter wheat (Stahlman and Miller 1990). This information suggests that

controlling *B. tectorum* in the interrow using interrow tillage, harrowing, or banded spray

applications could have a greater than proportional effect on the seed production and

resource acquisition of *B. tectorum*. Our results partially support this idea, but also

emphasize the potential impact of biotic and abiotic conditions in determining *B.*

tectorum performance. Specifically, we observed that in low and high N environments

(compared to the N environment imposed by recommended rates of N fertilizer), distance

from row only influenced *B. tectorum* biomass in disease-free environments, suggesting

that healthy wheat suppressed *B. tectorum* that was closest to the row. In contrast, wheat

inoculated with WSMV did not have this suppressive ability. A potential explanation for

this result could be that WSMV inoculation decreased the relative competitive ability of

wheat compared to *B. tectorum*, a less susceptible species (Ito 2011). Wheat inoculated

with WSMV may have had reduced competitive ability in high and low N environments

as infections inhibit wheat root growth, leading to a reduction in resource uptake (Price et

al. 2010). This reduced root growth in wheat may have reduced its ability to forage for

nutrients, allowing *B. tectorum* to compete effectively even close to wheat.

We observed a different pattern in the intermediate N environment, where

distance from row influenced *B. tectorum* performance only with the presence of WSMV.

Interestingly, the intermediate level of fertility in our study corresponded to

recommended rates for soil nitrate availability for wheat yield at the studied site

(Jacobson et al. 2005). Further, the effect of distance from row was most pronounced in

the intermediate level of fertility, where we observed that the percent increase in *B.

tectorum* biomass per cm from the row was highest. This result corresponds with

previous work suggesting that resource availability changes the impact of pathogens on

plant competitive ability (Alexander and Holt 1998). For example, Garcia-Guzman et al.

(1996) found that flower smut infection only changed *Bromus catharticus* Vahl

(rescuegrass) competitive ability under conditions of low nutrient availability and high

plant density. Our results have parallels in research conducted in additional rangeland

systems, where the competitive balance between *B. tectorum* and native perennial grasses

can shift at specific levels of soil nutrient availability (Vasquez et al. 2008a, b). However,

over most of the range of N availability we investigated, our results suggest that WSMV

inoculation impacted wheat's ability to suppress *B. tectorum*.

Conclusions and Management Implications

Previous work has established that wheat is more susceptible than *B. tectorum* to

WSMV infection (Ito 2011), and that crop vigor is reduced by this disease due to

physiological changes (Brakke et al. 1988, Price et al. 2010). Our results add to previous

knowledge, and suggest that competitive relationships between *B. tectorum* and winter wheat change with WSMV infection. More research into how the disease impacts the physiology of winter annual, grassy weed species of concern such as *B. tectorum* and *Aegilops cylindrica* (jointed goatgrass) could help us explain changes in competitive relationships seen in our study. In addition, it would be helpful to investigate if the patterns seen in our mechanically inoculated system are similar in more natural systems where the disease is vectored by the wheat curl mite.

This research highlights the importance of jointly considering multiple biological and environmental factors when assessing the potential impact of weeds on crop performance. We found interactive effects of disease, soil fertility, and crop competition on weed performance. These interactions are complex, as both fertility and disease can change both crop and weed competitive ability, and the effect of one factor may depend on the other. Further, because ecologically-based weed management hinges on sustaining competitive ability of the crop (Committee on Twenty-First Century Systems Agriculture; National Research Council 2010), effectively managing crop disease may in turn be an important aspect of weed management. As such, this research highlights the importance of incorporating an interdisciplinary perspective in the assessment of the impact and management of agricultural pests.

Tables and Figures

Table 3.1. Means, standard deviations, maximum values, and minimum values for wheat density and *Bromus tectorum* density 0.1 m^{-2} in a field study that assessed the impact of environmental and biological stressors on weed performance.

Year	Wheat density				*B. tectorum* density			
	Mean	SD	Max	Min	Mean	SD	Max	Min
2009	11[a]	5.0	35	0	12[a]	7.8	51	1
2010	14[b]	8.6	63	1	20[b]	15.3	94	1

Within plant species, superscript letters indicate differences in mean densities per year based on t-tests.

Table 3.2. Mean percent incidence of infection (standard deviation) for wheat mechanically inoculated with *Wheat streak mosaic virus*.

Year	N levels			
	1	2	3	4
2009	27 (14)[a]	35 (13)[a]	56 (20)[b]	65 (15)[b]
2010	9 (14)[a]	19 (11)[a]	35 (23)[b]	37 (23)[b]

Nitrate levels (N) were 1 (10-21 kg ha^{-1}), 2 (22-38 kg ha^{-1}), 3 (42-84 kg ha^{-1}), and 4 (100-207 kg ha^{-1}). Within year, superscript letters indicate differences in treatment means based on Tukey's HSD post-hoc tests.

Table 3.3. Results from ANOVA performed to assess the effect of nitrate level (N), *Wheat streak mosaic virus* (WSMV) inoculation, wheat density, *Bromus tectorum* density, and distance from wheat row (fixed effects) on individual *B. tectorum* biomass in most parsimonious linear mixed effects model.

	Num df	Den df	*F*-value	*p* value
(Intercept)	1	438	32.00	**< 0.001**
Wheat density	1	300	18.04	**< 0.001**
B. tectorum density	1	300	5.651	**0.018**
Distance	1	438	18.67	**< 0.001**
N	3	3	4.977	0.110
WSMV	1	4	1.249	0.326
Distance × N	3	438	0.389	0.761
Distance × WSMV	1	438	0.010	0.920
N × WSMV	3	4	4.560	0.088
Distance × N × WSMV	3	438	2.750	**0.042**

N levels were 1 (10-21 kg ha^{-1}), 2 (22-38 kg ha^{-1}), 3 (42-84 kg ha^{-1}), and 4 (100-207 kg ha^{-1}). WSMV 1 and 0 were plants inoculated and not inoculated, respectively, with *Wheat streak mosaic virus*. Distance is distance from the closest wheat row for each *B. tectorum* individual.

Table 3.4. Estimated slopes of the regression between distance from wheat row and *B. tectorum* biomass for the eight nitrate level (N) × *Wheat streak mosaic virus* (WSMV) combinations. *P*-values are for the null hypothesis that the slope is equal to zero.

Treatment combination	Estimate (SE)	*t* value	*p* value
N level 1 × WSMV 0	0.083 (0.030)	2.800	**0.005**
N level 1 × WSMV 1	0.031 (0.028)	1.137	0.256
N level 2 × WSMV 0	0.049 (0.029)	1.680	0.094
N level 2 × WSMV 1	0.035 (0.027)	1.266	0.206
N level 3 × WSMV 0	-0.002 (0.027)	-0.063	0.950
N level 3 × WSMV 1	0.12 (0.044)	2.796	**0.005**
N level 4 × WSMV 0	0.069 (0.034)	1.994	**0.047**
N level 4 × WSMV 1	0.038 (0.029)	1.308	0.191

Nitrate levels (N) were 1 (10-21 kg ha^{-1}), 2 (22-38 kg ha^{-1}), 3 (42-84 kg ha^{-1}), and 4 (100-207 kg ha^{-1}). WSMV 1 and 0 were inoculated and not inoculated, respectively, with *Wheat streak mosaic virus*. Estimates are presented in the natural log scale.
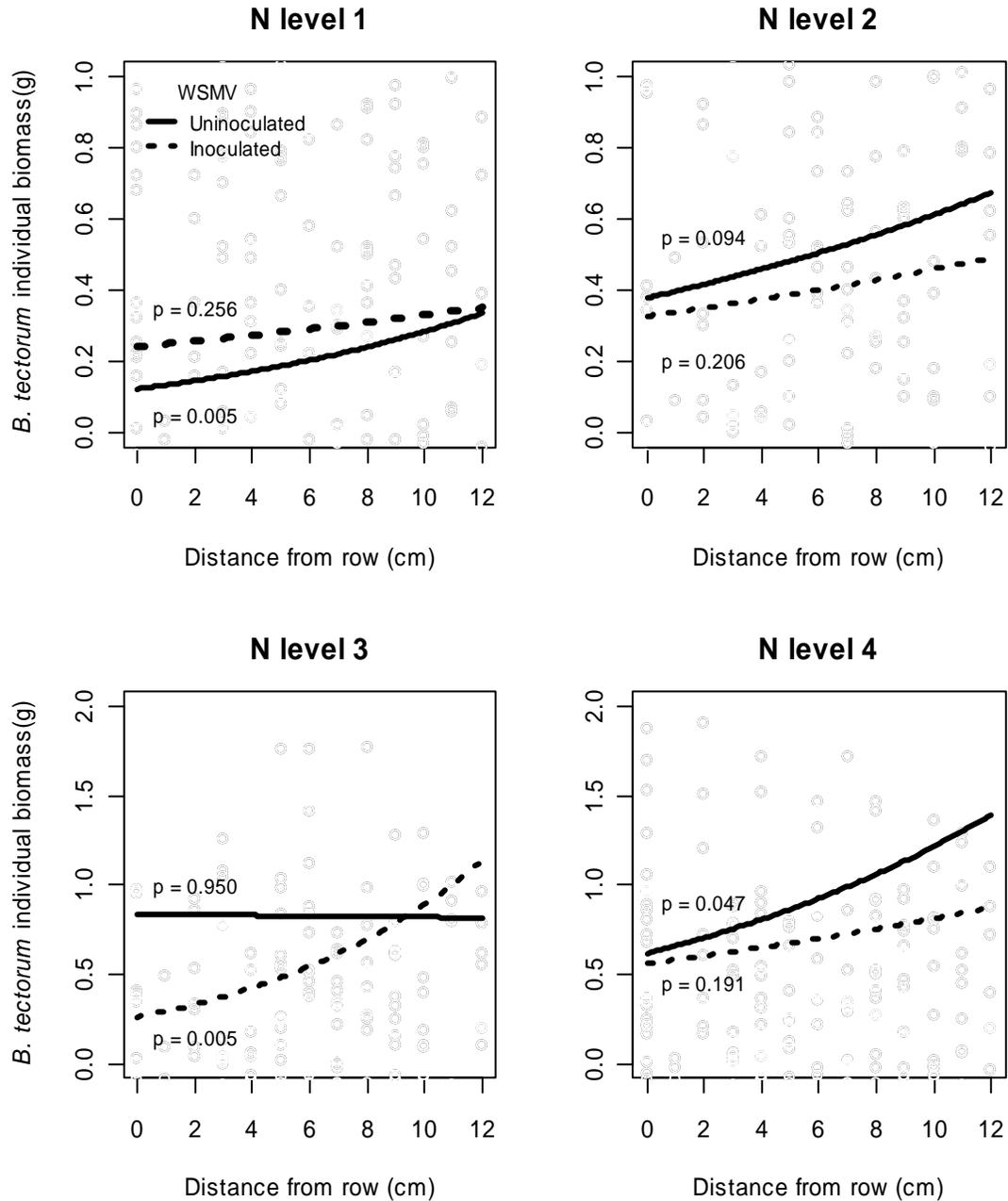
Figure 3.1. Predicted values for *Bromus tectorum* individual biomass by distance from closest wheat row in the four nitrate level (N) treatments. N levels were 1 (10-21 kg ha^{-1}), 2 (22-38 kg ha^{-1}), 3 (42-84 kg ha^{-1}), and 4 (100-207 kg ha^{-1}). The biomass values were backtransformed from the natural log scale, and mean covariate values (wheat density = 13, *B. tectorum* density = 16) were used for graphing purposes. Y-axis scale differs between panels. *P*-values are for the null hypothesis that the slope of the relationship between distance from row and *B. tectorum* individual biomass equals zero (α = 0.05).

CHAPTER FOUR

SUMMARY OF FINDINGS AND DIRECTIONS FOR FUTURE RESEARCH

Bromus tectorum has been called the most dominant invasive species in the western United States (Mack 2011). Its dominance and resulting ecological and economic impacts in both rangelands and croplands have arisen despite substantial management and research efforts to control its spread. Most published research about this species has focused either on its impacts or control methods. Less effort has been focused on investigating ecological processes that may play a mechanistic role in its success, though this is a necessary step for developing effective ecologically-based management. To expand the information about how ecological processes influence *B. tectorum* dynamics, we investigated how biotic and abiotic factors impact interactions between *B. tectorum* and desired vegetation. This research has implications for restoration of lands dominated by *B. tectorum* and management of *B. tectorum* in small-grain cropping systems.

Our first research objective applied to revegetation of *B. tectorum*-dominated rangelands with native perennial species. *Bromus tectorum* competition among other plant stressors may decrease establishment of desired species (Hull and Stewart 1948, Harris 1967, Allen 1995). Life history differences that cause seeded species to emerge after *B. tectorum* plants are actively growing, as well as differences in response to available resources, are two mechanisms hypothesized to lend a competitive advantage to *B. tectorum* over native perennial seedlings (Harris 1967, Harris and Wilson 1970, Aguirre and Johnson 1991, James 2008a, Vasquez et al. 2008a). Indeed, in a greenhouse experiment, we found that both relative time of emergence and resource availability play

a critical role in determining the competitive interactions between *B. tectorum* and *Pseudoroegneria spicata*, a native perennial bunchgrass often used in rangeland revegetation. Compared to concurrent sowing, *P. spicata* established prior to *B. tectorum* emergence effectively suppressed and avoided suppression, with its competitive effect increasing with cohort age. This result agrees with a growing body of research suggesting that order of emergence is an important mechanism influencing the competitive relationships between seeded species versus invasive species (Corbin and D'Antonio 2004, Abraham et al. 2009, Firn et al. 2010, Stevens and Fehmi 2011). In addition, though nitrogen (N) enrichment increased productivity of both species, the magnitude of increase did not differ between the two species. Consequently, and in contrast to our predictions, the ability of *B. tectorum* to suppress *P. spicata* growth did not increase with N availability.

Results from the study conducted under the first objective offer several opportunities for future research. This study was conducted in a greenhouse environment, and it would be beneficial to explore how our results extend to lands dominated by *B. tectorum*. Further research could also focus on how standard revegetation practices could be modified to achieve these differences in emergence time. Also, testing additional perennial species often used in revegetation projects would provide information that could lead to useful generalizations across species. Finally, previous research has shown that in conditions with higher soil fertility than was investigated in our study, *B. tectorum* may have an increasing impact on *P. spicata* growth (Wilson et al. 1966). Thus, conducting research to determine the role of relative time of emergence in soils with

higher fertility would provide useful information to improve seeding projects in old-field settings such as in Conservation Reserve Program lands where resource availability may be higher.

For our second research objective, we conducted a manipulated field experiment to explore how biotic and abiotic factors interact to determine *B. tectorum* performance in a winter wheat (*Triticum aestivum* L.) system. Previous research conducted in a controlled environment with no variation in resource availability showed that *B. tectorum* size increased proportionally to its distance from winter wheat (Stahlman and Miller 1990). We investigated how this relationship changed when the system was inoculated with *Wheat streak mosaic virus* (WSMV) over a range of N availability. Specifically, we evaluated the combined impact of proximity to wheat, N availability, and *Wheat streak mosaic virus* (WSMV) on *B. tectorum* biomass production. In accordance with previous research (Ito 2011), wheat was much more susceptible than *B. tectorum* to WSMV infection. We observed that in low and high N environments (compared to the N environment imposed by recommended rates of N fertilizer), distance from row only influenced *B. tectorum* biomass in disease-free environments, suggesting that healthy wheat suppressed *B. tectorum* that was closest to the row. In contrast, wheat inoculated with WSMV did not suppress *B. tectorum*. We observed a different pattern in the intermediate N environment, where distance from row influenced *B. tectorum* performance only with the presence of WSMV. Information gained in this experiment highlights the importance of jointly considering multiple biological and environmental factors when assessing the potential impact of weeds on crop performance. Because

ecologically-based weed management hinges on sustaining competitive ability of the crop, effectively managing crop disease may in turn be an important aspect of weed management.

Further research would be beneficial to explore how *B. tectorum* and WSMV jointly impact winter wheat cropping systems. While it has been established that wheat is more susceptible than *B. tectorum* to WSMV infection (Ito 2011), and that crop vigor is reduced by this disease due to physiological changes (Brakke 1998, Price 2010), additional research into how the disease impacts the physiology of winter annual, grassy weeds could help explain the mechanisms responsible for changes in competitive relationships. In addition, it would be helpful to investigate if the patterns seen in our mechanically inoculated system are similar to more natural systems where the disease is vectored by the wheat curl mite.

The results of our work contribute to the knowledge of *B. tectorum* ecology in both rangeland and cropland ecosystems. It is our hope that this information contributes to a more mechanistic understanding of *B. tectorum* success in varied ecosystems that will lead to effective ecologically-based *B. tectorum* management in the future.

APPENDIX A

SUPPLEMENTAL EXPERIMENTS, FIGURES, AND TABLES

Revegetation Demonstration Project: Justification,

Methods, and Preliminary Results

Introduction

Exotic annual grass invasion across arid and semi-arid rangelands of the western

United States has been associated with loss of sagebrush-steppe habitat, altered fire

regimes, species shifts, and widespread biotic impoverishment (D'Antonio and Vitousek

1992, Knapp 1996, Mack 2011). These grasses can become dominant on rangelands

following a disturbance, sometimes forming near monocultures that may prevent

recruitment of native species (Harris 1967, Humphrey and Schupp 2004, Chambers et al.

2007, Mack 2011). *Bromus tectorum* L. (downy brome or cheatgrass) and *Bromus*

japonicus Thunb. (Japanese brome) are two such exotic annual grasses. According to

Mack (2011), *B. tectorum* is the most dominant invasive species in the Intermountain

West, and it has also been identified as a major barrier to restoration efforts in degraded

lands (Allen 1995).

Desired perennial species can be lost from plant communities through decreased

recruitment and seed bank impoverishment due to long-term site dominance by exotic

annual grasses (Humphrey and Schupp 2001, 2004, Mack 2011). Consequently, simply

controlling exotic grasses may not be sufficient to restore plant communities. Instead,

revegetation should be integrated with weed control efforts as a long-term strategy to

suppress invasive exotic annual grasses and provide habitat for livestock and wildlife

(Di Tomaso 2000). However, re-establishing desired species is often difficult on lands

dominated by invasive annual grasses (Allen 1995, Di Tomaso 2000). Though many

factors (e.g. precipitation amount and timing, soil properties, plant materials chosen) can influence success of seeded perennial species, competition from invasive species may be a key factor in the failure of revegetation projects (Allen 1995). Specifically, competition from exotic annual grasses has been shown to decrease establishment of perennial grasses and cause failure of reseeding efforts (Hull and Stewart 1948, Romo and Eddleman 1987, Davies et al. 2010, but see James and Svejcar 2010).

Chemical control is the most common method of invasive plant management in rangeland systems and while it can be effective in managing exotic annual grasses (Di Tomaso 2000, Morris et al. 2009), misuse can result in unintended biological and environmental consequences (Smith et al. 2006, Rinella et al. 2009). Herbicide treatments that decrease annual grass abundance and competitive ability are important strategies for allowing perennial species to establish during revegetation. Imazapic is one herbicide that has been widely used to selectively control winter annual grasses such as *B. tectorum* and *B. japonicus* in rangelands (Shinn and Thill 2002, Morris et al. 2009, Owen et al. 2011). The integration of herbicide application with reseeding practices can favor seeded species, but it could result in non-target effects. For example, previous research has indicated that high rates of imazapic reduce seeded species establishment and damage remnant beneficial plants, though these effects are species-specific and depend on timing of herbicide application relative to seeding (Shinn and Thill 2004, Monaco et al. 2005, Sheley et al. 2007, Morris et al. 2009). Identifying perennial species that are competitive with annual grasses and tolerant of imazapic rates recommended for annual grass control will be useful to improve revegetation practices.

There is evidence that seeding a mix rather than single species is more effective for revegetation of rangeland dominated by invasive species. The ecological basis for this idea is that a diverse combination of species may fill multiple niches, leaving less space (i.e. resources and safe sites) available for unwanted plants (Tilman 1997). Indeed, Kirmer et al. (2011) determined that a seed mix with 55 species resulted in less colonization by unseeded species than a mix with three species, suggesting that the mix with higher species richness was more resistant to invasion. Further, successful plant establishment in rangeland communities hinges on episodic climate characteristics, such as rainfall at the right time for seed germination and seedling establishment (Call and Roundy 1991). When seeding a mix, it is more probable that some species will be able to tolerate site conditions which other species cannot, and that germination and establishment requirements are met for at least some of the species (Sheley and Half 2006). In accordance, previous research comparing establishment rates using seed mixes with high versus low species richness found higher seeded species establishment using the mix with a greater number of species (Kirmer et al. 2011).

The objectives of this study were to evaluate integration of herbicide (imazapic + glyphosate) and reseeding to restore sites dominated by annual *Bromus* species. Our goal was to detect an optimal herbicide application rate that would maximize the emergence and survival of seeded species by decreasing *Bromus* species competitive ability. Further, we hypothesized that seeding a combination of species would result in higher rates of establishment and decreased dominance of annual *Bromus* species than species seeded

singly. One field season of sampling has been conducted for this study; therefore preliminary results will be presented here.

<u>Materials and Methods</u>

Two study sites in Hill and Phillips Counties, Montana, U.S.A., that differed in land use history and annual *Bromus* species composition were chosen for this study (Table 1). Site selection was based on intensity and uniformity of *Bromus* infestation and ease of seeding machinery access. At each site, the experiment followed a randomized split-plot design with four replications arranged as blocks. Eight seeding treatments were assigned to 11.0 m by 2.4 m main plots, and the three herbicide rates were randomly assigned to 3.0 m by 2.4 m subplots. To minimize edge effects, there was a 1.2 m buffer between each main plot, and a 1 m buffer between subplots.

Herbicide treatments were applied before *Bromus* species emergence in fall 2009 with a CO_2 - pressurized backpack sprayer (31 August 2009 in Phillips County, and 1 September 2009 in Hill County). Herbicide (Journey®; BASF, Research Triangle Park, NC, U.S.A) application rates were control (no herbicide), low (66 g imazapic ha^{-1} + 132 g glyphosate ha^{-1}, 10 oz Journey ac^{-1}), and high (105 g imazapic ha^{-1} + 211 g glyphosate ha^{-1}, 16 oz Journey ac^{-1}). The high rate was the recommended rate for *Bromus* control and site preparation for the seeded grasses, while the low rate was recommended based on tolerance of the seeded forb to imazapic. We used a non-ionic surfactant mixed at a 0.25% volume/volume rate (1 ml surfactant: 400 ml water).

Seeding treatments were applied 19-20 April 2010, the spring following the herbicide application, utilizing a 120 cm - wide hoe seeder to seed eight rows in each plot

at 30 cm spacing and approximately two cm depth. We chose three species for each location based on site characteristics (e.g. precipitation and soil type) (Holzworth et al. 2003, Sheley et al. 2008), weed suppression ability (Holzworth et al. 2003), fall-applied Journey tolerance according to the product label, recommendations from local landowners and agricultural research station staff, and observations of plant communities in the area. Each species was sown singly, and in all combinations of two and three species for a total of eight seeding treatments including a non-seeded control. Species consisted of two grasses and a forb at each site and seeding rates for single species plots followed Sheley et al. (2008) (Table 2). A substitutive design was used in the species mixtures by adjusting seeding rates so the total number of seeds m^{-2} remained constant. Specifically, the single species seeding rate was adjusted for mixtures by dividing the rate for each species in the mix by two for two-species mixes and by three for three-species mixes.

Sampling was conducted in early summer (22 and 30 June in Phillips County and 7 July in Hill County) and fall (4 and 5 November) 2010 to determine seeded species emergence and survival to fall, annual brome control, and response of remnant perennial grasses to herbicide treatments. For all of these measurements, three 0.1 m^2 sampling frames were randomly placed in each subplot, each centered lengthwise on a seeded row. Frame locations were permanently marked for repeated sampling. Density of seeded species and *Bromus* were measured and percent canopy cover was estimated by species in these frames in spring and fall 2010.

Bromus biomass sampling locations differed from those used for density and cover sampling for two reasons. First, we did not expect the seeding treatment to impact *Bromus* biomass in the first season after seeding. Also, we did not clip *Bromus* biomass from the permanent sampling frame locations because removing *Bromus* may have impacted future seeded species establishment and growth. Thus, we randomly selected four subplots of each herbicide treatment in each replication, and placed two 0.1 m^2 sampling frames, making sure not to overlap these and the permanent frame locations. Then, we clipped all *Bromus* biomass within these two frames, dried it to constant mass in a 60º C oven, and weighed it to the nearest 0.1 gram.

At the Hill County site, we observed a visually evident increase in remnant perennial grass cover in subplots treated with imazapic + glyphosate (Fig. 1). These grasses included several native perennial grasses [e.g. *P. smithii* (western wheatgrass) and *Stipa viridula* Trin. (green needlegrass)] and introduced grasses [e.g. *Agropyron cristatum* (L.) Gaertn. (crested wheatgrass) and *Bromus inermis* Leyss. (smooth brome)] that were seeded approximately six years prior to this study by the landowner. These species were not apparent when we began the study due to substantial *B. tectorum* cover at the site and an associated thatch layer. To document these species' release from *Bromus* competition in response to our herbicide treatment, we estimated recruitment by counting seedlings and new ramets (i.e. seedlings with three or fewer leaves that were three or more cm from remnant grass) of existing perennial grasses within the permanent 0.1 m^2 frames discussed above. We collected this information in all herbicide treatment subplots within the unseeded control plots (*n* = 12 subplots).

Statistical Analysis. For all measurements, data collected in the sampling frames were averaged for each subplot and analyzed using R software, including the nlme and multcomp packages (Hothorn et al. 2008, R Development Core Team 2008, Pinheiro et al. 2011). Data from the Phillips and Hill County sites were analyzed separately due to differing plant communities, land use histories, and seeding treatments. To evaluate the impact of seeding and herbicide treatments on density and cover of seeded species and *Bromus* species, we performed split-plot ANOVA using mixed model techniques following Pinheiro and Bates (2000). Fixed variables were seeding treatment and herbicide rate, and random variables were herbicide rate nested in seeding treatment within block to account for blocking and the split-plot design. To determine *Bromus* biomass response to herbicide treatments, we performed one-way ANOVA where herbicide rate was the fixed variable. We examined histograms of the response variables, and both biomass and density of seeded species and *Bromus* species were natural log transformed to normalize the variables. Model fitting started with fixed effects and interactions included, non-significant parameters were omitted ($\alpha = 0.05$), and models were refitted to obtain the simplest models. Finally, to determine if remnant perennial grasses at the Hill County site increased recruitment (density of seedlings and new ramets) with increasing herbicide rate, we performed ANOVA, where recruitment was the response, herbicide rate was the fixed effect, and block was the random effect. Where treatment differences occurred, pairwise comparisons were made using Tukey's HSD (Honestly Significant Difference) tests ($\alpha = 0.05$).

Preliminary Results and Discussion

      Seeded Species Emergence and Survivorship. As expected, seeded species

emerged in spring 2010 at both sites. In Hill County, seeded species emergence depended

on both seeding treatment ($p < 0.001$, F stat $= 26.31$ on 7 and 21 df) and herbicide rate (p

$= 0.037$, F stat 3.470 on 2 and 62 df). According to pairwise tests, all seeding treatments

had better emergence than both the unseeded control and the native forb seeded alone,

but the other seeding treatments did not differ in seedling emergence (Fig. 2). Seeded

species emergence differed between the control and high rates of herbicide ($p = 0.037$

from Tukey's HSD test), but we could not detect a difference in emergence between the

control and low or low and high rates ($\alpha = 0.05$, Fig. 3).

      In Phillips County, there was a marginally significant effect of herbicide rate on

seeded species emergence ($p = 0.057$, F stat $= 3.011$ on 2 and 62 df), though post-hoc

pairwise tests indicated no differences in seedling emergence between rates ($\alpha = 0.05$,

Fig. 3). However, seedling emergence depended on seeding treatment ($p < 0.001$, F stat

15.07 on 7 and 21 df, Fig. 2). Again, the unseeded control had lower emergence than any

of the other treatments according to pairwise tests (Fig. 2). At this site, both the native

forb seeded alone and a mix of all three species had higher emergence than the

introduced grass seeded alone. However, none of the other seeding treatments differed in

seeded species emergence (Fig. 2).

      No seeded plants survived to fall sampling at the Hill County site, and very few

were found at the Phillips County site (data not presented). In Hill County we suspect that

competition from remnant perennial grasses in sprayed plots, and *B. tectorum* in control

plots may have caused the seeding to fail. According to the landowner in Phillips County

where the site is located, the seedlings may have been eaten by grasshoppers, which were

abundant in 2010. However, short term results of revegetation studies may not be

indicative of long-term outcomes (Rinella et al. 2011). Therefore, subsequent sampling at

both sites will be beneficial to determine if any of the seeded plants survived and if so,

what effect the herbicide and seeding treatments had on establishment.

Bromus Species Response to Herbicide and Seeding. Biomass of *Bromus* species

decreased with increasing herbicide rate at both Hill County ($p < 0.001$, F stat $= 60.83$ on

2 and 36 df) and Phillips County ($p < 0.001$, F stat $= 58.05$ on 2 and 38 df) (Fig. 4).

Bromus species density also depended on herbicide rate at both Hill County ($p < 0.001$, F

stat $= 26.04$, on 2 and 62 df) and Phillips County ($p < 0.001$, F stat $= 58.85$, on 2 and 62

df) (Fig. 4). Though our results indicate good control of annual grasses for the first

growing season after application, previous research indicates that *Bromus* populations

may rebound from herbicide treatment or other disturbance within two years due to

extensive seedbanks of these species (Humphrey and Schupp 2001, Sheley et al. 2007,

Morris et al. 2009, Owen et al. 2011). Further sampling would be useful to determine if a

similar pattern holds for this study.

Seeding treatments did not impact *Bromus* species density or biomass at either

site ($\alpha = 0.05$). As has been previously observed (Sheley et al. 2007), it may be several

years before we can detect differences in the ability of seeded species to resist annual

grass invasion.

Remnant Species Recruitment. We failed to detect a difference in remnant perennial grass recruitment in Hill County in response to herbicide treatment ($p = 0.207$, F stat = 2.072 on 2 and 6 df). However, this may be due to the small sample size (n = 12 subplots) as we did observe a trend of increasing recruitment with increased herbicide rate (Fig. 5). This pattern was probably due to a decrease in *Bromus* density and biomass in sprayed plots and a resulting release of perennial species from competition. Further assessment of the remnant perennial species would be valuable in assessing release from *B. tectorum* competition.

Conclusions and Future Directions. Though we have only collected data for one season after reseeding, this study presents useful directions for future research. We found that the herbicide treatments effectively controlled *Bromus* species at both sites for one season, and that seeded species establishment at each site was low or nonexistent. However, it is important to return to both sites to assess seeded species establishment and to determine if the impacts of the herbicide treatment on the annual grass population persist past the first growing season. Additionally, the apparent failure of the seeding treatment at the Hill County site may have been due to competition from remnant perennial grasses. If so, this seeding failure highlights the importance of assessing remnant plants prior to revegetation efforts. Further research into critical thresholds of the plant community where revegetation may or may not be necessary would be useful to identify situations where simply controlling invasive species may be adequate to restore desired vegetation.

Tables and Figures

Table 1. Site information for the two study sites in Hill and Phillips Counties, Montana, U.S.A.

Site	Dominant annual grass (mean % cover ± SD)	Land use	Latitude Longitude	Elevation	Precip (mm): 2010	Mean annual precip (mm): period of record
Hill County	*Bromus tectorum* (48 ± 32)	CRP	48º 26'55.40" N 109º 51'57.45" W	799 m	424	307
Phillips County	*Bromus japonicus* (4 ± 5)	Range	48º 08'23.59" N 107º 52'15.58" W	725 m	402	329

CRP is Conservation Reserve Program land. SD is standard deviation. Precipitation data obtained from WRCC (2008) for closest weather station to study sites (Ft. Assiniboine for Hill County, Malta for Phillips County).

Table 2. Seeded species and seeding rates for each site.

Site	Seeded species	Seeding rate (1 species)
Hill County	*Elymus lanceolatus* (Bannack) (thickspike wheatgrass)	12 kg PLS ha^{-1}
	Thinopyrum intermedium ssp. barbulatum (Luna) (pubescent wheatgrass)	16 kg PLS ha^{-1}
	Dalea purpurea (Bismarck) (purple prairieclover)	9 kg PLS ha^{-1}
Phillips County	*Pascopyron smithii* (Rosana) (western wheatgrass)	18 kg PLS ha^{-1}
	Thinopyrum intermedium ssp. barbulatum (Luna) (pubescent wheatgrass)	16 kg PLS ha^{-1}
	Dalea purpurea (Bismarck) (purple prairieclover)	9 kg PLS ha^{-1}

PLS (% purity × % germination) indicates pure live seeds. The single species seeding rate was adjusted for mixtures by dividing the rate for each species in the mix by two for two-species mixes and by three for three-species mixes.

Figure 1. Photograph depicting remnant perennial grass *Pascopyron smithii* increase in biomass relative to unsprayed areas in the background and foreground.
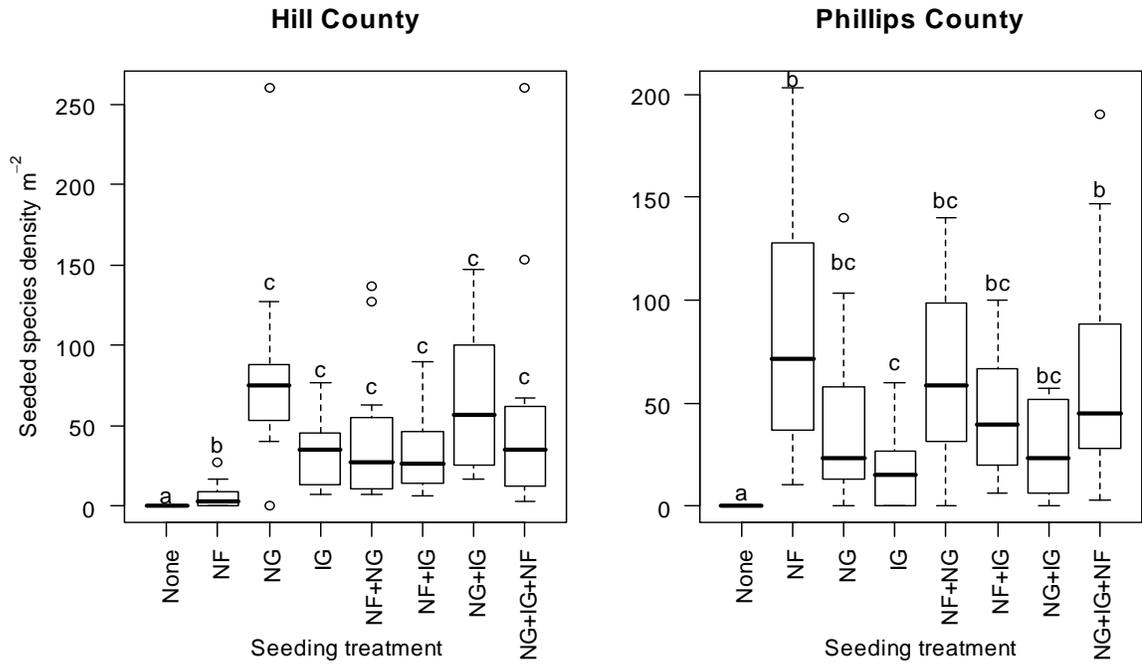
Figure 2. Seeded species density m^{-2} by seeding treatment measured four months after seeding. None is the non-seeded control, NF is the native forb (*Dalea purpurea*), NG is the native grass (*Elymus lanceolatus* in Hill County, *Pascopyron smithii* in Phillips County), and IG is the introduced grass (*Thinopyrum intermedium ssp. barbulatum*). Y-axis scale differs between sites. Letters separate treatment means that are significantly different according to Tukey's HSD post-hoc tests ($\alpha = 0.05$).

Hill County   **Phillips County**

Figure 3. Seeded species density m^{-2} by herbicide rate measured four months after seeding. Rates were control (no herbicide), low (66 g imazapic ha^{-1} + 132 g glyphosate ha^{-1}), and high (105 g imazapic ha^{-1} + 211 g glyphosate ha^{-1}). For the Hill County site, letters separate treatment means that are significantly different according to Tukey's HSD post-hoc tests (α = 0.05). Treatment means did not differ at the Phillips County site.
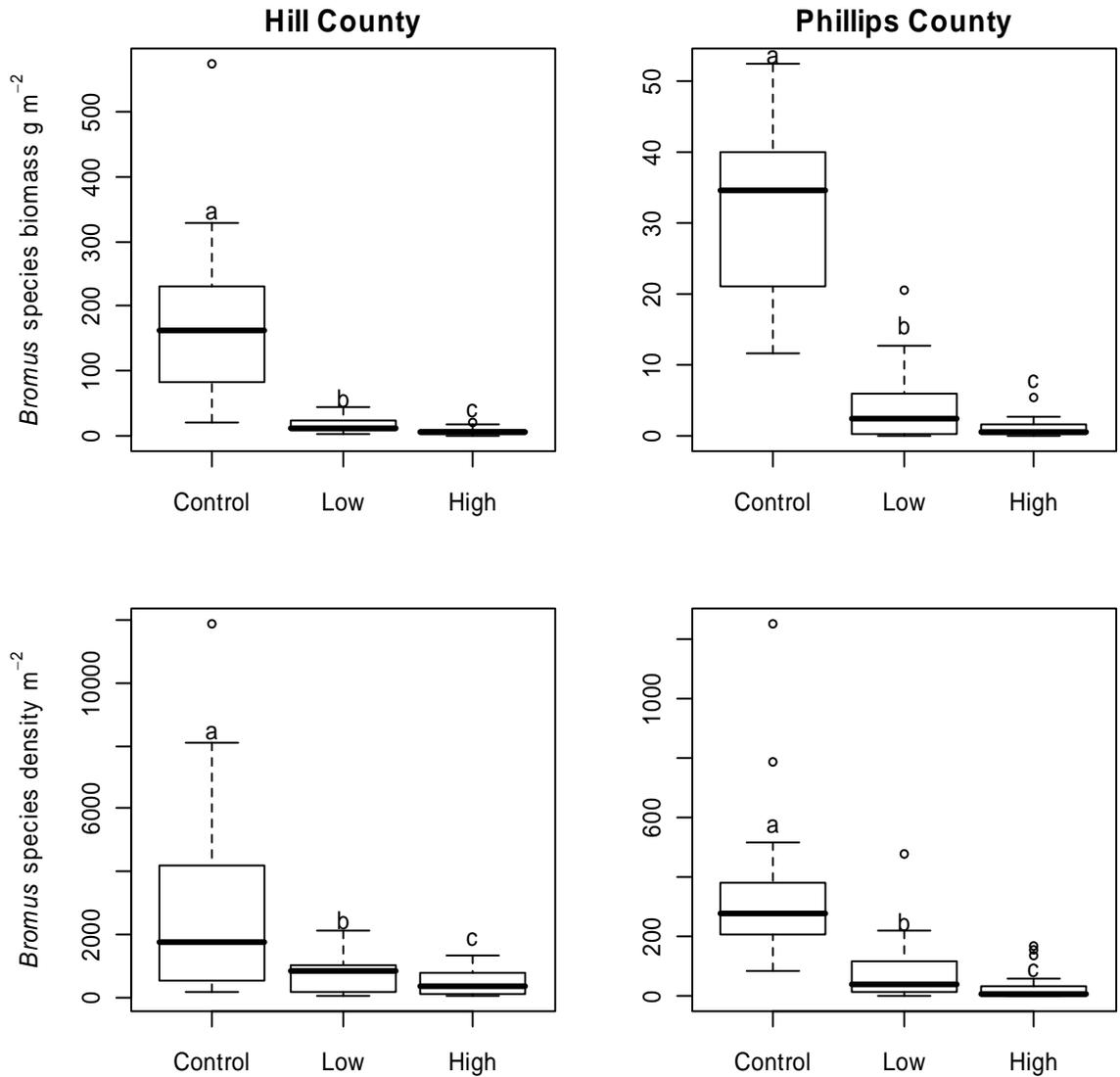
Figure 4. *Bromus tectorum* (Hill County) and *Bromus japonicus* (Phillips County) biomass m^{-2} and density m^{-2} responses to control (no herbicide), low (66 g imazapic ha^{-1} + 132 g glyphosate ha^{-1}), and high (105 g imazapic ha^{-1} + 211 g glyphosate ha^{-1}) rates. Letters separate treatment means that are significantly different according to Tukey's HSD post-hoc tests ($\alpha = 0.05$).

Hill County
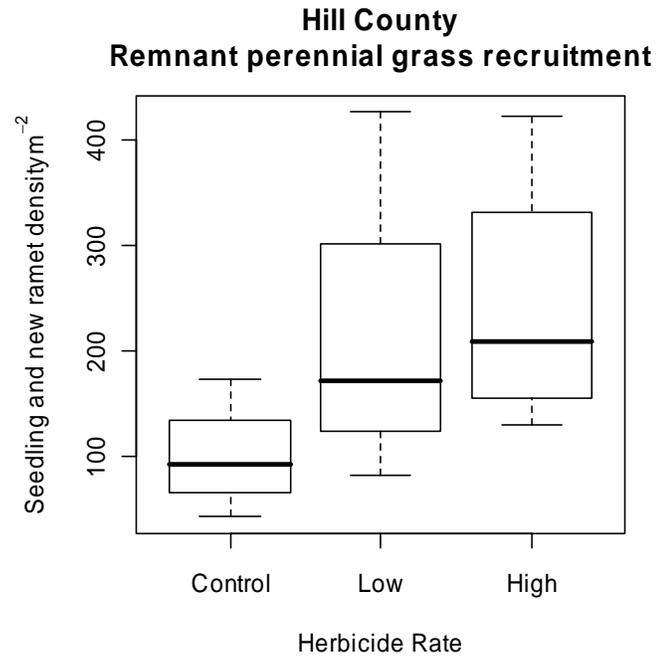**Remnant perennial grass recruitment**

Figure 5. Seedling + ramet density of remnant perennial grasses after treatment with control (no herbicide), low (66 g imazapic ha^{-1} + 132 g glyphosate ha^{-1}), and high (105 g imazapic ha^{-1} + 211 g glyphosate ha^{-1}). Seedling + ramet density did not differ by herbicide treatment (α = 0.05).

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