UNDERSTANDING MECHANISMS OF INVASION

AND RESTORING LANDS IMPACTED BY

NON-NATIVE ANNUAL GRASSES

by

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DEDICATION

For my dad,

Edward L. Majeski

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TABLE OF CONTENTS

TABLE OF CONTENTS CONTINUED

TABLE OF CONTENTS CONTINUED

LIST OF TABLES

LIST OF FIGURES

Figure Page

LIST OF FIGURES CONTINUED

Figure Page

LIST OF FIGURES CONTINUED

Figure Page

LIST OF EQUATIONS

ABSTRACT

European settlement and development of rangelands in the western U.S. has led to a shift in vegetation from native species to introduced species, some of which have become weedy and invasive. Effects of invasive plant species can vary but often include replacing native vegetation, altering ecosystems, affecting wildlife that relied on the native plants for food and shelter, and toxicity to livestock. Two introduced annual grasses of concern are *Ventenata dubia* and *Bromus tectorum*. These grasses are at different stages in their invasion in the western U.S. *Ventenata dubia* is a recent invasive species in the past ten years and *B. tectorum* has been dominant in the Intermountain West since the mid-1900s. Three independent studies were conducted to understand characteristics of *V. dubia* invasion and to test whether a seasonal priority effect could be shifted to *Pseudoroegneria spicata* to outcompete *B. tectorum* in range/pasturelands. A full-factorial design was executed in a greenhouse setting to examine if a plant-soil feedback contributes to *V. dubia* invasion and if *V. dubia* preferred specific nutrients for growth. *Ventenata dubia* biomass, shoot height and number of leaves and tillers (per plant) were higher when grown with field soil inoculum compared to sterilized greenhouse soil. *Ventenata dubia* growth varied among nutrient treatments, but trended higher with a full nutrient solution. A nested observational study was conducted to examine abiotic and biotic characteristics associated with *V. dubia* infestations. *Ventenata dubia* was positively associated with non-native perennial grasses and negatively associated with native perennial grasses, bare ground/rock and soil potassium concentration. A randomized split-plot design was performed in *B. tectorum*-infested range and pasturelands to test whether timing of herbicide application and seeding of *P. spicata* could create a seasonal priority effect for *P. spicata*. *Bromus tectorum* had lower cover and biomass (per m^2) with spring herbicide application. Higher *P. spicata* density, cover and biomass resulted with spring seeding after *B. tectorum* was reduced. These studies show that established and seeded native perennial grasses can compete with non-native, invasive annual grasses. When existing management tools (herbicide and revegetation) are applied in a different way, native perennial grasses benefit.

CHAPTER ONE

INTRODUCTION AND RESEARCH OVERVIEW

Literature Review

Rangelands

Global rangeland area is estimated at 3.7 billion hectares, encompasses grasslands, shrublands and tundra, and exists in arid and semi-arid regions in every continent except Antarctica (Havstad et al., 2007; Lund, 2007). Services and products provided by rangelands globally are poverty alleviation, feed for livestock, milk, production of food for game, manure (fertilizer and fuel), wool, hides, transportation, carbon storage, habitat for wildlife, watersheds for river systems, water and nutrient cycling, medicinal plants and minerals. Conservation of cultural areas and recreation also occur on rangelands (Havstad et al., 2007; Lund, 2007; Macleod & Brown, 2014).

In the United States, approximately 31% of total land area, 308 million hectares, is rangeland including deserts, alluvial valleys, coastal and inland foothills, high mountain meadows and arid inland plains (DiTomaso, 2000; Havstad et al., 2007). Rangelands are present in 16 states, and are defined as land where native vegetation is mostly grasses, grass-like plants, forbs or shrubs suitable for grazing or browsing (United States Environmental Protection Agency, 2020.). In 11 states west of the Mississippi River, 70% of the land area is designated as rangelands (Hess & Tanaka, 2012).

Short, tall and mixed-grass prairies consisting of *Bouteloua gracilis* (Wild. Ex Kunth) Lag. Ex Griffiths, *Buchloe dactyloides* (Nutt.) J.T. Columbus, *Pseudoroegneria spicata* (Pursh) À. Löve, along with *Artemesia* spp. were among the dominant vegetation before European settlement in western U.S. rangelands (Krueger, 1988; Menke & Bradford, 1992; Rottler, et al., 2015). Land use changed from an open prairie where bison (*Bison bison)*, deer (*Cervidae* spp.), elk (*Cervus canadensis)* and pronghorn antelope (*Antilocapra americanan)* grazed to areas with heavy domestic livestock grazing and the introduction of agriculture (Krueger, 1988). Those changes, and the establishment of new plants to the area brought by settlers, including beneficial species for agriculture, began the shift of rangeland native vegetation to introduced species, some of which were weedy and invasive (Menke & Bradford, 1992).

Invasive Plants in the Western United States

A weed is a plant that is undesired, but it may not be invasive (Radosevich et al., 2007b). When a plant is invasive, it can establish and spread to new areas; invasive plants may be either native or non-native to an area but are typically non-native (Radosevich et al., 2007b). Effects of invasive plant species can vary but often include replacing native vegetation, altering ecosystems, affecting wildlife that relied on the native plants for food and shelter, and toxicity to livestock (D'Antonio & Vitousek, 1992; DiTomaso, 2000). There are few shared characteristics among invasive plants, though they tend to be from different continents than where they have recently established and often grow in habitats similar to their native region (DiTomaso, 2000; Panetta & Mitchell, 1991).

In the western U.S., invasive plant species belong to many families: Apiaceae, Asteraceae, Boraginaceae, Brassicaceae, Convolvulaceae, Cupressaceae Eurphorbiaceae, Fabacaceae, Poaceae, Ranunculaceae, Rosaceae and Scrophulariaceae, (DiTomaso, 2000), highlighting that an invasive plant is not just one type of plant. Among these families, the most prevalent invasive species are *Bromus tectorum L.*, *Centaurea* *maculosa* auct. Non Lam., *Centaurea diffusa* Lam., *Centaurea solstitialis* L., *Cirsium arvense* (L.) Scop. and *Euphorbia esula* L., a majority in the Asteraceae family, occupying approximately 53 million hectares of land (Bradley & Marvin, 2011; DiTomaso, 2000).

Invasive Annual Grasses in Rangelands

Introduced annual grasses have become part of the landscape of the western U.S. due to human migration, intense cattle grazing and fire suppression (DiTomaso, 2000). *Bromus tectorum, Aegilops cylindrice* Host, and *Taeniatherum caput-medusae* (L.) Nevinski are major rangeland weeds in the western U.S. (DiTomaso, 2000). Specifically, *B. tectorum* and *T. caput-medusae* are strong competitors with perennial grasses and often outcompete them in revegetation projects (Harris, 1967). *Ventenata dubia* (Leers) Coss., another introduced annual grass, can affect range, pasture, and natural areas by decreasing plant community diversity and forage production and potentially increasing soil erosion due to the species' shallow root structure (Jones et al., 2018; Scheinost et al., 2009).

Bromus tectorum and *V. dubia* are at different stages of invasion in Montana. *Bromus tectorum* was first noted in the United States in the 1800s. By 1915, the grass was dominant in some areas and widespread in the Intermountain West (Mack, 1981). It now occupies 7 million hectares in the western United States and 35% of the Intermountain West (Belnap et al., 2005; Bradley et al., 2018). In Montana, *B. tectorum* was first observed in Missoula County in 1898 and was present in every county by 1980 (Menalled et al., 2017; State of Montana, n.d.).

Bromus tectorum is associated with doubling fire frequency and an increase in fire risk in the Great Basin desert (Balch et al., 2013; Bradley et al., 2018). Impacts of *B. tectorum* include larger and more frequent wildfires because of excess litter and continuity of fine fuel, along with soil erosion caused by exposed soil after fire, altered water and nutrient cycling, and reduced carbon sequestration (Balch et al., 2013; Blank et al., 2007; Rau et al., 2011; Wilcox et al., 2012). In the Snake River Plains in southern Idaho, fire intervals changed from 60-110 years to 3-5 years in *B. tectorum*-dominated regions (Whisenant, 1990). Fire may have stimulated *B. tectorum* establishment initially, and over time both an increase in fire occurrence and an increase in *B. tectorum* led to larger fires. The cumulative result was that *B. tectorum* became dominant where native vegetation previously existed (Whisenant, 1990). *Bromus tectorum* is considered by some as the most significant plant invasion in North America (D'Antonio & Vitousek, 1992).

Ventenata dubia has become a growing concern among land managers in the northwestern U.S., as it shares common life history and biological traits with *B. tectorum* (Jones et al., 2018; Prather & Steele, 2009; Wallace et al., 2015). Washington and Idaho first documented *V. dubia* in grassland areas in the 1950s (Crins, n.d.; University of Washington Herbarium, 2020). *Ventenata dubia* has spread quickly to rangelands and pastures throughout the inland Pacific Northwest and into the Northern Great Plains (Fountain, 2011; Gaskin et al., 2020; University of Wyoming, 2008; Wallace & Prather, 2011). *Ventenata dubia* was first recorded in Montana in the 1990s (University of Washington Herbarium, 2020) and was described as sporadic and ephemeral in highly disturbed areas (Lesica, 2012). As of 2020, *V. dubia* has been documented in 24 Montana counties where it is estimated to affect over 22,000 hectares (Harvey & Mangold, 2018).

It is a concern for livestock producers, public land managers, and researchers in Montana where it has been designated as a Priority 2A noxious weed; containment or eradication are management priorities (Montana Department of Agriculture, 2019).

Prather and Burke (2011) found that pasture, grass-hay and grasslands of north-central Idaho experienced a significant decline in forage production because of *V. dubia*. In some situations, timing of hay harvest schedules had to be altered to avoid export losses caused by *V. dubia* (Fountain, 2011; Wallace et al., 2015). A relationship between *V. dubia* and aphids carrying the barley yellow dwarf virus (BYDV) resulted in *V. dubia* being a susceptible host to and a transmitter of the virus (Ingwell & Bosque-Perez, 2015). Barley yellow dwarf virus reduces grain yield of many grasses including staple crops like wheat, rice and maize (D'Arcy & Domier, 2019). *Ventenata dubia* has been associated with a decline in nesting success of insect-eating birds due to a loss of biodiversity in conservation lands in northern Idaho (Mackey, 2014). Further, *V. dubia* is displacing *B. tectorum* in the Snake River Canyon grasslands of Idaho (Wallace et al., 2015) which is particularly alarming because *V. dubia* is considered unpalatable to livestock due to its silica content (Prather & Steele, 2009), while *B. tectorum* provides some grazing options (Mangold et al., 2019; Prather & Steele, 2009). With the change of one invasive grass to another in this area, it is unknown whether fire frequency or intensity will change (Brooks et al., 2004).

Biology and Invasive Characteristics of
Bromus tectorum and Ventenata dubia

The biology of *B. tectorum* and *V. dubia* are similar; they are winter annuals whose majority of seeds germinate in autumn, but germination can also occur in spring, resulting in a prolonged germination period (Harris, 1967; Hulbert, 1955; Northam & Callihan, 1994). *Bromus tectorum* can produce up to 5000 seeds per plant in an ideal environment (Young et al., 1987), while *V. dubia* produces 35 seeds per plant and can produce up to 43,000 seeds per m^2 when growing without competition (Pavek et al., 2011; Wallace et al., 2015). Seeds persist in the seedbank for up to three years with *B. tectorum*, with a majority (96 %) germinating in the first year, a small amount of seeds (4 %) carrying over into the second year, and an even smaller amount (0.4 %) into the third year (Smith et al., 2008). A similar pattern has been observed with *V. dubia* in a seed bank persistence study, with 82 % of seeds germinating after 30 days, and <1 % germinating at 13 months, 25 months and 37 months after burial. No viable *V. dubia* seeds remained by 49 months after burial (Wallace et al., 2015).

Both grasses grow to similar height. *Bromus tectorum* height ranges from 2 – 58 cm (Harris, 1967; Hulbert, 1955), and *V. dubia* height can be up to 46 cm (Scheinost et al., 2009). Low grass height keeps seed dispersal close to the plant, except when humans, equipment, vehicles or animals carry seeds to new locations (Radosevich et al., 2007c; Scheinost et al., 2009). Awns that protrude from *B. tectorum* and *V. dubia* seeds enable them to attach to the clothing of humans or fur of animals and also keep the seed in contact with the ground for subsequent burial, germination, and emergence. *Ventenata dubia's* awns are bent and become twisted, as opposed to *B. tectorum's* straight awns (Hulbert, 1955; Scheinost et al., 2009; Wiseman et al., 1977).

Seedling emergence in autumn allows roots of winter annual grasses to grow before reduced winter soil temperatures. This timing gives *B. tectorum* and *V. dubia* a growth advantage over perennial grasses, whose roots tend to go dormant earlier in autumn and remain dormant until later in the spring. Shallow root systems allow annual grasses to access water and nutrients just below the soil surface (Harris, 1967; Scheinost et al., 2009), yet rooting depth has been recorded at 117 cm, to access nutrients and water (Harris, 1967; Sperry et al., 2006). *Bromus tectorum*'s roots grow in a vertical direction, yet can branch horizontally when needed (Arredondo & Johnson, 1999). The vertical pattern allows *B. tectorum* roots to reach further soil depths before winter approaches (Harris, 1967). Under stressed conditions, such as variable nutrient solution treatments and experimental defoliation (80 % of shoots), *B. tectorum's* roots extended deeper than perennial grass roots (Arredondo & Johnson, 1999). Similarly, *B. tectorum*'s roots were deeper than the roots of the perennial grass *P. spicata* in a simulated field environment at six weeks and after 38 weeks when grown under conditions of intraspecific competition (Harris, 1967).

Less information is available about *V. dubia* root characteristics. One study compared root growth among *V. dubia*, *B. tectorum* and *T. caput-medusae*. *Ventenata dubia* had the lowest root growth under two different watering regimes (small/frequent, large/infrequent). This suggests that root response may be a reflection of amount of available water, rather than varied volume and pulses of water (Bansal et al., 2014), or that *V. dubia* allocates resources to other areas in the plant, such as shoot growth, when water is accessible (Arredondo & Johnson, 1999). In a growth chamber study where *V. dubia* and *B. tectorum* were grown together under current and elevated climate conditions, *V. dubia* had a higher root shoot ratio than *B. tectorum* (Harvey, 2019), indicating that further studies into root biology of *V. dubia* may provide insight into its invasive traits.

Soil and Moisture

Soil characteristics can contribute to how susceptible a site is to invasion by *B. tectorum* and *V. dubia* (Stachowicz & Tilman, 2005; Sperry et al., 2006). For example, soil texture affects soil water holding capacity as clays and organic matter in soil retain water because of chemical bonds between water and soil particles (Schaetzl & Thompson, 2015). Finer grained soils, with a higher percentage of silt and clay as opposed to sand, are able to hold more water because of high particle surface area. In addition, silt and clays provide a greater number of small pores where water can reside (Schaetzl & Thompson, 2015). Soil-water influence was evident when higher levels of silt and lower levels of sand facilitated moisture retention and *B. tectorum* invasion in a Utah study (Belnap & Phillips, 2001). Similarly, *V. dubia* was found growing in clayey soils in southwestern Idaho and eastern Oregon (Jones et al., 2018).

Factors Related to Non-Native Grass Invasion

Disturbance may lead to invasion (Lockwood et al., 2007; Rottler et al., 2015). Disturbances are discrete events, sometimes differing in spatial and temporal extent, that result in the partial or total disruption of plant biomass (Davis et al., 2000; Lockwood et al., 2007; Radosevich et al., 2007c). When vegetative biomass is disturbed by natural or human-caused events, availability of resources required for plant growth (e.g. nutrients, water, light) increases because less vegetation is utilizing those resources (Davis et al., 2000). An increase in resource availability can lead to an increase in susceptibility to invasion (Davis et al., 2000; James et al., 2010). Resources can fluctuate within a year and from year to year, and even small disturbance events can lead to invasion over time (Davis et al., 2000; Sheley & Smith, 2012).

Disturbance is not the only factor associated with invasive species presence, and oftentimes other factors may be equally important. Elevation, soil-water retention, and soil nutrient concentrations were related to *V. dubia* cover in sagebrush steppe rangeland in southern Idaho and eastern Oregon (Jones et al., 2018). In a different study, after two decades of exposed ground due to natural disturbance, *V. dubia* did not occupy bare ground even though it was prevalent nearby (Averett et al., 2016). Instead, there was a relationship between open tree canopy and *V. dubia* presence, showing preference to areas with more sun exposure for photosynthesis in this study (Averett et al., 2016).

Plant litter can affect annual grass seedling emergence. In a study in the Columbia Plateau of Washington, northeastern Oregon and northern Idaho, where varied *V. dubia* litter treatments were applied to pots with *V. dubia* seeds and placed outdoors, the presence of litter resulted in higher seedling emergence than the no-litter, bare-soil control pots. Also, seedling density declined in the no-litter control (Wallace et al., 2015). The studies described here suggest that multiple factors are necessary for non-native grass presence and invasion. Soil moisture retention, resource availability, elevation, and plant litter share roles in non-native species invasion and appear to be related to *V. dubia* invasion.

Belowground Ecology

Plant species are influenced by the soil they inhabit. Above and belowground relationships are often explored to understand species fecundity and mortality, which in turn, affect ecosystems (Bardgett, 2018). Belowground ecology studies can provide an understanding of how species function in a community. These studies entail many approaches that may include plant litter, root architecture and exudates, nutrient ratios, microbial community inventory, mycorrhizae studies, plant-soil feedbacks, among others (Arredondo & Johnson, 1999; Bardgett & Wardle, 2010; Bennett & Klironomos, 2018; Hawkes et al., 2006; Veen et al., 2015; Dostálek et al., 2016). For example, arbuscular mycorrhizal fungi (AMF) establish a symbiotic relationship with a plant in that the fungus gains carbohydrates from the plant, and the plant gains improved access to soil nutrients through the fungus (Bardgett & Wardle, 2010). In a meta-analysis of native and invasive species studies related to AMF, out of 67 studies, there was no difference in the AMF relationship between these types of species. Instead, differences occurred with functional groups, such as forbs or grasses (Bunn et al., 2015). Another study found that when roots were colonized by AMF, plants allocated resources to different areas of the plant: total biomass, shoot biomass or root biomass for species in the Asteraceae and Poaceae families (Reinhart et al., 2017).

A plant-soil feedback is when a plant species modifies the biotic composition of soil through nutrient cycling, root tissue or exudates, for example, such that the plant species continues to succeed or it declines or dies, thus altering the plant community (Bardgett & Wardle, 2010; Schaeffer et al., 2012; Van der Putten et al., 2013). Whether feedbacks are negative, positive, or have no effect is dependent upon the community, interactions within the community overall and which feedbacks are the most influential.

Plant-soil feedbacks are increasingly recognized as being important to plant community dynamics, including invasion by non-native annual grasses. For example, to understand the effect of rainfall regime and fine root feedback related to competition with a native forb and non-native grass, McKinney and Cleland (2014) conducted a greenhouse study where non-native grass root clippings were added to pots with topsoil and seeds either from native forb species, non-native forb species and non-native grass species, or in combination. Non-native grass root additions increased the average soil moisture providing additional soil organic matter, but did not increase plant growth (McKinney & Cleland, 2014). All plant growth was suppressed with the root additions and non-natives were more suppressed than natives, indicating a potential negative feedback (McKinney & Cleland, 2014). Once explored, plant-soil feedback studies can have the ability to demonstrate how species survive or decline, and potentially, how a species is able to be invasive.

Invasive Plant Management Recommendations and Ongoing Impacts to Rangelands

Invasive plant management is challenging, especially when a species is well-established and widespread. Ideally, prevention is the first tool used and most cost effective (Davies & Sheley, 2007; Ditomaso, 2000). Maintaining healthy and competitive vegetation reduces invasion by non-native annual grasses (Sheley et al., 1996). In some locations, Weed Prevention Areas have been established where community members take a proactive approach to management before invasive species arrive (Goodwin et al., 2012). Activities that limit propagule dispersal like washing vehicles (Rew et al., 2018), using weed seed-free forage and building materials, prohibiting cattle that have grazed in an infested area from grazing in a weed-free area are critical as well (Davies & Sheley, 2007; Radosevich et al., 2007a; Zimdahl, 2007b). Unfortunately, it can be difficult to show success for prevention, preventative actions are often ignored, and action is not taken until an invasive plant is a problem (Zimdahl, 2007b).

After prevention, invasive plant management approaches fall under four categories: biological, chemical, cultural, and physical (DiTomaso, 2000; Radosevich et al., 2007a). Biological control is the action of using natural enemies, pathogens, insects or animals, to reduce invasive species. The goal of biological control is to reduce the plant species density, not to eradicate it (Zimdahl, 2007a). Insects can extract fluid from plant stems or bore holes into roots and shoots, reducing a plant's viability (DiTomaso, 2000). *Bromus tectorum's* roots were reduced by 13%, 42% and 64% when a root-colonizing bacteria was applied in a lab and growth chamber, indicating some stress on the plant with biological control (Kennedy et al., 2001). However, the bacteria did not affect *B. tectorum* in several replicated field studies (Germino & Lazarus, *in press*; Pyke et al., *in press*; Reinhart et al., *in press*; Tekiela, *in press*).

Chemical control involves using herbicides, which are organic or synthetic chemicals, to reduce or kill unwanted vegetation (Radosevich et al., 2007a). Herbicides are the most common tool for weed control in rangelands (DiTomaso, 2000). Benefits of using herbicides include less human effort compared to hand-pulling or mechanical weeding, and large areas can be treated with the use of aircraft or helicopter (DiTomaso, 2000). Several studies have tested the efficacy of herbicides for controlling *B. tectorum* and *V. dubia* (Hirsch et al., 2012; Koby et al., 2019; Mangold et al., 2013; Rinella et al., 2014). A recently available herbicide, indaziflam, controlled the spread of *V. dubia* up to three years in southwestern Montana (Harvey, 2019). *Bromus tectorum* and *T. caput-medusae* were controlled for two years with imazapic in northeastern California (Kyser et al., 2013).

Examples of cultural control are using targeted grazing, applying prescribed fire, and seeding desired species to compete with weeds through revegetation. When grazing is applied, the type of animal species, quantity, and timing of grazing are important considerations that affect the undesired plant species (DiTomaso, 2000; Schmelzer et al., 2014). Multi-species grazers are an option when vegetation varies, as particular animals prefer certain types of plants. Further, some plant species are poisonous to certain grazers, such as cattle or horses, and harmless to others, notably sheep (DiTomaso, 2000). Timing of grazing can eliminate seed rain and subsequent seedling establishment with particular species (Daines, 2006). Fall cattle grazing of *B. tectorum* removed up to 80% of aboveground biomass in three years and reduced *B. tectorum* seedbank by 6 times (Schmelzer et al., 2014). In some situations, multiple grazing events may need to occur to reduce the targeted invasive plant species (Daines, 2006), or integrated methods, such as using herbicide with grazing may be successful in reducing *B. tectorum* (Lehnhoff et al., 2019).

Prescribed fire is a cultural management tool used to reduce some invasive plant species (Radosevich et al., 2007a). Careful consideration is needed with this approach as the undesired species may benefit from fire and increase its spread, or other invasive species may emerge (DiTomaso, 2000; Kyser et al., 2008), which occurred in a

California study where fire both reduced and enhanced cover of *T. caput-medusae* (Kyser et al., 2008). Site characteristics such as elevation and climate, along with species phenology are important contributors to prescribed fire success with *T. caput-medusae* (Kyser et al., 2008).

Integrated weed management, or combining multiple control strategies, is usually required for long-term success (DiTomaso, 2000; Mangold et al., 2015; Monaco et al., 2017) and involves using a combination of species removal methods along with revegetation (Ferrell et al., 1998; Mangold et al., 2015; Whitson & Koch, 1998). There are likely invasive species seeds in the seedbank which biomass removal does not address; this is why revegetation is needed. Revegetation creates competition among species and re-establishes diversity.

Revegetation has been integrated with invasive plant control methods to improve forage availability for domestic livestock and wildlife. It is an effective solution for both short and long-term management of invasive plants, and is particularly effective if the environmental conditions are appropriate for seeded species establishment (Ferrell et al., 1998; Hull & Stewart, 1948; Rinella et al., 2012). For example, without herbicides, cool-season grasses were seeded in the spring after fall tillage and were able to suppress *B. tectorum* by 32 % to 100 % three years after treatment (Whitson & Koch, 1998). Other studies included herbicide applications combined with revegetation. For example, establishing intermediate wheatgrass [*Thinopyrum intermedium* (Host, Barkworth and D.R. Dewey)] reduced canopy cover of the invasive forb *Euphorbia esula* to 15 % 10 years after seeding (Ferrell et al., 1998). In another study, biomass of the invasive forb

Centuarea maculosa was reduced by 93 % 15 years after seeding perennial grasses (Rinella et al., 2012).

Bromus tectorum has occupied rangelands in the Intermountain West for a century (Mack, 1981), and decades of revegetation studies related to restoring rangelands impacted by *B. tectorum* (Boyd & Lemos, 2015; Harris, 1967; Hull & Stewart, 1948; Mangold et al., 2015; Whitson & Koch, 1998) can help to direct future research as well as management actions for *B. tectorum* and other annual grasses like *V. dubia*. A meta-analysis conducted by Monaco et al. (2017) reviewed 119 articles published between 1948 and 2012 that reported on control methods used for *B. tectorum* in rangelands. Most common methods were herbicide application, burning, revegetation with perennial grasses, mowing or grazing, soil disturbance and soil amendments (Monaco et al., 2017). Each of these approaches reduced *B. tectorum* in the short term, but herbicide application and revegetation were the methods that were effective more than one year (Monaco et al., 2017).

Revegetation as a Restoration Strategy

Understanding life history population dynamics of a plant community can inform revegetation decisions and success (James et al., 2011; James et al., 2012; Radosevich et al., 2007b). For species that reproduce by seed only, such as annual grasses, there are multiple states and transition times where seeds or seedlings are vulnerable and could die. Life history stages for annuals are: seed, seedling, vegetative plant and flowering plant. These stages are connected with transition periods: seed dispersal, dormancy, germination, seedling establishment, resource capture, growth and seed production (James et al., 2011; James et al., 2012; Radosevich et al., 2007a). When an undesirable species is most at risk of mortality may be the best opportunity for revegetation with a more desired one (James et al., 2011; James et al., 2012). Life history stages were studied with perennial grasses (native and non-native) to explore whether there were differences in life history transition periods. Native species had higher survival rates than the non-native species after seedling establishment, or "emergence" (James et al., 2012). Emergence was a vulnerable stage for each species, as it occurred at different times; in February for the non-natives and in March for the native grasses. Exploiting different seedling emergent times could be explored further since timing of emergence, or seasonal priority effect, can have long-lasting effects on species survivorship (Weaver & Clements, 1938).

Seasonal priority effect. A species that emerges first in a community benefits from a seasonal priority effect (Ross & Harper, 1972; Weidlich et al., 2017). Upon first emergence, that seedling has access to and benefits from water and nutrients before other seedlings. The result of this advantage is more root and shoot biomass compared to nearby, smaller plants (Weaver & Clements, 1938), which can then affect the growth rate of the species (Ross & Harper, 1972).

Bromus tectorum benefits from a seasonal priority effect because of its biology as a winter annual. Seed germination usually occurs in autumn and roots begin to establish at that time, earlier than seeded perennial grass roots, which typically emerge and establish in spring. By spring, *B. tectorum* has a growth advantage over seeded perennial grasses. This advantage, or seasonal priority effect, may be how *B. tectorum* outcompetes perennial species during revegetation. For perennial grass seedlings to compete with *B.*

tectorum, a seasonal priority effect needs to be overcome during revegetation so that perennial grass seedlings are not at a competitive disadvantage.

Seeding timing. Experimenting with the idea of a seasonal priority effect has become a restoration endeavor where native species are seeded into annual grass-infested rangeland. In the arid region of eastern Oregon, *P. spicata* was seeded monthly in outdoor plots from September – December in 2008 and 2009. September and October seeding resulted in 80% germination of *P. spicata* and had a higher percent of emergence than the later seeding dates. However, seedling survival through the first growing season was higher for later seeding dates (Boyd & James, 2013).

A similar experiment was conducted in southwestern Montana where seeding of *P. spicata* was executed once in November, and weekly the following April through mid-May (Harvey, et al., 2020). The sites were tilled and weed free, as the first objective was to examine size and abundance of *P. spicata* based on seeding dates. November and early spring seeding dates resulted in larger plant size and higher density. (Harvey, et al., 2020). A second objective of Harvey et al. (2020) was to investigate the ability of *P. spicata* to resist invasion by *B. tectorum. Bromus tectorum* seeds were added to plots where *P. spicata* was previously established. Fall and early spring seeding dates had lower *B. tectorum* density than later spring dates, indicating higher *P. spicata* resilience to *B. tectorum* invasion (Harvey et al., 2020).

A seasonal priority effect may be obtained with appropriate timing of seeding. When life history and population dynamic concepts are combined with timing of seeding, successful competition for the desired species may be achieved. These components together create a seasonal priority effect, which can be considered an effective tool with ecology-based integrated weed management for rangelands.

Project Justification

Rangelands in the western U.S. are changing because of invasive, non-native annual grasses (Belnap et al., 2005; Humphrey & Schupp, 2004). Understanding how a species invades and proliferates can guide approaches to reduce invasion. Therefore, one objective of my research was to understand mechanisms contributing to *V. dubia* invasion. Two studies were conducted to this end. A greenhouse study was executed to explore plant-soil feedbacks and response to nutrient treatments related to *V. dubia*, and an observational study documented associations between species functional groups and soil characteristics and *V. dubia* to try to understand areas most susceptible to *V. dubia* invasion. The results of these studies will hopefully provide new insight into *V. dubia's* growth characteristics that can be leveraged to understand and reduce its invasion.

Using ecology-based integrated weed management could be a successful approach to address rangelands already infested with winter annual grasses. We can apply lessons learned from the long history of addressing *B. tectorum's* invasion to inform methods to minimize *V. dubia* invasion. Therefore, a second objective of my research was to test the importance of a seasonal priority effect when integrating chemical control and revegetation with *P. spicata* to reduce *B. tectorum* abundance in range and pasturelands. A third study, a revegetation experiment, tested whether timing of herbicide application and seeding (fall or spring) could be manipulated to provide a seasonal priority effect to a desired native grass in areas infested with *B. tectorum*. The result of this study will hopefully refine the practice of integrating herbicide and seeding to mitigate effects of annual grasses once they have invaded and are well-established across a region.

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CHAPTER TWO

VENTENATA DUBIA GROWTH RESPONDS TO FIELD SOIL INOCOLUM BUT NOT PHOSPHOROUS AND POTASSIUM TREATMENTS

Contribution of Authors and Co-Authors

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Contributions: Executed study, collected data, conducted data analysis and prepared written manuscript.

Co-Author: Dr. Catherine Zabinski

Contributions: Provided guidance with study execution. Reviewed and provided important feedback on manuscript.

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Contributions: Provided guidance with statistical analysis. Reviewed and provided important feedback on manuscript.

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Contributions: Conceived experimental design, obtained funding, conducted experiment, reviewed and provided guidance on manuscript.

Introduction

Ventenata dubia is a non-native, annual grass from southern Europe, western Asia and northern Africa (Alomran et al., 2019; Scheinost et al., 2009) that has increased its range in the Intermountain West over the last 10 years (Wallace & Prather, 2016). It was listed as a Priority 2A noxious weed by the Montana Department of Agriculture in 2019 (Montana Department of Agriculture, 2019b). Priority 2A noxious weeds are common in isolated areas of Montana, and management goals are eradication or containment (Montana Department of Agriculture, 2019a). *Ventenata dubia* is now present in 24 Montana counties, encompassing 22,000 hectares: Lincoln, Flathead, Sanders, Lake, Mineral, Missoula, Ravalli, Granite, Powell, Lewis and Clark, Cascade, Broadwater, Beaverhead, Madison, Gallatin, Park, Sweet Grass, Stillwater, Carbon, Yellowstone, Big Horn, Rosebud, Powder River and Carter (Harvey & Mangold, 2018, 2019).

Impacts of *V. dubia* have been increasingly recognized in the Intermountain West, in particular in Idaho and Washington, where the grass was first documented in 1952 (Crins, n.d.). In Idaho, *V. dubia* growing in *Phleum pretense* L. (timothy) hay fields caused 50% yield reduction (Prather & Steele, 2009), resulting in an economic impact to producers. Considering livestock production, *V. dubia* has low palatability because of high silica content (Mangold et al., 2019; Prather & Steele, 2009). The Palouse grassland region of southeastern Washington and western Idaho, which is a critically endangered and threatened ecosystem of the United States due to agricultural development (greater than 98% decline; United States Department of the Interior, 1995; Weddell, 2000), is now being threatened by *V. dubia* as well (Nyamai et al., 2011).

Information related to *V. dubia's* recent expansion in the Intermountain West is limited, but there is evidence that soil characteristics may contribute to its success. For example, *V. dubia* cover is higher in areas with higher clay content and lower phosphorous (P) and potassium (K) concentrations in sagebrush steppe in Idaho and Oregon (Jones et al., 2018). In a growth chamber study, *V. dubia* biomass was positively correlated with soil clay and nitrogen content and negatively correlated with soil pH (Bansal et al., 2014). In addition to abiotic soil factors possibly contributing to *V. dubia* success, biotic factors may also play a role. Since little is known about *V. dubia* invasion, and since *B. tectorum* shares a similar life history to *V. dubia*, studies related to *B. tectorum* may provide evidence for further exploration of *V. dubia.* For example, soil microbial relative abundance increased and greater nitrogen mineralization rates occurred in a *B. tectorum*-invaded site compared to a non-invaded site (Schaeffer et al., 2012). The change in nitrogen mineralization rates provided more plant-available nitrogen, compared to a non-invaded site, where nitrogen mineralization rates were slower and nitrogen was less available to plants (Schaeffer et al., 2012).

Understanding biotic plant-soil feedbacks may lend insight into non-native species invasion. A plant-soil feedback is where a plant species modifies soil characteristics through nutrient cycling, root tissue or exudates, for example, such that the plant species continues to succeed or it declines or dies, thus altering the plant community (Bardgett & Wardle, 2010b; Schaeffer et al., 2012; Van der Putten et al., 2013). Invasive plants may modify the soil microbial community in ways that benefit themselves (Bever, 2003; Callaway et al., 2004; Klironomos, 2002), while native plants may be harmed by changes in the soil environment (Bever, 2003; Reinhart et al., 2003).

During invasion, plant-soil feedbacks may favor the invader (Callaway et al., 2004) or have a less negative effect on the new species than on the resident native species (Van Grunsven et al., 2007).

Plant-soil feedbacks have been investigated in the context of *B. tectorum* invasion, and similar methods may be used to pursue questions related to *V. dubia* invasion (Belnap & Phillips, 2001; Busby et al., 2012a,b; Weber et al., 2015). With little documented literature on plant-soil feedbacks with *V. dubia*, I conducted a greenhouse study to explore potential interactions. I collected field soil from sites where *V. dubia* was growing and a nearby area where it was absent, and used these soils as inoculum in potting soil. The objective was to test whether field soil inoculum affected *V. dubia* growth when compared to potting soil without field soil added. I hypothesized that *V. dubia* biomass would be greater when *V. dubia* was growing in conetainers with field soil inoculum and the effect of inoculum would be more pronounced with the field soil from the *V. dubia*-infested site.

Since research shows that *V. dubia* abundance is associated with soils with low P and K concentrations (Jones et al., 2018; Mackey, 2014), I included nutrient treatments, focused on P and K, in the greenhouse study. I watered pots with either a full Hoagland's solution (Hoagland & Arnon, 1938) or one of two modified Hoagland solutions, one without P and one without P and K. I hypothesized that *V. dubia* biomass would be higher in low fertilizer (no P or no P and K) than high fertilizer treatments.

Materials and Methods

Experimental Design

I tested three soil inoculum treatments: 1) Field soil where *V. dubia* was growing, hereafter referred to as plus *V. dubia* (+V); 2) Field soil where *V. dubia* was absent, hereafter referred to minus *V. dubia* (-V); and 3) Greenhouse soil with no field soil added, hereafter referred to as none. I tested three nutrient treatments using a fertilizer (Hoagland) solution: 1) Full Hoagland's solution (control, P and K); 2) Full Hoagland's solution without P, hereafter referred to as minus P (-P); and 3) Full Hoagland's solution without P and K, hereafter referred to minus P minus K (-P-K). Treatments were factorially arranged for a total of nine treatments (Table 2.1), with eight replicates in each trial. Two trials were run with the first trial occurring from 23 January to 19 April 2019 and the second trial starting 30 days later, occurring 22 February to 20 May 2019. Both trials were executed similarly. Twenty-five to thirty conetainers were placed in supporting brackets, which were rotated weekly on the greenhouse bench. Additionally, approximately 30 conetainers were randomized within the brackets into new locations each week.

Table 2.1. Soil inoculum and nutrient treatments.

Soil Inoculum Treatment	**Nutrient Treatment**
None	Full Hoagland's
None	-P
None	-P-K
+V	Full Hoagland's
+V	-P
+V	-P-K
-V	Full Hoagland's
-V	-P
-V	-P-K

Soil Preparation

Field soil inoculum was collected from two areas in Bozeman, Montana (approximately 45°40'15.0"N, 111°01'39.0"W) on 9 November 2018. A population of *V. dubia* has been growing in one of the areas since 2005 (Matt Lavin, personal communication); the other area was nearby (within 30 m) and did not have any *V. dubia*. Both areas are of the Blackmore Soil Series, consisting of a silt loam (UC Davis, n.d.). Soil was collected with a golf ball cutter, 10 cm deep and 10 cm wide (approximately 785 cm^3), six five-liter Zip-loc® bags were filled with soil from each area. Before extracting soil from either area, I sterilized the golf ball cutter with 70% isopropyl alcohol wipes and a propane torch. Soil was stored at 5-7 °C at the Montana State University Plant Growth Center (PGC) until pots were prepared for planting. On 19 January 2019 field soil inoculum was removed from storage and homogenized by area (*V. dubia* present and *V. dubia* absent). If roots were in the soil, they were cut to pieces of about 1 to 2.5 cm in length. Field soil was dried at room temperature, and no further treat preparation occurred.

The greenhouse soil consisted of a 1:1 mix of topsoil and sand. Topsoil was a composite of mineral soil found from the area around Bozeman; sand was a 20/30 grit (medium – fine). Topsoil and sand were mixed for three minutes in a concrete mixer and aerated steam pasteurized at 70 °C for two hours. Soil was air-dried in an open room and stored for four hours (Trial One) and thirty days (Trial Two) until conetainers were prepared for planting. Nutrient analysis of the prepared greenhouse soil was conducted by Ward Lab, Wisconsin.

Ventenata dubia seeds were collected on 6 August 2018 near Belgrade, Montana (approximately 45°45'32.3"N, 111°08'39.3"W) from a road right-of-way co-dominated by perennial grasses and *V. dubia*. Seeds were kept dry and stored at approximately 22 °C. Seed germination rate was 53%.

Conetainers (6.5 cm in diameter x 25 cm height) were cleaned with 1% bleach solution prior to filling with soil. Conetainers were filled with the sand-soil mix to 1 cm from the top. Approximately 33 cm^3 of soil inoculum was added to designated conetainers in a 1 cm band and 1 cm from the conetainer top. Five *V. dubia* seeds were placed on the soil surface, and greenhouse soil was sprinkled on top of seeds. Supplemental light with GE Multi-Vapor MVR1000/C/U was used with a 14-hour photoperiod, and temperature was maintained at approximately at 21 °C during day and 13 °C during night.

<u>Water and Nutrient Application</u>

For 38 days, 8 mL of water was applied to conetainers twice per day. After 28 days of growth, seedlings were reduced to two per conetainer and then thinned to one per conetainer on the 33rd day. On the 38th day, watering was reduced to once per day and then was halted until the 43rd day, when plants were misted with water. Hoagland's solution 50 mL treatments were applied once per week for six weeks, starting on the 44th day, occurring for 39 days, and ending on the 85th day. Plants also received an additional 25 mL of water once per week.

The full strength solution was prepared with all nutrients and deionized water (Table 2.2). The nutrient solution minus P, was mixed without potassium dihydrogen phosphate (KH_2PO_4); the solution without P and K was prepared by omitting potassium nitrate (KNO_3), potassium chloride (KCl) and potassium dihydrogen phosphate

(KH_2PO_4). Hoagland's solution 50 mL treatments were applied once per week for six weeks, starting on the 44th day, occurring for 39 days, and ending on the 85th day. After sampling, post-treated soils from trials were combined and sent to Ward Lab for nutrient analysis. This was done to establish whether the nutrient treatments achieved the goal of creating different nutrient (P and K) environments.

Table 2.2. Nutrient treatments.

Full Hoagland's Solution	**Full Hoagland's minus P**	**Full Hoagland's minus P, minus K**
$Ca(NO_3)_2$	$Ca(NO_3)_2$	$Ca(NO_3)_2$
KCl	KCl	-
KH_2PO_4	-	-
KNO_3	KNO_3	-
$MgSO_4$	$MgSO_4$	$MgSO_4$
Fe-EDTA	Fe-EDTA	Fe-EDTA
Microelements*	Microelements*	Microelements*

*H_3BO_3, $MnCl_2$, $ZnSO_4$, $CuSO_4$, MoO_3

Sampling

Shoot height was measured to the nearest centimeter, tillers and leaves were counted for each plant, then shoots were clipped to just above the soil surface. Roots were rinsed in water for 2-3 minutes. Wet root length was measured to the nearest centimeter. Roots were placed in coin envelopes and dried for 72 hours at 35.6 °C and 9.9% humidity. Dried shoot-and root biomass were weighed to the nearest 0.0001g.

In both trials, *V. dubia* mortality was 25%. Date of mortality was recorded, and those conetainers no longer received the nutrient solution or water throughout the remainder of the experiment. Tillers and leaves were still counted at harvest, and shoots and roots were measured for length, dried and weighed to the nearest 0.0001g, as described above. Analysis was performed with the complete data set and with the dataset excluding dead individuals. Because means and relationships between groups were similar between the two data sets, results reported here include the full dataset.

A subset of the samples representing each nutrient treatment was visually analyzed for arbuscular mycorrhizal colonization with *V. dubia* roots (n=9). Roots were placed in a beaker and rehydrated with deionized water overnight, soaked in KOH for 48 hours, soaked for 12 hours in 3% HCL solution, and stained for 12 hours in trypan blue. Roots were cut, 12 segments were applied to glass slides per treatment (2 slides per treatment, for a total of 24 segments), and prepared for microscopy. Colonization was determined at 200x magnification.

Generalized linear models were used to analyze response variables: aboveground and belowground biomass (mg per individual), shoot height and root length (cm), number of tillers and leaves per plant (α= 0.05). Fixed variables were soil inoculum, nutrient treatments and trial number. To meet assumptions of constant variance and normality, response variables were log-transformed when needed. A Tukey HSD pairwise comparison was performed for significant factors. Finally, to establish whether there were differences among nutrient treatments at the end of the study, a generalized linear model with an analysis of variance was used to test differences between phosphorous and potassium concentrations (n=9). All statistical analysis and data visualization were conducted with R Software 3.6.1 with dplyr, emmeans and ggplot2 packages (Length, 2020; R Core Team, 2019; Wickam, 2016; Wickam et al., 2020).

Results

Aboveground biomass differed across trials with higher biomass in Trial 1 (107 ± 15.8 mg) than Trial 2 (70.1 ± 18.1 mg, $p<0.001$, Table 2.3). Differences in aboveground biomass were also observed with an interaction between nutrient and soil inoculum treatments ($p=0.0131$). Aboveground biomass was significantly lower without inoculum (None) compared to the +V treatment across all nutrient treatments (Figure 2.1). In the None inoculum treatment, aboveground biomass ranged from 3.38 ± 0.53 to 5.33 ± 1.16 mg compared to 107 ±14.7 mg to 217 ± 21.2 mg in the +V treatment. Aboveground biomass in the +V and -V inoculum treatments were similar to each other within a nutrient treatment. The highest aboveground biomass occurred when *V. dubia* was growing in the Full nutrient treatment and with soil inoculum, regardless of whether the inoculum was from an area without *V. dubia* (-V, 210 ± 31.5 mg) or with *V. dubia* (+V, 217 ± 21.2 mg) (Figure 2.1).

Table 2.3. Analysis of Variance (ANOVA) for aboveground biomass (Above Biomass), shoot height, number of leaves, number of tillers, belowground biomass (Below Biomass) and root length. Values in table represent the following in order: F/Chi^2, p-value, degrees of freedom. Bold p-values indicate significance (α=0.05).

	Above Biomass	Shoot Height	Number Leaves	Number Tillers	Below Biomass	Root Length
Nutrient	9.725 **<0.001** *2, 132*	10.822 **<0.001** *2, 130*	189.29 **<0.001** *2, 124*	125.659 **<0.001** *2, 124*	8.936 **<0.001** *2, 124*	0.207 0.814 *2, 136*
Soil	64.204 **<0.001** *2, 132*	19.997 **<0.001** *2, 130*	627.25 **<0.001** *2, 124*	211.372 **<0.001** *2, 124*	15.439 **<0.001** *2, 124*	85.166 **<0.001** *2, 139*
Trial	20.772 **<0.001** *1, 132*	12.310 **<0.001** *1, 130*	69.75 **<0.001** *1, 124*	68.577 **<0.001** *1, 124*	22.559 **<0.001** *1, 124*	1.827 0.179 *1, 138*
Nutrient*Soil	3.294 **0.0131** *4, 132*	3.067 **0.019** *4, 130*	57.52 **<0.001** *4, 124*	41.854 **<0.001** *4, 124*	5.106 **<0.001** *4, 132*	0.438 0.780 *4, 130*
Nutrient*Trial	0.143 0.8667 *2, 128*	0.584 0.559 *2, 128*	30.06 **<0.001** *2, 124*	47.830 **<0.001** *2, 124*	6.374 **0.002** *2, 124*	0.692 0.499 *2, 134*
Soil*Trial	0.584 0.5591 *2, 130*	3.225 **0.043** *2, 130*	3.52 0.172 *2, 124*	2.226 0.329 *2, 124*	3.872 **0.023** *2, 124*	0.152 0.859 *2, 128*
Nutrient*Soil*Trial	0.740 0.5661 *4, 124*	1.224 0.304 *4, 124*	28.46 **<0.001** *6, 124*	99.013 **<0.001** ***6, 124***	3.210 **0.015** *4, 124*	0.644 0.632 *4, 124*

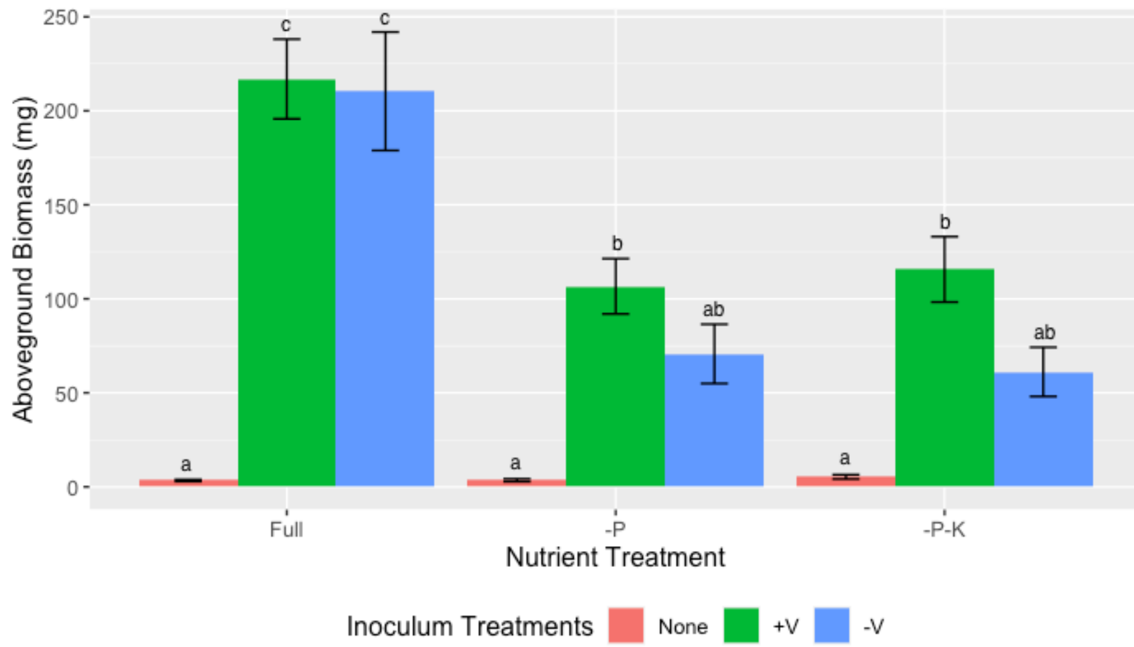

Figure 2.1. Mean aboveground biomass (mg) of *Ventenata dubia* as affected by nutrient and inoculum treatments. Similar letters indicate no difference in aboveground biomass across nutrient and inoculum treatments, conditional on trial (α=0.05). Error bars represent 1 standard error. Inoculum treatments are: (None) no inoculum added to greenhouse soil; (+V) soil from an area where *V. dubia* was present; (-V) soil from an area where *V. dubia* was absent.

Differences in *V. dubia* shoot height occurred among the two-way interactions of soil inoculum and nutrient treatments (p=0.019) and soil inoculum treatments and trial number (p=0.043, Table 2.3). Shoot height was lowest without soil inoculum (None) across all nutrient treatments with means ranging from 1.84 ± 0.19 cm to 2.59 ± 0.56 cm (Figure 2.2). Shoot height was similar among nearly all nutrient treatments with both field soil inocula (-V and +V).

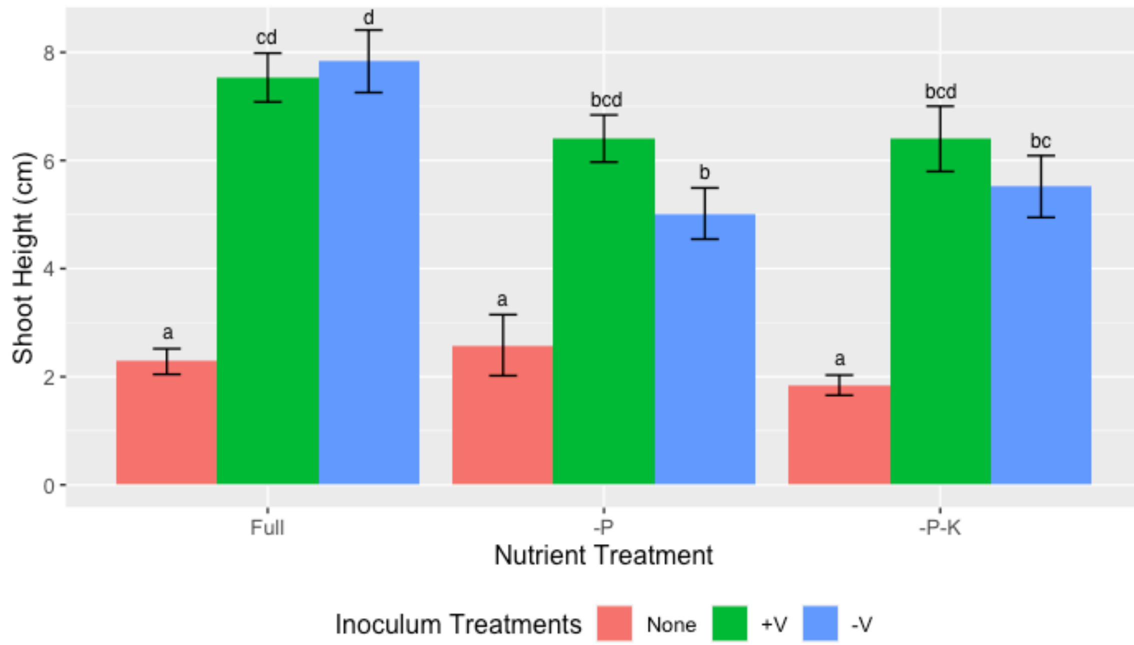

Figure 2.2. Mean shoot height (cm) of *Ventenata dubia* as affected by nutrient and soil inoculum treatments. Similar letters indicate no difference in shoot height across nutrient and inoculum treatments (α=0.05). Error bars represent 1 standard error. Inoculum treatments are: (None) no inoculum added to greenhouse soil; (+V) soil from an area where *V. dubia* was present; (-V) soil from an area where *V. dubia* was absent.

Shoot height was lowest in Trial 1 and Trial 2 without soil inoculum (None) with means of 2.24 ± 0.16 cm and 2.23 ± 0.40 cm, respectively (Figure 2.3). Inoculum treatments were similar to each other in both trials. The interaction was caused by differing shoot heights with -V and +V in each trial. Highest mean shoot height (-V and +V) in Trial 1 was 7.27 ± 0.46 cm and 5.70 ± 0.41 cm in Trial 2.

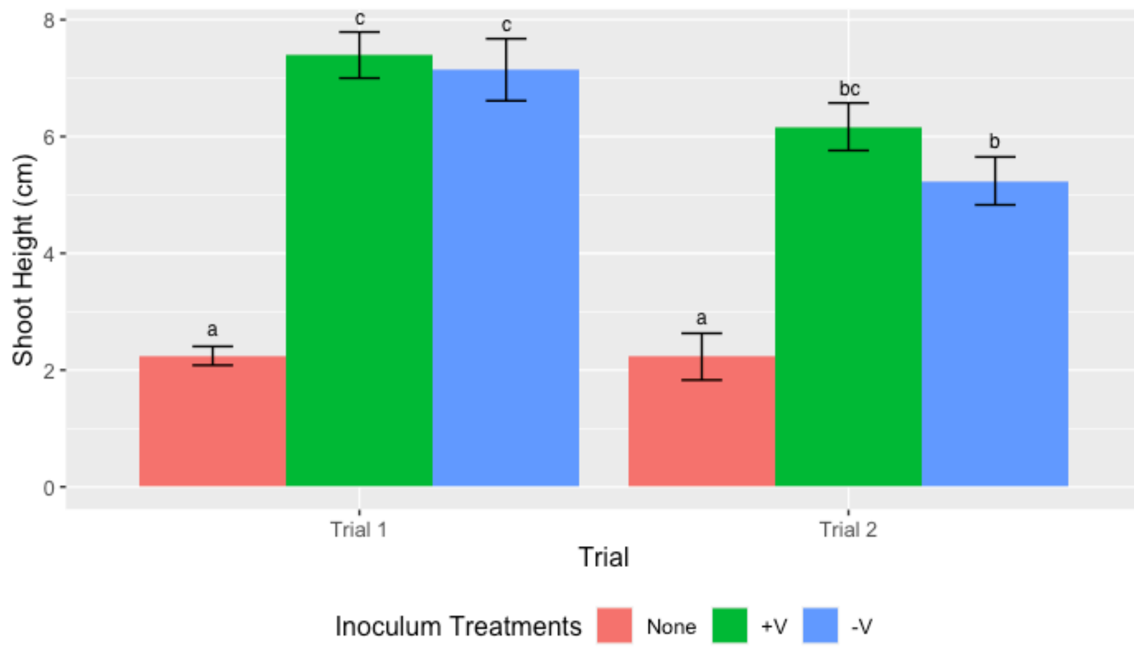

Figure 2.3. Mean shoot height (cm) of *Ventenata dubia* as affected by trial number and soil inoculum treatments. Similar letters indicate no difference in shoot height across both trials and inoculum treatments (α=0.05). Error bars represent 1 standard error. Inoculum treatments are: (None) no inoculum added to greenhouse soil; (+V) soil from an area where *V. dubia* was present; (-V) soil from an area where *V. dubia* was absent.

Number of leaves and tillers per plant were affected by the three-way interaction of nutrient treatment, soil inoculum treatments and trial ($p<0.001$, leaves and tillers, Table 2.3). Leaves and tillers in Trial 1 responded to treatments similarly to aboveground biomass (Appendix A, Figures 2.5, 2.6). In Trial 2, leaves and tillers were lowest among all nutrient treatments without field inoculum. Highest number of leaves in Trial 2 occurred with the full nutrient solution and either field soil inoculum (+V, -V). Number of tillers in Trial 2 was highest with the full nutrient solution with -V inoculum.

Differences in *V. dubia* belowground biomass were observed across a three-way interaction with soil inoculum, nutrient treatment and trial number ($p=0.015$, Table 2.3). The highest belowground biomass in both trials was with the full nutrient and

-V inoculum treatment, with means of 283 ± 26.7 mg and 255 ± 95.0 mg in Trial 1 and Trial 2, respectively (Figure 2.4). In Trial 1, belowground biomass varied among the remaining treatments but was typically higher in treatments where inoculum had been added compared to no inoculum. In Trial Two, aside from the Full nutrient -V treatment, the remaining treatments were all similar to each other, although the no inoculum treatment tended to appear lower, averaging about 2.13 ± 0.62 mg across nutrient treatments compared to 51.2 ± 16.0 averaged across the other treatments (Figure 2.4).

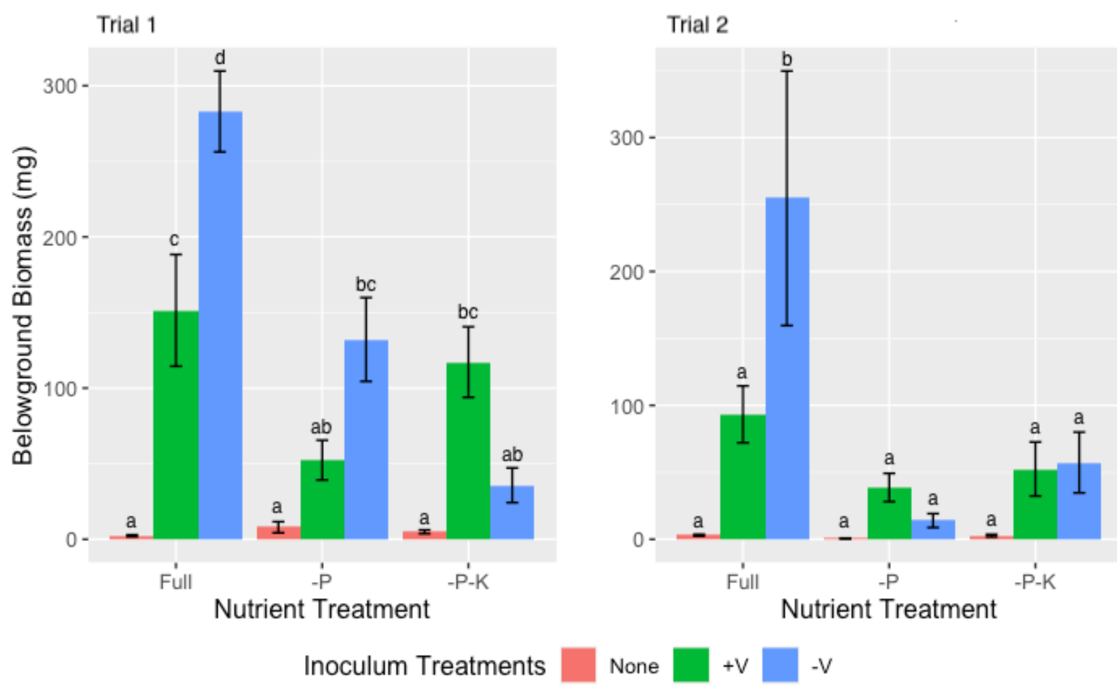

Figure 2.4. Mean belowground biomass (mg) of *Ventenata dubia* as affected by nutrient and soil inoculum treatments and trial. Similar letters indicate no difference in belowground biomass across nutrient and inoculum treatments within each trial (α=0.05). Error bars represent 1 standard error. Inoculum treatments are: (None) no inoculum added to greenhouse soil; (+V) soil from an area where *V. dubia* was present; (-V) soil from an area where *V. dubia* was absent.

Root length was affected by the soil inoculum treatment ($p<0.001$, Table 2.3) and there were no interactions. Inoculum treatments (-V and +V) were similar to each other and different from the non-inoculum treatment (None), with means of 19.5 ± 0.84 cm (-V), 20.3 ± 0.90 cm (+V) and 7.12 ± 0.67 cm (None), respectively.

Analysis of soil nutrient concentrations at the end of the study showed no difference in phosphorus (ANOVA: $F = 1.795$, df = 2, $p=0.225$) and potassium (ANOVA: $F = 2.139$, df = 2, $p=0.199$) concentrations in the -P, -P-K and Full nutrient treatments (Table 2.4). Arbuscular mycorrhizal fungi colonization was explored with *V. dubia* roots. Ocular observations performed with 200x microscope magnification resulted in no visible colonization on *V. dubia* roots.

Table 2.4. Mean ± 1 standard error phosphorous and potassium soil concentrations at the end of the study in the -P, -P-K, and Full nutrient treatments.

Treatments	Phosphorous (ppm)	Potassium (ppm)
-P	18.7 ± 0.33	177 ± 29.1
-P-K	19.3 ± 2.33	150 ± 15.6
Full	29.3 ± 7.36	221 ± 25.7

Discussion

In support of my first hypothesis, *V. dubia* biomass, shoot height, root length and number of leaves and tillers were higher when grown with field soil inoculum. Contrary to my hypothesis, however, the effect of field soil inoculum on *V. dubia* growth did not differ between the *V. dubia*-infested area and the non-infested area. *Ventenata dubia* soil biotic studies in the Intermountain West are limited, however, studies related to other non-native, winter annual grasses are useful for comparison. For example, *Taeniatherum caput-medusae* (L.) Nevski (medusahead) had higher biomass when grown in its own conditioned, clayey soil versus soil from other invasive and native grasses (Perkins & Nowak, 2013). Alternatively, *T. caput-medusae* had lower biomass when grown in a conspecific, sandy loam soil compared to biomass grown in conspecific, clayey soil (Perkins & Nowak, 2013), suggesting that soil texture, specifically clay, and its own-conditioned soil, positively affected plant growth for *T. caput-medusae*. Once soil was conditioned by *T. caput-medusae,* subsequent heterospecific plantings resulted in low plant performance of native and non-native grasses (Perkins & Nowak, 2013). Conversely, the invasive grass *Bromus diandrus* not only experienced a positive feedback when grown in soil previously occupied by native vegetation, it also demonstrated a stronger positive feedback when grown in pots with the native soil and with native forb species present (Hilbig & Allen, 2015).

In other studies, inoculum from field soils has led to greater growth of invasive plants, in particular invasive forbs, compared to greenhouse-only soil (Callaway et al., 2004; Mackay & Kotanen, 2008). In my study, whether the field soil was pre-conditioned by the invasive plant was not important. This is similar to another study where growth of *Ambrosia artemisiifolia* L., an invasive weedy annual forb in Europe that is native to North America; its growth was comparable with inoculum from field soil from where it was growing and from where it was absent (Mackay & Kotanen, 2008).

The strong effect of field inoculum in this study suggests naturally-occurring soil microbes are facilitating *V. dubia.* Alternatively, the strong effect could have occurred because soil microbes pathogenic to *V. dubia* were present in the greenhouse soil, in spite of pasteurization. These pathogens could have interacted with the microbial community introduced by the field inoculum. More specifically, when no inoculum was introduced (e.g. None treatment), greenhouse soil pathogens could have reduced *V. dubia* growth; in the presence of inoculum (+V or -V), pathogen(s) present in the greenhouse soil may have been overcome by the effect of field soil microbes. While my methods did not allow me to test for this, soil microbial ecology is complex with varied effects on aboveground growth (Bardgett & Wardle, 2010a).

The disparity between *V. dubia* growth with and without field soil inoculum prompted me to conduct a rudimentary analysis of *V. dubia* roots for arbuscular mycorrhizae fungi (AMF). A symbiotic relationship between AMF and plant roots provides carbohydrates for the fungi and nutrients to the plant (Smith et al., 2008). This relationship is often pursued to understand mechanisms of plant invasion (Bunn et al., 2015; Busby et al., 2012a; Hartnett & Wilson, 1999; Reinhart et al., 2017). For example, AMF colonized *B. tectorum* roots from germination to senescence, and the degree of colonization with hyphae, vesicles and arbuscules was related to soil temperature (Busby et al., 2012a), with higher colonization in May when florets developed. Soil inoculum in my study were collected in November when seedlings would be emerging, at least six months prior to flowering. Colonization was not evident with the *V. dubia* roots that were inspected. Though the sample size was small (n=9), 24 root segments per sample were observed, providing sufficient opportunity for AMF occurrence. However, soil inoculum were collected from one site, which limits inference to other sites. Arbuscular mycorrhizal colonization should be pursued further with *V. dubia,* and specifically from the field across multiple sites.

Arbuscular mycorrhizal fungi root colonization was examined in my study, yet, other endophyte and growth-promoting bacteria associations were not. Investigating fungi and bacteria associations can provide insight into aboveground community assembly and potentially, invasion. For example, in a sagebrush grassland, soil microbial differences existed in areas with native vegetation and where *B. tectorum* was dominant (Gasch et al., 2013). Native areas had slightly higher bacteria and less fungi than invaded areas. Also, invaded areas had overall lower microbial group abundance compared to uninvaded areas. Unraveling these ecological differences begins to shape an understanding of *B. tectorum's* relationship with soil biology. My study was exploratory with *V. dubia* plant-soil feedbacks and should be considered a first step in understanding the role of soil microbes in *V. dubia's* success. Since *V. dubia* growth was higher with both field soil inocula, growth-promoting fungi and bacteria could be contributing to *V. dubia* presence. Since we are in the early stages of understanding this species, studies assessing fungi and bacteria in a field setting with *V. dubia* present should be conducted.

Since low P and K soil concentrations were associated with higher *V. dubia* biomass in a field study (Jones et al., 2018), soil P and K treatments were pursued in this *V. dubia* greenhouse study. I hypothesized that *V. dubia* growth would be highest in conetainers watered with the modified (-P and -P-K) nutrient solutions compared to conetainers watered with full nutrient solution. In general, *V. dubia* growth was variable to somewhat similar across nutrient treatments. When differences did appear, *V. dubia* growth was higher in the Full nutrient treatment, which was contradictory to my hypothesis. However, soil analysis revealed that there were no differences in P and K concentrations among nutrient treatments (Full, -P, -P-K) at the end of the experiment (Table 2.4). It's possible that plants took up all available nutrients, so it is difficult to make conclusions about P and K related to *V. dubia* growth in my greenhouse study, especially related to a field study. *Ventenata dubia* may be able to grow better in the field where more nutrients are available rather than less, but because of competition in the high nutrient areas, *V. dubia* is not present there and therefore might occupy areas with reduced nutrients and less competition. Further investigating soil nutrients would be advantageous as soil nutrients had a positive effect on *T. caput-medusae* growth in a sandy loam soil (Perkins & Nowak, 2013), and *V. dubia* biomass was associated with low P and K concentrations in a field study (Jones et al., 2018).

High soil clay content (up to 40%) was noted as a positive environmental factor associated with *V. dubia* biomass in a Pacific Northwest field study (Jones et al., 2018). My *V. dubia* greenhouse study included an approximate 1:1 mix of mineral soil and sand, along with the addition of a small amount of silt loam for the soil inoculum treatments, likely resulting in lower silt and clay than other studies (Perkins & Nowak, 2013; Jones et al., 2018) have experienced. Although soil texture and organic matter were not analyzed in this study, it would be advantageous for future studies since they can influence nutrient availability. Clay and organic matter are negatively charged surfaces and influence the presence of cations, such as K, in the soil through cation exchange capacity (Rowell, 1994). Measuring soil properties with greenhouse and field soil throughout the study could elucidate differences in nutrient availability. It does appear that the soil inoculum played a large role in *V. dubia* growth, which suggest that soil biota, in addition to soil texture, as demonstrated in other studies (Callaway et al., 2004; Hilbig & Allen, 2015; Mackay & Kotanen, 2008), may be a strong contributor to *V. dubia* growth. Future *V. dubia* research should pursue soil texture in the context of nutrient concentrations, especially related to soil microbial communities, as they interact and are related (Morris et al., 2016; Schaeffer et al., 2012).

This is the first known study of *V. dubia* plant-soil feedbacks in the Intermountain West. Since *V. dubia* growth was positively related to inoculum from field soil, regardless of whether the field soil was collected from an area where *V. dubia* was present or absent, the evidence for a plant-soil feedback is not strong. Rather, there appears to be a positive relationship with *V. dubia* and field soil in general. Since *V. dubia* did not grow well with the sterilized greenhouse soil, it seems that the field environment provides *V. dubia* the microbes and nutrients it needs to survive. This indicates that once seeds fall, *V. dubia* will be able to establish, even in areas with low nutrient concentrations and areas not previously occupied by *V. dubia*.

Reports of *V. dubia* presence have increased in Montana. It is unknown whether those reports are because of heightened awareness or greater plant spread. If *V. dubia* is spreading, its likely distribution in North America could be large, ranging from central California to Alaska based on latitudes where it has occurred in its native range (Alomran et al., 2019). Management should include control measures to prevent its spread and monitor nearby areas so it can be quickly managed when found. Further soil biotic and nutrient investigations should be pursued to better understand *V. dubia's* mechanisms of invasion. Nutrient cycling, fungal and bacteria associations, and soil texture are a few avenues to consider.

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APPENDIX A

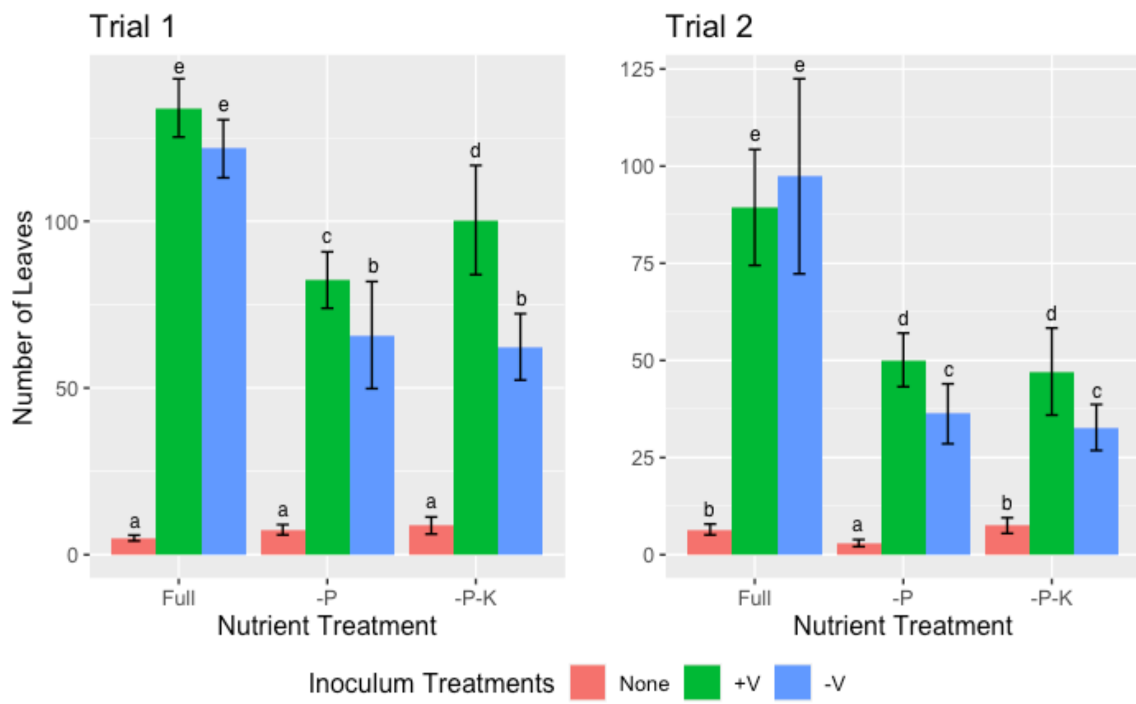

Figure 2.5. Mean number of *Ventenata dubia* leaves as affected by nutrient and soil inoculum treatments and trial. Similar letters indicate no difference in number of leaves across nutrient and inoculum treatments, by trial (α=0.05). Error bars represent 1 standard error. Inoculum treatments are: (None) no inoculum added to greenhouse soil; (+V) soil from an area where *V. dubia* was present; (-V) soil from an area where *V. dubia* was absent.

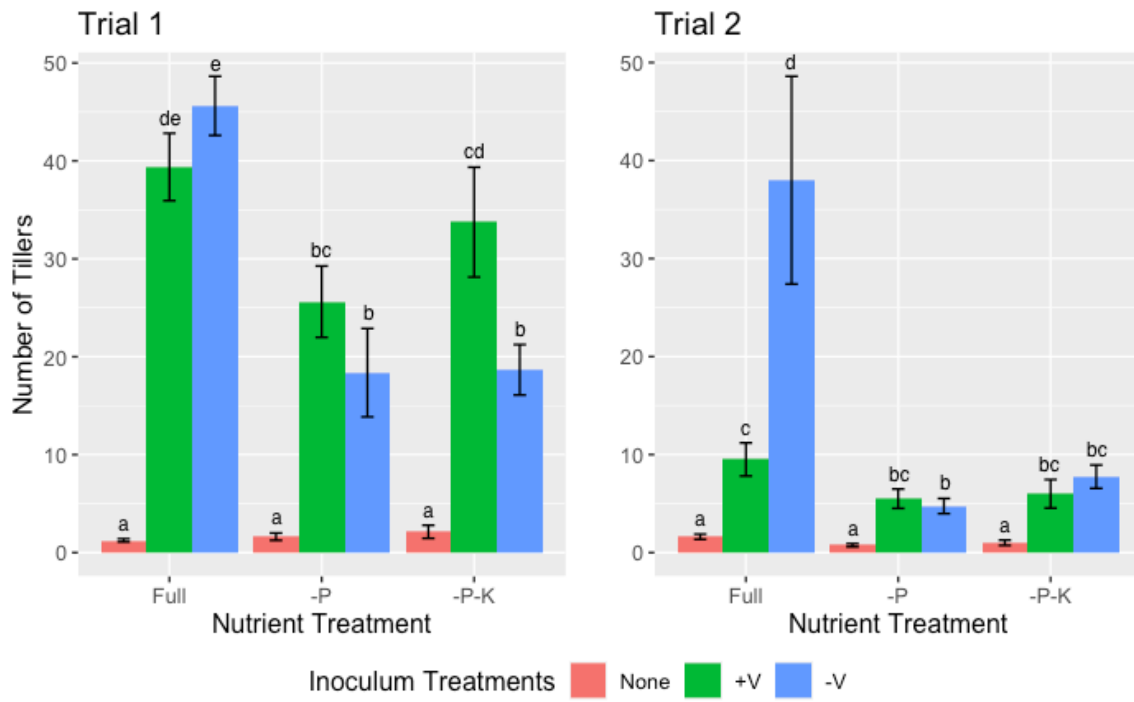

Figure 2.6. Mean number of *Ventenata dubia* tillers per plant as affected by nutrient and soil inoculum treatments and trial. Similar letters indicate no difference in number of tillers across nutrient and inoculum treatments, within each trial (α=0.05). Error bars represent 1 standard error. Inoculum treatments are: (None) no inoculum added to greenhouse soil; (+V) soil from an area where *V. dubia* was present; (-V) soil from an area where *V. dubia* was absent.

Manuscript Information

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CHAPTER THREE

VENTENATA DUBIA WAS ASSOCIATED WITH PERENNIAL GRASSES, BARE GROUND AND SOIL POTASSIUM CONCENTRATION

Contribution of Authors and Co-Authors

Manuscript in Chapter 3

Author: Michelle Lynn Majeski

Contributions: Executed study, collected data, conducted data analysis and prepared written manuscript.

Co-Author: Dr. Catherine Zabinski

Contributions: Reviewed and provided important feedback on manuscript.

Co-Author: Dr. Lisa J. Rew

Contributions: Provided guidance with statistical analysis. Reviewed and provided important feedback on manuscript.

Co-Author: Dr. Jane Mangold

Contributions: Conceived experimental design, obtained funding, conducted experiment, reviewed and provided guidance on manuscript.

Introduction

Ventenata dubia is a winter annual grass that is spreading across the Intermountain West (Alomran et al, 2019; Jones et al., 2018). Native to eastern Europe, western Asia, and northern Africa, it was first recorded in North America in the early 1950s in Washington and Idaho (Crins, n.d.; University of Washington Herbarium, 2020); it was first reported in Montana in the mid-1990s (University of Washington Herbarium, 2020). As of 2019, *V. dubia* was documented in 24 Montana counties, which is more than a 100% increase from 2018, when it was noted in nine counties encompassing 22,000 hectares (Harvey & Mangold, 2019). This expansion contributed to its noxious weed designation in Montana in June 2019 (Montana Department of Agriculture, 2019).

Impacts of *V. dubia* have been documented in Idaho and Washington. For example, reduced vegetative biodiversity on conservation land in northern Idaho was associated with *V. dubia*, which resulted in a decline in nesting success of insect-eating birds (Mackey, 2014). In grasslands in the Snake River Canyon of Idaho, *V. dubia* has displaced *B. tectorum* (Wallace et al., 2015). This change in vegetation affects livestock grazing; *B. tectorum* can serve as early-season forage for cattle (Murray et al., 1978), but cattle may avoid *V. dubia* due to its silica content (Mangold et al., 2019; Prather & Steele, 2009).

Soil, topography, elevation and climate contribute to plant species distribution (Radosevich et al., 2007a). The relationship between community composition and environmental factors are often studied to understand invasion (Bansal & Sheley, 2016; Blank et al., 2007; Radosevich et al., 2007a). Topography and elevation affect soil moisture, which modifies access to nutrients for plants (Blank et al., 2007; Radosevich et al., 2007a). In the Great Basin of the United States, cover of *B. tectorum* and other non-native annual grasses was positively associated with increasing soil temperatures and lower elevations (Bansal & Sheley, 2016); conversely, precipitation as snow, perennial grass cover, biological soil crust cover, and higher elevations were associated with a decrease in non-native annual grasses (Bansal & Sheley, 2016). Land aspect is often studied related to invasion susceptibility. For example, driest hill aspects in an Oregon canyon grasslands were more susceptible to vegetation change after land-use disturbances, such as grazing and cultivation (Bernards & Morris, 2017), and *V. dubia* was associated with south-facing aspects on low hillsides in southern Idaho and eastern Oregon (Jones et al., 2018).

Soil texture also influences moisture retention and nutrient availability (Schaetzl & Thompson, 2015). Increased moisture is associated with high amounts of silt and clay in soil and is sometimes associated with abundance of certain plant species. *Bromus tectorum, Taeniatherum caput-medusae* (L.) Nevski and *V. dubia* shoot biomass was positively associated with clay content and soil nitrogen in a growth chamber study (Bansal et al., 2014). In the field, in southern Idaho and eastern Oregon, *V. dubia* was positively associated with clayey soils and topographical areas that retained moisture, such as along ephemeral streams (Jones et al., 2018). At the same time, *V. dubia* cover was higher in soils with low phosphorous (P) and potassium (K) concentrations (Jones et al. 2018), demonstrating that not all associations between non-native annual grasses and soil texture or nutrient concentrations are positive.

In addition to abiotic environmental factors serving as indicators of plant species abundance, sometimes plant species associations can be used to identify areas susceptible to invasion by non-native annual grasses (Radosevich et al., 2007b). In the sagebrush steppe of the western United States, *B. tectorum* abundance was positively associated with *Artemisia tridenta* Nutt. ssp. *wyomingensis* Bettle and Young (Brummer et al., 2016). Also, 95 percent of sites where *B. tectorum* canopy cover was estimated as low to zero, native grass canopy was at least 25%, indicating a negative association between the two functional groups (Brummer et al., 2016). In another example from sagebrush steppe environments, *V. dubia* was associated with *A. tridenta* species and *A. arbuscula* Nutt, along with other annual grasses, *T. caput-medusae*, *B. japonicus* Houtt*, B. tectorum,* and *Apera interrupta* (L.) Beauv. (Jones et al., 2018). In another study in southwestern Montana, *V. dubia* was associated with *B. inermis* Leyss. (Harvey, 2019).

Given the recent increase in *V. dubia* across the Intermountain West, including Montana, I examined biotic and abiotic characteristics associated with established infestations of *V. dubia* to help identify areas vulnerable to future invasion. Five sites infested with *V. dubia* were selected across Montana. At each site, I surveyed plant communities where *V. dubia* was present and nearby areas where it was absent. I measured vegetative functional groups and environmental factors (soil texture and soil chemical characteristics). Based on studies from Idaho, Oregon and Montana, my hypotheses were: 1) *V. dubia* would be positively associated with non-native annual grasses and negatively associated with native perennial grasses and 2) *V. dubia* would be positively associated with soils with high clay content and negatively associated with soil P and K concentrations.

Materials and Methods

Experimental Design

Five sites were chosen based on prior knowledge of *V. dubia* presence in Montana: Arlee, Bozeman, Florence, Lodge Grass and Missoula. Each site consisted of two areas, approximately 50 m x 60 m each (Table 3.1): 1) where *V. dubia* was present (hereinafter referred to as *V.dubia*-present); and 2) where *V. dubia* was absent (hereinafter referred to as *V.dubia*-absent). At each site, eight transects (four within *V. dubia*-present and four within *V. dubia*-absent) were established to survey plant species functional groups and collect soil for chemical and texture analysis.

Sampling

In each area, four 50 m transects were established that were approximately 10 m apart. Along each transect, I estimated canopy cover to the nearest 1% of *V. dubia*, native annual forb, non-native annual forb, native perennial forb, non-native perennial forb, native annual grass, non-native annual grass (excluding *V. dubia*), native perennial grass, non-native perennial grass, bare ground/rock and litter in five (0.1 m^2) frames. The first frame of each transect was randomly located within the first 10 m of the 50 m transect, and the remaining four frames were located at 10 m intervals. At Missoula, 30 m transects were used instead of 50 m transects to accommodate smaller *V. dubia* patches, therefore points were 6 m apart instead of 10 m to account for the shorter transects. Soil was collected to a depth of 10-12 cm using an 8 cm diameter tulip bulb planter in each frame (5 frames/transect) and composited for one soil sample per transect. Soil pH, texture, organic matter (OM), nitrate (NO_3^-), phosphorous (P), potassium (K), sulfate (SO_4^{2-}), calcium (Ca), magnesium (Mg), sodium (Na) and cation exchange capacity

(CEC) were analyzed at Ward Lab, Wisconsin. Elevation, slope and aspect were recorded in *V. dubia*-present and absent areas within each site (Table 3.1).

Ventenata dubia cover was analyzed for similarities between sites with a generalized linear model and a Tukey HSD pairwise comparison. In the *V. dubia*-present areas, to determine whether biotic functional groups were associated with *V. dubia*, a mixed effects model was used. The response variable was *V. dubia* cover and fixed effects were functional groups. Random effects were nested with site and transect. To meet normality and constant variance assumptions, response and predictor variables were natural log transformed and estimated medians are reported. Correlations between *V. dubia* cover and abiotic predictor variables of soil texture (sand, silt and clay percent), soil organic matter, soil pH, soil nutrients (NO_3^-, P, K, SO_4^{2-}, Ca, Mg, Na) and CEC were analyzed with mixed effect models. A datum related to *V. dubia* cover had a Cook's Distance of 0.8, appeared to show leverage and was removed from the dataset as models with and without the datum showed different results. The response variable was *V. dubia* cover with fixed effects of each separate abiotic factor and the random effect of site. Predictor variables were further analyzed for mean differences by area (*V. dubia*-present, *V. dubia*-absent) with a mixed effects model. Response variables were abiotic factors with area as a fixed effect and site as a random effect. All analysis included $\alpha = 0.1$. Statistical analysis and data visualization were conducted with R Software 3.6.1 with dplyr, and lmer packages (Bates et al., 2015; R Core Team, 2019; Wickam et al., 2020).

Table 3.1. Site characteristics by area. Precipitation and temperature are for 2019.

Site Area	Latitude Longitude	Aspect	Elevation (m)	Precipitation Avg. (cm) July – Sept.	Slope (%)	Soil Series	Temperature Avg. High/Low °C (June – Aug)
Arlee *V. dubia* absent	N47º14'33.7 W114º10'39.3	NW	868	3.6	1	Gird series, silt loam	26 / 8
V. dubia present	N47º14'34.3 W114º10'47.9	E	870	3.6	3	Gird series, silt loam	26 / 8
Bozeman *V. dubia* absent	N45º54'44.7 W111º04'27.4	SW	1664	3.3	5	Sawicki series, cobbly loam	28 / 10
V. dubia present	N45º54'37.3 W111º04'28.5	SW	1664	3.3	5	Sawicki series, cobbly loam	28 / 10
Florence *V. dubia* absent	N46º43'11.5 W114º01'01.5	W	1223	3.0	11	Bigarm series, very gravelly loam	28 / 11
V. dubia present	N46º43'07.4 W114º00'55.6	SW	1238	3.0	13	Bigarm series, very gravelly loam	28 / 11
Lodge Grass *V. dubia* absent	N45º16'25.7 W107º35'02.2	N	746	3.3	5	Wayden series, silty clay	28 / 10
V. dubia present	N45º16'17.4 W107º35'16.9	S	1145	3.3	4	Wayden series, silty clay	28 / 10
Missoula *V. dubia* absent	N46º53'56.5 W113º57'01.1	S	4568	5.3	13	Minesinger, very stony loam	17 / 8
V. dubia present	N46º53'55.6 W113º56'58.3	S	4568	5.3	23	Minesinger, very stony loam	17 / 8

Results

Ventenata dubia cover in the *V. dubia* – present area differed among sites (ANOVA: F = 4.127, df = 4, p=0.004). Lowest cover was at Missoula with 4.1 ± 1.2 %, and highest cover occurred at the remaining sites, averaging 20 ± 3.9 %.

Table 3.2. T-test results for *Ventenata dubia* cover associated with measured variables. *Ventenata dubia* and biotic predictor variables were natural log-transformed (1st section of table). For abiotic predictor variables on *Ventenata dubia* response, variables were not transformed (2nd section of table). Bold p-values indicate significance (α=0.1).

Biotic predictor variables	Degrees of freedom	T-value	P-value
Bare ground / Rock	1, 92	-1.724	**0.088**
Litter	1, 84	-0.957	0.341
Native annual forb	1, 92	-0.900	0.371
Non-native annual forb	1, 87	-0.629	0.531
Native perennial forb	1, 88	-0.601	0.550
Non-native perennial forb	1, 74	-0.700	0.486
Native annual grass	1, 87	-0.647	0.519
Non-native annual grass	1, 94	0.949	0.345
Native perennial grass	1, 85	-2.592	**0.011**
Non-native perennial grass	1, 68	2.086	**0.041**
Abiotic predictor variables			
CEC	1, 4	-1.342	0.246
Clay	1, 10	-1.546	0.151
Sand	1, 7	0.397	0.704
Silt	1, 10	0.413	0.688
Calcium	1, 4	-1.749	0.164
Magnesium	1, 9	-1.032	0.329
Nitrate	1, 8	1.103	0.303
Phosphorous	1, 14	-1.028	0.321
Potassium	1, 16	-1.833	**0.086**
Sodium	1, 5	0.300	0.776
Soil organic matter	1, 10	-1.679	0.125
Soil pH	1, 14	-0.043	0.967
Sulfate	1, 17	0.505	0.619

Ventenata dubia cover was negatively associated with bare ground/rock cover (p=0.088) and native perennial grass cover (p=0.011) and positively associated with non-native perennial grass cover (p=0.041, Table 3.2, Eq. 3.1).

$$\hat{\mu}\ \{\ln\ (\textit{V. dubia})\ |\ \ln\ (\text{biotic functional group})\} = \qquad \text{[Eq. 3.1]}$$
$$2.023 - 0.087 \cdot (\ln)\ \textit{Bare ground/Rock} - 0.175 \cdot (\ln)\ \textit{Native perennial grass} + 0.158 \cdot (\ln)\ \textit{Non-Native perennial grass} + (1|\ \text{Site / Transect})$$

The model variation explained by the random and fixed effects was 67%. Associations with *V. dubia* were for every 10 % increase in bare ground/rock cover, there was an estimated 1 % decrease in median *V. dubia* cover (CI: -0.19 to 0.01), for every 10 % increase in native perennial grass cover, there was an estimated 2 % decrease in median *V. dubia* cover (CI: -0.30 to -0.04) and for every 10 % increase in non-native perennial grass cover, there was an estimated 2 % increase in median *V. dubia* cover (CI: -0.01 to 0.30, Figure 3.1).

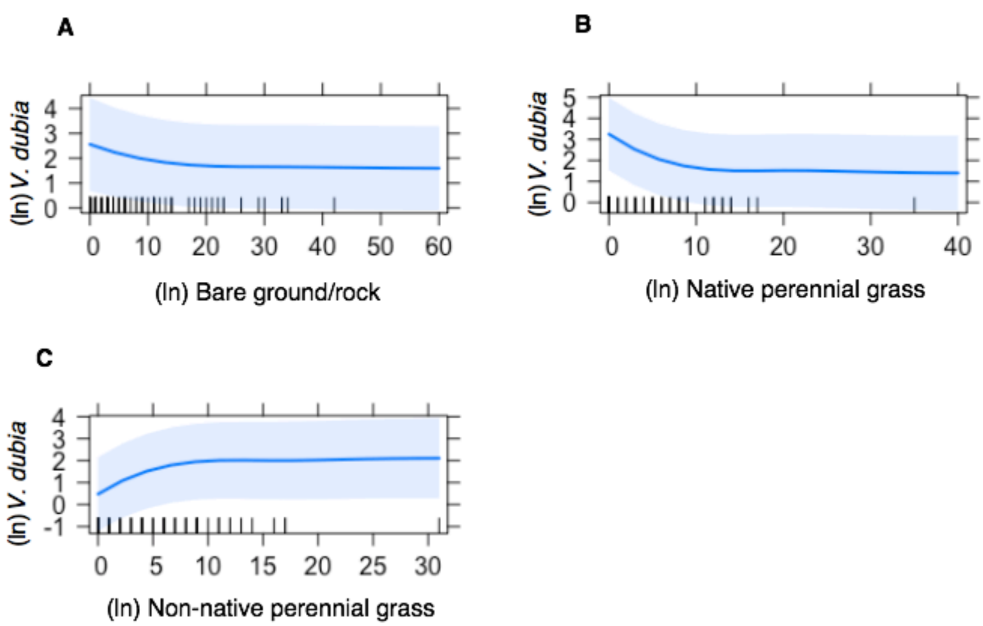

Figure 3.1. Effects plots showing: (A) (ln) bare ground/rock cover (%), (B) (ln) native perennial grass cover (%) and (C) (ln) non-native perennial grass cover (%), as related to (ln) *Ventenata dubia* cover (%) for the estimated model. Blue bands represent 95% confidence intervals. Tick marks on x-axis reflect data points.

There was a negative association between *V. dubia* cover and soil K concentration ($p=0.086$, Table 3.2, Eq. 3.2). Fixed and random effects explained 63% variability in the model. For every increase in 1 ppm soil K concentration, *V. dubia* estimated mean cover decreased by about 0.05 % (95% CI: -0.098 to 0.005, Figure 3.2).

$$\hat{\mu}\{V.\ dubia \mid \text{potassium}\} = 36.57 - 0.048 \cdot \text{soil } K\ concentration + (1 \mid \text{Site}) \qquad \text{[Eq. 3.2]}$$

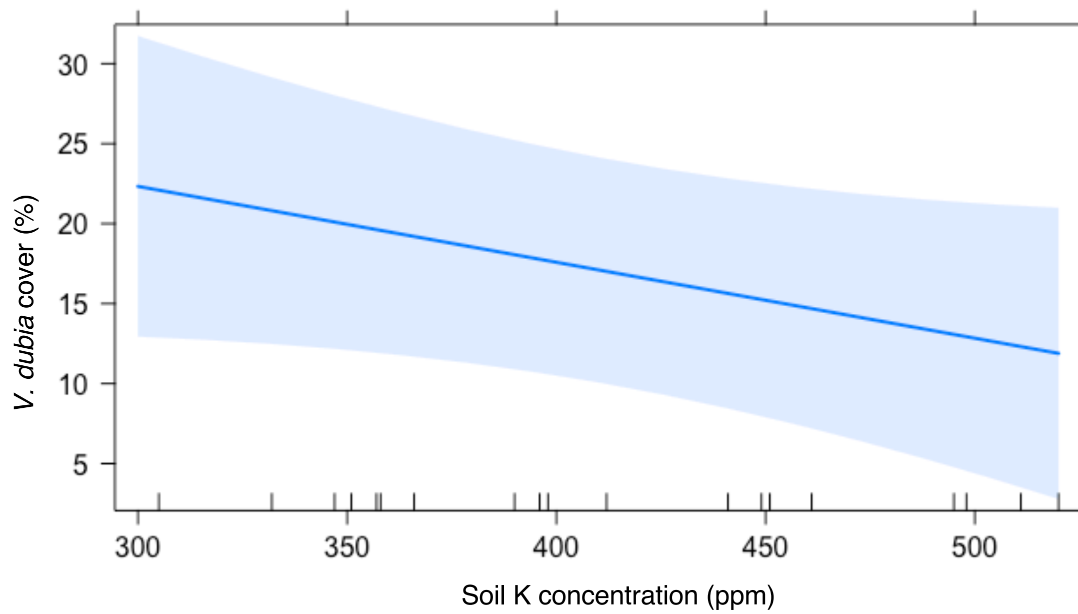

Figure 3.2. Effects plot of soil K concentration (ppm) versus *Ventenata dubia* cover (%) for the estimated model. Blue band represents 95% confidence intervals. Tick marks on x-axis indicate data points.

Most abiotic factors differed between the *V. dubia*-absent and *V. dubia*-present areas across all sites. Differences occurred with CEC ($p<0.001$) and soil texture: percent clay ($p<0.001$), percent sand ($p<0.001$) and percent silt ($p=0.001$). Soil nutrients that differed among areas were: Ca ($p<0.001$), Mg ($p=0.028$), P ($p=0.045$), Na ($p<0.001$) and SO_4^{2-} ($p<0.001$). Soil organic matter ($p<0.001$) and pH ($p<0.001$) also differed between the *V. dubia*-absent and *V. dubia*-present areas (Table 3.3)

Table 3.3. T-value, P-value, and means (± 1 standard error) for abiotic factors by area, i.e. *Ventenata dubia*-present and -absent. Degrees of freedom are 1, 194. Bold p-values indicate significance (α=0.1).

			Means for each variable	
Variable	T-value	P-value	*V. dubia*-absent	*V. dubia*-present
CEC (me/100g)	-7.165	**<0.001**	17.9 ± 0.39	14.8 ± 0.48
Clay (%)	-6.549	**<0.001**	30.0 ± 1.0	25 ± 0.4
Sand (%)	4.731	**<0.001**	40.0 ± 1.0	43 ± 0.7
Silt (%)	3.317	**0.001**	30.0 ± 0.4	32 ± 0.6
Calcium (ppm)	-8.664	**<0.001**	2709 ± 68.6	2018 ± 77.4
Magnesium (ppm)	2.208	**0.028**	321 ± 7.96	336 ± 9.84
Nitrate (ppm)	0.968	0.334	2.6 ± 0.2	2.8 ± 0.2
Phosphorous (ppm)	2.015	**0.045**	23 ± 1.2	24 ± 1.1
Potassium (ppm)	0.767	0.444	411 ± 13.3	419 ± 6.88
Sodium (ppm)	6.473	**<0.001**	15 ± 1.6	19 ± 1.8
Soil organic matter (%)	-11.65	**<0.001**	6.3 ± 0.2	4.9 ± 0.1
Soil pH	-6.378	**<0.001**	7.0 ± 0.1	6.8 ± 0.1
Sulfate (ppm)	-6.22	**<0.001**	9.0 ± 0.3	7.09 ± 0.2

Discussion

My first hypothesis, that *V. dubia* would be positively associated with non-native annual grasses and negatively associated with native perennial grasses, was partially met. There was no association between *V. dubia* and non-native annual grasses in my study, but *V. dubia* was negatively associated with native perennial grasses. *Ventenata dubia* has invaded perennial grasslands and sagebrush steppe communities in the Intermountain West in the last decade (Jones et al., 2018; Wallace et al., 2015; Wallace & Prather, 2011), and these areas may continue to be susceptible to invasion. Similar to my study, in a larger area encompassing sagebrush steppe communities within 11 states, another non-native, invasive annual grass, *B. tectorum*, was also negatively associated with native perennial grasses (Brummer et al., 2016). Likewise, in sagebrush steppe rangelands in southern Idaho and eastern Oregon, native species richness was low when *V. dubia* cover was high (> 12.5 %, Jones et al., 2018), indicating a similar trend to my study. Interestingly, *V. dubia* was positively associated with non-native perennial grasses in my study, which is the first to demonstrate such a relationship. Identifying indicator species related to *V. dubia* is a way to distinguish areas that may be susceptible to future invasion. Knowledge of areas where invasion may be low is helpful when management resources are limited and efforts can be directed to other areas. This study, along with others, indicates that where native perennial grasses are abundant, *V. dubia* cover will be low. Such areas can be low priority for monitoring, and resources should instead be directed to monitoring areas where native perennial grass abundance has been compromised.

This study found a distinction between the nativity of perennial grass and the type of association with *V. dubia*. While *V. dubia* had a negative association with native perennial grasses, it was positively associated with non-native perennial grasses. *Poa compressa* L., *Poa bulbosa* L. and *Agropyron cristatum* (L.) Gaertn. were species noted in *V.dubia*-present areas, though specific species were not analyzed for associations with *V. dubia*. A southwest Montana study found a similar relationship with *V. dubia* and a non-native perennial grass, *B. inermis,* which was positively associated with *V. dubia* (Harvey, 2019). Monitoring areas where native perennial grasses have been replaced by non-native perennial grasses could be a first step for identifying areas susceptible to *V. dubia* invasion.

A positive or negative correlation with *V. dubia* with respect to native or non-native perennial grasses could be a function of many factors: historical land use, level of disturbance, elevation, climate, etc. Whether an invasive species associates with native or non-native species may be determined by whether the site is a historically intact ecosystem versus one that is disturbed. Non-native annual grasses and non-native perennial grasses, especially if their nativity is similar, may be able to co-exist more so than annual and perennial grasses of different nativity. For example, in a California coastal grassland study, the non-native annual grass *Bromus diandrus* Roth suppressed two native perennial grasses more than it did a non-native perennial grass (Abraham et al., 2009). A similar situation could be occurring with *V. dubia* in the Intermountain West. If this is the case, it could be beneficial to use non-invasive, non-native perennial grasses as a managed successional stage for restoring areas invaded by annual grasses where native perennial grass establishment is initially unsuccessful.

This approach has been tried with positive results. In a *B. tectorum*-infested area in Wyoming, seeding introduced perennial grasses resulted in 85 to 100 % *B. tectorum* control three years later (Whitson & Koch, 1998). Similarly, in an area that was infested with *T. caput-medusae,* seeding a non-native perennial grass at the edge of the infestation created a competition buffer and reduced *T. caput-medusae* by 42-fold three years later in the buffer area (Davies et al., 2010). These studies show that over a short time period, non-native perennial grasses can reduce non-native annual grasses in infested areas.

Ventenata dubia had a negative association with soil K concentration, which supported my second hypothesis, that *V. dubia* would be negatively associated with soil P and K concentrations. This result is similar to findings from Jones et al. (2018), where *V. dubia* abundance was correlated with soils with low K concentration in southern Idaho and eastern Oregon. Potassium concentration ranged from 305 to 547 ppm in my study, which is also similar to Jones et al. (2018) where soil K concentrations ranged from 200 to 520 ppm. There are now two field studies, encompassing Montana, Idaho and Oregon, with evidence that *V. dubia* is associated with lower soil K concentrations. This was not the case in a greenhouse study (See Chapter 2 where low K conditions did not improve *V. dubia* growth compared to high K conditions), however greenhouse studies may not represent conditions as they occur in the field. Realistically, *V. dubia* may be able to grow among a variety of nutrient environments and tolerate less than superior conditions, given the opportunity. If low nutrient areas are the only places available for *V. dubia* to grow, it may be able to tolerate those conditions more so than high nutrient areas where there is strong vegetation competition. Low nutrient areas may be the only available niche for *V. dubia* at certain locations.

I hypothesized that *V. dubia* would be associated with soil P concentration and clay content. Contrary to this, *V. dubia* was not associated with soil P concentration or clay content like it was in Jones et al. (2018). However, my findings somewhat align with a growth chamber study investigating the effect of soil texture on *V. dubia, B. tectorum* and *T. caput-medusae* (Bansal et al., 2014). In that study, the growth of these species was compared in nine soils with varying amounts of clay. There was no difference in *V. dubia* biomass among the different soils, demonstrating that *V. dubia* may have a wide range of soil textures in which it can grow and reproduce
(Bansal et al., 2014).

My study also analyzed soil factors by area (*V. dubia*-absent and *V. dubia*-present). Most of the factors differed by area except for nitrate and K (Table 3.3). Most of the areas were not more than 400 m from each other, except for one site (Lodge Grass, 410 m), and soil series were the same per site (Table 3.1). Since no significant associations were found between soil characteristics and *V. dubia* presence (except K), *V. dubia* presence or absence may best be explained by vector pathways rather than differences in soil characteristics. Since *V. dubia* is an annual, and reproduces by seed only, locations where seeds have dispersed and established may be a more important determinant of *V. dubia* presence than soil characteristics. Since *V. dubia's* height usually does not exceed 50 cm (Scheinost et al., 2009), seeds typically stay close to the parent plant, and *V. dubia's* twisted awns help seeds reach the soil. These physical traits, along with the presence of native vegetation, are more likely why *V. dubia* was somewhat contained in the *V.dubia*-present areas rather than physical and chemical differences in the soil. If seeds disperse beyond current infestations, it is likely that *V. dubia* will be successful in new locations as well. Management strategies should focus on identifying vector pathways and limiting dispersal into new areas (Davies & Sheley, 2007).

This study expands the current knowledge on *V. dubia* in the Intermountain West, specifically related to abiotic and biotic factors. Still, little is known about *V. dubia* in this region and further research is needed to understand its niche, environmental associations and invasion mechanisms. This is an opportunity, as *V. dubia* awareness appears to be building and interest in reducing or eradicating it has been the topic of recent trainings, studies, conference presentations (Libbey, 2019) and conversations.

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CHAPTER FOUR

SPRING SEEDING PROVIDES A SEASONAL PRIORITY EFFECT FOR PSEUDOROEGNERIA SPICATA IN BROMUS TECTORUM-INVADED RANGELANDS

Contribution of Authors and Co-Authors

Manuscript in Chapter 4
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Contributions: Executed study, collected data, conducted data analysis and prepared written manuscript.

Co-Author: Stacy C. Simanonok

Contributions: Gathered materials and executed experimental design at Belgrade site, assisted with data collection in 2018.

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Contributions: Conceived experimental design, obtained funding, executed experimental design at Corvallis sites, will review manuscript prior to publication submittal.

Co-Author: Dr. Lisa J. Rew

Contributions: Provided guidance with statistical analysis. Reviewed and provided important feedback on manuscript.

Co-Author: Dr. Jane Mangold
Contributions: Conceived experimental design, obtained funding, conducted experiment, reviewed and provided guidance on manuscript.

Introduction

Bromus tectorum L. is one of the most widespread invasive annual grasses in the western United States, occupying 7 million hectares of land (Belnap et al., 2005). The impacts of this vegetation change from native perennial species to a non-native winter annual grass are considerable and complex. Wildlife that once relied on native vegetation for forage and shelter pursue habitat in other areas (Ditomaso, 2000). Water, nutrient cycling, and soil food webs are altered when there is a change in plant species composition to *B. tectorum* (Belnap et al., 2005; Chambers et al., 2007; Sperry et al., 2006). Increased soil erosion occurs as a result of *B. tectorum* invasion because of its shallow roots (Ditomaso, 2000). *Bromus tectorum* senesces earlier in the summer than native perennial grasses, extending wildfire season and increasing the likelihood of burning (Bradley et al., 2018).

Chemical control is the most commonly used method for reducing impacts associated with *B. tectorum*, however control is typically short-lived unless herbicide applications are made repeatedly (Hirsch et al., 2012; Mangold et al., 2013; Monaco et al., 2017). Longer term management, beyond one year, requires that chemical control be integrated with revegetation (Monaco et al., 2017). Timing of herbicide application is important and must consider *B. tectorum's* growth stage (Mangold et al., 2013). However, precipitation and temperature patterns vary even within a region, particularly large ecoregions with heterogeneous elevation and topography, resulting in different local peaks in the growth stage of *B. tectorum* (Bansal & Sheley, 2016; Brummer et al., 2016), consequently affecting the ideal timing of herbicide application by location.

Revegetation, when successful, establishes desired perennial species that can compete against *B. tectorum* and thereby provide control that extends beyond one season (Whitson & Koch, 1998). For example, in a meta-analysis comparing *B. tectorum* control methods over a 64-year period, herbicide application combined with revegetation was the only approach that resulted in successful long-term (> 2 yrs.) control (Monaco et al., 2017). Revegetation, however, is not always successful. Appropriate seed mixture, seeding rate, moisture availability and removal of undesired species are factors that contribute to success or failure of revegetation (Chambers et al., 2007; Nyamai et al., 2011). Understanding life history stages of seeded species proves to be an important factor for revegetation (Boyd & James, 2013; James et al., 2011). James et al. (2011) found that the transition from germination to emergence was a critical time for perennial grass seedling establishment. *Bromus tectorum,* a winter annual grass, emerges in the fall, becomes dormant in the winter, regrows early in the spring and has a rapid growth rate. Seeded perennial grasses typically emerge in the spring and then grow more slowly and beyond one year, which reduces their competitive ability relative to *B. tectorum*, at least in the short-term (one year or less). Once established, perennial grasses become more competitive with *B. tectorum* and may outcompete it (Harvey et al., 2020; Orloff et al., 2013; Schantz et al., 2016).

Early-emerging species benefit by having first access to soil nutrients and water, and this can result in a more developed root structure (Weidlich et al., 2017) as well as greater aboveground biomass and cover than slower-emerging competitor, creating a seasonal priority effect (Weidlich et al., 2017; Zimdahl, 2007). *Bromus tectorum* benefits from a seasonal priority effect because of its biology as a winter annual. This seasonal priority effect needs to be overcome during revegetation so that perennial grass seedlings are not at a competitive disadvantage.

Overcoming the seasonal priority effect of *B. tectorum* when seeding native, perennial grasses has been the focus of recent studies (Harvey et al., 2020; Orloff et al., 2013; Schantz et al., 2016; Wainwright et al., 2012). *Pseudoroegneria spicata* Pursh A. Löve (bluebunch wheatgrass), for example, is a ubiquitous, long-lived native bunchgrass in the Intermountain West, well-suited for managed grazing because of its high protein content and palatability to all classes of livestock (Boyd & James, 2013; Ogle et al., 2013). Orloff et al. (2013) found that when *P. spicata* had a four-leaf size advantage, approximately four weeks of growth, over emerging *B. tectorum* in a greenhouse study, it had higher plant density and was able to more effectively suppress *B. tectorum*. In the field, November and December planting dates of *P. spicata* resulted in higher emergence and increased survival compared to September and October planting dates in eastern Oregon rangelands; once established, 50% of *P. spicata* plants survived beyond two years (Boyd & James, 2013). In southwest Montana, seeding timing (fall or multiple dates in spring) of *P. spicata* was tested in a weed-free, fallow field. Fall seeding led to bigger yet fewer plants, while early spring seeding resulted in smaller yet denser plants; fall and early spring seeding led to an increase in resistance to invasion by *B. tectorum* (Harvey et al, 2020).

Timing of seeding desired, native, perennial grass appears to influence revegetation success (Boyd & James, 2013; Harvey et al., 2020), and integrating chemical control with revegetation to reduce *B. tectorum* long-term is usually required (Monaco et al., 2017). However, incorporating timing of seeding with timing of herbicide application to overcome the seasonal priority effect typically demonstrated by winter annual grasses like *B. tectorum* has yet to be explored and was therefore the objective of this study. More specifically, I attempted to shift the seasonal priority effect typical for *B. tectorum* to *P. spicata*. My hypotheses were: 1) Early spring seeding as opposed to fall seeding will result in higher abundance (density and cover) of *P. spicata* and lower abundance (cover) of *B. tectorum* and other weedy species; and 2) Integrating an herbicide application with seeding will result in lower abundance of *B. tectorum* and other weedy species and higher abundance of *P. spicata* compared to not integrating herbicide application; however, timing of herbicide application (fall or spring) will have no effect.

Materials and Methods

Study Sites

Three field sites were located in Montana at the following locations: Belgrade (45°48'02.3"N, 111°09'10.6"W), with a Beaverell series loam soil classification; Corvallis West at the Montana State University Western Agricultural Research Center (46°1 9'40.3"N, 114°05'06.4"W), with a soil classification of coarse-loamy in the Burnt Fork series; and Corvallis East, located approximately 5.6 km east of Corvallis West on Soft Rock Road (46°19'34.4"N, 114°00'08.2"W), where soil is classified as coarse-loamy of the Burnt Fork-Wimper-Fairway complex series (Univeristy of California & Service, n.d., Table 4.1).

Table 4.1. Site elevation and average temperature and precipitation during the first growing season of the study (NOAA, 2020).

	Belgrade	Corvallis-West	Corvallis-East
Elevation (m)	1363	1096	1424
Avg. Temp. °C (Hi/Lo., 2018 Mar – May)	13 / -1	14 / 2	14 / 2
Avg. Temp. °C (Hi/Lo., 2018 June – Aug.)	27 / 8	26 / 8	26 / 8
Avg. Precip., mm (2018 Mar – May)	53.8	32.5	46.0
Avg. Precip., mm (2018 June – Aug.)	42.7	40.1	40.9

Experimental Design

A randomized block, split-plot design was used to test six seeding treatments and two herbicide treatments. The six seeding treatments were no seeding (the control), one fall date, and four spring dates starting in April and occurring about every two weeks through May. The herbicide treatments were glyphosate applied in fall or spring. Seeding treatments were applied to whole-plots (6 m x 3.7 m), and herbicide treatments were applied to split-plots (3 m x 3.7 m). Treatments were replicated three times at each site. Due to variation in climate across the three sites, treatment application at Corvallis East and Corvallis West started about two weeks earlier than at Belgrade (Table 4.2).

Table 4.2. Dates of *Pseudoroegneria spicata* seeding, herbicide applications and growing degree days at Corvallis East and West and Belgrade. Cumulative growing degree days (GDD = sum of average daily temperature °C – temperature base 4.4 °C between 1March 2018 to 31 May 2018) for *Pseudoroegneria spicata.*

Corvallis East and West		**Belgrade**	
Seeding Dates	*Growing Degree Days*	*Seeding Dates*	*Growing Degree Days*
30 October 2017	-	15 November 2017	-
3 April 2018	20.9	21 April 2018	34.3
19 April 2018	47.6	3 May 2018	85.7
4 May 2018	117.8	17 May 2018	200.7
15 May 2018	209.7	31 May 2018	337.8
Herbicide Application Dates		*Herbicide Application Date*	
15 October 2017		19 October 2017	
11 April 2018		N/A	

Seeding and Herbicide Treatments

Pseudoroegneria spicata, Goldar variety, (Bruce Seed Farm, Townsend, Montana) was seeded at 12 kg/ha pure live seed (PLS) using a Landpride® No-till drill with as seeding depth of 0.5 – 1.25 cm at Corvallis East and Corvallis West sites. At Belgrade, *P. spicata* was broadcasted by hand at 24 kg/ha rate. Seeding rates followed those of Orloff et al. (2013). Herbicide treatments consisted of a 2% glyphosate solution applied using a backpack sprayer with a single fan nozzle. At Corvallis East and West, glyphosate was applied as Roundup® plus 120 mL liquid ammonia to help with absorption, and indicator dye (4.2 l/ha, includes 120 mL liquid ammonia and indicator dye). At Belgrade, glyphosate was applied as Accord® plus 296 mL Activator 90 surfactant, and indicator dye (8.5 l/ha, includes 296 mL surfactant and indicator dye). Fall was the only herbicide treatment applied to Belgrade, therefore herbicide treatment hereafter is referred to as not treated or treated for this site.

In the second year (2019), all sites displayed an abundance of broad-leaved weedy species, so all plots were treated with a broad-leaved herbicide. Two,4-D was applied at a rate of 2.5 l/ha with a tractor sprayer at Corvallis West on 6 May 2019 and on 15 May 2019 at Corvallis East. In Belgrade a backpack sprayer with a single fan nozzle was used to apply 2,4-D at the same rate on 29 May 2019.

Sampling

Since two seeding methods (drill-seed and broadcast) were used across the three sites, two sampling methods were executed. For Corvallis East and West, a 1-meter stick was placed along an initial randomly-selected drill row for each split-plot. Along the middle 50 cm of the 1 m stick, *P. spicata* density was counted. *Pseudoroegneria spicata* density was converted from linear meter to m^2 by multiplying linear meter by 5 to accommodate the number of drill rows within a meter. This conversion allowed for *P. spicata* density comparison across sites. A Daubenmire, 50 cm x 20 cm, frame was placed in the center of the 1 m stick, and *P. spicata* and *B. tectorum* ocular cover were estimated within this frame, along with functional groups (perennial forb or perennial grass). This sampling procedure (stick + frame) occurred three times in each split-plot, and sampling locations were permanent from 2018 to 2019. Sampling occurred on 26 June 2018 and 2 July 2019 at Corvallis West and 27 June 2018 and from 2 - 4 July 2019 at Corvallis East.

In 2018 at Belgrade, which was broadcast seeded, 3 50 cm x 100 cm permanent frames were randomly located in each split-plot. *Pseudoroegneria spicata* density and cover, *B. tectorum* and perennial grass cover were estimated within the frames. Sampling occurred 10 July 2018 and 21, 23, 26-27 June 2019.

In the second year (2019), biomass of *P. spicata, B. tectorum*, and the co-dominant functional group was sampled. Aboveground biomass was clipped, placed in paper bags and dried at the Montana State University Plant Growth Center (approximately 34.6 °C, 13.8 % humidity) for 48 hours and weighed to the nearest 0.1 g. Generalized linear models were used to analyze response variables: *P. spicata* density, cover and biomass; *B. tectorum* cover and biomass; functional group cover and biomass. Poisson distribution was used for *P. spicata* density and Gaussian distribution was used for cover and biomass. Fixed effect variables were herbicide application (one-two times), seeding date (five times), year (two) and block (three). To meet assumptions of constant variance and normality, response variables were natural log-transformed for cover or biomass. Each site was analyzed separately due to different protocols (i.e. seeding, spraying, and sampling methods) and the site's dominant functional group. Control plots were included in the analyses for *B. tectorum* and functional groups to compare the effect of herbicide timing to no management, but they were not included in *P. spicata* analyses since seeding was not employed in the control plots and no *P. spicata* was expected to be found. A Tukey HSD pairwise comparison was performed for significant factors with $\alpha = 0.05$. Statistical analysis and data visualization were conducted with R Software 3.6.1 with dplyr, emmeans, and ggplot2 packages (Lenth, 2020; R Core Team, 2019; Wickam et al., 2020; Wickham, 2016)

Results

Belgrade

Pseudoroegneria spicata, B. tectorum and perennial grass abundance were analyzed for Belgrade. The species co-dominant with *B. tectorum* were *Agropyron intermedium* (Host) P. Beauv and *Agropyron smithii* Rydb. Domestic cattle grazing is the primary use at this site, and perennial grasses are desired.

Pseudoroegneria spicata. *Pseudoroegneria spicata* density was affected by an interaction between seeding date and herbicide application ($p<0.001$), an interaction between seeding date and year ($p<0.001$) and an interaction between herbicide application and year ($p<0.001$, Table 4.3).

The interaction between seeding date and herbicide application resulted in higher *P. spicata* density with Spring 3 and Spring 4 seeding dates with herbicide treatment (20 ± 4.6 plants per m^2) compared to all other seeding dates and no treatment, except

Spring 2 Seeding date with herbicide (Figure 4.1). *Pseudoroegneria spicata* density with Spring 2 Seeding date and herbicide treatment was 13 ± 2.2 plants per m^2, while remaining treatments resulted in an average of 2.6 ± 1.0 plants per m^2 (Figure 4.1). Except for Fall and Spring 1 seeding dates, *P. spicata* density was higher with an herbicide treatment versus none.

Table 4.3. Belgrade site Analysis of Variance (ANOVA) table for *Pseudoroegneria spicata*, *Bromus tectorum* and perennial grass cover (2018, 2019) and biomass (2019). Density measured for *P. spicata* only (2018, 2019). Values in table represent the following in order: F/Chi^2, p-value, degrees of freedom. Bold p-values indicate significance (α=0.05).

	P. spicata density	*P. spicata* cover	*P. spicata* biomass 2019	*B. tectorum* cover	*B. tectorum* biomass 2019	Perennial grass cover	Perennial grass biomass 2019
Block	13.73 **0.001** *2, 158*	1.187 0.308 *2, 166*	0.209 0.812 *2, 78*	3.494 **0.032** *2, 197*	2.764 0.068 *2, 95*	2.838 0.061 *2, 201*	1.720 0.185 *2, 95*
Herbicide	6.29 **0.012** *1, 162*	4.550 **0.034** *1, 168*	18.28 **<0.001** *1, 80*	23.46 **<0.001** *1, 197*	8.541 **0.004** ***1, 97***	91.35 **<0.001** *1, 203*	88.49 **<0.001** *1, 97*
Seeding	370..7 **<0.001** *4, 162*	4.577 **0.002** *4, 168*	1.728 0.152 *4, 80*	8.702 **<0.001** *5, 197*	5.159 **<0.001** *5, 97*	5.891 **<0.001** *5, 203*	2.525 **0.034** *5, 97*
Year	0.61 0.436 *1, 162*	76.46 **<0.001** *1, 168*	-	37.38 **<0.001** *1, 197*	-	48.71 **<0.001** *1, 203*	-
Herbicide * Year	23.58 **<0.001** *1, 162*	34.55 **<0.001** *1, 168*	-	2.092 0.150 *1, 196*	-	5.081 **0.025** *1, 203*	-
Seeding * Year	66.13 **<0.001** *4, 162*	1.900 0.113 *4, 162*	-	3.115 **0.010** *5, 197*	-	0.379 0.863 *5, 196*	-
Seeding * Herbicide	57.67 **<0.001** 4, 162	2.957 **0.022** *4, 168*	3.194 **0.017** *4, 80*	9.289 **<0.001** *4, 197*	6.066 **<0.001** *4, 97*	4.830 **<0.001** *4, 203*	5.085 **<0.001** *4, 97*

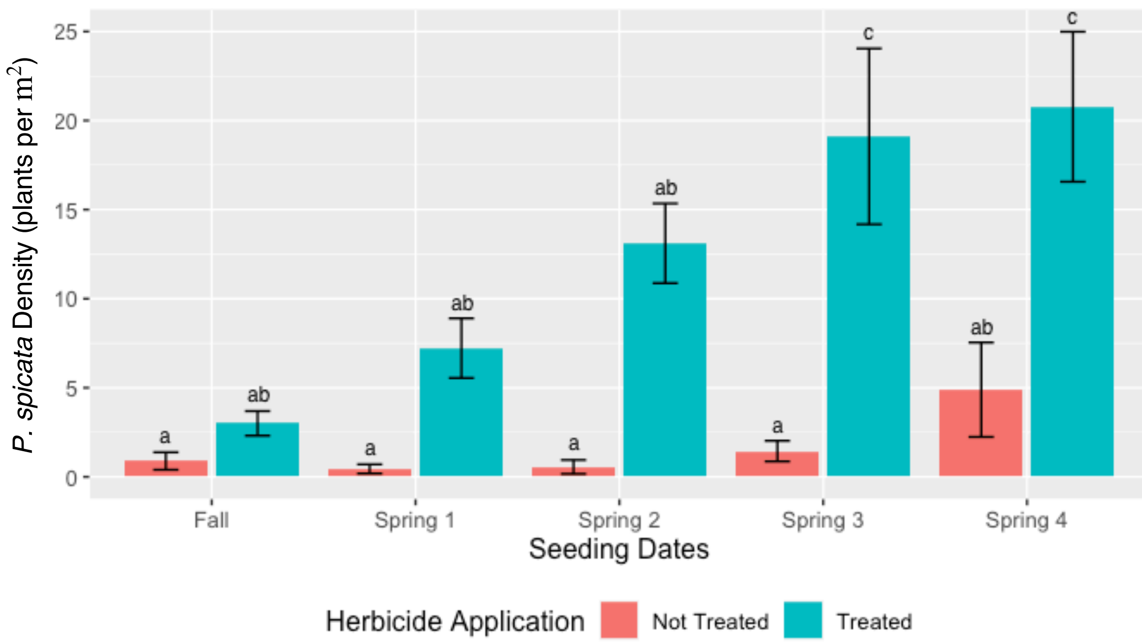

Figure 4.1. Mean *Pseudoroegneria spicata* density (plants per m^2) by seeding date and herbicide application at Belgrade, averaged across both years. Similar letters indicate no difference in density across seeding dates and herbicide application at α=0.05. Error bars represent ± 1 standard error.

Pseudoroegneria spicata density varied between year and seeding dates. In 2018, *P. spicata* was highest with Spring 3 and Spring 4 Seeding dates, with an average of 18 ± 5.0 plants per m^2 (Figure 4.2). Lowest density in 2018 occurred with Fall Seeding, with a mean of 2.0 ± 0.7 plants per m^2. *Pseudoroegneria spicata* density was mostly similar in 2019 across all seeding dates with an average of 4.1 ± 1.4 plants per m^2, though Spring 2 and 4 Seeding dates were higher than Fall and Spring 1 (Figure 4.2).

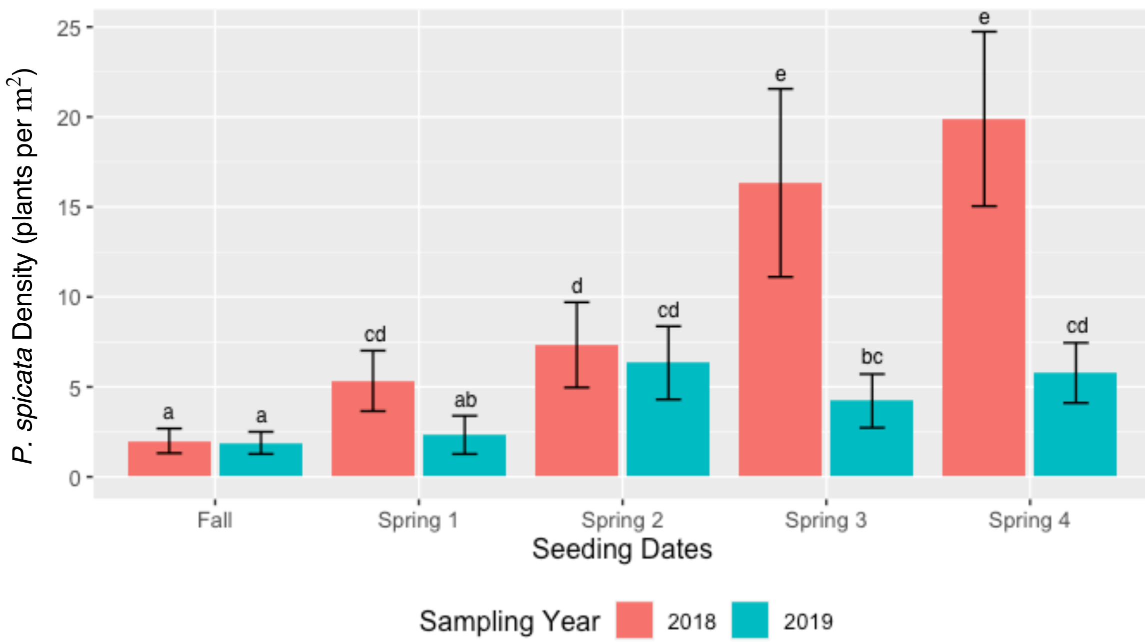

Figure 4.2. Mean *Pseudoroegneria spicata* density (plants per m^2) by seeding date and year at Belgrade. Similar letters indicate no difference in density across seeding dates and year at α=0.05. Error bars represent ± 1 standard error.

The interaction of year and herbicide application resulted in highest *P. spicata* density in 2018 with treated (18 ± 2.8 plants per m^2) followed by treated in 2019 (7.8 ± 1.1 plants per m^2). Density was generally lowest when no herbicide was applied (Figure 4.3).

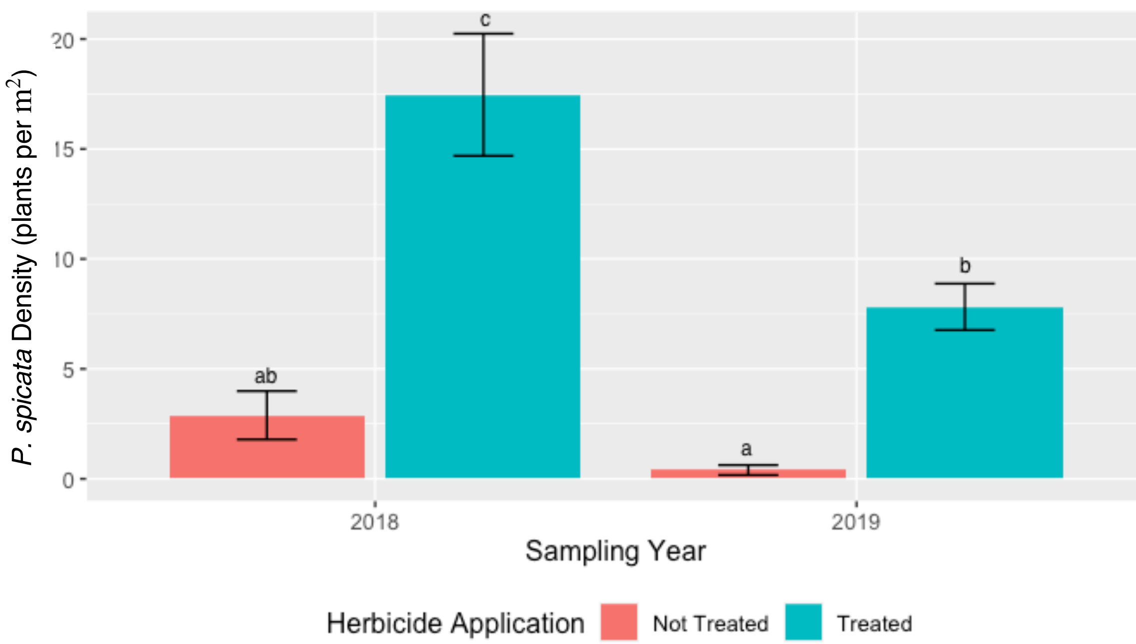

Figure 4.3. Mean *Pseudoroegneria spicata* density (plants per m^2) by herbicide application and sampling year at Belgrade. Similar letters indicate no difference in density across sampling year and herbicide application at $\alpha=0.05$. Error bars represent $\pm$ 1 standard error.

Differences in *P. spicata* cover (per .5 m^2) were observed with the interaction of seeding date and herbicide application ($p=0.022$) and the interaction of herbicide application and year ($p<0.001$, Table 4.3). Cover of *P. spicata* was generally low (<6%) overall. Higher *P. spicata* cover occurred with Spring 2 Seeding date and herbicide treatment (5.2 $\pm$ 1.9 %) compared to Fall Seeding with herbicide, and all seeding dates without herbicide application.

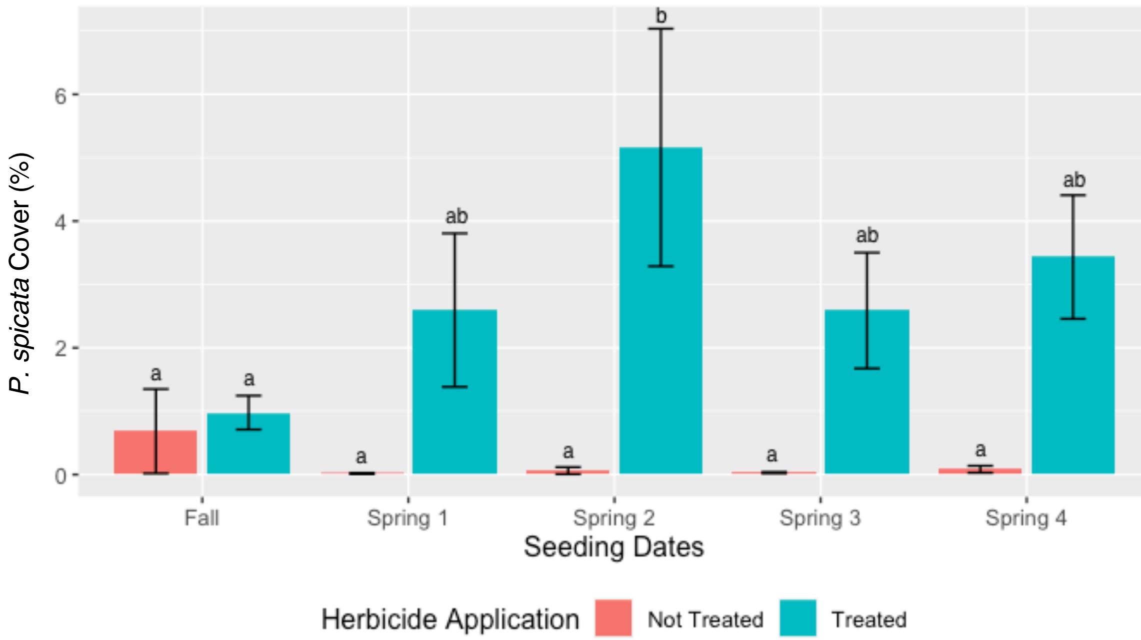

Figure 4.4. Mean *Pseudoroegneria spicata* cover (%) by seeding date and herbicide application at Belgrade, averaged across both years. Similar letters indicate no difference in cover across seeding dates and herbicide application at α=0.05. Error bars represent ± 1 standard error.

Herbicide application and year also affected *P. spicata* cover. Highest cover occurred in 2019 when herbicide was applied, with a mean of 5.7 ± 0.9 %. Cover was less than one percent across remaining treatments and years (Figure 4.5).

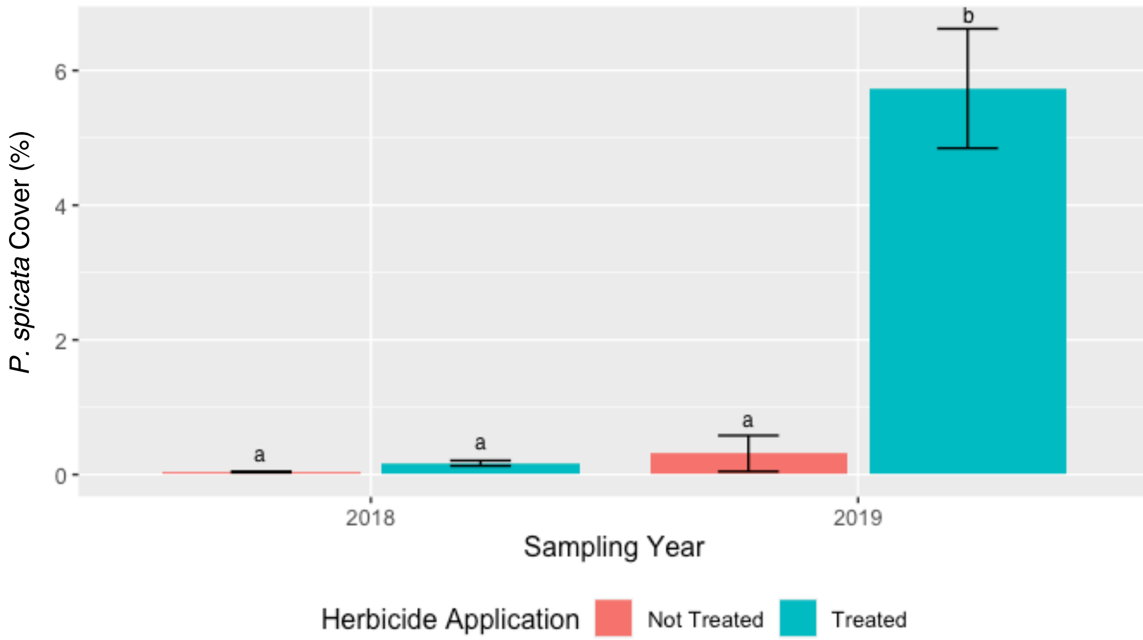

Figure 4.5. Mean *Pseudoroegneria spicata* cover (%) by herbicide application and sampling year at Belgrade. Similar letters indicate no difference in cover across years and herbicide application at α=0.05. Error bars represent ± 1 standard error.

In 2019 the interaction of seeding date and herbicide application affected *P. spicata* biomass (p=0.017, Table 4.2). Effects on biomass paralleled results for *P. spicata* cover (Figure 4.4). Higher *P. spicata* biomass was a result of Spring 2 Seeding date and herbicide application with 48 ± 17 g per m^2, compared to Fall Seeding date with or without herbicide application, and all spring seeding dates without herbicide application, where biomass averaged 3.1 ± 2.3 g per m^2 (Figure 4.6).

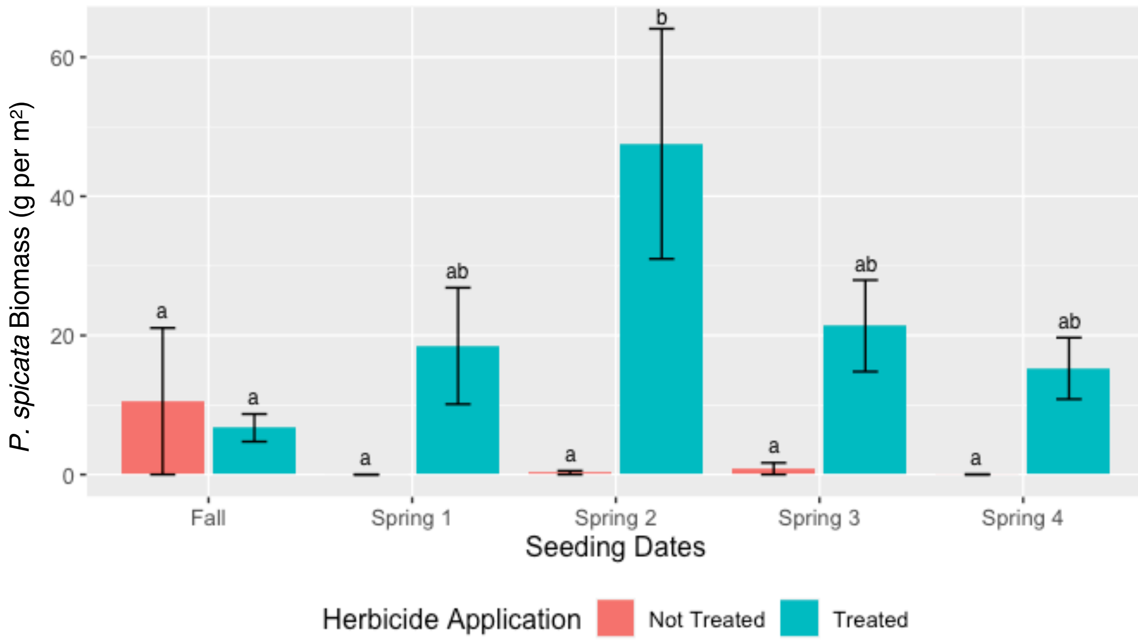

Figure 4.6. Mean *Pseudoroegneria spicata* biomass (g per m^2) by seeding date and herbicide application at Belgrade. Similar letters indicate no difference in biomass across seeding dates and herbicide application at α=0.05. Error bars represent ± 1 standard error.

Bromus tectorum. *Bromus tectorum* cover was affected by the interaction between seeding date and herbicide application ($p<0.001$, Table 4.3). Cover was generally low (<5 %), except for Spring 2 Seeding date and no herbicide application, where *B. tectorum* cover was 17 ± 4.6 % (Figure 4.7).

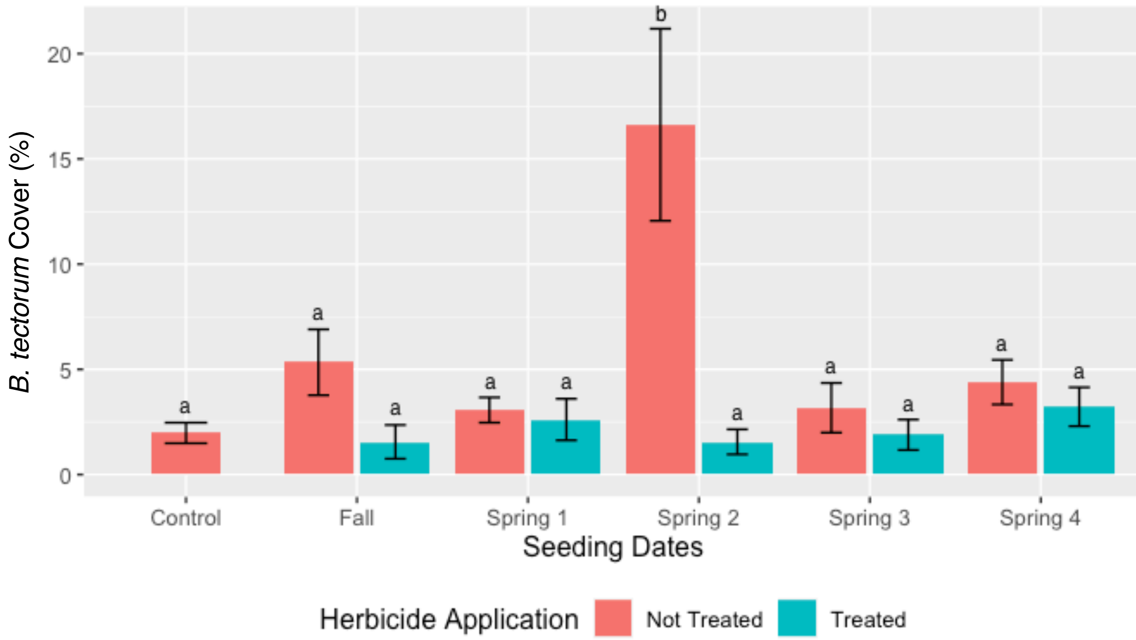

Figure 4.7. Mean *Bromus tectorum* cover (%) by seeding date and herbicide application at Belgrade, averaged across both years. Similar letters indicate no difference in cover across seeding date and herbicide application at α=0.05. Error bars represent ± 1 standard error.

An interaction between year and seeding date also affected *B. tectorum* cover (p=0.010, Table 4.3). Cover was highest in the Spring 2 seeding in 2019, 15 ± 4.5 %. All other seeding dates were similar to each other across both years, averaging 2.0 ± 0.9% (Figure 4.8).

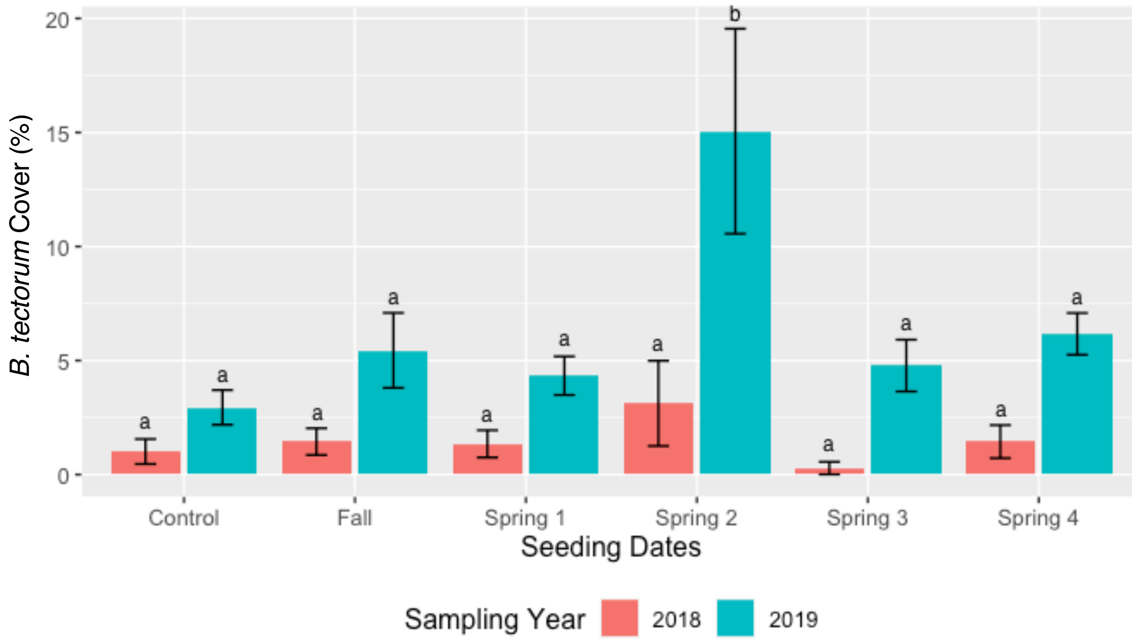

Figure 4.8. Mean *Bromus tectorum* cover (%) by seeding date and sampling year at Belgrade. Similar letters indicate no difference in cover across seeding dates and year at α=0.05. Error bars represent ±1 standard error.

Bromus tectorum biomass was affected by seeding date and herbicide application ($p<0.001$, Table 4.3). Biomass was highest in the Spring 2 Seeding date and no herbicide application, with a mean of 95 ± 25 g per m^2. Remaining seeding dates and herbicide treatment combinations produced similarly low biomass, averaging 21 ± 7.1 g per m^2 (Figure 4.9).

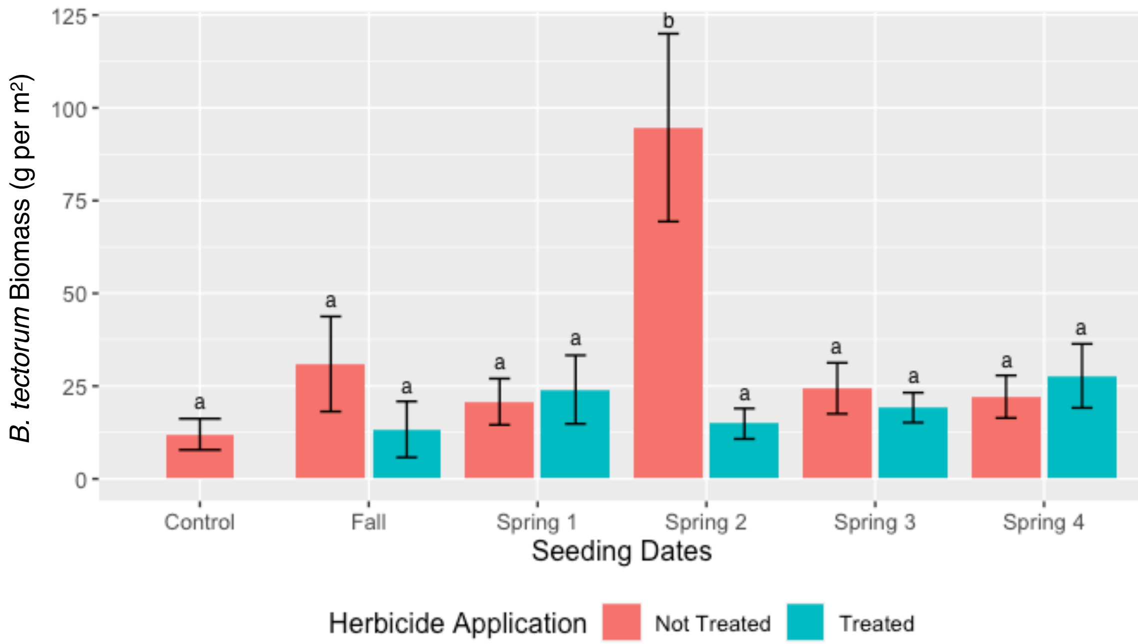

Figure 4.9. Mean *Bromus tectorum* biomass (g per m^2) by seeding date and herbicide application at Belgrade. Similar letters indicate no difference in cover across seeding dates and herbicide application at α=0.05. Error bars represent ±1 standard error.

<u>Perennial grass.</u> Perennial grass cover responded to an interaction between seeding date and herbicide application ($p<0.001$) and an interaction between herbicide application and year ($p=0.025$, Table 4.3). With the combination of seeding date and herbicide application, application tended to reduce perennial grass cover compared to no application across all seeding dates and compared to the Control. Perennial grass cover was highest in the Control and the Fall, Spring 3 and Spring 4 Seeding dates with no herbicide application ranging from 39 ± 3.4 % to 30 ± 4.6 % (Figure 4.10).

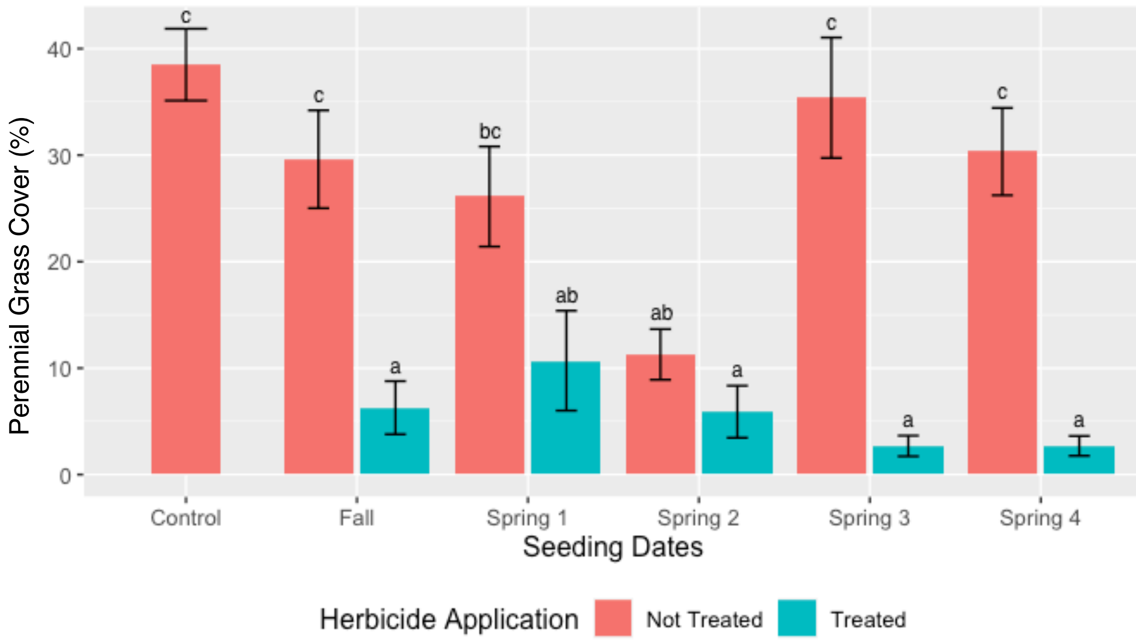

Figure 4.10. Mean perennial grass cover (%) by seeding date and herbicide application at Belgrade, averaged across both years. Similar letters indicate no difference in cover across seeding dates and herbicide application at α=0.05. Error bars represent ±1 standard error.

The interaction of herbicide application and year resulted in the lowest perennial grass cover in both years (2018, 2019) when herbicide was applied (Figure 4.11). Perennial grass cover was highest where no herbicide was applied in 2019, 39 ± 2.3 %.

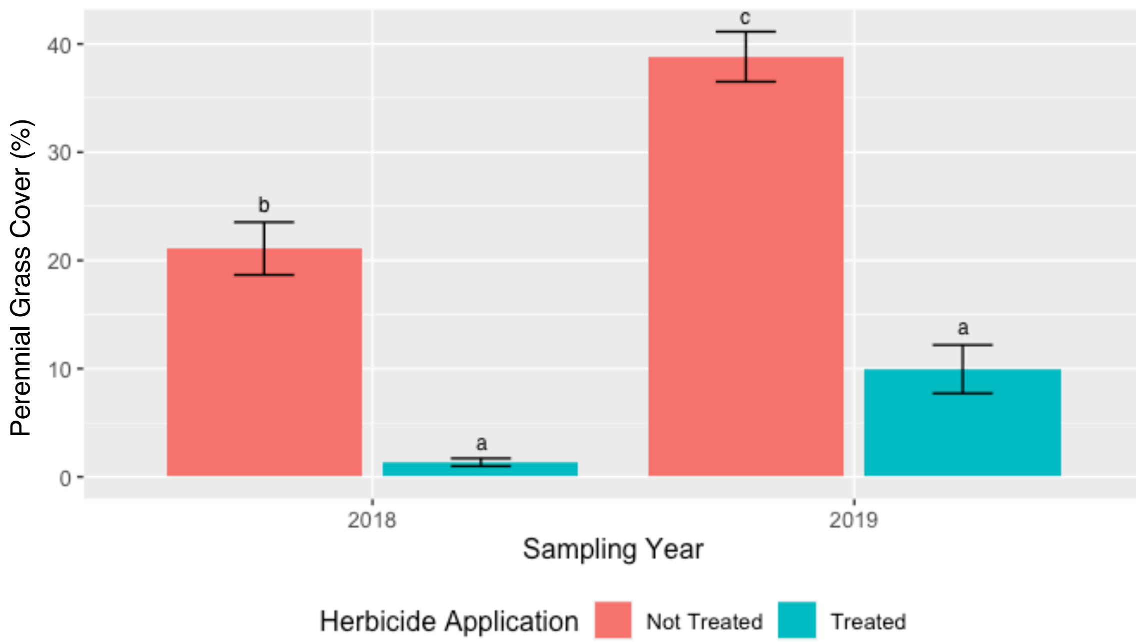

Figure 4.11. Mean perennial grass cover (%) by herbicide application and sampling year at Belgrade. Similar letters indicate no difference in cover across years and herbicide application at α=0.05. Error bars represent ±1 standard error.

Perennial grass biomass was affected by seeding date and herbicide application ($p<0.001$, Table 4.3). Generally, herbicide application reduced perennial grass biomass compared to no application. The exception to this was Spring 1 and Spring 2 seeding dates where there was no difference between herbicide treatments, despite perennial grass biomass appearing lower when sprayed versus not sprayed (Figure 4.12).

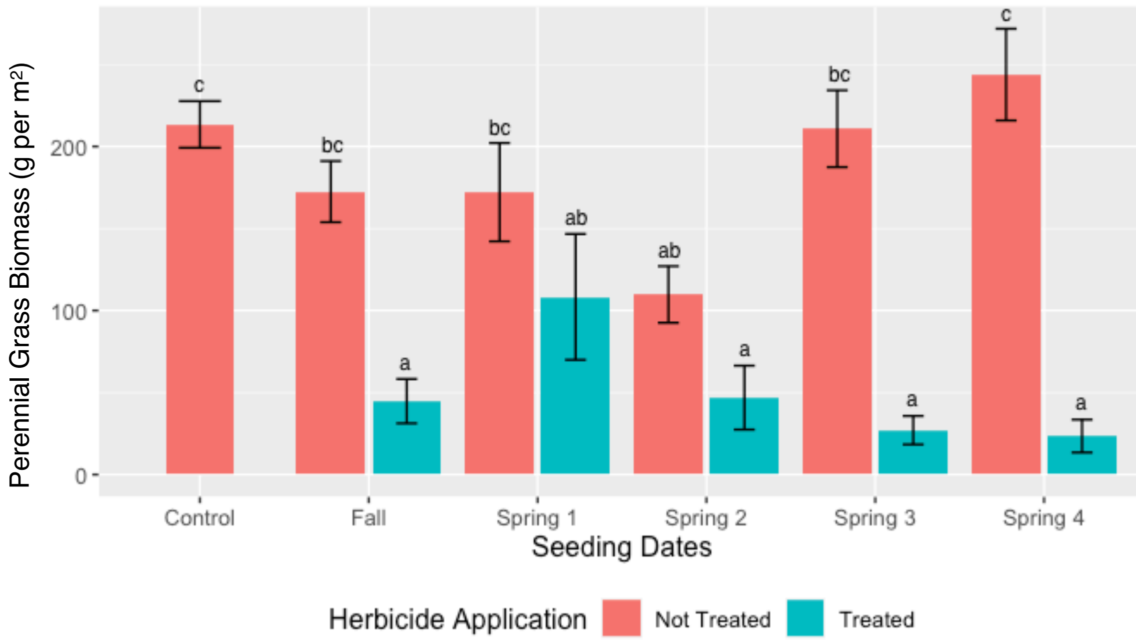

Figure 4.12. Mean perennial grass biomass (g per m^2) by seeding date and herbicide application at Belgrade. Similar letters indicate no difference in biomass across seeding dates and herbicide application at $\alpha=0.05$. Error bars represent ± 1 standard error.

Corvallis West

The co-dominant functional group along with *B. tectorum* at Corvallis West was perennial forb; dominant perennial forbs included *Tragopogon dubuis* Scop. and *Centaurea stoebe* L. This site is an agricultural research station with land use focused on research, and the study area had been in perennial vegetation for decades and used as a biological control insectary.

Pseudoroegneria spicata. *Pseudoroegneria spicata* density responded to an interaction between seeding date and herbicide application ($p<0.001$), an interaction between seeding date and year ($p<0.001$) and an interaction between herbicide application and year ($p<0.001$, Table 4.4).

Table 4.4. Corvallis West site, Analysis of Variance (ANOVA) table for *Pseudoroegneria spicata*, *Bromus tectorum* and perennial forb cover (2018, 2019) and biomass (2019). Density measured for *P. spicata* only (2018, 2019). Values in table represent the following in order: F/Chi^2, p-value, degrees of freedom. Bold p-values indicate significance (α=0.05).

	P. spicata density	*P. spicata* cover	*P. spicata* biomass - 2019	*B. tectorum* cover	*B. tectorum* biomass - 2019	Perennial forb cover	Perennial forb biomass - 2019
Block	235.8 **<0.001** *2, 162*	1.215 0.299 *4, 166*	0.476 0.623 *2, 78*	0.742 0.478 *2, 208*	0.272 0.762 *2, 99*	0.629 0.534 *2, 196*	1.634 0.200 *2, 103*
Herbicide	2.88 0.090 *1, 162*	42.69 **<0.001** *1, 168*	*25.36* **<0.001** *1, 80*	1.988 0.139 *2, 210*	2.140 0.123 *2, 105*	72.56 **<0.001** ***1, 198***	5.477 **0.005** *2, 105*
Seeding	799.0 **<0.001** *4, 162*	8.118 **<0.001** *4, 168*	2.326 0.063 *4, 80*	0.852 0.494 *4, 200*	0.9823 0.4208 *1, 101*	2.853 **0.025** *4, 198*	0.081 0.988 *4, 99*
Year	444.7 **<0.001** *1, 162*	8.570 **0.004** *1, 168*	-	19.92 **<0.001** *1, 208*	-	120.2 **<0.001** *1, 198*	-
Herbicide * Year	256.5 **<0.001** *1, 162*	4.980 **0.027** *1, 168*	-	3.567 **0.030** *2, 208*	-	31.70 **<0.001** *1, 198*	-
Seeding * Year	182.7 **<0.001** *4, 162*	1.091 0.363 *4, 162*	-	0.214 0.930 *4, 196*	-	3.747 **0.006** *4, 198*	-
Seeding * Herbicide	372.2 **<0.001** *4, 162*	7.233 **<0.001** *4, 168*	2.772 **0.035** *4, 80*	0.739 0.566 *4, 200*	0.579 0.678 *4, 95*	3.694 **0.006** *4, 198*	0.818 0.516 *4, 95*

Spring seeding dates resulted in mostly similar *P. spicata* density among each other and with both herbicide treatments. Spring 1 seeding date, however, produced higher *P. spicata* density compared to Spring 4 and Spring 3 combined with fall herbicide. Differences occurred with Spring 3 Seeding date among herbicide applications. Fall seeding tended to result in lower *P. spicata* density than spring seeding, especially when combined with spring herbicide (Figure 4.13).

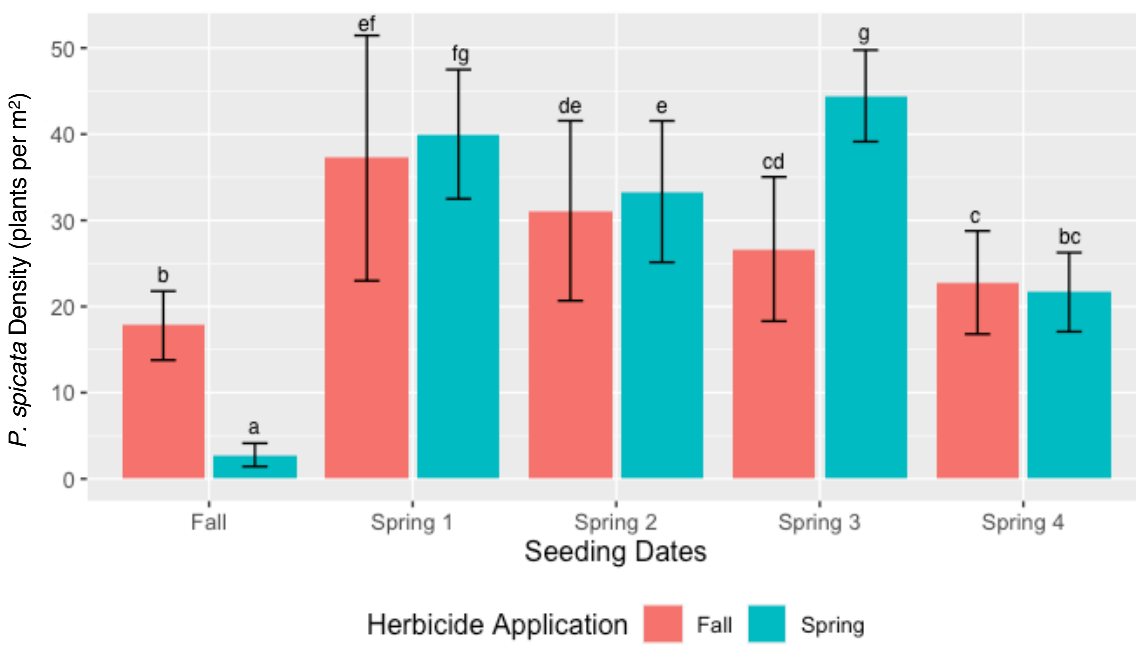

Figure 4.13. Mean *Pseudoroegneria spicata* density (plants per m^2) by seeding date and herbicide application at Corvallis West. Similar letters indicate no difference in density across seeding dates and herbicide application at α=0.05. Error bars represent ±1 standard error.

Pseudoroegneria spicata density trended lower in 2019 than 2018 except for Fall seeding date. Density was mostly similar across seeding dates and year, though there was one major difference. Higher *P. spicata* density occurred with Spring 1 and Spring 3 seeding dates in 2018 with an average mean of 48.3 ± 10.6 plants per m^2 compared to Fall seeding date (both years) and Spring 4 seeding date in 2019 (Figure 4.14).

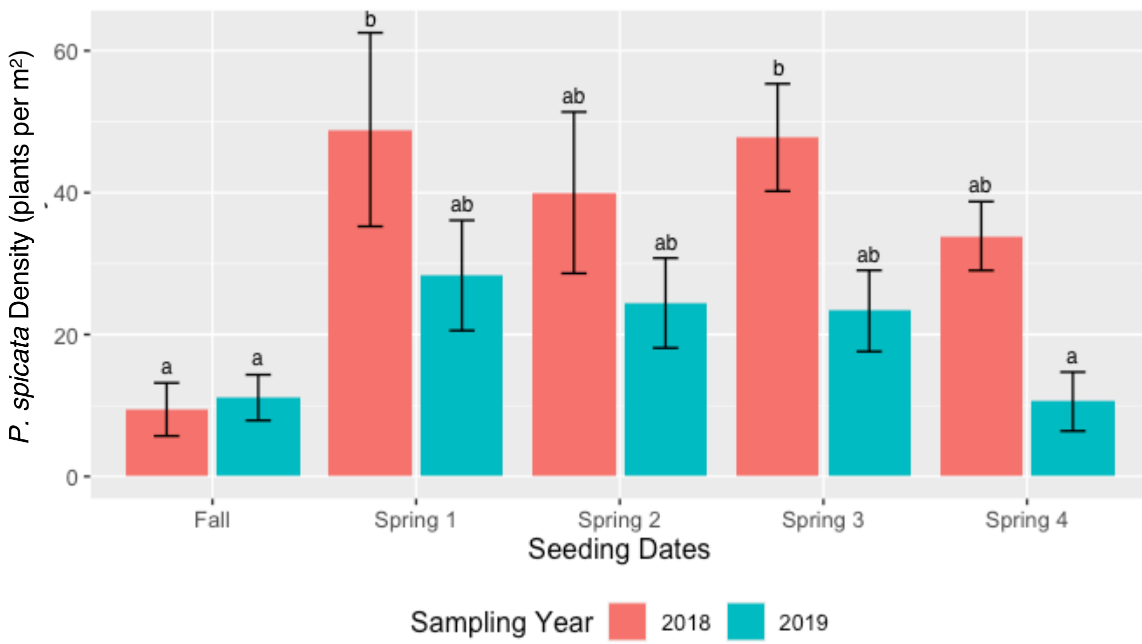

Figure 4.14. Mean *Pseudoroegneria spicata* density (plants per m^2) by seeding date and sampling year at Corvallis West. Similar letters indicate no difference in density across seeding dates and year at α=0.05. Error bars represent ±1 standard error.

Pseudoroegneria spicata density decreased between 2018 and 2019 with Fall herbicide treatment but not with Spring herbicide treatment (Figure 4.15). Density was 40.2 ± 7.2 plants per m^2 in 2018 and decreased to 14.0 ± 3.1 plants per m^2 with Fall treatment, while density remained at about 28.4 ± 4.3 plants per m^2 in the Spring treatment.

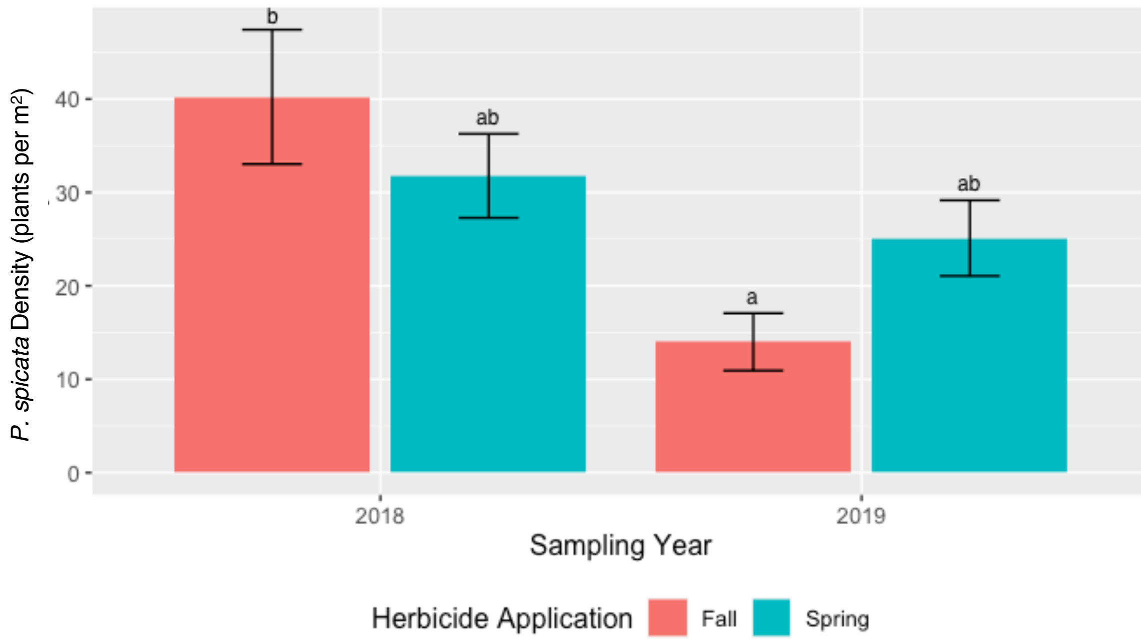

Figure 4.15. Mean *Pseudoroegneria spicata* density (plants per m^2) by herbicide application and sampling year at Corvallis West. Similar letters indicate no difference in density across herbicide application and year at α=0.05. Error bars represent ±1 standard error.

The interaction of seeding date and herbicide application influenced *P. spicata* cover ($p<0.001$), as did the interaction of herbicide application and sampling year ($p=0.027$, Table 4.3). Highest *P. spicata* cover was found with Spring 1 and Spring 3 seeding dates combined with Spring herbicide application, at 13 ± 3.0 % and 10 ± 2.0 %, respectively. All other seeding dates and herbicide applications were lower, ranging from 6.3 ± 1.3 % to 1.0 ± 0.2 % (Figure 4.16).

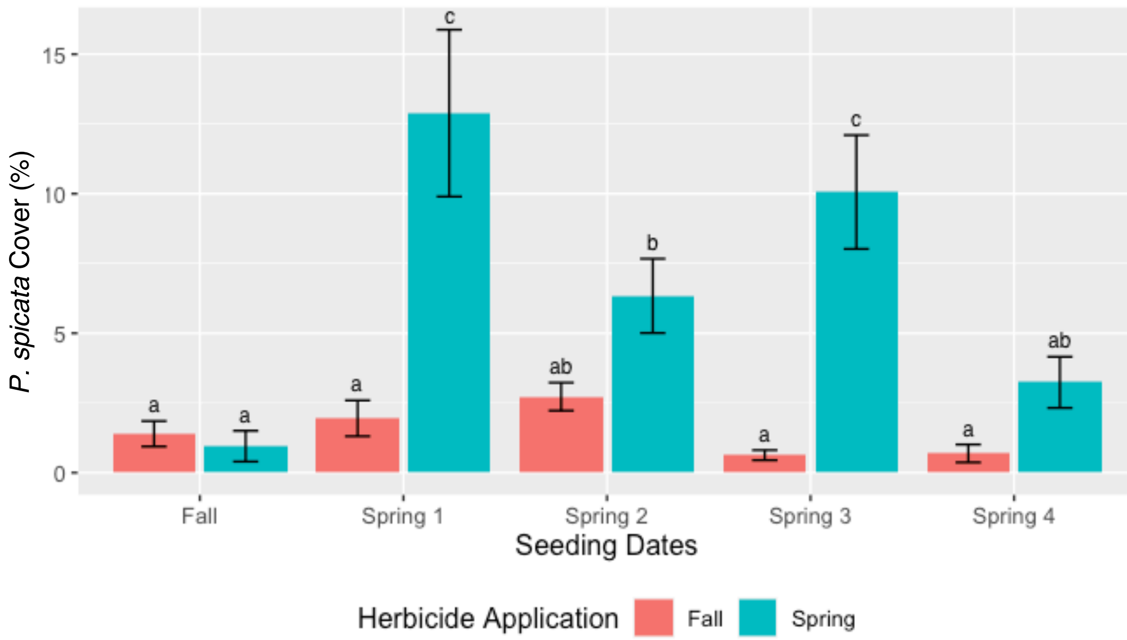

Figure 4.16. Mean *Pseudoroegneria spicata* cover (%) by seeding date and herbicide application at Corvallis West. Similar letters indicate no difference in cover across seeding date and herbicide application at α=0.05. Error bars represent ±1 standard error.

Pseudoroegneria spicata cover (per 0.1 m^2) increased in the Spring herbicide application from 4.6 ± 0.8 % in 2018 to 8.8 ± 1.6 % in 2019, while cover remained the same in the Fall herbicide treatment from one year to the next. Averaged across both years, *P. spicata* cover in the Fall herbicide treatment was 1.5 ± 0.3 % (Figure 4.17).

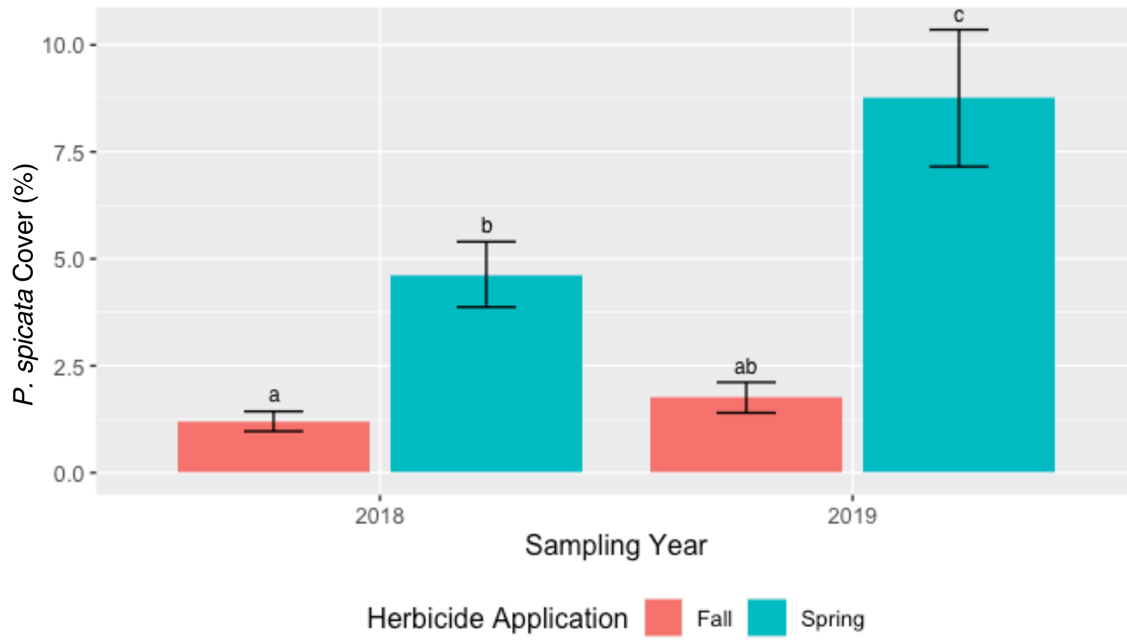

Figure 4.17. Mean *Pseudoroegneria spicata* cover (%) by herbicide application and sampling year at Corvallis West. Similar letters indicate no difference in cover across sampling year and herbicide application at α=0.05. Error bars represent ±1 standard error.

The interaction of seeding date and herbicide application influenced *P. spicata* biomass (p=0.035, Table 4.4). Fall herbicide application tended to have lower *P. spicata* biomass than spring herbicide application, although the difference was only significant for Spring 3 seeding date. Biomass in the Spring 3 Seeding combined with Spring herbicide application was higher than most other seeding date and herbicide application combinations, with a mean of 156 ± 55 g per m^2 (Figure 4.18).

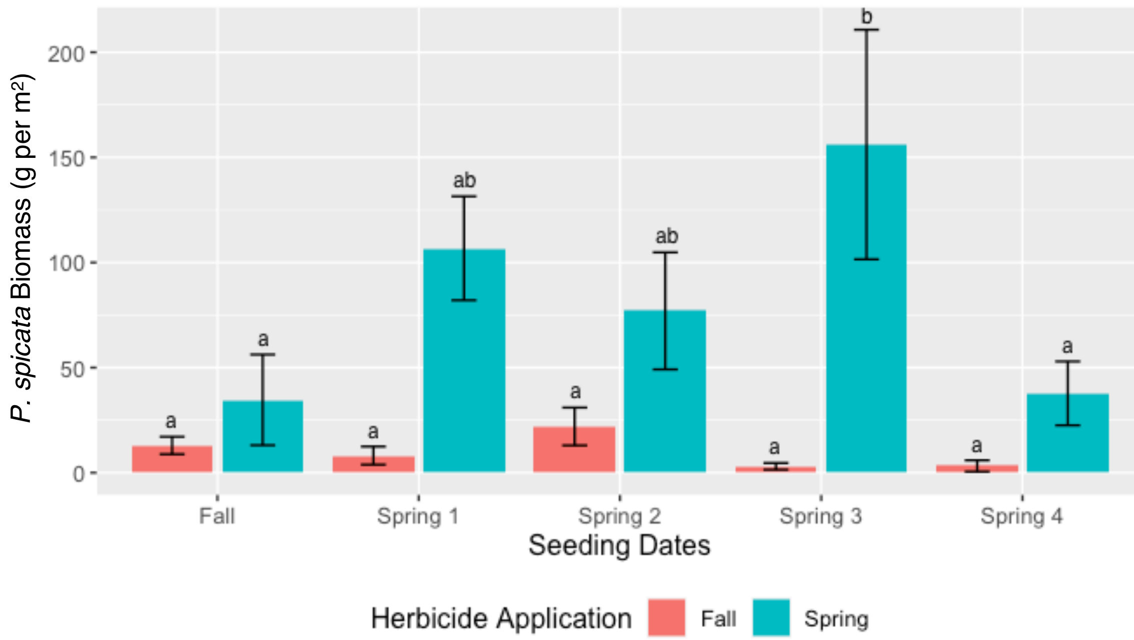

Figure 4.18. Mean *Pseudoroegneria spicata* biomass (g per m2) by seeding date and herbicide application at Corvallis West. Similar letters indicate no difference in biomass across seeding date and herbicide application at α=0.05. Error bars represent ±1 standard error.

<u>*Bromus tectorum*</u>. *Bromus tectorum* cover was affected by the interaction of herbicide application and year (p=0.030, Table 4.4). Cover tended to be lower in 2018, where it was similar among herbicide applications and the Control. However, in 2019 *B. tectorum* cover increased to 16 ± 3.7 % in the Fall herbicide treatment and 18 ± 8.0 % in the Control (Figure 4.19). Cover in the Spring herbicide treatment remained similar to cover in 2018.

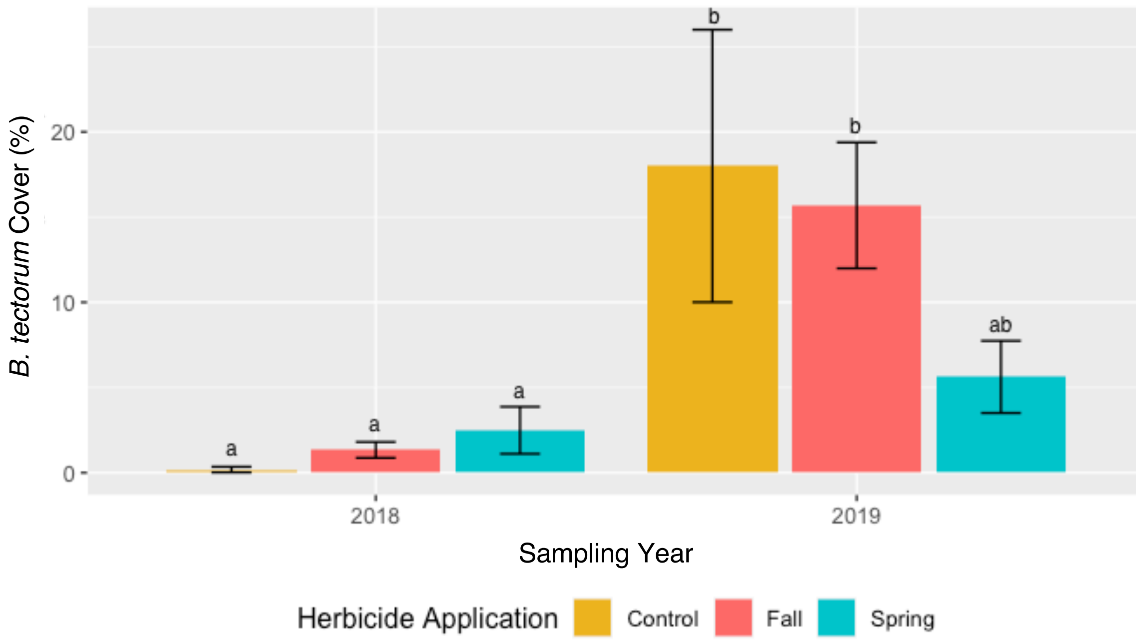

Figure 4.19. Mean *Bromus tectorum* cover (%) by herbicide application and sampling year at Corvallis West. Similar letters indicate no difference in cover across year and herbicide application at $\alpha=0.05$. Error bars represent ±1 standard error.

<u>Perennial Forb.</u> Perennial forb cover responded to the interaction between seeding date and herbicide application (p=0.006), the interaction between seeding date and year (p=0.006) and the interaction between herbicide application and year (p<0.001, Table 4.4). Generally, perennial forb cover was lower with Spring herbicide application (all seeding dates), with an average of 5.5 ± 1.4 % (averaged across all seeding dates), compared to Fall herbicide application (15 ± 2.8 %, averaged across all seeding dates). The Control had perennial forb cover of 16 ± 1.8 % (Figure 4.20).

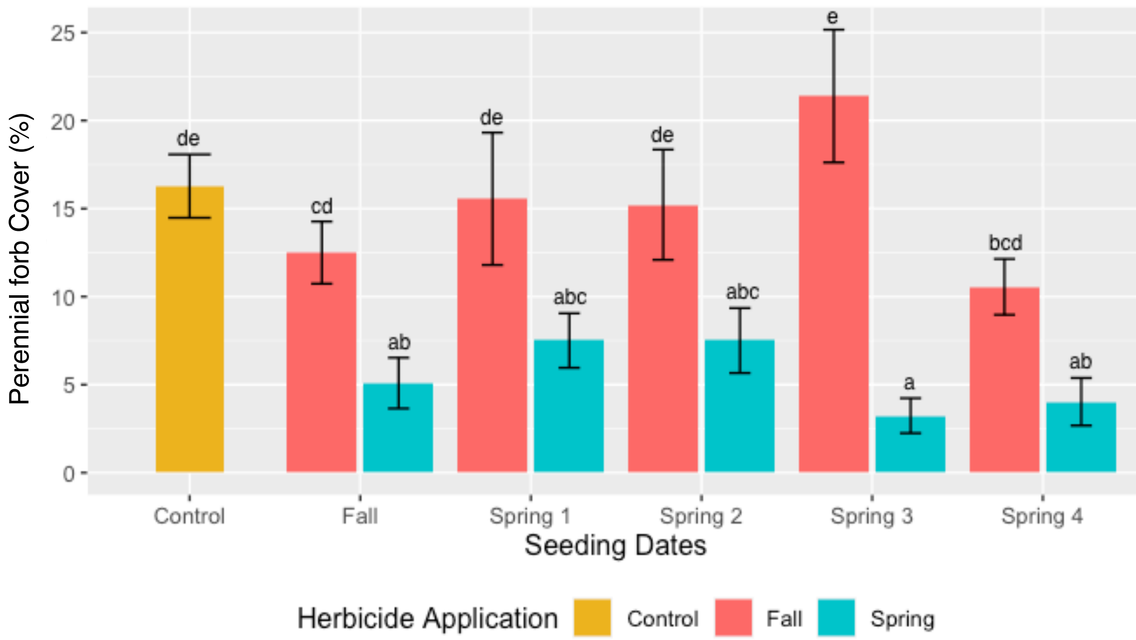

Figure 4.20. Mean perennial forb cover (%) by seeding date and herbicide application at Corvallis West. Similar letters indicate no difference in cover across seeding date and herbicide application at α=0.05. Error bars represent ±1 standard error.

Perennial forb cover was generally lower across all seeding dates and the Control in 2019 compared to 2018 (Figure 4.21). Spring 1, 2 and 3 Seeding dates in 2018 tended to have higher perennial forb cover compared to 2019 with an average mean of 19 ± 3.4 %. Looking across seeding dates within each year, seeding date did not affect cover except for the comparison between Spring 4 and the Control in 2018; Spring 4 seeding date reduced perennial forb cover from 21 ± 2.6 % to 10 ± 1.9 % (Figure 4.20).

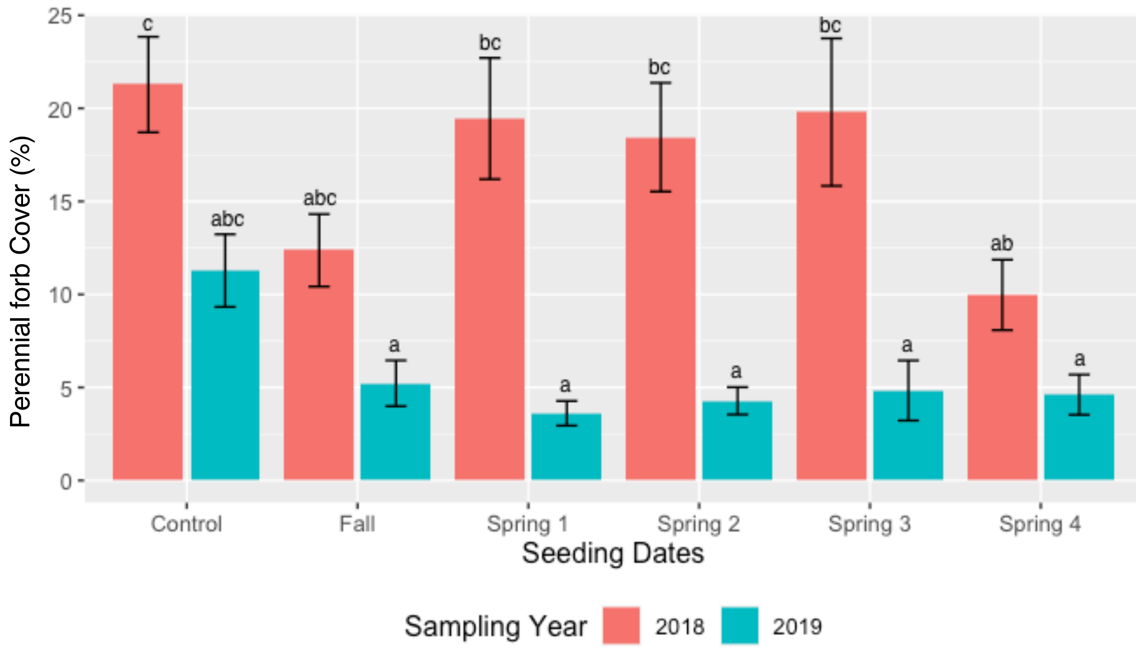

Figure 4.21. Mean perennial forb cover (%) by seeding date and sampling year at Corvallis West. Similar letters indicate no difference in cover across seeding date and year at α=0.05. Error bars represent ±1 standard error.

Differences in perennial forb cover occurred among herbicide application and year. In 2018, perennial forb cover was lower with Spring herbicide (8.1 ± 1.1 %) than Fall herbicide application (24 ± 1.8 %), and Fall was similar to the Control (21 ± 2.6 %). In 2019, Spring herbicide application resulted in perennial forb cover of 2.9 ± 0.4 % followed by Fall herbicide application at 0.1 ± 0.8 % and the Control at 11 ± 2.0 % (Figure 4.22).

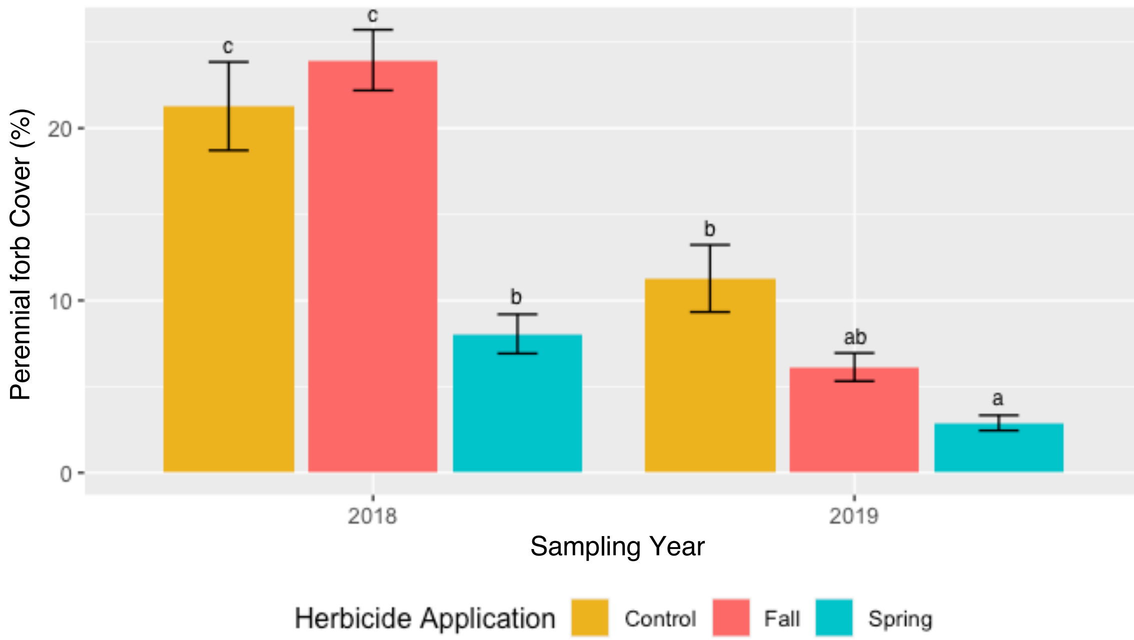

Figure 4.22. Mean perennial forb cover (%) by herbicide application and sampling year at Corvallis West. Similar letters indicate no difference in cover across year and herbicide application at α=0.05. Error bars represent ±1 standard error.

Perennial forb biomass responded to herbicide application (p=0.005, Table 4.4). Biomass was lowest with Spring herbicide at 34 ± 7.4 g per m^2 and highest in the Control at 77 ± 13 g per m^2. Biomass with Fall herbicide (61 ± 8.0 g per m^2) was similar to the Control.

<u>Corvallis East</u>

Perennial grasses, annual forbs and perennial forbs were co-dominant with *B. tectorum* at Corvallis East. *Galium aparine* L., *Carduus nutans* L., *Elymus repens* L. (Gould), and *Dactylis glomerata* L. were present. *Galium aparine* is a native forb, but considered weedy because of its abundance at the site. Wildlife habitat is the primary use at this site.

<u>*Pseudoroegneria spicata*</u>. *Pseudoroegneria spicata* density responded to the interaction between seeding date and herbicide application ($p<0.001$), the interaction with seeding date and year ($p<0.001$) and the interaction among herbicide application and year ($p=0.001$, Table 4.5).

Overall, this site had little *P. spicata* establishment, with most treatments producing almost 4, but not more than 9 plants per square meter. Spring 4 Seeding date with Spring herbicide application produced highest *P. spicata* density at 21 ± 6.6 plants per m^2. All other seeding dates and herbicide applications were lower, ranging from 0.0 ± 0.0 to 8.9 ± 4.2 plants per m^2 (Figure 4.23).

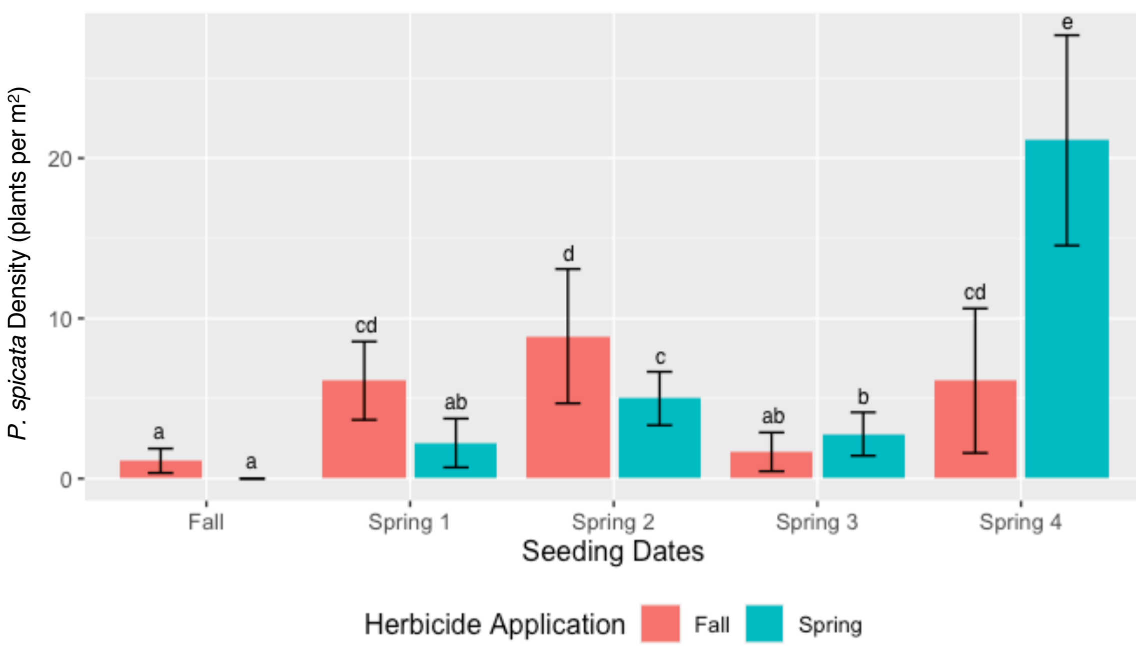

Figure 4.23. *Pseudoroegneria spicata* density (plants per m^2) by seeding date and herbicide application at Corvallis East. Similar letters indicate no difference in density across seeding dates and herbicide application at α=0.05. Error bars represent ±1 standard error.

Table 4.5. Corvallis East site, Analysis of Variance (ANOVA) table for *Pseudoroegneria spicata*, *Bromus tectorum* and perennial grass cover (2018, 2019) and biomass (2019). Density measured for *P. spicata* only (2018, 2019). Values in table represent the following in order: F/Chi^2, p-value, degrees of freedom. Bold p-values indicate significance (α=0.05).

	P. spicata density	*P. spicata* cover	*P. spicata* biomass - 2019	*B. tectorum* cover	*B. tectorum* biomass - 2019	Perennial grass cover	Perennial grass biomass – 2019
Block	23.34 **<0.001** *2, 162*	0.699 0.499 *2, 171*	0.663 0.518 *2, 82*	2.837 0.061 *2, 208*	0.766 0.468 *2, 100*	10.02 **<0.001** *2, 200*	2.187 0.118 *2 ,99*
Herbicide	17.12 **0.001** *1, 162*	3.873 0.051 *1, 178*	1.679 0.198 *1, 88*	11.02 **<0.001** *2, 210*	0.519 0.473 *1, 99*	2.137 0.145 *1, 200*	3.227 0.075 *1, 101*
Seeding	684.6 **<0.001** *4, 162*	1.714 0.149 *4, 173*	0.979 0.424 *4, 84*	0.165 0.956 *4, 204*	1.753 0.129 *5, 102*	3.121 **0.016** *4, 200*	3.602 **0.005** *5, 102*
Year	376.1 **<0.001** *1, 162*	2.534 0.113 *1, 177*	-	12.81 **<0.001** *2, 210*	-	12.90 **<0.001** *1, 200*	-
Herbicide * Year	53.52 0.225 *1, 162*	0.804 0.371 *1, 170*	-	6.419 **0.002** *2, 210*	-	3.331 **0.038** *4, 200*	-
Seeding * Year	183.1 **<0.001** *4, 162*	0.961 0.430 *4, 166*	-	0.302 0.876 *1, 196*	-	0.893 0.469 *4, 196*	-
Seeding * Herbicide	273.1 **<0.001** *4, 162*	0.669 0.614 *4, 162*	0.561 0.692 *4,78*	0.466 0.761 *4, 200*	2.183 0.077 *4, 95*	2.627 **0.036** *2, 200*	1.358 0.254 *4, 95*

Among the seeding date and year interaction and similar to the other two sites, *P. spicata* density generally declined from 2018 to 2019. Density was highest with Spring 4 seeding date in 2018 at 23 ± 7.1 plants per m^2; second highest *P. spicata* density occurred with Spring 2 seeding in 2018 at 11 ± 4.1 plants per m^2; remaining combinations resulted in less than 5 plants per m^2 (Figure 4.24).

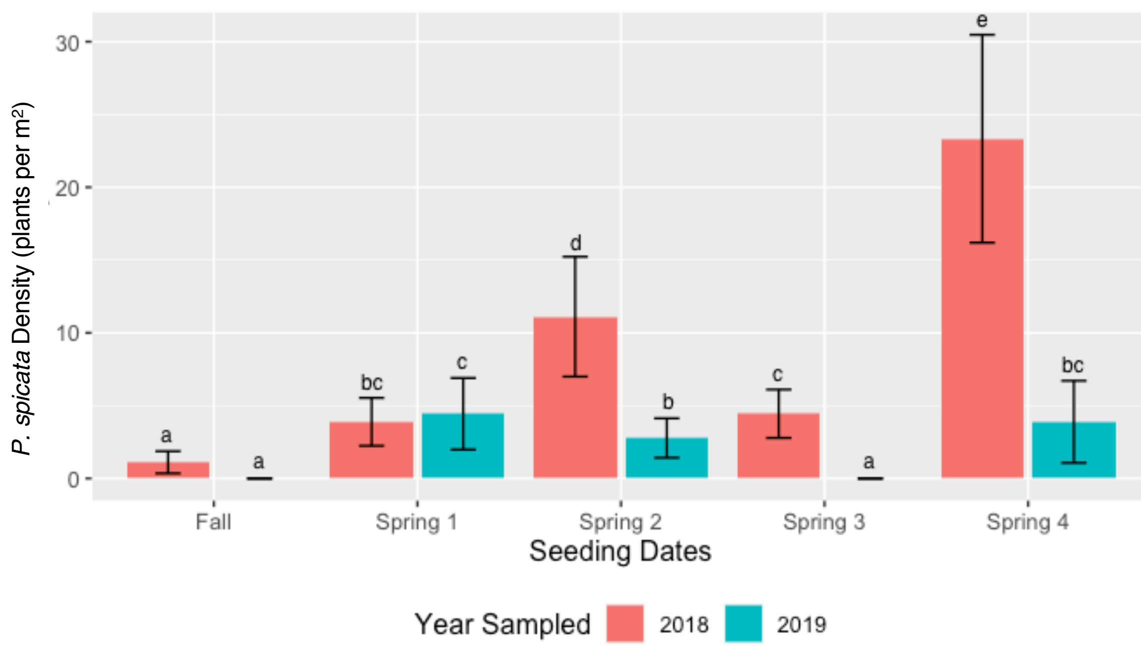

Figure 4.24. *Pseudoroegneria spicata* density (plants per m^2) by seeding date and years sampled at Corvallis East. Similar letters indicate no difference in density across seeding dates and year at α=0.05. Error bars represent ±1 standard error.

<u>*Bromus tectorum.*</u> *Bromus tectorum* cover responded to the interaction between herbicide application and year ($p=0.002$, Table 4.5). In 2018, cover (per 0.1 m^2) was low across all treatments (<2 %, Figure 4.25). In 2019, cover in the Control (12 ± 5.1 %) was almost 4 times higher than when herbicide was applied in either Fall (1.8 ± 0.3 %) or Spring (2.6 ± 0.8 %).

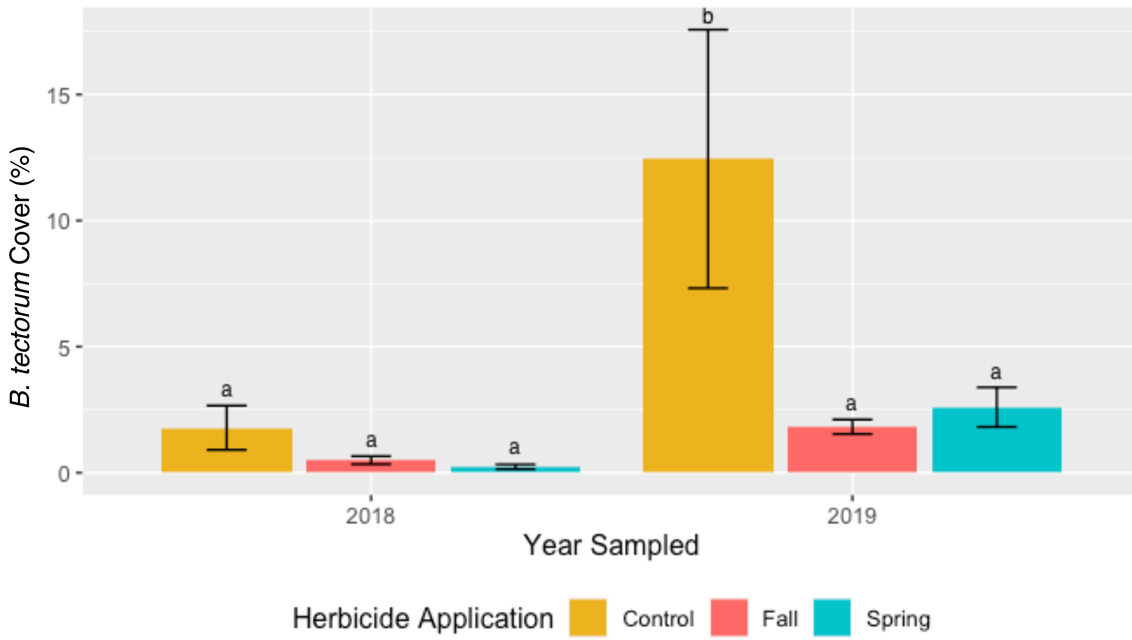

Figure 4.25. *Bromus tectorum* cover (%) by herbicide application and year at Corvallis East. Similar letters indicate no difference in cover across years and herbicide applications at α=0.05. Error bars represent ±1 standard error.

Perennial grasses. Perennial grass cover was affected by the interaction between seeding date and herbicide application (p=0.036) and the interaction of herbicide application and year (p=0.038, Table 4.5). Spring 3 seeding date with Fall herbicide resulted in the highest perennial grass cover at 15 ± 2.7 %. All other seeding dates and herbicide application combinations were similar to each other and ranged from 3.7 ± 1.2 % to 7.6 ± 2.3 % (Figure 4.26).

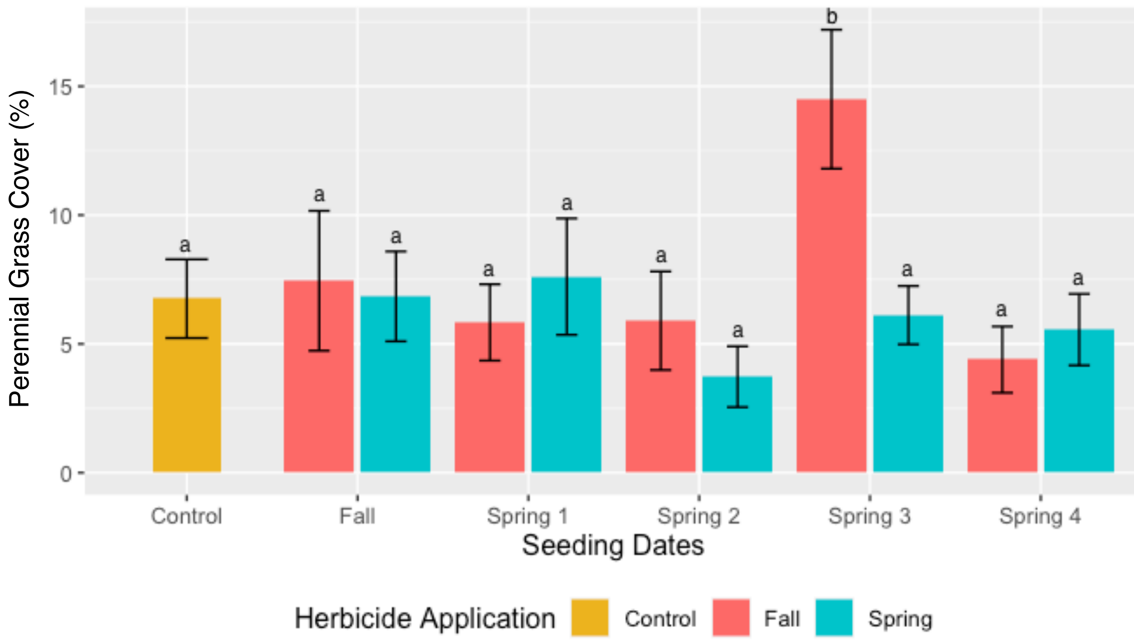

Figure 4.26. Perennial grass cover (%) by seeding date and herbicide application at Corvallis East. Similar letters indicate no difference in cover across seeding date and herbicide applications at α=0.05. Error bars represent ±1 standard error.

The difference in perennial grass cover that resulted from herbicide application and year was mostly reflected in the Control plots. Cover increased from 2018 to 2019 in the Control but not in the other herbicide treatments. Within each year, cover was similar across all herbicide treatments (Figure 4.27).

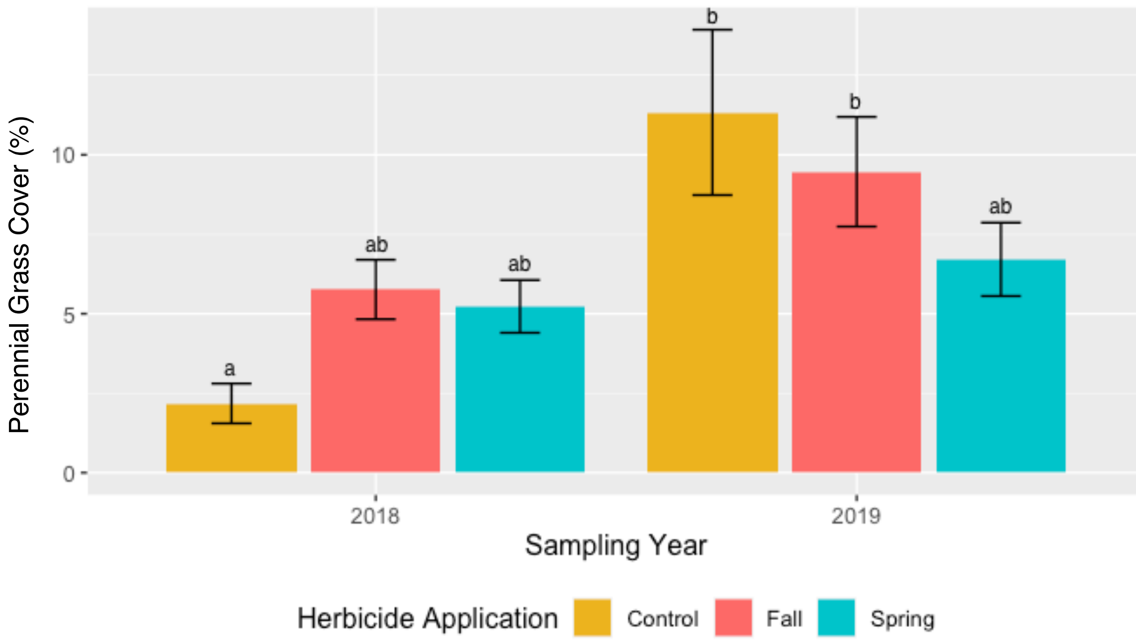

Figure 4.27. Perennial grass cover (%) by herbicide application and sampling year at Corvallis East. Similar letters indicate no difference in cover across herbicide applications and sampling year at α=0.05. Error bars represent ±1 standard error.

Perennial grass biomass responded to seeding date (p=0.005, Table 4.5). Biomass was highest in the Spring 3 Seeding date (144 ± 22 g per m^2) and lowest in the Spring 4 Seeding date (40 ± 13 g per m^2). Fall, Spring 1 and 2 Seeding dates resulted in intermediate biomass (91 ± 26 g per m^2, averaged across all three seeding dates).

Discussion

Given the extent of and challenges associated with *B. tectorum* invasion, managers need better information to effectively restore invaded rangelands. While seeding and herbicide are effective tools, strategic timing of their use could further benefit degraded rangelands. My first hypothesis, that early spring versus fall seeding will result in higher abundance of *P. spicata* and lower abundance of *B. tectorum* and other weedy species was partially supported. *Pseudoroegneria spicata* density (plants per m^2) was higher with early Spring seeding dates when compared to the Fall seeding date. At Belgrade, this occurred with Spring 2 (3 May), Spring 3 (17 May) and Spring 4 (31 May) Seeding dates. At Corvallis West, this included Spring 1 (3 April), Spring 2 (19 April) and Spring 3 (4 May) and at Corvallis East, Spring 2 (19 April) and Spring 4 (15 May) Seeding dates. Differences in seeding date effect among sites on *P. spicata* establishment could be due to growing degree days between the Corvallis sites and Belgrade (Table 4.2). However, since *P. spicata* density differed between spring seeding dates at the Corvallis sites, precipitation and species competition may be stronger limiting factors for *P. spicata* establishment.

Pseudoroegneria spicata performance was not as strong at the Corvallis East site compared to Corvallis West and Belgrade. This could be due to the high amount of broadleaf weedy species present at that site, specifically *C. nutans* and *G. aparine*, which appeared to not be controlled with glyphosate applications in either fall 2017 or spring 2018. Even though 2-4, D was applied in spring 2019 to reduce such species, the application was likely too late to benefit *P. spicata* establishment, most of which would have occurred during its first season of growth in 2018. Additionally, it is not uncommon for seeding outcomes to differ between sites (Orloff et al., 2015).

Once *P. spicata* was established, abundance tended to decline between 2018 and 2019. Seeded species mortality is not unusual in revegetation studies (Fansler & Mangold, 2011; Schantz et al., 2016). For example, a reduction in perennial grass density (plants per m^2) and biomass occurred in the second year after seeding in shrub-steppe in eastern Oregon (Schantz et al., 2016). In another study, *P. spicata* biomass decreased from one to three years after seeding in the northern Great Basin (Boyd & Lemos, 2015). Seeded species' mortality between years could be a result of competition between *P. spicata* and other vegetation at the sites. For example, at Belgrade other perennial grasses increased from 2018 to 2019, and at Corvallis West *B. tectorum* increased across the two years. Glyphosate, the herbicide used in this study, does not provide any residual control (EPA, 2016) and was only expected to control weedy vegetation for a short period of time.

Even with the decline in *P. spicata* from 2018 to 2019, results of this study are encouraging. In the second year, *P. spicata* density at Belgrade was 6 plants per m^2 with Spring 2 and 4 seeding dates and at Corvallis West, 25 plants per m^2 were present with Spring 1, 2 and 3 seeding dates. Revegetation is considered successful when desired vegetation is > 5 plants per m^2 in rangelands (Valentine, 1989). At Corvallis West, not only was revegetation successful, but the plants that survived to 2019 were bigger, as cover increased from 2018 to 2019. This is encouraging, especially considering that some revegetation studies have shown that initial, sometimes less-promising results can improve over the long term, e.g., 4 and up to 15 years after treatment (Mangold et al., 2015; Rinella et al., 2020; Rinella et al., 2012).

Herbicide is often used to reduce *B. tectorum* either pre- or post-emergence, depending on site conditions and management objectives and can often provide control beyond one year, especially if integrated with seeding (Kyser et al., 2013; Mangold et al., 2013; Monaco et al., 2017). In this study, abundance of *B. tectorum* cover and other weedy species did not decline with *P. spicata* seeding, but herbicide application resulted in at least a short-term decline in *B. tectorum* and other weedy species. *Pseudoroegneria* *spicata* establishment was improved when herbicide was applied to *B. tectorum*, as demonstrated at Belgrade, which supports my second hypothesis that integrating herbicide would reduce *B. tectorum* and other weedy species abundance in favor of *P. spicata* abundance. Once *B. tectorum* and other weedy species (*T. dubuis*, *C. stoebe*, *G. aparine*, and *C. nutans*) no longer accessed resources essential for plant growth, such as soil nutrients, water and light, *P. spicata* was able to take advantage of the available resources and grow more abundantly.

Furthermore, timing of herbicide application mattered, with spring applications working better than fall. Spring tended to result in higher *P. spicata* cover and biomass at the Corvallis sites, which differs from the second part of my second hypothesis that suggested there would be no seasonal effect of herbicide treatment. *Bromus tectorum* generally germinates and emerges in fall but can also do so in spring (Mack & Pyke, 1983). Spring herbicide application was likely more effective because it was able to reduce weeds that overwintered from fall and lower the abundance of spring-emerging seedlings, including *B. tectorum*. *Pseudoroegneria spicata* benefitted from this timing and was able to establish since the weedy species were no longer consuming resources that it needed to survive. Spring herbicide application benefitted *P. spicata* with spring seeding, but was detrimental to *P. spicata* with fall seeding. When *P. spicata* was able to establish with fall seeding, spring herbicide reduced its growth along with other weedy species. The combination of fall seeding and spring herbicide application proved to be ineffective.

The objective of this study was to see whether timing of seeding and herbicide application could help to overcome the seasonal priority effect typically demonstrated by

B. tectorum and instead shift the seasonal priority effect to *P. spicata*. Was a seasonal priority effect created for *P. spicata* establishment? It appears so, and specifically with spring seeding following spring herbicide application. Seeding throughout the month of April in Corvallis with a drill seeder resulted in higher abundance of *P. spicata*, while a similar effect occurred in Belgrade with hand-broadcasting of seed in May. The difference in timing between sites is not surprising due to elevation differences and variation in climate. Studies have suggested that spring seeding of perennial grasses could be a viable alternative to fall seeding in *B. tectorum*-dominated rangelands (Boyd & Lemos, 2015; Harvey, 2019; Schantz et al., 2016). My study indicates that spring may be the preferred seeding time of *P. spicata* in the Intermountain West.

This study provides multiple tools and lessons for invasive plant management. First, controlling weedy species like *B. tectorum* with herbicide is needed for *P. spicata* establishment; this study used herbicide as a weed control tactic, but other tactics should not be dismissed (Monaco et al., 2017). Since the Corvallis East site had low *P. spicata* response compared to the other sites, that site would have likely benefitted from improved weed control prior to seeding of *P. spicata*. Second, while the timing of glyphosate application (fall or spring) did not affect *B. tectorum* abundance, spring application generally resulted in higher *P. spicata* abundance than fall application. Third, since spring *P. spicata* seeding was more effective than fall seeding, spring may be the preferred revegetation timing for *P. spicata* in the Intermountain West. At the very least, spring seeding should be considered as an alternative to fall seeding. My results, combined with other studies (Harvey et al, 2020; Schantz et al., 2016), suggest that spring seeding following application of a non-selective, no residual herbicide like glyphosate, may be the best practice when seeding native perennial grasses like *P. spicata*. Rangeland managers have a more strategic and ecologically-based option when it comes to timing of herbicide application and seeding *P. spicata* based on the results of this study, which is promising for *B. tectorum*-infested areas.

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CHAPTER FIVE

CONCLUSIONS

Summary of Findings and Implications

The primary goal of this thesis was to understand mechanisms of invasion and to apply current restoration tools in a new way on rangelands impacted by non-native annual grasses. *Ventenata dubia* is a recent invasive species in the Intermountain West, with impacts affecting hay producers, conservation areas, wildlife and domestic livestock. In 2019, *V. dubia* was added to the Montana noxious weed list, requiring control or eradication and has been a recent concern for land managers. Gaining insight into how *V. dubia* is a successful invader and identifying areas of potential invasion is the start of prevention, the most effective tool against invasive species. If areas become invaded with non-native annual grasses, leveraging ecologically-based invasive plant management strategies, such as seeding desired species to exploit seasonal priority effects, as demonstrated with my revegetation study, proved to be effective.

The field soil inoculum and nutrient treatment greenhouse study revealed that *V. dubia* did not create a positive plant-soil feedback loop, which I hypothesized. Rather, *V. dubia* had equally greater growth (higher biomass, shoot height, number of leaves and tillers) with field soil inoculum from the *V.dubia*-absent and *V. dubia*-present areas, as opposed to the greenhouse-only sterilized soil. While a plant-soil feedback did not occur, there is an indication that *V. dubia* is benefitting from microbes in the field soil that the sterilized soil could not provide. However, a sub-sample of roots were investigated for arbuscular mycorrhiza fungi colonization, and none of the examined roots showed colonization in this study. This is the first exploratory study of field soil inoculum with *V. dubia* in the Intermountain West and it provides evidence that further soil biology research should be explored to better understand *V. dubia* invasion.

The nutrient treatment portion of the greenhouse study showed that *V. dubia* grew better with the full nutrient treatment as opposed to the -P and -P-K treatments, which was contrary to my hypothesis. Aboveground biomass, belowground biomass, shoot height, number of leaves and tillers indicated more growth with the full nutrient solution, especially when in combination with the field soil inoculum. An end-of-study soil nutrient analysis revealed no difference in P or K concentrations among the three treatments, possibly indicating that *V. dubia* sequestered the available nutrients and did not prefer one treatment over another. Nutrient treatments were pursued in this study because a field study in Idaho, Oregon and Washington indicated that *V. dubia* was associated with low P and K concentrations in the soil (Jones et al., 2018). My greenhouse study did not prove similar results, but greenhouse studies do not always reflect what is occurring in the field.

The second *V. dubia* study identified vegetation and soil characteristic associations with *V. dubia*-infested areas across Montana. *Ventenata dubia* was negatively associated with bare ground/rock and native perennial grasses and positively associated with non-native perennial grasses, which partially supported my hypothesis. This is the first vegetation association study of *V. dubia* in the Intermountain West grasslands and the first to reveal a different relationship with perennial grass nativity. Since native perennial grasses had a negative association with *V. dubia*, revegetating with such grasses could prevent or limit *V. dubia* invasion. Because non-native perennial grasses had a positive association with *V. dubia*, areas with such vegetation may require annual preventive monitoring if *V. dubia* is growing nearby and seeds may be transported to close-proximity areas.

Soil K concentration was negatively associated with *V. dubia*, which supported my hypothesis. This is the second field study in the region noting such relationship (Jones et al., 2018). When comparing this finding with the results from my greenhouse study, it appears that *V. dubia* may grow well in nutrient-rich and nutrient-limited areas. When soil characteristics and nutrient concentrations were compared in the *V.dubia*-absent and *V.dubia*-present areas, few differences occurred. This is not surprising since the areas were not more than 400 m apart per site, except for Lodge Grass. A logical reason for the difference in *V. dubia* abundance between areas could be the presence of its seeds in the seed bank and lack of dispersal to *V. dubia*-absent areas. *Ventenata dubia's* seeds have bent awns that facilitate contact with the ground. Seed awns can easily attach to clothing, animal fur, equipment and vehicles, transporting seed to new areas and assisting establishment. Likely, *V.dubia* seeds have not yet travelled beyond the infested areas at my sites, which is why *V. dubia* was somewhat contained. A management approach would be to identify vector pathways at each site to prevent seed transport to new areas.

Once invasive annual grasses have established, utilizing ecologically-based invasive plant management techniques are effective. In *B. tectorum*-infested rangeland, glyphosate herbicide application reduced the infestation and provided an opportunity for *P. spicata* to establish, as demonstrated at Belgrade in my last study. Although I did not predict that timing of herbicide would be important for *B. tectorum* reduction, it was. Spring herbicide was more effective at reducing *B. tectorum* than fall herbicide, which was demonstrated at the Corvallis sites. Once *B. tectorum* was reduced with spring herbicide, spring *P. spicata* seeding created a seasonal priority effect in favor of *P. spicata,* resulting in higher density and cover than fall seeding. Without an herbicide application, seeding timing was not effective at reducing *B. tectorum*, as demonstrated at Belgrade. Historically, fall seeding has been used with *P. spicata* revegetation projects. This study showed that spring seeding is more effective than fall, and specifically when it follows spring herbicide application. Land managers can use the existing tools of herbicide application and revegetation in a new way, by altering their timing for improved *P. spicata* establishment in *B. tectorum*-dominated rangelands.

Combined, these independent studies provide a new understanding of *V. dubia* invasion, associated vegetation with its invasion, and refined restoration tools for *B.tectorum*-invaded rangelands. Knowledge of *V. dubia* is in its infancy. Since *V. dubia* shares similar biology to *B. tectorum*, studies related to *B. tectorum* could be pursued to shape further understanding of and reducing *V. dubia* in the Intermountain West.

Future Research

Ventenata dubia appears to be benefitting from field soil for its growth. Pursuing soil ecology, such as bacteria and fungal community composition, would be a logical next step in gaining insight into its invasion. Understanding which bacteria and fungi species are present, and their abundance, at each life history stage could advance the knowledge of *V. dubia* invasion. Further, additional observational studies associating *V. dubia* with plant species would be beneficial in identifying areas vulnerable to invasion, as well as identifying species that may limit or prevent invasion. Since *V. dubia* is a new invader in the region, applying successful restoration strategies from *B. tectorum* studies would likely be promising.

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