UNDERSTANDING THE BIOLOGY, ECOLOGY, AND INTEGRATED MANAGMENT OF *VENTENATA DUBIA*

by

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DEDICATION

For my grandparents,

Susie H. Lee
Jack Lee
Nellie Y. Harvey
Andrew Harvey Sr.

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ABSTRACT

Ventenata dubia (Leers) Coss., common name ventenata or African wire grass, is a non-native winter annual grass of increasing concern in western Montana. In North American, *V. dubia* appeared in the early 1950s; since then it has successfully established in the northeastern and northwestern United States. It is known to invade areas previously inhabited by *Bromus tectorum* (cheatgrass) and *Taeniatherum caput-medusae* (medusahead). In the Intermountain Pacific Northwest, *V. dubia* has caused substantial ecological and economic impacts in perennial grass habitats. Varying disturbance regimes contribute to its rapid expansion over the last decade. Impending climate change threats have the potential to exacerbate the spread of this invasive species. Three independent studies were conducted to explore the biology, ecology, and integrated management of *V. dubia* populations in Montana to alleviate impacts by this species and other invasive annual grasses. A growth chamber study tested the effects of elevated carbon dioxide and temperature on seedling growth of *V. dubia* in response to climate change and in competition with *B. tectorum*. This competition replacement study indicated that at elevated climate conditions *V. dubia* and *B. tectorum* grow smaller and competition with *V.dubia* has the potential to decrease *B. tectorum* growth. A field-based herbicide efficacy trial utilizing the active ingredient indaziflam compared it to other commonly used herbicides to determine long-term control of *V. dubia* and potential plant community changes at 8, 11, 20, and 23 months after treatment. Foliar cover, species richness, and functional group biomass were collected. Findings indicated indaziflam can control *V. dubia* up to three years with positive implications for plant community dynamics. A revegetation study was used to determine the optimum seeding time for perennial grass species, *Pseudoroegneria spicata*, and the effects seeding time can have with competition dynamics with *B. tectorum*. A randomized complete block design was established and *P. spicata* grown for one season prior to *Bromus tectorum* seeding. After the second growing season, tillers and biomass were collected for both species. Findings indicated priority effects can occur with fall and early spring seeding of *P. spicata*, with implications for suppression of *B. tectorum* at earlier seeding dates.

CHAPTER ONE

INTRODUCTION AND RESEARCH OBJECTIVES

Ventenata dubia (Leers) Coss., African wire grass or ventenata, is an non-native winter annual grass of increasing concern in Montana. The first reports of this species in North America were in 1952 in Washington State; since then it has successfully established in the northeastern and northwestern United States, including California, Idaho, Maine, Montana, New York, Oregon, Utah, Wisconsin, and Wyoming (Scheinost, Stannard, & Prather, 2008). It is known to invade areas previously inhabited by *Bromus tectorum* (cheatgrass, downy brome) and *Taeniatherum caput-medusae* (medusahead) (Wallace, Pavek, & Prather, 2015). In the Intermountain Pacific Northwest (IPNW), *V. dubia* has caused substantial ecological and economic impacts in perennial grass habitats (Wallace et al., 2015). As it matures, it becomes unpalatable for livestock and wildlife (Scheinost et al., 2008). The shallow root system creates the potential for soil erosion in areas of monotypic invasions, thus decreasing land productivity (Scheinost et al., 2008). A more robust understanding of *V. dubia*'s biology and ecology in varying climates and disturbance regimes can provide greater insight on its current and future establishment in Montana.

My research explored the response of *V. dubia* to three independent studies which can be used to develop integrated management practices that may alleviate impacts associated with this species. This work addressed: testing the effects of elevated carbon dioxide (CO_2) and temperature on *V. dubia* seedling growth, a herbicide trial of a new herbicide mode-of-action, and mitigating revegetation efforts as a means to promote native perennial grass establishment in plant communities infested with annual grasses. Current management of invasive winter annual grass infestations (e.g., *B. tectorum*, *B. japonicus*, *T. caput-medusae*, and *V. dubia*) largely relies upon herbicide applications, further deepening the need for better understanding of *V. dubia* traits in order to develop a more diverse array of control strategies.

Literature Review

Distribution and Habitat

Ventenata dubia originates from northern Africa and southern Europe and has been expanding in North America, with significant impacts in the IPNW (Scheinost et al., 2008). Primary germination occurs in the fall indicating a preadaptation to characteristic Mediterranean climates with cool, wet winters and hot, dry summers (Wallace et al., 2015). In its native range, it is considered a rare species (Paszko, 1998). Of the five known species in the genus of *Ventenata*, *V. dubia* is the only species established in North America (Scheinost et al., 2008). Its transcontinental migration is unknown, but its primary spread in North America is through contaminated hay and annual crops. Roadside infestations also suggest that it spreads through transportation corridors. Since its first occurrence in Washington State in 1952, it moved into northern Idaho (Kootenai County) by 1956 (Northam & Callihan, 1992). Field observations have noted it growing abundantly in areas with moderate annual precipitation from 35 to 112 cm and elevations ranging from 10 to 1,800 meters (Scheinost et al., 2008). Grass-hay productions systems, primarily *Phleum pratense* L. (timothy hay), have seen significant impacts over the last decade (Wallace et al., 2015). Invasions have occurred in perennial grassland, pastures, rangeland, winter grain and hay fields, Conservation Reserve Program (CRP) lands, and sagebrush steppe habitats (Northam & Callihan, 1992; Wallace et al., 2015). Highly vulnerable sagebrush ecosystems in the western United States have been subject to intensifying invasive annual grass infestations, where *V. dubia* has been observed overtaking communities where *B. tectorum* was once prevalent (Northam & Callihan, 1992). Infestations of *V. dubia* are known to occur in Montana, however the extent of its distribution is poorly understood. To date it is known to occur in Beaverhead, Broadwater, Flathead, Gallatin, Granite, Lewis and Clark, Lake, Madison, Mineral, Missoula, Powell, Ravalli, Sanders Counties in western Montana and Big Horn, Carbon, Park, Rosebud, and Yellowstone Counties in southcentral Montana where it grows in native rangeland, improved pasture, and along roadsides (Harvey & Mangold, 2018).

Identification

Mature *V. dubia* individuals have slim, erect culms that range from 10 – 46 cm in height (Figure 1.1) (Scheinost et al., 2008). Open and airy panicles emerge in late May through June, during which time the stems will noticeably harden and become unpalatable to livestock and wildlife (Scheinost et al., 2008). Seedling and mature leaves are narrow and folded lengthwise. Culms are covered with many thin minuscular hairs. Mature culms have a distinguishing long, membranous ligule from 1 – 8 mm in length and reddish-black nodes (Figure 1.1).

Figure 1.1. Mature *Ventenata dubia* showing shallow roots (left panel), node, and ligule (right panel). Photos by Inna Smith (left) and Pamela Scheinost (right).

Figure 1.2. Mature *Ventenata dubia* seeds with notable bent awns. Photo by Matt Lavin.

Awns are a distinguishing feature in the *Aveneae* tribe, where *V. dubia* is no exception with bent and twisted awns that are most evident from July through August (Figure 1.2). At maturity, when the plant senesces, the awns are approximately 1 – 2.5

mm in length (Figure 1.2) (Scheinost et al., 2008). In the absence of competition, seed rain can produce up to 40,000 seeds per m^2, furthering the need to address infestations (Wallace et al., 2015).

Germination

Scientists have only begun to understand seed germination characteristics of *V. dubia*, in which experimental evidence is limited to research conducted by Wallace et al. (2015). Foremost, it is similar to species such as *B. tectorum* in that it has been observed to typically germinate in the fall, generally about two weeks after *B. tectorum* (Wallace et al., 2015). In vitro germination experiments by Wallace et al. (2015) specifically addressed *V. dubia* germination in relation to a range of constant temperatures, after-ripening periods, seed aging, and cold stratification treatments. Germination did not occur below 8.6 °C and no maximum temperature was found at which germination terminated, however the maximum temperature evaluated in this study was 29.2 °C. An increased period of incubation of *V. dubia* seeds at room temperature (21°C) increased the total cumulative germination rate (seeds per day). At room temperature total cumulative germination was 87% with mean number of days to reach 50% germination of 10.7 days. Seeds that were incubated at 5 °C for 5 and 10 days had a total cumulative germination rate of 28 and 35%, with mean number of days to reach 50% germination of 35.0 and 39.9 days, respectively. Fifty percent of non-dormant seeds at 5 °C and 7.8 °C were recorded to germinate after approximately 42 days (Wallace et al., 2015). The optimum temperature range for maximum seed germination (%) and highest germination rate ranges from 23.3 to 29.2 °C (Wallace et al., 2015). This range of temperatures resulted in a germination time of 7 – 13 days at a 76 – 99% total cumulative germination rate. It was also found that non-dormant seeds germinated across a range of constant temperatures from 8 to 28 °C.

Life History

Emergence and growth of *V. dubia* appears to be affected by total accumulated precipitation and moisture availability rather than precipitation pulses (short-frequent vs long-infrequent intervals) (Bansal, James, & Sheley, 2014). Wallace et al. (2015) found that cumulative precipitation that fell between 2 and 42 growing degree days (GDD) prompted initial seedling emergence with 95% seedling emergence at 33 – 94 GDD. Specific knowledge to regions in Montana where *V. dubia* has been found is mostly limited to local observations, where seedling emergence was observed in early fall (September), approximately within the later GDD recorded in the IPNW experiments.

Though primary seed germination and seedling emergence occurs in fall, ground litter and soil temperature regulates local conditions that can naturally impose secondary dormancy and spring seedling emergence (Wallace et al., 2015). Particularly, seedling emergence was minimal in CRP habitats but was observed to the greatest extent in hay and rangeland systems (Wallace et al., 2015). The distinction in hay fields dominated by *Phleum pratense* L. was suspected to be due to soil temperatures that quickly decreased in fall and slowly increased in the spring due to the higher latitudes within this study (Wallace et al., 2015). In rangelands, spring seedling emergence was associated with low soil moisture years in the fall as compared to fields of *Phleum pratense* L. and CRP lands. Being more inland than IPNW, Montana range and wildland areas differ in overall climate where *V. dubia* infestations are increasing, and the extent of these infestations are unclear.

Climate Change Effects on Invasive Annual Grasses

Advantageous environmental conditions for invasive grasses have the potential to alter ecosystem functions in arid regions that will affect the fire cycle and reduce biodiversity at multiple scales (A. L. Smith et al., 2012). Increased fire intensity and frequency has been a consequence of the 22 million hectares, as of 2005, of *B. tectorum* invasions in the western United States (Duncan et al., 2004). Characterizing species-specific traits that allow invaders to be successful in varying climates will be important for understanding the extent of *V. dubia* invasions. In 2013, the Intergovernmental Panel on Climate Change (IPCC) released a fifth climate change assessment report indicating the Earth's surface to be continually warmer in each of the last three decades than any period of time before 1850. It is projected that hot weather extremes will be more frequent over longer durations, and cold weather extremes will be less frequent with the incessant rise in global mean surface temperature (IPCC, 2014).

In mid-latitude regions, extreme precipitation events are expected to become more intense and frequent (IPCC, 2014). Research by Bansal et al. (2014), analyzed the effects of two potential precipitation regimes for the Great Basin on three invasive annual grasses: *B. tectorum*, *T. caput-medusae*, *V. dubia.* Short-frequent pulses and long-infrequent pulses of precipitation were used to mimic climate change scenarios. *Ventenata dubia* had the lowest root growth in response to both short-pulsed and large-infrequent precipitation regimes as compared to *B. tectorum* and *T. caput-medusae*

(Bansal et al., 2014). Root biomass and whole plant biomass had similar responses between *B. tectorum* and *V. dubia,* whereas *T. caput-medusae* had the highest and most significant response to precipitation regimes (Bansal et al., 2014). Though *B. tectorum* and *V. dubia* did not respond significantly to precipitation pulses at this experimental scale, they were suggested to share similar evolutionary responses to soil properties. Their findings also indicated that cumulative soil moisture was more important than the frequency and duration of precipitation events for both *B. tectorum* and *V. dubia*. It is currently unclear the response invasive annual grasses will have to shifting precipitation patterns, or how those patterns may shift; though changes are expected and will play a significant role in effects on soil properties thus plant community assemblage.

Soil properties, such as pH, clay content, moisture, have a strong relationship with nutrient availability and were found to play a significant role in the growth of *V. dubia* (Bansal et al., 2014). Invasive annual grasses are known to outcompete native species due to their efficient use of soil moisture and water retention in semi-arid ecosystems (Melgoza, Nowak, & Tausch, 1990). In the same study by Bansal et al. (2014), cited above, shoot biomass of the three invasive annual grasses had an overall positive response to soil nitrogen and clay content, where *V. dubia* had the highest shoot biomass in soils with higher clay content in comparison to *B. tectorum* and *T. caput-medusae* (Bansal et al., 2014). Other soil nutrient studies (James et al., 2008) suggest specific root length to be greater for *V. dubia* than *B. tectorum* with increasing nitrogen availability. A high specific root length allows annual plants to move through more soil volume per unit of root biomass, and is said to be a character favorable for nutrient-rich soils (James et al., 2008). Contrary studies suggest *V. dubia* is less efficient at nitrogen assimilation under high nitrogen regimes as compared to other invasive grasses (Wallace & Prather, 2016). More research is needed to further parse invasibility characteristics of *V. dubia* in relation to soil nutrient and composition.

Warming temperatures have provided a more precise prediction of invasive grass response in both experimental and observational settings than elevated CO_2 concentrations (Blumenthal, Kray, Ortmans, Ziska, & Pendall, 2016; Larson, Lehnhoff, & Rew, 2017). Warming temperatures may have the greatest impact on nitrogen uptake for annual grasses and may explain species-specific differences that can occur (Leffler, James, & Monaco, 2013; Leffler, Monaco, & James, 2011). In one study, *B. tectorum* root-shoot ratio was found to have an inverse relationship with temperature (25 °C), while *T. caput-medusae* root-shoot ratio increased (Leffler et al., 2011). High root-shoot ratios of *T. caput-medusae* exhibit higher nitrogen uptake than *B. tectorum* and are a factor of overall mass-specific absorption rate in which annual grasses generally have faster absorptions rates as compared to native perennial species (James, 2008a; Leffler et al., 2013). Rapid nitrogen uptake by annual grasses in the fall greatly benefit their success into the spring. The differences in these physiological and morphological characteristics may also be true for *V. dubia*, which exhibits similar growth patterns as *T. caput-medusae.*

It is currently unclear the response invasive annual grasses will have to shifting climate patterns, or how those patterns may shift soil nutrient dynamics; though changes are expected and will likely play a role in plant community dynamics, particularly communities infested with new invasive annual grasses like *V. dubia*. Future studies need to consider interactions among soil moisture, nutrients, elevated temperatures, and elevated CO_2, as they will all impact future management.

Integrated Management for Invasive Annual Grasses and *Ventenata dubia*

Land managers have limited integrated management strategies for *V. dubia* in the various ranges of perennial grass habitats that it invades. Primary control has been with herbicide applications similar to management of other invasive annual grasses such as *B. tectorum*. The newly marketed herbicide Esplanade® 200 SC (active ingredient (a.i.) indaziflam) shows promise for multiple-year control of invasive annual grasses, especially in combination with spring nitrogen fertilizer applications that promote perennial plant growth (D. Sebastian, J. Sebastian, Nissen, & Beck, 2016). There are no known biological controls for *V. dubia*. Mechanical control, such as mowing, is impractical due to the bents awns and wispy stature of the plant (Lass & Prather, 2007). In combination with potentially useful herbicide applications, multiple integrated control tactics are necessary for long-term control of this species. Management may include combinations of promoting competitive perennial grass growth (i.e. nitrogen additions to poor soil) (Goodwin, Marks, & Sheley, 2006), prescribed fire to reduce litter (DiTomaso, Brooks, Allen, & Minnich, 2006), and revegetation of disturbed habitats. Presently, the effectiveness of these additional management tactics are unknown for long-term control due to the limited biological and ecological knowledge of this new invasive species.

A study by Wallace and Prather (2016) investigated several common invasive annual grass herbicide treatments in pre- and post-emergence applications to *V. dubia*.

Herbicides of interest included: flufenacet plus metribuzin (303 + 73 g a.i. per ha), propoxycarbazone-sodium (49 g a.i. per ha), rimsulfuron (53 g a.i. per ha), sulfosulfuron (53 g a.i. per ha), and imazapic (105 g a.i. per ha). Pre-emergence treatments of rimsulfuron and flufenacet plus metribuzin resulted in over 90% control 10 months after application. In addition, nine months after application, rimsulfuron and sulfosulfuron that had been applied during early post-emergence resulted in over 90% control. In post-emergence applications of rimsulfuron and sulfosulfuron, minimal damage was seen on desired grass species including *Thinopyrum intermedium* (intermediate wheatgrass), *B. inermis* Leyss. (smooth brome), *Dactylis glomerata* L. (orchard grass), *Pseudoroegneria spicata* (Pursh) Á. Löve (bluebunch wheatgrass), and *P. pratense* L. Conversely, imazapic applied early post-emergence provided 72 – 91% control nine months after treatment but resulted in the most damage to local perennial grass species. Propoxycarbazone had the lowest control in pre- and post-emergence applications across all herbicides tested in this study (Wallace & Prather, 2016). Additional herbicide studies have investigated the growth regulators aminopyralid and picloram, which, with pre-emergence application, proved successful in the control of *B. tectorum* and *T. caput-medusae* (Rinella, Bellows, & Roth, 2014). When applied at the seedling stage of *V. dubia*, aminopyralid was shown to reduce seed production. However, overall growth inhibitor herbicides had minor effects on biomass and still did not provide control beyond the seedling period of development.

Currently, there are no herbicides available that provide reliable control of winter annual grasses over several growing seasons that do not injure neighboring desirable plants (D. Sebastian, J. Sebastian, et al., 2016). As mentioned above, there are timing and selectivity issues associated with each herbicide currently used for invasive annual grass control. An emerging herbicide that may aid in long-term control in rangeland is indaziflam, a cellulose biosynthesis inhibiting herbicide (D. Sebastian, J. Sebastian, et al., 2016). A recent evaluation found that it provided 89 – 100% control of *B. tectorum* two years after treatment and 83 – 100% three years after treatment, as compared to commonly used herbicides glyphosate, imazapic, and rimsulfuron, whose effectiveness dropped from about 80% in the first year after treatment to 30% by the third year (D. Sebastian, J. Sebastian, et al., 2016). In addition, it was found species richness of the local plant community was not impacted by indaziflam applications. Though advances in herbicide technology may alleviate annual grass impacts, integrated management approaches are nevertheless needed.

Various other management strategies are sometimes employed for invasive annual grasses, though they are largely underdeveloped due to the lack of basic biological understanding of *V. dubia*. In hay systems, producers will alter harvest schedules to avoid substantial loss in hay exports (Wallace et al., 2015). Manual removal, or mowing, is difficult due to the bent character of the awns which become tangled and unmanageable throughout the growing season (Scheinost et al., 2008). Some producers note having minimal success with aggressive, repeated mowing during the early growing season, which ultimately prevents plants from producing seed once soil moisture becomes too limited (Scheinost et al., 2008). Research on integrated management strategies, outside or in combination with herbicide control, are lacking for *V. dubia* and more options for prevention and control of infestations are needed.

Project Justifications and Objectives

The aim of this research was to provide additional knowledge on the biology and ecology of *V. dubia*, so that land managers are better prepared at utilizing integrated management strategies in the control of this species. Three independent studies were conducted to this end, and they are presented in three separate chapters.

The second chapter is a growth chamber study which looked at the effects of elevated temperatures and CO_2 concentrations on the growth of *V. dubia* and *B. tectorum*. Above and below ground biomass were sampled to determine effects of current and elevated temperature and CO_2 concentrations on growth of these two species.

The third chapter tested effectiveness of a new herbicide mode-of-action for controlling the annual grass species *V. dubia* (primary invader) and *B. tectorum* (secondary invader), while accounting for injury of the local plant community. Plant cover and herbicide injury were evaluated for ten herbicide treatments, half of which included the new mode-of-action.

The fourth chapter addresses how the seeding of a native perennial grass may be used in revegetation of invasive plant-infested plant communities. Particularly, the competitive dynamics between an invasive grass and native grass species were observed in a controlled field experiment. The first growing season explored fall and spring seeding dates effect on native grass establishment. In the second year of the study, an invasive grass species was seeded into the seeding treatment plots to determine how seeding date of the native grass would influence invasion dynamics.

The final chapter is a summary of findings from each study that synthesizes results to inform integrated management practices of *V. dubia*. This chapter also highlights future research concerning non-native annual grasses.

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CHAPTER TWO

THE EFFECTS OF ELEVATED TEMPERATURE AND CO_2 CONCENTRATION ON SEEDLING GROWTH OF *VENTENATA DUBIA* AND *BROMUS TECTORUM*

Contribution of Authors and Co-Authors

Manuscript in Chapter 2, 3, and 4

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Contributions: Conceived and designed the growth chamber experiment, collected data, conducted data analyses, and prepared written manuscript.

Co-Author: Dr. Jane Mangold

Contributions: Assisted with the design of the growth chapter experiment, conducted experiment, reviewed, and provided guidance on manuscript.

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Co-Author: Dr. Timothy Prather

Contributions: Assisted with the design of the growth chapter experiment, reviewed, and provided important feedback on manuscript.

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____ Accepted by a peer-reviewed journal
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CHAPTER TWO

THE EFFECTS OF ELEVATED TEMPERATURE AND CO_2 CONCENTRATION ON SEEDLING GROWTH OF *VENTENATA DUBIA* AND *BROMUS TECTORUM*

Introduction

Impacts of climate change are expected to alter the abundance and distribution of invasive annual grasses, such as *Ventenata dubia* (ventenata) and *Bromus tectorum* (cheatgrass), further impacting ecosystems in arid and semi-arid climates (Blumenthal et al., 2016; Bradley, Curtis, & Chambers, 2016). Earth's surface has warmed in each of the last three decades more so than any period of time before 1850 (Bradley et al., 2016; Whitlock, Cross, Maxwell, Silverman, & Wade, 2017). It is projected high temperature extremes will be more frequent for longer time periods and low temperature extremes will be less frequent. Additionally, increased atmospheric CO_2 is expected to double across all ecosystems, even in the most conservative estimates (Whitlock et al., 2017). These climate changes draw concern for the potential success for winter annual grasses (Blumenthal et al., 2016) and interactions with other vegetation in arid and semi-arid plant communities. We have limited capacity to predict how species or ecosystems will respond to changing dynamics. Information on *B. tectorum*'s potential biological response to climate change in laboratory and field experiments are available, however, more knowledge is needed on *V. dubia*'s response to climate change and competition with other species.

In greenhouse settings, where nutrients and water were readily available, *B. tectorum* in monoculture consistently has a positive growth response to elevated CO_2 concentrations (Jabran & Doğan, 2018; Larson, Lehnhoff, Noffsinger, & Rew, 2018; S. D. Smith, Strian, & Sharkey, 1987; Ziska, Reeves, & Blank, 2005). For example, CO_2 conditions were recreated for early 19th century (270 µmol mol^{-1} CO_2), 1960s (320 µmol mol^{-1} CO_2), 2005 (370 µmol mol^{-1} CO_2), and “future” 2020 conditions (420 µmol mol^{-1} CO_2), and *B. tectorum* biomass increased with increasing CO_2 concentrations, supporting the enduring historical success of this species in western states over the last century (Ziska et al., 2005). Despite such findings in greenhouse settings, field studies utilizing free-air CO_2 enrichment treatments have measured varying responses from *B. tectorum*. For instance, in a free-air CO_2 enrichment study in the Mohave Desert ecosystem, Smith et al. (2000) determined that seed production and above-ground biomass of *B. tectorum* increased at elevated CO_2 concentrations as compared to native annual grasses. Contrary, *B. tectorum* monocultures also responded positively to increased CO_2, but not when grown in competition with native perennial grasses (Larson et al., 2018). In other CO_2 enrichment studies, *B. tectorum* tissue were less palatable to herbivores and more combustible when grown at 470 µmol mol^{-1} CO_2 as compared to 270 µmol mol^{-1} CO_2 (Blank, Morgan, Ziska, & White, 2011; Blank, White, & Ziska, 2006; Ziska et al., 2005).

Increased temperatures are expected in all climate change scenarios, and increased temperatures are the most predictable explanatory condition for *B. tectorum* productivity, particularly the early onset of warming spring temperatures and elevated winter temperatures (Bradley et al., 2016). Air and soil temperatures are drivers of germination timing and rates, seedling establishment, and maturation of plants (Ball, Frost, & Gitelman, 2004; Hulbert, 1955; Klemmedson & Smith, 1964; Thill, Schirman, & Appleby, 1979). Consistent findings of rapid maturation and an increase in *B. tectorum* biomass as a result of warming temperatures are well-known in both greenhouse and field experiments when grown in monocultures (Bansal & Sheley, 2016; Blumenthal et al., 2016; Boyte, Wylie, & Major, 2016; Compagnoni & Adler, 2014; Larson et al., 2018, 2017; Zelikova et al., 2013).

Climate experiments that incorporate competition with *B. tectorum* are lacking. As previously indicated, *B. tectorum* tends to have a positive response to elevate climate conditions in monoculture, but these findings do not extend to more recent competition studies. At elevated temperatures, the local native grass community was the most significant factor in suppressing *B. tectorum* biomass and cover in Montana sagebrush steppe (Larson et al., 2017). Furthermore, Larson et al. (2018) also found that *Pseudoroegneria spicata* (bluebunch wheatgrass) had a more suppressive effect on *B. tectorum* when grown under increased CO_2. Such competition studies are important when addressing changing climates, as species are not singularly affected by changing conditions, rather the whole community will respond. Furthermore, water and nutrient uptake are species-specific (Blumenthal et al., 2016; Wolkovich et al., 2013; Wolkovich & Cleland, 2011), and water and nutrient availability is greatly affected by precipitation and soil conditions (Compagnoni & Adler, 2014; Zelikova et al., 2013) which adds to the complexity of how a community will respond to climate change.

This study examined the effects of elevated temperatures and CO_2

concentrations on the growth of *V. dubia* and *B. tectorum* in relation to current (year 2018) and predicted regional end-of-century (year 2100) values. *Bromus tectorum* is the most dominant and widely studied invasive annual grass in the sagebrush steppe biome due to its extensive presence. More recently new winter annual grasses are invading areas once infested with *B. tectorum*, such as in the Intermountain Pacific Northwest with *V. dubia* (Scheinost et al., 2008). Our current understanding of these new non-native annual grasses is limited, but the little information we do have suggests they may not respond similarly to *B. tectorum*, (Bansal et al., 2014; Jones, Norton, & Prather, 2018). Additionally, invasive grasses are found in a wide range of habitats (i.e. grass-shrublands, open forests, and mountain habitats) which all vary widely in environmental conditions, furthering the complexity of understanding their species specific responses to climate change (Averett et al., 2016; Bashkin et al., 2003; Jones et al., 2018). An exploration of potential climate scenarios for *V. dubia* growth in the Northern Rockies Ecoregion is needed to determine this species' range and potential infestation severity as compared to *B. tectorum*. Empirical climate change research focusing on the biological fitness of *V. dubia* and consequential competition with *B. tectorum* are explored in this chapter.

The objectives were to determine: 1. Differences in growth (shoot and root biomass, shoot length, and number of leaves) for each species under current and elevated climate treatments, and 2. Differences in growth (shoot and root biomass, shoot length, and number of leaves) as a response to inter-specific competition under current and elevated climate conditions. In concert with previous controlled CO_2 and temperature studies, I hypothesize that *B. tectorum* and *V. dubia* shoot and root biomass would be greater when growing under elevated temperature and CO_2 concentrations compared to current climate levels, and the magnitude of the difference would be greater for *B. tectorum* than *V. dubia*. I also expected *B. tectorum* to have higher shoot biomass than *V. dubia* under either climate condition and to therefore exert more of a competitive effect on *V. dubia* than *V. dubia* would exert on *B. tectorum*.

Methods

Estimated changes in elevated temperature (°C) and CO_2 concentration (ppm) for southwestern Montana (Whitlock et al., 2017) were used to determine seedling growth responses for two different competition scenarios. For this study I used the 30-year (1985 – 2015) historical average maximum and minimum temperatures in September for southwestern Montana, 23 °C and 4 °C, respectively (Table 2.1) (Time and Date AS, 2017). Optimal range for *V. dubia* germination is 23.3 °C to 29.2 °C (78 – 99% germination with 7 – 13 days to germination) (Wallace et al., 2015). Decreased *V. dubia* germination occurs at 5 °C (28 – 35% germination) (Wallace et al., 2015). Current estimates of CO_2 concentrations are approximately 400 ppm which is what was used. Elevated climate estimates were based on Representative Concentration Pathway (RCP) 8.5 from the Intergovernmental Panel on Climate Change (IPCC) which predicts future greenhouse gas emissions based on assumptions about future energy use, global population, and economic activity (IPCC, 2014; Whitlock et al., 2017). RCP 8.5 scenario describes emissions that will continue to increase into year 2100 (end-of-century) due to unsuccessfully controlling emissions (Whitlock et al., 2017); current social trends indicate a likely RCP 8.5 scenario. For end-of-century values I used the predicted values of 29.6 °C and 10.6 °C, respectively (Table 2.1). Predictions for CO_2 concentrations range from 525 to 925 ppm for end-of-century, with estimates greater than 800 ppm matching that of RCP 8.5 (Whitlock et al. 2017) which is what was used. These treatments were established within growth chambers, where light emission was 0 and 800 μ moles per m^2 per second to reflect 12 hour diurnal fluctuations for each treatment, which was also matched by diurnal day-night changes in temperature (Table 2.1). Total annual precipitation for southwestern Montana has not changed between 1950 and 2015 and is currently estimated to be 53.8 cm (Whitlock et al., 2017). Future precipitation conditions are not expected to significantly change and were therefore not treated as a factor in this experiment; pots were watered daily throughout the experiment (approximately 30 mm per day once seedlings were established).

Table 2.1. Climate treatments.

Time	Temperature (°C)	CO_2 (ppm)
Current Conditions		
07:00 – 19:00	23	400
19:00 – 07:00	4	400
Elevated Conditions		
07:00 – 19:00	29.6	800
19:00 – 07:00	10.6	800

Each climate treatment was conducted sequentially where the first treatment mimicked current environmental conditions followed by elevated conditions. Seeds of both species were collected near Bozeman, Montana, during summer 2017 and were determined to be 100% germinable. A replacement design was used with a total of 4 plants per pot (10 cm x 10 cm x 12.5 cm): *V. dubia* alone, *B. tectorum* alone, and *V.*

dubia with *B. tectorum*, with 10 replications per competition type. Twenty seeds were sown per plot and, after 14 days, thinned to 4 individuals per pot for the intra-specific competition treatment or 2 individuals per species per pot for the inter-specific treatment. MSU Plant Growth Center (PGC) “MSU Mix” (1:1:1 by volume mineral soil, Canadian Sphagnum Peat Moss, and washed concrete sand) was used and Aqua-Gro 2000G, a wetting agent, was added at the rate of 0.59 kg per cubic meter; the mix was aerated steam pasteurized for one hour at 70 °C. All pots were rotated weekly to account for variation within chamber.

Plants grew for 22 days under the current climate treatment and 19 days under the elevated climate treatment. The difference in growth periods between the two climate treatments was due to time limitations for using the CO_2 growth chamber that is shared among PGC users. Shoot length was measured (to nearest 0.1 cm) and leaves counted for all plants in each pot prior to biomass processing. Total plant material in each pot was collected all at once, then separated from the soil by first removing large debris. After shoot biomass was harvested by clipping green foliage from bottom of plant, root biomass was carefully rinsed for 10 minutes in cold water using 1 and 2 mm sieves. All biomass, separated by shoot and root portions, were placed into coin envelopes, dried at 37 °C for 72 hours, and weighed to the nearest 0.0001 grams.

To determine differences in shoot and root biomass (g per individual), root-shoot ratios, number of leaves per individual, and maximum shoot length (cm) as a response to climate and competition treatments, all response variables were log-transformed to meet normalization assumptions; mean values are reported. The most parsimonious model was used for all responses and were evaluated for independence and constant variance. Independent factors for climate variables were current and elevated climate treatments and for competition levels were inter-specific (*B. tectorum* and *V. dubia*) and intra-specific for each species (*B. tectorum* only and *V. dubia* only) treatments. A Tukey HSD pairwise comparison was conducted for significant factors. Graphical interpretations and analyses were conducted using R Software 3.5.1, specifically emmeans, dplyr, and ggplot2 packages (Lenth, Singmann, Love, Buerkner, & Herve, 2018; Wickham, 2016; Wickham, Romain, Henry, Müller, & RStudio, 2018; R Core Team, 2018).

Results

Differences in seedling shoot and root biomass were evident across species, competition, climate, and the interaction between competition and climate treatments (p<0.001) (Table 2.2). For root-shoot ratios, differences were evident across species (p<0.001) and competition (p=0.019) and weakly evident for climate (p=0.054) (Table 2.2).

Table 2.2. Analysis of variance (ANOVA) table for average shoot biomass, root biomass, and root-shoot ratio. Bold p-values indicate significance at p<0.05.

Main Effects and Interactions	*df*	Shoot Biomass		Root Biomass		Root-Shoot Ratio	
		F-value	p-value	F-value	p-value	F-value	p-value
Species	1,73	2,064	**<0.001**	768.5	**<0.001**	50.15	**<0.001**
Competition	2,73	15.31	**<0.001**	20.28	**<0.001**	4.195	**0.019**
Climate	1,73	266.9	**<0.001**	183.6	**<0.001**	3.824	0.054
Competition*Climate	2,73	23.04	**<0.001**	11.57	**<0.001**	1.929	0.153

Bromus tectorum growing in current conditions had the largest shoot biomass and responded similarly across intra- and inter-specific competition treatments at 0.0556 and

0.0549 g per individual, respectively (Figure 2.1). Shoot biomass of *B. tectorum* was lower when grown in elevated conditions, and the intra-specific competition treatment resulted in higher shoot biomass than the inter-specific treatment, at 0.0254 and 0.0131 g per individual, respectively (Figure 2.1). Shoot biomass of *V. dubia* under current conditions was similar across competition treatments at 0.0029 g per individual for inter-specific and 0.0025 g per individual for intra-specific competition (Figure 2.1). Elevated climate conditions resulted in lower *V. dubia* shoot biomass, and shoot biomass was greater in the intra-specific competition treatment at 0.0014 g per individual than the inter-specific competition treatment at 0.0005 g per individual (Figure 2.1).

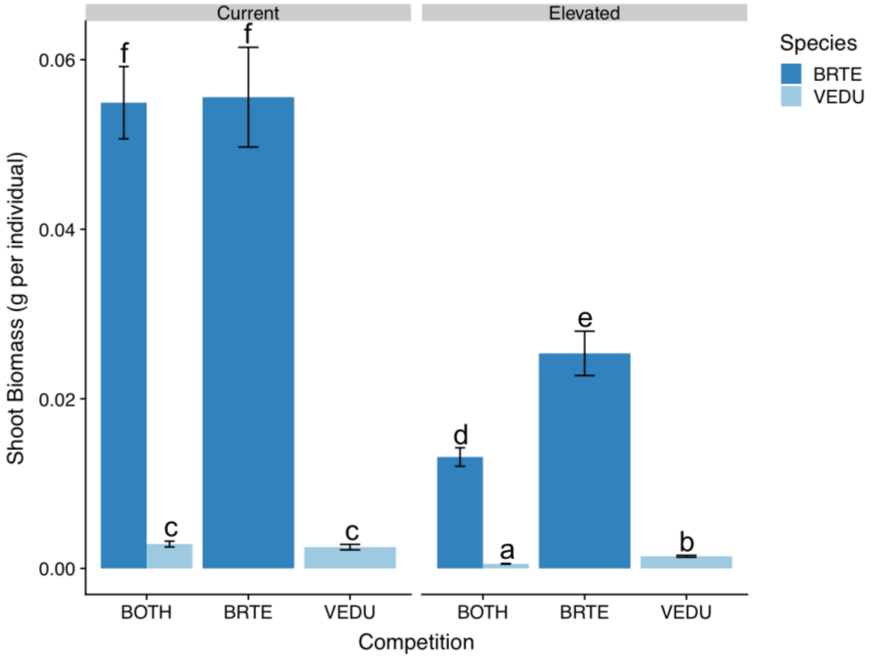

Figure 2.1. Mean shoot biomass (g per individual) for each species in competition and climate treatments. Competition treatments are indicated by BOTH = *B. tectorum* + *V. dubia*, BRTE = *B. tectorum* only, VEDU = *V. dubia* only. Similar letters indicated no difference in shoot biomass across all climate and competition treatments at α=0.05.

Similar to shoot biomass, *B. tectorum* growing in current conditions in both intra- and inter-specific competition treatments had the largest and similar root biomass at 0.0589 and 0.0403 g per individual, respectively (Figure 2.2). The second highest *B. tectorum* root biomass was found in the elevated climate, intra-specific competition treatment at 0.0176 g per individual, followed by the inter-specific competition treatment at 0.0093 g per individual (Figure 2.2). Root biomass of *V. dubia* grown in current climate in intra- and inter-specific competition treatments, and elevated climate, intra-specific conditions all had a similar response at 0.0038, 0.0040, and 0.0020 g per individual, respectively (Figure 2.2). The lowest *V. dubia* root growth occurred in elevated climate, inter-specific conditions at 0.0006 g per individual (Figure 2.2).

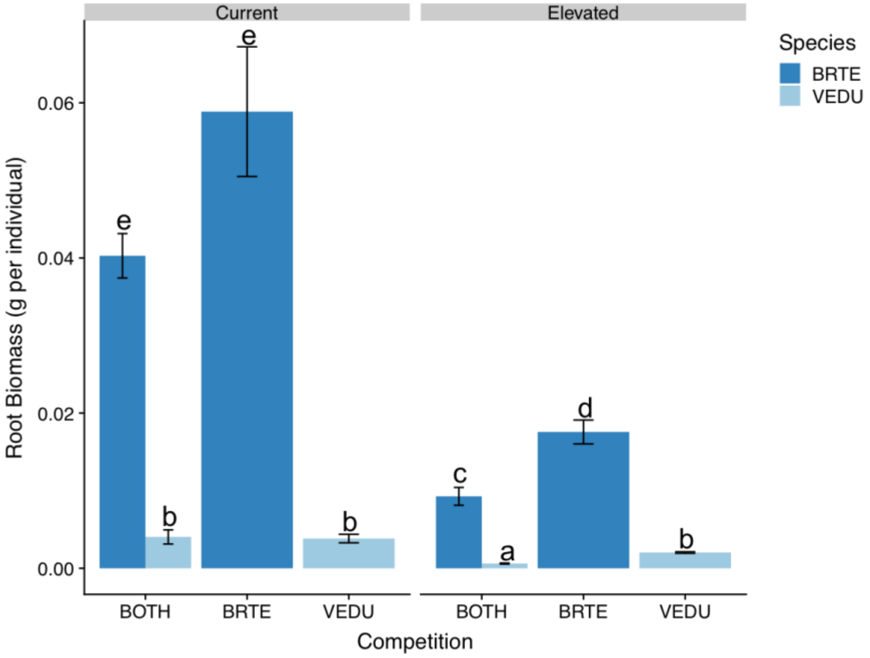

Figure 2.2. Mean root biomass (g per individual) for each species in competition and climate treatments. Competition treatments are indicated by BOTH = *B. tectorum* + *V. dubia*, BRTE = *B. tectorum* only, VEDU = *V. dubia* only. Similar letters indicated no difference in root biomass across all climate and competition treatments at α=0.05.

There was a difference in root-shoot ratios between species (p<0.001) and competition treatments (p<0.001) (Table 2.1). *Bromus tectorum* root-shoot ratios ranged from 0.701 to 1.06 with an average of 0.80 across climate and competition treatments (Figure 2.3). *Ventenata dubia* root-shoot ratios were higher and ranged from 1.15 – 1.57 with an average of 1.40 across climate and competition treatments. Intra-specific treatments had an average root-shoot ratio of 1.21 and inter-specific treatments had an average root-shoot ratio of 0.99 (Figure 2.3). There was also a trend (p=0.056) indicating current conditions had higher root-shoot ratios than elevated conditions (Table 2.1).

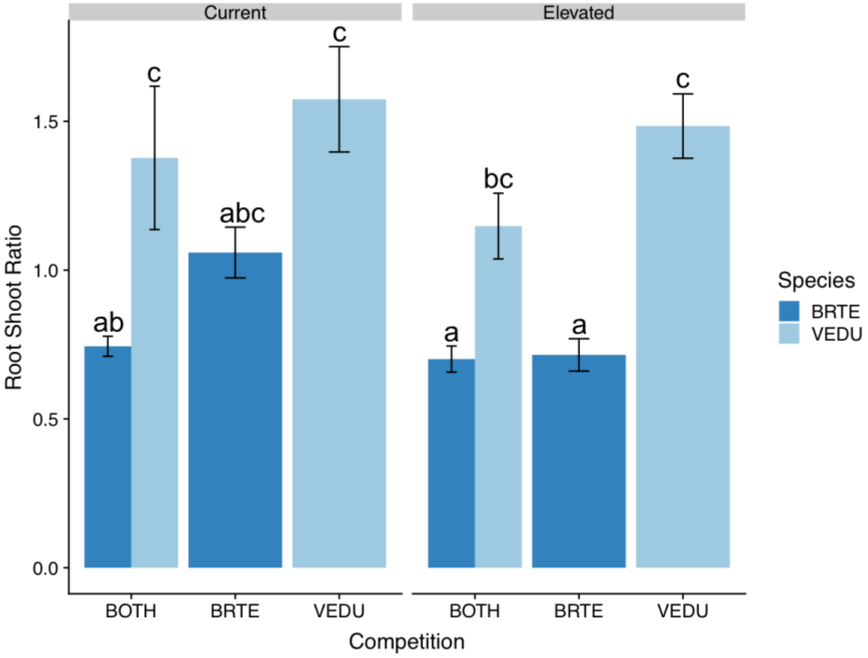

Figure 2.3. Mean root-shoot ratios for each species in competition and climate treatments. Competition treatments are indicated by BOTH = *B. tectorum* + *V. dubia*, BRTE = *B. tectorum* only, VEDU = *V. dubia* only. Similar letters indicated no difference in root-shoot ratios across all climate and competition treatments at α=0.05.

Shoot length differed by species (p<0.001), climate treatments (p<0.001), and the interaction of competition and climate treatments (p=0.020) (Table 2.3). Number of leaves per individual differed across species (p<0.001) and climate treatments (p<0.001).

Table 2.3. Analysis of variance (ANOVA) table for maximum shoot length (cm) per pot and number of leaves per individual. Bold p-values indicate significance at p<0.05.

Main Effects and Interactions	*df*	Shoot Length		Leaves	
		F-value	p-value	F-value	p-value
Species	1,73	1305	**<0.001**	432.4	**<0.001**
Competition	2,73	0.8300	0.439	0.6850	0.509
Climate	1,73	107.2	**<0.001**	48.87	**<0.001**
Competition*Climate	2,73	4.134	**0.020**		

Bromus tectorum had the longest shoot length under current conditions in both inter- and intra-specific treatments at 11.1 cm and 10.9 cm in comparison to elevated conditions and competition treatments (Figure 2.4). This was followed by *B. tectorum* growing under elevated conditions in either competition treatment at 7.4 cm and 7.8 cm (Figure 2.4). For *V. dubia*, only the inter-specific current and elevated conditions differed significantly at 3.6 cm and 2.4 cm. All other *V. dubia* shoot length responses were similar. There was a general trend of shorter *V. dubia* shoot length under elevated conditions compared to current conditions.

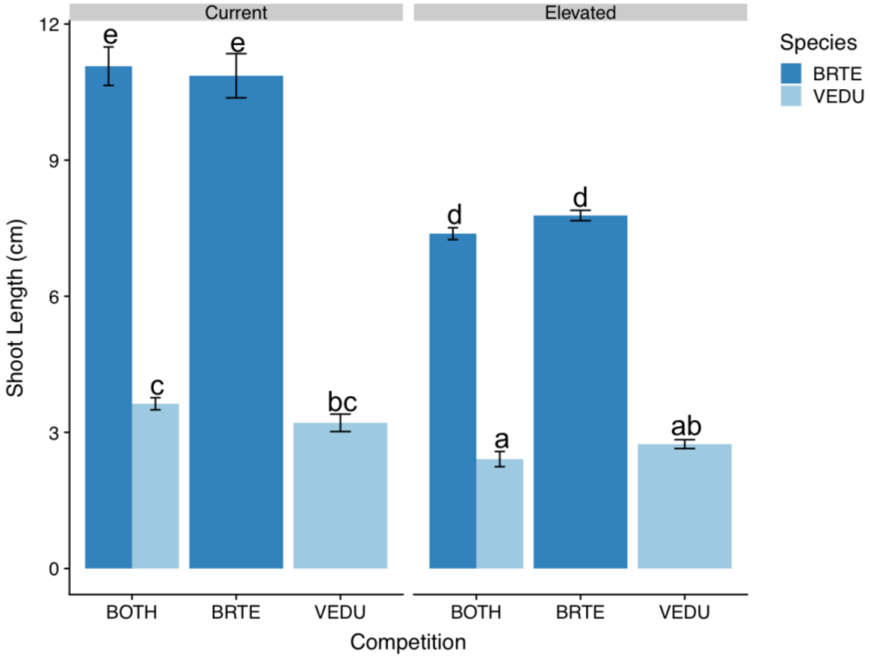

Figure 2.4. Mean shoot length (cm) for each species in competition and climate treatments. Competition treatments are indicated by BOTH = *B. tectorum* + *V. dubia*, BRTE = *B. tectorum* only, VEDU = *V. dubia* only. Similar letters indicated no difference in shoot length across all climate and competition treatments at α=0.05.

Bromus tectorum had more leaves per individual (28.5) than *V. dubia* (10.5) when averaged across both climate and competition treatments (p<0.001) (Table 2.3). Across species, under current conditions the number of leaves per individual was 2.0 and 1.7 under elevated conditions. The number of leaves per individual *B. tectorum* plant was 33.5 in the current climate treatment and 23.6 in the elevated climate treatment (p<0.001) (Table 2.3). The number of leaves per individual *V. dubia* plant was 12.0 in the current climate treatment and 8.9 in the elevated climate treatment.

Discussion

In support of my hypotheses, *B. tectorum* had more shoot and root biomass than *V. dubia* in current and elevated climates, and inter- and intra-specific competition treatments. These findings are consistent with previous research where *B. tectorum* and *V. dubia* biomass were compared under varying nitrogen concentrations and precipitation amounts, and *V. dubia* consistently was smaller than *B. tectorum* (Bansal et al., 2014; James, 2008b, 2008a). This trend is further supported by *B. tectorum* having longer shoot length and more leaves per individual compared to *V. dubia* under both competition and climate treatments. However, the pattern of response between these species and treatments is of interest as it can help guide future research and management of invasive annual grasses.

At elevated conditions, *B. tectorum* decreased in overall size in both competition treatments, whereas *V. dubia* had varying responses. Negative growth responses by *B. tectorum* in the presence of competition were found in another growth chamber study at elevated CO_2 (800 ppm) and watering (38 mm) (Larson et al., 2018) similar to my study. Contrary to *B. tectorum*'s decreasing root biomass response, *V. dubia*'s root biomass and shoot length was similar in the absence of competition. Maintaining shoot length and root biomass at elevated conditions could increase the abundance and distribution of *V. dubia* in the future and is an indication of *V. dubia* having high plasticity to changing conditions. Limited knowledge is available on non-native annual grass response to changing climate conditions, and these responses can be further affected by competition.

Interestingly, there was no effect of competition on each species' biomass under current climate conditions, but both species grew bigger in intra-specific treatments than inter-specific treatments under elevated climate conditions. In my study the effect of inter-specific competition was most evident in elevated climate conditions where *B. tectorum* shoots and roots were smaller when grown with *V. dubia* compared to *B. tectorum* growing alone. Similarly, *V. dubia* did not grow differently in competition treatments under current climate conditions, whereas in elevated conditions *V. dubia* grew bigger in the absence of *B. tectorum* competition. No effect of competition treatments under current climate conditions on biomass may be due to lower transpiration rates by both species at these temperatures, where a higher density or longer duration of treatment may have yielded differences. However, under elevated climate conditions, the relative higher temperatures may have contributed to higher transpiration rates thus there was a stronger effect of competition. Elevated climate conditions can perpetuate the distribution of invasive grass monocultures, and species-specific responses can change competition dynamics with dominant annual grasses.

Even though *B. tectorum* always grew larger than *V. dubia*, root-shoot biomass allocation was higher for *V. dubia*, particularly in elevated climate conditions. In fact, *B. tectorum* root-shoot ratios decreased under elevated climate conditions. Greater root growth is seen as an adaptive growth strategy in dry climates for invasive annual grasses, and favors higher nitrogen use and subsequent leaf nitrogen productivity (James, 2008b). Higher root allocation is a known adaption by native perennial species and a trait shared by *V. dubia*, particularly in the seedling growth stage (James, 2008b). A high specific root length allows annual plants to move through more soil volume per unit of root biomass, and is said to be a character favorable for nutrient-rich soils (James 2008b). Previous research has shown *V. dubia* to have overall lower biomass and root length than *B. tectorum* and another invasive winter annual grass, *Taeniatherum caput-medusae* (medusahead), and although *V. dubia* was also smaller than *B. tectorum* in this study, there was also evidence for potentially more root allocation by this species in elevated climate conditions.

Higher CO_2 concentrations and temperatures can enhance the water use efficiency of C3 plants like *B. tectorum* (Bazzaz, 1990). Under current conditions, I found some evidence of *V. dubia* having more access to limiting soil resources than *B. tectorum*. Anecdotal evidence has indicated *V. dubia* is displacing *B. tectorum*, where initial establishment of *V. dubia* is known to favor moist conditions (Jones et al., 2018). A field study in California that enhanced CO_2 (723 mol^{-1} CO_2) found *Avena* species, which are in the same taxonomical tribe as *V. dubia,* to double in water use efficiency when compared to ambient CO_2 levels (Jackson, Sala, Field, & Mooney, 1994). My study supports the potential for *V. dubia* to have effective water use in current and elevated conditions, thus potentially enhancing its seedling growth over that of *B. tectorum* and possibly contributing to *B. tectorum*'s present displacement.

Characterizing species-specific responses of annual invasive species and perennials to climate change is important for invasions across the western United States. Understanding the extent of newest annual grass invader, *V. dubia,* in new environments is critical to determining its potential distribution. Management should consider the effects of shifting competitive relationships between invasive plant species due to increasing temperatures and CO_2, where protecting and maintaining native perennial systems from disturbance is the principal goal. These impending changes in climate are cause for concern due to intensifying catalyst events that encourage invasive species expansion, like wildfires, in addition to creating more conducive conditions favoring invasive species establishment. At the seedling stage, when establishment and survival is most important, we also find support of *V. dubia* to have a greater water use efficiency than *B. tectorum* due to its relatively higher root-shoot ratio and maintaining its root biomass in changing conditions. Lastly, this study supports annual grasses have lower growth at elevated conditions which is contrary to previous findings and also has implications for future species distribution. Characterizing species-specific responses to climate change will be important for understanding the extent of *V. dubia* invasions across the western United States where competition with dominant invasive annual grasses is likely.

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CHAPTER THREE

INDAZIFLAM PROVIDED UP TO THREE-YEARS OF CONTROL FOR *VENTENATA DUBIA* IN SOUTHWESTERN MONTANA

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CHAPTER THREE

INDAZIFLAM PROVIDED UP TO THREE-YEARS OF CONTROL FOR *VENTENATA DUBIA* IN SOUTHWESTERN MONTANA

Introduction

Herbicides can be used to minimize impacts from annual grass invasions and promote desired vegetation. Presently, herbicides control winter annual grasses, including *Ventenata dubia*, for one or two years with minor injury to resident, desirable plants (Hirsch, Monaco, Call, & Ransom, 2012; Kyser et al., 2007; Mangold et al., 2013; D. Sebastian, J. Sebastian, et al., 2016; Wallace & Prather, 2016). A herbicide now available that may enable long-term control in pasture, rangeland and non-crop areas is indaziflam (Esplanade® 200 SC, Bayer CropScience LP), a cellulose biosynthesis inhibiting herbicide, that is effective on controlling annual grasses prior to seedling emergence (Sebastian, Nissen, De, & Rodrigues, 2016; D. Sebastian, J. Sebastian, et al., 2016). Indaziflam may expand our flexibility in managing annual grasses with herbicide, through its potential of longer duration of control.

Ventenata dubia is a recent, non-native annual grass invader in southwestern Montana. It has caused up to 50% yield loss in croplands across eastern Idaho and Washington (Wallace & Prather, 2015a, 2016). The first reports of this species in North America were in the early 1950s; since then it has successfully established in the northeastern and northwestern United States, with a growing presence in Montana

(Scheinost et al., 2008). It is known to invade areas previously inhabited by *Bromus tectorum* (cheatgrass or downy brome) and *Taeniatherum caput-medusae* (medusahead) (Jones et al., 2018; Wallace et al., 2015a; Wallace & Prather, 2015b). In the Intermountain Pacific Northwest (IPNW), *V. dubia* has caused substantial ecological and economic impacts in perennial grass habitats (Wallace et al., 2015a). As it matures, it becomes unpalatable for livestock and wildlife. The shallow root system creates the potential for soil erosion in areas of monotypic invasions, thus decreasing land productivity and value (Scheinost et al., 2008). In Montana, *V. dubia* distribution is increasing with confirmed infestations in range, pasture, and along roadsides in at least 20,000 hectares across 18 counties (Harvey & Mangold, 2018).

Invasive annual grasses are notorious for growing across a broader range of seasons than native perennial grasses due to their ability to germinate and grow at low temperatures (Thill et al., 1979). While this extended growing season can provide an advantage for annual grasses, it also presents an opportunity for selective chemical control that targets newly germinated seedlings. Indaziflam is typically applied pre-emergent to inhibit growth, specifically seedling root growth. Fall applications in northern Colorado provided 89 – 100% control of *Bromus tectorum* two years after treatment and 83 – 100% control three years after treatment; this was compared to the more commonly used herbicides glyphosate, imazapic, and rimsulfuron, whose effectiveness dropped from about 80% in the first year after treatment to 30% by the third year (D. Sebastian, J. Sebastian, et al., 2016). In that same study, plant community species richness was not impacted by indaziflam. The use of indaziflam in Montana and information about the effectiveness and non-target injury of the product for *V. dubia* are limited and need further exploration. Recently, *V. dubia* was included on a supplemental label for Esplanade® (a.i. indaziflam) for use in natural areas, not including pasture or cropland (“Esplanade®”, 2018). In addition, *V. dubia* is listed on three herbicide labels that are primarily used in croplands: Axiom®DF (a.i. flufenacet), Osprey® (a.i. mesosulfuron-methyl), and Sinbar®WDG (a.i. terbacil), and a rangeland specific label is not yet available (“Axiom®DF”, 2015; “Osprey®”, 2015; “Sinbar®WDG”, 2010; Greenbook, 2018). An extension bulletin from the Pacific Northwest Weed Management Handbooks also indicates the use of imazapic (product name Plateau® or Panoramic) and sulfosulfuron (product name Outrider®) for herbicide control (Prather, Miller, & Hulting, n.d.).

This study compared the effectiveness of indaziflam to commonly used herbicides for controlling annual grasses, while accounting for non-target injury to desired vegetation, and subsequent shifts in plant community composition. The study was specifically interested in control of the annual grass, *V. dubia*. Over a two-year period, *V. dubia* control and non-target injury were assessed across ten herbicide treatments: a non-sprayed control, indaziflam, propoxycarbazone-sodium (Lambient™, Bayer CropScience LP), rimsulfuron (Matrix®SG, DuPont), imazapic (Plateau®, BASF Corporation), glyphosate (Accord® XRT II, Dow AgroSciences LLC), and indaziflam combined with each of the other four active ingredients (a.i.). Based on previous studies (Sebastian, Fleming, Patterson, Sebastian, & Nissen, 2017; Sebastian, Nissen, et al., 2016; D. Sebastian, J. Sebastian, et al., 2016), I hypothesized that indaziflam alone and in combination with the other herbicides would provide longer-term control (i.e. at least 2 years) of *V. dubia* compared to the other herbicides applied alone. Further, I sought to document changes to species richness and diversity. Finally, I examined non-target plant injury (perennial grass, perennial forb, and annual forb), expecting injury to vary across treatments, but injury would be most evident in perennial grass biomass and abundance due to comparable biological structure to that of annual grass (Kyser et al., 2007; Sebastian, Nissen, et al., 2016).

Methods

The study site was located near Bozeman (45°52'51.0"N 111°03'24.0"W), at the foothills of the Bridger Mountain Range in southwestern Montana. Mean annual precipitation is 15.5 mm and temperature is 6 °C. Soil (0 – 15 cm) at this location was loam (41% sand, 38% silt, 21% clay) with a 6.2 soil pH and 2.7% organic matter. The site was dominated by *Bromus inermis* (smooth brome), interspersed with *Agropyron smithii* (western wheatgrass), *Bromus carinatus* (mountain brome) and a uniform infestation of *V. dubia* (Lesica, Lavin, & Stickney, 2012). Ten herbicide treatments, replicated three times, were arranged in a randomized complete block design (Table 3.1). On 4 November 2016, 9.1 m x 3.1 m plots were established and herbicide treatments applied using a CO_2 backpack sprayer that delivered 182.4 liters water per hectare at 289.6 kPa. The non-ionic surfactant Induce® (Helena Chemical Company) was applied at a 0.25% v/v rate along with each herbicide treatment. At the time of treatment, *V. dubia* was in the one- to two-leaf stage.

Table 3.1. Treatments applied to *Ventenata dubia*-infested study site.

Treatment	Common Product Name	Application Rate (grams a.i. /hectare)
Non-sprayed	Not applicable	Not applicable
Indaziflam	Esplanade® 200 SC	102.4
Propoxycarbazone-sodium	Lambient™	60.0
Rimsulfuron	Maxtrix® SG	70.1
Imazapic	Plateau®	122.7
Glyphosate	Accord® XRT II	533.0
Indaziflam + Propoxycarbazone-sodium	Esplanade® 200 SC + Lambient™	102.4 and 60.0
Indaziflam + Rimsulfuron	Esplanade® 200 SC + Maxtrix® SG	102.4 and 70.1
Indaziflam + Imazapic	Esplanade® 200 SC + Plateau®	102.4 and 122.7
Indaziflam + Glyphosate	Esplanade® 200 SC+ Accord® XRT II	102.4 and 533.0

Visual control ratings of *V. dubia* were conducted on 13 July and 10 October 2017 and 5 July and 16 October 2018 to represent 8, 11, 20, and 23 months after treatment (hereafter referred to as MAT), respectively. Ratings were conducted by walking through each plot and assigning a percentage value of *V. dubia* control (based on canopy cover) in comparison to the non-sprayed treatment. Particular observation was given to emerging *V. dubia* seedlings at 11 and 23 months after treatment. Visual control ratings were arcsine transformed to meet normalization of proportional data and evaluated for independence and constant variance. To determine treatment effectiveness, an analysis of variation (ANOVA) on a mixed effects model was used to account for plot-to-plot variation, where fixed effects were treatments and MAT. A Tukey HSD post hoc test was used on statistically significant treatment responses to determine all pairwise differences for *V. dubia* control throughout the study.

On 12-13 July 2017 and 3-5 July 2018, foliar cover for each species was measured using three randomly located 20 cm x 50 cm Daubenmire (1959) frames per plot. Cover (%) of all observed species (based on Lesica et al., 2012), bare ground and rock (combined) were measured and trace values were replaced with 0.1 for analyses. On 3 and 5 July 2018, aboveground biomass (g per m^2) was harvested by functional group in the same frames that were used for estimating foliar cover. Aboveground biomass was clipped to 2 cm from the soil surface and categorized as: *V. dubia*, annual forbs, perennial grasses, and perennial forbs. Samples were returned to the Montana State University Plant Growth Center and dried at 37 °C for 72 hours then weighed to the nearest 0.1 g.

To evaluate non-target injury and any changes in plant community composition, an ANOVA was used to determine differences across functional group biomass, species richness, and Simpson's Diversity. A decline in biomass (g per m^2) was interpreted as injury to that functional group as a result of treatment. There was an overall increase in species richness across the site from 8 to 20 MAT, and 20 MAT was evaluated for community composition using a Poisson distribution across treatments. Simpson's diversity excluded target species data and was analyzed across treatments and MAT. In addition, relative species abundance (% per m^2) was used to evaluate alpha-diversity differences and changes to the community structure across all herbicide treatments at 8 and 20 MAT. Although annual grasses were not included in biomass analyses, *B. japonicus* (Japanese brome) and *B. tectorum* were included for species richness and relative species abundance calculations. An alpha level of 0.05 was used for all statistical tests and all models were evaluated for normality, independence, and constant variance assumptions. A Tukey HSD post hoc test was used to determine significant pairwise differences for all models. Graphical interpretations and analyses were conducted using R

Software 3.5.1, specifically using routines within dplyr, lme4, emmeans, vegan, and ggplot2 packages (Bates, Mächler, Bolker, & Walker, 2015; Lenth et al., 2018; Oksanen et al., 2018; Ram, Wickham, Richards, & Baggett, 2018; R Core Team, 2018; Wickham, 2016; Wickham et al., 2018).

Results

Control of *Ventenata dubia*

Differences in *V. dubia* visual control ratings were evident across all treatments for all months after treatment ($p<0.001$) (Table 3.2). Differences were also found across main effects of treatments and months after treatment for visual control ratings ($p<0.001$) (Table 3.2).

Table 3.2. Analysis of variance (ANOVA) table for treatment effects on *V. dubia* control across 8, 11, 20, and 23 months after treatment (MAT). Bold numbers are significant at α=0.05.

Main Effects and Interaction	*df*	*V. dubia* Control	
		F-Value	*p-Value*
Treatment	9,78	165.62	**<0.001**
MAT	3,78	7.57	**<0.001**
Treatment*MAT	27,78	4.81	**<0.001**

Eight MAT indaziflam plus glyphosate had the highest control at 98%. This was followed by indaziflam plus rimsulfuron at 96%, indaziflam plus imazapic at 95%, indaziflam plus propoxycarbazone-sodium at 93%, and rimsulfuron at 90%, which all shared a similar response as the highest control treatment ($p<0.5$) (Table 3.3). Indaziflam alone exhibited 70% control, which was comparable to imazapic at 63% control ($p<0.05$)

(Table 3.3). Propoxycarbazone-sodium had 22% control, which was similar to the non-sprayed treatment.

Eleven MAT indaziflam plus any of the other herbicides had the highest control, ranging from 89 – 98% ($p<0.05$) (Table 3.3). At 11 MAT, the indaziflam alone treatment resulted in control of 67%, which was similar to indaziflam plus propoxycarbazone-sodium or glyphosate and rimsulfuron (46%). Propoxycarbazone-sodium and imazapic had similar control ratings 11 months after treatment (23% and 20%, respectively), with imazapic sharing similar ratings as the non-sprayed treatment and glyphosate.

Table 3.3. Mean absolute *Ventenata dubia* control (% ± SE) as affected by all treatments at 8, 11, 20, and 23 months after treatment MAT).

Treatment	Months After Treatment*			
	8	11	20	23
Non-sprayed	0 ± 0 a	0 ± 0 a	0 ± 0 a	0 ± 0 a
Indaziflam	70 ± 15 bc*	67 ± 24 cd*	98 ± 2 c^{+}	76 ± 11 b*
Propoxycarbazone-sodium	22 ± 13 a*	23 ± 7 b*$^{+}$	53 ± 4 b^{+}	8 ± 4 a*
Rimsulfuron	90 ± 5 bcd^{o}	46 ± 21 bc^{+}	17 ± 10 ab*	5 ± 1 a*
Imazapic	63 ± 12 b^{+}	20 ± 12 ab*	20 ± 6 b*	11 ± 2 a*
Glyphosate	0 ± 0 a	0 ± 0 a	0 ± 0 a	0 ± 0 a
Indaziflam+ Propoxycarbazone-sodium	93 ± 2 bcd	89 ± 7 de	99 ± 1 c	97 ± 1 b
Indaziflam+ Rimsulfuron	96 ± 1 cd	98 ± 1 e	99 ± 1 c	99 ± 0 b
Indaziflam+ Imazapic	95 ± 1 bcd	98 ± 1 e	100 ± 0 c	96 ± 3 b
Indaziflam+ Glyphosate	98 ± 2 d	96 ± 1 de	98 ± 2 c	98 ± 1 b

*Within MAT, similar letters following means indicate no difference across treatments and similar superscripted symbols indicate no difference in each treatment across MAT ($\alpha=0.05$).

Twenty and twenty-three MAT indaziflam combined with the other four herbicides continued to provide the highest control at 96 – 100% ($p<0.05$) (Table 3.3).

Herbicides applied alone, including indaziflam, performed variably at 20 and 23 months after application. Compared to 8 and 11 MAT, indaziflam increased in control to 98% at 20 months after treatment; control decreased to 76% at 23 months, however this was still comparable to all high ratings of indaziflam combined treatments. Rimsulfuron provided 17% control 20 MAT and decreased to 5% at 23 MAT. Imazapic also decreased from 20% to 11% during this time. Propoxycarbazone-sodium increased in control at 53% 20 MAT, but this decreased to 8% at 23 MAT. At 23 MAT herbicides other than indaziflam that were applied alone did not differ from the non-sprayed treatment. For all sampling periods, glyphosate (0%) alone exhibited no *V. dubia* control.

Plant Community Responses at Peak Growing Season

Differences in *V. dubia* ($p=0.005$) and perennial grass ($p=0.037$) biomass were found across all herbicide treatments at 20 MAT, but herbicide treatments did not affect annual ($p=0.447$) or perennial forb ($p=0.547$) biomass (Table 3.4).

Table 3.4. Analysis of variance (ANOVA) table for treatment effects on functional group biomass at 20 months after treatment (MAT). Bold numbers are significant at $\alpha=0.05$.

Functional Group	Treatment Effects		
	df	F-value	p-value
Ventenata dubia	9,19	4.018	**0.003**
Annual Forb	9,19	0.956	0.447
Perennial Grass	9,19	2.487	**0.037**
Perennial Forb	9,19	0.839	0.547

The glyphosate treatment had the highest *V. dubia* biomass at 81.3 g per m^2, similar to the non-sprayed treatment at 38.4 g per m^2, propoxycarbazone-sodium at 21.1 g per m^2, and imazapic at 23.9 g per m^2 ($p<0.05$) (Table 3.5). Similar *V. dubia* biomass was found in indaziflam alone at 10.5 g per m^2, rimsulfuron at 14.4 g per m^2, and indaziflam plus glyphosate at 4.2 g per m^2. These treatments were also not different where no *V. dubia* was found in indaziflam plus propoxycarbazone-sodium, indaziflam plus rimsulfuron, and indaziflam plus imazapic treatments ($p<0.05$) (Table 3.5). There were no Tukey pairwise differences across perennial grass biomass. Perennial grass biomass ranged from 68.4 g per m^2 in the non-sprayed treatment to 202 g per m^2 in the indaziflam treatment.

Table 3.5. Mean absolute functional group biomass (g per m^2 ± SE) as affected by all treatments 20 months after treatment (MAT). VEDU = *Ventenata dubia*, AF = annual forb, PG = perennial grass, and PF = perennial forb.

Treatment	Functional Group*				
	V. dubia		AF	PG	PF
Non-sprayed	38.4 ± 17.1	ab	20.0 ± 9.90	68.4 ± 5.40	33.1 ± 22.7
Indaziflam	10.5 ± 10.5	a	66.9 ± 31.4	202 ± 29.7	39.1 ± 39.1
Propoxycarbazone-sodium	21.2 ± 15.1	ab	28.2 ± 15.0	108 ± 4.80	0 ± 0
Rimsulfuron	14.4 ± 2.90	a	30.0 ± 17.5	147 ± 25.2	49.8 ± 24.9
Imazapic	23.9 ± 8.70	ab	52.5 ± 18.8	104 ± 28.6	12.6 ± 12.6
Glyphosate	81.3 ± 27.5	b	45.1 ± 18.6	77.4 ± 44.1	32.9 ± 20.3
Indaziflam+ Propoxycarbazone-sodium	0 ± 0	a	65.3 ± 7.10	146 ± 39.0	0 ± 0
Indaziflam+ Rimsulfuron	0 ± 0	a	41.1 ± 17.4	116 ± 5.40	0 ± 0
Indaziflam+ Imazapic	0 ± 0	a	42.2 ± 7.40	105 ± 22.9	13.4 ± 13.3
Indaziflam+ Glyphosate	4.20 ± 4.20	a	19.6 ± 8.30	190 ± 35.3	27.3 ± 15.0

*Within functional group, similar letters following means indicate no difference in biomass ($\alpha=0.05$).

Differences in species richness were found across treatments ($x^2(1, n = 40) = <0.001$) at 20 MAT. Propoxycarbazone-sodium, rimsulfuron, and imazapic alone had the highest species richness at 13, 14, and 14, respectively ($p<0.05$) (Table 3.6). Indaziflam plus rimsulfuron had the lowest species richness at 4.7 and all other treatments were similar (Table 3.6).

Table 3.6. Mean species richness (± SE) as affected by treatment at 20 months after treatment (MAT).

Treatment	Species Richness
Non-sprayed	12 ± 0.0 abc
Indaziflam	6.3 ± 1.3 abc
Propoxycarbazone-sodium	13 ± 1.8 c
Rimsulfuron	14 ± 1.9 c
Imazapic	14 ± 2.0 c
Glyphosate	13 ± 2.0 bc
Indaziflam+Proxycarbazone-sodium	5.0 ± 1.0 ab
Indaziflam+Rimsulfuron	4.7 ± 0.6 a
Indaziflam+Imazapic	8.0 ± 2.3 abc
Indaziflam+Glyphosate	7.3 ± 2.3 abc

Similar letters indicate no difference in species richness (α=0.05)

Table 3.7. Analysis of variance (ANOVA) table for Simpson's Diversity at 8 and 20 months after treatment (MAT). Bold numbers are significant at α=0.05.

Main Effects and Interaction	*df*	*Deviance*	*Pr(>Chisq)*
Treatment	9,50	40.71	**<0.001**
MAT	1,49	41.85	**<0.001**
Treatment*MAT	9,40	36.66	**0.011**

Simpson's diversity was affected by the interaction of treatment and months after treatment ($x^2(1, n = 40) = <0.011$) (Table 3.7). Eight MAT there were no pairwise differences found across treatments (Figure 3.1). During this time, Simpson's diversity ranged from 1.74 in the indaziflam plus rimsulfuron treatment to 3.50 in the glyphosate treatment. At 20 MAT Simpson's diversity was highest in propoxycarbazone-sodium and imazapic treatments at 6.78 and 6.45, respectively (Figure 3.1). Diversity was lowest in indaziflam plus propoxycarbazone-sodium (2.94), indaziflam plus glyphosate (2.86), indaziflam (2.70), and indaziflam plus rimsulfuron (2.14) treatments. All other treatments were similar for rimsulfuron (5.09), indaziflam plus imazapic (5.07), glyphosate (3.81), and the non-sprayed (3.82) treatments.

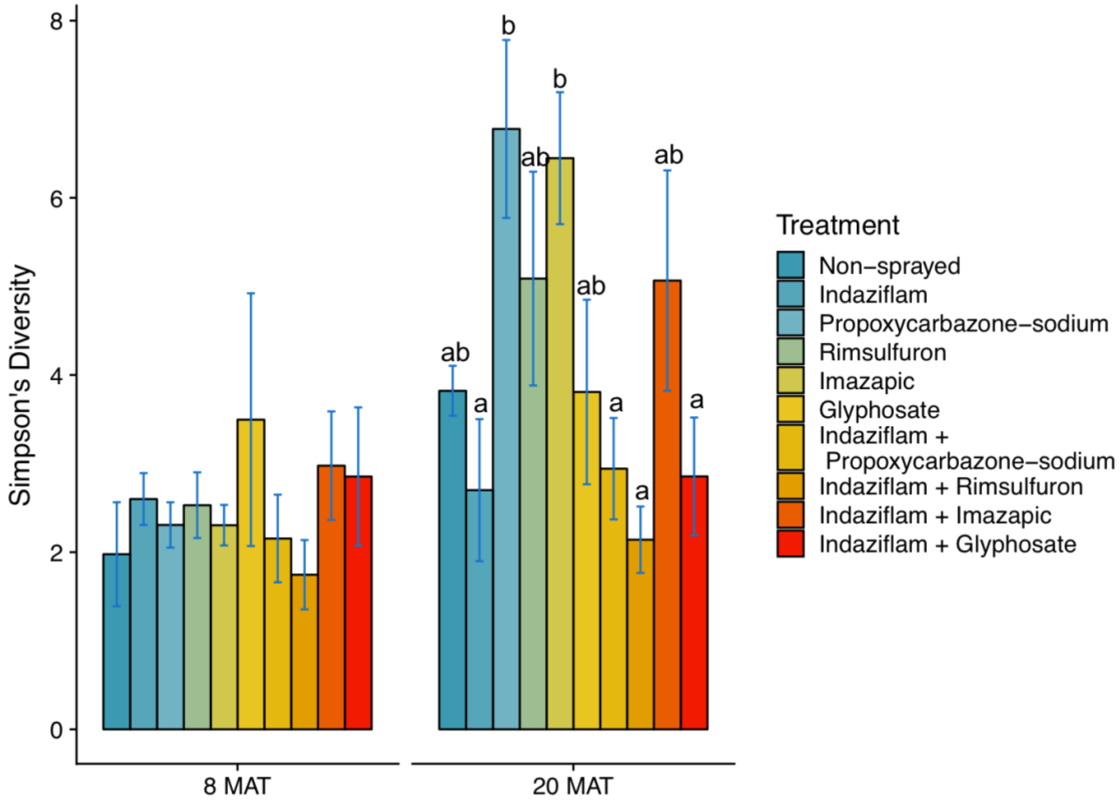

Figure 3.1. Simpson's diversity across treatments at 8 and 20 months after treatment (MAT). Letters indicate Tukey pairwise differences (α=0.05) across treatments within MAT; no pairwise differences in diversity were found 8 MAT.

Eight months after treatments were applied the non-sprayed treatment had a *V. dubia* relative species abundance of 63% per m^2 followed by *Bromus inermis* at 21.6% (Figure 3.2). At 20 months in the non-sprayed treatment *V. dubia* was still highest in abundance at 21.2% per m^2, followed by *Rumex acetosella* at 5.2% (Figure 3.2). Perennial *Bromus* species decreased at 20 months after the treatments were applied but were the next most abundant at 5.5% per m^2. Two annual forbs were found at 8 MAT making up <0.02% per m^2; annual forbs increased to 11 species during the study to account for <4% cover at 20 months. Bare ground and rock cover was 3.0% per m^2 (SE=2.0) at 8 MAT and 0.3 % per m^2 (SE= 0.3) at 20 MAT.

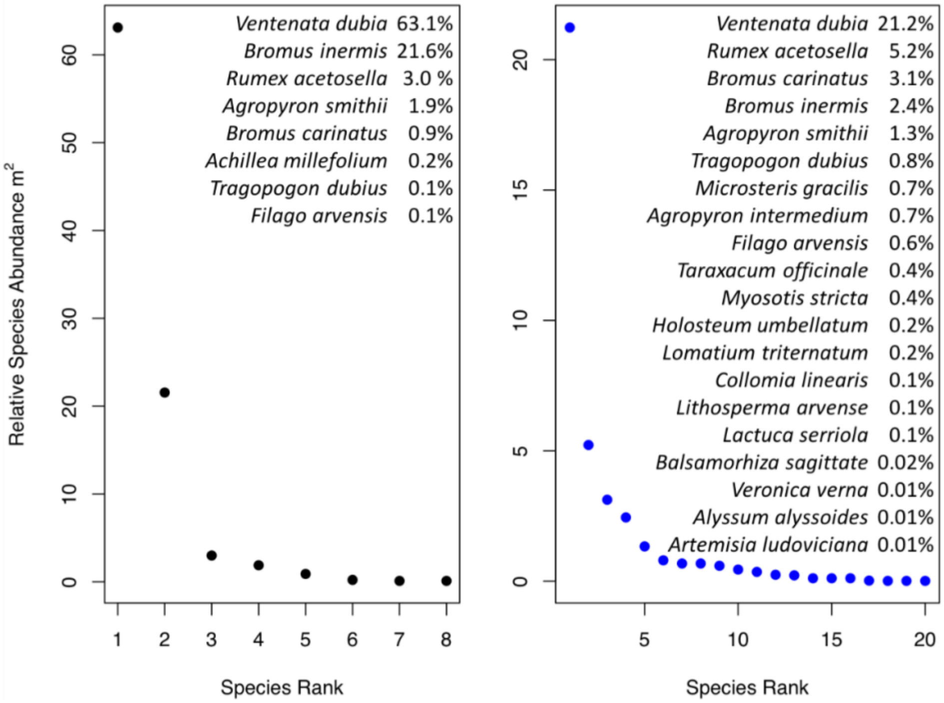

Figure 3.2. Relative species abundance (RSA, % per 1m^2) for non-sprayed treatment, 8 (left panel) and 20 (right panel) months after treatment. Each circle represents a species with its respective abundance (RSA). Species are listed in descending order.

Bromus inermis was the highest ranking species in the indaziflam treatment at 15.4% per m^2, followed by *V. dubia* at 10.0%, and *B. carinatus* at 9.1% 8 MAT (Figure 3.3). Twenty MAT perennial *Bromus* species were the highest at about 11% per m^2, and *V. dubia* decreased to 0.2% (Figure 3.3). This was followed by *Agropyron* species at 3.7% in the first year to about 3% in the second year. *Agropyron intermedium* and *Pseudoroegneria spicata* (0.1% per m^2) were two new perennial grass species found 20 MAT. Annual forb species increased from 2 species (0.4% per m^2) to 5 species (<2% per m^2). Two perennial forbs found 8 MAT, *Achillea millefolium* and *Artemisia ludoviciana*, were not found again 20 MAT, but two other perennial forbs not present 8 MAT were present 20 MAT, *Lomatium triternatum* and *Balsamorhiza sagittata.* Bare ground and rock cover was 1.6% per m^2 (SE=1.1) 8 MAT and 1.5% per m^2 (SE= 0.5) 20 MAT.

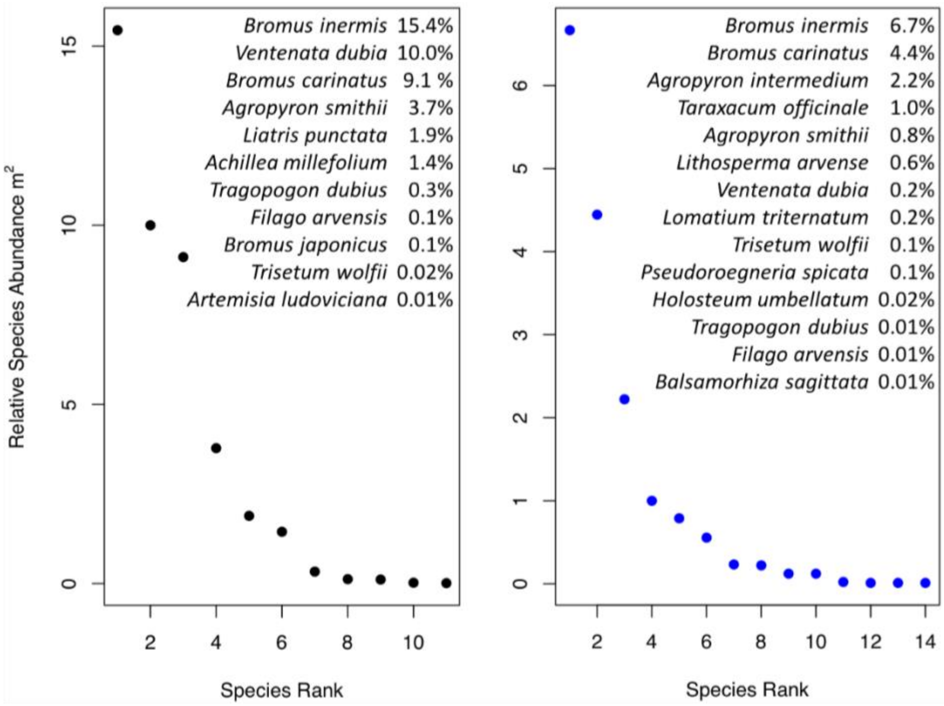

Figure 3.3. Relative species abundance (RSA, % per 1m^2) after indaziflam treatment, 8 (left panel) and 20 (right panel) months after treatment. Each circle represents a species with its respective abundance (RSA). Species are listed in descending order.

In the propoxycarbazone-sodium treatment in both 8 and 20 MAT, the most abundant cover was that of *V. dubia* at 22.2% and 7.3% per m^2, respectively (Figure 3.4). *Bromus japonicus* was not found 8 MAT but was found in trace amounts (0.3% per m^2) 20 MAT. Perennial *Bromus* species were at 8.7% and *Agropyron smithii* was at 4.6% 8 MAT. *Achillea millefolium* (0.3% per m^2) was the only perennial forb found 8 MAT in this treatment, and no perennial forbs were found 20 MAT. Instead, annual forbs increased by 7 new species with a total cover of about 11% per m^2. Bare ground and rock cover was 0.8% per m^2 (SE=0.4) 8 MAT and 2.8% per m^2 (SE=0.8) 20 MAT.

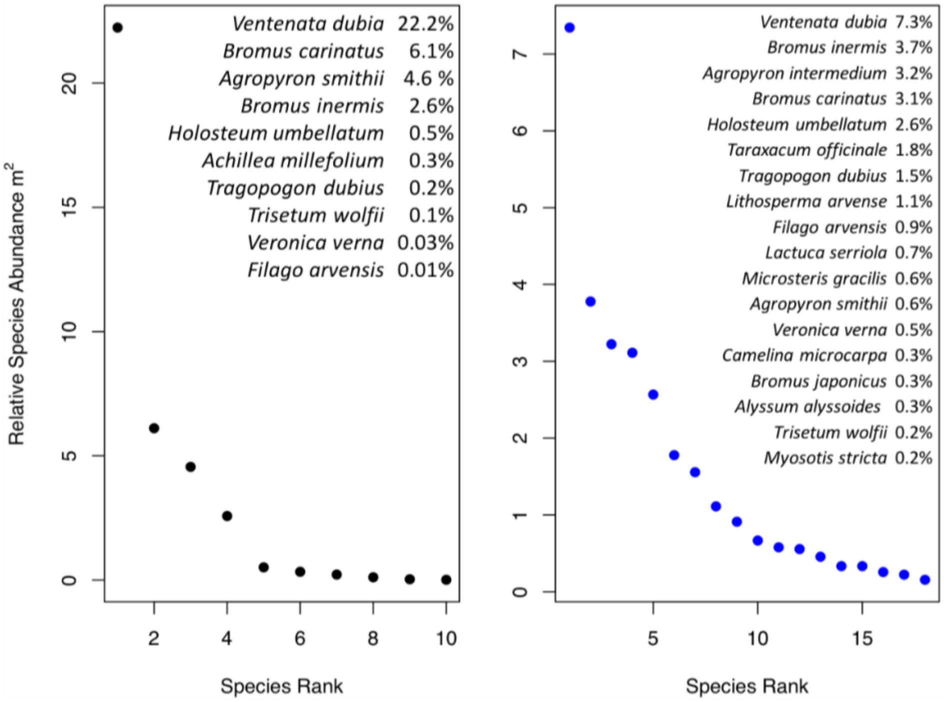

Figure 3.4. Relative species abundance (RSA, % per 1m^2) after propoxycarbazone-sodium treatment, 8 (left panel) and 20 (right panel) months after treatment. Each circle represents a species with its respective abundance (RSA). Species are listed in descending order.

In the rimsulfuron treatment perennial *Bromus* species covered 12.5% per m^2 followed by *A. smithii* at 4.1% 8 MAT. *Ventenata dubia* was found 8 MAT at 0.2% per m^2 and increased to the fourth most abundant species at 1.8% per m^2 20 MAT (Figure 3.5). Twenty MAT, perennial *Bromus* species accounted for 8.6% of cover. *Agropyron* species decreased to 2.2% cover per m^2, and *Buchloe dactyloides* (1.8% per m^2) was not found again 20 MAT, but *Trisetum wolfii* was found in trace amounts (0.6% per m^2). Annual forbs increased from 4 species at 1% per m^2 to 10 species covering 8% in 2018.

Bromus japonicus appeared 20 MAT in trace amounts (0.01%). Bare ground and rock cover was 1.7% per m^2 (SE=1.7) 8 MAT and 1.7% per m^2 (SE=0.8) 20 MAT.

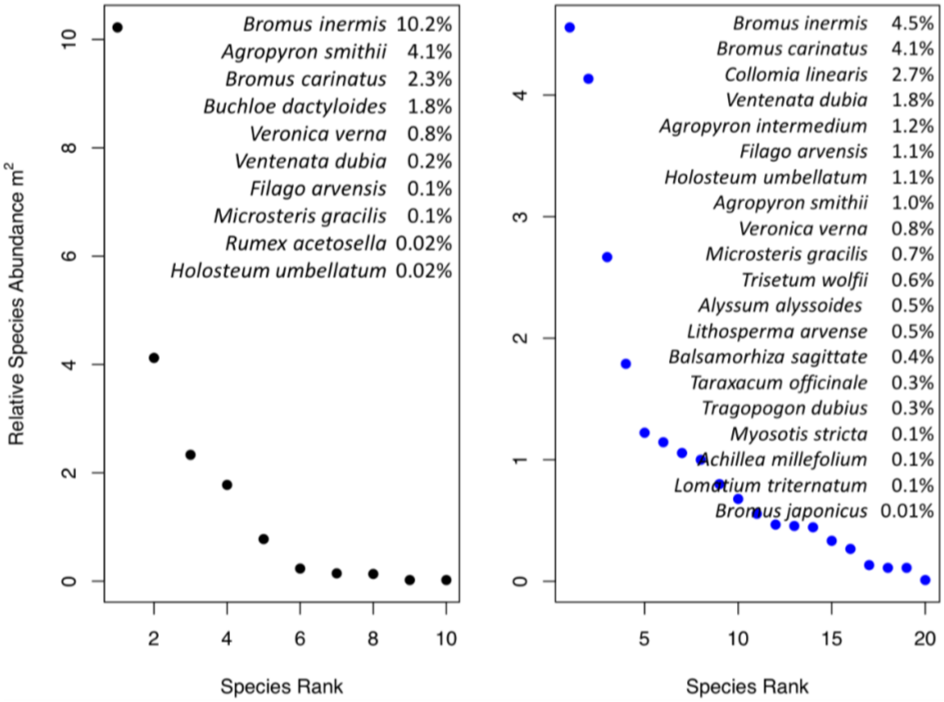

Figure 3.5. Relative species abundance (RSA, % per $1m^2$) after rimsulfuron treatment, 8 (left panel) and 20 (right panel) months after treatment. Each circle represents a species with its respective abundance (RSA). Species are listed in descending order.

In the imazapic treatment 8 MAT, perennial *Bromus* species covered about 22.1% per m^2 followed by *Agropyron smithii* at 12.6% per m^2 (Figure 3.6). *Ventenata dubia* at 10.2% and *A. ludoviciana* (2.2% per m^2) were also among the most abundant species 8 MAT. Twenty MAT perennial *Bromus* species decreased in overall relative abundance to 3.3% per m^2. During this period, *V. dubia* cover decreased to 4.8% per m^2 and was the most dominant 20 MAT. *Agropyron smithii* was still the second most abundance but decreased to 2.7% per m^2. *Veronica verna* and *H. umbellatum* increased in relative abundance to 2.2% and 2.1% per m^2, respectively. Perennial forb *A. ludoviciana* (0.1%)

decreased 20 MAT. Four annual forb species covered about 1.2% per m^2 8 MAT, and this increased to 12 species at about 8.6% per m^2 20 MAT. Bare ground and rock cover was 0.9% per m^2 (SE=0.4) 8 MAT and 1.0% per m^2 (SE=0.6) 20 MAT.

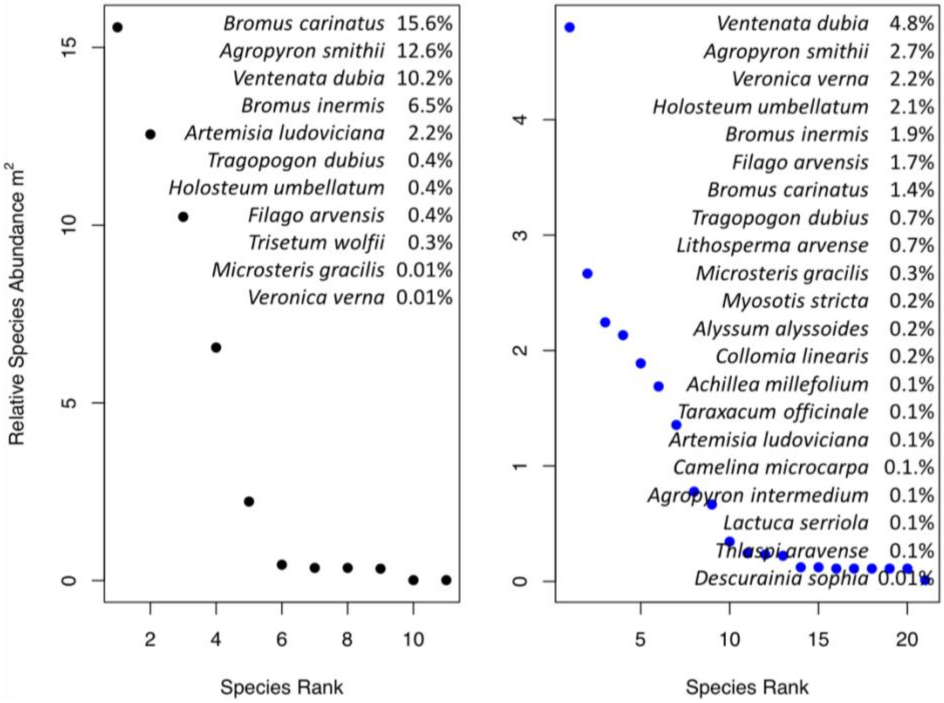

Figure 3.6. Relative species abundance (RSA, % per 1m^2) after imazapic treatment, 8 (left panel) and 20 (right panel) months after treatment. Each circle represents a species with its respective abundance (RSA). Species are listed in descending order.

Eight and 20 MAT *V. dubia* was the most dominant species in the glyphosate treatment at 41.7% per m^2 and 36.3% per m^2, respectively (Figure 3.7). Perennial *Bromus* species were the second most abundant in both periods at 8% per m^2 8 MAT and 4.5% per m^2 20 MAT. *Artemisia ludoviciana* (4.5% and 4.4% per m^2), *Filago arvensis* (2.4% to 1.2% per m^2), and *H. umbellatum* (1.4% and 0.7% per m^2) decreased over time. Annual forb species increased from 5 to 10 species but decreased in cover from 4.7% per

m^2 to about 3% per m^2. Bare ground and rock cover was 2.3% per m^2 (SE=1.9) 8 MAT and 2.7% per m^2 (SE=2.0) 20 MAT.

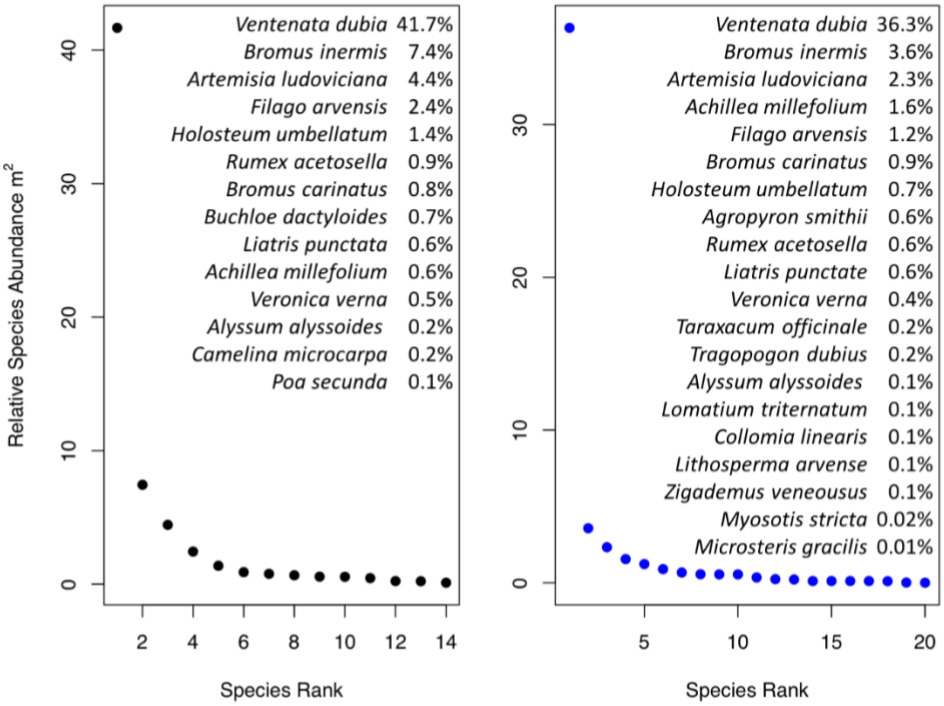

Figure 3.7. Relative species abundance (RSA, % per $1m^2$) after glyphosate treatment, 8 (left panel) and 20 (right panel) months after treatment. Each circle represents a species with its respective abundance (RSA). Species are listed in descending order.

Eight MAT perennial *Bromus* species were the most abundant in the indaziflam plus propoxycarbazone-sodium treatment at about 17.6% per m^2, and this decreased to 14% 20 MAT (Figure 3.8). *Agropyron* species were the next most abundant at 1.7% per m^2 8 MAT and 3.3% 20 MAT. *Agropyron intermedium* and *T. wolfii* were new perennial grass species 20 MAT. *Ventenata dubia* was found at 1.8% 8 MAT and not found 20 MAT. *Rumex acetosella*, one of two perennial forbs 8 MAT, increased from 1.3% to 3.0% per m^2 20 MAT. *Artemisia ludoviciana*, the one other perennial forb 8 MAT (0.8%), was not found again 20 MAT. Annual forb species were found in trace amount in both periods (0.2% 8 MAT and 0.1% in 20 MAT), with one less species 20 MAT. Bare ground and rock cover was 2.2% per m^2 (SE=1.3) 8 MAT and 3.0% per m^2 (SE=1.2) 20 MAT.

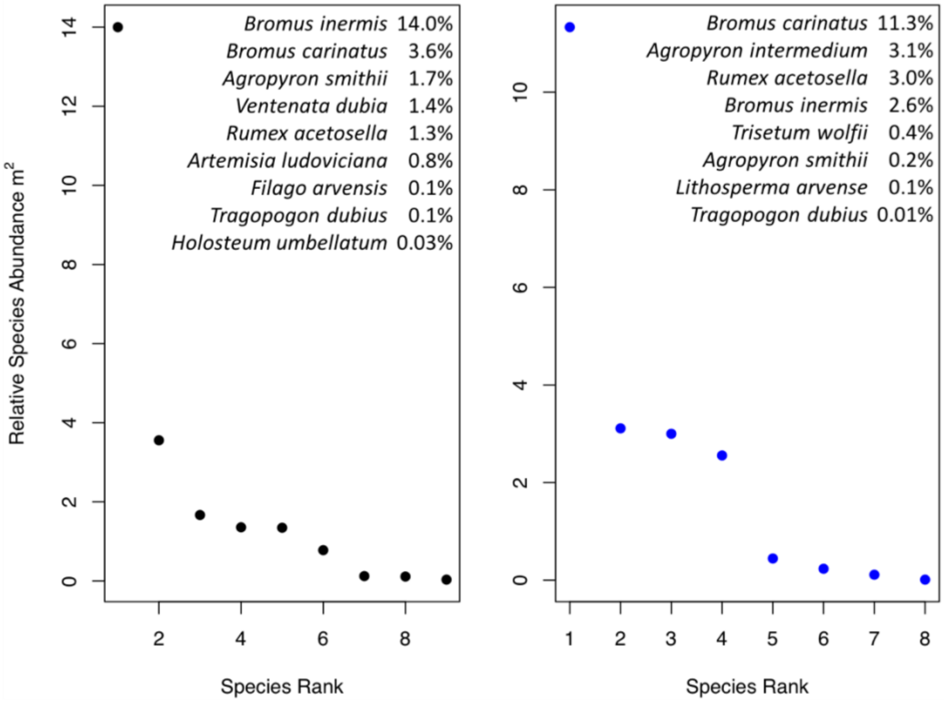

Figure 3.8. Relative species abundance (RSA, % per $1m^2$) after indaziflam plus propoxycarbazone-sodium treatment, 8 (left panel) and 20 (right panel) months after treatment. Each circle represents a species with its respective abundance (RSA). Species are listed in descending order.

In the indaziflam plus rimsulfuron treatment, perennial *Bromus* species were the most abundant at about 27% per m^2 8 MAT and 17.5% 20 MAT (Figure 3.9). *Agropyron* species decreased from 1.2% 8 MAT to 0.2% per m^2 20 MAT. *Ventenata dubia* was not found 8 MAT, but it was found in low abundance (0.01% per m^2) 20 MAT. *Buchloe dactyloides, A. ludoviciana,* and *T. dubius* were not found 20 MAT in spite of being present 8 MAT. The two perennial forbs, *A. millefolium* and *A. ludoviciana*, were found 8

MAT (1.6 per m^2) but not found again 20 MAT. Annual forb cover increased from trace amounts at 0.2% per m^2 8 MAT to 2.6% 20 MAT. Bare ground and rock cover was 3.1% per m^2 (SE=3.1) 8 MAT and 4.9% per m^2 (SE=1.2) 20 MAT.

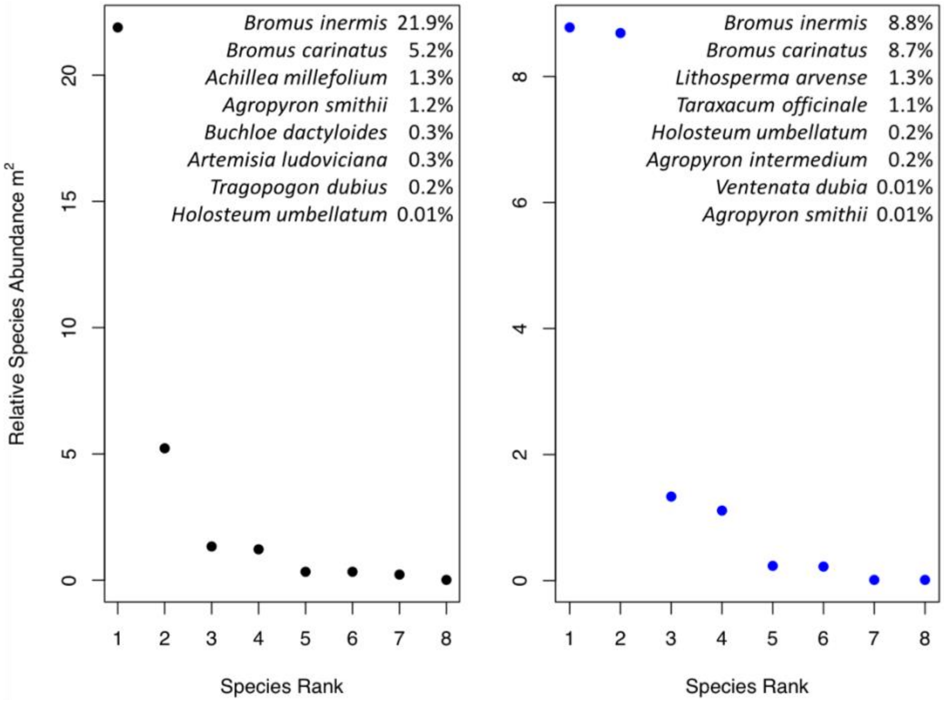

Figure 3.9. Relative species abundance (RSA, % per $1m^2$) after indaziflam plus rimsulfuron treatment, 8 (left panel) and 20 (right panel) months after treatment. Each circle represents a species with its respective abundance (RSA). Species are listed in descending order.

Eight MAT the indaziflam plus imazapic treatment saw perennial *Bromus* species as the most dominant at about 24%, followed by *A. smithii* at 4.0% per m^2 (Figure 3.10). Twenty MAT perennial *Bromus* species decreased to 4.2%. *Agropyron smithii* was third most abundant 8 MAT (4.0% per m^2) and became the most abundant 20 MAT (3.4% per m^2). Perennial forbs covered about 3.5% 8 MAT and decreased to 2.1% per m^2 20 MAT. In spite of the decrease in perennial forbs, one new species, *Zigadenus venenosus*, was found in trace amounts (0.02% per m^2) 20 MAT. Three annual forbs accounted for about 3.0% cover 8 MAT, and 20 MAT 6 species were found that accounted for 3.4% per m^2. *Ventenata dubia* (0.4%) and *B. japonicus* (0.01%) were only found in low abundances 8 MAT. Bare ground and rock cover was 0.7% per m^2 (SE=0.5) 8 MAT and 5.1% per m^2 (SE=2.8) 20 MAT.

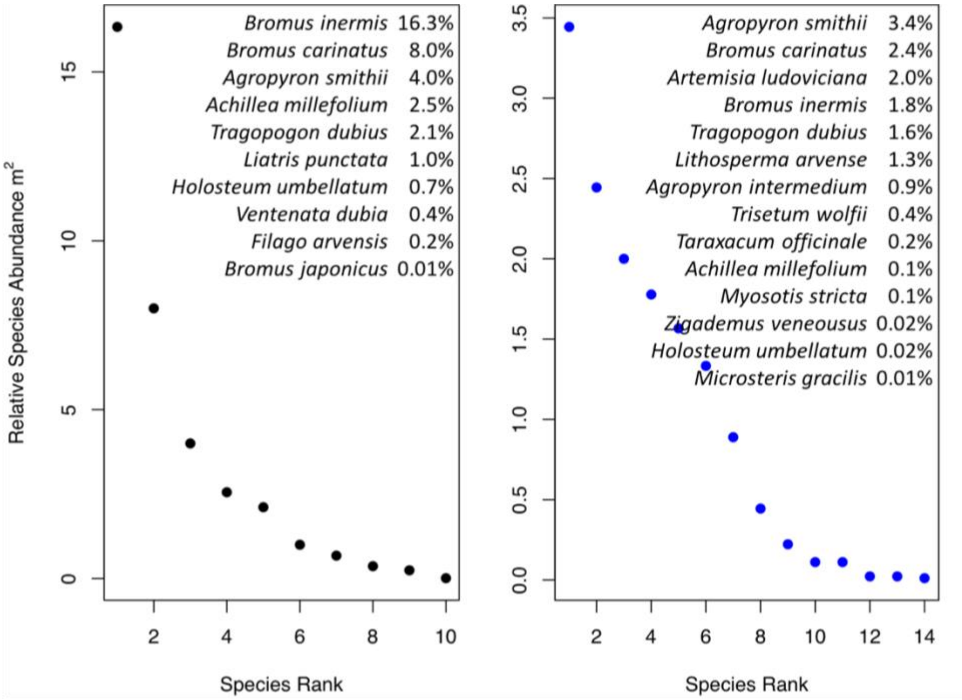

Figure 3.10. Relative species abundance (RSA, % per 1m^2) after indaziflam plus imazapic treatment, 8 (left panel) and 20 (right panel) months after treatment. Each circle represents a species with its respective abundance (RSA). Species are listed in descending order.

The indaziflam plus glyphosate treatment increased in number of species and relative abundances between 8 and 20 MAT (Figure 3.11). *Bromus inermis* was the most abundant over that time at 12.6% and 9.8% per m^2, respectively. *Achillea millefolium* was the second most abundant 8 MAT (7.6% per m^2) and third most abundant (1.7% per m^2) 20 MAT. Eight MAT *H. umbellatum* and *F. arvensis* were third and fourth most abundant, both at 3.1%; neither of these species were found 20 MAT. A different group of annual forbs were present 8 MAT compared to 20 MAT and covered about 1.7% per m^2. *Ventenata dubia* decreased from 1.3% 8 MAT to 0.1% per m^2 20 MAT. There was an increase of perennial forbs from 2 species (8.5% per m^2) to 6 species (3% per m^2) over the course of the study. Bare ground and rock cover was absent 8 MAT but increased to 29.8% per m^2 (SE=9.0) 20 MAT.

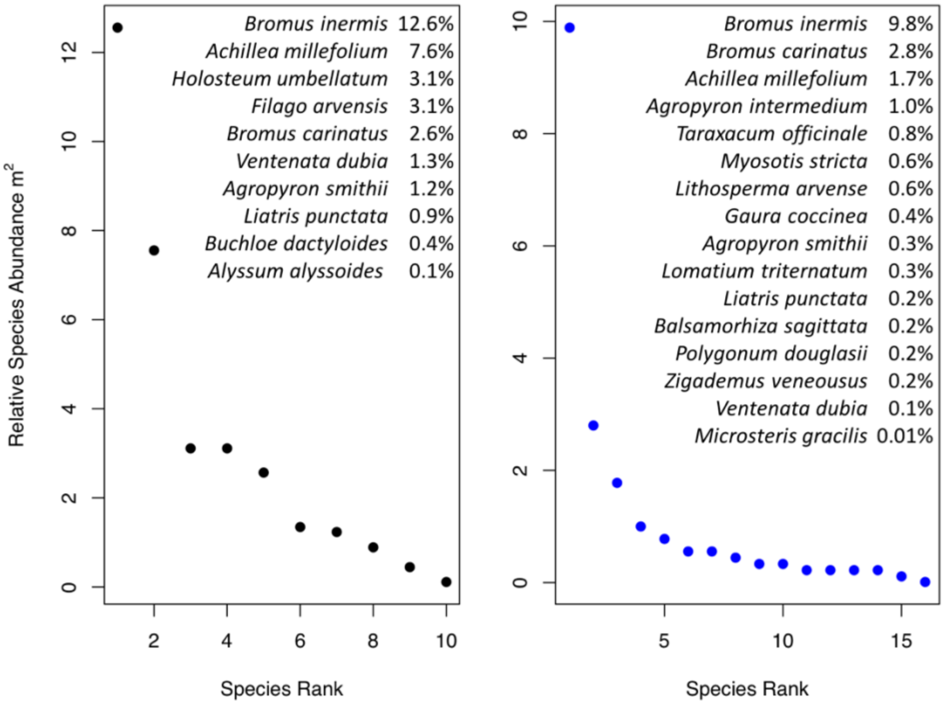

Figure 3.11. Relative species abundance (RSA, % per $1m^2$) after indaziflam plus glyphosate treatment, 8 (left panel) and 20 (right panel) months after treatment. Each circle represents a species with its respective abundance (RSA). Species are listed in descending order.

Discussion

All indaziflam treatments provided the highest and most persistent control of *V. dubia* at 8, 11, 20, and 23 months after treatment. Combination treatments had the highest control (89 – 100%) and to a varying extent, the indaziflam alone treatment also remained one of the most effective (68 – 98%) throughout the duration of the study.

Assuming the cohort of *V. dubia* seedlings at 23 months would be indicative of control ratings summer 2019 (approximately 32 months after treatment), treatments containing indaziflam may provide a third year of *V. dubia* control at my study site in southwestern Montana. At species-level assessments, indaziflam plus propoxycarbazone-sodium and indaziflam plus imazapic were the only treatments to have no annual grasses found 20 MAT, though negligible amounts of *V. dubia* seedlings were observed in these treatments at 23 months after treatment during visual control ratings. Propoxycarbazone-sodium, rimsulfuron, and imazapic treatments all tended to decrease in effectiveness over the course of the study, which was contrary to findings by Wallace & Prather (2016) where these same herbicides were applied at early post-emergent growth stage for *V. dubia* in a *B. inermis* field in Idaho. In their study, these same herbicides provided at least 82% control 9 MAT, and *V. dubia* cover was 14 – 21% at 21 MAT. In my study rimsulfuron increased in *V. dubia* cover 20 MAT, and at 23 months after treatment, was one of the treatments with the lowest control ratings. The most obvious ineffective treatment was glyphosate, which demonstrated no control for all months of evaluation and the highest amount of *V. dubia* biomass across all treatments 20 MAT.

Overall there was an increase in species richness, which was not the case in another study (D. Sebastian, J. Sebastian, et al., 2016). However, my species richness findings are in line with more recent studies by Sebastian et al. (2017) where indaziflam was applied at 102 g a.i. g per hectare in a *B. tectorum* infested field in northern Colorado. In that study species richness increased after 24 MAT, particularly with perennial grasses and annual forbs. Similar changes in plant community diversity (i.e.

increases in Simpson’s diversity and species abundance) from one year to the next coincide with my findings. However, in my study, the increase in number of perennial grass species did not parallel the overall reduction of perennial grass abundance (e.g. cover) relative to other functional groups across all indaziflam treatments. This finding was not unique to indaziflam, where in general, we found any decrease in perennial grass and *V. dubia* abundance resulted in a notable increase of annual forbs abundance. For instance, in the rimsulfuron only treatment, overall perennial grass abundance decreased by 7.0%, *V. dubia* decreased by 1.6%, and annual forb species increased by 6.8%. The non-sprayed treatment also had similar patterns in plant community composition, which suggests herbicide treatments alone do not solely impact succession.

Two distinct patterns of succession and plant injury emerged for the two treatments with no *V. dubia* at 20 months after treatment (indaziflam plus propoxycarbazone-sodium and indaziflam plus imazapic). First, indaziflam plus propoxycarbazone-sodium treatments had limited colonization by annual forbs, and perennial grass abundance was maintained over two growing seasons. In the indaziflam plus imazapic treatment, annual forb abundance was maintained while perennial grasses decreased by 19%. Perennial grass injury was likely due to imazapic application for the latter treatment, as the imazapic only treatment also had a significant reduction in perennial grass abundance. Imazapic labeling (“Plateau®” 2011) describes potential season-long suppression to *Bromus* and *Agropyron* species when applied fall post-emergent at high application rates ranging from 105.0 – 210.0 g a.i./hectare (my study used 122.7 g a.i./hectare). The pattern of *Bromus* species injury by imazapic is also consistent with previous findings by Wallace & Prather (2016) where more injury was observed by imazapic than propoxycarbazone-sodium and rimsulfuron.

Contrary to my prediction that non-target plant injury would be most evident for perennial grasses, there was no treatment effect on perennial grass biomass at 20 months after treatment. This finding does not imply there were no changes in perennial grass abundance, which was evident in species-level assessments and previously highlighted by indaziflam plus propoxycarbazone-sodium and indaziflam plus imazapic injury patterns. In fact, it appeared imazapic (29% reduction) and indaziflam (13.9% reduction) treatments had the most perennial grass injury, in terms of relative species abundance, from 8 to 20 months after treatment. This is in comparison to other single herbicide applications of propoxycarbazone-sodium at 2.6% reduction, rimsulfuron at 7% reduction, and glyphosate at 3.9% reduction. Indaziflam plus rimsulfuron (10% reduction) may also have experienced perennial grass injury, though it is difficult to discern indaziflam-related injury in combination treatments.

Inter-annual variability in *V. dubia* abundance is not uncommon (Wallace & Prather, 2016) and, in addition to treatments, may explain the overall reduction in *V. dubia* cover, including changes in the plant community in the non-sprayed treatments from 8 to 20 MAT. Non-native annual grass abundance can be strongly influenced by precipitation and temperature (Bradley et al., 2018; Bradley & Mustard, 2005; Clinton et al., 2010). At this site, spring (March – May) 2018 was wetter and cooler than spring 2017 (NOAA, 2018a). Comparatively, the non-sprayed treatment had 12 more species 20 MAT. This may coincide with the significantly higher precipitation in June 2018 (83.1

mm) than the previous year (40.1 mm) and may explain the flush of annual forbs and overall increase in number of species (NOAA, 2018a). This indicates that plant community changes are not only due to treatments, but climate and treatment interactions as previously stated. Additionally, imazapic herbicide trials targeting non-native annual grasses have also shown inter-annual variability related to site-specific temperature and precipitation events in Montana (Ehlert, Engel, & Mangold, 2015; Orloff, Mangold, & Menalled, 2015).

No detrimental effect of treatments was found for annual and perennial forb biomass, and instead increases in trace coverage and number of species were apparent 20 MAT. The complex nature of a cellulose biosynthesis inhibiting herbicide makes it difficult to pinpoint the exact mode of action on monocot and dicot cellulose synthesis, but indaziflam is known to act more on monocots (Brabham et al., 2014; Sebastian, Fleming, et al., 2017). In this study, we found no evidence of overall species decline (richness, diversity, and relative species abundance) typical of non-selective herbicides. There is limited knowledge of the effects to targeted monocot and dicot proteins by cellulose synthesizers in other field tolerance studies (Sebastian, Fleming, et al., 2017), though I found no strong evidence of non-crop species decline. However, more investigation of non-crop species tolerances are needed.

Ventenata dubia management and the restoration of range and wildlands depend highly on the long-term integrated use of chemical and cultural tactics, like grazing, prescribed burning, or revegetation. In this study, I showed indaziflam can be an effective tool for land managers needing two, and possibly three, years of invasive annual grass control. This is encouraging since *V. dubia* seeds are viable about 4 years (Wallace et al., 2015a). Sequential applications of indaziflam, 2 or 3 times after initial treatment, have been recommended to have substantial impact on the seed bank over several years (Sebastian, Fleming, et al., 2017). Our findings indicate indaziflam plus propoxycarbazone-sodium or indaziflam plus imazapic applications can provide the best multi-year control, with the caveat that community assemblage varies in conjunction with other factors, such as climate, for each herbicide. Use of indaziflam needs to consider plant community shifts which were prevalent in all treatments at 20 MAT. Land managers may find success with indaziflam applications to reduce *V. dubia* coverage and in combination treatments, maintain perennial grass abundance or facilitate the succession of annual and perennial forbs during wet years.

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CHAPTER FOUR

EFFECT OF SEEDING DATE OF *PSEUDOROEGNERIA SPICATA* (BLUEBUNCH WHEATGRASS) ON ESTABLISHMENT AND SUBSEQUENT ABILITY TO RESIST INVASION BY *BROMUS TECTORUM* (CHEATGRASS)

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CHAPTER FOUR

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Introduction

Degraded range and wildlands are difficult to revegetate due the persistence of annual grasses and secondary invasion that occurs when target invaders are controlled (Pearson, Ortega, Runyon, & Butler, 2016; Schantz, Sheley, James, & Hamerlynck, 2016). In habitats dominated by invasive annual grasses, seedlings of these species can outcompete native perennial grass seedlings due to advantages on spatial and temporal scales (Wainwright, Wolkovich, & Cleland, 2012). Earlier germination and emergence by invasive annual grasses compared to native plants allows for primary access to water and nutrient resources (Dickson, Hopwood, & Wilsey, 2012; Mangla, Sheley, James, & Radosevich, 2011b). These benefits are amplified after germination and emergence because invasive plants grow faster than native plants, thus have primary and ample use of local resources (Grotkopp & Rejmánek, 2007; James, 2008a; James & Drenovsky, 2007). Being the first to fill a vacant ecological niche is known as a priority effect (Wainwright et al., 2012). The seed banks of weed-infested lands are often dominated by invasive plants, minimizing the recruitment of native plants. Therefore, the direct planting of native seeds can be used to offset this disadvantage and re-establish a more diverse plant community.

Strategically seeding native plants to overcome the priority effects of invasive annual grasses during revegetation, used in combination with integrated weed control methods, can be an ecologically-based management tool for improving native species recruitment and establishment (Farrell & Fehmi, 2018; James, Drenovsky, Monaco, & Rinella, 2011). For example, in a greenhouse setting, the native grass *Pseudoroegneria spicata* (bluebunch wheatgrass) suppressed the invasive annual grass *Bromus tectorum* (cheatgrass or downy brome) when seeded four weeks prior to seeding of *B. tectorum* (Larson et al., 2018; Orloff, Mangold, & Menalled, 2013). Similar studies also support the effectiveness of seeding early to improve native grass establishment over invasive annual plants (Boyd & James, 2013; Grman & Suding, 2010). However, the success of native grass establishment from fall versus spring seeding remains largely unknown in a field setting and in relation to overcoming weed infestations over multiple years.

Secondary invasion, or re-invasion, by target and non-target species can have substantial impacts on community assembly when biotic and abiotic influences, like wildlife and livestock foraging and seasonal precipitation, diminish the local seed environment and reduce native species recruitment (Mangla et al., 2011b; Young, Zefferman, Vaughn, & Fick, 2015). In addition, natural seed availability, survival, and dispersal strongly influences the realized niche of annual and perennial native species (Schantz, Sheley, & James, 2015). During invasion or restoration, the realized niche specifies appropriate conditions for germination and establishment of native plants in the presence of invasive plants (Satterthwaite, 2007; Schantz et al., 2016). Direct seeding can alleviate limitations associated with these natural conditions particularly when knowing the appropriate time to seed during revegetation to maximize establishment. Priority effects can be granted to seeded species particularly during secondary invasion where competition with non-target species is likely (Pearson et al., 2016).

During revegetation of invasive plant-infested areas, seeding of native perennial grasses like *P. spicata* often follows a summer or fall herbicide application aimed at controlling the target invasive plant. The seeds are expected to remain dormant throughout winter and emerge in the spring at the earliest opportune time (Boyd & James, 2013), however unanticipated germination can put seedlings at risk of failure during winter freeze-thaw cycles (James, Rinella, & Svejcar, 2012). Failure can also result due to the slow growing nature of native perennial grasses that do not typically reach reproductive maturity in the first growing season, in contrast to quickly growing invasive annual grasses that complete their life cycle in less than a year (Schantz et al., 2016). Though fall dormant seedings are common practice, they eliminate the option of a spring herbicide application to control spring-emerging invasive plants because such an application would also injure seedlings of seeded species.

Delaying seeding until spring as an alternative to seeding in the fall has demonstrated limited success in terms of biomass and density of perennial grasses (Schantz et al., 2015, 2016). Particularly, with the addition of water during the first growing season and low annual grass propagule pressure (between 150 – 1500 seeds per m^2), perennial grasses were able to effectively establish within an annual-grass dominated system (Schantz et al., 2016). In semi-arid climates, however, delaying seeding until spring can be risky. Seedlings emerge but may not obtain enough size, particularly root length, to survive seasonal drought (Schantz et al., 2016). Addressing how late in the spring seeding can occur while still resulting in sufficient native perennial grass establishment is necessary to improve revegetation of invasive plant-infested range and wildland.

The first objective of this study was to examine whether fall or early to late spring seeding resulted in the best establishment of the native perennial grass *P. spicata* over a two-year period. Consistent with previous studies, I hypothesized perennial grass density to be highest for fall and early spring-seeded cohorts when compared to late spring-seeded cohorts (Boyd & James, 2013; Boyd & Lemos, 2015). The second objective addressed secondary invasion and native-invasive plant competition dynamics in the second year of *P. spicata* growth. Specifically, this objective aimed to determine if *P. spicata* seeding date affected the suppression of the invasive annual grass *B. tectorum*. I hypothesized *B. tectorum* biomass and density would be lowest where *P. spicata* was seeded in fall and early spring, when compared to late spring seeding, due to the potentially more biomass and tillers of *P. spicata* plants in the first growing season.

Methods

Two field sites were located at the Arthur H. Post Research Farm (hereafter referred to as Post Farm) and Fort Ellis Research Farm (hereafter referred to as Fort Ellis) near Bozeman, Montana, at 45°40'38.01"N 111° 9'19.49"W and 45°40'13.19"N 110°58'48.13"W, respectively. Elevation at Post Farm and Fort Ellis are 1,450 m and

1,484 m, respectively. At Post Farm, average 2016 and 2017 spring (March – May) precipitation and minimum/maximum temperatures were 4.22 cm and 1.3 °C/14.6 °C (NOAA, 2018b). Average 2016 and 2017 summer (June – August) precipitation and minimum/maximum temperatures were 2.1 cm and 9.9 °C/27.9 °C (NOAA, 2018b). At Fort Ellis, average 2016 and 2017 spring precipitation and minimum/maximum temperatures were 6.76 cm and 1.0 °C/ 12.9 °C (Weather Underground, 2018). Average 2016 and 2017 summer precipitation and minimum/maximum temperatures were 3.81 cm and 10.0 °C/26.7 °C (Weather Underground, 2018).

Prior to setting up the study, existing vegetation was manually removed and fields were tilled to remove competition. A completely randomized split-plot design was used to test eight seeding dates of *P. spicata* (main plots, 1 m x 2 m with 0.5 m buffer lanes between main plots) and two levels (absent and present) of *B. tectorum* competition (split-plots, 1 m x 1 m). In total, seeding treatments were replicated four times at each site for a total of 32 main plots and 64 split-plots per site (Figure 4.1).

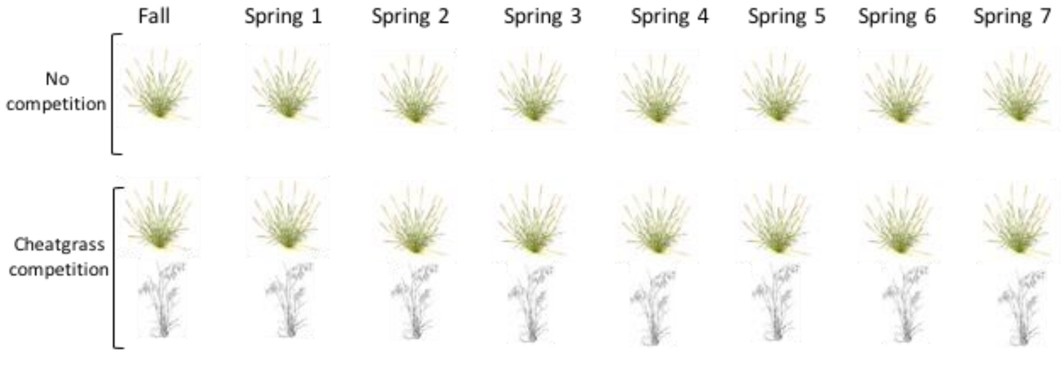

Figure 4.1. Visual representation of study design with different seeding dates of *Pseudoroegneria spicata* as main plots and level of competition with *Bromus tectorum* as sub-plots. Each treatment combination was replicated four times at two sites (n=64).

The eight seeding date treatments were 8 November 2015 (fall) and seven weekly spring seeding dates from 1 April 2016 to 12 May 2016 (early to late spring, Table 4.1). Seeds of *P. spicata* (Goldar cultivar) were hand broadcasted evenly on the soil surface at 667 seeds per m^2 (following Orloff et al. 2013) for each treatment at each site. Seeds were obtained from Bruce Seed Farm near Townsend, Montana, approximate 100 km from the study sites. To minimize the risk of stand failure throughout the first year of the study, supplemental irrigation was applied, as needed, to mimic 30-year mean precipitation (Western Regional Climate Center) for Post Farm. However, supplemental irrigation was only necessary twice at both sites on 21 – 22 June 2016 and 30 June 2016 – 1 July 2016, when the equivalent of 1.27 cm of precipitation per split-plot was applied by hand using watering cans. Non-target species were manually removed to ensure only target species were growing in plots and buffer strips.

Table 4.1. Seeding dates for *Pseudoroegneria spicata.*

Treatment	Seeding Date
Fall and Control	November 11, 2015
Spring 1 (S1)	April 1, 2016
Spring 2 (S2)	April 7, 2016
Spring 3 (S3)	April 13, 2016
Spring 4 (S4)	April 21, 2016
Spring 5 (S5)	April 29, 2016
Spring 6 (S6)	May 5, 2016
Spring 7 (S7)	May 12, 2016

The emergence of *P. spicata* was measured weekly as soon as seedlings were observed (early April 2016) and continued for 12 weeks until late June 2016. In September 2016, after the first growing season, *P. spicata* density (tillers per m^2) were measured within no competition and competition subplots.

For the second year investigating competition dynamics, *B. tectorum* seeds were sown to mimic natural seed rain in fall 2016. *Bromus tectorum* seeds were collected from various sites near Bozeman, Montana, in summer 2015. Prior to seeding, seed germination was determined in the lab over a 14-day period. *Bromus tectorum* was seeded into competition plots on 1 September 2016 at 1,112 seeds per m^2 (following Orloff et al. 2013). Non-target species were removed throughout the second growing season up until data were collected from 23 June 2017 – 10 July 2017. Three randomly-placed 50 cm x 20 cm Daubenmire frames per split-plot were used to sample density (tillers per 0.3 m^2) and aboveground biomass (g per 0.3 m^2) of *P. spicata* and *B. tectorum*. Biomass was clipped to 2 cm above ground level, dried at 37 °C for 48 hours, and weighed to the nearest 0.1 gram.

For objective one, an analysis of variance (ANOVA) was used on a log-linear model to analyze differences in *P. spicata* density (tillers per m^2) by seeding group for each site. Data were over-dispersed so a Quasi-Poisson distribution was used. One replication of the Spring 5 seeding data at Post Farm were removed from analysis because the plots were accidentally irrigated and produced abnormally high *P. spicata* densities. In the first year, *P. spicata* density across main plots (1 m x 2 m, n=12) were used to determine establishment for all cohorts. In the second year, *P. spicata* density from the no competition plots were used to determine second-year establishment for all seeding treatments. Tukey pairwise comparisons were used to determine differences across seeding groups for each site.

For objective two, tillers and biomass (per 0.3 m^2) data from the second-year were scaled up to full 1 m^2 subplots for graphical interpretations, but were analyzed on their original scale. When analyzing *P. spicata* density and biomass, an ANOVA was used on a linear mixed effects model to account for plot-to-plot variation, where fixed effects were seeding treatments, competition treatments, and sites. When analyzing *B. tectorum* density, an ANOVA was used with a general linear model to determine seeding date treatment effects across sites. Data were over-dispersed so a Quasi-Poisson distribution was used. When analyzing *B. tectorum* biomass, an ANOVA was used on a linear model to determine seeding date treatment effects across sites. Tukey pairwise comparisons were used to determine differences between seeding groups and competition levels (no competition versus *B. tectorum* competition). For all analyses, parsimonious models were used and explored for violations of normality, independence, and constant variance assumptions. Graphical interpretations and analyses were conducted using R Software 3.5.1, specifically dplyr, lme4, emmeans, ggplot2 packages (Bates et al., 2015; Lenth et al., 2018; R Core Team, 2018; Wickham, 2016; Wickham et al., 2018).

Results

Pseudoroegneria spicata Density and Biomass

After one growing season, seeding treatments affected *P. spicata* density across both sites (p=0.011, Table 4.2). At Fort Ellis, Spring 2 resulted in 1,180 tillers per m^2 (SE=168.5), which was similar to Fall (1,009 tillers per m^2, SE=176.4), Spring 1 (1,038 tillers per m^2, SE=121.7), Spring 3 (856.1 tillers per m^2, SE=179.6), and Spring 5 (829 tillers per m^2, SE=222.9) (Figure 2). Spring 4, Spring 6, and Spring 7 had similar responses and resulted in the lowest densities at 472 tillers per m^2 (SE=71.5), 561 tillers per m^2 (SE=133.8), and 349 tillers per m^2 (SE=62.9), respectively.

Table 4.2. Analysis of variance (ANOVA) table for *Pseudoroegneria spicata* density (tillers per m^2) in 2016. Bold numbers are significant at α=0.05.

Main Effects and Interaction	Density		
	df	*F-Value*	*p-Value*
Seeding	7,188	5.444	**<0.001**
Site	1,117	57.35	**<0.001**
Seeding*Site	7,110	2.759	**0.011**

At the Post Farm, no pairwise differences were found across seeding groups. Densities ranged from 1,706 tillers per m^2 (SE=206.9) in Spring 1 to 1,054 tillers per m^2 (SE=47.0) in Spring 4.

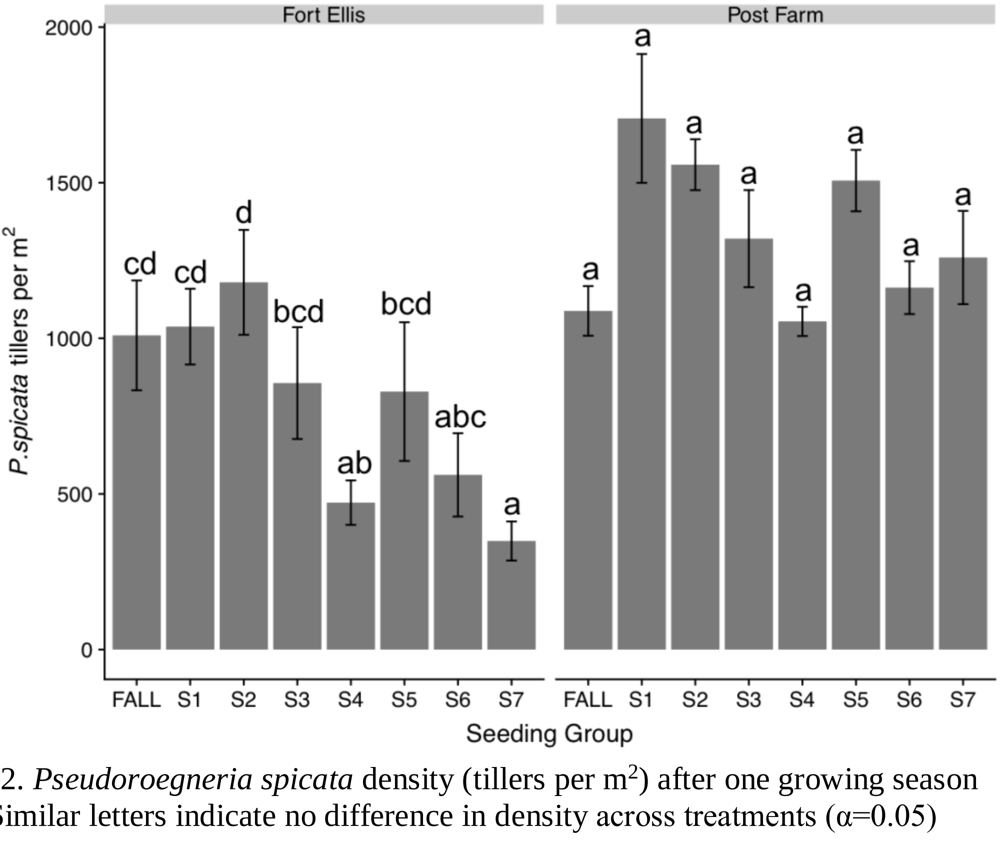

Figure 4.2. *Pseudoroegneria spicata* density (tillers per m^2) after one growing season (2016). Similar letters indicate no difference in density across treatments (α=0.05)

After two growing seasons, density ($p=0.005$) and biomass ($p=0.030$) of *P. spicata* was affected by competition treatments, and the effect varied by site ($p<0.05$) (Table 4.3). Density ($p=0.010$) and biomass ($p=0.005$) were also different across seeding treatments (Table 4.3). There was no effect of seeding across competition treatments for density ($p=0.218$) and biomass ($p=0.301$) (Table 4.3).

Table 4.3. Analysis of variance (ANOVA) table for *Pseudoroegneria spicata* density (tillers per m^2) and biomass (g per m^2) in 2017. Bold numbers are significant at $\alpha=0.05$.

Main Effects and Interactions	*df*	Density		Biomass	
		F-Value	*p-Value*	*F-Value*	*p-Value*
Seeding	7,54	2.994	**0.010**	3.297	**0.005**
Competition	1,54	8.706	**0.005**	5.139	**0.030**
Site	1,54	7.832	**0.007**	35.50	**<0.001**
Seeding*Competition	7,54	1.416	0.218	1.234	0.301
Competition*Site	1,54	23.63	**<0.001**	9.731	**0.003**

At Fort Ellis no competition treatments (control) yielded higher density of *P. spicata* (1,735 tillers per m^2, SE=122) than all *B. tectorum* competition treatments (1,161 tillers per m^2, SE=107) (Table 4.4). No differences were found across competition treatments at Post Farm. Across sites, Post Farm yielded higher density (1,748 per m^2, SE=55) as compared to Fort Ellis (1,448 tillers per m^2, SE=88).

Table 4.4. Mean *Pseudoroegneria spicata* density (tillers per m^2 ± SE) across competition treatments at each site in 2017.

Competition Treatment	Site	
	Post Farm	Fort Ellis
No competition	1,671 ± 75 a	1,735 ± 122 a
B. tectorum competition	1,825 ± 80 a	1,161 ± 107 b

Similar letters indicate no difference in density between competition treatments within a site ($\alpha=0.05$).

Averaged across both sites, density of *P. spicata* was similar across most seeding treatments and ranged between 1,988 tillers per m^2 (SE=145) and 1,414 tillers per m^2 (SE=150) (Table 4.5). The only exception to this was Spring 7, which resulted in 1,221 tillers per m^2 (SE=158); this was lower than Spring 2 and Spring 1, but similar to the other seeding treatments.

Table 4.5. Mean *Pseudoroegneria spicata* density (tillers per m^2 ± SE) across seeding treatments.

Seeding Treatment	*P. spicata* density	
Fall	1,687 ± 163	ab
Spring 1	1,988 ± 145	b
Spring 2	1,895 ± 110	b
Spring 3	1,635 ± 117	ab
Spring 4	1,415 ± 150	ab
Spring 5	1,427 ± 171	ab
Spring 6	1,475 ± 127	ab
Spring 7	1,221 ± 158	a

Similar letters indicate no difference in biomass across treatments (α=0.05)

With regard to biomass, there was a site effect ($p<0.001$); at Fort Ellis, no competition treatments yielded higher *P. spicata* biomass (686.8 g per m^2, SE=57.2) than *B. tectorum* competition treatments (455.1 g per m^2, SE=51.8) (Table 4.6). No pairwise differences were found across competition treatments at Post Farm. Across sites, Post Farm yielded more biomass (859.4 g per m^2, SE=31.2) as compared to Fort Ellis (570.9 g per m^2, SE=41.0).

Table 4.6. Mean *Pseudoroegneria spicata* biomass (g per m^2 ± SE) across competition treatments at each site.

Competition Treatment	Site	
	Post Farm	Fort Ellis
No competition	837 ± 44.7 a	687 ± 57.2 a
B. tectorum competition	881 ± 43.8 a	455 ± 51.8 b

Similar letters indicate no difference in biomass between competition treatments within a site (α=0.05)

When looking at the effect of seeding treatment averaged across both sites, *P. spicata* biomass was similar across most seeding treatments and ranged between 887.6 g per m^2 (SE=77.9) and 550.6 g per m^2 (SE=88.9) (Table 4.7). The only exception to this was Spring 7 and Spring 4, which resulted in 559.6 g per m^2 (SE=88.9) and 578.6 g per m^2 (SE=74.6), respectively; this was lower than Fall, but similar to the other seeding treatments.

Table 4.7. Mean *Pseudoroegneria spicata* biomass (g per m^2 ± SE) across seeding treatments.

Seeding Treatment	*P. spicata* biomass
Fall	887.6 ± 77.9 b
Spring 1	845.4 ± 90.0 ab
Spring 2	828.2 ± 73.6 ab
Spring 3	707.4 ± 58.3 ab
Spring 4	578.6 ± 74.6 a
Spring 5	608.6 ± 84.8 ab
Spring 6	674.6 ± 80.2 ab
Spring 7	559.6 ± 88.9 a

Similar letters indicate no difference in biomass across treatments (α=0.05)

Bromus tectorum Density and Biomass

There was a difference in *B. tectorum* density ($p<0.05$) and biomass ($p<0.05$) due to the main effects of seeding treatment and site (Table 8). Fort Ellis had higher density of *B. tectorum* (1019 tillers per m^2, SE=59) than Post Farm (356 tillers per m^2, SE=29)

(Table 4.8). Averaged across sites, *Bromus tectorum* density was similar across most seeding dates and ranged from 943 tillers per m^2 (SE=188) to 553 tillers per m^2 (SE=88.0), except for Spring 2 (480 tillers per m^2, SE=101) which was lower than Spring 7 (Table 4.9).

Table 4.8. Analysis of variance (ANOVA) table for *Bromus tectorum* density (tillers per m^2) and biomass (g per m^2) in 2017. Bold numbers are significant at α=0.05.

Main Effects and Interaction	Density			Biomass		
	df	*F-Value*	*p-Value*	*df*	*F-Value*	*p-Value*
Seeding	7,55	4.163	**<0.001**	7,54	3.027	**0.009**
Site	1,54	160.4	**<0.001**	1,54	428.3	**<0.001**

Fort Ellis had higher *B. tectorum* biomass (635.9 g per m^2, SE=53.4) than Post Farm (26.3 g per m^2, SE=6.0) (Table 4.8). Averaged across sites, *B. tectorum* biomass was similar across most treatments ranging from 532.9 g per m^2 (SE=206.3) to 226.6 g per m^2 (SE=80.70). The only exception was Fall which was lower than Spring 7 (Table 4.9).

Table 4.9. Mean *Bromus tectorum* density (tillers per m^2 ± SE) and biomass (g per m^2) across seeding treatments in 2017.

Seeding Treatment	Density	Biomass
Fall	553 ± 88.0 ab	226.6 ± 80.70 a
Spring 1	655 ± 172 abc	254.3 ± 105.3 ab
Spring 2	480 ± 101 a	236.9 ± 120.6 ab
Spring 3	624 ± 161 abc	324.1 ± 127.0 ab
Spring 4	819 ± 177 bc	425.8 ± 154.1 ab
Spring 5	647 ± 159 abc	377.8 ± 154.9 ab
Spring 6	816 ± 122 bc	314.1 ± 108.9 ab
Spring 7	943 ± 188 c	532.9 ± 206.3 b

Similar letters indicate no difference in density or biomass across seeding treatments (α=0.05)

Discussion

My study indicates that fall (i.e. November) or early spring (i.e. April) seeding results in acceptable establishment of bluebunch wheatgrass after one and two growing seasons. Five plants per m^2 is often the restoration goal in semi-arid grasslands (Boyd & James, 2013; Rinella & James, 2017); in fall 2016 the minimum number of *P. spicata* plants per m^2 in this study was about 10 at Fort Ellis and 7 at Post Farm, which was also the minimum density across seeding groups. These results are consistent with my first hypothesis and previous studies that indicate fall and early spring seeding will produce larger perennial grasses than late spring seeding dates (Boyd & Lemos, 2015; James et al., 2012). It should be noted, however, that these results are limited to one cultivar of *P. spicata*, and other native grasses may differ in optimal seeding time. Of the recommended USDA cultivars, ‘Goldar,’ which was used in this study, is best known for its rapid growth under dry conditions at or above 30.5 cm of annual rainfall (USDA-NRCS, 2012). Established *P. spicata* are also expected to be highly competitive against secondary invasion (USDA-NRCS, 2012).

Furthermore, my study took place in fallow fields and establishment of seeded native perennial grasses may differ in more natural settings, including degraded rangeland, where seeded grasses may have to compete with weedy species at the seedling stage. In natural settings environmental stressors, such as wildlife foraging and drought, can also diminish the local seed environment by reducing seedling recruitment of native plants (Johnson, Vavra, Parks, & Willis, 2013). Despite these limitations, this study supports that land managers can continue to use direct seeding during the fall or delay seeding to early spring for effective native grass establishment. If seeding is delayed until spring, seeding after the first week of May is not recommended as it could result in decreased establishment.

My second hypothesis was also supported, where I expected *B. tectorum* biomass and density to be lowest where *P. spicata* was highest in fall and early spring treatments. In particular, the high density of *P. spicata* in the Spring 2 treatment (i.e. seeded second week of April) had the greatest competitive effect on *B. tectorum* density; and *P. spicata* biomass was greatest in the Fall seeding which subsequently led to lower *B. tectorum* biomass. This study also indicates that seeding after the first week of May is not advised as there was a trend of decreasing *P. spicata* abundance and subsequent increase in *B. tectorum* abundance at the latest spring seeding date. This trend was consistent across sites, suggesting results found here may hold true across multiple locations.

Across both sites there was minimal effect of competition from *B. tectorum* on *P. spicata* once *P. spicata* was well-established (second year of study), which suggests large and robust perennial grasses can limit invasion by annual grasses like *B. tectorum*. My results support those of James et al. (2008) who found that large, productive bunchgrasses were more effective than other functional groups in resisting invasion by the annual grass *Taeniatherum caput-medusae* (medusahead). Wetter conditions at Fort Ellis compared to Post Farm did not have a substantial impact on *P. spicata* establishment and competitive dynamics with *B. tectorum*. However, it should be noted that there was more variability at Fort Ellis in the response of *P. spicata* density to seeding date during the first year of the study, and there was an effect of the competition treatment during the second year of the study. The findings from this study are in line with experimental observations in Oregon where additional watering to fall seeding (Boyd & James, 2013) and spring seeding (James & Svejcar, 2010) of *P. spicata* had no effect on final density and biomass.

Continued practice of fall dormant seeding at the recommended rate (667 seeds per m^2, approximately 17 pounds per acre) (Sheley, Mangold, Goodwin, & Marks, 2008) is supported by my study, even though another study has shown that fall seeded perennial grasses experience more competition with annual grasses than spring-seeded perennial grasses (Schantz et al., 2016). In that study, which took place in eastern Oregon, the threshold for annual grass dominance following fall and spring perennial grass seeding occurred at *B. tectorum* seeding rates comparable to my study (1,500 seeds per m^2) (Schantz et al., 2016). Different seeding densities, which can influence competition between two species (S. Mangla, Sheley, James, & Radosevich, 2011b; S. Mangla, Sheley, James, & Radosevich, 2011), were not tested in this study, but the results lend support to the idea that seeding native grasses like *P. spicata* at high rates (greater than 2,500 seeds per m^2; Schantz, Sheley, & James, 2018) may not be necessary. Instead, promoting priority establishment of *P. spicata* or other perennial grasses may be more a more effective tactic for suppressing non-native annual grasses.

One of the foremost risks to seeding a degraded site with native species is the immediate competition with invasive seedlings (Ray-Mukherjee, Jones, Adler, & Monaco, 2011), which was not a condition in this experimental design. Maintaining or reducing the seed bank to a level that allows native species to establish (less than 1,500 seeds per m^2; Schantz et al., 2016) can prove difficult when natural seed rain of *B. tectorum* can be as high as 12,000 seeds per m^2 (Humphrey & Schupp, 2001). Integrated management tools applied over multiple years or preemergent herbicides with multiple years of annual grass control can reduce the seed bank of invasive annual grasses (Sebastian, Fleming, et al., 2017; Sebastian, Nissen, Sebastian, & Beck, 2017; D. Sebastian, J. Sebastian, et al., 2016). Because early spring seeding provided similar *P. spicata* establishment as fall seeding, spring seeding would allow the application of a non-selective, non-persistent herbicide like glyphosate to control *B. tectorum* seedlings that emerged over the winter and into early spring (Kyser, Creech, Zhang, & DiTomaso, 2012; Kyser, Wilson, Zhang, & Ditomaso, 2013). In summary, the wide range of effective seeding times (fall through early May) found in this study can be integrated with control methods to restore *B. tectorum*-impacted rangeland. This could result in priority effect advantages for perennial grass species that would then reduce competition with invasive seedlings and suppress invasive grasses into the future.

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CHAPTER FIVE

CONCLUSIONS

Summary of Findings and Implications

The overarching goal of this thesis was to provide insight on the biology and ecology of *V. dubia* so that we can continue to develop control strategies for its management in range and wildland habitats. Integrated weed management employs a multi-control approach for long-term management, but biological and ecological research is lacking on the singular and integrated response of management approaches for less common invasive annual grasses. For example, we know mowing and grazing of *V. dubia* is ineffective, even when these options are practical for *B. tectorum* (Fryer, 2017; Harvey & Mangold, 2018). As *V. dubia* is an increasing concern for regions outside the Intermountain Pacific Northwest, there is an increasing need by land managers for a broader range of management options.

The growth chamber study revealed elevated temperature and CO_2 concentrations can potentially affect the growth and competition dynamics between *V. dubia* and *B. tectorum.* I focused on these two species because information is lacking on growth responses by species other than the commonly studied *B. tectorum.* Also, anecdotal evidence indicates *V. dubia* is displacing *B. tectorum*, and it is speculative that the rapid expansion of *V. dubia* over the last decade may be partly attributed to climate change. The first objective was to determine differences in growth for both species under current and elevated conditions. Under elevated conditions, there was an overall decrease in growth by both species compared to current conditions, which was the opposite of what I hypothesized. The decrease in growth could be associated with limits in photosynthesis with excess CO_2. My second hypothesis was supported in which I found *B. tectorum* to have greater growth than *V. dubia* across all climate and competition treatments. The second objective of this study was to determine differences in both species as a response to inter-specific competition. Because I expected *B. tectorum* to have greater growth, I also expected it to exert more competition on *V. dubia*. My hypothesis regarding competition was not fully supported as *B. tectorum* had less growth in the presence of *V. dubia* in elevated inter-specific treatments. Interestingly, there was a general trend of *V. dubia* allocating more growth to its roots across all treatments, and this effect was greatest where *V. dubia* was grown alone under elevated conditions. Another important finding of this study was *V. dubia*'s similar root biomass across current and elevated treatments, indicating this species may have more plasticity in responding to changing environmental conditions compared to *B. tectorum*. More allocation to root growth across different environmental conditions suggests *V. dubia* may have an advantage over *B. tectorum* in water use efficiency.

My second study, the field-based herbicide efficacy trial, determined a new herbicide mode of action can provide up to three years of control of annual grasses, with potential changes to plant community composition. My objective was to determine the effectiveness of indaziflam and commonly used herbicides on *V. dubia* and plant community responses to each treatment over a 23-month period. It was found that indaziflam can provide up to three years of control as compared to other commonly used herbicides on annual grasses, particularly in combination treatments that address pre- and post-emergent growth. Indaziflam may present an opportunity for longer-term activity on the seed bank of *V. dubia*. The second part of my objective was to determine the effects of herbicide treatments on the plant community composition and address potential injury. Little is known about the effects of indaziflam on non-target species, so this study addressed potential injury and changes to the local plant community. It was found indaziflam caused no substantial reduction in perennial grass, perennial forb, and annual forb biomass across all treatments. Another important finding is that plant community changes do not solely depend on herbicide treatments as indicated by the increase in overall species richness at the site and interannual variability observed in the non-sprayed plots.

The revegetation study determined priority effects can occur with fall and early spring seeding of *P. spicata*, with implications for restoring grasslands impacted by invasive annual grasses like *V. dubia.* The first objective was to determine the effect of fall or spring seeding on the establishment of *P. spicata* after one growing season. It was found that fall (November) and early spring (April) seedings resulted in acceptable establishment of *P. spicata*. Acceptable perennial grass establishment from fall and early spring seedings held true in the second growing season as well. The second objective was to determine if *P. spicata* seeding date affected the suppression of *B. tectorum* during the second growing season. There was minimal effect of competition from *B. tectorum* on *P. spicata* once *P. spicata* was well-established, which suggests large and robust perennial grasses can limit invasion by annual grasses like *B. tectorum*. Land managers appear to have a wide opportunity of seeding (fall to early spring) with the expectation that encouraging perennial grass establishment lessens invasion by annual grasses. In this case, *B. tectorum* was used as a model invasive species, but we expect similar effects of perennial grass establishment in the presence of other invasive annual grasses at locations outside the study area.

The combination of these independent studies aids in increasing our understanding of the biology of *V. dubia* and developing chemical and cultural controls for integrated weed management practices. Our awareness and knowledge of this species is currently limited, and more research is needed on this species. By having a more comprehensive understanding of *V. dubia*, we can use this knowledge to develop a broader range of effective management tools to enhance the control of invasive grasses in range and wildland habitats.

Future Research

More information is need on the biology and ecology of *V. dubia*. There are no known biological controls for this species and expanding this research in this area would add to current management options. In terms of climate change and competition with other species, more research is needed on inter-specific and community level interactions that can change due to elevated conditions. Findings from the growth chamber study reveal growth allocation is much different for *V. dubia* than *B. tectorum*, and more knowledge is needed on how nutrient absorption changes the overall growth of invasive annual grasses over a range of densities. Finally, because maintaining native perennial grass stands is arguable one of the most effective ways to limit invasion, more research is need on how to promote the establishment of desired species in disturbed areas. Research could include utilizing indaziflam with seeding of native perennial grasses over several years to look at the pre-emergent herbicide effects on seeding. Overall, additional research is needed on other ways to reduce the seed bank of invasive annual grasses as this allows for more effective establishment of desired species.

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APPENDIX A

CHAPTER THREE SUPPLEMENTAL INFORMATION

List of all species found at the herbicide trial site. Scientific names (Lesica et al. 2012) correspond with four-letter species code, common name, functional group, and species status from the NRCS/USDA Plant Database.

Scientific Name	Species Code	Common Name	Functional Group	Status
Achillea millefolium	ACMI	Yarrow	Perennial forb	Native/Introduced
Agropyron intermedium	AGIN	Intermediate wheatgrass	Perennial grass	Introduced
Agropyron smithii	AGSM	Western wheatgrass	Perennial grass	Native
Alyssum alyssoides	ALAL	Yellow alyssum	Annual/biennial forb	Introduced
Artemisia ludoviciana	ARLU	White sagebrush	Perennial forb	Native/Introduced
Balsamorhiza sagittata	BASA	Arrowhead balsamroot	Perennial forb	Native
Bromus carinatus	BRCA	Mountain brome	Perennial grass	Native
Bromus inermis	BRIN	Smooth brome	Perennial grass	Native/Introduced
Bromus japonicus	BRJA	Japanese brome	Annual grass	Introduced
Bromus tectorum	BRTE	Cheatgrass	Annual grass	Introduced
Buchloe dactyloides	BUDA	Buffalo grass	Perennial grass	Native
Camelina microcarpa	CAMI	Littlepod false flax	Annual/biennial forb	Introduced
Collomia linearis	COLI	Tiny trumpet	Annual forb	Native
Descurainia sophia	DESO	Tansy mustard	Annual/biennial forb	Introduced
Filago arvensis	FIAR	Field fluffweed	Annual forb	Introduced
Gaura coccinea	GACO	Scarlet guara	Perennial forb	Native
Holosteum umbellatum	HOUM	Jagged chickweed	Annual forb	Introduced
Lactuca serriola	LASE	Prickly lettuce	Annual/biennial forb	Introduced
Liatris punctata	LIPU	Dotted blazing star	Perennial forb	Native
Lithospermum arvense	LIAR	Corn-gromwell	Annual forb	Introduced
Lomatium triternatum	LOTR	Nineleaf biscuitroot	Perennial forb	Native
Microsteris gracilis	MIGR	Slender phlox	Annual forb	Native
Myosotis stricta	MYST	Small-flowered forget-me-not	Annual forb	Introduced
Poa secunda	POSE	Sandberg bluegrass	Perennial grass	Native
Polygonum douglasii	PODO	Douglas knotweed	Annual/biennial forb	Native

Pseudoroegneria spicata	PSSP	Bluebunch wheatgrass	Perennial grass	Native
Rumex acetosella	RUAC	Sheep sorrel	Perennial forb	Introduced
Taraxacum officinale	TAOF	Common dandelion	Perennial forb	Introduced
Thlaspi arvense	THAR	Field pennycress	Annual forb	Introduced
Tragopogon dubius	TRDU	Yellow salsify	Annual/biennial forb	Introduced
Trisetum wolfii	TRWO	Wolf's trisetum	Perennial grass	Native
Ventenata dubia	VEDU	Ventenata	Annual grass	Introduced
Veronica verna	VEVE	Spring speedwell	Annual forb	Introduced
Zigadenus venenosus	ZIVE	Meadow death camas	Perennial forb	Native