OPTIMIZING EFFICACY OF *BROMUS TECTORUM* (CHEATGRASS, DOWNY BROME) BIOLOGICAL CONTORL IN CROPS AND RANGELANDS

by

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ABSTRACT

Management of *Bromus tectorum* L., an annual grass invasive in western North America, has focused on single and integrated methods across crop and non-crop settings. Extensive literature does not exist on the integration of *Pyrenophora semeniperda,* a generalist grass pathogen for *B. tectorum* control, which has been used experimentally with some success to control *B. tectorum*. However, questions remain about (1) the risk of non-target effects on grassy species, (2) efficacy as part of an integrated management plan, and (3) efficacy under different environmental conditions and on different *B. tectorum* populations. I sought to answer these questions with three distinct studies. First, I assessed the risk of *P. semeniperda* on *B. tectorum* and 15 co-occurring grass species in a greenhouse setting. *Pyrenophora semeniperda* reduced *B. tectorum* density by 40% but also negatively affected density of 60% of the non-target species tested, particularly native rangeland grasses. Second, I integrated *P. semeniperda* as part of a two-year rangeland revegetation management plan that included an herbicide (imazapic), a fungicide seed treatment, and different perennial grass seeding rates. Application of *P. semeniperda* did not increase inoculum loads above ambient levels, and there was no effect of seeding rate or seed treatment on *B. tectorum* or seeded perennial grass density or biomass. However, *B. tectorum* density was reduced by 60% the first year with a single imazapic application. Lastly, I compared the effects of temperature (13°C, 17°C, 21°C, 25°C, 32°C) and *B. tectorum* populations (range, crop, sub-alpine) on infection and mortality rates caused by *P. semeniperda* using a temperature gradient table. Infection rates by *P. semeniperda* peaked at intermediate temperatures (17°C, 21°C, 25°C) for range and sub-alpine populations, but were generally low and not as influenced by temperature in the crop population. Overall, *B. tectorum* control with *P. semeniperda* is possible, provided (1) non-target effects are considered, especially for range species, (2) research is conducted to increase *P. semeniperda* inoculum loads above ambient levels and revegetation is used with other control tactics, and (3) we take into account how distinct *B. tectorum* populations respond to *P. semeniperda*.

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CHAPTER ONE

PROJECT BACKGROUND, THEORETICAL FRAMEWORK, PROJECT SIGNIFICANCE, AND OBJECTIVES

Project Background

Plant invasions have far-reaching consequences that affect humans and ecological systems (Vitousek et al. 1997). The simple addition of one species can change the interactions that govern a system's composition and dynamics, altering key functions such as primary productivity, nutrient and hydrologic cycling, and decomposition (Vitousek and Walker 1989). Invasive plants become a major component in the invaded community (Callaway and Maron 2006), potentially displacing native species and decreasing biodiversity (Heywood 1989). Consequently, millions of dollars are lost every year in the form of reduced crop, rangeland, and forestry yields, reduction in the provision of ecosystem services, and costs associated with prevention and control efforts (Tilman et al. 2012, Vitousek et al. 1997). These efforts focus on restoring invaded communities and thereby, improve biodiversity and ecosystem production, which is becoming vital because of Earth's expanding population and increasing demand on ecosystem services (Cardinale et al. 2012).

Bromus tectorum L. (cheatgrass, downy brome), an annual grass native to Eurasia, currently infests millions of hectares of cropping, forage, and rangeland systems in western North America (Mack 1981, Rice 2005). Its impacts include decreased native plant diversity (Humphrey and Schupp 2001), altered fire regimes (Epanchin-Niell et al.

2009), economic losses through control costs, and decreased forage (Ganskopp and Bohnert 2001) and crop (Zimdahl 2004) quality and yields. The success of *B. tectorum* in western North America is believed to result from propagule pressure and abiotic and biotic characteristics. Specifically, *B. tectorum* dominance is attributed to its prolific seed production and widespread seed dispersal, often by anthropogenic factors, and life cycle. An individual *B. tectorum* plant is capable of producing up to 6,000 seeds (Young and Evans 1978), creating seedbank densities that may reach up to 19,000 seeds m^{-2} (Hempy-Mayer and Pyke 2008, Humphrey and Schupp 2001), depending on precipitation (Smith et al. 2008). While *B. tectorum* invasion in the Great Basin was partly due to overgrazing in the late 1800s that led to substantial range deterioration into the early 1900s (Pickford 1932, Vale 1974), this species also seized an unoccupied niche because of the lack of native annual grasses (Knapp 1996). Moreover, *B. tectorum* is typically a winter annual that germinates in fall but can behave as a summer annual that germinates in spring (Espeland et al. 2016). This prolonged germination period is due to secondary dormancy (Harmon et al. 2012) brought on by abiotic conditions such as temperature and precipitation. Seeds entering secondary dormancy during the winter add to the carryover spring seedbank (Young and Evans 1975, Young et al. 1969).

Management of *B. tectorum* has focused on tools such as herbicides (Mangold et al. 2013, Morris et al. 2009, Rinella et al. 2010, Whitson and Koch 1998), prescribed grazing (Murray et al. 1978, Rice 2005, Schmelzer et al. 2014), revegetation (Cox and Anderson 2004, Davies et al. 2010, Orloff et al. 2015), and to a lesser degree biological control (Beckstead et al. 2010, Ehlert et al. 2014, Meyer et al. 2007). While success has been demonstrated with all of these tools, my research focuses on manipulating ecological processes through the management strategies of herbicides, revegetation, and biological control. Specifically, I investigated the impact of the herbicide imazapic, a biological control pathogen, *Pyrenophora semeniperda*, as well as the seeding of native perennial species on the management of *B. tectorum*. While these management strategies have been investigated previously, they have not been considered in the context of potential drivers of invasion, for example propagule pressure, abiotic characteristics, and biotic characteristics.

Catford et al. (2009) proposed that these drivers of invasion (i.e. propagule pressure, abiotic characteristics, and biotic characteristics) could serve as a unifying theoretical framework, the "PAB framework," for multiple invasion theories. Overall, Catford et al.'s (2009) theory rests on the idea that focusing on PAB provides a top-down approach to organizing research questions about factors leading to plant invasions. First, influential factors (propagule pressure, abiotic characteristics, biotic characteristics) are identified, and then causal mechanisms such as dispersal and competition help narrow the focus of a multidimensional approach to the invasion process. My research utilizes *B. tectorum* as a model organism for contextualizing the PAB framework (Catford et al. 2009) within a management realm.

Theoretical Framework:
Drivers of Invasion and Mediating Ecological Processes

Integrated weed management (IWM) strategies focus on using a mix of physical, biological, and chemical control methodologies (Norris 2011) that ideally ameliorate or limit the impact of invasive plants on our ecosystems, and thus, the ecosystem services they provide, by utilizing an ecological approach to weed control in the context of an entire system (Buhler 1996, Wyse 1992). Moreover, this idea is further expanded upon by the concept of "many little hammers," which explains that integrating several control tactics that by themselves have marginal control, may cumulatively amount to substantial control (Liebman and Gallandt 1997). This is advantageous because a single "hammer" or control method is often ineffective in achieving sustainable control (DiTomaso 2000, Sheley and Krueger-Mangold 2003), can result in unintended consequences such as herbicide resistance or soil erosion, (Heap 2017, Wysocka-Czubaszek and Czubaszek 2014), and can cause shifts from dominance of one weed to another (Buhler et al. 1997, Holt 1994, Pearson et al. 2016). Successful IWM focuses on the ecological processes that mediate plant community dynamics (Hobbs and Humphries 1995). My research was framed within the context of three drivers of invasion, which are mediated by ecological processes that, in turn, I manipulated through cultural (e.g. seeding, seedbed preparation, species selection and performance), chemical (e.g. herbicides), and biological IWM strategies (James et al. 2010, Krueger-Mangold et al. 2010, Sheley et al. 2010) (Figure 1.1). Below, I outline each of these drivers of invasion, as well as the ecological processes that mediate them. Finally, I discuss which management strategies I used to manipulate the associated ecological processes.

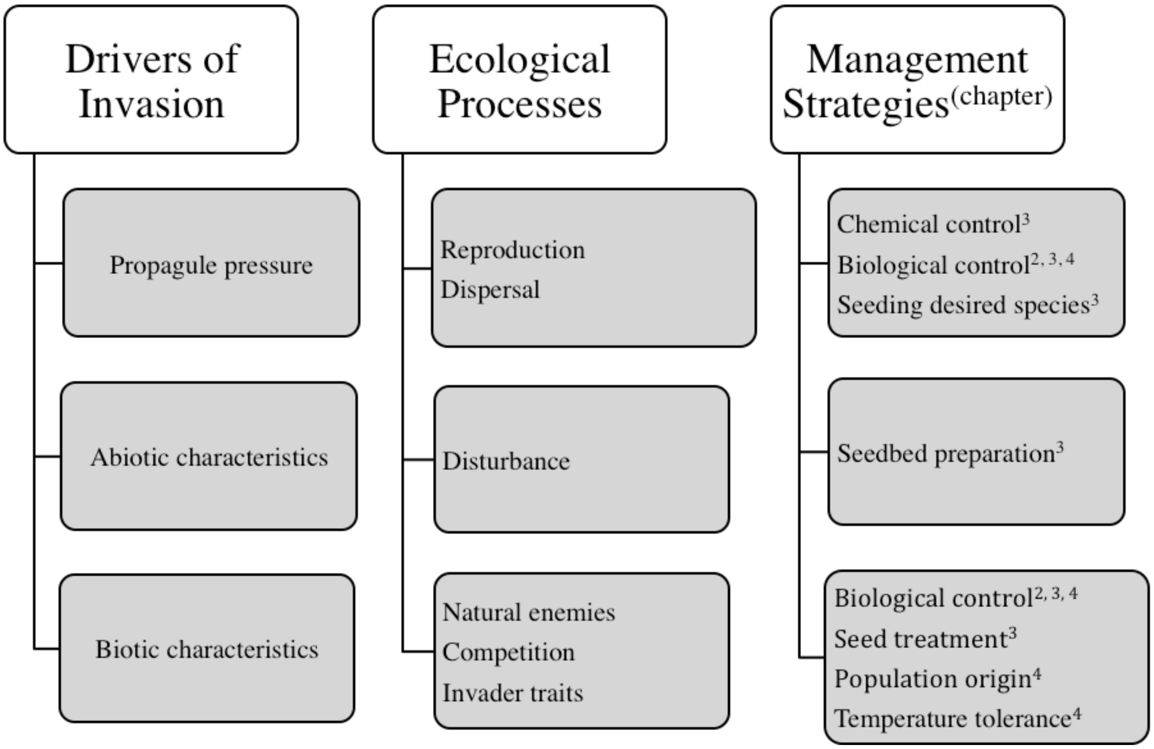

Figure 1.1. The theoretical framework of my research is based on three drivers of invasion (Catford et al. 2009). These are mediated by ecological processes that can be manipulated through management strategies. Superscript numbers on the management strategies correspond to my dissertation chapters:
2. Impacts of *Pyrenophora semeniperda* on non-target, economically important grassy species: implications for biological control of *Bromus tectorum* L. (cheatgrass, downy brome).
3. Impact of native species seeding, herbicides, and fungicides in perennial grass establishment in *Bromus tectorum* L. (cheatgrass, downy brome) infested habitats
4. Role of temperature on efficacy of *Pyrenophora semeniperda* as a biological control agent of three distinct, locally-adapted populations of *Bromus tectorum* L. (cheatgrass, downy brome).
Management strategies are discussed in the context of each experiment in the appropriate chapter.

Propagule Pressure

Propagule pressure in invasion ecology is most often thought of as the number of individuals introduced in a single event ("propagule size," Simberloff 2009) multiplied by the number of introductions ("propagule number," Simberloff 2009) (Eppstein and Molofsky 2007). It has been cited as playing a determinant role in invasion success (Crawley et al. 1996, Colautti et al. 2006, Lockwood et al. 2005, Simberloff 2009). Specifically, Colautti et al. (2006) posit that invasion success or failure is attributed to the amount of propagule pressure. This is because propagule pressure has been found to be a predictor of both invasiveness (the ability of species to establish in, spread to, or become abundant in novel communities) and invasibility (the susceptibility of habitats to the establishment or proliferation of invaders) (Colautti et al. 2006).

There are several ecological processes that mediate propagule pressure (Catford et al. 2009) including the number of propagules and frequency of each introduction, as well as propagule characteristics. Reproduction and dispersal are the ecological processes that I manipulated in the context of my research. Therefore, I discuss each in turn below, followed by a description of the management strategies I tested within the *B. tectorum* model system.

Reproduction

Fecundity, the time it takes for an individual to become a reproductive adult, and fertility, the number of offspring per female, is correlated with invasiveness (Baker and Stebbins 1965, Elton 1958, Sutherland 2004). Thus, many invasive plant species produce a large number of seeds or have a reserve of seeds in the seedbank (Crawley et al. 1996). In addition, repeated introductions from different source populations results in high genotypic and phenotypic plasticity (Baker and Stebbins 1965, Elton 1958), avoiding a genetic bottleneck that may occur if only a few individuals initiate an invasion (Simberloff 2009).

The type of reproduction, sexual (i.e. seed production) or asexual (i.e. vegetative), that a species exhibits influences its invasiveness and governs its evolutionary response to environmental change (Barrett 2011). Sexual reproduction results in genetic recombination and gene flow among different populations, which assists the invader in the process of evolving to local adaptation (Barrett 2011, Garcia-Ramos and Rodriquez 2002, Kaltz and Bell 2005). Moreover, sexual reproduction has been associated with a higher projected population growth rate for invasive species compared to their noninvasive closely related-species (Burns et al. 2013). Specifically, sexually reproducing species with life history strategies that allocate to fecundity either by already having higher fecundity or by responding to pulses of resource availability are more likely to become invasive (Burns 2008, Davidson et al. 2011, Van Kleunen 2010).

Bromus tectorum. As an annual, *B. tectorum* has prolific seed production with individual plants capable of producing up to 6,000 seeds (Young and Evans 1978), and 4,800 to 19,000 seeds m^{-2} can be found in unburned *B. tectorum*-dominated communities within the Great Basin (Hempy-Mayer and Pyke 2008, Humphrey and Schupp 2001). *Bromus tectorum* seed production depends on precipitation patterns, with above-normal precipitation resulting in higher seed rain (approximately 14,000 seeds m^{-2}), relative to drought conditions (approximately 3,500 seeds m^{-2}) (Smith et al. 2008). The likelihood of these seeds establishing is increased by *B. tectorum*'s genotypic variation and high phenotypic plasticity that occur when it cross-pollinates (Ashley and Longland 2007).

Thus, *B. tectorum* can create novel genetic recombinants that have hybrid vigor that confers advantage over natives within the highly variable environments where it invades (Ashley and Longland 2007, Mack and Pyke 1983).

Management strategies. Because *B. tectorum* reproduces via seed, controlling seed production in rangelands is critical to its management. Current management strategies in rangeland and natural areas focus on chemical control and revegetation efforts. However, chemical control options on rangelands are limited and research indicates that herbicide efficacy is inconsistent (Mangold et al. 2013). Chemical control is also problematic because few herbicides selectively control annual grasses like *B. tectorum* without negatively affecting surrounding grasses. Further, long-term control with chemicals is often difficult to achieve because of *B. tectorum*'s large seedbank and prolonged emergence period that can last from fall of one year to spring of the next. Other rangeland and natural area control methods are grazing (Klemmedson and Smith 1964, Murray et al. 1978, Rice 2005), prescribed fire (DiTomaso et al. 2010), and revegetation (Cox and Anderson 2004, Davies e al. 2010). Yet, these methods are often ineffective unless integrated with one another or chemical methods (Davies 2010, Calo et al. 2012, DiTomaso et al. 2010).

I utilized imazapic, a member of the imidazolinone herbicide family (Davison and Smith 2007, Elseroad and Rudd 2011, Morris et al. 2009) to control *B. tectorum* seed production, in addition to a biological control fungal pathogen, *Pyrenophora semeniperda* (see "Dispersal," page 10). Imazapic is an ALS inhibitor that is absorbed through leaves, stems, and roots (Peterson et al. 2010). Imazapic efficacy has been evaluated across the western U.S. with variable results. For example, in Oregon imazapic reduced *B. tectorum* frequency to zero without affecting native species abundance in semiarid grassland and shrub-steppe (Elseroad and Rudd 2011), and in Nevada *B. tectorum* biomass decreased by more than 50% with imazapic application relative to a non-sprayed control after two growing seasons (Davison and Smith 2007). In Montana imazapic efficacy has achieved 20% to above 90% control, depending on application timing (Mangold et al. 2013).

Efficacy of imazapic usually depends on a tradeoff between *B. tectorum* control and injury to desired perennial species, which is often site-dependent. For example, Morris et al. (2009) assessed variable rates of imazapic and seeding of five perennial species [two sources each of Siberian wheatgrass (*Agropyron fragile*), prostrate kochia (*Bassia prostrata*), and Russian wildrye (*Psathyrostachys juncea*)] and observed increased plant establishment with increasing imazapic rates up to 105 g ai ha^{-1} at one site, while establishment declined at rates above 35 g ai ha^{-1} at a second site. Efficacy was related to site differences such as precipitation, soil organic matter, and disturbance history (Morris et al. 2009). Similarly, Shinn and Thill (2004) reported imazapic rates that reduced *B. tectorum* abundance (140 g ai ha^{-1}) also severely injured perennial forage grasses [big bluegrass (*Poa juncifolia*), smooth brome (*Bromus inermis*), meadow brome (*B. biebersteinii*), sheep fescue (*Festuca ovina*), hard fescue (*Festuca brevipila*), orchardgrass (*Dactylis glomerata*), crested wheatgrass (*Agropyron cristatum*), western wheatgrass (*Pascopyrum smithii*), intermediate wheatgrass (*Thinopyrum intermedium*), and bluebunch wheatgrass (*Pseudoroegneria spicata*)].

Dispersal

Spatial dispersal of propagules is a function of several factors such as plant height, number of seeds, mechanism of dispersal, and activity of dispersing agents (Harper 1977). In general, distribution of seeds from the parent plant follows a normal distribution, with a large number of seeds dispersing a short distance from the parent plant, while few seeds disperse over longer distances (Neubert and Caswell 2000). Further, research has demonstrated a negative relationship between seed mass and dispersal, with small seeds better adapted for long distance seed dispersal (Cadotte and Lovett-Doust 2002, Rejmanek and Richardson 1996). Seeds are dispersed spatially via wind, water, animals, and humans (Radosevich et al. 2007). The likelihood of being dispersed via one of these vectors can be aided by fleshy fruit, seed appendages and modifications such as plumes, hooks, and barbs (Radosevich et al. 2007).

Temporal dispersal is a function of seedbank abundance and seed dormancy (Radosevich et al. 2007). This is particularly important for annual plants because seeds are the only link between generations. Consequently, annual plants rely on a seedbank that acts as a storehouse where seed deposits are made via seed rain from production and dispersal, while seed withdrawals occur through germination, senescence, death, and predation (Harper 1977). For species that exhibit dormancy, the majority of seeds within a seedbank is dormant at maturity and passes through conditional dormancy when environmental conditions promote after-ripening (Baskin and Baskin 1998). Within a species, seeds become non-dormant as after-ripening continues and can germinate over a wide range of environmental conditions; however, if conditions are unfavorable, seeds enter secondary dormancy and rely on a more narrow range of conditions to induce germination (Baskin and Baskin 1998).

Bromus tectorum. Seeds of *B. tectorum* have barbed awns that allow spatial dispersal via wind, animals, and humans. While spatial dispersal is important (Johnston 2011), *B. tectorum* relies heavily on temporal dispersal in the form of its seedbank and associated dormancy. *Bromus tectorum* seeds generally germinate quickly in the fall once they lose dormancy (Allen and Meyer 2002, Roundy et al. 2007). However, if there is insufficient fall precipitation, seeds enter secondary dormancy and overwinter, thereby adding to the carryover seedbank (Evans and Young 1975, Young et al. 1969). Although these seeds rarely persist beyond the second carryover year (Smith et al. 2008), there can be a sufficient proportion of seeds remaining the first carryover year to emerge in subsequent years.

Unlike *B. tectorum,* perennial grass species do not invest in reproduction and dispersal until survival requirements such as growth, storage, and defense have been met (Crawley 1997). Consequently, the dispersal of perennial species onto sites where they do not occur, including *B. tectorum* invaded systems, is limited (Marlette and Anderson 1986). Research has focused on seeding competitive native and introduced perennial species into *B. tectorum*-infested lands (Cox and Anderson 2004, Davies et al. 2010, Hull and Stewart 1948). Selecting desirable species adapted to the site's soil, elevation, climate, precipitation, and fire regimes improves the probability of successful establishment (DiTomaso 2000, Epanchin-Niell et al. 2009, Jacobs et al. 1998), and seeding may be the best option for long-term, sustainable management of *B. tectorum* invasions (DiTomaso 2000). For example, one model parameterized for the Wyoming big sagebrush community predicted that if revegetation was not implemented, 72% of the landscape would be covered by a *B. tectorum* monoculture after 50 years (Epanchin-Niell et al. 2009).

<u>Management strategies</u>. I utilized the biological control fungal pathogen *Pyrenophora semeniperda* to reduce the temporal dispersal of *B. tectorum*. *Pyrenophora semeniperda* begins its life as conidia in the soil that are carried by germ tubes to grass inflorescences where they infect the developing ovary during anthesis (Campbell and Medd 2003, Medd et al. 2003). The fungus consumes starch resources within the ovary, resulting in seed mortality or reduced seedling vigor, thereby negatively impacting *B. tectorum*'s seedbank. Infected mature host grass seeds disperse to the ground where *P. semeniperda* remains as mycelium for the rest of summer. Stromata develop from the mycelium, protrude from infected seeds as black finger-like appendages, and produce more conidia to further the infection cycle.

In addition, I directly influenced the dispersal of desired species through seeding perennial grasses into *B. tectorum* infestations. Severely deteriorated rangelands that have been dominated by *B. tectorum* for a long time are associated with a loss of desired perennial species' seed bank and recruitment (Humphrey and Schupp 2001, Masters and Sheley 2001). Successful management of *B. tectorum* has sometimes resulted in an increase in desired perennial species (Davies and Sheley 2011, Elseroad and Rudd 2011), but more often than not niches opened by control efforts are filled by seeds of *B. tectorum* or another undesirable species present in the propagule pool

(Connell and Slatyer 1977, Egler 1954, Svejcar et al. 2014, Pearson et al. 2016). Consequently, attention has focused on increasing propagule pressure of desired species through seeding. If successful, this management strategy diminishes *B. tectorum*'s abundance while simultaneously improving ecosystem function, niche occupation, and desired species competitiveness, establishment and growth (DiTomaso et al. 2010, Masters and Sheley 2001, Tilman 1997).

Abiotic Characteristics

Invasion depends on not only propagule pressure, but also abiotic parameters that govern whether a site's environmental conditions are hospitable to a given species. Abiotic characteristics include geographical location with respect to dispersal routes, conditions such as temperature and rainfall, resource availability, and disturbances (Catford et al. 2009). Of these, I manipulated disturbance, e.g. an event that affects the survivorship of individuals directly (Hobbs et al. 1992).

Disturbance

Resource fluctuations and changes in the physical environment (Davis and Pelsor 2001, Elton 1958, Hobbs et al. 1992, Rejmanek and Richardson 1996) are brought about by disturbance. Fire, floods, herbivory, and anthropogenic disturbances like urbanization and the use of herbicides, plowing, and seedbed preparation are all forms of disturbance (Gerhardt and Collinge 2003, Lockwood et al. 2007). These often result in species mortality, thereby increasing available space and resources (Catford et al. 2009, Davis et al. 2000), as well as reduced competition (Crawley et al. 1999). Thus, disturbance is an important component of ecosystems and can affect ecosystem and community structure and function (Hobbs and Huenneke 1992, Huston 2004), depending on the frequency and intensity of disturbance.

Naturally occurring disturbances can result in open niches that invasive, weedy species can occupy (Hobbs and Huenneke 1992, DiTomaso et al. 2000); at the same time, disturbance associated with weed management efforts (i.e. herbicides, seedbed preparation) also occurs in invaded rangelands. Ecological theory (Connell 1978) as well as empirical evidence (Hobbs and Huenneke 1992) suggests that moderate or intermediate frequency and intensity of disturbance results in maximum species richness. Thus, from a management perspective, the frequency and intensity of disturbance needs to be considered to effectively restore desired species to lands currently infested by *B. tectorum*.

<u>Bromus tectorum</u>. Disturbance is closely tied to *Bromus tectorum*'s spread. Specifically, rangelands were overgrazed in the late 1800s, heavy plowing practices were implemented, and homesteads were abandoned during the Great Depression (Pickford 1932, Rickard and Cline 1980). The result of these factors was disturbed sites suitable for *B. tectorum* invasion, easily invaded because of a lack of perennial species suited to compete against *B. tectorum*. Fire has also been identified as a disturbance that favors *B. tectorum* (Davies and Nafus 2013, Monty et al. 2012, Taylor et al. 2014). It has been suggested that *B. tectorum* is more tolerant to frequent disturbances compared to native plants (D' Antonio and Vitousek 1992). Consequently, applying integrated weed management to lands infested by *B. tectorum* should focus on reducing the intensity and

frequency of disturbance to suppress *B. tectorum* and favor desired species (DiTomaso et al. 2010).

Management strategies. I employed two management strategies to shift the disturbance regime in favor of desired perennial species: use of an herbicide (imazapic) and seedbed preparation prior to perennial grass seeding. Imazapic controls *B. tectorum* (see "Propagule Pressure: Reproduction: Management Strategies," page 8) thus opening niches suitable for perennial grass seeds. To ensure the highest probability of successful grass establishment, an ideal seedbed should have adequate seed-soil contact but soil loose enough to allow the coleoptile to emerge and the radicle to penetrate the soil (Goodwin et al. 2006). Consequently, light raking followed by simulated drill seeding was used to provide safe sites, areas suitable for germination and growth (Goodwin et al. 2006), for perennial seeds.

Biotic Characteristics

Biotic characteristics are the final driver of invasion and encompass community interactions and internal dynamics of invader traits (Catford et al. 2009). Interactions with other plant species or natural enemies can be either gained or lost upon an invader's entry into its introduced range and thereby influence invasion success and impact (Joshi and Vrieling 2005, Lau 2008, Mitchell et al. 2006, Ricciardi and Atkinson 2004). These interactions are mediated by invader traits and may include mutualism, commensalism, competition, and antagonism with natural enemies (Catford et al. 2009). For my research, I focused on invader traits, competition, and the negative impact of a natural enemy on its host.

Invader Traits

Extensive research has been conducted on traits that enable invaders to succeed (Blumenthal 2005, Funk et al. 2008, Pysek and Richarson 2007, Seastedt 2009, Sutherland 2004), such as their life history, stress tolerance, and seed weight. Life history constitutes the phenological, physiological, and behavioral traits (Radosevich et al. 2007) and thus can contribute to a species' invasiveness and placement along the successional trajectory (Connell and Slayter 1977). Invaders may take on characteristics of r or K-strategists, or a combination of both (MacArthur 1962), depending on where they are in the successional trajectory (Connell and Slatyer 1977). For example, early successional species (i.e. colonizers) are more r-strategists because they grow quickly, exploit less-crowded ecological niches, and allocate resources to reproduction and dispersal (MacArthur 1962). However, without disturbance, these species may be eliminated because they lack competitive structure (MacArthur 1962). In contrast, late successional species are more K-strategists (MacArthur 1962) that grow slowly, live longer, and allocate resources toward belowground growth instead of reproduction, making them tolerant to stressors such as drought and low-nutrients (MacArthur 1962). Most invasive plants are considered r-strategists (Bazzaz 1986, Radosevich et al. 1997), although some possess traits such as a long life span (greater than one year) that are associated with K-strategists (Radosevich et al. 1997).

Although not explicit in addressing r- vs K-selection, empirical research has investigated the correlation between life history and invasiveness. Davis (2005) developed a comparative study investigating smooth cordgrass (*Spartina alterniflora* Loisel.) from sites in an invasive population and sites in native populations and found higher reproductive output from individuals in the invasive population, thus suggesting those plants exhibited r-traits relative to the native population. Gerlach and Rice (2003) investigated life history traits of congeneric plant species and found that differences in invasiveness were attributed to life history correlates, such as fecundity. On a similar note, Sutherland (2004) compared ten life history traits for nearly 20,000 plants that occur in the U.S. and found that life span was the most significant life history trait for weeds. In particular, weeds were more likely to be annuals and biennials and less likely to be perennials compared to non-weeds (Sutherland 2004).

Life history is closely linked with stress tolerance, which is outlined by the competitive-stress tolerant-ruderal (C-S-R) theory (Grime 1979) and can further explain an invader's invasiveness and a system's invasibility. This theory posits three evolutionary strategies: competitors, stress tolerators, and ruderals, which exist along a continuum that indicates the relative intensity of competition, stress, and disturbance, respectively (Grime 1979). Competitors prosper in areas of low intensity stress and disturbance and out-compete other species, while stress tolerators persist because they have the ability to survive through demanding conditions like low nutrients and drought (Diamond 1975). Lastly, ruderals thrive under conditions of low stress and high disturbance, allocating their resources to seed production (Grime 1979). According to

Radosevich (1997), invaders possess characteristics that are associated with competitors and ruderals; for example, a small proportion of annual production devoted to seeds and annual flowering of established plants (associated with competitors) compared to a large proportion of annual production devoted to seeds and a high frequency of flowering (associated with ruderals).

The C-S-R theory (Grime 1979) has been empirically tested and used for classifying alien species accordingly. Specifically, Vicente et al. (2010) used C-S-R theory to investigate patterns and drivers of invasion at a regional scale. Likewise, Vicente et al. (2013) utilized C-S-R theory to classify species as competitors, stress tolerators, or ruderals, and used this information to explore the impact of invasive species on ecosystem services. In both instances, Vicente et al. (2010, 2013) found C-S-R theory to be a good indicator of species' invasiveness and impacts. Moreover, C-S-R scores (reflectance spectra) of peatland vegetation have been mapped with airborne imaging spectroscopy (Schmidtlein et al. 2012), demonstrating links between C-S-R strategies and visible traits. These studies underscore the ability of ecological theories such as C-S-R (Grime 1979) to transcend decades and be applied to modern day invasive plant ecology.

Propagule seed size or weight is another species’ trait associated with invasiveness (Pysek and Richardson 2007), although generalizations are somewhat ambiguous (Pysek and Richardson 2007). Lightweight seeds have been positively correlated with invasion success (Hamilton et al. 2005). Specifically, lightweight seeds are advantageous because they are easily dispersed by wind, persist longer in the soil compared to heavy, larger seeds (Thompson et al. 1993), and are correlated with increased seed output (Henry and Westoby 2001). However, seed weight is also a valid measure of seed vigor (Pepper 2002, Singn and Bai 1988) and is inversely correlated with susceptibility to phytotoxins (Liebman and Sundberg 2006) and pathogens (Crist and Freise 1993). Thus, species with lightweight seeds are less stress tolerant to phytotoxins and pathogens than heavier seeds. In general, heavier seeds have higher germination and emergence and can produce larger and more vigorous seedlings (Black 1956, Harper and Obeid 1967, Schaal 1980).

Bromus tectorum. As previously stated, *B. tectorum* generally behaves as a winter annual (Page 2). Further, it has characteristics associated with r-strategists (MacArthur 1962) and competitive ruderals (Grime 1979, Radosevich et al. 1997). Specifically, Mangla et al. (2011) studied *B. tectorum* in a competition experiment and found an increase in competition as nitrogen availability increased, supporting the C-S-R theory (Grime 1979) that competition intensifies in resource-rich environments compared to resource poor environments. *Bromus tectorum* dominates many areas of western North America because of disturbances such as overgrazed rangelands, plowing for cultivation, and wildfires (Bradford and Lauenroth 2006, Melgoza and Nowak 1991, Knapp 1996). After such disturbances, niches were left open for *B. tectorum* to invade, which was fairly easy because of its prolific seed production (see "Reproduction," page 6), ease of dispersal due to barbed awns (see "Dispersal," page 10), and competitive abilities (see "Competition," page 21). Although propagule seed weight is associated with invasiveness, no research has been conducted that directly identifies seed weight - either of *B. tectorum* or desired species - as being a predictor of successful germination.

Management strategies. Research to date has not investigated whether intraspecific variation in seed weight or genetic differences in populations influence susceptibility to the grass pathogen and potential biological control agent *P. semeniperda*. Thus, I collected seeds from three locally adapted *B. tectorum* populations in order to test if intraspecific genetic variation in seed weight affects susceptibility to *P. semeniperda* (Crawley 1997). Further, *B. tectorum* populations exhibit high phenotypic plasticity (Mack 1981), which plays a significant role in its invasive success (Anderson 1996, Mack and Pyke 1983). Specifically, *B. tectorum* has been found along elevational gradients, which suggests phenotypic plasticity due to environmental differences (Allen and Meyer 2002, Brown and Rowe 2004, McCarlie et al. 2003, Meyer et al. 1997). Thus, *B. tectorum* traits such as germination, growth rates (McCarlie et al. 2003), and seed production (Rice and Mack 1991b, c) differ either due to environmental differences, genetic variation, or interactions between the two.

Consequently, I also investigated the effect of temperature on *P. semeniperda* infection of the three distinct *B. tectorum* populations. Infection may vary because of phenotypic differences among the populations or because efficacy of *P. semeniperda* shifts depending on temperature. Specifically, Brown and Rowe (2004) investigated *B. tectorum* seed dormancy and germination response along an elevational gradient in Colorado, and their results revealed differences among populations and local adaptation, the evolved difference in populations due to selective pressures from their local environment. Further, laboratory research has found an optimal temperature for *P. semeniperda* growth to be 23°C (Campbell et al. 1996, 2003), but the temperature at which *P. semeniperda* loses efficacy has not been reported. Finally, research has found that *B. tectorum* germination can occur at temperatures just above freezing (5°C) (Evans and Young 1972), but is inhibited above 30°C (Harris and Gobel 1976). Thus, there may be an ideal temperature at which *B. tectorum* is stressed enough to forfeit germination and become susceptible to *P. semeniperda*, which could predict what sites and conditions *P. semeniperda* may be suited for based on soil temperatures.

Competition

Community composition plays a role in regulating invasion (Levine 2000, Seabloom et al. 2003). Specifically, a system's invasibility can be reduced by interspecific competition from the surrounding plant community (Burke and Grime 1996, Catford et al. 2009, Emery and Gross 2006). Interspecific competition occurs when an increase in the population density or biomass of a single species results in a decrease in the population growth rate and density or biomass of another species (Tilman 1997). Moreover, competition regularly occurs over resources such as light, water, and nutrients. Specifically, Davis et al. (2000) posit that communities are invasible if there is a lack of competition for resources from resident species, and that an increase in resource availability can occur if the resident species' use declines or the resource supply increases faster than the resident vegetation is able to utilize it. Thus, systems are less invasible if species' niches, as they relate to resource availability, do not overlap and instead, species with similar niches are partially incompatible (Daleo et al. 2009) conferring biotic resistance.

Competition manifests itself as biotic resistance to invasion (Elton 1958, Levine et al. 2004) when competitors, herbivores, and pathogens in the introduced range limit the colonization, naturalization, and persistence of the invader (Alpert 2006, Levine et al. 2004, Parker and Hay 2005), because the invader is ill equipped to compete or lacks defenses to protect itself (Catford et al. 2009). A meta-analysis review (Levine et al. 2004) found that biotic resistance reduced the establishment of individual invaders and constrained invasive species' abundance once they successfully established. In severely degraded plant communities, biotic resistance can be increased through the seeding of desired species (Funk et al. 2008), which will fill empty niches and increase competition (Shea and Chesson 2002).

Bromus tectorum. Competitive traits allow *B. tectorum* to outperform natives, in addition to its life history characteristics of having prolific seed production and a carryover seedbank (see "Invader traits," page 16). Under a wide range of available nitrogen environments, *B. tectorum* produces more biomass, tillers, and root length per unit nitrogen relative to native seedlings (Vasquez et al. 2008). Further, *B. tectorum* also efficiently utilizes water relative to native plants (Pellant 1996) and has greater root length relative to perennial grass species like bluebunch wheatgrass (*Pseudoroegneria spicata*), bottlebrush squirreltail (*Elymus elymoides*), and crested wheatgrass (*Agropyrum desertorum*) under varying soil nitrogen levels (James 2008). Thus, *B. tectorum* effectively uses soil moisture and nutrients, making them less available to neighboring native plants (Chambers et al. 2007, Harris 1967, Sperry et al. 2006, Stewart and Hull 1949).

Competition from desired species has been associated with resistance to *B. tectorum* invasion and has been studied extensively (Allen and Meyer et al. 2014, Beckstead and Augspurger 2004, Chambers et al. 2007, Mangla et al. 2011, McGlone et al. 2011, Orloff et al. 2013). Despite these studies, only Mazzola et al. (2011) manipulated native species seeding rates in a factorial combination with *B. tectorum* densities. High native species seeding rate (600 seeds m^{-2}) resulted in the highest number of native seedlings when *B. tectorum* density was low (150 seeds m^{-2}) and the lowest number of native seedlings when *B. tectorum* density was high (1200 seeds m^{-2}) (Mazzola et al. 2011). This demonstrates the potential for successful desired species establishment, but only in the context of reduced *B. tectorum* populations and increased number of desired species propagules.

Establishing desired perennial grasses in *B. tectorum*-infested systems may fail because of biotic factors that affect seedling recruitment (Svejcar et al. 2014). For example, soil pathogens are ubiquitous within the soil and can have saprophytic or pathogenic effects on desired species' seeds (Christensen 1989), thereby reducing their survival (Crist and Friese 1993, Dalling et al. 1998, O'Hanlon-Manners and Kotanen 2004). *Pyrenophora semeniperda* has demonstrated non-target effects on native grasses that co-occur with *B. tectorum* (Beckstead et al. 2010, Mordecai 2013a, b). If *P. semeniperda* is developed as a biological control agent for *B. tectorum,* research is needed to evaluate if its non-target effects on desired species can be mitigated. Seed treatments such as fungicides have been suggested to improve desired species establishment in weed-infested rangelands (Jacobs et al. 1998), and they could protect seeded grasses from *P. semeniperda* mortality. While fungicides have successfully increased tree sapling survival in forests (Dalling et al. 1998, O'Hanlon-Manners and Kotanen 2004), to my knowledge no such research has been reported concerning native grass establishment in rangelands of the western North America.

Management strategies. *Bromus tectorum* control methods are often integrated with seeding of desired species when rangeland is so severely degraded that few desirable species are present (DiTomaso et al. 2010; see "Dispersal," page 10). Thus, I directly manipulated interspecific competition between *B. tectorum* and the surrounding plant community in three ways. First, I reduced *B. tectorum* with imazapic (see "Reproduction," page 6), which in turn reduced competition for space and resources like water and soil nutrients. Second, I increased biotic resistance of the remaining plant community by seeding perennial grasses (see "Dispersal," page 10). Finally, I utilized a fungicide seed treatment to protect the seeded perennial grasses from *P. semeniperda* and other soil pathogens.

Natural Enemies

The enemy release hypothesis (ERH) states that an invader's success in its introduced range could be attributed to the lack of natural enemies (e.g. pathogens, insects, herbivores) that once regulated the invader's population in its native range (Elton 1958, Keane and Crawley 2002). Empirical research of introduced plant populations demonstrates support for the ERH. Specifically, introduced populations are exposed to fewer species of insect herbivores and pathogens (Hinz and Schwarzlaender 2004, Torchin and Mitchell 2004) and thus feel fewer or less negative effects on growth and fitness in the introduced range (DeWalt et al. 2004, Reinhart and Callaway 2004, Torchin and Mitchell 2004, Wolfe et al. 2005) compared to conspecific native populations.

Invasive plants are more completely released from specialist than generalist enemies (Andow and Imura 1994, Hinz and Schwarzlaender 2004, Knevel et al. 2004, Torchin and Mitchell 2004, Van der Putten et al. 2005), resulting in increased susceptibility to generalist pathogens and increased risk of pathogen accumulation. Specifically, pathogen accumulation is positively correlated with time since introduction (Hawkes 2007), geographical range of the invader (Clay 1995, Strong and Levin 1975), and diversity of invaded habitats (Mitchell et al. 2010). The longer an invader is present in its introduced range, the higher the likelihood that a natural enemy will be introduced from its native range (Hawkes 2007). Further, highly dense stands of invaders increase the probability of encountering inoculum and promote the spread of disease because of shorter distances between hosts (Garrett and Mundt 1999). Dense stands can also modify pathogen transmission by changing environmental conditions like temperature and humidity (Alexander 2010, Burdon and Chilvers 1982) to favor the natural enemy.

There are three possible outcomes of pathogen accumulation (Flory and Clay 2013). First, pathogen accumulation can decrease invader density and the extent of invasions, allowing resident species to recover (Flory and Clay 2013). Second, the invader can act as a pathogen reservoir and increase disease on co-occurring native hosts, rendering them unable to compete (Colautti et al. 2004). Lastly, an invader may not feel any effects of pathogen accumulation if it possesses tolerance or compensatory traits, or phenotypic plasticity (Alexander 2010, Flory and Clay 2013, Gilbert and Parker 2006).

Bromus tectorum. Three pathogens and one bacterium that target different stages of *B. tectorum*'s life history are the focus of current biological control research (Ehlert et al. 2014, Kennedy et al. 2001, Meyer et al. 2008a). First, *Ustilago bullata,* a head smut pathogen with high host-specificity is endemic in nearly every *B. tectorum* population and is easily grown in culture (Meyer et al. 2008a). However, major differences exist in *U. bullata* susceptibility among *B. tectorum* genotypes because of resistance polymorphism among and within *B. tectorum* populations (Meyer et al. 2001). Second, *Tilletia fusca* is a host specific chestnut bunt that infects seedlings and can persist long term because of a soil spore bank (Meyer et al. 2008a). However, *Tilletia fusca* is most likely effective in mesic habitats where autumn precipitation and persistent snow cover is likely to occur (Meyer et al. 2008a). Finally, isolates of *Pseudomonas fluorescens*, a deleterious rhizobacterium, reduce seedling vigor and are in various stages of development as bioherbicides. However, *B. tectorum* seeds inoculated with *P. fluorescens* isolate D7 did not experience mortality under laboratory conditions (Kennedy et al. 1991), and there are few published results from field studies (Kennedy et al. 2015). Further, EPA registration has been obtained for isolate D7, which has been released as a commercial bioherbicide and isolate ACK55 is in the process of EPA registration (Kennedy et al. 2015).

Pyrenophora semeniperda is a generalist grass fungal pathogen that causes minor leaf spot, seed infection, and death of at least 36 genera of annual and perennial grasses (Meyer et al. 2008a, Medd et al. 2003). The name "black fingers of death" is ascribed to this pathogen because of black finger-like stromata that emerge from infected seeds

(Meyer et al. 2008a). *Pyrenophora semeniperda* over-summers as mycelium in seed and plant debris, with stromata developing from the mycelium to produce conidiophores and conidia (Medd et al. 2003). Conidia that are carried to the inflorescence directly infect the developing ovary of *B. tectorum* seeds during anthesis, resulting in seed death (Medd et al. 2003), thereby negatively impacting the seed bank and *B. tectorum*'s temporal dispersal.

A major concern of using *P. semeniperda* as a biological control is spillover effects on to sensitive crops and native grasses (Medd and Campbell 2005). Pathogen spillover occurs when one host species supports high pathogen loads, causing indirect disease-mediated consequences for co-occurring host species (Beckstead et al. 2010). Because *B. tectorum* acts as the dominant pathogen reservoir for *P. semeniperda*, the potential exists for *P. semeniperda* to negatively impact native grasses and grassy crops indirectly at the seed stage before germination or emergence has taken place (Beckstead et al. 2010). Beckstead et al. (2010) reported spillover effects on five native grasses that co-occur with *B. tectorum*, with some species experiencing seed mortality up to 80%.

<u>Management strategies</u>. I utilized *P. semeniperda* as a natural enemy of *B. tectorum,* which if effective, would reduce propagule pressure of *B. tectorum* by affecting seeds in the seedbank, (see "Dispersal," page 10), and consequently, *B. tectorum* competitive effects would be reduced (see "Competition," page 21). In addition, I utilized a fungicide seed treatment to assess the impact of *P. semeniperda* on *B. tectorum,* while at the same time preventing spillover onto desired grass species that were seeded into *B. tectorum*-infested rangeland. Ultimately, biological control with *P. semeniperda*

integrated with fungicide seed treatments for seeded grass species may improve *B. tectorum* management by addressing biotic factors contributing to *B. tectorum* invasion.

Project Significance

Several ecological theories of invasion outline the where, when, why, and how of plant invasions (Davis et al. 2000, Keane and Crawley 2002, Levine et al. 2004); however, no single theory encompasses all mechanisms governing a successful invasion. Catford et al. (2009) outlined an invasion framework that focuses on three different drivers of invasion: propagule pressure, abiotic characteristics, and biotic characteristics ("PAB framework"). Ecological processes such as reproduction, disturbance, and natural enemies mediate each driver. In turn, these ecological processes can be manipulated by different management strategies. Thus, this project sought to place the PAB framework (Catford et al. 2009) within a management realm (Figure 1.1.), using the *Bromus tectorum-Pyrenophora semeniperda* pathosystem as a model. In addition, the prevalence of *Bromus tectorum* in western North America requires integrated management strategies that rely less heavily on herbicides alone and instead incorporate many "little hammers" (Liebman and Gallandt 1997) such as seeding, seed treatments, and biological control. Moreover, management strategies of *B. tectorum* have been propositioned as "one size fits all," even though many authors suggest that site-specific management recommendations are needed (Morris et al. 2009, Orloff et al. 2015, Sheley et al. 2010). This project not only manipulated ecological processes, but also sought to understand the role of temperature and *B. tectorum* population in determining efficacy of alternative management strategies, that is the biological control fungal pathogen *P. semeniperda*.

The goals of this project were twofold: first, an understanding of how ecological processes can be manipulated by management strategies and second, management recommendations for the *B. tectorum-P. semeniperda* pathosystem. This chapter of my dissertation explored how propagule pressure, abiotic characteristics, and biotic characteristics are mediated by select ecological process that may play a significant role in the *B. tectorum-P. semeniperda* pathosystem. The second chapter investigates the role of propagule size and a biological control agent (*P. semeniperda*) on non-target species. I then discuss the role of reproduction, dispersal, disturbance, natural enemies, and competition on revegetation of *B. tectorum*-invaded rangeland (Chapter 3). In Chapter 4, I investigate how propagule size, natural enemies, and invader traits interact to influence the susceptibility of *B. tectorum* populations to *P. semeniperda*. I end my dissertation with a discussion on integrating ecological processes into management recommendations and provide a direction for future research focused on the *B. tectorum-P. semeniperda* pathosystem.

Objectives

1. Evaluate the role of seed weight on susceptibility of *Bromus tectorum* and non-target, economically important grasses to the generalist grass seed pathogen *Pyrenophora semeniperda*.
2. Assess the effect of integrating imazapic, *P. semeniperda*, perennial grass seeding, and fungicide seed treatment on revegetation of a *B. tectorum*-infested plant community.

3. Investigate *P. semeniperda* efficacy as a biological control agent across varying temperatures in different *B. tectorum* populations.

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CHAPTER TWO

IMPACTS OF *PYRENOPHORA SEMENIPERDA* ON NON-TARGET, ECONOMICALLY IMPORTANT GRASSY SPECIES: IMPLICATIONS FOR BIOLOGICAL CONTROL OF *BROMUS TECTORUM* L. (CHEATGRASS, DOWNY BROME)

Introduction

Adding biological control to the arsenal of tools for integrated weed management may mitigate problems associated with excessive reliance on herbicides such as ground and surface water contamination, non-target effects, and evolved herbicide resistance (Charudattan 2001). In a successful classical biological control program, agents are able to self-perpetuate beyond initial introduction and respond in a density-dependent manner to an invasive species population density, thereby regulating the invader's abundance below an economic threshold level (Culliney 2005). However, a potential disadvantage of biological control is the requirement of an ideal and often specific environment for the natural enemy/target species relationship to exist (Bale et al. 2008). Furthermore, a natural enemy may have non-target effects on desirable species (Culliney 2005, Fowler et al. 2012). Thus, environmental adaptation and high host-specificity are preferred traits of a successful biological control program.

Bromus tectorum L. (cheatgrass, downy brome), an annual grass native to Eurasia, currently infests millions of hectares of cropping, forage, and rangeland systems in western North America (Mack 1981, Miller et al. 2013, Rice 2005). Its impacts include decreased native plant diversity, altered fire regimes, economic losses through control costs (BLM 1999), and decreased forage (Ganskopp and Bohnert 2001) and crop (Zimdahl 2004) quality and yields. *Bromus tectorum* invaded range and pastures often require expensive revegetation to restore desired perennial species (Epanchin-Niell et al. 2009).

Bromus tectorum's competitive advantages result from its prolific seed production, life cycle, and germination pattern. An individual *B. tectorum* plant is capable of producing 6,000 seeds (Young and Evans 1978), creating seedbank densities that may reach 19,000 seeds m^{-2} (Hempy-Mayer and Pyke 2008, Humphrey and Schupp 2001), depending on precipitation (Smith et al. 2008). *Bromus tectorum* typically acts as a winter annual species that germinates in fall but may behave as a summer annual that germinates in spring. This prolonged germination period is due to secondary dormancy (Harmon et al. 2012). Seeds entering secondary dormancy during the winter add to the carryover spring seedbank (Young and Evans 1975, Young et al. 1969).

Recent *B. tectorum* biological control research (Beckstead et al. 2010, 2014; Ehlert et al. 2014; Meyer et al. 2007, 2008) has focused on exploiting the natural enemy/invader relationship utilizing a generalist soil-borne fungal grass pathogen, *Pyrenophora semeniperda* (Brittlebank and Adam) Shoemaker (Ascomycotina: Pyrenomycetes). *Pyrenophora semeniperda* begins its life as conidia in the soil that are carried by germ tubes to grass inflorescences where they infect the developing ovary during anthesis (Campbell and Medd 2003, Medd et al. 2003). The fungus consumes starch resources within the ovary, resulting in seed mortality or reduced seedling vigor.

Infected mature host grass seeds disperse to the ground where *P. semeniperda* remains as mycelium for the rest of summer. Stromata develop from the mycelium, protrude from infected seeds as black finger-like appendages, and produce more conidia to further the infection cycle.

Host seeds that quickly capitalize on their seed reserves may germinate and effectively outcompete *P. semeniperda* for starch resources within the ovary, while slow-germinating and dormant seeds are more susceptible to mortality. This differential mortality has been described as a "race for survival" between *P. semeniperda* and the targeted host seed (Beckstead et al. 2007). Host species' seed weights, a valid measure of seed vigor (Pepper 2002, Singn and Bai 1988), could influence the "race for survival" between *P. semeniperda* and its host seed. For example, seed weight is inversely correlated with susceptibility to phytotoxins (Liebman and Sundberg 2006), with heavyweight seeds more stress tolerant than lightweight seeds. Moreover, heavyweight seeds have less vulnerability to pathogens (Crist and Freise 1993), higher germination and emergence, and can produce larger and more vigorous seedlings (Black 1956, Harper and and Obeid 1967, Schaal 1980) than lightweight seeds.

As a generalist pathogen, *P. semeniperda* affects seeds of at least 36 genera of annual and perennial grasses (Medd et al. 2003, Meyer et al. 2008), and Beckstead et al. (2010) documented 35-80% seed mortality in five grasses native to rangeland in the western United States. *Pyrenophora semeniperda* mortality could vary across species as lightweight and slow germinating seeds such as native rangeland species may be more likely to be impacted by *P. semeniperda* in comparison to heavyweight and quickly germinating crop and forage species. However, the extent to which *P. semeniperda* could negatively impact crop, forage, and range species is largely unknown. To fill this knowledge gap, a greenhouse experiment was conducted and exposed groups of crop, forage, and range grassy species commonly found growing in competition with *B. tectorum* to *P. semeniperda* to investigate the role of interspecific variations in seed weight on pathogen susceptibility. Although seed weight cannot be isolated as causing variation in susceptibility to *P. semeniperda,* it was chosen because of its ease of use. The hypothesis was that species with heavier seeds would be less susceptible to *P. semeniperda*, such as crop species, compared to lighter seeds such as forage and range species.

Materials and Methods

Seeds

Seeds of crop, forage, and range grassy species were obtained from Montana State University and commercial outlets (Western Native Seed, Coaldale, CO). *Bromus tectorum* seeds were collected at a cropland site located near Amsterdam, MT. All species were assessed for germinability prior to *P. semeniperda* treatment application by placing four replications of 25 seeds each on moistened blotter paper in germination boxes for seven days in the greenhouse (21.1°C day, 12.8°C night). Blotter paper was re-wetted as needed, and germination was assessed on day seven. To determine the mean weight of each species (Table 2.1), four samples of 100 seeds were dried (50°C for 72 hr) and weighed (National Seed Laboratory).

Pyrenophora semeniperda Inoculum Preparation

A *Pyrenophora semeniperda* inoculum was prepared using the modified single conidia isolation method (Stewart 2009). Isolates of *P. semeniperda* were obtained from the same site where *B. tectorum* seeds were collected. Plant material and soil were collected from 20 locations within a 1 ha area. Stromata from *B. tectorum* seeds that carried the isolate were removed with sterilized tweezers and placed onto damp blotter paper for 24 h to produce conidia. Stromata bearing conidia were placed into a 1.5 mL vial containing a 1% Tween®/H_20 solution, which was shaken vigorously for 15 sec to release the conidia. The solution was evenly spread using a sterile glass rod onto a Petri dish containing water agar. Conidia were allowed to germinate at room temperature (20˚C) for 14-16 h. Using a dissecting microscope, germinated conidia were identified based on the presence of a clear germination tube, as long as or longer than the conidia. An X-Acto® knife dipped in ethanol and flame-sterilized was used to transfer a single conidium onto a Petri dish containing modified alphacel medium (Stewart 2009). Four-40 watt cool-white and four-40 watt black light florescent tubes were positioned 40 cm above Petri dishes to provide a 12 h near visible ultraviolet (320-420 nm) photoperiod and maintained at room temperature (20°C). Petri dishes were checked for contaminants every two to three days, and an X-Acto® knife dipped in ethanol and flame-sterilized was used to remove bacterial contaminants. After 12 d, conidia were harvested from Petri dishes by rinsing the surface with 5 mL of sterile deionized water and gently scraping the surface with a rubber-tipped glass-stirring rod. Additional water was used as needed to gently scrape the surface clean. The conidia solution was poured into a sterile glass jar. A haemocytometer was used to quantify conidia concentration, and sterile deionized water was added until a 5,000 conidia mL^{-1} concentration was achieved for the inoculum (Beckstead et al. 2007). Inoculum was stored at 5˚C until seed inoculation.

Experimental Design

The experiment was conducted in a greenhouse at the Montana State University Plant Growth Center, Bozeman, MT. It consisted of a factorial of two *P. semeniperda* treatments (inoculated, non-inoculated) and 16 grass species: *B. tectorum* and 15 species that co-occur with *B. tectorum* in crop (5 species), forage (5 species), and range (5 species) environments (Table 2.1). The non-inoculated treatment is hereafter referred to as the control. All treatments were replicated four times in a randomized complete block design. The experiment was concurrently repeated in two different greenhouses (trial 1: 7 May to 4 June 2013, trial 2: 13 May to 10 June 2013).

Inoculum Application and Planting

The aim was to achieve a density of 20 plants per pot. Therefore, for each species the number of seeds subjected to the *P. semeniperda* treatment and subsequently planted into pots was adjusted accordingly based on the species' germinability (Table 2.1). Prior to inoculation, all seeds were surface sterilized to remove unwanted debris and microbial material by submerging them for 60 sec in 70% ethanol, 60 sec in 10% bleach, 60 sec in 70% ethanol, and rinsing with deionized water for 30 sec (Stewart 2009). The inoculated treatment consisted of the appropriate number of seeds being placed in Petri dishes containing 1 mL *P. semeniperda* inoculum per 5 seeds. Control seeds received an equivalent amount of deionized water. Inoculated and control seeds were then placed on a shaker table for 14 h at 50 rpm to allow for absorption of *P. semeniperda* inoculum.

For each species, inoculated and control seeds were planted to a depth of 0.5 cm into pots (2.2 L, 15 cm diameter) containing a steam-sterilized growing medium that was equal parts by volume of loam mineral soil, washed concrete sand, peat moss, and vermiculite. Greenhouse lights (1000 watt, GE Multi-Vapor MVR1000/C/U, General Electric Company, Cleveland, OH) supplemented ambient light as needed to achieve 12 hr days, and greenhouse temperature was maintained at 21.1°C day and 12.8°C night. Pots were moved every five to seven days to minimize effect of location within the greenhouse on plant emergence and growth. Pots were watered daily as needed to avoid visual signs of drought stress (i.e. wilting). Seedling emergence was recorded daily. After 28 d from the day of planting, final density was recorded and aboveground biomass was clipped, dried (50°C for 72 hr), and weighed (mg plant^{-1}) to the nearest 0.001g.

Statistical Analysis

Seed Weight. Species were grouped by the system they are more frequently associated with: crop, forage, or range. To evaluate if seed weight differed among all species and groups of species, three separate analyses of variance (ANOVA) were conducted. Species and groups (crop, forage, range), respectively, were model predictors and seed weight was the response variable for two of the ANOVAs. A third ANOVA was conducted separately for each group, with species as the model predictor and seed weight as the response.

Time to 50% Emergence. Time to 50% emergence (T_{50}) was calculated according to the formula of Coolbear et al. (1984) modified by Farooq et al. (2005):

$$T_{50} = t_i + \frac{(\frac{N}{2} - n_i)(t_j - t_i)}{(n_j - n_i)},$$

where N is the final number of seeds emerged, and n_i and n_j are the total number of seeds germinated by adjacent counts at time t_i and t_j where $n_i < (N/2) < n_j$. To evaluate the relationship between T_{50} and seed weight for the control and inoculated treatment, an analysis of covariance (ANCOVA) was conducted with time to 50% emergence (T_{50}) as the response, seed weight as the predictor, and *P. semeniperda* treatment as a multiplicative covariate. The error term was block nested within trial.

Plant Density and Biomass. To determine if *P. semeniperda* affected species density and biomass of seedlings, two separate ANOVAs were used with species, *P. semeniperda* treatment, and their interaction as predictors and either density or biomass as response variable. The error term was block nested within trial. Density counts were logit transformed, after 0.01 was added, to meet assumptions of normality. Biomass was natural log transformed to meet the statistical assumption of homogeneity of variance. Density and per capita biomass are presented as relative to the non-inoculated control to underscore the effect of *P. semeniperda*. Relative values were calculated as:

$$Relative\ plant\ biomass\ (bm)\ \boldsymbol{or}\ density\ (d)\ = \frac{(bm\ \boldsymbol{or}\ d_{inoculated28d}/n_{planted})}{(bm\ \boldsymbol{or}\ d_{control28d}/n_{planted})},$$

Where $bm_{inoculated28d}$ or $d_{inocualted\ 28d}$ is biomass or density of inoculated seedlings at 28 d, $bm_{control28d}$ or $d_{control28d}$ is biomass or density of control seedlings at 28 d and $n_{planted}$ is the number of seeds planted per pot. All analyses were performed using R software (R Core Team 2016). When significant variables were found, means were separated using least squared means (LSD) ($\alpha < 0.05$) in the lsmeans package (Lenth and Hervé 2016).

Results

Seed Weight

Seed weight differed across all species ($P < 0.01$), within each group of species ($P < 0.01$ for crop, forage, and range), and across species' groups ($P < 0.01$). Overall, crop species had larger seed weights than those of *B. tectorum* and forage and range species (Table 2.1). In general, the crop and forage groups had some similarities among species seed weight, and in the range group, all five species were different from one another (Table 2.1).

Time to 50% Emergence vs. Seed Weight

Within the group of crop species, the effect of seed weight depended on *P. semeniperda* treatment (seed weight x *P. semeniperda* treatment, $P = 0.02$). There was a negative relationship between T_{50} and seed weight for both control and inoculated seeds; as seeds got heavier, they emerged faster (Figure 2.1.a), with a steeper slope for the control compared to the inoculated treatment. Within the group of forage species, T_{50} was not affected by seed weight ($P = 0.23$), but was influenced by *P. semeniperda* treatment ($P < 0.01$). Time to 50% emergence was 1.4 d later for inoculated seeds compared to control seeds (Figure 2.1b). Within the group of range species, T_{50} was affected by *P. semeniperda* treatment ($P < 0.01$) and marginally affected by seed weight ($P = 0.06$). Inoculated seeds emerged 1.1 d later than control seeds, and there was a positive trend between T_{50} and seed weight, particularly for inoculated seeds.

Density and Biomass

The effect of *P. semeniperda* on seedling density differed among species ($P < 0.01$). Negative impacts of *P. semeniperda* were most common in lightweight range species where inoculation affected four out of five species, reducing relative density 20% to 80% (Figure 2.2). *Hordeum vulgare* and *S. cereal* were the two crop species that were negatively affected by *P. semeniperda* inoculation, with relative density reduced by 8% and 33%, respectively. Three of five forage species were negatively affected by inoculation. On average, inoculation reduced density of *A. cristatum*, *B. inermis*, and *E. junceus* by 30% relative to the control. There was a 40% reduction in *B. tectorum* density with inoculation, relative to the control.

Pyrenophora semeniperda differently impacted species growth as reflected by the interaction between species identity and biomass ($P = 0.02$). Specifically, *P. semeniperda* inoculation negatively affected biomass in three of the 16 species tested (Figure 2.3). In particular, inoculation reduced biomass of X *Triticosecale*, *B. inermis*, and *E. junceus* by 25%. Biomass of a single species, *S. scoparium*, increased in response to inoculation.

Table 2.1. Percentage germination, number of seeds planted per pot, and 100-seed weight for crop, forage, and range species that co-occur with *Bromus tectorum* (cheatgrass, downy brome). ^ Means separations within a column indicate 100-seed weight means that differ from one another ($\alpha = 0.05$).

	Species	Germination (%)	Seeds Planted	100-Seed Weight (mg ± SE)	Across Species^	Within a Group	Across Groups
	BRTE*	75	26	303 ± 4	C	■	**A**
Crop	HOVU	88	22	3540 ± 50	G	*d*	2762 ± 161 **B**
	AVSA	52	38	1309 ± 9	D	*a*	
	SECE	94	21	3363 ± 43	F	*c*	
	TRITI2	96	21	2848 ± 23	E	*b*	
	TRAE	100	20	2752 ± 46	E	*b*	
Forage	AGCR	68	29	148 ± 1	B	*b*	239 ± 19 **A**
	DAGL	38	52	110 ± 1	AB	*a*	
	ELJU	88	23	291 ± 3	C	*c*	
	BRIN2	80	25	338 ± 9	C	*d*	
	FEAR3	82	28	306 ± 6	C	*c*	
Range	BOGR2	80	25	75 ± 2	AB	*b*	138 ± 20 **A**
	PSSP6	50	40	305 ± 6	C	*e*	
	FEID	70	29	111 ± 0	AB	*c*	
	SCSC	42	48	173 ± 4	B	*d*	
	KOMA	50	40	24 ± 0	A	*a*	

*Symbols of species according to USDA Plants Database. **BRTE**: Cheatgrass, downy brome, *Bromus tectorum* L.; **HOVU**: Barley, *Hordeum vulgare* L.; **AVSA**: Oat, *Avena sativa* L.; **SECE**: Rye, *Secale cereal* L.; **TRITI2**: Triticiale, X *Tritosecale* ex A. Camus; **TRAE**: Winter wheat, *Triticum aestivum* L.; **AGCR**: Crested wheatgrass, *Agropyron cristatum* (L.) Gareth; **DAGL**: Orchardgrass, *Dactylum glomerata* L.; **ELJU**: Russian wildrye, *Elymus junceus* (Fisch.); **BRIN2**: Smooth brome, *Bromus inermis* Leyss.; **FEAR3**: Tall fescue, *Festuca arudianacea* Schreb.; **BOGR2**: Blue grama, *Bouteloua gracilis* (Willd. ex Kunth) Lag. ex Griffiths; **PSSP6**: Bluebunch wheatgrass, *Pseudoroegneria spicata* (Pursh) Á. Löve; **FEID**: Idaho fescue, *Festuca idahoensis* Elmer; **SCSC**: Little bluestem, *Schizachyrium scoparium* (Mirchx.) Nash; **KOMA**: Prairie junegrass, *Koeleria macrantha* (Ledeb.) Schu

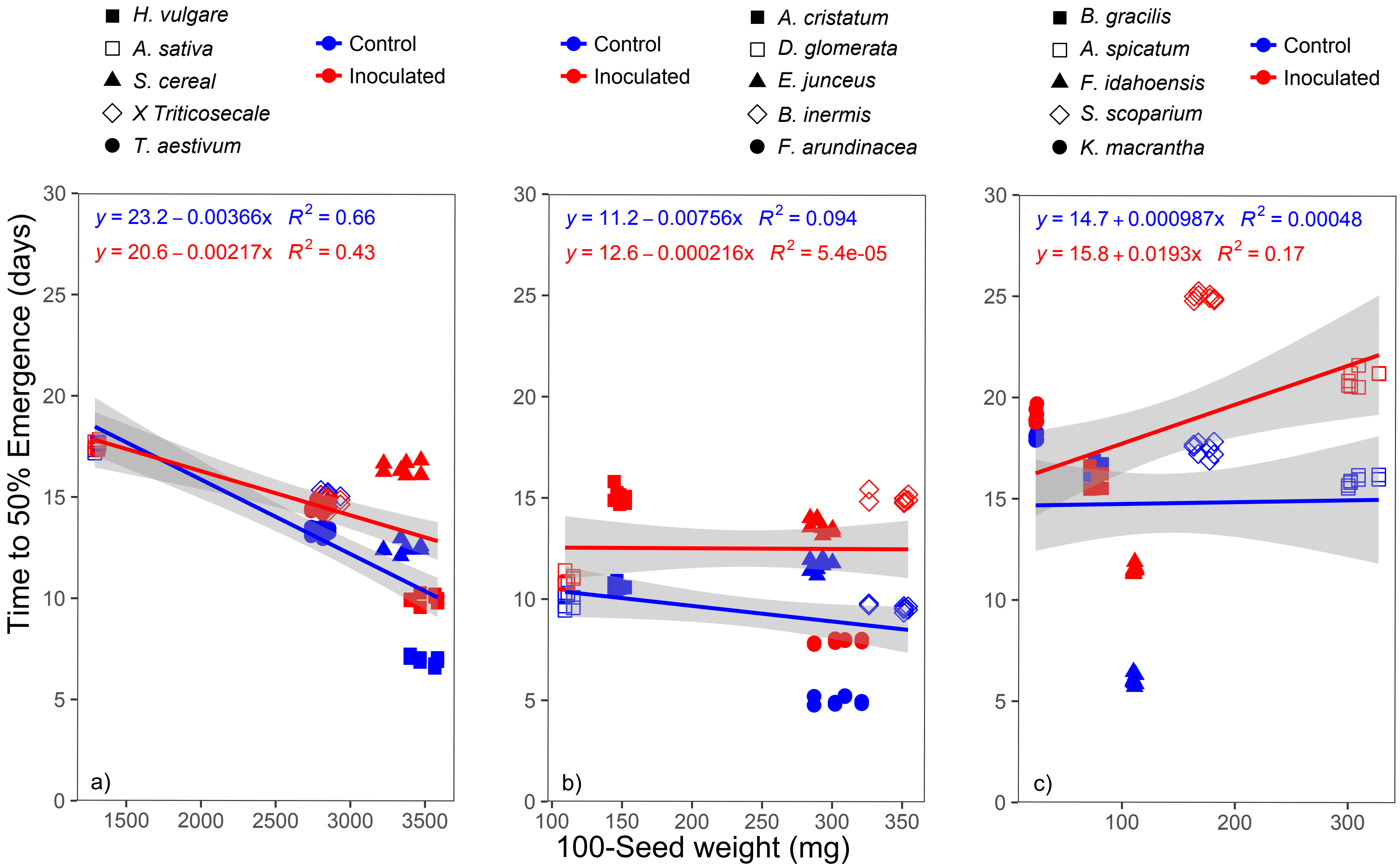

Figure 2.1. The effect of seed weight on time to 50% emergence (T_{50}) for a) crop, b) forage, and c) range species. Shadow represents ± SE.

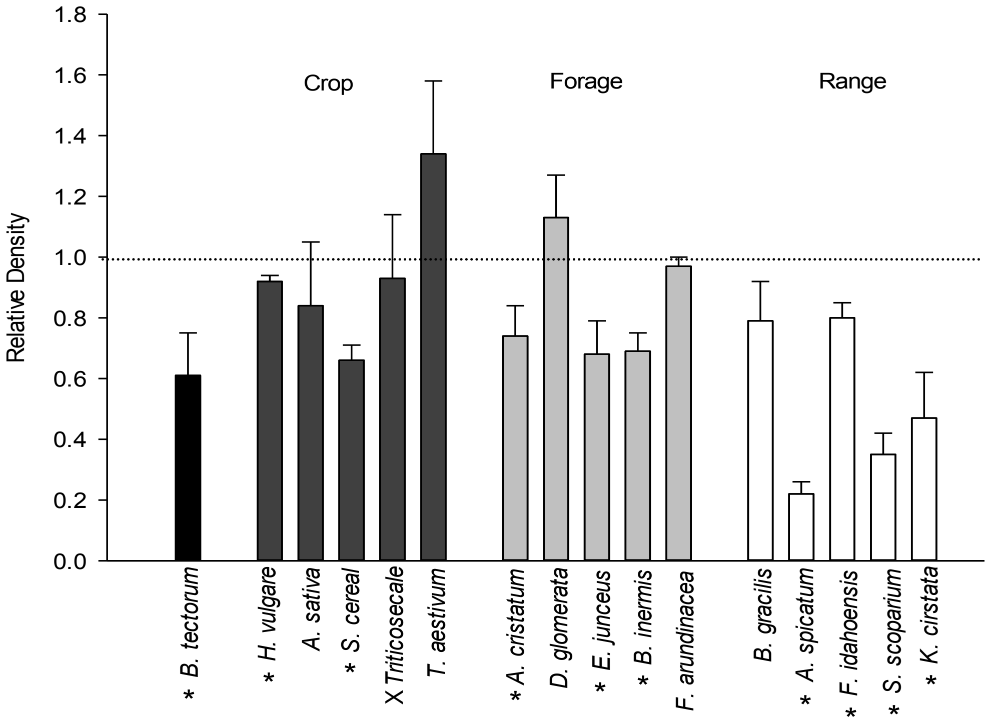

Figure 2.2. Relative density of 16 grass species inoculated with *Pyrenophora semeniperda*. Relative densities are presented as the density of the inoculated treatment relative to the density of the non-inoculated control. The dashed line at 1.0 represents the control. An asterisk (*) next to a species name indicates a difference between the control and *P. semeniperda* ($\alpha < 0.05$).

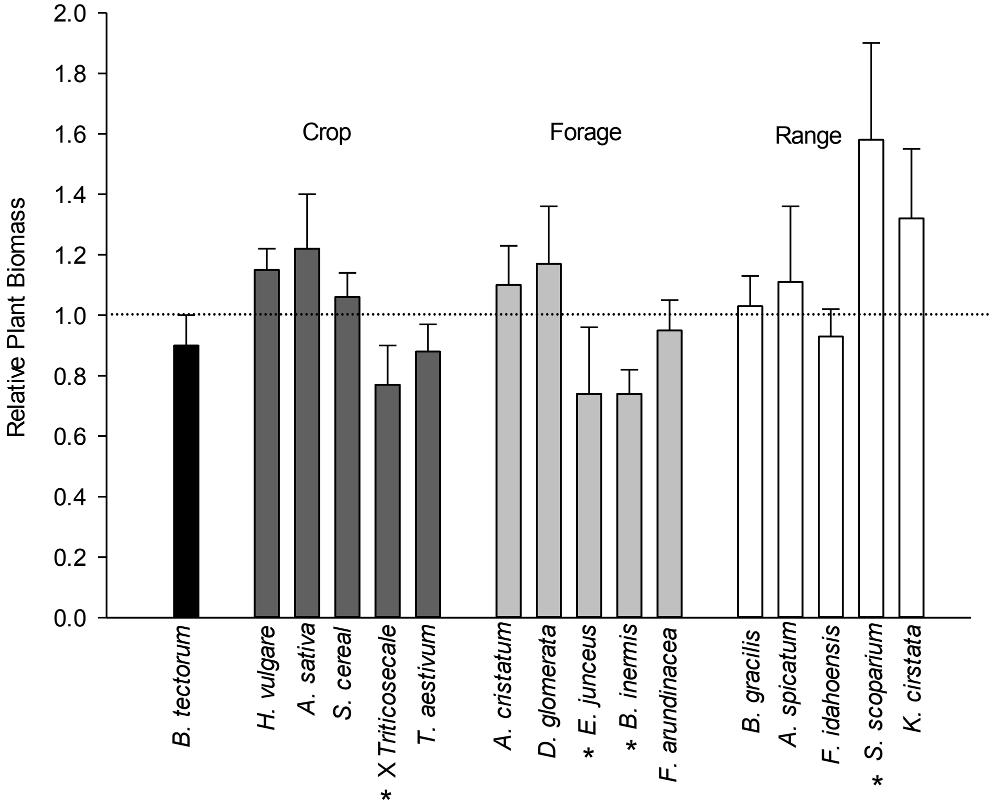

Figure 2.3. Relative per capita plant biomass of 16 grass species inoculated with *Pyrenophora semeniperda*. Relative plant biomass is presented as the biomass of the inoculated treatment relative to the biomass of the non-inoculated control. An asterisk (*) next to a species name indicates a difference between the control and *P. semeniperda* ($\alpha < 0.05$).

Discussion

Previous studies suggested the possibility of utilizing *P. semeniperda*, a generalist grass pathogen, for biological control of *B. tectorum*, despite the risk of non-target effects on desirable species found in crop, forage, and range systems (Beckstead et al. 2010, Ehlert et al. 2014, Meyer et al. 2007, 2008). While providing valuable information, these studies did not address groups of crop and forage species as well as other range species that co-occur with *B. tectorum*. Also, these studies tested *P. semeniperda* susceptibility in a sterile environment (i.e. Petri dishes). This study furthers the understanding of non-target impacts of *P. semeniperda* across crop, forage, and range species, particularly in the context of a non-sterile environment (i.e. soil). Furthermore, by assessing the relative impact of *P. semeniperda* as a function of seed size, a simple indicator of susceptibility, this study allowed us to predict the effect that *P. semeniperda* could have on species outside of those tested.

While the number of species screened was not exhaustive, 60% (9 of 15 species) was negatively affected by *P. semeniperda*, specifically when considering density of emerged seedlings, and rangeland species were especially susceptible. Moreover, only 20% (3 of 15) exhibited a reduction in biomass with *P. semeniperda* infection, and *B. tectorum* emergence was reduced by 40% and its biomass was unaffected. Due to the intensive nature of this study, I could not test if effects differ among *P. semeniperda* isolates. Thus, conclusions on non-target species susceptibility to *P. semeniperda* are limited to the isolate used. However, other researchers have also utilized a single *P. semeniperda* isolate (Beckstead et al. 2007, 2011; Ehlert et al. 2014; Parkinson, Mangold, Miller, *personal communication*).

Beckstead et al. (2010) explained the relationship between *P. semeniperda* and the target seed as a "race for survival," where slower germinating species are more susceptible to *P. semeniperda*-caused mortality because the fungus usurps starch resources within the seed before it can germinate and begin assimilating carbon through photosynthesis. Slower germinating species typically have smaller seeds (Black 1956, Harper and Obeid 1967, Schaal 1980) and are thus less vigorous (Pepper 2002), less stress tolerant to phytotoxins (Liebman and Sundberg 2006), and more vulnerable to pathogens (Crist and Freise 1993). In general, time to 50% emergence was affected by inoculation, and there were differences between the control and inoculated treatment. Specifically, control seeds emerged faster than inoculated seeds for the crop and forage species. Moreover, the speed of emergence for forage species was not affected by seed weight, and range species were only slightly affected, and then there was only a clear trend for the inoculated seeds between time to 50% emergence and seed weight. Results suggest that seed weight accounted for 66% of the variability for crop species when predicting T_{50} in the absence of *P. semeniperda*, and accounted for nearly none of the variability for forage and range species. Moreover, seed weight accounted for about 17% and 43% of the variability when predicting T_{50} in the presence of *P. semeniperda* for range and crop species, respectively. Taken together, this suggests that unless species are particularly heavy (i.e. crop species), seed weight alone is insufficient in predicting a species response to *P. semeniperda*. Moreover, it is important to consider species-specific, while correlated with seed weight, may be due to other factors (e.g. genetic, environmental) that determine susceptibility and tolerance to *P. semeniperda*.

Despite the risk of non-target effects on desirable species, steps can be taken to mitigate the effects of *P. semeniperda* should it be adopted for biological control of *B. tectorum*. First, desired crop, forage, and range grass seeds can be treated with a fungicide (Meyer et al. 2008) prior to applying *P. semeniperda*. Second, species that are less susceptible to *P. semeniperda* can be chosen for rangeland revegetation (Meyer et al. 2008). For example, in this study *P. semeniperda* negatively impacted *A. spicatum* but did not positively or negatively impact *B. gracilis*. Thus, if *B. gracilis* meets other species' and site-specific trait requirements for revegetation, it may be a possible candidate for integrated rangeland revegetation that combines biological control practices with seeding. Moreover, testing *P. semeniperda* under field conditions is necessary as species-specific germination time and associated soil temperature, moisture, and chemistry may influence *P. semeniperda* effects on *B. tectorum* and desired grassy species. Third, heavier crop species reach T_{50} faster in the absence of *P. semeniperda*, suggesting that crop species with a 100-seed weight greater than 1750 mg will succeed in germinating prior to attack by *P. semeniperda*. Finally, despite *P. semeniperda* being a generalist, there is the potential to select isolates with high host-specificity (Campbell et al. 1996) within crop, forage, and range systems. Overall, as with any management tool, precautions should be taken if and when *P. semeniperda* is implemented as a biological control on a large scale (Meyer et al. 2008).

Integrated management can address limitations of different strategies for *B. tectorum* control. *Pyrenophora semeniperda* should be considered one of many "little hammers" (Liebman and Gallandt 1997) in the weed manager's toolbox as *P. semeniperda* inoculation caused a 40% reduction in *B. tectorum* density. Incorporating *P. semeniperda* with other management techniques such as herbicides (Ehlert et al. 2014), seed treatments (e.g. fungicide), and using heavier species for revegetation could potentially yield better results than any single tool used alone. For example, imazapic is commonly used to control *B. tectorum* in rangeland settings (Mangold et al. 2013); however, as a growth regulator herbicide it only controls individuals that have emerged and are actively growing. Integrating imazapic with *P. semeniperda* may therefore provide a multi-pronged management approach where *B. tectorum* emergence is reduced with *P. semeniperda*, and imazapic controls *B. tectorum* seedlings that escaped *P. semeniperda* (Ehlert et al. 2014). Utilizing *P. semeniperda* (40% reduction in density in my study) for *B. tectorum* control should be weighed against both the risk of non-target effects on desirable species and its overall efficacy relative to other management techniques.

Future research should include field trials with *P. semeniperda* to understand if and how greenhouse results scale to the field, where spatial, temporal, and environmental factors may lead to different outcomes. Furthermore, we need to study the role of *P. semeniperda* in both intra- and interspecific relationships. *Pyrenophora semeniperda* may not only impact non-target species, but may also affect interactions that non-target species have with each other and with *B. tectorum* (i.e. pathogen-mediated apparent competition, Power and Mitchell 2004). For example, *P. semeniperda* spillover can lead to coexistence, native grass exclusion, priority effects (Mordecai 2013a), or even native grass persistence (Mordecai 2013b). Further research should explore how long *P. semeniperda* persists in the soil and the consequent effect on offspring of already established desired species. These suggestions, in addition to a cost-benefit analysis, are needed to determine if *P. semeniperda* can become part of an integrated *B. tectorum* management program in crop, forage, and range systems.

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CHAPTER THREE

IMPACT OF NATIVE SPECIES SEEDING, HERBICIDES, AND FUNGICIDES IN PERENNIAL GRASS ESTABLISHMENT IN *BROMUS TECOTRUM* L. (CHEATGRASS, DOWNY BROME) INFESTED HABITATS

Introduction

Bromus tectorum L. (downy brome, cheatgrass) is a winter annual grass that currently infests millions of hectares of cropping, forage, and rangeland systems in western North America (Mack 1981, Miller et al. 2013, Rice 2005). This invasive species negatively impacts native plant communities by competing for moisture and nutrients prior to perennial grass growth in the spring (Epanchin-Niell et al. 2009). *Bromus tectorum* long-term dominance in rangelands has been associated with a loss of desired perennial species' seedbank and recruitment (Humphrey and Schupp 2001, 2004). Successful management of *B. tectorum* has sometimes resulted in an increase in desired perennial species (Davies and Sheley 2011, Elseroad and Rudd 2011). However, on many occasions niches created by control efforts may be filled by *B. tectorum* or other undesirable species present in the propagule pool (Connell and Slatyer 1977, Egler 1954, Svejcar et al. 2014). Consequently, attention has focused on ecologically-based management strategies such as revegetation that aim at diminishing *B. tectorum*'s abundance while simultaneously improving ecosystem function, niche occupation, and desired species competitiveness, establishment and growth (DiTomaso et al. 2010).

Imazapic, an acetolactate synthase inhibitor and member of the imidazolinone family, is an herbicide commonly used to manage *B. tectorum*-invaded rangeland; however, its efficacy varies depending on application timing and rate (Mangold et al. 2013). Efficacy of imazapic usually depends on the tradeoff between *B. tectorum* control and injury to desired perennial species, which is often site-dependent. For example, Morris et al. (2009) assessed variable rates of imazapic and seeding of five perennial species [two sources each of Siberian wheatgrass (*Agropyron fragile*), prostrate kochia (*Bassia prostrata*), and Russian wildrye (*Psathyrostachys juncea*)] and observed increased plant establishment with increasing imazapic rates up to 105 g ai ha^{-1} at one site, while establishment declined at rates above 35 g ai ha^{-1} at a second site. Similarly, Shinn and Thill (2004) reported imazapic rates that reduced *B. tectorum* abundance (140 g ai ha^{-1}) also severely injured perennial forage grasses [big bluegrass (*Poa juncifolia*), smooth brome (*Bromus inermis*), meadow brome (*B. biebersteinii*), sheep fescue (*Festuca ovina*), hard fescue (*Festuca brevipila*), orchardgrass (*Dactylis glomerata*), crested wheatgrass (*Agropyron cristatum*), western wheatgrass (*Pascopyrum smithii*), intermediate wheatgrass (*Thinopyrum intermedium*), and bluebunch wheatgrass (*Pseudoroegneria spicata*)].

Revegetation of *B. tectorum* infested systems can also fail because of biotic factors that affect seedling recruitment (Svejcar et al. 2014). For example, soil pathogens are ubiquitous within the soil and can have saprophytic or pathogenic effects on desired species' seeds (Christensen 1989), thereby reducing their survival (Crist and Friese 1993, Dalling et al. 1998, O'Hanlon-Manners and Kotanen 2004). One such soil-borne pathogen is *Pyrenophora semeniperda* (Brittlebank and Adam) Shoemaker (Ascomycotina: Pyrenomycetes), a generalist grass pathogen. *Pyrenophora semeniperda* kills *B. tectorum* seeds in the seedbank (Beckstead et al. 2007, Meyer et al. 2007, 2008a, b), but it has demonstrated non-target effects on co-occurring native grasses (Beckstead et al. 2010, Mordecai 2013a, b). *Pyrenophora semeniperda* could potentially serve as a biological control agent for *B. tectorum,* but research is needed to evaluate if its non-target effects on desired species can be mitigated. Seed treatments such as fungicides have been suggested to improve desired species establishment in weed-infested rangelands (Jacobs et al. 1998), and they could protect seeded grasses from *P. semeniperda* mortality. While fungicides have successfully increased tree sapling survival in forests (Dalling et al. 1998, O'Hanlon-Manners and Kotanen 2004), to my knowledge no such research has been reported in the rangelands of western North America, especially *B. tectorum*-invaded systems treated with *P. semeniperda*.

Synergistic, additive, or antagonistic interactions may occur when management practices are combined as part of an integrated weed management (IWM) strategy (Sciegienka et al. 2011). One approach to develop an IWM strategy is to combine "many little hammers" management strategies that by themselves are marginally effective but collectively may result in sustainable, economical, and successful weed control (Liebman and Gallandt 1997). While this approach has been proven successful to manage weeds in agricultural settings (Westerman et al., 2005), relatively less knowledge exists in rangelands (Smith et al 2006). Previous studies assessed integrated strategies to control *B. tectorum* in rangeland conditions have focused on integrating herbicides and revegetation (Morris et al. 2009, Orloff et al. 2015, Owen et al. 2011, Sbatella et al. 2011, Whitson and Koch 1998), with few studies incorporating other "little hammers" such as a biological control (Dooley and Beckstead 2010, Ehlert et al. 2014), seeding rates, and seed treatments. Accordingly, the objective was to assess the potential of improving *B. tectorum* management by integrating imazapic and *P. semeniperda* with varying rates of perennial grass seeding and a fungicide seed treatment. The hypothesis was that the integration of any of these methods would yield better *B. tectorum* control and perennial grass establishment compared to either method used singularly.

Materials and Methods

Site and Study Description

The field study was conducted over two years (Year 1: September 2013 to August 2014, Year 2: September 2014 to August 2015) at a site located 10.5 km northwest of Amsterdam, MT, (45.756958, -111.426554) where a naturally occurring *B. tectorum* infestation existed. The site was on private land used primarily for agriculture, but it had not been in production for three years. Soil at the site is a Beaverell-Beavwan complex composed of cobbly loam (0 to 17.8 cm depth) and very cobbly clay loam (17.8 to 50.8 cm depth) (NRCS Soil Survey 2016). The Western Regional Climate Center (WRCC) database was accessed for temperature and precipitation data during the duration of the study as well as long-term averages (1967 to 2015, 48 years) collected from the Bozeman Experimental Farm (Station #241047), located 23.3 km from my study site. Plots (1 m x 2 m) were established in fall 2013 as a randomized complete-block design with four blocks. A factorial combination of two herbicide treatments (non-sprayed, sprayed), two perennial grass seeding rates [recommended rate (1X), two times recommended rate (2X)], two *P. semeniperda* treatments (non-inoculated, inoculated), and two seed-fungicide treatments (non-treated, treated) was randomly assigned to plots.

Herbicide, Fungicide, and Seeding Treatments

Imazapic [Plateau®, WSC; 120 g ai ha^{-1}] was mixed with water plus a non-ionic surfactant (Penetrator®, Helena Chemical Company, 0.10% volume/volume) and applied to treated plots using a CO_2 backpack sprayer delivering 210 L ha^{-1} water at 294 kPa across a boom width of 1 m. Non-treated plots received an equal amount of water. Application occurred on 3 November 2013 when *B. tectorum* was at the 4-leaf stage.

Pseudoroegneria spicata (bluebunch wheatgrass) and *Koeleria macrantha* (prairie Junegrass) (Western Native Seed, Coaldale, CO) were chosen as my revegetation species because they are ubiquitous within the Northern Rocky Mountain region and are susceptible to *P. semeniperda* (Ehlert et al., *unpublished data*). Difenoconazole and mefenoxam (Dividend Extreme®, 12 g ai 100 kg^{-1} seed difenoconazole and 3 g ai 100 kg^{-1} seed mefenoxam) was applied to seeds receiving the fungicide treatment by placing seeds in plastic bags and shaking the bags to evenly distribute the fungicide. The bags were opened and allowed to air dry for 1 hr prior to seeding. *Pseudoroegneria spicata* and *K. macrantha* were hand seeded as a mix on 18 April 2014 at the rate of either 13.5 or 27.0 kg ha^{-1} (1X or 2X) and 2.2 or 4.4 kg ha^{-1} (1X or 2X), respectively. Rates were calculated according to Goodwin et al. (2006) and accounted for differences in seed germinability. Prior to seeding, gentle hand raking was used to break up the soil surface as part of seedbed preparation. Drill seeding was simulated by using garden hoes to establish a furrow (no greater than 2.5 cm depth) for each row. Four rows were planted within the center of each plot, with 30 cm row spacing. Seeds were evenly distributed among the four furrows and gently covered with soil.

Vegetation Sampling

Vegetation density was sampled on 29-30 July 2014 and 25-26, 29-30 June 2015. Sampling dates corresponded to 100 and 433 d after perennial grasses were seeded and 268 and 603 d after imazapic was applied, respectively. A 20 cm x 50 cm frame (Daubenmire 1959) was placed over two randomly selected rows of seeded perennial grasses in each plot to record density of co-occurring species. Due to its high density, *B. tectorum* was counted within a 20 cm x 12.5 cm section of each frame. Seeded perennial grass density was counted along a linear meter (i.e. 1 m transect) of each randomly selected row. *Pseudoroegneria spicata* and *K. macrantha* were not separated by species during data collection because of difficulty distinguishing these species at the seedling stage. All other vegetation was sampled within the entirety of the frame. At the 2015 sample dates (2 years post seeding), biomass was clipped from the Daubenmire frames and grouped into functional groups for density and biomass analysis. Functional groups included *B. tectorum*, seeded perennial grasses, non-seeded perennial grasses (*Hordeum jubatum*, *Elymus trachycaulus*, *Poa compressa*), exotic perennial forbs, annual grasses, and native forbs. Biomass was dried at 65°C for 72 hours in the Plant Growth Center, Montana State University, Bozeman, MT, USA and weighed to the nearest 0.001 g.

Abundance of *Pyrenophora semeniperda*

Soil samples were collected from all plots on 28 August 2014 and 1 October 2015. These dates were 339 d and 738 d, respectively, after *P. semeniperda* was applied. At each sampling date, one soil core was collected to a depth of 7.5 cm at two random locations within each plot using a 7 cm diameter tulip bulb planter. The two soil cores collected from each plot were composited and placed in 1 L Ziploc® bags and placed in cold-wet storage within 4 h of sampling. Each sample was placed in a plastic bin to gently distribute the soil and 50 *B. tectorum* seeds per sample were collected with tweezers. Seeds were visually inspected for *P. semeniperda* stromata and scored as infected or non-infected.

Statistical Analysis

To evaluate *P. semeniperda* prevalance, a repeated measures logistic regression model was conducted using glmer in the lme4 package (Bates et al. 2015) of R (R Core Team 2016). The response was the proportion of seeds infected with *P. semeniperda*. The model had the fixed effect of *P. semeniperda* treatment (inoculated, non-inoculated), year, and their interaction, and the random effect of year nested within plot, nested within block (Crawley 2013).

To evaluate the effect of treatments (herbicide application, perennial grass seeding rate, and fungicide) on vegetation density, a repeated measures analysis of variance (ANOVA) was conducted in R (R Core Team 2016). The response variable was functional group (*B. tectorum,* seeded perennial grasses, non-seeded perennial grasses, exotic perennial forbs, annual grasses other than *B. tectorum*, and native forbs) density. Predictor variables were herbicide application, seeding rate, fungicide, year, and their interactions, and the error term was year nested within plot, nested within block (Crawley 2013). To evaluate the effect of treatments on biomass collected in Year 2, an ANOVA was conducted with functional group (*B. tectorum,* seeded perennial grasses, non-seeded perennial grasses, exotic perennial forbs, annual grasses, and native forbs) biomass as the response and predictor variables were herbicide application, seeding rate, fungicide, and their interactions. The error term was plot nested within block (Crawley 2013). Response variables for density and biomass models were log transformed + 1, if needed, to meet the assumption of normally distributed errors. When interactions occurred, means separations were conducted using the lsmeans package (Lenth 2016) in R (R Core Team 2016).

Results

Weather

During the study, the average monthly temperature was generally similar between the first and second year and was within 5°C of the long-term average (Figure 3.1a). Mean annual temperature was 6.5°C ± 0.8 in Year 1 and 8.2°C ± 0.7 in Year 2; the annual long-term average is 6.5°C ± 0.7. Average temperature from March to June in Year 1 was 13.2 ± 2.8°C, which was within the range of the long-term average of 12.6 ± 2.8°C during the same time period. Total monthly precipitation varied between Year 1 and Year 2 (Figure 3.1b). Specifically, months in Year 1 that had high precipitation had low precipitation in Year 2 compared to the long-term average. This is particularly evident from March to June, a critical period for both *B. tectorum* and perennial grass growth. Unlike mean annual temperature, mean annual precipitation decreased from 39.4 mm ± 2.2 in Year 1 to 26.5 mm ± 1.6 in Year 2; the long-term average is 34.1 mm ± 1.6.

Pyrenophora semeniperda Prevalence

There was no difference in the proportion of *B. tectorum* seeds infected with *P. semeniperda* between inoculated and non-inoculated plots ($P = 0.88$), indicating that the *P. semeniperda* application was insufficient to increase its prevalence above ambient levels. Specifically, average infection of collected seeds was 22.1 ± 3.6% and 20.9 ± 3.3% in non-inoculated and inoculated plots, respectively. Consequently, data were pooled across the *P. semeniperda* treatment for the statistical analysis of density and biomass.

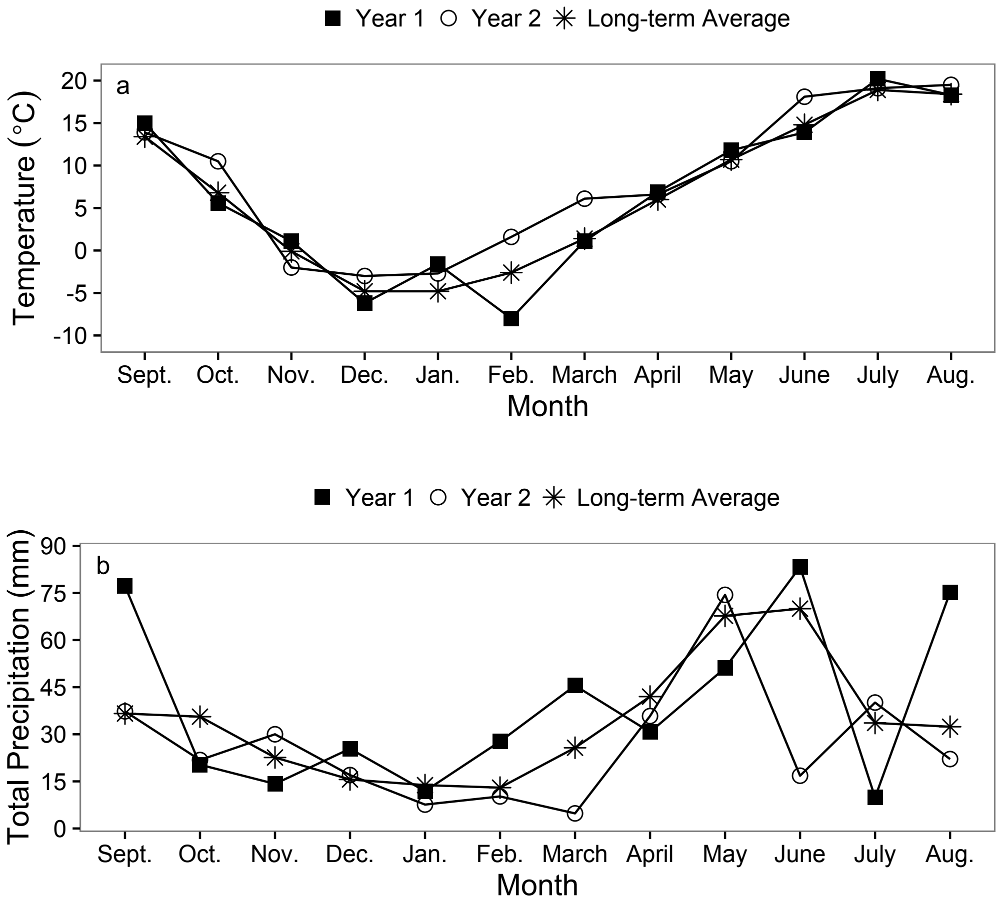

Figure 3.1. a) Average monthly temperature and b) Total monthly precipitation for Year 1: 2013 to 2014, Year 2: 2014 to 2015, and the long-term average (1967 to 2015, 48 years) at the study site.

Vegetation Density and Biomass

The effects of herbicide and fungicide seed treatment on *B. tectorum* density depended on year (Table 3.1). *Bromus tectorum* density in Year 1 was higher in non-sprayed (1382 ± 518 tillers m^{-2}) compared to sprayed (576 ± 312 tillers m^{-2}) plots (Figure 3.2). The effect disappeared in Year 2 when both treatments resulted in similar *B. tectorum* densities with 9090 ± 1571 tillers m^{-2} in non-sprayed and 7274 ± 1557 tillers m^{-2} in sprayed plots. *Bromus tectorum* density did not differ between the fungicide treated and non-treated plots within each year (Figure 3.3), but density increased within each treatment from Year 1 to Year 2. Treated plots increased by a factor of seven from 1069 ± 370 tillers m^{-2} in Year 1 to 7551 ± 1634 tillers m^{-2} in Year 2, and non-treated plots increased by a factor of 10 from 889 ± 520 tillers m^{-2} in Year 1 to 8814 ± 1528 tillers m^{-2} in Year 2.

Seeded perennial grass density was affected by herbicide across both years (Table 3.1). Seeded perennial grass density was higher (25 ± 7 tillers m^{-1}) in sprayed plots than in non-sprayed plots (13 ± 6 tillers m^{-1}).

The effect of herbicide on non-seeded perennial grass density depended on year (Table 3.1). Non-seeded perennial grass density was similar between non-sprayed and sprayed plots in Year 1. However, in Year 2 density was lower at 30 ± 30 tillers m^{-2} in the non-sprayed plots compared to sprayed plots where density was 291 ± 202 tillers m^{-2}, an order of a magnitude greater (Figure 3.4).

Exotic annual forb density was influenced by the individual effects of seeding rate and year (Table 3.1). Averaged between years, exotic annual forb density was higher at 63 ± 31 plants m^{-2} in the 1X seeding rate compared to the 2X seeding rate at 39 ± 23 plants m^{-2}. Exotic annual forb density decreased from 90 ± 35 individuals m^{-2} in Year 1 to 13 ± 9 individuals m^{-2} in Year 2.

Bromus tectorum, seeded perennial grasses, and exotic annual fob biomass was unaffected by treatments in Year 2 (Table 3.2). However, non-seeded perennial grass biomass was marginally affected by herbicide (Table 3.2). Averaged between years, non-seeded perennial grass biomass was 4.98 ± 3.15 g m^{-2} in non-sprayed plots compared to 94.66 ± 60.61 g m^{-2} sprayed plots. There were too few observations of annual grasses and native forbs to conduct statistical models for density and biomass.

Table 3.1. F-statistics and P-values from a repeated measure analysis of variance to test for the treatment effects of fungicide, seeding rate, herbicide, and their interactions on density of plant functional groups. Significant effects (α < 0.05) in bold.

		Bromus tectorum	Seeded Perennial Grasses	Non-seeded Perennial Grasses	Exotic Annual Forbs
Parameter	df	P	P	P	P
Fungicide	1, 53	0.42	0.74	0.65	0.34
Seeding rate	1, 53	0.99	0.17	0.34	**0.03**
Herbicide	1, 53	**< 0.01**	**< .01**	**0.03**	0.41
Year	1, 56	**< 0.01**	0.22	**0.03**	**< .01**
Fungicide x Seeding rate	1, 53	0.69	0.86	0.09	0.46
Fungicide x Herbicide	1, 53	0.70	0.34	0.49	0.90
Herbicide x Seeding rate	1, 53	0.80	0.51	0.16	0.14
Fungicide x Year	1, 56	**0.03**	0.91	0.21	0.39
Seeding rate x Year	1, 56	0.30	0.70	0.59	0.44
Herbicide x Year	1, 56	**0.03**	0.89	**0.01**	0.75
Fungicide x Seeding rate x Herbicide	1, 53	0.53	0.16	0.56	0.74
Fungicide x Seeding rate x Year	1, 56	0.36	0.32	0.83	0.58
Fungicide x Herbicide x Year	1, 56	0.88	0.23	0.91	0.58
Seeding rate x Herbicide x Year	1, 56	0.80	0.95	0.75	0.74
Fungicide x Seeding rate x Herbicide x Year	1, 56	0.97	0.70	0.57	0.66

Table 3.2. F-statistics and P-values from a linear mixed effects analysis of variance to test for the treatment effects of fungicide, seeding rate, herbicide, and their interactions on biomass of each functional group collected in Year 2.

		Bromus tectorum	Seeded Perennial Grasses	Non-seeded Perennial Grasses	Exotic Annual Forbs
Parameter	df	P	P	P	P
Fungicide	1, 53	0.14	0.34	0.52	0.26
Seeding rate	1, 53	0.23	0.86	0.83	0.30
Herbicide	1, 53	0.70	0.14	0.05	0.73
Fungicide x Seeding rate	1, 53	0.29	0.50	0.65	0.81
Fungicide x Herbicide	1, 53	0.33	0.26	0.90	0.56
Seeding rate x Herbicide	1, 53	0.45	0.78	0.85	0.17
Fungicide x Seeding rate x Herbicide	1, 53	0.15	0.41	0.92	0.79

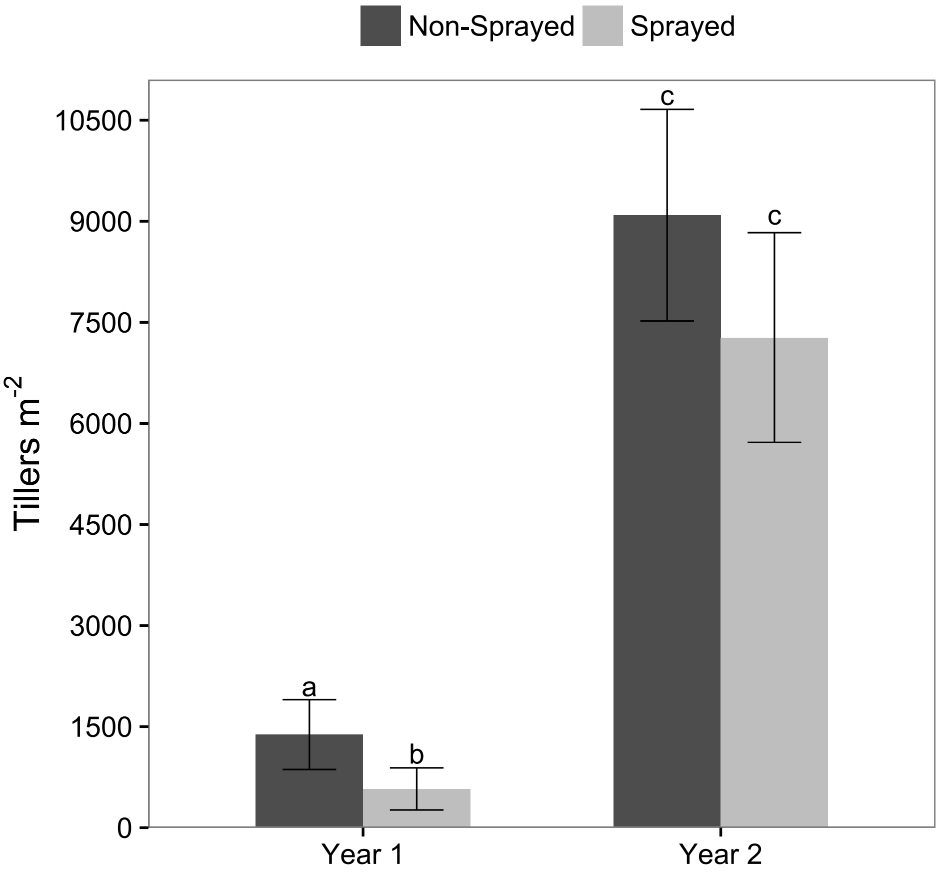

Figure 3.2. *Bromus tectorum* density (tillers m^{-2}) as affected by herbicide and year. Error bars indicate the 95% confidence interval around the mean. Bars with different letters indicate means that are different from each other ($\alpha = 0.05$).

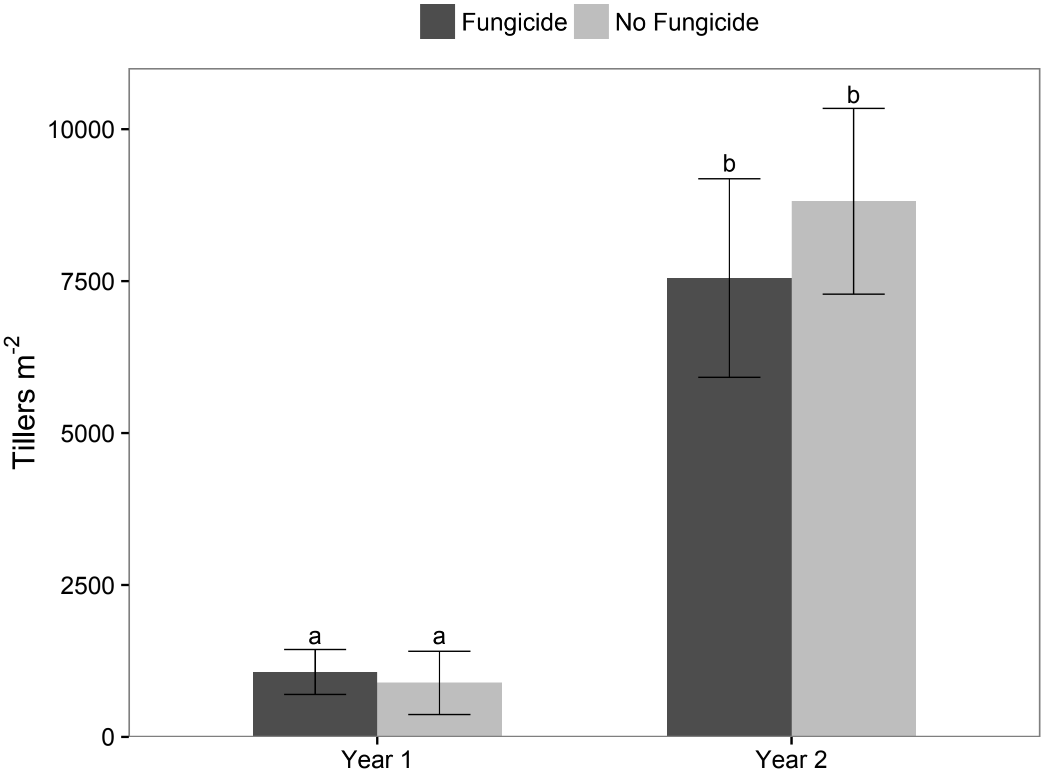

Figure 3.3. *Bromus tectorum* density (tillers m^{-2}) as affected by fungicide and year. Error bars indicate the 95% confidence interval around the mean. Bars with different letters indicate means that are different from each other ($\alpha = 0.05$).

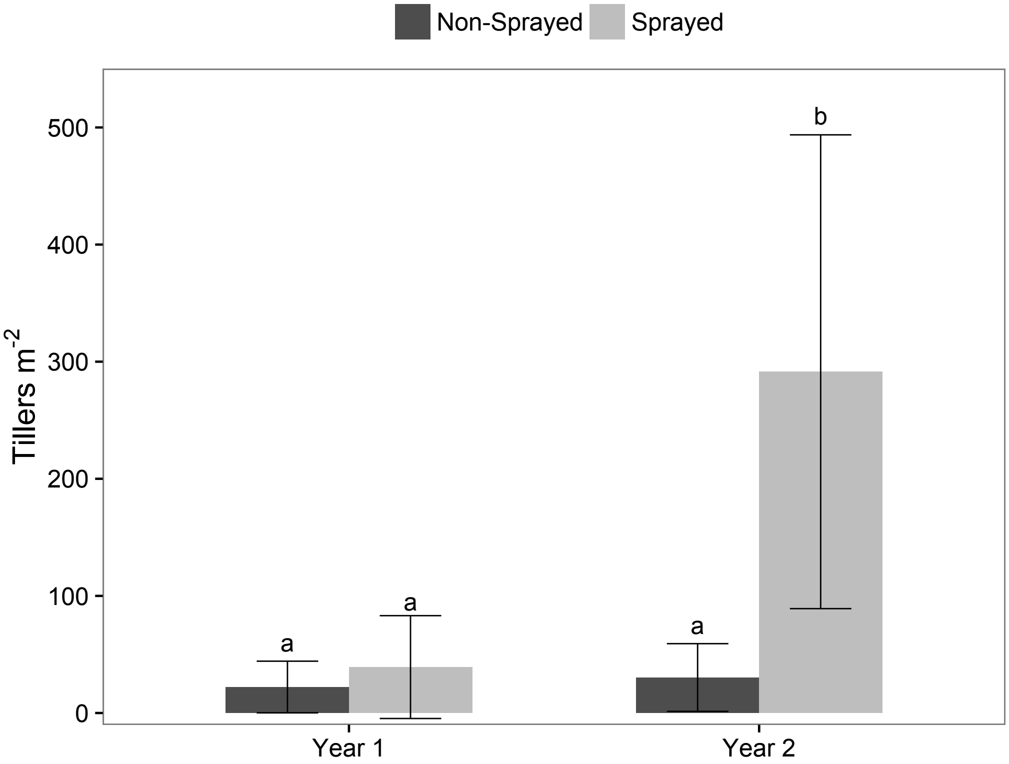

Figure 3.4. Non-seeded perennial grass density (tillers m^{-2}) as affected by herbicide and year. Error bars indicate the 95% confidence interval around the mean. Bars with different letters indicate means that are different from each other ($\alpha = 0.05$).

Discussion

Integrating multiple management approaches into an ecologically-based management plan could help overcome common causes of revegetation failure in rangeland settings, including unsuccessful control of the target weed, residual effects of herbicides, insufficient propagule pressure of desired species, and exposure of desired species to soil pathogens (Christensen 1989, Svejcar et al. 2014). In this study, imazapic and *P. semeniperda* were integrated with two rates of perennial grass seeding and a fungicide seed treatment as an approach to revegetate a *B. tectorum* infested site.

This study adds to the knowledge of integrated management in *B. tectorum*-invaded systems, as there were positive effects of treatments, particularly short-term impacts of herbicide application, and gained knowledge of the efficacy of seeding rates and fungicide seed treatments.

Imazapic efficacy on *B. tectorum* can be site and year specific (Orloff et al. 2015), and its effect on seeded perennial grasses may be affected by the time between imazapic application and seeding. In Year 1, *B. tectorum* density decreased with the 120 g ai ha^{-1} imazapic rate compared to non-sprayed plots, while in Year 2 its density increased and was similar between sprayed and non-sprayed plots. This imazapic rate did not affect emergence of perennial grasses 166 d after herbicide application and instead resulted in a two-fold increase in seeded perennial grass density. In contrast, in Idaho, Shinn and Thill (2004) observed injured perennial grasses that were seeded and then sprayed 1 d later with imazapic at 140 g ai ha^{-1}. In Utah Morris et al. (2009) applied four imazapic rates (35, 70, 105, and 140 g ai ha^{-1}) to *B. tectorum* at two sites and seeded perennial plants 12 d later; but successful *B. tectorum* control with a consequent increase in perennial grasses establishment occurred at only one site with imazapic rates of 105 g ai ha^{-1} and 140 g ai ha^{-1} (Morris et al. 2009). These results suggest that fall-applied imazapic may lead to poor seeded perennial grass establishment if seeding also occurs in the fall. This is supported, in part, by Ehlert et al. (2015) who found that fall-applied imazapic (80, 160, and 240 g ai ha^{-1}) persisted into the spring in a semiarid environment, and all rates similarly degraded 160 d after application, relative to its half-life of 120 d (Tu et al. 2001). Degradation of imidazolinone herbicides is primarily due to microbial activity and therefore limited or slowed by low moisture and temperatures (Mangels 1991, Prostko et al. 2005). Taken together, these results suggest that imazapic applied at 120 g ai ha^{-1} degraded to concentrations non-lethal to perennial grasses by the time of seeding. Further, these results suggest that an imazapic rate between 80 and 120 g ai ha^{-1} may be beneficial for one year of *B. tectorum* control in revegetation scenarios, depending on site-specific characteristics such as temperature and precipitation.

Imazapic was applied in November of Year 1 when *B. tectorum* was at the 4-leaf growth stage, which Mangold et al. (2013) found to be less effective in achieving *B. tectorum* control compared to applying imazapic when *B. tectorum* is at a 1-2 leaf growth stage. However, the study site received 137.1 mm precipitation from August to November in Year 1, which was higher than the long-term average of 110.4 mm received during the same time period. Due to the precipitation that occurred prior to herbicide application, it is likely that most *B. tectorum* seedlings had already emerged at the time of imazapic application, exposing these seedlings to the effects of the herbicide, which may have been enhanced under the cool and wet conditions (Mangels 1991, Prostko et al. 2005).

Temperature and precipitation also influence germination and establishment of both *B. tectorum* and desired species (Hardegree et al. 2003, Meyer et al. 2000, Rawlins et al. 2012a, b), and at the study site, were generally higher in spring than fall. Successful perennial grass establishment was likely due to these warm temperatures combined with 175.0 mm of precipitation received from March to June in Year 1.

Although planting date was not manipulated, common drawbacks of fall planting (Boyd and James 2013) may have been avoided by planting in the spring. Specifically, perennial species planted in the fall may germinate prior to winter onset, thereby resulting in pre-emergent mortality (Boyd and James 2013, James et al. 2011, Laude 1956).

Intra- and interspecific competition may explain the absence of a seeding rate effect on perennial grass establishment. Mangla et al. (2011) studied intra- and interspecific competition between invasive annual grasses [*B. tectorum* and *Taeniatherum caput-medusae* (medusahead)] and native species [*P. spicata* and *Poa secunda* (Sandberg bluegrass)] in greenhouse settings. Their results revealed that intraspecific competition in native species during initial growth stages contributed to smaller seedlings, because individuals shared similar resource requirements.

There was no effect of seeding rate, and seedbed preparation and planting method, while not formally tested, may explain the observed establishment of perennial grasses. Drill seeding was simulated by hand seeding with garden hoes, which allowed accurate seed depth and good seed-soil contact. James and Svejcar (2010) investigated different seeding techniques (rangeland drill, hand seeding) of desired species [*P. spicata, Agropyron desetorum* (desert wheatgrass), *Agropyron smithii* (western wheatgrass), *Leymus cinereus* (basin wildrye), *Elymus wawawaiensis* (Snake River wheatgrass), *Poa secunda* (Sandberg bluegrass), *Agropyron fragile* (Siberian wheatgrass), *Achillea millefolium* (common yarrow), and *Linum perenne* (blue flax)] and found that seedling density increased from 12.2 ± 6.1 plants m^{-2} with a rangeland drill to 18.4 ± 4.6 plants m^{-2} with hand seedling. Although different seeding techniques were not tested, perennial grass densities of 13 to 25 tillers m^{-1} were achieved across herbicide treatments two years after seeding. Such densities are more promising than densities reported in other annual grass revegetation studies where drill seeding (Cox and Anderson 2004, Mangold et al. 2015, Sheley et al. 2006) or broadcast seeding (Cox and Anderson 2004, Sheley et al. 2006) was implemented and support the need for improvements in seeding technology (James and Svejcar 2010). Further, there was flooding and silt deposition at the field site prior to treatment application, which may have influenced both *B. tectorum* and seeded perennial grasses, with respect to available soil moisture and nutrients.

Perennial grass seeds were treated with a fungicide prior to planting, because emergence can by inhibited by soil-borne fungal pathogens (Harper 1977). However, there was no effect of the fungicide seed treatment, except for interannual variability. This may have occurred because temperature and moisture conditions were favorable for perennial grass establishment and emergence, which may have reduced the impact of soil pathogens. The efficacy of *P. semeniperda*, the pathogen evaluated as a *B. tectorum* control agent, is temperature-dependent (Campbell et al. 1996, Campbell and Medd 2003), which is crucial since it competes against the seed for seed reserves necessary for germination (Beckstead et al. 2007, Meyer et al. 2007, 2008a, b). Thus, there may not have seen either an effect of *P. semeniperda* or fungicide because of favorable temperatures for perennial grasses, allowing germination and negating any need for seed protection. In contrast, previous laboratory studies show that *P.*

semeniperda may work on *B. tectorum* populations of cold deserts in Idaho and Utah (Meyer et al. 2007) and salt desert shurblands and sagebrush steppes in Utah (Beckstead et al. 2007). Furthermore, studies have demonstrated that fungicides can protect seeds from susceptibility to pathogen attack (Dalling et al. 1998, O'Hanlon-Manners and Kotanen 2004), suggesting they can be useful tools when *P. semeniperda* is considered as a biological control agent of *B. tectorum*. At the same time, a fungicide did not increase the seedbank survival of two native species in the presence of an invader, *Lonicera maackii* (Caprifoliaceae) (Orrock et al. 2012). Land managers can thus save resources by not treating seeds prior to planting, unless knowledge exists about other pathogenic soil microbes at a site or the effectiveness of the proposed pathogenic biological control agent.

While there did not see an effect of *P. semeniperda* in this study, *B. tectorum* was effectively controlled for one year with a single imazapic application and there was strong perennial grass establishment two years after treatment. Future research should test *P. semeniperda* against *B. tectorum* from a range of environments to determine exactly how environmental conditions, particularly temperature, play a role in its efficacy. This is crucial as temperature plays a role in both *P. semeniperda* efficacy and *B. tectorum* germination. Moreover, a temperature that is beneficial for *P. semeniperda* infection may not be for *B. tectorum* germination and vice versa. Seeding technologies need to be developed and tested to provide the accurate seed depth and seed-soil contact achieved with hand seeding, as this will likely save land managers time, money, effort, and reduce frustration associated with *B. tectorum* control. Overall, there is optimism that research advances - such as seeding technologies and biological control with *P. semeniperda* - will result in better control of *B. tectorum* populations in rangelands.

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CHAPTER FOUR

ROLE OF TEMPERATURE ON EFFICACY OF *PYRENOPHORA SEMENIPERDA* AS A BIOLOGICAL CONTROL AGENT OF THREE DISTINCT, LOCALLY-ADAPTED POPULATIONS OF *BROMUS TECTORUM* L. (CHEATGRASS, DOWNY BROME)

Introduction

Bromus tectorum (cheatgrass, downy brome) is a ubiquitous invasive annual grass in western North America where it infests millions of hectares of cropping, forage, and rangeland systems (Mack 1981, Rice 2005). The range of *B. tectorum* is expected to expand with increasing temperatures (Bradley 2009). For example, Blumenthal et al. (2016) suggested that increased temperatures will directly impact *B. tectorum* invasions as they will expand its phenological niche by decreasing limitations on recruitment and growth, particularly at higher elevations. In accordance, Suring et al. (2005) reported that current *B. tectorum* invasions are more severe in warm, dry, low elevation sites compared to cold and wet high elevation sites.

Bromus tectorum typically behaves as a winter annual species and germinates in the fall, but if temperature and precipitation conditions are favorable it can also behave as a summer annual and germinate in the spring (Espeland et al. 2016). This prolonged germination period is due to secondary dormancy (Harmon et al. 2012) that is brought on by low winter temperatures (Young and Evans 1975). Seeds entering secondary dormancy during winter add to the carryover spring seedbank (Young and Evans 1975, Young et al. 1969). As temperatures warm in the spring, secondary dormancy breaks but spring-germinated plants are often smaller and less vigorous than fall-germinated ones that underwent a longer vernalization period (Stewart and Hull 1949).

Bromus tectorum populations exhibit high phenotypic plasticity (Mack 1981), which plays a significant role in its invasiveness potential (Anderson 1996, Mack & Pyke 1983). Specifically, *B. tectorum* has been found along elevational gradients, which suggests phenotypic plasticity to environmental conditions (Allen and Meyer 2002, Brown and Rowe 2004, McCarlie et al. 2003, Meyer et al. 1997). In accordance, *B. tectorum* traits such as germination, growth rates (McCarlie et al. 2003), and seed production (Rice and Mack 1991b, c) differ either due to environmental differences or genetic variation.

The efficacy of *B. tectorum* management strategies may be impacted by environmental conditions or genetic variation. For example, Orloff et al. (2015) reported site-specific responses to imazapic in annual brome invaded old-field and rangeland sites that had existing and seeded perennial grasses. Similarly, Elseroad and Rudd (2011) and Morris et al. (2009) found variation in the duration of *B. tectorum* control due to site-specific responses, and Sheley et al. (2010) suggested that site-specific factors such as climate and genetic differentiation of the target population influence restoration success. In accordance, Zelikova et al. (2013) determined that *B. tectorum*'s response to warming conditions depended on a site's climate characteristics (e.g. temperature, precipitation) and *B. tectorum* genotype.

Understanding the effects of temperature on weed-biological control interactions may shed light on site-specific outcomes and responses of these interactions in a warming climate (Bebber et al. 2013). Classical biological control agents, i.e. herbivorous insects, have demonstrated varying levels of efficacy depending on climate variables such as temperature (Lu et al. 2013, Ortega et al. 2012). Warming conditions impact biological control insects by extending the growing season, changing the timing of emergence, and altering geographical distributions (Gitay et al. 2002, Porter et al. 1991). Despite this research, little is known about the effect of climate change on fungal pathogens used as biological control agents.

Previous research (Beckstead et al. 2007, 2010, Ehlert et al. 2014, Meyer et al. 2007, 2008) has focused on using a soil-borne fungal pathogen, *Pyrenophora semeniperda* (Brittlebank and Adam) Shoemaker (Ascomycotina: Pyrenomycetes), as a biological control agent of *B. tectorum*. *Pyrenophora semeniperda* conidia in the soil are carried via germination tubes to grass inflorescences where they infect developing ovaries during anthesis (Medd et al. 2003). Infected mature host grass seeds disperse to the ground where *P. semeniperda* remains as mycelium for the rest of summer. The fungus prevents seeds from germinating by usurping starch resources within the ovary. Consequently, *P. semeniperda*'s efficacy has been linked to how quickly host seeds capitalize on their seed reserves (Beckstead et al. 2007); seeds that germinate quickly either due to phenotypic plasticity or genetic variation can effectively outcompete *P. semeniperda* for starch resources within the ovary, while slow-germinating and dormant seeds are more susceptible to mortality.

The efficacy of *P. semeniperda* has been linked to temperature (Campbell et al. 1996, 2003). In a laboratory setting, Campbell et al. (2003) found that 23°C *in vitro* resulted in the greatest sporulation of *P. semeniperda*. In addition, heavy seeds have demonstrated less vulnerability to pathogens (Crist and Freise 1993), higher germination and emergence, and can produce larger and more vigorous seedlings (Black 1956, Harper and Obeid 1967, Schaal 1980) compared to light seeds. Previous research has demonstrated that *P. semeniperda* impacts species with lower seed weight more than heavy-seeded species (Ehlert et al., *unpublished data*). However, research to date has not investigated whether intraspecific variation in seed weight influences susceptibility to *P. semeniperda*. To address this knowledge gap, the objective was to assess *P. semeniperda* efficacy as a biological control agent with varying temperatures across three distinct, locally-adapted populations of *B. tectorum*. The hypothesis was that (1) *P. semeniperda* infection will increase and (2) *B. tectorum* germination will decrease with increasing temperature and (3) *B. tectorum* populations will respond differently to *P. semeniperda* across a temperature gradient, depending on their seed weight.

Materials and Methods

Bromus tectorum Seed Sources

Bromus tectorum seeds were collected in 2015 from three environments (range, crop, sub-alpine) that had established *B. tectorum* infestations (Table 4.1). The rangeland system was located on private land 26 km northwest of Dillon, MT. The cropping system was located at Montana State University's Arthur H. Post Agronomy Research Farm, 8.8 km west of Bozeman, MT. The sub-alpine system was located 10.4 km northwest of Norris, MT. Seeds collected from these environments are hereafter referred to as the range, crop, and sub-alpine populations, respectively. To determine mean seed weight, three samples of 100 seeds of each population were dried (50°C for 72 hr) (National Seed Laboratory) and weighed to the nearest 0.01 g.

Pyrenophora semeniperda Inoculum Preparation

An isolate of *P. semeniperda* was obtained from a sagebrush steppe system (39.613524, -112.002022) 17.4 km southwest of Nephi, UT, (Susan Meyer, *personal communication*) in the form of air-dried conidia. Air-dried conidia were placed on Petri dishes containing modified alphacel medium (Stewart 2009). Four-40 watt cool-white and four-40 watt black light florescent tubes were positioned 40 cm above Petri dishes to provide a 12 h near visible ultraviolet (320-420 nm) photoperiod and maintained at room temperature (20°C). Petri dishes were checked for contaminants every two to three days, and an X-Acto® knife dipped in ethanol and flame-sterilized was used to remove bacterial contaminants. After 12 d, conidia were harvested from Petri dishes by rinsing the surface with 5 mL of sterile deionized water and gently scraping the surface with a rubber-tipped glass-stirring rod. Additional water was used, as needed, to gently scrape the surface clean and the conidia solution was poured into a sterile glass jar. A haemocytometer was used to quantify conidia concentration, and sterile deionized water water was added until a 5,000 conidia mL^{-1} concentration was achieved for the inoculum (Beckstead et al. 2007). Inoculum was stored at 5˚C until seed inoculation, approximately 60 days after preparation.

Experimental Design

The experiment was conducted on a thermo-gradient table at Montana State University that had six parallel aluminum plates (101.6 cm long x 15.2 cm wide x 1.0 cm thick). Temperature was controlled with a 200 W fluid loop chiller and a 260 W fluid heater at opposite ends of the table, resulting in a 19°C temperature gradient. The experiment consisted of two *P. semeniperda* treatments [inoculated, non-inoculated (control)], three *B. tectorum* populations (range, crop, sub-alpine), and five temperatures [(13.0°C, 17.2°C, 20.9°C, 24.6°C, 32.0°C (± 0.1°C)]. All treatments were replicated three times in a randomized block design. Two trials were conducted from 23 October 2015 to 22 November 2015 (Trial 1) and 21 January 2016 to 20 February 2016 (Trial 2). Each trial lasted 30 days.

Inoculum Application and Data Collection

Prior to inoculation, all *B. tectorum* seeds were surface sterilized to remove unwanted debris and non-*P. semeniperda* microbial material by submerging them for 60 sec in 70% ethanol, 60 sec in 10% bleach, 60 sec in 70% ethanol, and rinsing with sterile deionized water for 30 sec (Stewart 2009). Inoculated seeds were placed in Petri dishes (35 mm x 11 mm) containing *P. semeniperda* inoculum (5 seeds, 1 mL inoculum per Petri dish), and control seeds received an equivalent amount of sterile deionized water. All seeds were placed on a shaker table for 14 h at 50 rpm to allow for absorption of *P. semeniperda* inoculum.

Five inoculated and five control *B. tectorum* seeds of each population were placed in individual Petri dishes containing autoclaved filter paper (32 mm diameter) that was wetted with 1 ml of sterile deionized water. Petri dishes were sealed with Parafilm® (Bemis, Oshkosh, WI) to prevent the filter paper from drying out. Filter paper was re-wetted with 1 mL sterile deionized water as needed. *Pyrenophora semeniperda* infection and seed germination were recorded at day 30. Infection was based on the presence of stromata (i.e. black fingers-like appendages) emerging from the seed, and seeds were considered germinated if a radicle greater than 1 mm was present.

Statistical Analysis

To evaluate if seed weight differed among *B. tectorum* populations, an analysis of variance (ANOVA) was conducted with population (range, crop, sub-alpine) as the model predictor and seed weight as the response variable. To determine if population and temperature influenced infection at day 30, a subset of data of only the inoculated treatment was used, as there was no infection present in the control. An ANOVA was performed with population, temperature, trial, and their interactions as predictor variables. The error term was block nested within trial. To determine if population, temperature, and *P. semeniperda* influenced germination at day 30, an ANOVA was conducted with population, temperature, *P. semeniperda*, trial, and their interactions as predictor variables. The error term was block nested within trial. Counts of infection and germination were logit transformed, after adding 0.01, to meet assumptions of normality. All analyses were performed using R software (R Core Team 2016). When significant models were found, means were separated using least squared means (LSD) ($\alpha < 0.05$) in the lsmeans package (Lenth and Hervé 2016).

Table 4.1. Seed source information for the range, crop, and sub-alpine *Bromus tectorum* seeds used in this study.

Population	Seed Source	Elevation (m)	Location	Soil^	Precipitation* (mm)	Mean Annual Temperature* (°C)
Range	Hogsback Ranch	1444	45.7570, -111.7953	Nuley clay loam; 0-18 cm clay loam 18-38 cm clay loam	337	7.4
Crop	MSU Arthur H. Post Agronomy Research Farm	1432	45.6775, -111.1560	Amsterdam-Quagle silt loam; 0-20 cm silt loam 20-38 cm silt loam	410	4.7
Sub-alpine	Preacher Creek in Tobacco Root Mountains#	1770	45.5950, -111.8310	Branham Rock Outcrop complex; 0-10 cm coarse sandy loam 10-30 cm gravelly coarse sandy loam	450	5.2

#Information on sub-alpine population obtained from Seipel et al. (2016).
*(WRCC 2016)
^(USDA-NRCS 2016)

Results

Seed Weight

Seed weight differed among populations (P < 0.01). Specifically, the sub-alpine population had the lowest seed weight of 191.7 ± 4.3 mg, while the crop population had the highest seed weight of 299.3 ± 2.2 mg. The range population had an intermediate seed weight of 224.3 ± 1.5 mg.

Infection

The effect of temperature on infection varied by population (temperature x population, P = 0.03, Table 4.2), and the interaction was largely driven by differences between the crop population and the other two populations at 17°C, 21°C, and 25°C (Figure 4.1). At 17 °C infection was the same for the range (66.7 ± 9.9%) and sub-alpine populations (46.7 ± 12.3%); the sub-alpine population was also similar to the crop population (20.0 ± 7.3%), averaged across trials. At 21°C and 25°C, there was similar and higher infection rate for the range and sub-alpine populations compared to the crop population. Infection was similar for all three populations at 13°C and 32°C.

The effect of temperature on infection depended on trial (temperature x trial, P < 0.01, Table 4.2), and the temperature by trial interaction was driven by differences between trials at 32°C. Specifically, infection was 44.4 ± 8.0% in trial 1 and 6.7 ± 4.7% in trial 2 at 32°C (Figure 4.2). The two trials resulted in similar infection at 13°C, 17°C, 21°C, and 25°C with 35.5 ± 5.3%, 44.4 ± 7.2%, 61.1 ± 7.1%, and 61.1. ± 8%, respectively, averaged across trials and populations.

Table 4.2. P-values from an analysis of variance to test for the effects of trial, population, and temperature on seed infection. Significant effects ($\alpha = 0.05$) in bold.

Parameter	df	P
Trial	1	0.186
Population	2	**< 0.01**
Temperature	4	**< 0.01**
Population x Temperature	8	**0.03**
Population x Trial	2	0.06
Temperature x Trial	4	**< 0.01**
Population x Temperature x Trial	8	0.55

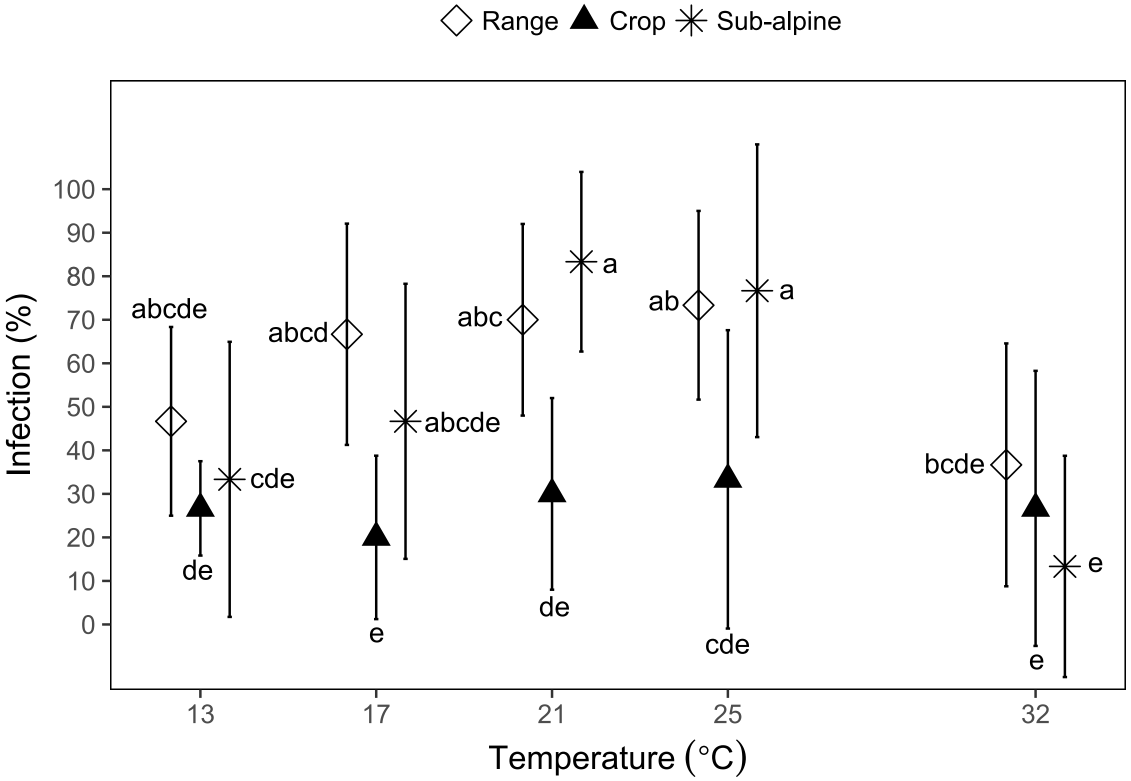

Figure 4.1. Infection as affected by temperature and population. Error bars indicate a 95% confidence interval around the mean. Letters indicate means that are different from one another ($\alpha = 0.05$).

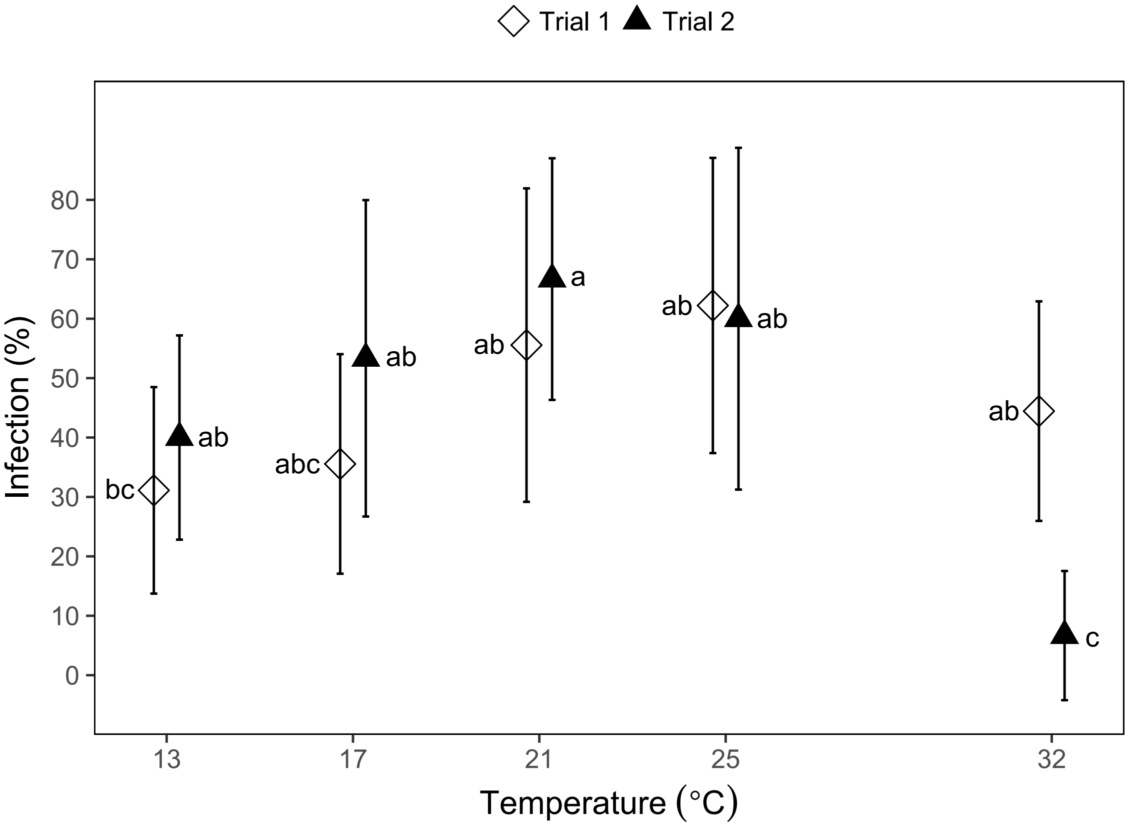

Figure 4.2. Infection as affected by temperature and trial. Error bars indicate a 95% confidence interval around the mean. Letters indicate means that are different from one another ($\alpha = 0.05$).

Germination

The effect of temperature on germination depended on *P. semeniperda* treatment (temperature x *P. semeniperda,* P = 0.05, Table 4.3). The interaction was driven by differences between the control and inoculated treatment at 13°C. Specifically, germination was 38.9 ± 8.2% and 22.2 ± 5.3% in the control and inoculated treatment, respectively, averaged across populations and trials (Figure 4.3). The four other temperatures resulted in similar germination between the control and inoculated treatment.

Table 4.3. P-values from an analysis of variance to test for the effects of trial, population, *P. semeniperda,* and temperature on seed germination. Significant effects (α = 0.05) in bold.

Parameter	df	P
Trial	1	0.89
Population	2	**< 0.01**
P. semeniperda	1	0.08
Temperature	4	**< 0.01**
Population x *P. semeniperda*	2	0.54
Population x Temperature	8	0.39
P. semeniperda **x Temperature**	4	**0.05**
Population x Trial	2	**< 0.01**
P. semeniperda x Trial	1	0.95
Temperature x Trial	4	**< 0.01**
Population x *P. semeniperda* x Temperature	8	0.17
Population x *P. semeniperda* x Trial	2	0.49
Population x Temperature x Trial	8	**0.05**
P. semeniperda x Temperature x Trial	4	0.06
Population x *P. semeniperda* x Temperature x Trial	8	0.48

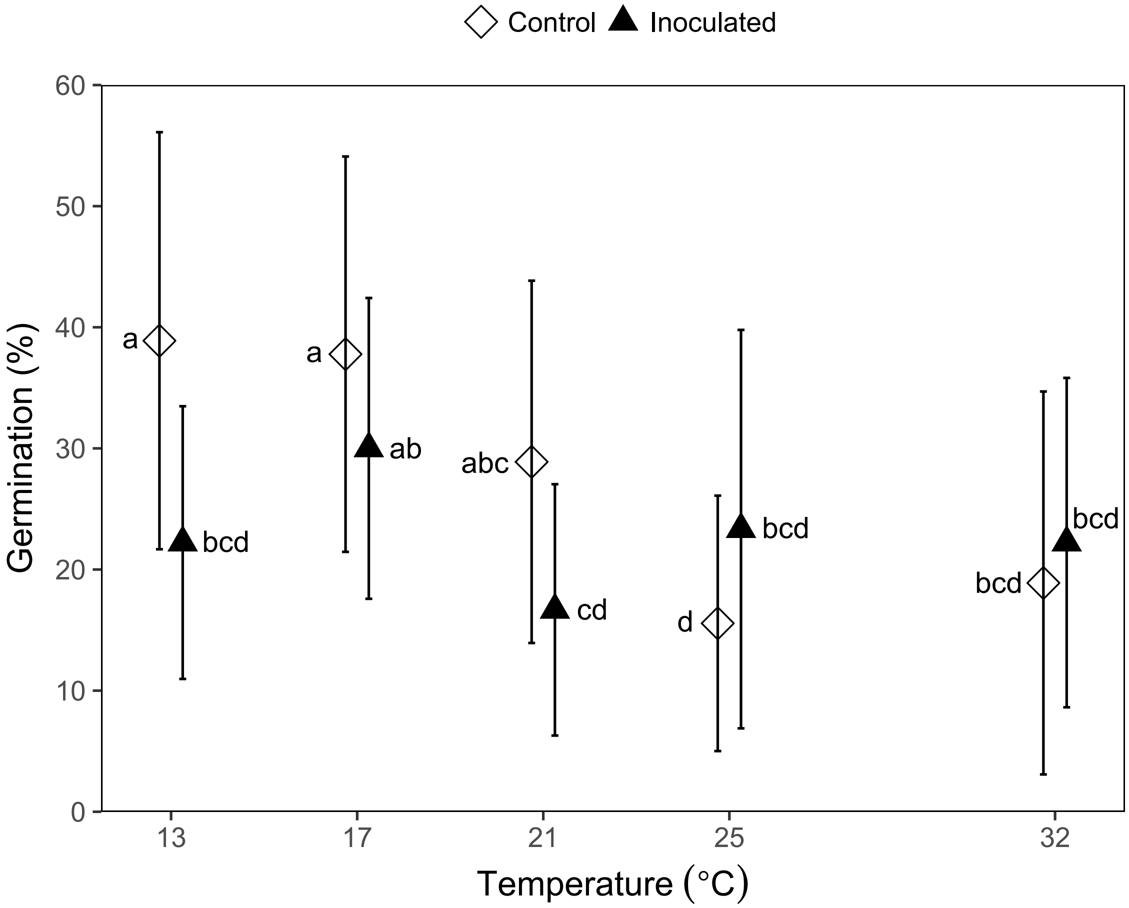

Figure 4.3. Germination as affected by temperature and *P. semeniperda* treatment. Error bars indicate a 95% confidence interval around the mean. Letters indicate means that are different from one another ($\alpha = 0.05$).

The effect of temperature on germination depended on population and trial (population x temperature x trial, $P = 0.05$, Table 4.3, Figure 4.4). The three-way interaction was driven by differences between populations and temperatures across trials (population x trial, $P < 0.01$; temperature x trial, $P < 0.01$, Table 4.3). The population by trial interaction was driven by differences between trial 1 and trial 2 for the sub-alpine population (Figure 4.5). Specifically, the sub-alpine population's germination was 21.3 ± 4.4% in trial 1 and 35.3 ± 5.0% in trial 2. Averaged across trials, germination was lowest for the range population (5.7 ± 1.7%), intermediate for the sub-alpine population (28.3 ±

3.4%), and highest for the crop population (42.3 ± 4.0%). The temperature by trial interaction was driven by differences at the two temperature extremes of 13°C and 32°C. At 13°C, germination was 46.6 ± 7.2% and 14.4 ± 4.5% in trial 1 and trial 2, respectively; in contrast, at 32°C, germination was 1.1 ± 1.1% in trial 1 and 40.0 ± 7.2% in trial 2. Intermediate temperatures did not differ in germination between the two trials; averaged across trials and populations, germination decreased as temperature increased with 33.9 ± 4.8%, 22.8 ± 4.4%, and 19.4 ± 4.6% at 17°C, 21°C, and 25°C, respectively.

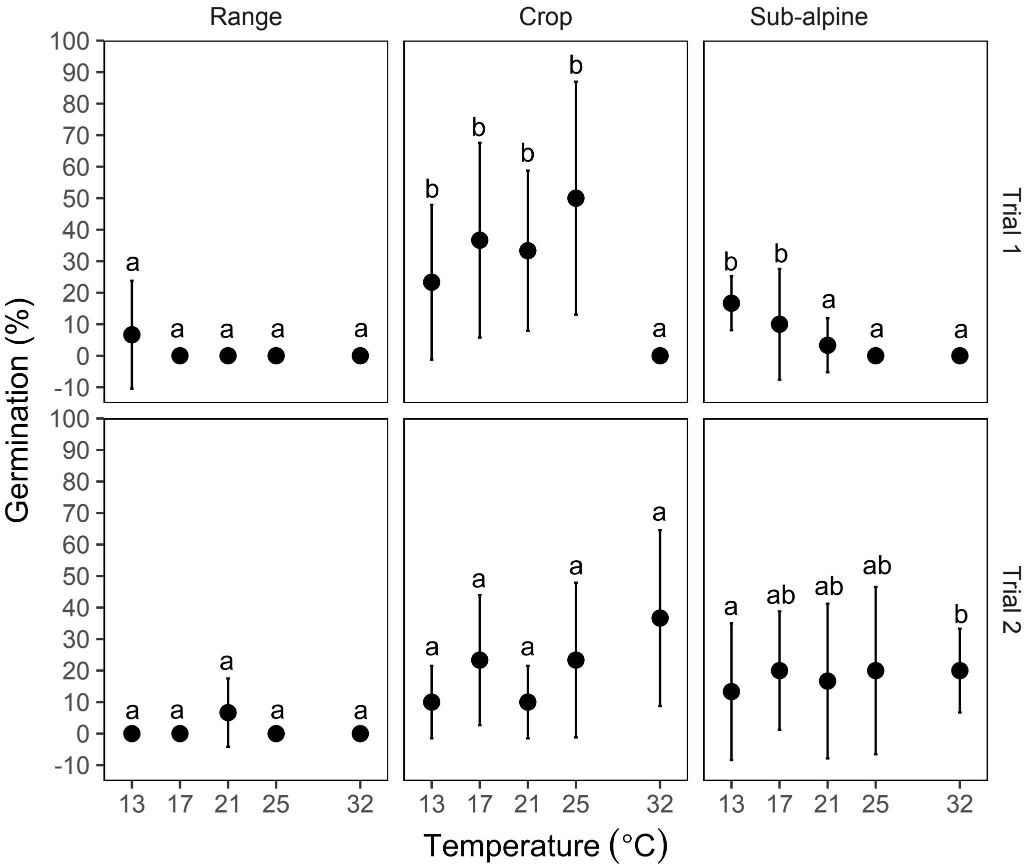

Figure 4.4. Germination as affected by population, temperature, and trial. Error bars indicate a 95% confidence interval around the mean. Letters indicate means that are different from one another (α = 0.05) within each population by trial combination.

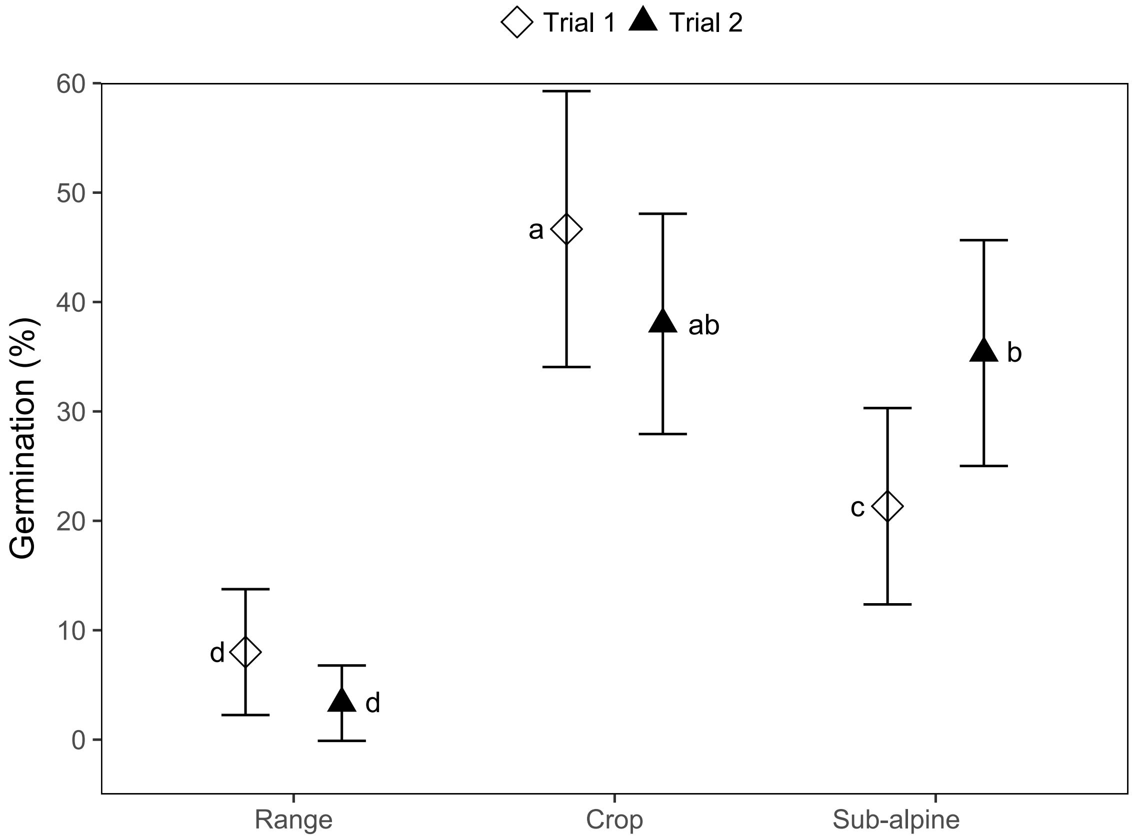

Figure 4.5. Germination as affected by population x trial. Error bars indicate a 95% confidence interval around the mean. Letters indicate means that are different from one another ($\alpha = 0.05$).

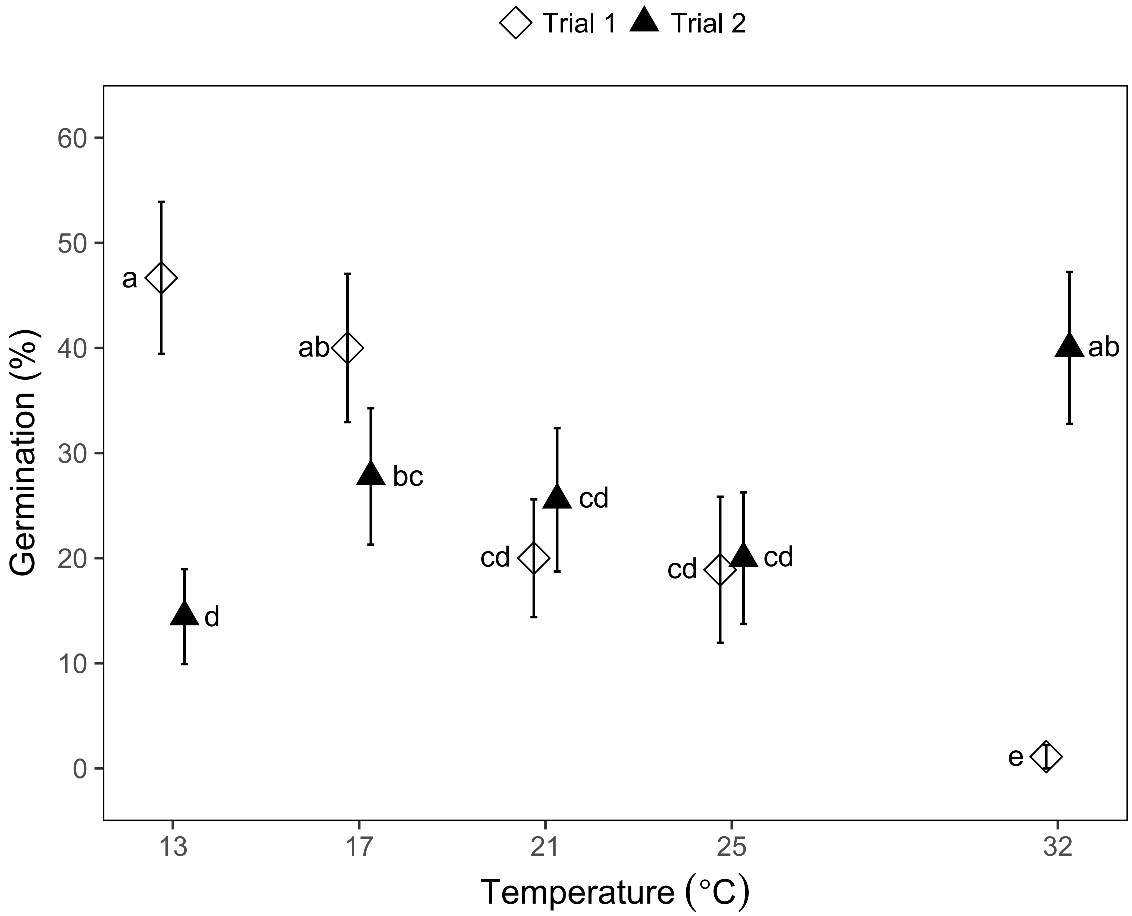

Figure 4.6. Germination as affected by temperature and trial. Error bars indicate a 95% confidence interval around the mean. Letters indicate means that are different from one another (α = 0.05).

Discussion

The development of an alternative management strategy for *B. tectorum* that incorporates the biological control agent *P. semeniperda* has been underway for some time (Beckstead et al. 2007, 2010, Ehlert et al. 2014, Meyer et al. 2007, 2008), and further advancement is needed as climate change influences the distribution of *B. tectorum* (Bradley et al. 2009, 2010, Concilio et al. 2013, Taylor et al. 2014, Zelikova et al. 2013) as well as efficacy of current control methods (Hellmann et al. 2008). To date, laboratory, greenhouse, and field research with *Pyrenophora* has used singular, isolated populations of *B. tectorum* and *P. semeniperda* (Beckstead et al. 2007, Campbell and Medd 2003, Ehlert et al. 2014). Although field research with *P. semeniperda* has utilized different sites, differences in *P. semeniperda* efficacy were attributed to site differences such as precipitation (Meyer et al. 2007) and failed to consider the potential impact of differences among *B. tectorum* populations. To fill this knowledge gap, the impact of *P. semeniperda* on different *B. tectorum* populations under varying temperatures was assessed. Further evaluation looked at differences in *B. tectorum* population seed weight and the influence on *P. semeniperda* infection.

Results indicated that response of *P. semeniperda* infection to temperatures was not consistent among *B. tectorum* populations. The range population was equally susceptible to infection while *P. semeniperda* was less effective at infecting the crop population, regardless of temperature. In contrast, the sub-alpine population experienced high levels of infection at 21°C and 25°C. Seed size was associated with infection rates. Lightweight populations (i.e. range and sub-alpine) are more susceptible to *P. semeniperda* infection compared to a heavier population (i.e. crop). The range and sub-alpine populations differed in seed weight by 32.6 mg and had similar levels of infection. In contrast, the crop population was 75.0 mg and 107.6 mg heavier than the range and sub-alpine populations, respectively, and experienced ~ 30% less infection. These results suggest that small differences in intraspecific seed weights could potentially have consequences for *P. semeniperda* infection. Results support the concept that small seeds are less vigorous (Pepper 2002), less stress tolerant (Liebman and Sundberg 2006), and therefore more vulnerable to pathogens (Crist and Freise 1993). In accordance, previous research found this to be true for grass species that co-occur with *B. tectorum* (Ehlert et al., *unpublished data*).

Differences in *B. tectorum* population susceptibility to *P. semeniperda* infection may be linked to local adaptation as a result of environmental differences (Allen and Meyer 2002, Meyer et al. 1997, McCarlie et al. 2003) and consequent novel recombinant populations (Novak and Mack 2001). The sites where these three populations were collected had different environmental characteristics, and germination was highest and infection lowest for the crop population, while the opposite occurred for the range population. Brown and Rowe (2004) investigated *B. tectorum* seed dormancy and germination response along an elevational gradient in Colorado, and their results revealed differences among populations and local adaptation, with evolved differences in populations due to selective pressures from their local environment. Taken together, these trends suggest that the strain of *P. semeniperda* tested and the *B. tectorum* populations used may have slightly different environmental ranges that they exist within, influencing susceptibility of *B. tectorum* to *P. semeniperda*. For example, the temperature optima of *P. semeniperda* and *B. tectorum* may overlap (Elton 2001, Grinnell 1917, Hutchinson 1957) in such a way that there are finite environmental parameters that allow *B. tectorum* to exist in a stressed state and *P. semeniperda* to flourish. Thus, utilizing *P. semeniperda* for *B. tectorum* control may be too environmentally constrained to warrant production on a commercial scale, unless locally adapted *P. semeniperda* is used.

Because *P. semeniperda* is a living organism, temperatures can have a large impact on growth and sporulation, and therefore, efficacy as a biological control. In this experiment temperature had an effect on *P. semeniperda* infection and influenced the effect of *P. semeniperda* treatment on germination. Laboratory research has found an optimal temperature for *P. semeniperda* growth to be 23°C (Campbell et al. 1996, 2003), but the temperature at which *P. semeniperda* loses efficacy has not been reported. In this experiment, as temperature increased, fewer seeds germinated. High soil temperatures such as 25°C and 32°C are unlikely to occur during the fall and spring months when *B. tectorum* germinates. Other research has found that germination can occur at temperatures just above freezing (5°C) (Evans and Young 1972) but is inhibited above 30°C (Harris and Gobel 1976).

Overall, results support the hypothesis. Although there were trial differences, *P. semeniperda* infection increased and germination decreased with increasing temperature and populations with different seed weights experienced different levels of infection. However, conclusions are limited because of the single inoculum source and small sample size, which was dictated by the amount of inoculum that was able to produce. Despite this, this study provides further insight into the temperature requirements of *B. tectorum* and *P. semeniperda* as intraspecific variations in seed weight were found that also influence *P. semeniperda* infection. Although *P. semeniperda* by itself is not a silver bullet for *B. tectorum,* it may have a place in the future as part of site-specific integrated management strategies.

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CHAPTER FIVE

SUMMARY OF FINDINGS AND DIRECTIONS FOR FUTURE RESEARCH

The invasion of cheatgrass is one of the most significant plant invasions in North America. Most published research about *Bromus tectorum* has focused on the use of individual tools such as herbicides, prescribed grazing, revegetation, and biological control. In contrast, my research manipulated ecological processes such as reproduction, disturbance, and relationships with natural enemies (Figure 1.1.) through the integration of herbicides, revegetation, and biological control. Specifically, I investigated the herbicide imazapic and a biological control pathogen, *Pyrenophora semeniperda*, as well as the seeding of native perennial species and evaluated their effects within the context of the three drivers of invasion: propagule pressure, abiotic context, and biotic characteristics. Once identified, the drivers of invasion served to narrow focus onto causal mechanisms, i.e. ecological processes that can be manipulated through management strategies.

My first objective was to evaluate interspecific variation in *P. semeniperda* susceptibility. Within this context, I utilized *P. semeniperda* as a natural enemy to prevent *B. tectorum* emergence and to understand its potential for spillover on to non-target grasses that co-occur with *B. tectorum* in a range of environments (crop, forage, range). I tested the "race for survival" hypothesis that slow-germinating seeds are more susceptible to *P. semeniperda* infection. While the number of species screened was not exhaustive, the majority saw reduced density when inoculated with *P. semeniperda*. In addition, *B. tectorum* saw a reduction in density with inoculation. Biomass was generally unaffected by inoculation. Emergence dynamics modified *P. semeniperda* impact. Specifically, I found that non-inoculated seeds emerge faster than those that are inoculated for the crop, forage, and range species tested. Moreover, I discovered that unless species are particularly heavy, like crop species, then seed weight alone is insufficient in predicting a species response to *P. semeniperda*.

My second objective was to assess the effect of integrating imazapic, a commonly used herbicide in rangeland, *P. semeniperda*, perennial grass seeding, and fungicide seed treatment on revegetation of a *B. tectorum*-infested plant community. I again utilized *P. semeniperda* as a natural enemy to prevent the temporal dispersal of *B. tectorum* and sought to impact its reproduction by targeting it with imazapic. I directly manipulated the dispersal of desired species by seeding native perennial grasses into a carefully crafted seedbed, which minimized disturbance, and I took precautions to protect the seed from *P. semeniperda* and other fungal pathogens by applying a fungicide seed treatment. I successfully controlled *B. tectorum* for one year with a single imazapic application, and it is possible that the rate of imazapic used (120 g ai ha^{-1}) had degraded to concentrations non-lethal to perennial grasses by the time of seeding. Combined with the careful seeding technique, this likely allowed for strong perennial grass establishment two years post treatment. In addition, there was no effect of either the fungicide seed treatment or the different rates of perennial grass seeding. Finally, I was unable to achieve *P. semeniperda* inoculum loads that were above ambient levels, consequently leading to no effect of *P. semeniperda* on either *B. tectorum* or seeded perennial grasses.

My third objective was to investigate *P. semeniperda* efficacy as a biological control agent across varying temperatures with different *B. tectorum* populations. Again, I depended on *P. semeniperda* as a natural enemy to prevent *B. tectorum* germination. Instead of focusing on a single *B. tectorum* population, I investigated how three distinct *B. tectorum* populations (range, crop, sub-alpine), each with their own environmental characteristics, respond to varying temperatures in the presence and absence of *P. semeniperda*. Germination was highest and infection by *P. semeniperda* was lowest for the crop population, while the opposite was true for the range population. Taken together, these trends suggest that the effect of the strain of *P. semeniperda* I tested differed across the *B. tectorum* populations I used.

Ultimately, the main benefit of using *P. semeniperda* (reducing propagule pressure from the seedbank) may not be enough to overcome its non-target effects, particularly onto highly susceptible, lightweight range species, difficultly achieving high inoculum loads in the field, and differing effects on distinct *B. tectorum* populations, depending on environmental constraints like temperature. Future research on *P. semeniperda* should include additional field trials to better understand the environmental constraints that exist for the *B. tectorum-P. semeniperda* pathosystem. A better understanding of how to increase *P. semeniperda* inoculum loads above ambient levels is needed if and when *P. semeniperda* is implemented as a biological control agent for *B. tectorum*. Further investigation is required into how long *P. semeniperda* persists in the soil and whether residual effects, if any, are felt by the offspring of already established species. In addition, seeding technologies need to be developed to provide the accurate seed depth and seed-soil contact that was achieved with hand seeding. *Pyrenophora semeniperda* needs to be evaluated for site-specific management strategies in the context of highly virulent and locally adapted inoculum. Finally, an economic cost-benefit analysis would help demonstrate the potential, or lack thereof, of implementing *P. semeniperda* on a large scale.

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