PEST MANAGEMENT CHALLENGES AND CLIMATE CHANGE IN WATER LIMITED WINTER WHEAT AGROECOSYSTEMS IN SOUTHWESTERN MONTANA

By

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DEDICATION

I dedicate this thesis to where it all started. In 2013 I was hired as an undergraduate research assistant in the Rangeland and Agricultural Weeds Laboratory by Dr. Fabián Menalled. I had emailed many professors, unsure of what I was interested in. I am so grateful that Dr. Menalled was the one who replied and hired me. I feel very fortunate, lucky really, to have been a part of the incredible research, and supportive, loving community that stemmed from the Weed's lab (a.k.a. the Fab Lab) and extended throughout the LRES and PSPP departments. To everyone who helped make this research come to fruition, this is for you.

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TABLE OF CONTENTS

TABLE OF CONTENTS CONTINUED

LIST OF TABLES

Table Page

LIST OF FIGURES

Figure Page

LIST OF FIGURES CONTINUED

Figure Page

LIST OF FIGURES CONTINUED

Figure Page

LIST OF FIGURES CONTINUED

ABSTRACT

Dryland winter wheat production is influenced by many environmental factors including climate, disease, and resource availability. In Montana, *Bromus tectorum* (cheatgrass) and *Fusarium pseudograminearum* (a fungus causing root crown rot) are major winter wheat pests; reducing yield and grain quality. However, little is known how climate change and resource availability impact winter wheat, *B. tectorum*, and *F. pseudograminearum* individually as well as their multi-trophic interactions. Thus, this research aimed to 1) Determine the susceptibility of *B. tectorum* to *F. pseudograminearum* and assess how CO_2 and nitrogen impact their growth, and 2) Evaluate how elevated temperature, reduced precipitation, and plant competition impact winter wheat and *B. tectorum* growth and reproduction.

Utilizing growth chambers, high and low nitrogen treatments, fungal inoculated and uninoculated treatments, and ambient and elevated CO_2 treatments, *Bromus tectorum* was found to be a host of *F. pseudograminearum*, and the fungus significantly reduced root, shoot and total biomass, as well as primary physiological processes of *B. tectorum*. *Fusarium pseudograminearum* infection was not impacted by nitrogen or CO_2 level. Low nitrogen increased emergence and root production early on, while high nitrogen increased shoot production at later growth stages. Low nitrogen also improved stomatal conductance and transpiration rate. High CO_2 increased *B. tectorum* root, shoot, and biomass production, as well as intercellular CO_2. An interaction between ambient CO_2 and low nitrogen resulted in the greatest shoot relative growth rate between the first and second harvest.

Field tests, using three climate treatments (ambient, increased temperature, reduced precipitation with increased temperature) and three plant competition levels (monoculture winter wheat, monoculture *B. tectorum*, and biculture of the two), found that for both winter wheat and *B. tectorum* monocultures, ambient and warmer climates produced similar yields and biomass, respectively, whereas the drier with warmer treatment reduced these factors. Additionally, *B. tectorum* presence increased winter wheat grain protein. A quadratic interaction model of winter wheat yield as a function of *B. tectorum* biomass by climate treatment suggests that at low to moderate *B. tectorum* biomass levels, winter wheat yield was negatively impacted by the warmer and drier treatment, whereas ambient and warmer treatment results were similar.

CHAPTER ONE

LITERATURE REVIEW, PROJECT SIGNIFICANCE & OBJECTIVES

Introduction

Agricultural systems responses to climate change are not fully understood, but predictions suggest overall adverse impacts on food production (Core Writing Team et al., 2014) Climate change may significantly alter the geographic distribution of invasive plant species, insect pests, and plant pathogens, as well as associated crop-pest interactions (Fuhrer, 2003; Germino et al., 2016). Bebber et al. (2013) suggest an average poleward shift of 2.7 ± 0.8 km yr^{-1} since 1960, based on observations of hundreds of pests and pathogens, but with high levels of variation among taxonomic groups. The distribution and severity of wheat pathogens and insect pests are among those that may shift in response to climate change (Bebber et al., 2013; Fuhrer, 2003; Melloy et al., 2010; Váry et al., 2015).

In Montana, climate data reveals an increasing trend in mean annual temperature, from 4.5° C in 1895 to 6° C in 2016, (National Oceanic and Atmospheric Administration [NOAA], 2017a). According to the Montana Climate Assessment, average annual temperatures, minimum and maximum temperatures, days over 32°C, and frost-free days increased in Montana between 1950-2015, and temperatures are expected to continue to rise across the state throughout the 21st century regardless of season or greenhouse gas emissions scenario (Whitlock et al., 2017). Precipitation data between 1895 to 2017 show an increasing trend in eastern areas of Montana, compared to a decreasing trend in western parts of the state (NOAA, 2017b). Precipitation is projected to be increasingly variable, with a rising trend across the state in all seasons except summer, when it will likely decrease (Whitlock et al., 2017).

The invasive winter annual grass *Bromus tectorum* L. (cheatgrass, downy brome) is a prominent weed in Montana winter wheat production (Mack, 1981), where it competes with the crop (Challaiah et al., 1986) and can serve as an alternate host for pathogens and insect vectors (Ito et al., 2012; Perez-Mendoza et al., 2006; Ranabhat et al., 2017). Increasing temperature and altered precipitation regimes will likely expand the range of suitable environments for *B. tectorum* in the Intermountain West northward and create an ecological advantage for this species in some areas (Bradley et al., 2009, 2016; Taylor et al., 2014). In addition, elevated atmospheric CO_2 has been shown to increase the growth of *B. tectorum* but make it less competitive to perennial grasses (Larson et al., 2018). Interactions between crops, pests, and climate change are complex; dependent on many factors such as phenology and physiology, host-pest synchronization, phenotypic and genotypic flexibility, and the type and extent of climate change experienced (Fuhrer, 2003). Climate change varies geographically and therefore regionally specific studies are necessary to make effective management recommendations at the local level (Core Writing Team et al., 2014). The overarching goal of this research was to gain a deeper understanding of how altered climate scenarios may affect dryland winter wheat growth, *B. tectorum* competitive ability, as well as crop-weed-pathogen interactions in Montana. First, a field experiment was implemented to address the effects of increased temperature and decreased precipitation on winter wheat and *B. tectorum* growth and yield. Second, a growth chamber experiment was used to assess the effects of elevated CO_2, *Fusarium pseudograminearum* (root crown rot), and nitrogen (N) fertilizer on the growth of *B. tectorum*.

Literature Review

Bromus tectorum Origin and Distribution

Native to Eurasia (Klemmedson & Smith, 1964; Mack, 1981), *B. tectorum* has been introduced to many countries worldwide, including the U.S, Canada, Argentina, Chile, New Zealand, and Australia, to name a few (Novak & Mack, 2001; Valliant et al., 2007). *Bromus tectorum* likely made its way to North America via contaminated ship ballasts and crop seed (Hulbert, 1955; Klemmedson & Smith, 1964; Mack, 1981; Morrow & Stahlman, 1983; Stewart & Hull, 1949) and was first officially recorded in Pennsylvania in 1861 (Morrow & Stahlman, 1983). In North America, multiple introductions as well as multidirectional spread of *B. tectorum* likely occurred during western expansion (Novak & Mack, 2016). Since its introduction, *B. tectorum* naturalized in all U.S.A. continental states and Canada Provinces and is especially invasive in the Intermountain West (Mack, 1981; Morrow & Stahlman, 1983; Novak & Mack, 2001). The first record of *B. tectorum* in Montana is from 1898 and it spread to every Montana county by 1980 (Rice, 2003).

The rapid and expansive invasion of *B. tectorum* across North America and other regions has been attributed to its preadaptation to semi-arid landscapes, the co-occurrence of land disturbance with its introduction, and lack of effective competitors, pathogens, and predators in the new environments (Mack, 1981). Introduced *B. tectorum* readily populates disturbed land such as cropland, overgrazed rangeland, and land disturbed by mining operations (Hulbert, 1955; Mack, 1981; Stewart & Hull, 1949). In 2005, *B. tectorum* reportedly covered nearly 23 million ha in 17 western states (Rice, 2005).

Bromus tectorum Biology, Environmental Requirements and Phenology

Biology: *Bromus tectorum* is an annual monocotyledonous species that typically self-pollinates but is capable of cross-pollination, reproduces from viable caryopses on or beneath the soil surface, and is capable of producing dozens of tillers with thousands of seeds per plant (Klemmedson & Smith, 1964; G. Stewart & Hull, 1949; Thill et al., 1983). For example, Ostlie & Howatt (2013) observed that *B. tectorum* plants produced up to 60 tillers and over 7,500 seeds when densities were below two plants m^{-2} and no control was administered. Seeds of *B. tectorum* are highly viable from the time the plants turn a reddish-purple color during maturation (Klemmedson & Smith, 1964). Seed survival in the seedbank is short with 0.4-50% viable seeds after one year of dispersal, depending on seed depth, timing of seed deposition, precipitation, and farming system (Wicks, 1997).

Environmental Requirements: Numerous habitats are suitable for *B. tectorum* establishment and success. *Bromus tectorums'* optimal growth conditions range between 10-20°C (McCarlie et al., 2001) and 15-56 cm of annual precipitation. Plants establish in many soil types and can survive in elevations over 2,700 m (Stewart & Hull, 1949; Hulbert, 1955; Klemmedson & Smith, 1964; Morrow & Stahlman, 1983).

Phenology: As a winter annual species, adequate late-summer and fall precipitation allows for germination and emergence of *B. tectorum.* Sparse fall precipitation may initiate germination, but seedlings may not survive a warm fall (Hull & Pechanec, 1947). Fall-emerged seedlings undergo vernalization during the winter months and renew growth in the spring. Plants mature from late May through June, during which time they turn a reddish-purple color, and thereafter seeds fall to the ground (Hull & Pechanec, 1947). When fall precipitation is inadequate, *B. tectorum* can act as a summer annual, however, the delay in germination can come with a fitness cost (Stewart & Hull, 1949; Hulbert, 1955).

Impacts of *Bromus tectorum*

Bromus tectorum competes with native and desirable species across its invasive range via water, nutrient, and light competition, and can alter nutrient cycling (D'Antonio & Vitousek, 1992; Sperry et al., 2006). In arid and semiarid regions, *B. tectorum* may alter fire regimes as it matures into highly flammable fine fuel mid-summer, during the annual window of fire activity, resulting in increased fuel surface-to-volume ratio, horizontal fuel continuity, and fuel packing ratio, which together facilitates greater fire frequency (Brooks et al., 2004). Increased fire frequency due to *B. tectorum* invasions has been correlated with negative effects on plant and animal diversity, ecosystem services, agricultural and recreational economies, and social wellbeing particularly in regions of the Great Basin (Brooks et al., 2004; D'Antonio & Vitousek, 1992; Pimentel et al., 2005). In rangeland of the northeastern region of the sagebrush steppe Larson et al. (2017) found no evidence of negative impacts of *B. tectorum* on biodiversity, but did observe an increase in *B. tectorum* fecundity due to fire. In cropland, competition between *B. tectorum* and desired plant species is of great concern.

The ecological similarities between *B. tectorum* and wheat are responsible for the negative impacts on crop growth and yield and the control of *B. tectorum* in wheat cropping systems has long been studied (Blackshaw, 1993, 1994b; Challaiah et al., 1986; Ostlie & Howatt, 2013; Rydrych, 1974; Rydrych & Muzik, 1968; Stahlman & Miller, 1990). Rydrych and Muzik (1968) found that fewer than 54 *B. tectorum* plants per m^2 reduced winter wheat yield by 28% in eastern Washington. The relative time of emergence of *B. tectorum* in relation to winter wheat has been found to be more influential on yield loss than *B. tectorum* density. Specifically, a study conducted in Lethbridge, Alberta, Canada found that at comparable densities, *B. tectorum* that emerged within three weeks of winter wheat caused 2- to 5-fold greater yield reduction than the plants that emerged six weeks after winter wheat emergence (Blackshaw, 1993).

Bromus tectorum Management

Much research has been conducted on *B. tectorum*, yet the management of this species remains a challenge. Documentation from the mid-20th century describes scientists and land managers in the western U.S.A. relying on grazing, tillage, reseeding of native grasses, and fire to control *B. tectorum*. Currently, ecologically based integrated pest management (EBIPM) of *B. tectorum* is the most promising tenet for its control (Krueger-Mangold et al., 2006; Monaco et al., 2016; Sheley & Smith, 2012). Ecologically based integrated pest management programs emphasize ecological understanding of the system, integrate physical, chemical, cultural, and biological practices, and promote social, economic, and environmental sustainability of the operation (Koul & Cuperus, 2007; Sheley & Smith, 2012). Furthermore, researchers are calling for the inclusion of an eco-evolutionary tenet to the EBIPM framework in order to reduce the risk of herbicide resistant weed biotypes (Menalled et al., 2016).

Chemically Based Management of *B. tectorum*: Chemicals are often used to manage *B. tectorum* control in agricultural (Ostlie & Howatt, 2013) as well as natural lands (Monaco et al., 2016). Several herbicides are registered to manage *B. tectorum*, particularly acetolactate synthase (ALS)-inhibitors (Reddy et al., 2013). High rates of *B. tectorum* control in wheat with pre- and post-emergence chemicals are achieved with a fall application of herbicide, as opposed to early spring application (Ostlie & Howatt, 2013; Reddy et al., 2013). Winter wheat-fallow rotations often include chemical burn down of weeds during the fallow period with non-selective herbicides, such as glyphosate (Roundup®) (Rydrych & Muzik, 1968; Wicks & Smika, 1973). Clearfield™ wheat varieties are tolerant to imidazolinone herbicides (i.e. imazapyr, imazapic, imazamox), which allow producers to control *B. tectorum* post-crop emergence. However, imidazolinone herbicides may facilitate the selection of herbicide resistant biotypes (Tan et al., 2005).

Herbicide Resistance: Excessive reliance on herbicides imposes strong selection pressures on weed populations. Weed biotypes that have the innate ability to survive and reproduce after what should be lethal applications of herbicide (i.e., herbicide resistant biotypes) pose a threat to agricultural as well as natural landscapes (Menalled et al., 2016). Selection for herbicide resistance impacts genetic composition of weed populations, leading to adaptation that further increases weed density, resulting in greater weed densities that require alternative management (Menalled et al., 2016). Documentation of *B. tectorum* herbicide resistance in the U.S.A. spans 20 years. Specifically, resistant biotypes to ALS-inhibitors [(B/2), imazamox, primisulfuron-methyl, sulfosulfuron] were found in Kentucky bluegrass in Oregon in 1997 (Mallory-Smith, Hendrickson, & Mueller-Warrant, 1999), ACCase-inhibitors [(A/1), clethodim, fluazifop-P-butyl, quizalofop-P-ethyl, sethoxydim] in Oregon grass seed in 2005 (Park & Mallory-Smith, 2004), and ALS inhibitors [(B/2), imazamox, procarbazone-sodium, pyroxsulam] in Montana wheat in 2016 (ALS inhibitors (B/2), imazamox, procarbazone-sodium, pyroxsulam) (Heap, 2017). Risk of herbicide resistant *B. tectorum* biotypes can be reduced by adopting eco-evolutionary principles, such as utilizing a combination of crop rotations, cover crops, intercropping, tillage, rotating herbicide modes of action, and appropriate use of herbicides and soil amendments (Menalled et al., 2016).

<u>Mechanical Management:</u> Soil disturbance practices (i.e., tillage, disking, plowing) effectively control *B. tectorum* and other weeds (Camara et al., 1996; Hansen et al., 2012; Massee, 1976; Young et al., 1994), but can result in soil erosion, reduced soil organic matter, lower levels of organic carbon and nitrogen, reduced soil aggregation and water infiltration, and altered abundance and diversity of soil biota (Alvarez & Steinbach, 2009; Havlin et al., 1990; Rhoton et al., 2002). As a result, adoption of no-till agricultural systems are increasing worldwide, including in the U.S.A. (Derpsch et al., 2010). In 2008, roughly one-third of small grain production in the U.S.A. was under no-till management (Conservation Technology Information Center [CTIC], 2008). Montana’s

cropland is dominated by no-till (>2.77 million hectares) and conservation tillage (>708,000 hectares), as opposed to conventional tillage practices (>764,000 hectares) (United States Department of Agriculture [USDA], 2014). *Bromus tectorum* control is challenging without soil disturbance practices (Blackshaw, 1994b; Camara et al., 1996; Hansen et al., 2012; Massee, 1976; Young et al., 1994), but weed control in no-till systems is improved when multiple methods are integrated, including diverse crop rotation, cover cropping, and increased crop competitiveness (Blackshaw, 1994b; Halde et al., 2015; Tautges et al., 2016).

Cultural Management: Several cultural management tactics such as crop diversification, cover cropping, and crop competition can be used to manage *B. tectorum.* Diverse crop rotations, as opposed to continuous wheat and wheat-fallow systems, are capable of suppressing weeds, disrupting pest cycles, improving soil characteristics, and increasing if not maintaining wheat yields and overall profitability (Anderson, 2015; Liebman & Davis, 2000; Smith et al., 2017). For example, Smith et al. (2017) reported higher wheat protein in a rotation with a legume green manure. In addition, their research found that a wheat-canola (*Brassica napus* L.)-wheat-dry pea (*Pisum sativum* L.) rotation was more profitable than a conventional wheat system. Lyon and Baltensperger (1995) assessed the extent to which crop rotation can suppress winter annual grass weeds including *B. tectorum, Aegilops cylindrica* Host (jointed goatgrass), and *Secale cereale* L (cereal rye) in dryland winter wheat production. In this study, the winter wheat-sunflower-fallow and winter wheat-proso millet-fallow rotations had the least weeds per square meter compared to the continuous wheat, wheat-fallow, and wheat-fallow-fallow cropping systems. Although the 2- and 3-year cropping systems did not differ in winter wheat yields, the three-year systems reduced grain contamination from weeds and allowed for more opportunity to recover from management mistakes. A similar study found that winter annual weed densities were reduced tenfold after two cycles of a 3-year rotation, compared to one cycle, and 100-fold compared to the 2-year rotations. Three-year rotations were economically competitive with the 2-year rotations and provided superior control of winter annual grass weeds (Daugovish et al., 1999).

Cover crops can have a number of positive influences on ecosystem properties, including weed suppression, improvement of soil physical characteristics, reduced nutrient leaching and erosion, and the addition of nitrogen if legumes are included (Liebman & Davis, 2000). In using cover crops to control weeds, the goal is to replace an unmanageable weed population with a manageable cover crop, by preempting the niche occupied by weed populations (Teasdale, 1996). In semiarid environments, where soil moisture is a limiting factor for crop production, adoption of cover crops and green manures can be challenging as they could compromise subsequent crop yield, due to their water use (Robinson & Nielsen, 2015). A 12-year study (Allen et al., 2011) determined that green manures can be a viable option for spring wheat producers in the Northern Great Plains. Spring wheat-Indianhead lentil (*Lens culinaris* Medikus cv. Indianhead) systems where no synthetic nitrogen fertilizer was added produced similar wheat yields to conventional wheat-fallow and continuous wheat systems after five years due to 26% greater spring soil nitrate (0-0.6m) availability. Grain protein was similar after four years, and water use for green manure and fallow periods was alike when lentil was terminated at full bloom. Furthermore, high seeding rates of lentil resulted in near elimination of a serious green foxtail (*Setaria viridis* (L.) P. Beauv) problem (Allen et al., 2011).

Living mulches (i.e., cover crops that continue growth with the main crop), and intercrops (two or more crops grown simultaneously) exhibit potential for effective in-crop weed control (Hiltbrunner et al., 2007; Liebman & Davis, 2000), but their adoption has been limited in semi-arid environments. Successful integration of cover crops, green manures, intercrops, or living mulches is a viable option for reducing *B. tectorum* populations in cropping systems, but their effectiveness depends on many factors including climate, weather, species, timing, and the relative impact of the other management tactics applied (Liebman & Davis, 2000; Nielsen et al., 2016; Robinson & Nielsen, 2015).

Competitive cultivars can suppress and/or tolerate weed competition (Andrew et al., 2015). For example, Blackshaw (1994a) reported 14-30% wheat yield reduction caused by *B. tectorum* in the semi-dwarf cultivars, compared to tall varieties. Aside from height, wheat can exhibit other competitive traits such as vigor and erect growth at tillering, high leaf area index at stem extension, and resilient grain yield under weedy conditions (Worthington et al., 2014). Decreased row spacing and increased seeding density can increase weed suppression by wheat (Chen et al., 2008; De Vita et al., 2017).

Bromus tectorum is usually a larger threat to early seeded winter wheat than late because it is easier to control before the crop emerges (Wicks, 1983). Producers can adjust planting date and other management strategies based on *B. tectorum* phenology. For instance, if precipitation occurs near the planned seeding date, planting can be delayed in order for *B. tectorum* to emerge and management steps taken, to enhance wheat competitiveness (Wicks, 1983).

Biological Control: Overstocking of domestic grazing animals and a lack of grazing rotational practices helped perpetuate the spread and success of *B. tectorum* in the Intermountain West. Nevertheless, sustainable grazing practices, such as proper stocking density, rotation, and seasonal timing can help control this species (Hulbert, 1955; Klemmedson & Smith, 1964; Platt & Jackman, 1946; Stewart & Hull, 1949).

There are five identified soilborne pathogens that can have negative effects on *B. tectorum* seed bank dynamics, seedling emergence, and seed production: *Ustilago bullata* Berk. (head smut pathogen), *Pyrenophora semeniperda* (Brittlebank & Adams) Shoemaker (black fingers of death (BFOD) pathogen), *Tilletia bromi* (Brockm.) Nannf, (chestnut bunt pathogen), *Fusarium* Link sp. n. (*Fusarium* seed rot pathogen), and Rutstroemiaceae sp. (bleach blonde syndrome pathogen). These pathogens rarely compete directly, but can interact to exacerbate their impact on *B. tectorum* stand structure and potentially result in stand failure (Meyer et al., 2016).

One of the most promising fungal biocontrols is *Pyrenophora semeniperda*, an ascomycete fungus that attacks mature grass seeds, including those of *B. tectorum* (Meyer et al., 2008). The fungus is unique in that it attacks the seed bank, but it is less virulent to rapidly germinating seeds. BFOD is a generalist pathogen and its impact on crop seed is not fully known (Meyer et al., 2008). However, Ehlert (2017) found that barley and rye densities were reduced by 8% and 33%, respectively, when inoculated with BFOD in greenhouse settings, whereas winter wheat, oat, and triticale densities were not impacted by the fungus. Forage species, range species, and *B. tectorum* were also included in the latter experiment. Their findings suggest that seed weight alone is not sufficient to predict a species' response to BFOD, unless the seeds are heavier (i.e. wheat, other crops) and can therefore germinate more rapidly and avoid a BFOD attack. Ehlert, Mangold, & Engel (2014) reported a significant reduction in *B. tectorum* emergence and density in response to BFOD, with the greatest responses for seed placed below the soil surface. The latter study also achieved greater *B. tectorum* control with sub-soil BFOD combined with post-emergent application of imazapic. Ehlert (2017) reported that *B. tectorum* density was reduced by BFOD by 40%, but biomass was unaffected. Ehlert et al. (2019) assessed BFOD infection rates on *B. tectorum* seed collected from crop, range, and subalpine sites. Higher temperatures and lighter-weight seeds resulted in increased infection. *Bromus tectorum* seed from cropland had greater germination and therefore lower infection rate compared to those from range and subalpine areas.

Climate Change: Past, Present, and Future

Climate change poses uncertainties and challenges to all aspects of biotic and abiotic systems on earth (Core Writing Team et al., 2014). In its fifth assessment report, the Intergovernmental Panel on Climate Change (IPCC) reported that it is 'extremely likely' that increases in anthropogenic greenhouse gas emissions are responsible for more than half the observed increases in global average surface temperature between 1951 and 2010. Between 1880 and 2012, the globally averaged combined land and ocean surface temperature anomaly was 0.85 °C, and climate models project a quasi-linear relationship between rising CO_2 emissions and increasing global mean surface temperature to the year 2100 (Core Writing Team et al., 2014).

Extreme weather and climate events have observably changed since the 1950's. For example, large parts of Europe, Asia, and Australia have experienced an increased frequency of heat waves, and North America and Europe have experienced an increased frequency and intensity of precipitation events (Core Writing Team et al., 2014). For many regions, it is very likely that heat waves will happen more often and with longer duration, extreme precipitation events will become more intense and frequent, and the oceans will continue to warm, acidify, and rise (Core Writing Team et al., 2014).

Over a century of meteorological data (1895-2006) from 9 weather stations in western Montana revealed that on average, days with temperatures below -17.8°C have decreased in number and conclude 20 days earlier, whereas days with temperature greater than 32°C are three times more frequent and occur in a seasonal window of 24 days longer (Pederson et al., 2009). Northwestern and southwestern Montana weather station temperature data varied in timing and rates of change, and the number of days at or below 0°C decreased by an average of 16 days, with the most dramatic reduction of these freeze/thaw days occurring between 1986-2006 (Pederson et al., 2009). Mean annual precipitation for the whole state of Montana does not exhibit a clear increasing or decreasing trend between 1895-2016. However, a decreasing trend in mean annual precipitation has been seen for western, southwestern, northcentral, and central Montana, compared to an increasing trend for southcentral, northeastern and southeastern Montana during the same period (NOAA, 2017b). For Montana, the palmer drought severity index

(PDSI) and palmer modified drought index (PMDI) show decreasing trends (indicating increasingly severe drought conditions) between 1895-2016, with a mean PDSI and PMDI of 0.45 and 4.96, respectively (National Oceanic and Atmospheric Administration [NOAA], 2017b).

The Montana Climate Assessment reported that between 1950-2015, average annual temperatures, minimum temperature, maximum temperatures, days over 32°C, frost-free days, and growing season increased (Whitlock et al., 2017). Temperature projections for Montana show continued warming across the state, in all seasons, and under all greenhouse gas emission scenarios throughout the 21st century. Average statewide temperatures are projected to increase 1.7-3.9°C by 2050, with the greatest warming occurring in summer and winter, and in southeastern Montana (Whitlock et al., 2017).

According to the Montana Climate Assessment, there were no changes in average annual precipitation between 1950 and 2015, but there were anomalies in average seasonal precipitation. Average winter precipitation decreased by 2.3cm, largely due to natural variability and an increase in El Niño events, particularly in western and central regions of Montana. Spring precipitation increased during this same time period by 3.3-5.1cm in the eastern regions of Montana (Whitlock et al., 2017). Precipitation projections show an increase across the state for winter, spring, and fall, but a decrease in summer. The greatest precipitation increases are projected in spring in the southern regions of Montana, whereas the largest reductions are projected for summer in central and southern areas of the state. Increased year-to-year precipitation variability is also projected. The number of consecutive dry days are not expected to change drastically in Montana throughout the 21st century. However, increased precipitation variability indicates the possibility for greater occurrence of severe droughts, namely coinciding with climate oscillations (Whitlock et al., 2017).

Snowpack is crucial for many regions worldwide, including the Northern Great Plains. Adequate spring runoff from mountain snowpack is crucial for the ecological, economic, and social wellbeing of the immediate locations as well as globally. Effects of climate change on mountain snowpack vary greatly by location, latitude, and elevation, among other factors. Generally, warmer temperatures reduce precipitation as snowfall, reduce snowpack, and cause spring runoff to occur earlier. In the western U.S.A, 75% of gauges have reported a reduction of precipitation of snow, whereas the Rocky Mountain range has seen both increases and decreases (Stewart, 2009). Trends found in data from 20 meteorological stations across the Northern Great Plains between 1951 and 2010 suggest that the minimum temperature and days with precipitation increased at most of the stations, and reduced winter albedo was more common among the stations (Fassnacht et al., 2016).

Agriculture and Climate Change

In 2010, agriculture contributed 11.2 ± 0.4% of total anthropogenic greenhouse gas emissions, and continue to increase by roughly 1% annualy (Tubiello et al., 2015). Furthermore, crop and livestock production is the dominant source of agriculture, forestry, and other land use GHG emissions (Tubiello et al., 2015). According to the IPCC (2014), the percent of crop (mainly wheat, maize, rice, and soy) yield projections showing yield decreases over the course of the 21st century outnumber those reporting yield increases.

Wheat was the 4th most produced crop globally in 2013 and continues to be an important food source throughout the world (Food and Agriculture Organization [FAO], 2015). In order to meet increasing food demands imposed by a growing human population by 2050, annual global cereal production needs to increase by nearly 1 billion tonnes, with 90% of growth coming from yield increases and greater cropping intensity and the remainder from arable land expansion (FAO, 2009). Wheat yields are decreasing in many areas of the Great Plains, including parts of Montana, western North Dakota, South Dakota, Kansas, Texas and eastern Colorado (Ray et al., 2013).

Montana ranks 3rd in the U.S.A. for all wheat production and 4th for winter wheat production. In 2015, winter wheat production exceeded $4.36 million in total value for more than 898,000 harvested hectares in Montana. Dryland winter wheat in 2015 made up 98% of winter wheat production in the state. In Gallatin County, Montana, where my field research was conducted, there were over 8,903 harvested hectares of winter wheat in 2015, valued at over $6.3 million (Montana Department of Agriculture [MDA; USDA-NASS], 2016).

Montana agriculture has long been exposed to weather volatility, variability and extreme events, and this trend will continue under the projected climate scenarios. Climate in Montana is not homogenous across the state. Due to its large size (it is the 4th largest state in the U.S.A) and location, the state is subject to various weather systems stemming from the Pacific Ocean, Arctic, and occasionally subtropical regions. In addition, the Continental Divide splits the state into western wet and eastern dry climate regions (Whitlock et al. 2017).

In Montana, climate change will likely have both positive and negative consequences on agriculture. Increases in spring and winter precipitation may improve soil water and irrigation availability during the growing season, yet extreme events and unfavorable timing could lead to crop damage or failure (Melillo et al., 2014). Higher temperatures could lengthen the growing season and diversify crop rotations but are also projected to increase demand and competition for water and energy resources. Higher winter temperatures and shifts in the timing and quantity of precipitation have observably altered crop growth cycles; requiring altered and novel management practices (Melillo et al., 2014). Warmer winters could allow certain weeds and insect pests to survive the winter months that historically they could not, and winter crops that emerge from snow cover earlier in the spring would be vulnerable to spring freezes. Climate change will affect food security locally and globally as volatility in crop yields and prices impacts all levels of food systems, from production to consumption (Melillo et al., 2014).

Effects of Climate Change on Wheat: Climate change adds significant complexity and uncertainty to agroecosystems worldwide (Coakley et al., 1999). Crops are influenced by climate change, due to shifts in atmospheric CO_2 level, temperature, precipitation and transpiration regimes, extreme temperature and precipitation events, and pest pressure (Tubiello et al., 2007). Hundreds of studies, utilizing diverse methods and plant species have reported a positive relationship between elevated atmospheric CO_2 and plant biomass and yield, due to photosynthetic stimulation resulting in improved plant productivity and altered water and nutrient cycles (Tubiello et al., 2007). A review of free air CO_2 enrichment (FACE) studies concluded that elevated CO_2 stimulates photosynthetic carbon gain and net primary production, improves plant nitrogen use efficiency, reduces water use, stimulates dark respiration, and can indirectly stimulate carbon gain under drought conditions (Leakey et al., 2009). A FACE study conducted across three years in Germany reported increased aboveground biomass (+11.8%) and yield (+10.4%) of spring wheat, reduced grain protein concentration (-7.4%), and grain size distributions shifted towards smaller grains, when enriched with 150 $\mu l \cdot l^{-1}$ CO_2 above ambient concentration (Högy et al., 2009). Experimental settings may overestimate the positive effects of elevated CO_2 on plant growth under farm-scale field conditions, due to limiting biotic and abiotic factors. The individual and interactive effects between elevated CO_2 and factors such as water, soil nutrients, and pest pressure are still under much investigation (Tubiello et al., 2007).

In 2015, 98.4% and 94.9% of winter wheat and spring wheat acreage, respectively, was non-irrigated in Montana (MDA; USDA-NASS, 2016). Therefore changes in climate and interactions between CO_2 and temperature are of great concern. Varga et al. (2016) explored the combined effects of elevated CO_2 and drought stress on various winter wheat cultivars in growth chambers. This study concluded that higher CO_2 levels reduced water uptake and improved water use efficiency (WUE) under drought conditions, and showed an interaction between CO_2 and cultivar that influenced WUE. Sionit et al. (1980) found that CO_2 fertilization effects on wheat yield can be limited in drought conditions. Spring wheat grown in growth chambers under high (1,000 ppm)

CO_2 with adequate water increased tiller production (+43%) and increased yield, total dry matter production, and grain size when compared to well-watered, low (350 ppm) CO_2 wheat. In contrast, water-limited, high CO_2 wheat yields and biomass production were similar to those of low CO_2, well-watered wheat (Sionit et al., 1980).

Nitrogen availability can limit the benefits of higher CO_2 (Reich et al., 2006). Kimball et al. (2001) conducted FACE experiments with spring wheat grown under elevated (550 mmol mol^{-1}) or ambient CO_2, with either high (350 kg N ha^{-1}) or low (70 and 15 kg N ha^{-1}, for trial one and two, respectively) nitrogen application. Elevated CO_2 tended to worsen the negative effects of low nitrogen (-33% and -39% grain protein for ambient and elevated CO_2, respectively), compared to a 5% grain protein reduction for elevated CO_2 with high nitrogen and ample irrigation. Furthermore, elevated CO_2 reduces the rate of nitrate assimilation, thereby lowering the concentration of nitrogen in plant tissues. A data synthesis concluded an average of 14% reduction of nitrogen concentration in plant tissue under elevated CO_2 conditions, with C3 plants exhibiting larger deficits (Cotrufo et al., 1998). Bloom et al. (2014) analyzed the ratio of nitrate to total nitrogen concentration and the stable isotope ratios of organic nitrogen and free nitrate in wheat leaf tissues, reporting that elevated CO_2 slowed the rate of nitrate assimilation in wheat. There is concern that reductions in crop nitrogen concentration reduces nutritional quality of food and in the case of wheat producers, threatens their ability to achieve grain protein levels sufficient for protein premiums. Simply increasing fertilizer levels may not fully compensate for the deficit if nitrate assimilation is too limited, which poses risks of nitrate leaching and nitrous oxide emissions from unassimilated nitrogen (Bloom et al., 2014; Högy et al., 2009).

Temperature highly influences crop success, particularly during the pollination and grain fill periods (Wienhold et al., 2017). Ferris et al. (1998) reported spring wheat yields and root biomass were negatively correlated with high temperature extremes at mid-anthesis. According to a simulation modelling study, the impact of temperature has been underestimated, and variations in average growing season temperautres of ±2°C can reduce wheat grain yields by up to 50% (Asseng et al., 2011).

Numerous studies have assessed interactive effects between temperature and other environmental effects on crop growth and yield. Wheeler et al. (2009) reported that winter wheat biomass and yield increases resulting from elevated (700 μmol mol$_{-1}$) CO_2 were offset by an increase of mean seasonal temperature of only 1-1.8°C, compared to wheat grown at ambient CO_2 levels. The latter study did not limit nutrient and water supply, and grew one cultivar. Dias De Oliveira et al. (2013) evaluated the impact of elevated CO_2 (700 μL L$_{-1}$), high temperature (+2,4,6°C), and terminal drought (applied at 50% anthesis) on biomass accumulation and grain yield for vigorous and non-vigorous wheat genotypes. Regardless of watering regime, biomass and yield were enhanced for both genotypes under elevated CO_2 + 2°C above ambient temperature, whereas elevated CO_2 + 4°C and 6°C above ambient temperature tended to reduce these outcomes. Under elevated CO_2 + 2°C, reductions in biomass and grain yield (45-50%) caused by terminal drought were less severe (21-28%). Elevated CO_2 combined with +2°C ameliorated the negative effects of terminal drought due to a 63% increase in net leaf photosynthetic rate of the vigorous cultivar, and a 39% increase in tillering and leaf area in the non-vigorous cultivar (Dias De Oliveira et al., 2013).

Models have been used to understand future crop yields under various climate scenarios. Yang et al. (2017) combined outputs from a wide range of general circulation models with observational data to produce detailed projections of the impact of increasing heat stress events on wheat yield. The model was run at 36 representative sites in China with baseline data from 1996-2005. By 2100, projected increases in heat stress would lead to yield reductions of -7.1% (probability 80%) and -17.5% (probability 96%) for winter wheat and spring wheat, respectively, under irrigated conditions. Losses could be fully compensated by CO_2 fertilization, but caution is needed because existing crop dynamic models are not able to incorporate the effect of CO_2 acclimation and other offsetting forces (Yang et al., 2017). Asseng et al. (2015) tested 30 different wheat crop models of the Agricultural Model Intercomparison and Improvement Project against field experiments in which growing season mean temperatures ranged 15°C-32°C. Models simulated yields well but were less accurate at higher temperatures, and their ensemble median was more accurate than any single model at simulating crop temperature response. Extrapolating the model ensemble temperature response indicated that warming is already slowing yield gains at a majority of wheat-growing locations, global wheat production is estimated to fall by 6% for each 1°C of further temperature increase, and become more variable over space and time (Asseng et al., 2015).

Effects of Climate Change on *B. tectorum*

Invasion risk can expand or contract due to climate change, as altered precipitation and temperature regimes can make them less or more suitable for an invasive plant species. In addition, currently invaded landscapes can become unsuitable for an invasive plant species due to altered climate conditions (Bradley et al., 2009). Peters et al. (2014) categorizes climate change effects on agricultural weeds into three types of shifts at different scales: 1) range shifts in landscapes, 2) niche shifts in communities, and 3) trait shifts of species in populations. Plant species can adjust to novel environmental conditions by way of phenotypic plasticity, natural selection, and migration (Nicotra et al., 2010), and *B. tectorum* is capable of all of the above (Hufft & Zelikova, 2016). For instance, Wade and Loik (2017) provided new insight into the mechanisms responsible for *B. tectorum* over-competing with four native species in the eastern Sierra Nevada, where *B. tectorum* has recently invaded. Specifically, when a springtime pulse of precipitation was added in a drought year, CO_2 assimilation for *B. tectorum* increased 78% over the controls, compared to the three native perennials with increases ranging from 2 to 29%. Further, *B. tectorum* exhibited the largest increase in stomatal conductance (27%) and had the most responsive instantaneous electron transport rate. These results suggest that *B. tectorum's* ability to rapidly upregulate carbon uptake in response to precipitation in drought conditions could enhance its spread into higher elevations (Wade & Loik, 2017).

Bromum tectorum biomass and seed production have been shown to respond positively to elevated CO_2 (Ziska et al., 2005). Ziska et al. (2005) collected *B. tectorum* seeds from three elevations between 1220-2171m in Nevada, grew seeds in controlled chambers under 270, 320, 370, or 420 μmol mol^{-1} CO_2, and provided optimal water and nutrient levels. Results indicated that *B. tectorum* aboveground biomass increased 1.5-2.7g per plant for every 10μmol mol^{-1} increase in CO_2, sensitivity to CO_2 decreased in seeds from higher elevations, and the lowest elevation seeds reduced the time to reproductive maturity by ~10 days and doubled reproductive biomass with increasing CO_2 (Ziska et al., 2005). However, CO_2 fertilization effects are limited by environmental factors such as soil water availability and soil nutrient levels (Hikosaka et al., 2011; Miyagi et al., 2007; Reich et al., 2014). Furthermore, Blumenthal et al. (2016) found that elevated levels of atmospheric CO_2 may not be the most influential factor of climate change affecting plant growth, reproduction, and geographical distribution. A FACE study applying 600 ppmv CO_2 and infrared warming (+1.5°C day/3°C night) on *B. tectorum* in a mixed-grass, semi-arid prairie found that warming more than tripled *B. tectorum* biomass and seed production, due to increased recruitment and growth. The latter results were consistent under low and high competition from native species, wet and dry conditions, and despite reduced soil water availability due to warming. Elevated CO_2 had minimal effect on *B. tectorum* invasion or soil water, while reducing soil and plant nitrogen. The latter study concluded that warming might facilitate the expansion of *B. tectorum's* phenological niche, specifically into northern mixed-grass prairies, and that elevated CO_2 could have limited effects on *B. tectorum* and other nitrophilic invasive species (Blumenthal et al., 2016).

In an agricultural setting, such as no-till winter wheat, the evolution of *B. tectorum* and other weed species in a changing climate is of interest, so that cropping systems and weed management approaches can evolve simultaneously. *Bromus tectorum* can tolerate a wide range of habitats due to genetic variation among populations, a range of locally adapted ecotypes, and high levels of phenotypic plasticity, but the full ecological limits, genetic mechanisms responsible for success, and interaction between plasticity and genetic adaptation of this species are poorly understood (Hufft & Zelikova, 2016). Zelikova et al. (2013) reported that warming *B. tectorum* field plots (+2 and +4°C) advanced growth initiation, flowering, and senescence, following a wet winter and early spring. Seeds were then collected from the field study and grown in a greenhouse setting. Results showed that seeds from warmed *B. tectorum* plots had higher biomass and germination rates, and lower mortality than seeds from ambient plots. However, two dry years ensued and no phenological differences were observed in the field and warming tended to have a negative effect on *B. tectorum* biomass and reproduction (Zelikova et al., 2013). In a controlled chamber study, *Bromus rubens* L. plants were grown in either ambient (360 μmol mol$_{-1}$) or elevated (700 μmol mol$_{-1}$) CO_2, and their seeds were collected to evaluate parental effects of elevated CO_2 on seed quality. Results indicated that seeds from parents grown in elevated CO_2 had larger pericarp surface area, and higher C:N ratio, but did not differ in percent germination or mean germination time, and had smaller seed reserves, compared to ambient-developed seeds. In addition, seedlings from elevated CO_2-developed seeds had reduced relative growth rate and smaller final mass compared to the controls (Huxman et al., 1997). The latter study did not, however, incorporate other environmental factors and only explored two generations, which leaves many questions about the species' ability to acclimate and evolve under elevated CO_2, and how the interactive effects of climate variables influence seed quality.

A seven-year FACE study in the Mojave Desert using *Bromus madritensis* ssp. *rubens* (red brome) found that populations exposed to elevated CO_2 had lower rates of leaf stomatal conductance; a physiological adaptation for water conservation. This adaptation was accompanied by reduced plasticity in increasing stomatal conductance when CO_2 was more limiting, which suggests that genetic assimilation may be proceeding (Grossman & Rice, 2014). Another study exploring parental CO_2 effects and offspring nutrient environment on *B. rubens* growth and photosynthesis concluded that elevated CO_2 reduced photosynthesis and growth rates in successive generations (Huxman et al., 2001). Drake et al. (2017) analyzed a collection of grasses, including *B. tectorum,* gathered in New Mexico since 1892. The results revealed an increase in internal CO_2 partial pressure (c_i) in response to increasing atmospheric CO_2 and that increased c_i could have provided some drought resistance to the grasses by increasing the availability of CO_2 during a time of reduced stomatal conductance due to short-term water stress (Drake et al., 2017).

Multi-generational, multi-environmental factor, parental effect studies are lacking for *B. tectorum,* both in-situ and in controlled environments. The latter types of studies have not been completed in cropping system settings, as *B. tectorum* climate change research has primarily been focused in natural and rangeland landscapes. In order to maintain crop yields and develop effective weed management strategies for cropping systems, there needs to be improvement in estimations of the damage potential of weeds in cropping systems in future climate scenarios (Peters et al., 2014).

Effects of Climate Change on Wheat Pathogens

Like weeds, the effects of climate change on plant pathogens largely depend on the type of host-pathogen system, are complex, and are difficult to predict (Fuhrer, 2003; Patterson et al., 1999). Plant fungal and bacterial pests are highly influenced by temperature, precipitation, humidity, radiation, and dew. Survival, growth, and spread of plant pathogens, as well as host resistance, depend heavily on climate conditions (Fuhrer, 2003). Altered climate regimes can change pathogen stages and development rates, influence host resistance, and modify the physiology of host-pathogen interactions. The geographical distribution of pathogens and their hosts, as well as efficacy of control strategies, are likely to shift due to climate change, resulting in altered crop losses (Coakley et al., 1999). It is expected that pathogens will migrate with their associated hosts, potentially at different rates, and with varying degrees of success (Goudriaan & Zadoks, 1995). Temperature and precipitation anomalies and their timing can expand and contract the range of pathogens, as well as enhance or reduce their severity (Fuhrer, 2003).

The dryland root rot complex, causing seedling blight, and rotting of roots, stems, and crowns, commonly affects wheat crops in dry and semiarid conditions worldwide. The dryland root rot complex includes several species, including *Fusarium pseudograminearum*, causing crown rot of wheat (Moya-Elizondo, 2013). Crown rot of small grains is most commonly caused by *F. culmorum*, *F. graminearum*, and *F.*

pseudograminearum in Montana and the Pacific Northwest (Paulitz et al., 2002). Numerous crops (i.e. wheat, oats, barley, maize, sorghum) and other grassy weeds such as *Avena fatua* (wild oat) and *B. tectorum* are susceptible to *Fusarium* species (Akinsanmi et al., 2007; Meyer et al., 2016). *Fusarium pseudograminearum*, previously known as *F. graminearum* Group 1, (teleomorph: *Gibberella coronicola*) is haploid, heterothallic, necrotrophic, and produces the potent trichothecene mycotoxin deoxynivalenol (DON), a toxic esterogenic metabolite that causes hyperestrogenism in animals (Aoki & O'Donnell, 1999).

In wheat, *Fusarium pseudograminearum* more frequently inhabits crowns, causing root crown rot, but can also infect wheat heads and cause fusarium head blight (Akinsanmi et al., 2004). *Fusarium pseudograminearum* survives mainly as mycelium in plant residue, such as wheat stubble, as well as resilient chlamydospores (Paulitz et al., 2002). Adoption of conservation tillage methods have likely increased FCR severity due to more crop residue available for fungal inoculum (Paulitz et al., 2002). Graham et al. (2015) reported that *F. pseudograminearum* prevented durum wheat grown in New South Wales from extracting plant available water by as much as 49mm, reduced grain quality, and reduced yield by 17.8-64.3%. Symptoms of FCR include yield loss, stand reduction, rotting of seeds, seedlings, roots, crowns, subcrowns, and lower stem tissue, and white-heads or premature tiller death (Moya-Elizondo, 2013). A survey of 91 Montana fields during the 2008-2009 crop season detected FCR in 57% of fields, with 8% *F. culmorum* and 13% *F. pseudograminearum* incidence based on isolation from individual tillers (Moya-Elizondo et al., 2011). Field trials comparing the aggressiveness of *Fusarium* species on multiple spring and durum wheat varieties found that *F. pseudograminearum* caused the greatest yield reductions compared to *F. graminearum* and *F. culmorum* (Dyer et al., 2009).

A review by Moya-Elizondo (2013) conveyed that increased drought incidence and alterations of rainfall regimes associated with climate change may increase the prevalence of the dryland root rot complex, especially FCR, in wheat cropping areas. Research conducted in Australian wheat fields reported that yield losses from crown rot were greatest when precipitation during crop maturation (September and October) was below the long-term average. Crown rot reduced durum wheat yield the most, compared to bread wheat, and least of all barley. *Fusarium pseudograminearum* and *F. culmorum* caused similar yield losses. In addition, DNA concentrations of *F. pseudograminearum* and *F. culmorum* in pre-seeding soil samples were positively related to crown rot symptoms and negatively related to grain yield. The experiments were conducted across a range of geographic areas and years, therefore these yield loss patterns and ecological relationships could be expected in other cereal production areas (Holloway et al., 2013). A study evaluating the effect of increasing diurnal temperature (15/15°C, 20/15°C, 25/15°C, 28/15°C) on *F. pseudograminearum* pathogenic fitness concluded that stem browning and DON production were greatest at the lowest temperature treatment, and generally decreased with increasing temperature. The latter study suggests that rising temperatures combined with improvements in host genetic resistance could reduce fitness of *F. pseudograminearum* and crown rot, but other environmental variables should be included in these types of studies to provide more realistic scenarios (Sabburg, Obanor, & Aitken, 2015).

Research evaluating the effects of elevated CO_2 on *Fusarium* spp., their hosts, and disease development are on the rise. Melloy et al. (2010) reported fungal biomass of *F. pseudograminearum* and wheat stem browning increased in response to elevated CO_2. The authors suggested that elevated CO_2 and increased host biomass will facilitate more severe and rapid colonization of *F. pseudograminearum* inoculum in susceptible wheat stubble, unless a wheat variety completely inhibits infection. Melloy et al. (2014) conducted a greenhouse study evaluating the effects of elevated CO_2 and higher temperature on the incidence, severity, and fungal biomass of *F. pseudograminearum* on 16 wheat genotypes commonly grown in Australia. Elevated CO_2 (690 µmol-mol) with ambient temperature (24°C day, 15°C night) as well as elevated CO_2 with higher temperature (28°C day, 20°C night) increased *F. pseudograminearum* incidence and severity compared to ambient CO_2 (470 µmol-mol) with ambient temperature. Furthermore, wheat grown in high CO_2 with ambient temperature exhibited the highest rate of increase of crown rot severity and fungal biomass between the node development, anthesis, and soft dough stages. Both elevated CO_2 treatments resulted in crown rot symptoms expressed more rapidly and further up the stem compared to the control. Genotype influenced crown rot severity and incidence but the exact role and altered host susceptibility was not clearly understood (Melloy et al., 2014).

Assessing acclimation of pathogens and their hosts to altered climate regimes is necessary to better understand how these interactions will evolve, and the consequences for crop production and food safety. Váry et al. (2015) explored the effects of *F. graminearum* and wheat acclimation to elevated CO_2 and assessed pathogen development. Wheat-*F. graminearum* acclimation to elevated CO_2 (780 ppmv) resulted in increased head blight severity and yield loss. Furthermore, when the latter was tested on a disease resistant cultivar grown in elevated CO_2, pathogen acclimation increased disease levels and yield loss, indicating a decrease in the crops' defense mechanisms.

Mycotoxigenic fungi, like *Fusarium* species, are of particular concern for food production and safety and altered climate regimes could result in increased disease, mycotoxin production in their hosts, and greater mycotoxin contamination in cereal grains (Chakraborty & Newton, 2011; Medina et al., 2017; Miraglia et al., 2009). Climate and weather are the most important factors that determine DON accumulation in cereal crops, followed by agronomic practices; the most important being cultivar (Schaafsma & Hooker, 2007). Temperature, moisture, humidity, and CO_2 could impact grain quality during post-production storage and processing as well. For example, excessive storage moisture levels can perpetuate DON concentration, and the extent to which other climate factors will play in post-harvest grain quality is not understood (Chakraborty & Newton, 2011).

Project Significance

Scientific research has documented the negative impact of *B. tectorum* and *F. pseudograminearum* on wheat yield (Akinsanmi et al., 2004; Blackshaw, 1993, 1994a, 1994b; Challaiah et al., 1986; Dyer et al., 2009; Graham et al., 2015; Moya-Elizondo, 2013; Stahlman & Miller, 1990) and the ability of several *Bromus* spp. to host various

Fusarium species (Inch & Gilbert, 2003; Kazan & Gardiner, 2017; Lofgren et al., 2017). Also, climate change studies suggest that both *B. tectorum and F. pseudograminearum* could thrive in a warmer, drier environment, such as that proposed for much of Montana (Blumenthal et al., 2016; Bradley et al., 2016; Magan et al., 2011; Melloy et al., 2010, 2014; Sabburg et al., 2015; Singh et al., 2009; Zelikova et al., 2013; Ziska et al., 2005). However, *F. pseudograminearum* colonization has not been documented in *B. tectorum* specifically, in controlled or field settings. There is some evidence that numerous wild grasses are not only hosts of mulitple *Fusarium* species, but also have lower trichothecene levels compared to infected wheat, suggesting that the wild grasses sampled accomodate the toxigenic fungi differently from wheat, which could inform future crop improvement (Lofgren et al., 2017). These findings further the need to increase data and understanding of associations between *B. tectorum* and *F. pseudograminearum*, in current and predicted climate conditions, as they are both serious pests in no-till, dryland wheat production and *B. tectorum* could be a reservoir for this pathogen.

Crop rotation is an effective way to control soilborne pathogens (Moya-Elizondo, 2013) as well as *B. tectorum* populations in wheat (Blackshaw, 1994b). However, in-crop and/or field edge *B. tectorum* populations that persist in non-cereal rotation years could harbor *F. pseudograminearum*, and subsequent wheat crops could be at risk. Chapter two presents a growth chamber study assessing *F. pseudograminearum* growth in *B. tectorum* under elevated CO_2 and low and high soil N levels. I hypothesized: (1) Elevated CO_2 and higher nitrogen would increase (a) *B. tectorum* biomass and relative growth rate, and (b)

F. pseudograminearum DNA copy number; (2) *F. pseudograminearum* would reduce *B. tectorum* biomass and relative growth rate; (3) An interaction may be detected between elevated CO_2, nitrogen, and *F. pseudograminearum*.

Wheat has also been a focus of climate change related studies (Bloom et al., 2014; Cotrufo et al., 1998; Dias De Oliveira et al., 2013; Ferris et al., 1998; Högy et al., 2009; Kimball et al., 2001; Leakey et al., 2009; Varga et al., 2016). More recently, research addressing climate-pest-crop associations have increased (Fuhrer, 2003; Lyon & Broders, 2017; Melloy, 2015; Melloy et al., 2010, 2014; Tiedemann & Firsching, 2000), and modelling agroecosystem performance and relationships under potential future climate scenarios is improving (Asseng et al., 2011, 2015; Battilani, 2016; Bradley et al., 2017; O'Leary et al., 2015; Schaafsma & Hooker, 2007; Schauberger et al., 2017). However, predicted climate change is not homogenous on a global scale, nor across the state of Montana (Whitlock et al., 2017), and climate influenced crop-pest interactions are inherently specific, unique and complicated. To improve understanding and predictions about how climate change will impact Montana cropping systems, research needs to be site, crop, and pest specific and consider numerous biotic and abiotic factors. To my knowledge there are no published studies addressing how elevated temperature and decreased moisture will impact the growth, reproduction, and competition of winter wheat and *B. tectorum* in a no-till, rainfed cropping system, in southwest Montana or elsewhere. Filling these knowledge gaps would provide insight into how winter wheat grown in this region would be impacted by *B. tectorum* in warmer and drier growing conditions. Chapter three describes a field study assessing the impact of increased temperature and reduced soil moisture availability on winter wheat and *B. tectorum* moncultures and bicultures of these species in a no-till, dryland field setting. I hypothesized: (1) a warmer environment with ambient precipitation would enhance (a) monoculture winter wheat biomass, yield and grain quality, (b) monoculture *B. tectorum* biomass and seed production, and (c) *B. tectorum* competitive ability over winter wheat in a biculture; (2) a warmer, drier environment would (a) negatively impact winter wheat biomass, yield, and grain quality, (b) reduce *B. tectorum* biomass and seed production, and (c) exhibit that *B. tectorum* is more resilient to this climate scenario than wheat; possibly indicating an interaction between *B. tectorum*, higher temperature, and reduced precipitation.

The concluding chapter discusses the results of the growth chamber and field experiments, implications for no-till, dryland winter wheat production in southwest Montana, and addresses future research needs regarding climate-crop-pest interactions in Montana cropping systems.

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CHAPTER TWO

EFFECTS OF ELEVATED CO_2, NITROGEN AVAILABILITY, AND *FUSARIUM PSEUDOGRAMINEARUM* ON THE GROWTH AND PRIMARY PHYSIOLOGY OF *BROMUS TECTORUM*

Introduction

To sustain and enhance future crop yields it is crucial to improve the understanding of how the impact of agronomic pests will be modified by predicted climate change. Two important pests in Montana wheat production are the stubble-born necrotrophic fungus *Fusarium pseudograminearum*, which causes root crown rot in wheat and barley (Akinsanmi et al., 2004), and the invasive winter annual grass *Bromus tectorum* L. (cheatgrass, downy brome) (Mack, 1981). *Fusarium pseudograminearum* survives mainly as mycelium on plant residue (e.g. wheat stubble) and as resilient chlamydospores (Paulitz et al., 2002). The *Fusarium* genera has a broad host range, including various *Bromus* species (Lofgren et al., 2017; Meyer et al., 2016). To our knowledge, *F. pseudograminearum* has not been isolated from *Bromus tectorum* L. (cheatgrass, downy brome), yet it has the potential to persist on this and other grassy weed host species (Burgess et al., 1993). Therefore, it would be beneficial to identify how climate and environmental conditions influence the relationships between these two species under current and predicted climate conditions.

Fusarium pseudograminearum, previously known as *F. graminearum* Group 1, (teleomorph: *Gibberella coronicola*) is a haploid, heterothallic, necrotrophic fungus, and produces the potent trichothecene mycotoxin deoxynivalenol (DON), a toxic esterogenic metabolite that causes hyperestrogenism in animals (Aoki & O'Donnell, 1999). This pathogen typically causes root crown rot in wheat and barley, but can also infect the heads leading to head blight (Akinsanmi et al., 2004). *Fusarium* crown rot (FCR) symptoms include yield loss, stand reduction, rotting of seeds, seedlings, roots, crowns, subcrowns, and lower stem tissue, as well as white-heads or premature tiller death (Moya-Elizondo, 2013). Graham et al. (2015) reported that *F. pseudograminearum* reduced water uptake by durum wheat by as much as 49 mm, caused yield reduction of 17.8-64.3%, and lowered grain quality. In Montana, *F. pseudograminearum* is a significant pathogen in wheat fields across the state and can result in yield losses ranging from 3% to 35% (Dyer et al., 2009; Moya-Elizondo et al., 2011).

Increased drought incidence and altered precipitation regimes due to climate change could potentially increase the prevalence of FCR in wheat cropping systems (Moya-Elizondo, 2013). This phenomena has been documented in Australian wheat fields, where yield losses from FCR were most severe when precipitation during crop maturation was below the long-term average (Holloway et al., 2013). In relation to warming, researchers reported that increasing temperatures had a negative effect on *F. pseudograminearum* pathogenic fitness, including reduced DON production and stem browning (Sabburg et al., 2015). Finally, elevated atmospheric CO_2 (550 µmol mol^{-1}) was reported to have a positive impact on *F. pseudograminearum* in wheat; resulting in an increase in wheat stem browning and fungal biomass (Melloy et al., 2010). Furthermore, Melloy et al. (2014) found that both elevated CO_2 (690 µmol-mol) with ambient (24°C day, 15°C night) and higher (28°C day, 20°C night) temperature increased *F. pseudograminearum* incidence and severity in wheat, with the most severe results occuring with elevated CO_2 coupled with an ambient temperature environment.

Bromus tectorum competes with desirable species via water, nutrient, and light competition, can alter nutrient cycling (D'Antonio & Vitousek, 1992; Sperry et al., 2006b), and impact fire regimes by facilitating greater fire frequency (Bradley et al., 2017; Brooks et al., 2004; Brooks & Matchett, 2006; D'Antonio & Vitousek, 1992). Severe infestations of *B. tectorum* can result in upwards of 92% wheat yield loss (Rydrych & Muzik, 1968). A particular concern for cropping systems is *B. tectorums*' ability to serve as an alternate host for numerous agricultural pests and pathogens, including wheat streak mosaic virus (Ito et al., 2012; Ranabhat et al., 2018) and the wheat stem sawfly (*Cephus cinctus* Norton) (Perez-Mendoza et al., 2006). While studies have evaluated mechanical (Camara et al., 1996; Hansen et al., 2012; Massee, 1976; Young et al., 1994), cultural (Anderson, 2015; Liebman & Davis, 2000; Smith et al., 2017), and biological (Ehlert, 2017; Ehlert et al., 2014; Meyer et al., 2016) methods of *B. tectorum* control, efforts have largely focused on chemically-based approaches in both agricultural (Ostlie & Howatt, 2013) and natural landscapes (Monaco et al., 2016). This overreliance on herbicides has resulted in the selection of herbicide resistant *B. tectorum* biotypes (Heap, 2017; Mallory-Smith et al., 1999; Park & Mallory-Smith, 2004), which complicates current and future management of this invader species, and deepens uncertainty how its interactions with other pests and pathogens will impact desirable plant species.

Bromus tectorum can grow and survive in a variety of habitats due to its inter-population genetic diversity, phenotypic plasticity, and a span of locally adapted ecotypes; allowing this species to maintain fitness in both marginal and high-quality environments (Hufft & Zelikova, 2016). These traits could benefit *B. tectorum* survival in altered climate conditions. The range of suitable environments for *B. tectorum* in the Intermountain West will likely expand northward in response to rising temperature and altered precipitation regimes (Bradley et al., 2009, 2016). In response to CO_2, Ziska, Reeves, & Blank (2005) reported a 1.5-2.7 g/plant increase in *B. tectorum* aboveground biomass for every 10μmol mol^{-1} increase in CO_2. However, CO_2 fertilization effects may not be the most influential climate change factor impacting *B. tectorum*. Blumenthal et al. (2016) conducted a FACE (free-air CO_2 enrichment) study and reported that a warming treatment (+1.5°C day/3°C night) more than tripled *B. tectorum* biomass and seed production due to recruitment and growth, whereas elevated CO_2 (600 ppmv) had minimal effects. Above ambient temperatures have shown to enhance *B. tectorum* seed weights and germination rates, and lower seed mortality (Zelikova et al., 2013). Also, when precipitation was a limiting factor, Zelikova et al. (2013) reported no phenological differences and warming (+2 and +4°C) negatively impacted *B. tectorum* biomass and reproduction.

Research addressing the combined effects of nitrogen on *F. pseudograminearum* and *B. tectorum* is lacking. Rowaished (1981) compared the effects of NO_3 and NH_4, as well as nitrogen concentration, in *F. graminearum* infected and healthy winter wheat. Infected seedling death increased with greater nitrogen concentration, and NH_4

application resulted in more seedling death and disease severity compared to NO_3. Smiley (2019) found that whitehead incidence in wheat due to *Fusarium* crown rot increased with increasing nitrogen rate. *Bromus tectorum* has been found to increase biomass and culms m^{-2}, and to inhibit positive responses of winter wheat to nitrogen (NH_4NO_3 at 56 kg/ha). Additionally, when precipitation was 70% of normal, nitrogen applied in winter wheat infested with *B. tectorum* reduced crop yield from 12% to 28% (Anderson, 1991). Similarly, other research found that *B. tectorum* in winter wheat prevented otherwise positive yield benefits of split nitrogen (32% aqua ammonia solution) application. Nitrogen applications during the growing season further reduced winter wheat yield while *B. tectorum* biomass increased when precipitation was moderate. However, neither species benefitted from growing season nitrogen applications during a dry year (Ball et al., 1996)

Montana wheat and barley production could be at great risk if the impact of *B. tectorum, F. pseudograminearum,* and their potential interactions are augmented by climate change. Mean annual temperatures in the state have increased (~4.5° C in 1895 to ~6° C in 2016) (National Oceanic and Atmospheric Administration [NOAA], 2017) and projections show a continued warming trend (+1.7-3.9°C by 2050) across the state, in all seasons, and under all greenhouse gas emission scenarios throughout the 21st century (Whitlock et al., 2017). Changes in average precipitation in Montana are not as drastic as temperature, but have decreased 2.3 cm in the winter (Whitlock et al., 2017). Precipitation is projected to decrease in summer and increase in all other seasons, as well as become more variable; increasing possibility of severe droughts (Whitlock et al., 2017). Atmospheric CO_2 is expected to continue to rise, and depending on emissions scenario could reach upwards of 1000 ppm by 2100 (Intergovernmental Panel on Climate Change [IPCC], 2014). The current body of research indicates that a drier environment under further elevated CO_2 could be beneficial to *F. pseudograminearum* and *B. tectorum* success (Blumenthal et al., 2016; Holloway et al., 2013; Melloy et al., 2010, 2014; Moya-Elizondo, 2013; Zelikova et al., 2013; Ziska et al., 2005), while a warmer environment may benefit *B. tectorum* but not *F. psuedograminearum* (Blumenthal et al., 2016; Sabburg et al., 2015).

The goal of this study was to identify if *B. tectorum* is susceptible to *F. pseudograminearum* and if so, evaluate the impact of infection, assess how elevated CO_2 and nitrogen impact *B. tectorum* and *F. pseudograminearum*, and bring to light interactions between these biotic and abiotic variables. The research questions of this study were as follows: 1) How do *B. tectorum* emergence, biomass, relative growth rate, and primary physiology respond to elevated CO_2 with low and high nitrogen? 2) How does *F. pseudograminearum* growth respond to elevated CO_2 with low and high nitrogen? 3) Are there any interactions occurring between these biotic and abiotic variables? We expected that elevated CO_2 and high nitrogen availability would result in greater *B. tectorum* emergence, biomass, and relative growth rate as well as augment *F. pseudograminearum* infection. Photosynthetic rate and intercellular CO_2 were expected to be enhanced, and stomatal conductance and transpiration rate were expected to be reduced under elevated CO_2, compared to ambient climatic conditions. We predicted that increasing fungal infection would negatively impact *B. tectorum* growth but were uncertain of the degree. We could not anticipate how these factors would interact, as the current knowledge base is limited.

Materials and Methods

Experimental Design and Treatment Application

This research was conducted in two growth chambers at the Montana State University Plant Growth Center. Two trials (t1: 12 February 2016 to 6 May 2016, t2: 31 May 2016 to 23 August 2016) were conducted using the same two growth chambers. The design was a randomized factorial combination of two nitrogen (N) levels (63 kg N/ha, 219 kg N/ha), two pathogen levels (*F. pseudograminearum* inoculated and uninoculated), and two CO_2 levels [ambient (385 ppm) and elevated (750 ppm)]. The ambient growth chamber (Conviron PGR15, 1.5 m_2) utilized a mixture of incandescent (Sylvania, FP39/841/ho/eco) and halogen (Halogen Bulbs, Cleveland, OH) bulbs. The elevated growth chamber (Conviron BDR16, 1.5 m_2) utilized an equal amount of 400-watt high-pressure sodium bulbs (Phillips Alto, Solmerset, NJ) and 400-watt metal halide bulbs (Venture, Solon, OH). Growth chamber temperatures were set at 24°C day and 18°C night.

For each trial, 154 black plastic pots (10 cm X 10 cm X 30 cm) were filled with 1:1:1:3 mixture by volume of steam-pasteurized mineral soil, Canadian sphagnum peat moss (Aquagro 2000G; Aquatrols, Paulsboro, NJ), washed concrete sand, and Sunshine Mix number 2 Basic (Sun Gro Horticulture, Vancouver, BC, Canada). Prior to each trial, soil in each pot was leached to reduce soil N by saturating with water and draining once a day for 7 days. During this period, pots were housed in a greenhouse with a 16 h photoperiod of natural sunlight supplemented with mercury vapor lamps (165 μmol m^{-2} sec^{-1}) and 18.3-26.7°C day and 10-23.9°C night temperatures. After the leaching period, soil samples from ten randomly selected pots were analyzed for NPK and percent organic matter (Agvise Laboratories, Northwood, SD) (Table 2.1).

Table 2.1. Mean percent organic matter, nitrate, phosphorus, and potassium from pots leached prior to each trial ± SE.

	Trial 1	Trial 2
% Organic Matter	5.13 ± 0.12	4.58 ± 0.09
Nitrate (ppm)	4.25 ± 1.35	2.05 ± 0.78
Phosphorus (ppm)	13.9 ± 0.56	6.4 ± 0.22
Potassium (ppm)	296.4 ± 6.08	191.1 ± 2.59

Bromus tectorum seeds, locally collected in the summer of 2015, were surface sterilized (60 sec. EtOH, 60 sec. 10% bleach, 60 sec. EtOH, 30 sec. H_2O) and dried at room temperature. Six *B. tectorum* seeds were seeded 2.5 cm deep in each pot. All pots were fertilized with either a high or low dose of urea, in addition to 0.05 g P_2O_5 powder and 0.05 g K_2O powder. Urea was delivered by dissolving urea prills in water at a rate of 9.76 g urea prills/1000 mL of water (high nitrogen), and 2.78 g urea prills/1000 mL (low nitrogen). The K_2O powder was dissolved in water prior to application, while P_2O_5 was added to the soil surface and watered in. Two additional NPK fertilizations were carried out for each trial (t1: 38 d and 59 d, t2: 45 d and 50 d).

Seedling emergence was recorded daily and seedlings were thinned to the most phenologically advanced plant 19 and 15 days after seeding for trial one and two, respectively. Fungus treated plants were infested with 1 mL of *F. pseudograminearum* inoculum (preparation described below) pipetted onto the crown of *B. tectorum* plants 26 and 36 days after seeding for trial one and two, respectively.

Three harvests occurred in each trial: early growth stage, peak biomass, and maturation. The first harvest took place 34 and 44 days after seeding for trial 1 and 2, respectively, when the plants had between 4-18 tillers. The second harvest occurred 55 and 62 days after seeding for trial 1 and 2, respectively. The third and final harvest took place 84 days after seeding for both trials.

Fusarium pseudograminearum Inoculum Preparation

Fusarium pseudograminearum isolate 2228 (Fpg2228) was chosen for this study due to its aggressiveness and vigor in previous studies (Dyer et al., 2009; Moya-Elizondo et al., 2011). Cultures of *F. pseudograminearum* were maintained on potato dextrose agar (PDA) at room temperature and conidial suspensions were obtained following the protocol of Bai and Shaner (1996). In short, 500 ml flasks were filled with 250 ml of autoclaved mung bean medium, inoculated with two *F. pseudograminearum* plugs, and placed on a shaker for 1 week at room temperature. The resulting conidial suspension was then diluted with reverse osmosis water to obtain a ~2.5 million spores per 1 mL of solution.

Bromus tectorum Physiological Data Collection

The broadest part of one representative *B. tectorum* leaf in each pot was selected to evaluate the impact of growing conditions on primary physiological parameters including photosynthetic rate (μmol CO_2 m^{-2} s^{-1}), stomatal conductance (mol CO_2 m^{-2} s^{-1}), intercellular CO_2 concentration (μmol mol^{-1}), and transpiration rate (mmol H_2O m^{-2} s^{-1}). All measurements were obtained using a LI-6400 portable photosynthesis system (Li-Cor Inc). A light intensity of 1400 μmol photons m^{-1} s^{-1} (10% blue and 90% red light) was used inside the chamber with an airflow rate of 500 μmol s^{-1}. Ambient and elevated CO_2 plants were exposed to a reference CO_2 concentration of 385 μmol CO_2 mol^{-1} and 750 μmol CO_2 mol^{-1}, respectively. Measurements were obtained at 62 and 63 days after seeding in trial one and two, respectively.

Bromus tectorum Biomass and Data Collection

Pots selected for the third harvest of each trial were soil sampled and analyzed for NPK and percent organic matter after the plant biomass was collected (Agvise Laboratories, Northwood, SD). Table 2.2 displays soil nitrate levels. Results of phosphorus and potassium levels are not shown as they were not treatment levels and merely used to monitor soil nutrient levels. For each harvest, above and belowground biomass was harvested and dried at 60 °C to constant mass and weighed to the nearest 0.001g. Following Hoffmann and Poorter (2002) Relative Growth Rate (RGR) between the first and second harvest (RGR_{2-1}), second and third harvest (RGR_{3-2}), and third and first harvest (RGR_{3-1}); was calculated as:

$$RGR_{2-1} = (\overline{lnW_2} - \overline{lnW_1})/(t_2-t_1)$$

$$RGR_{3-2} = (\overline{lnW_3} - \overline{lnW_2})/(t_3-t_2)$$

$$RGR_{3-1} = (\overline{lnW_3} - \overline{lnW_1})/(t_3-t_1)$$

Where W_1, W_2, and W_3 are plant dry weights (g) at times t_1, t_2, and t_3.

Table 2.2. Mean nitrate (ppm) ± SE for each treatment from final harvest of each trial.

Treatment	Trial 1	Trial 2
AmbL-	1.40 ± 0.187	0.50 ± 0.00
AmbL+	1.17 ± 0.105	4.58 ± 1.71
AmbH-	1.92 ± 0.30	2.25 ± 0.512
AmbH+	5.08 ± 2.09	14.5 ± 2.82
ElevL-	1.25 ± 0.214	0.58 ± 0.083
ElevL+	1.75 ± 0.309	0.67 ± 0.166
ElevH-	2.00 ± 0.532	0.70 ± 0.122
ElevH+	35.3 ± 10.95	9.79 ± 4.55

Treatments included: Ambient CO_2-Low N-No *Fusarium* (AmbL-), Ambient CO_2-Low N-Plus *Fusarium* (AmbL+), Ambient CO_2-High N-No *Fusarium* (AmbH-), Ambient CO_2-High N-Plus *Fusarium* (AmbH+), Elevated CO_2-Low N-No *Fusarium* (ElevL-), Elevated CO_2-Low N-Plus *Fusarium* (ElevL+), Elevated CO_2-High N-No *Fusarium* (ElevH-), Elevated CO_2-High N-Plus *Fusarium* (ElevH+).

Fusarium pseudograminearum Detection and Quantification

Isolation of *F. pseudograminearum* on PDA: *Bromus tectorum* lower stems and crowns were harvested, stored at 5 °C, and processed within four days for visual detection of *F. pseudograminearum* on PDA as well as for real-time quantitative PCR (qPCR). For visual assessment of fungal infection, six crown and lower stem pieces from each sample were surface sterilized (60 sec. 70% EtOH, 60 sec. 10% bleach, 30 sec. RO water), plated on acidified half-strength potato dextrose agar, and stored at room temperature for ~1 week. Results were recorded as the number of plant tissue segments growing *F. pseudograminearum* per plate.

Real-Time Quantitative PCR: Ten lower stem and crown samples, or the maximum stem number grown if less than ten were produced, were bulked from each pot to generate an overall DNA sample for each experimental unit. For analysis, the latter was standardized by dividing DNA copy number by shoot biomass. Plant tissue was cleaned of any soil and leaf tissue prior to sampling. To isolate *F. pseudograminearum* DNA from *B. tectorum*, three-mm pieces were cut from the lower crown tissue of the plant samples using a double-blade rotary knife to ensure consistent excision of plant tissue. Samples were processed using FastDNA kits (QBiogene Inc., Irvine, CA) (Hogg et al., 2007). DNA samples were subsequently diluted 1:10 with molecular-grade water prior to qPCR analysis.

Real-time quantitative PCR was used to quantify *F. pseudograminearum* DNA in *B. tectorum* plant tissue. The probes utilized in the qPCR procedures were dual-labeled with 6-carboxyfluorescein fluorescent reporter dye and 6-carboxyltetramethylrhodamine fluorescence quencher (TaqMan® TAMRA probe). The primer-probe combination is specific to the trichodiene synthase (*tri5)* gene of *F. pseudograminearum, F. culmorum*, and *F. graminearum* (Hogg et al., 2007; Strausbaugh et al., 2005).

The Bio-Rad CFX Connect Real-Time System (BioRad USA) was used to conduct all qPCR assays. A two-step protocol was used with the following thermocycling parameters: 55°C for 2 minutes, 94°C for 10 minutes, and subsequent 43 cycles of 15 seconds at 94°C and 62°C for 60 seconds. The 25 μl qPCR reaction included 2.5 μl of 2μM TaqMan probe, 2.25 μl of a 1:1 mixture of 20 μM forward and reverse primers (Integrated DNA Technologies, Inc. Coralville, IA), 12.5 μl of Universal TaqMan Master Mix (Applied Biosystems, Carlsbad, CA), 2.75 μl of molecular-grade water, and 5 μl of 1:10 diluted DNA sample. One positive control, extracted from *F. pseudograminearum* grown on PDA, and one negative control, *Cochliobolus sativus* DNA, were included on each qPCR plate. Each qPCR plate also contained three technical replicates of a dilution series of five DNA standards, ranging from 10^2 – 10^6 DNA copies, these standards were derived from a cloned fragment of the *tri5* gene isolated from *F. culmorum* (Hogg et al., 2007).

Each *B. tectorum* DNA sample was run with three technical replicates and the mean population value for each sample was calculated using the three replicates. The standard deviation of *Cq* values - the number of cycles required for a sample to amplify above the detection threshold of fluorescence - between technical replicates was inspected to ensure that the standard deviation did not surpass 0.5 cycles. The number of *F. pseudograminearum* DNA copies reported in the plant samples by qPCR was interpreted as a proxy for the quantified lower stem and crown population of *F. pseudograminearum.*

Statistical Analysis

Data from trial one and two were combined for analysis unless the patterns between the two trials were dissimilar. Interactions between treatment factors are only discussed if found to be statistically significant. Log transformations were applied when necessary to meet assumptions of normality and homoscedasticity. All datasets from this experiment were log-transformed, except for percent emergence, PDA infection, relative growth rate, photosynthetic rate, and intercellular CO_2 level. Biomass data, although log-transformed for analysis, is graphically displayed as untransformed for impact. With the exception of fungal infection rate on PDA, which was analyzed with generalized linear models, linear models were used for analysis of all other datasets. Table 2.1 displays the predictors used in analysis. The *Fusarium* treatment was not included in emergence analyses because the fungal inoculum was not applied before or during seedling emergence.

Table 2.3. Datasets and predictor variables

Dataset	Predictor Variables
Percent Emergence	Nitrogen and CO_2
Time to 50% Emergence	Nitrogen and CO_2
PDA Infection Rate	Nitrogen, CO_2, Harvest Number
qPCR	Nitrogen, CO_2, Harvest Number, Trial
Biomass (Root, Shoot & Total)	Nitrogen, CO_2, *F. pseudograminearum*, Harvest Number
Relative Growth Rate (RGR) * RGR_{2-1}, RGR_{3-2}, and RGR_{3-1}	Nitrogen, CO_2, *F. pseudograminearum*, Harvest Number
Primary Physiology	Nitrogen, CO_2, *F. pseudograminearum*

All analyses were completed in the statistical analysis program R (version 3.3.2, R Development Core Team, 2016). Linear models were built with the lme4 package (Bates et al., 2018) and lmerTest package (Kuznetsova et al., 2017). Analysis of variance (ANOVA) was used to assess models, and when significant models were fit, estimated marginal means (EMM’s) were calculated using the emmeans package, with a significance level of $P < 0.05$ based on T-ratios and using the Tukey adjustment method (Lenth et al., 2018).

Results

Bromus tectorum Emergence

For time to 50% emergence (t50), CO_2 level was marginally significant ($P = 0.052$), but pairwise comparisons showed that the 95% confidence levels of the CO_2 treatments overlapped, and therefore were not significantly different. The untransformed means±SE t50 for ambient and elevated CO_2 were 4.35±0.086 and 4.6±0.11 days, respectively. *Bromus tectorum* seeds in the high nitrogen treatment had a greater mean t50 compared to those treated with less nitrogen ($P < 0.005$) (Fig. 2.1).

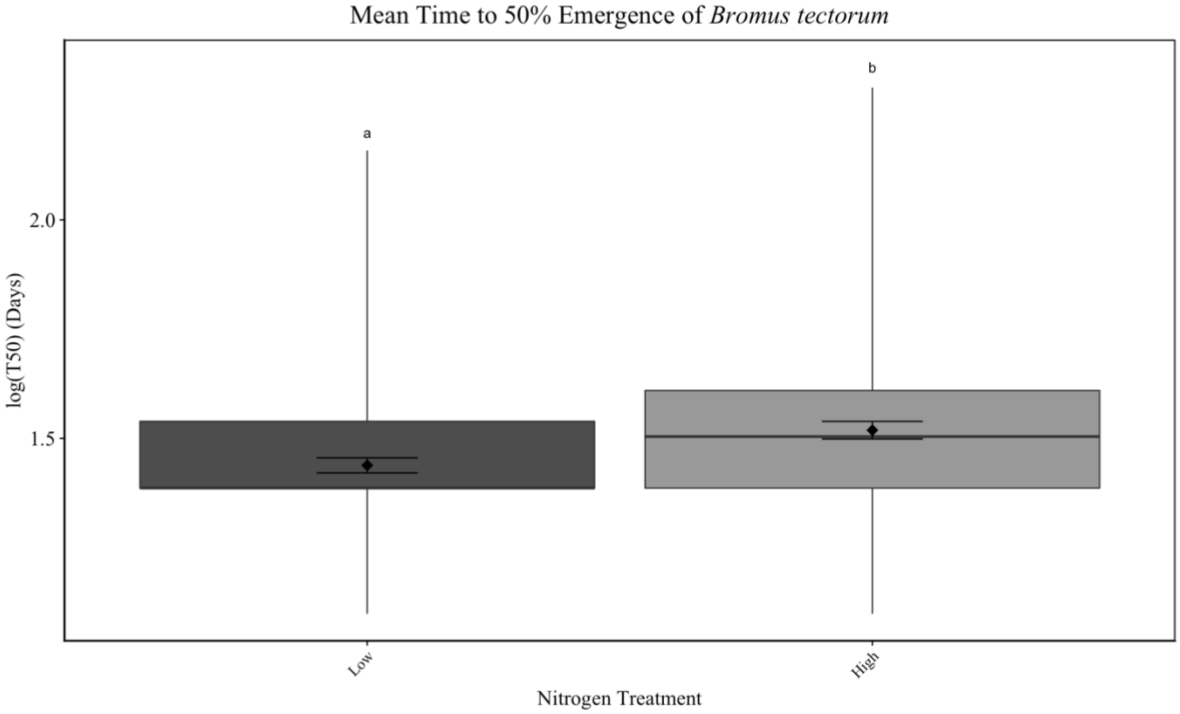

Figure 2.1. Effects of nitrogen level (low N, n=120; high N, n=114) on mean time to 50% emergence [log(t50)] of *Bromus tectorum*, measured in days after seeding, ± the standard error of the mean. Treatments with different letters are significant at the 0.05 level.

Both CO_2 and nitrogen fertilization impacted the percentage of emergence of *B. tectorum* seedlings. When compared to ambient CO_2, elevated CO_2 had a positive effect ($P < 0.0005$) on *B. tectorum* emergence, and the low nitrogen treatment increased *B. tectorum* emergence ($P < 0.0001$), compared to the high nitrogen treatment (Fig. 2.2).

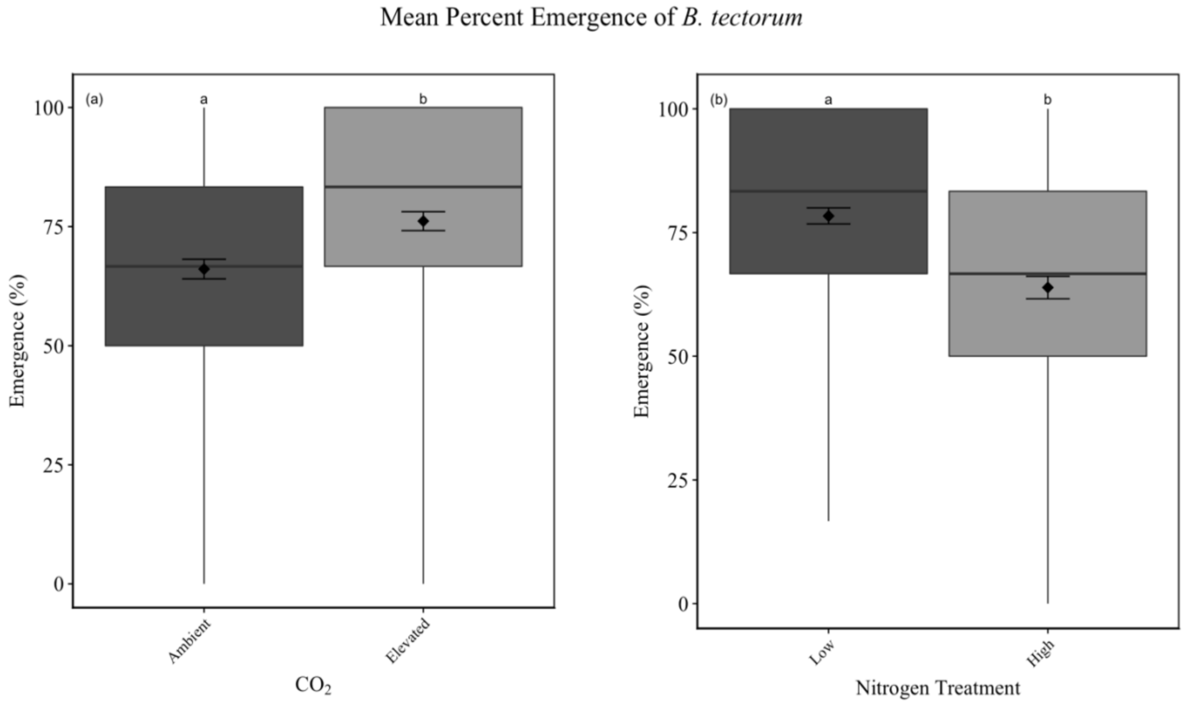

Figure 2.2. Effects of CO_2 [ambient (n=144), elevated (n=144)] and nitrogen (low N, n=144; high N, n=144) level on mean percent emergence of *Bromus tectorum* seedlings ± the standard error of the mean. Treatments with different letters are significant at the 0.05 level.

Analysis of the fungal infection on PDA revealed that *F. pseudograminearum* inoculation of *B. tectorum* was successful in both trials. Pairwise comparisons revealed that neither nitrogen or CO_2 level had a significant impact on the success of fungal infection ($P > 0.05$). Mean percent infection increased between harvest two and three ($P < 0.0001$) (Table 2.2).

Fusarium pseudograminearum Detection and Quantification

Table 2.4 Mean percent infection of *F. pseudograminearum* in *B. tectorum* after the second and third harvest (59 and 84 days after seeding [DAS], respectively).

Harvest Number	Control (%±SEM)	Inoculated (%±SEM)
II	0	81.9%±4.03
III	10.64%±3.87	99.04%±0.71

Results from the qPCR analysis indicated that neither nitrogen or CO_2 influenced the number of *F. pseudograminearum* DNA copies detected in *B. tectorum* samples. Inoculated plants from harvest 3 had significantly greater numbers of fungal DNA than those in harvest 2 ($P < 0.001$). Inoculated plants in the second trial had significantly greater fungal DNA copies compared to those in trial 1 ($P < 0.05$). Trials displayed similar patterns of DNA copy number, and the log(mean) fungal DNA copy number for inoculated plants in harvest 2 and harvest 3 were 9.36±0.52 and 13.89±0.23, respectively.

Impact of Nitrogen on *B. tectorum* Biomass Production and Primary Physiology

Bromus tectorum biomass differed across harvests, reflecting their growth stage difference ($P < 0.0001$). Nitrogen was not a significant factor for *B. tectorum* total biomass at any harvest. However, at the first harvest, plants in the low nitrogen treatment had, on average, greater root production than those in the high nitrogen treatment ($P < 0.005$) (Fig. 2.3). Plants in the high nitrogen treatment collected in the second and third harvests exhibited, on average, greater shoot production compared to those from the low nitrogen treatment ($P < 0.0001$) (Fig. 2.4).

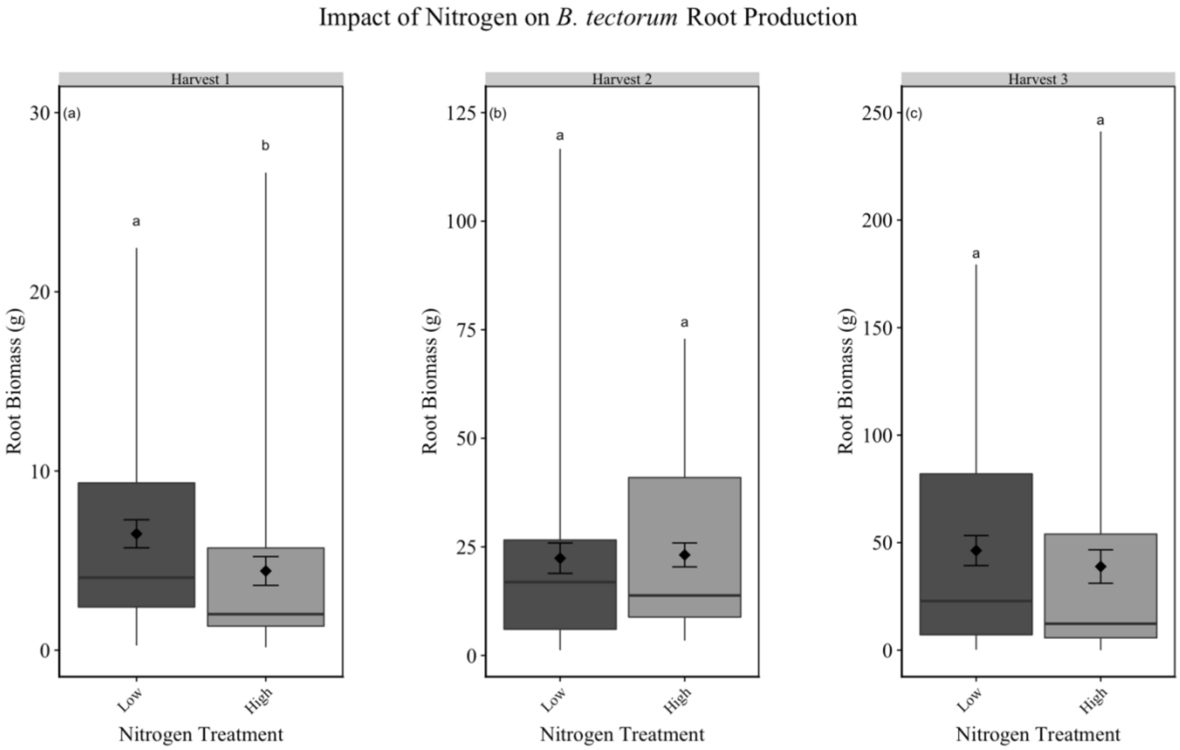

Figure 2.3. Effects of nitrogen fertilization on untransformed root biomass of *B. tectorum* at 39, 59, and 84 DAS (harvest 1, 2 and 3, respectively) ± the standard error of the mean. Low and high nitrogen (n=48, each). Treatments with different letters are significant at the 0.05 level.

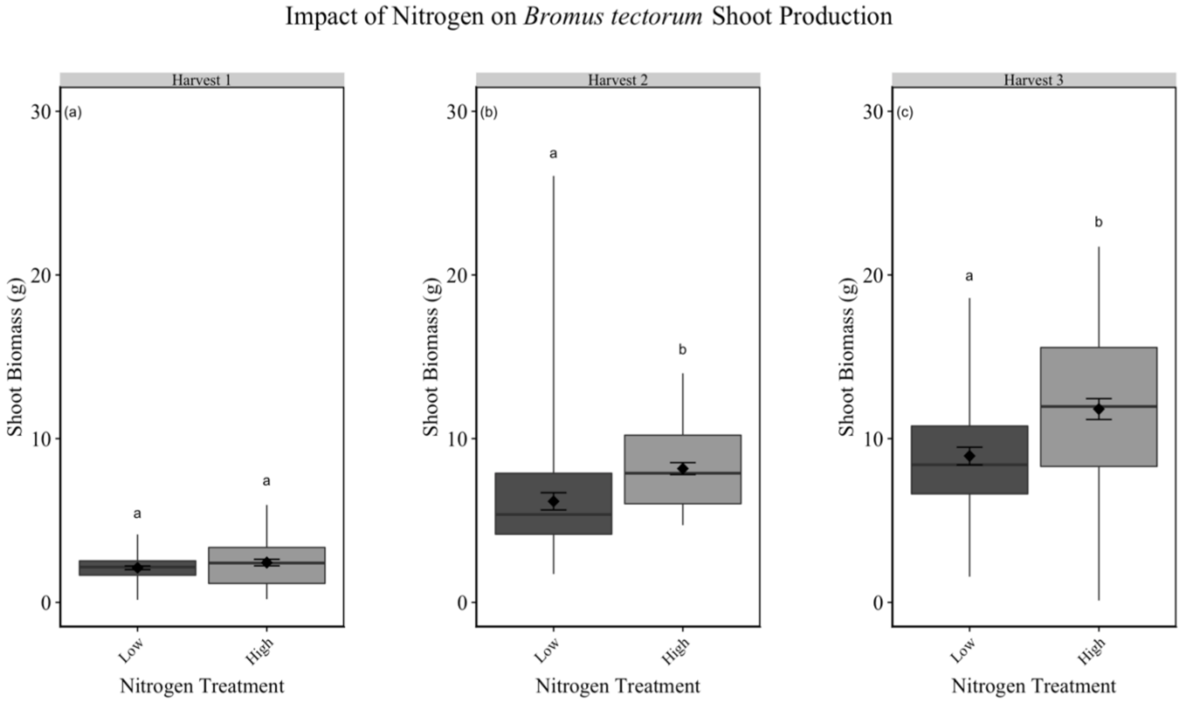

Figure 2.4. Effects of nitrogen fertilization on shoot biomass of *B. tectorum* 39, 59, and 84 DAS (harvest 1, 2, and 3, respectively) ± the standard error of the mean. Harvest 2 and 3 low nitrogen, n=48, each; harvest 2 high nitrogen, n=45; harvest 3 high nitrogen, n=50. Treatments with different letters are significant at the 0.05 level.

The mean RGR of total *B. tectorum* biomass between the first and second harvest for plants treated with low nitrogen was greater than those treated with high nitrogen ($P < 0.05$) (Fig. 2.5). An interaction was found where the mean RGR of shoot biomass between the first and second harvest was greatest in *B. tectorum* plants in the low nitrogen and ambient CO_2 treatments ($P = 0.005$) (Fig. 2.6).

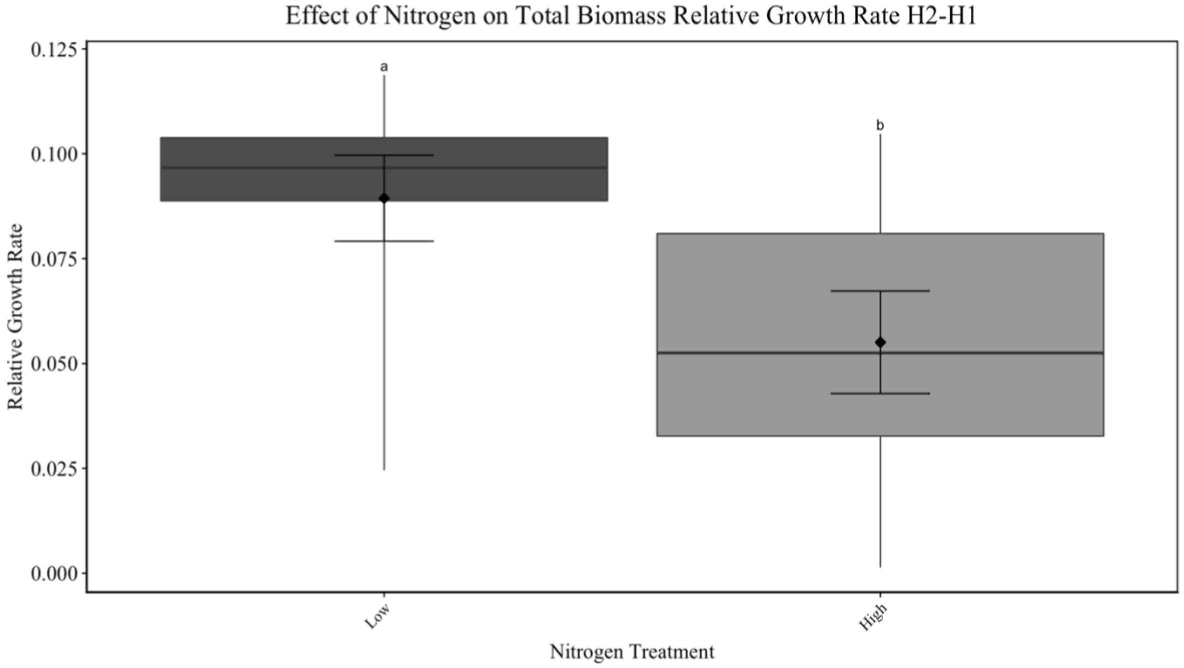

Figure 2.5. Effects of nitrogen fertilization on the relative growth rate of *B. tectorum* between 39 and 59 DAS (harvest 1 and 2, respectively) ± the standard error of the mean. Low and high nitrogen, n=8 each). Treatments with different letters are significant at the 0.05 level.

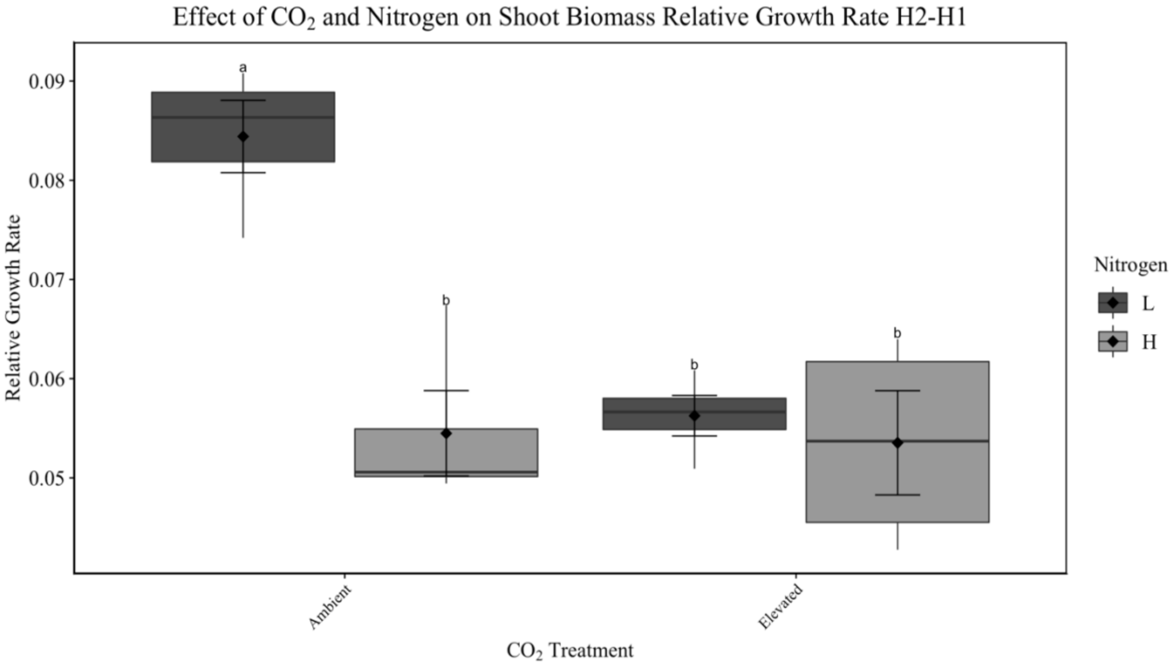

Figure 2.6. Effects of nitrogen and CO2 on the relative growth rate of *B. tectorum* between 39 and 59 DAS (harvest 1 and 2, respectively) ± the standard error of the mean. Ambient low, ambient, high, elevated low, and elevated high n=8, each. Treatments with different letters are significant at the 0.05 level.

Bromus tectorum treated in the low nitrogen treatment had, on average, greater stomatal conductance and transpiration rate ($P < 0.05$) than those treated with high nitrogen (Fig. 2.7).

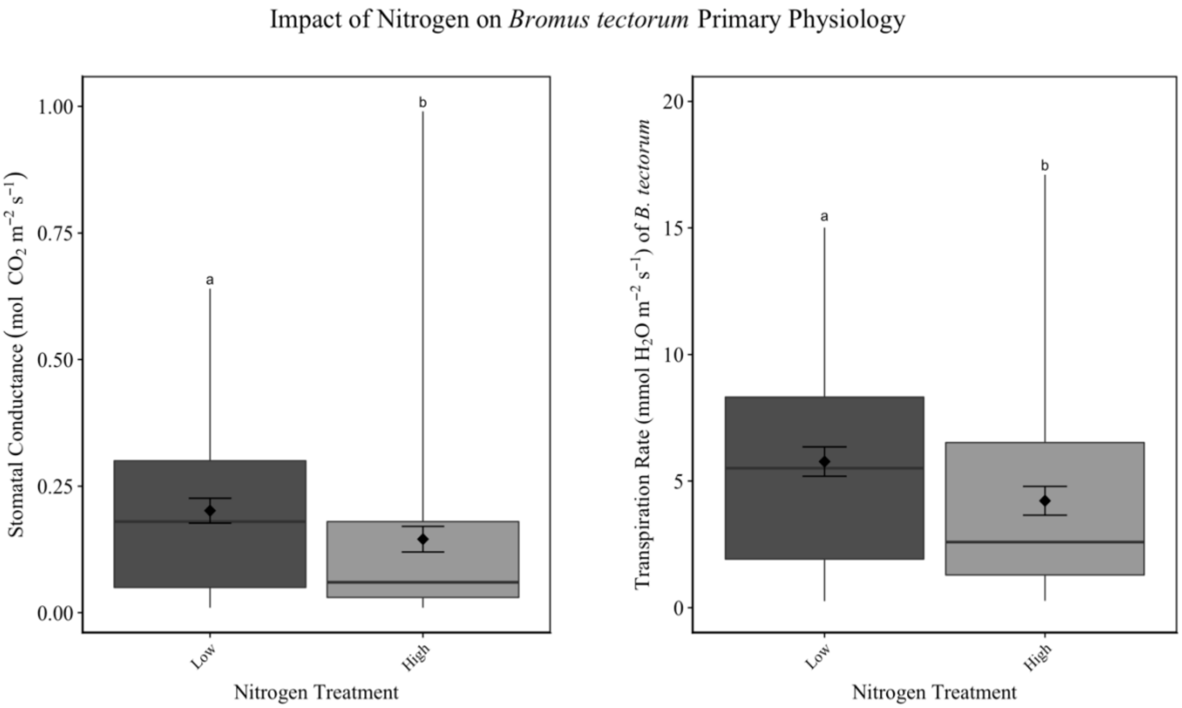

Figure 2.7. Effects of nitrogen fertilization on *B. tectorum* stomatal conductance and transpiration rate ± the standard error of the mean. Low and high nitrogen. n=8, each). Treatments with different letters are significant at the 0.05 level.

Impact of CO_2 on *B. tectorum* Biomass Production and Primary Physiology

Bromus tectorum total biomass production was impacted by CO_2 ($P < 0.0001$). The elevated CO_2 treatment resulted in greater mean total ($P < 0.0001$) (Fig. 2.8) and root ($P < 0.0005$) (Fig. 2.9) biomass production of *B. tectorum* for harvests 1 and 2, but not harvest 3. Elevated CO_2 increased mean shoot production for all three harvests ($P < 0.0005$) (Fig. 2.10).

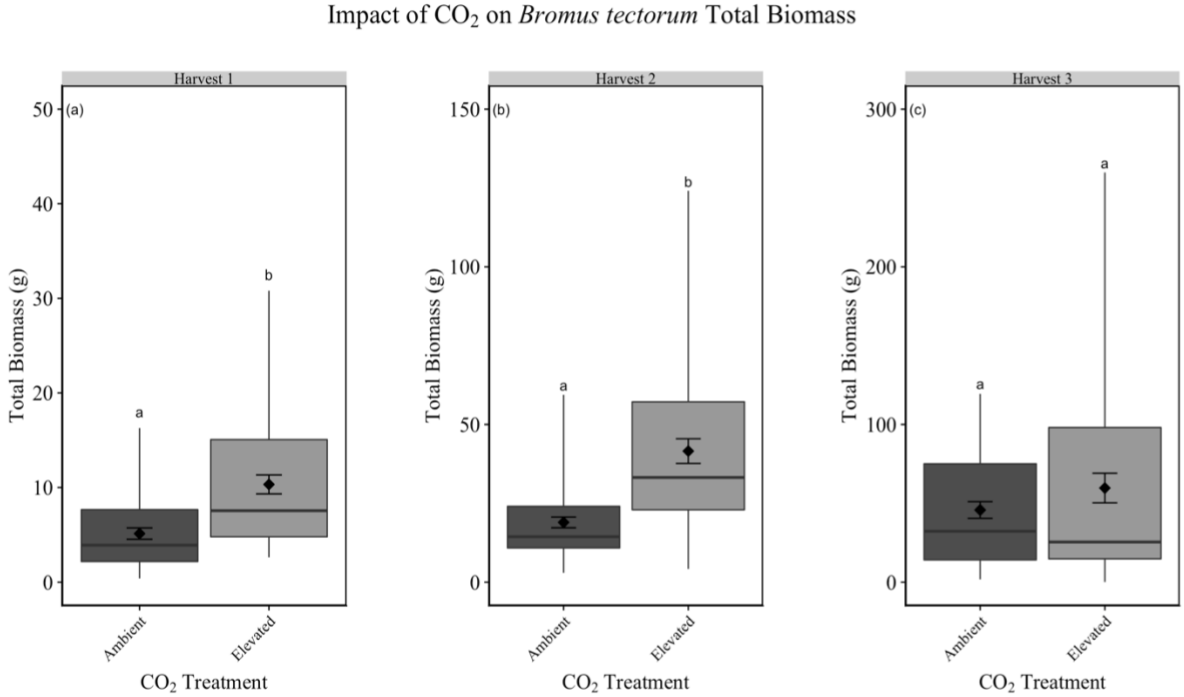

Figure 2.8. Effects of CO_2 on untransformed total biomass production of *B. tectorum* for 39, 59, and 84 DAS (harvest 1, 2, and 3, respectively) ± the standard error of the mean. Harvest 1, 2 and 3 ambient CO_2, and harvest 1 elevated CO_2, n=48; harvest 2 elevated CO_2, n=45. Treatments with different letters are significant at the 0.05 level.

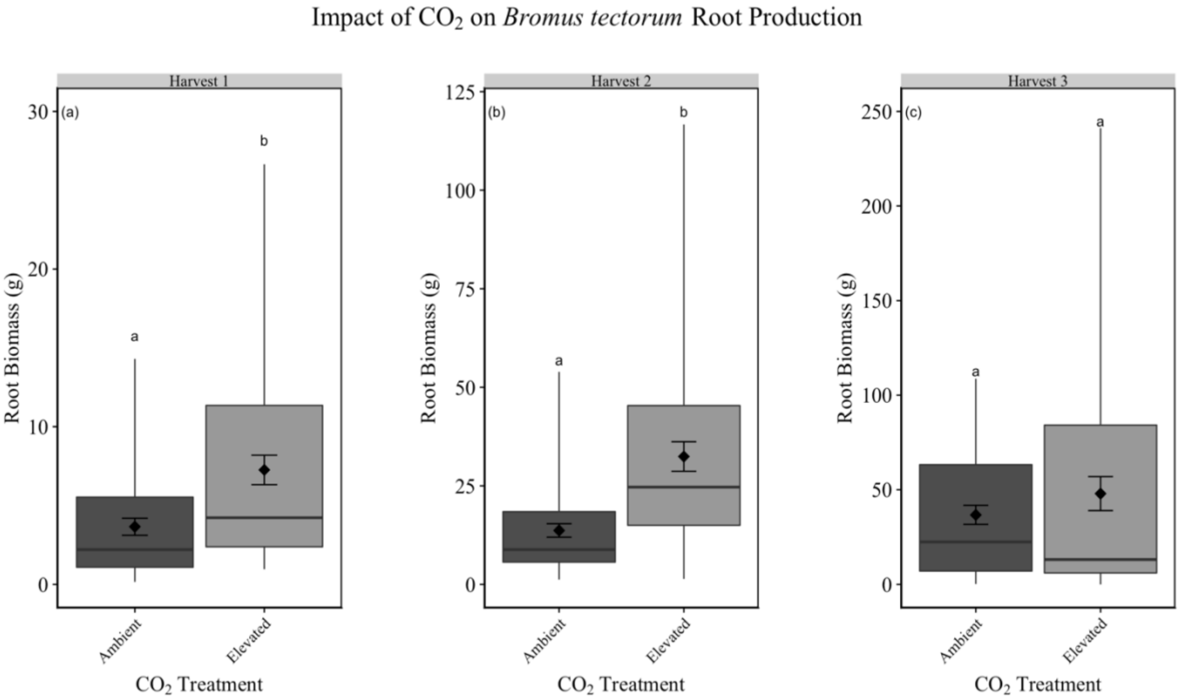

Figure 2.9. Effects of CO_2 level on untransformed root biomass production of *B. tectorum* for 39 and 59 DAS (harvest 1 and 2, respectively) ± the standard error of the mean. Harvest 1 and 2 ambient CO_2, and harvest 1 elevated CO_2 (n=48), harvest 2 elevated CO_2 (n=45).

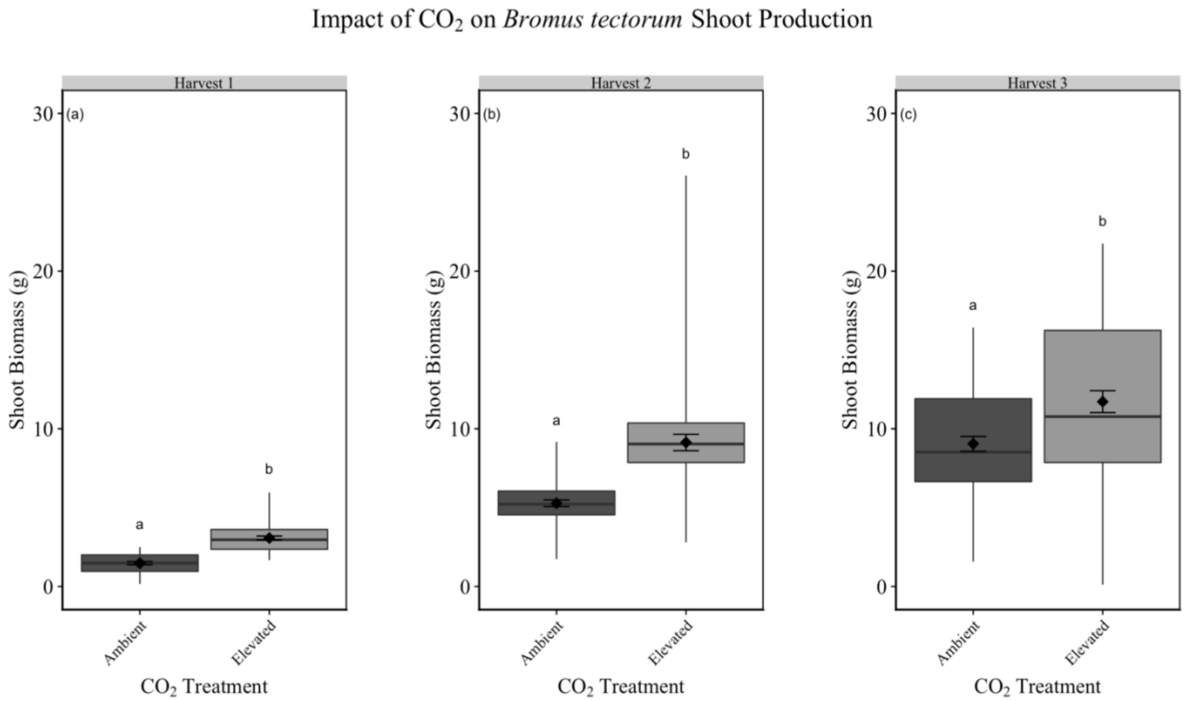

Figure 2.10. Effects of CO_2 level on untransformed shoot biomass production of *B. tectorum* for 39, 59, and 84 DAS (harvest 1, 2, and 3, respectively) ± the standard error of the mean. Harvest 1, 2 and 3 ambient CO_2, and harvest 1 elevated CO_2 (n=48), harvest 2 elevated CO_2 (n=45). Treatments with different letters are significant at the 0.05 level.

Plants grown in ambient CO_2 had a greater shoot RGR than those in elevated CO_2 conditions between the first and third harvest ($P < 0.05$) (Fig. 2.11). *Bromus tectorum* grown under elevated CO_2 conditions exhibited higher levels of intercellular CO_2 compared to those in ambient CO_2 conditions ($P < 0.0001$) (Fig. 2.12).

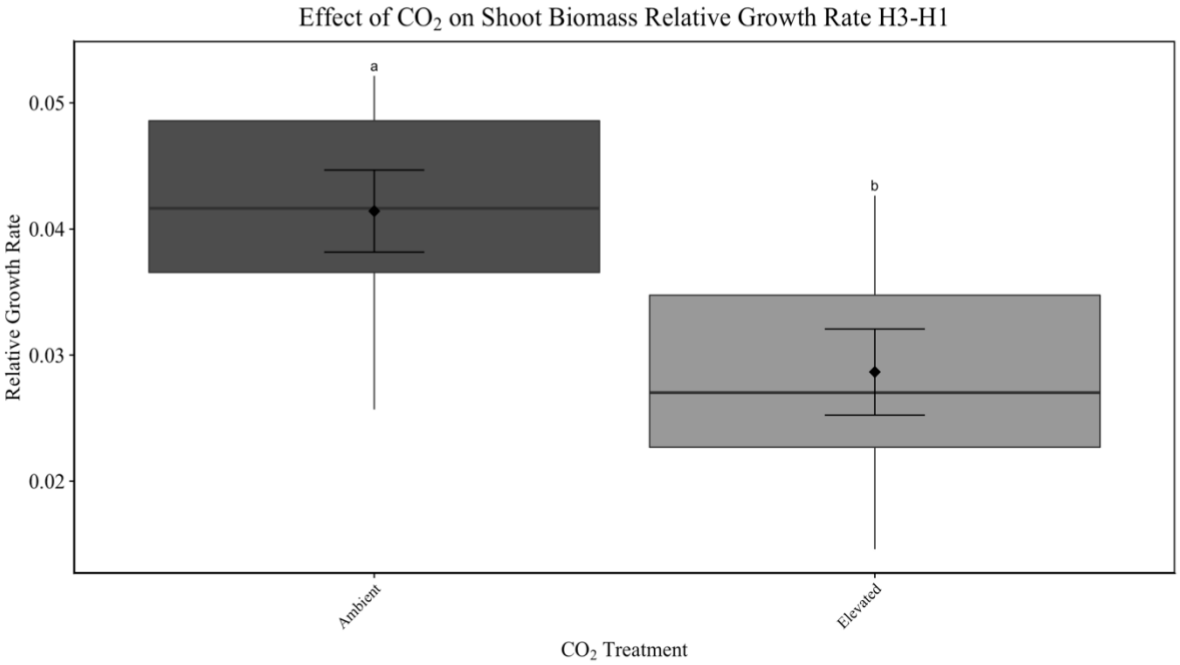

Figure 2.11. Effect of CO_2 treatment on the relative growth rate of *B. tectorum* shoot biomass between 39 and 84 DAS (harvest 1 and 3, respectively) ± the standard error of the mean. Ambient and elevated (n=8, each).

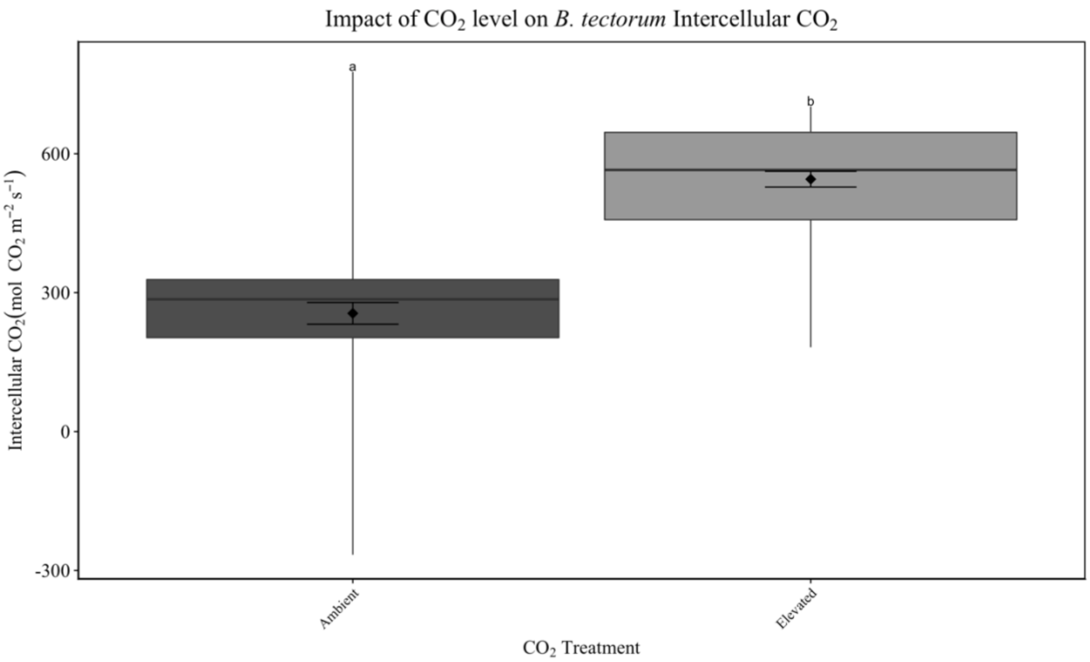

Figure 2.12. Effect of CO_2 treatment on intercellular CO_2 level of *B. tectorum* leaves ± the standard error of the mean. Ambient and elevated (n=8, each).

Impact of F. pseudograminearum Inoculation on B. tectorum Biomass Production and Primary Physiology

Bromus tectorum total biomass production was impacted by *F. pseudograminearum* inoculation ($P < 0.0001$), resulting in less total biomass production between harvests 2 and 3 ($P < 0.0005$) (Fig. 2.13). Inoculated plants from harvest 2 and 3 had less mean root mass ($P < 0.0001$) (Fig. 2.14) compared to healthy plants. Mean shoot mass of inoculated plants from harvest 3 was significantly lower than that of healthy plants ($P < 0.0005$) (Fig. 2.15).

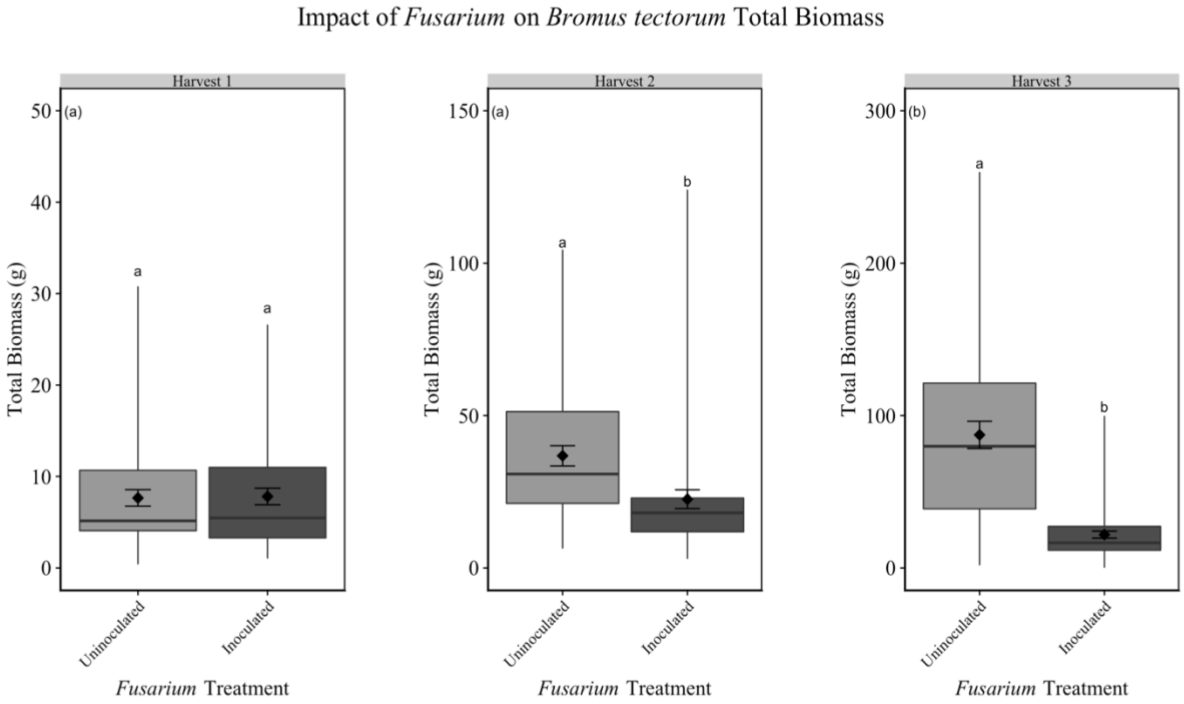

Figure 2.13. Effects of *F. pseudograminearum* inoculation on untransformed total biomass production of *B. tectorum* for 59 an 84 DAS (harvest 2 and 3, respectively) ± the standard error of the mean. Harvest 2 uninoculated and harvest 3 inoculated (n=48), harvest 2 inoculated (n=45), harvest 3 uninoculated (n=47), harvest 3 inoculated (n=52).

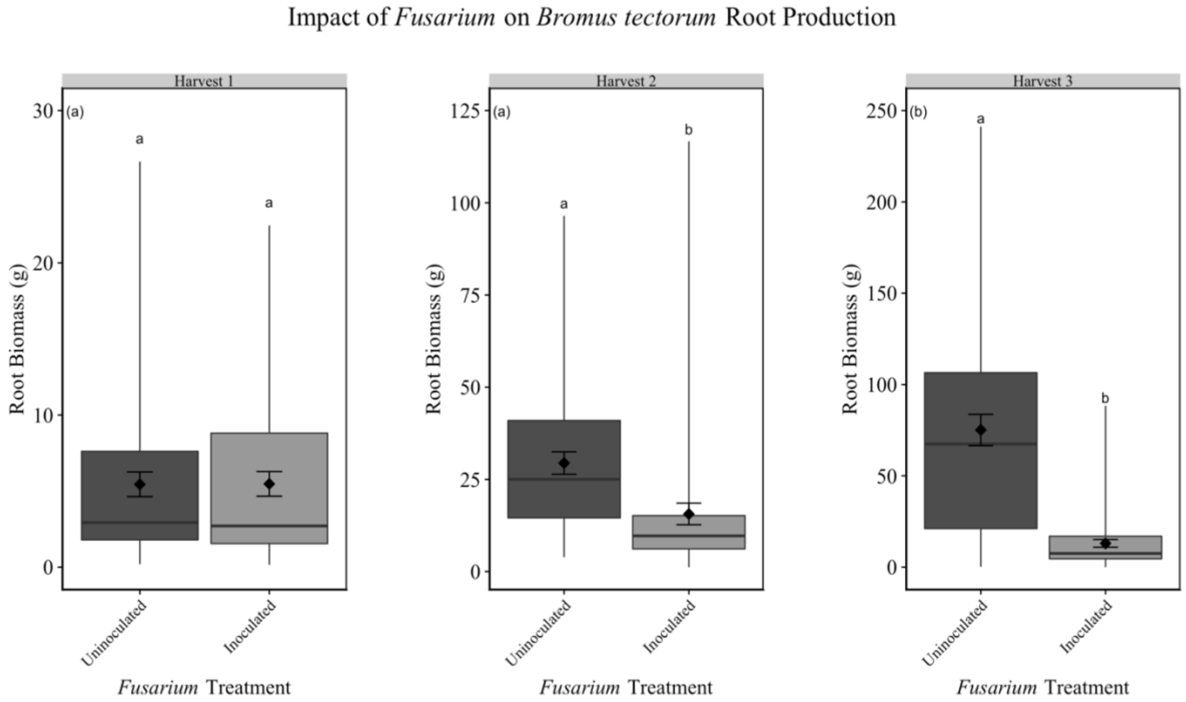

Figure 2.14. Effects of *F. pseudograminearum* inoculation on untransformed root biomass production of *B. tectorum* for 59 and 84 DAS (harvest 2 and 3, respectively) ± the standard error of the mean. Harvest 2 uninoculated and harvest 3 inoculated (n=48), harvest 2 inoculated (n=45), harvest 3 uninoculated (n=47), harvest 3 inoculated (n=52).

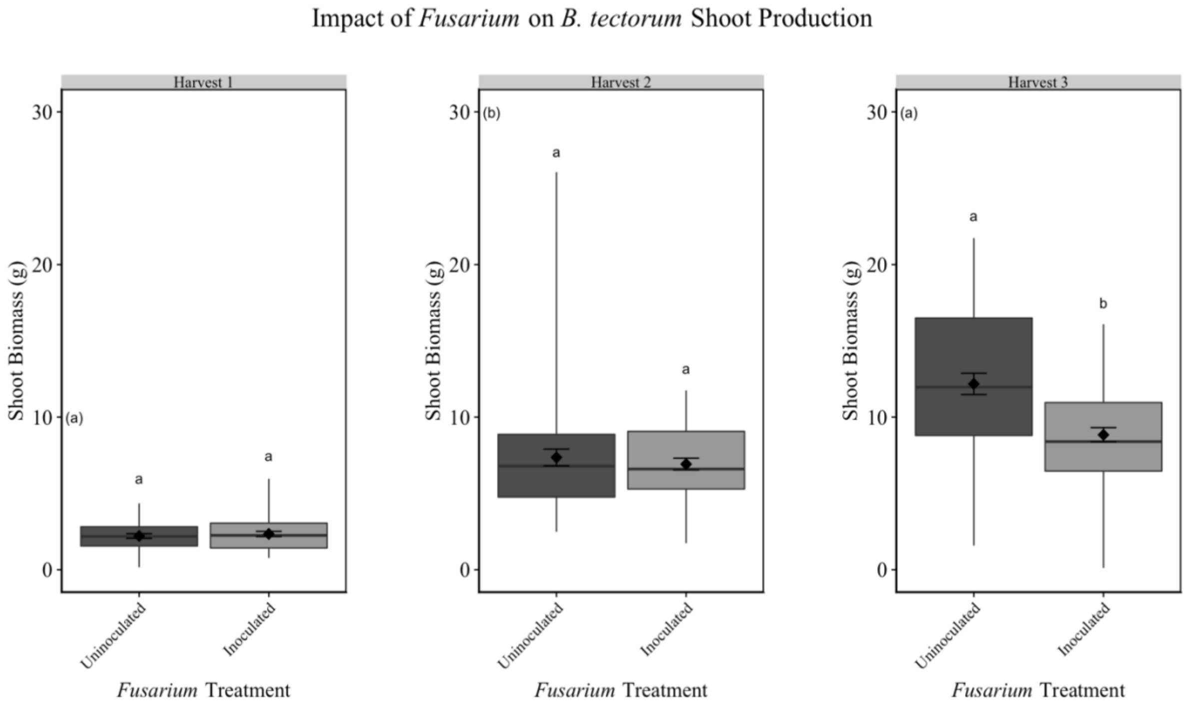

Figure 2.15. Effects of *F. pseudograminearum* inoculation on untransformed shoot biomass production of *B. tectorum* for 39, 59, and 84 DAS (harvest 1, 2, and 3, respectively) ± the standard error of the mean. Harvest 3 uninoculated (n=47), harvest 3 inoculated (n=51).

Fusarium pseudograminearum had a consistent impact on *B. tectorum* RGR. Between the second and third harvest, and the third and first harvest, inoculated plants had significantly lower mean total ($P < 0.0001$) (Fig. 2.16) and root relative growth rates ($RGR_{3-2} = P < 0.05$, $RGR_{3-1} = P < 0.0005$) (Fig. 2.17), compared to healthy plants. Shoot biomass relative growth rates were not impacted by the fungus ($P > 0.05$).

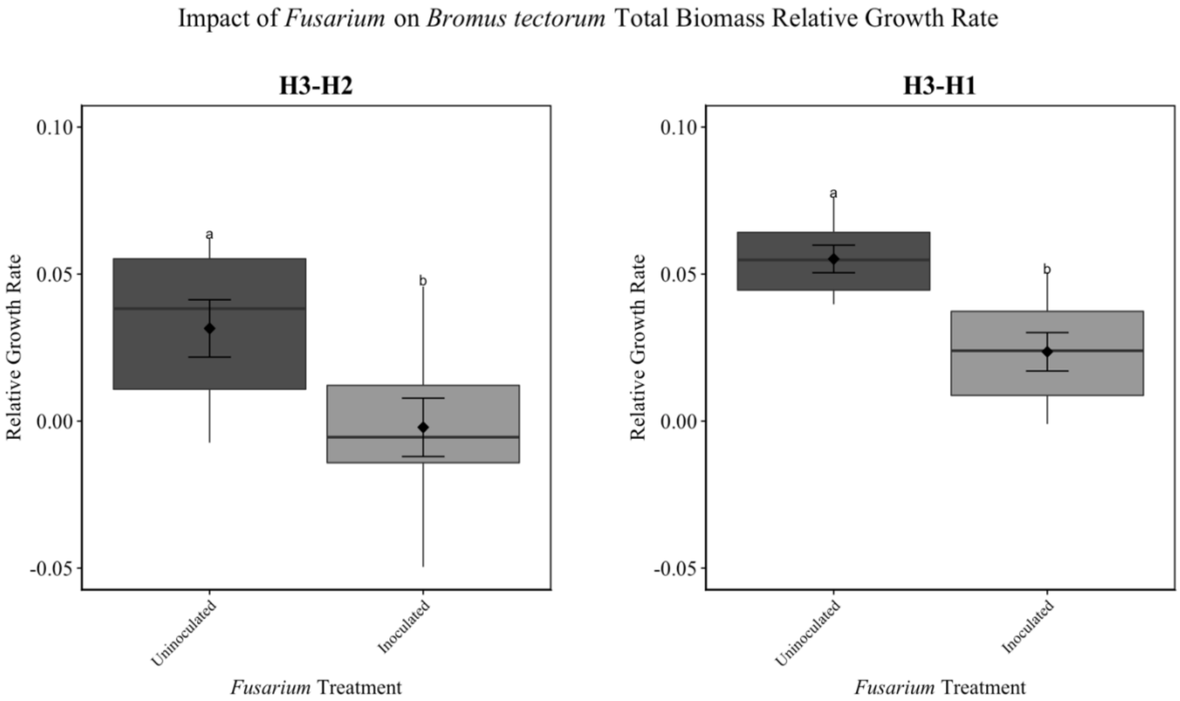

Figure 2.16. Effect of *F. pseudograminearum* treatment on the total biomass relative growth rate of *B. tectorum* between 59 and 84 DAS (harvest 2 and 3, respectively) ± the standard error of the mean. Uninoculated and inoculated (n=8, each).

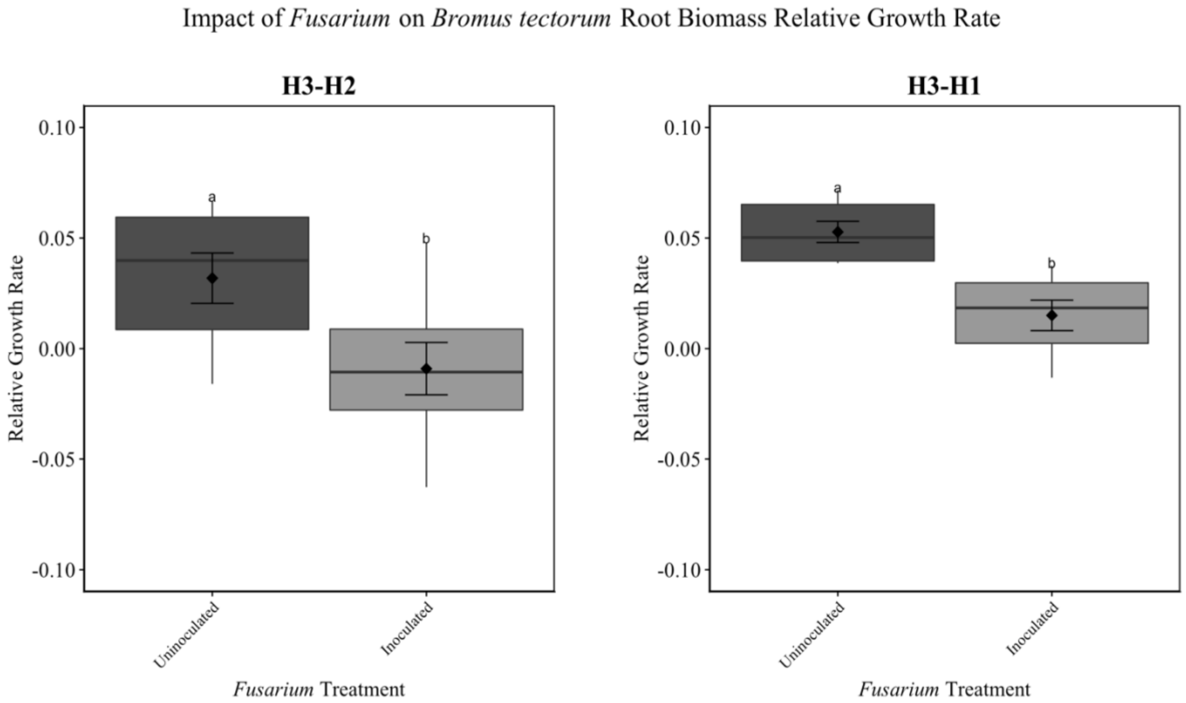

Figure 2.17. Effect of *F. pseudograminearum* treatment on the relative growth rate of *B. tectorum* root biomass between 59 and 84 DAS (harvest 2 and 3, respectively) ± the standard error of the mean. Uninoculated and inoculated (n=8, each).

Bromus tectorum plants infected with *F. pseudograminearum* had reduced photosynthetic rate ($P < 0.005$), stomatal conductance ($P < 0.0001$), intercellular CO_2 ($P < 0.05$), and transpiration rate ($P < 0.0001$) (Fig. 2.18).

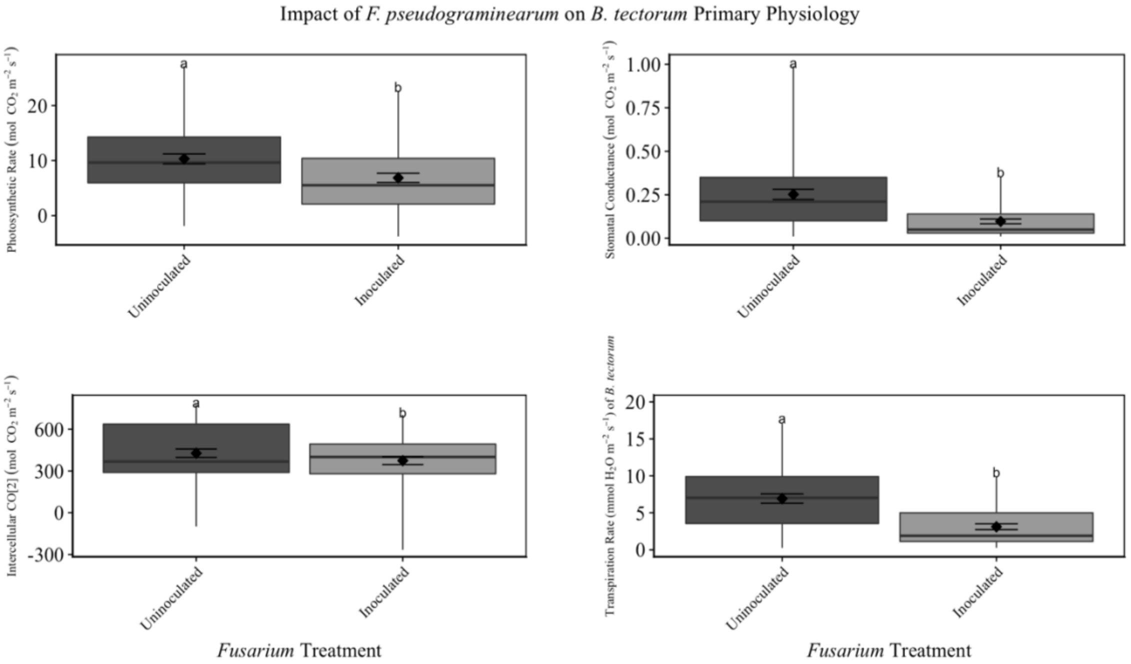

Figure 2.18. Effect of *F. pseudograminearum* treatment on the primary physiology of *B. tectorum* ± the standard error of the mean. Trial 1 and 2 combined. Uninoculated and inoculated (n=8, each).

Discussion

The geographic distribution of invasive plant species and plant pathogens, as well as their associated crop-pest interactions, has and will likely continue to be altered by climate change (Fuhrer, 2003; Germino et al., 2016). For major wheat growing areas like Montana, U.S.A., it is imperative to understand how wheat-associated pests such as *B. tectorum* and *F. pseudograminearum* respond to various climatic and management conditions. Previous research has confirmed that *B. tectorum* and *F. pseudograminearum* have adverse effects on wheat production (Akinsanmi et al., 2004; Aoki & O’Donnell, 1999; D’Antonio & Vitousek, 1992; Dyer et al., 2009; Graham et al., 2015; Ito et al., 2012; Moya-Elizondo et al., 2011; Moya-Elizondo, 2013; Perez-Mendoza et al., 2006;

Ranabhat et al., 2018; Rydrych & Muzik, 1968; Sperry et al., 2006a). Elevated atmospheric CO_2 can benefit the growth and success of both *B. tectorum* and *F. pseudograminearum* (Blumenthal et al., 2016; Holloway et al., 2013; Melloy et al., 2010, 2014; Moya-Elizondo, 2013; Zelikova et al., 2013; Ziska et al., 2005). Further, the cumulative and interactive effects of climatic and environmental factors ultimately impact the establishment and severity of *B. tectorum* and *F. pseudograminearum* (Hikosaka et al., 2011; Miyagi et al., 2007; Reich et al., 2014; Sabburg et al., 2015; Smiley, 2019; Zelikova et al., 2013).

Studies addressing the impact of climate change on *B. tectorum* and *F. pseudograminearum* are lacking for cropping system settings, although both of these pests are prominent in wheat production. Furthermore, to our knowledge *F. pseudograminearum* has not been isolated specifically from *B. tectorum*, even though these two species can persist in the same environments (Dyer et al., 2009; Moya-Elizondo, et al., 2011; Perez-Mendoza et al., 2006; Rydrych, 1974; Rydrych & Muzik, 1968). We believe it was necessary to investigate whether *B. tectorum* is in fact a host to *F. pseudograminearum* and shed light on the impact of, and interactions between, atmospheric CO_2 and soil nitrogen level on the growth and primary physiology of these pests.

Due to the logistics of this study, *F. pseudograminearum* fungal inoculum was not applied at seeding, and we are aware that in a field setting *Fusarium* species attack non-dormant seeds during early stages of germination (Franke et al., 2014; Meyer et al., 2018). Our nitrogen rates represent extreme low and high ends of those typical for a wheat production system, and therefore a mid-range nitrogen treatment would have been ideal if space allowed. Ideally the *B. tectorum* seeds used in this study would have experienced vernalization so as to allow the plants to undergo a complete life cycle, but the growth chambers did not allow for a low enough temperature.

We found that *B. tectorum* t50 was only impacted by nitrogen level, where the lower rate resulted in shorter t50. Low nitrogen increased the percent of *B. tectorum* seeds that emerged, compared to the high nitrogen treatment. At the first harvest, low nitrogen resulted in greater root biomass compared to the high nitrogen treatment, and nitrogen level at this early growth stage did not affect shoot production. Mid and later root production (harvest 2 and 3) was not affected by nitrogen treatment, but *B. tectorum* treated with high nitrogen had greater shoot production at these later growth stages. Total biomass was not significantly affected by nitrogen level, however, the total biomass relative growth rate between harvest 1 and 2 was greater on average for plants treated with low nitrogen. With regards to nitrogen, we speculated that in the early stages of growth, *B. tectorum* emergence and root production benefitted more from the low nitrogen treatment, suggesting that the higher level of nitrogen was detrimental to these factors early on, but enhanced shoot production as the plant matured. The low nitrogen rate increased both stomatal conductance and transpiration rate, suggesting that the higher nitrogen level was more stressful to *B. tectorum*. In a cropland setting, if higher rates of nitrogen slow early *B. tectorum* root production, *F. pseudograminearum* infection of germinating *B. tectorum* seeds could increase. Research has shown that nitrogen rate has little to no impact on *Fusarium* disease severity in wheat (Davis et al., 2009; Lemmens et al., 2004), so applying higher rates of nitrogen could further benefit a wheat crop susceptible to *B. tectorum* competition and *F. pseudograminearum* infection, in addition to yield and protein benefits.

Elevated CO_2 did not impact *B. tectorum* t50 or *F. pseudograminearum* infection but did increase percent emergence. Elevated CO_2 significantly increased *B. tectorum* total and root biomass for the first and second harvest, as well as shoot biomass for all harvests. Ambient CO_2 had a greater RGR for shoot biomass between harvest 1 and 3. We also found an interaction between ambient CO_2 and low nitrogen, where this combination resulted in the highest shoot RGR between harvest 1 and 2. With respect to primary physiology, elevated CO_2 increased intercellular CO_2 of *B. tectorum*, but had no impact on other physiological characteristics that were measured. Overall, elevated CO_2 benefitted biomass production of *B. tectorum*. The interaction between ambient CO_2 and low nitrogen on early-mid growth stage RGR suggests the combination of elevated CO_2 and higher levels of nitrogen are not beneficial to *B. tectorum* growth. The latter findings, put in context with finding no CO_2 impact on *F. pseudograminearum* and limited impact on *B. tectorum* primary physiology, suggest that the role of atmospheric CO_2 is not the most important factor in *B. tectorum* and *F. pseudograminearum* success in a crop such as wheat, let alone in interactions between these two pests.

Bromus tectorum was found to be a highly susceptible host to *F. pseudograminearum*. The number of fungal DNA copies found in inoculated plants were not influenced by nitrogen or CO_2 treatment, but were abundant. Total and root biomass were greatly impaired by the fungus at harvest 2 and 3, as well as shoot biomass at the third harvest. This was expected as plants were inoculated after the first harvest, and this fungus targets crown and lower stem tissue. Total and root biomass RGR between the third and second, and third and first harvests were greater for uninoculated plants. Furthermore, control plants had greater levels of stomatal conductance, transpiration rate, photosynthetic rate, and intercellular CO_2 levels than inoculated plants.

We were able to confirm *B. tectorum* as a host of *F. pseudograminearum* and show that this fungus has detrimental impacts on the biomass production and physiological success of this invasive species. Nitrogen (low early on and high as the plants matured) and elevated CO_2 level benefitted *B. tectorum* in a number of ways, but *F. pseudograminearum* had the most dramatic impact on the plants overall. Research should further our findings by looking at the relationships between *B. tectorum* and *F. pseudograminearum* in-situ with wheat, under various climate conditions, to assess whether *F. pseudograminearum* is a viable control of *B. tectorum* in crop land, the fitness cost to the wheat crop, and how climate (CO_2, temperature, precipitation) alters these relationships.

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CHAPTER THREE

EFFECTS OF INCREASED TEMPERATURE AND REDUCED PRECIPITATION ON THE SUCCESS OF, AND COMPETITION BETWEEN WINTER WHEAT AND *BROMUS TECTORUM* IN A DRYLAND, NO-TILL SYSTEM IN SOUTHWEST MONTANA

Introduction

Wheat, the fourth most produced crop globally (Food and Agriculture Organizaiton [FAO], 2015), is a key component of agriculture in Montana, which ranks third for all wheat production and fourth for winter wheat production in the U.S.A. Wheat production occurs in the majority of counties across the state, primarily those east of the Rocky Mountains, and is concentrated in central and north central region of Montana (United States Department of Agriculture-National Agricultural Statistics Service [USDA-NASS], 2017). Montana is a large state (236,638 km^2) (Montana State Library, n.d.), and much of Montana crop production is dryland, including 98% of winter wheat (Montana Department of Agriculture & USDA-NASS, 2016). Warmer temperatures and uncertain precipitation patterns could have dramatic effects on winter wheat production in Montana, yet in-situ research is lacking for the state.

Montana has experienced increases in average annual temperature (+1.5°C) and annual minimum and maximum temperatures (+1.8°C) between 1950-2015, and increases in days over 32°C (+11days) and growing season length (+12 days) between 1951-2010 (Whitlock, Cross, Maxwell, Silverman, & Wade, 2017). Average temperature projections show continued warming (+1.7-3.9°C by mid-century) across the state, in all seasons, and under all greenhouse gas emission scenarios throughout the 21st century, with the greatest warming expected in summer and winter, and in southeastern Montana (Whitlock et al., 2017). Between 1950-2015, average winter precipitation (rain and snow combined) decreased by 0.36 cm statewide, most likely due to increased El Niño events since 1950. Precipitation projections show an increase across the state for winter, spring, and fall, but a decrease in summer (Whitlock et al., 2017). The number of consecutive dry days is not expected to change drastically in Montana throughout the 21st century, however, increased precipitation variability indicates possibility for greater occurrence of severe droughts (Whitlock et al., 2017).

The exact impacts of climate change on agriculture in the Northern Great plains is uncertain, but there will likely be both negative and positive consequences. Areas that experience increased precipitation could benefit from enhanced yields, depending on the timing and severity of precipitation events (Melillo et al., 2014). Higher temperatures may extend the growing season in some areas and make it possible to diversify crop rotations but could also stress water and energy resources. Despite these potential benefits, weeds and other pests that normally could not survive winters in the Northern Great Plains may be able to do so during warmer winters (Melillo et al., 2014).

Bromus tectorum (cheatgrass, downy brome), native to Eurasia, is an invasive winter annual grass with high phenotypic plasticity that can inhabit a wide range of environments (Klemmedson & Smith, 1964; Mack, 1981). It is capable of producing dozens of tillers and thousands of seeds per plant, and has spread to every county in

Montana (Klemmedson & Smith, 1964; Rice, 2003; Thill, Beck, & Callihan, 1983). *Bromus tectorum* is problematic in cropping systems, natural areas, and rangelands as it competes with desired species for light, soil nutrients, and water, has the ability to alter nutrient cycling, and can change fire regimes by adding fine fuel loads (Brooks et al., 2004; D'Antonio & Vitousek, 1992; Pimentel, Zuniga, & Morrison, 2005; Sperry, Belnap, & Evans, 2006). *Bromus tectorum* can also serve as an alternate host for wheat pathogens and insect vectors (Ito et al., 2012; Perez-Mendoza et al., 2006; Ranabhat et al., 2018). Furthermore, *Bromus tectorum* can significantly reduce wheat yields (Rydrych & Muzik, 1968). It remains unclear how *B. tectorum* infestations in winter wheat systems will interfere with yield under projected altered temperature and precipitation regimes.

Consequences of climate change, such as increasing atmospheric CO_2, shifts in temperature, precipitation, and transpiration regimes, and increased extreme weather events and pest pressure greatly affect crop production (Tubiello et al., 2007). Wheat, like many crops, is most susceptible to temperature during pollination and grain fill (Wienhold, Vigil, Hendrickson, & Derner, 2017). In the Great Plains region of the U.S.A, Stewart, Thapa, Xue, and Shrestha (2018) assessed how rising temperatures impacted winter wheat production using historical temperature and winter wheat yield data from 1939-2016. Analysis revealed that average annual temperatures increased in all areas, but more so in the northern Great Plains. The northern regions of the Great Plains experienced an increasing wheat yield trend, versus decreasing in more southern regions (i.e. North Central Texas), since 1990. Northern regions of the Great Plains are historically colder and less suitable for winter wheat, which explains why increased winter temperatures tended to improve yield due to reduced winter kill and more growing degree days during critical growth periods. However, researchers argue that earlier heading dates due to increased temperatures result in the crop missing exposure to full growing season precipitation, likely causing shorter grain fill periods and ultimately reduced yield (Stewart et. al., 2018). In addition, elevated temperature has been shown to increase aphid and weed pressure, while reducing arbuscular michorizal fungi colonization, which indirectly augmented winter wheat yield loss (Tian et al., 2018). Xiangnan et al. (2015) reported that winter wheat exposed to above average temperatures in winter was more susceptible to damage from low temperature stress in spring.

Water and temperature stress are major concerns for dryland wheat producers. Balla et al. (2011) reported that post-anthesis winter wheat exposed to drought, as well as heat in conjuction with drought, had significantly greater yield loss and reduced grain quality than plants treated with heat stress alone. Through the use of modelling, researchers found that across 11 wheat varieties grown in Kansas between 1985-2011, warming, drought, and warming with drought reduced wheat yield by 11%, 22%, and 33% respectively. Furthermore, newer yield varieties had greater yields than older varieties, but this advantage was lessened under warmer and drier conditions (Tack et al., 2014).

Research addressing the impacts of climate change on *Bromus tectorum* in an agricutlural setting is lacking. There is evidence that warmer temperatures will benefit the reproductive as well as geograhical success of *B. tectorum* in the intermountain west (Bradley et al., 2016). Zelikova et al. (2013) observed that *B. tectorum* seed quality and successive seedlings benefitted from a warmed environment when precipitation was normal, but were negatively effected by higher temperature in drought conditions. Due to *B. tectorum* high phenotypic plasticity, competitiveness, wide environmental requirements, and large reproductive capacity (Klemmedson & Smith, 1964; Mack, 1981; Thill et al., 1983), it is of concern how this weed will behave under predicted climate scenarios in wheat systems.

To our knowledge there is no research that addresses the individual and combined effects of elevated temperature and reduced precipitation on *B. tectorum* and winter wheat growth, reproduction, and interaction in a reduced-till, dryland field setting. Our research questions were: 1) How do elevated temperature and reduced moisture affect winter wheat and *B. tectorum* biomass and seed production? 2) Do *B. tectorum* – winter wheat competitive interactions change when moisture is limiting and/or temperatures are elevated? 3) Are there interactive effects between the climate variables and winter wheat and *B. tectorum*? We hypothesized that warming (+1-3° C) with normal precipitation would benefit both wheat and *B. tectorum* monocultures, whereas increased temperature with reduced precipitation (~50% reduction) conditions would reduce biomass and yield for both species. Furthermore, we hypothesized that when grown together, *B. tectorum* would have a competitive advantage over winter wheat in warmer conditions, and the latter would be exacerbated in warmer, drier treatments.

Materials and Methods

Site Description

This experiment was conducted between August 2014 and July 2017 at the Montana State University Arthur H. Post Research Farm in Bozeman, MT (45°40’N, 111°9’W), 1451 m elevation. The soil at the sites consists of Amsterdam-Quagle silt loams with 0-4% slopes and pH 7.8 (Natural Resources Conservation Service [NRCS], 2016). The research sites were chosen because of the long history of small grain production and access to equipment necessary to conduct this field study. All sites were chemically fallowed the summer before each trial was conducted. Long-term average annual precipitation (1966-2016) at the site was 411.7 mm (Western Regional Climate Center, 2017) and total precipitation in 2014, 2015, and 2016 was 408, 361, and 389 mm, respectively. Mean monthly temperatures and total monthly precipitation from 2014-2017 at the site are presented in Table 3.1.

Table 3.1. Mean monthly air temperature (°C) and total monthly precipitation (mm) for Arthur H. Post Agronomy Farm for 2014-2017 (U.S. Department of the Interior Bureau of Reclamation, 2017). Long term averages consist of data collected between 1996-2016 (Western Regional Climate Center, 2016).

Month	2014 Precip.	2015 Precip.	2016 Precip.	2017 Precip.	Long Term Mean Precip.
January	9.07	11.7	12.5	12.4	13.7
February	19.8	11.4	4.37	16.1	12.7
March	46.5	13.7	33.3	38.9	25.9
April	36.1	44.7	34	60.4	42.7

May	46.9	72.6	63.5	64.2	68.3
June	70.4	14.9	18.8	53.4	70.1
July	9.4	38.6	26.9	3.9	33.5
August	69.1	19.1	21.1	11.8	32.5
September	31.5	30.7	51.6	68.0	36.6
October	13.2	39.6	-83.1	21.1	35.8
November	32.3	36.1	14.7	50.4	22.6
December	19.8	29.7	25.2	40.9	15.7

Month	2014 Temp.	2015 Temp.	2016 Temp.	2017 Temp.	Long Term Mean Temp.
January	-2.11	-3.89	-8.83	-8.82	-4.74
February	-8.22	0.72	1.78	-1.74	-2.52
March	0.83	5.56	3.11	5.16	1.5
April	6.06	5.67	8.17	5.74	6.02
May	11.1	9.78	10.1	10.24	10.7
June	13.1	17.9	17.4	15.22	14.9
July	20.2	18.1	19.2	21.58	18.9
August	17.3	18.7	18.4	19.06	18.4
September	12.9	14.7	12.2	12.29	13.5
October	9.44	9.67	8.22	6.01	7.37
November	-2.22	-2.22	4.06	-0.13	-0.09
December	-2.67	-3.72	-8.17	-6.28	-4.76

Experimental Design

The experiment consisted of three trials (August to July in 2014-2015, 2015-2016, and 2016-2017) and followed a complete randomized block design with four blocks, each 25 by 22 m. Treatments included a full factorial combination of three climate levels [ambient (AMB), increase temperature (OTC), and reduced moisture + increased temperature (ROS+OTC)], and three plant competition levels [winter wheat monoculture, *B. tectorum* monoculture, and winter wheat-*B. tectorum* biculture]. Plots were circular, measuring 1.6 m in diameter, and spaced no closer than 3 m from each other (Figure 3.1). Prior to the initiation of each trial, 32 soil samples were collected from four quadrants within each block to a depth of 0-15 cm and 15-30 cm, submitted to an independent laboratory (Agvise Laboratories, Northwood, SD), and analyzed for NPK and percent organic matter (Table 3.2).

Table 3.2. Pre-seeding Mean ± SE soil chemical characteristics.

	Trial 1	Trial 2	Trial 3
% Organic Matter	1.92 ± 0.095	2.41 ± 0.022	2.16 ± 0.086
Nitrate (ppm)	60.78 ± 6.42	13.37 ± 1.36	12.87 ± 1.65
Phosphorus (ppm)	18.18 ± 2.76	18.5 ± 1.13	14.78 ± 2.15
Potassium (ppm)	297.56 ± 28.5	372.5 ± 8.97	303.78 ± 26.1

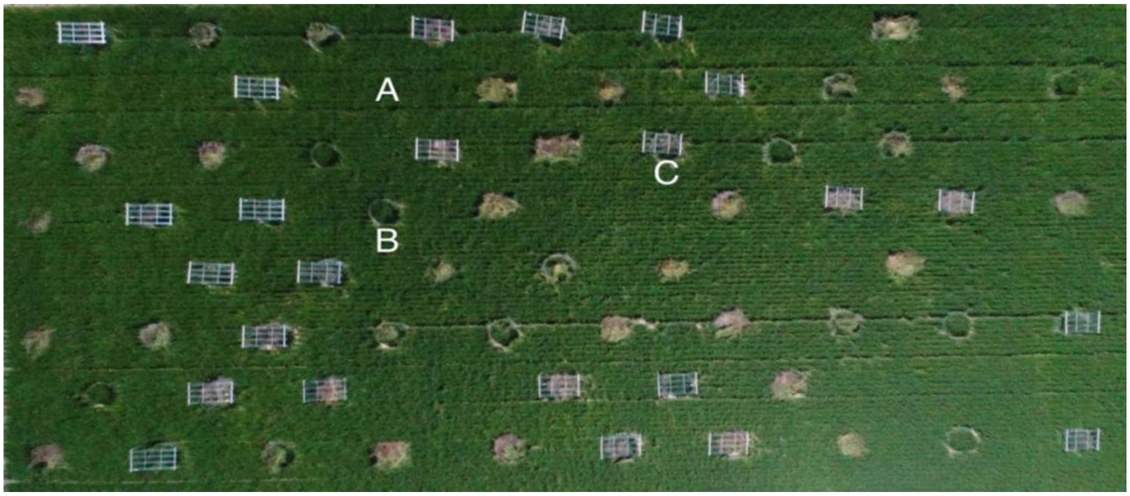


Figure 3.1. Aerial photograph of a field trial conducted to assess the impact of temperature and moisture on winter wheat – *B. tectorum* growth, reproduction, and competitive interactions. The letter A marks an ambient plot (AMB), B an increased temperature (OTC) plot, and C indicates a reduced moisture + increased temperature (ROS+OTC) plot.

Open top cone chambers (OTC's) (Figure 3.2) were utilized to increase temperature by 1-2°C (Larson, Lehnhoff, & Rew, 2017) and were constructed based on the design outlined in the International Tundra Experiment (ITEX) second edition manual (Molau & Mølgaard, 1996). OTCs measured 40 cm tall, 160 cm bottom diameter, 100 cm top diameter, and were constructed using Sun-Lite® HP fiberglass glazing (Solar Components Corporation, Manchester, NH).

Figure 3.2. Open top chamber (OTC) (left) designed to generate a warming effect of ~ 2°C on the plot, while receiving ambient moisture levels. Rain out shelter with open top chamber (ROS+OTC) (right) intended to reduce ~50% of precipitation from entering the plot as well as facilitate warming.

Rain out shelters (ROSs) (Figure 3.2), coupled with OTCs, provided the increased temperature + reduced moisture treatment (ROS+OTC). ROSs intercepted approximately 50% of precipitation and were modeled after Yahdijan and Sala (2002), with rectangular tops approximately 100 cm x 180 cm, and elevated by two long (63.5 cm) and two short (45.5 cm) wooden legs, creating an angle ample enough to prevent precipitation from accumulating on the shelters. In trial 1, OTC's were installed in September after winter wheat was planted and ROS's were installed in late March. In trial 2 and 3, OTC's and ROS's were installed in August after *B. tectorum* was seeded.

Winter Wheat and *Bromus tectorum* Seeding and Weed Management

In August 2014, trial 1 site was prepared with a heavy harrow; which was not necessary in other trials. Approximately 860 *B. tectorum* seeds m_{-2} were scattered on the soil surface of *B. tectorum* treated plots and lightly incorporated with a rake on October 3, 2014, August 19, 2015, and August 17, 2016, for trial 1, 2, and 3, respectively. Due to concerns of low weed emergence, five hundred additional *B. tectorum* seeds per weedy plot were added in trial 2 on September 10, 2015. In trial 2, 11.4 liters of water were added to ambient and OTC plots, whereas 7.5 liters of water were added to ROS+OTC plots, to encourage emergence of winter wheat and *B. tectorum* on October 28, 2015.

Winter wheat (Warhorse variety, MTS0808) was seeded in all plots at 67.25 kg ha^{-1} with a Fabro Goose Mechanics pull type no-till seed drill with seven double-disk openers, 25.4 cm spacing on a 1.8 m wide planting swath. Seed was drilled to a depth of 5 cm and side-banded with 112 kg ha^{-1} of 17-17-17 NPK on September 23, 2014; September 22, 2015; and September 20, 2016 for trial 1, 2, and 3, respectively. In trial 1, winter wheat growing in *B. tectorum*-only plots was terminated post-emergence with glyphosate (248 g ha^{-1} a.i.), and hand weeding was used to control all other weeds inside plots. In addition, glyphosate (248 g ha^{-1} a.i.) was used to control emerged weeds in alleyways outside of plots in trial 1. Winter wheat in *B. tectorum*-only plots and other weeds were hand pulled in trial 2 and 3, and no weed control was required in alleyways. In each trial, spring emerged broadleaf weeds were controlled in March. Trial 1 was sprayed with 149 g ha^{-1} a.i. of octanoic and heptanoic acid ester of bromoxynil, and 2-ethylhexyl ester of MCPA (BRONATE Advanced™), and trial 2 and 3 with 159.7 g ha^{-1} a.i. of florasulam and fluroxypyr (Starane® Flex).

Soil Temperature and Soil Moisture Data Collection

Soil temperature was assessed using Maxim® 1921G iButton temperature loggers buried 2.5 cm under the soil surface at the center of each plot. Trial 1 iButtons were set at 180 min recording intervals October through April, and 210 min recording intervals April through August. Trial 2 and 3 iButtons had 210 min recording intervals September through July. Soil moisture was monitored using Delmhorst® gypsum soil moisture blocks following Aho and Weaver (2008). Soil moisture sensors were buried approximately 10 cm under the soil surface at the center of each plot and data was collected using a Delmhorst® soil moisture reader. Gypsum block data were collected weekly when weather conditions permitted between March and July, as that is when the bulk of growth occurred in winter wheat and *B. tectorum* (Feekes 3-11).

Winter Wheat and *B. tectorum* Harvest and Processing

Bromus tectorum was harvested June 30, 2015, June 28, 2016, and June 29, 2017. Winter wheat was harvested July 30, 2015, July 28, 2016, and July 28, 2017. Winter wheat and *B. tectorum* samples were dried for ~1 week at 40° C before being weighed to the nearest 0.1 g. Winter wheat biomass was threshed using a Vogel thresher (custom built by Bill's Welding, Pullman, WA) and *B. tectorum* was hand-threshed. The Cereal Quality Laboratory at Montana State University, Bozeman, analyzed winter wheat seed for protein content.

Virus Incidence

Wheat and *B. tectorum* were monitored for wheat streak mosaic virus (WSMV). Ten winter wheat flag leaves and ten *B. tectorum* leaves were collected from the center 1 m circular area of each plot and observed for wheat curl mites (*Aceria tosichella* Kiefer). Leaf samples were processed using indirect enzyme linked immunosorbent assay (ELISA), as described by Ito et al. (2012). WSMV positive samples were required to have an optical density (OD) at least three standard deviations larger than the mean OD of the negative controls (healthy wheat and *B. tectorum*) on the corresponding plate (Miller et al., 2014).

Statistical Analysis

All analyses were completed in the statistical analysis program R (version 3.3.2, R Development Core Team, 2016). Linear models were built with the lme4 package (Bates et al., 2018) and lmerTest package (Kuznetsova, Brockhoff, & Christensen, 2014). Analysis of variance (ANOVA) was used to assess models, and when significant models were fit, estimated marginal means (EMM's) were calculated using the emmeans package, with a significance level of $P < 0.05$ based on T-ratios and using the Tukey adjustment method (Lenth et al., 2018).

Soil Temperature and Moisture: Data collected with the Delmhorst® soil moisture reader was transformed to MPa using the methods of Aho and Weaver (2008). All raw values lower than 5 were changed to 4.9 prior to transformation, as readings lower than 5 are not accurate for this particular technology (Aho & Weaver, 2008). Linear mixed effect models were fit to determine the effects of climate treatment on soil temperature and soil moisture. Climate treatment and month were fixed effects and block was a random effect. Trials were analyzed separately due to variation, but overall trends between trials were similar.

Impact of Climate and Competition on Winter Wheat Yield and *Bromus tectorum* Growth: Linear mixed effect models were fit to determine the effect of climate treatments on monoculture winter wheat yield and monoculture *B. tectorum* biomass production, as well as the impact of climate treatment and *B. tectorum* competition on winter wheat seed protein content (%). Climate treatment was a fixed effect, while block and trial were random effects. In trial 3 no protein results were able to be obtained for bi-culture+OTC plots, due to the lack of wheat seed production.

To model the impact of *B. tectorum* and climate conditions on winter wheat yield we fit three candidate models: an additive, an interaction, and a quadratic interaction model and compared them using the adjusted R_2 method (Faraway, 2004) (Table 3.3).

Table 3.3. Summary of adjusted R_2 for the three candidate models.

Model	Adjusted R_2
Additive	0.7003
Interaction	0.7292
Quadratic Interaction	0.7548

The quadratic interaction model:

$$\mathrm{ww.yield}_i = \beta_0 + \beta_1 I_{otc,i} + \beta_2 I_{ros,i} + \beta_3 \mathrm{cg.biomass}_i + \beta_4 I_{otc,i}\mathrm{cg.biomass}_i + \beta_5 I_{ros,i}\mathrm{cg.biomass}_i + \beta_6 I_{otc,i}\mathrm{cg.biomass}^2_i + \beta_7 I_{ros,i}\mathrm{cg.biomass}^2_i + \varepsilon_i$$

Where:

- The β's are the true (unknown) coefficients for the model terms,
- The I's are indicator functions that equal one if the observation falls within the climate treatment group indicated by the function and zero otherwise,
- ε_i is the error associated with observation i.

- The intercepts and the curvilinear relationships of the three climate treatments were allowed to vary.

The quadratic interaction model had the highest adjusted R_2 and was therefore selected as best model for the available data. Block was not included in the above model, because the response (winter wheat yield) and predictor (*B. tectorum* biomass) were both outcomes of the experiment. Block is related to variability in both the response and predictors, therefore it is unreasonable to include blocking as a term in the model. An ANOVA was used to assess the strength of evidence for the inclusion of terms in the model.

Results

Soil Temperature

Soil temperature differences between climate treatments were similar across trials. Looking across trials, both OTC and ROS+OTC increased mean, minimum, and maximum soil temperatures between October-November. In addition, ROS+OTC had the greatest mean, minimum, and maximum temperatures in trial 2 and 3 compared to both ambient and OTC plots, whereas in trial 1 OTC and ROS+OTC had equally warmer soil temperatures than ambient plots. Similar to the fall months, OTC and ROS+OTC had increased mean, minimum, and maximum soil temperatures compared to ambient between February and May, but the ROS+OTC treatment was more consistently warmer compared to the OTC treatment. ROS+OTC significantly increased mean, minimum, and maximum soil temperature from June-July, while OTC did not, with the exception of maximum soil temperature in trial 2. Furthermore, there were many instances where OTC soil temperatures did not differ from, or were cooler, than those of ambient plots, namely from June-July (Table 3.4).

Table 3.4. Temperature response to climate treatments recorded at the Arthur H. Post Agronomy Farm October 2014-July 2017. Trial and season (Oct.-Nov., Feb.-May, and June-July) were analyzed separately and the superscripts indicate statistical significance (*P* < 0.05).

			Soil Temperature (°C)		
Season	Trial	Temperature Variable	Ambient	OTC	ROS+OTC
Oct.- Nov.	1	Mean ± SEM	4.71 ± 0.17 $_{a}$	5.24 ± 0.16 $_{b}$	5.18 ± 0.16 $_{b}$
		Min	0.45$_{d}$	2.14$_{e}$	1.94$_{e}$
		Max	10.58$_{g}$	9.21$_{h}$	9.34$_{h}$
Feb.-May	1	Mean ± SEM	6.31 ± 0.13$_{a}$	6.77 ± 0.13$_{b}$	6.92 ± 0.14$_{b}$
		Min	1.97$_{d}$	2.31$_{e}$	2.46$_{e}$
		Max	12.57$_{g}$	13.28$_{h}$	13.28$_{h}$
June-July	1	Mean ± SEM	18.22 ± 0.14$_{a}$	18.04 ± 0.12$_{a}$	18.72 ± 0.13$_{b}$
		Min	13.88$_{d}$	13.92$_{d}$	14.55$_{e}$
		Max	23.95$_{gh}$	23.66$_{g}$	24.41$_{h}$
Oct.-Nov.	2	Mean ± SEM	5.55 ± 0.09$_{a}$	6.08 ± 0.10$_{b}$	6.87 ± 0.11$_{c}$
		Min	4.15$_{d}$	4.61$_{e}$	5.26$_{f}$
		Max	7.33$_{g}$	8.02$_{h}$	8.93$_{i}$

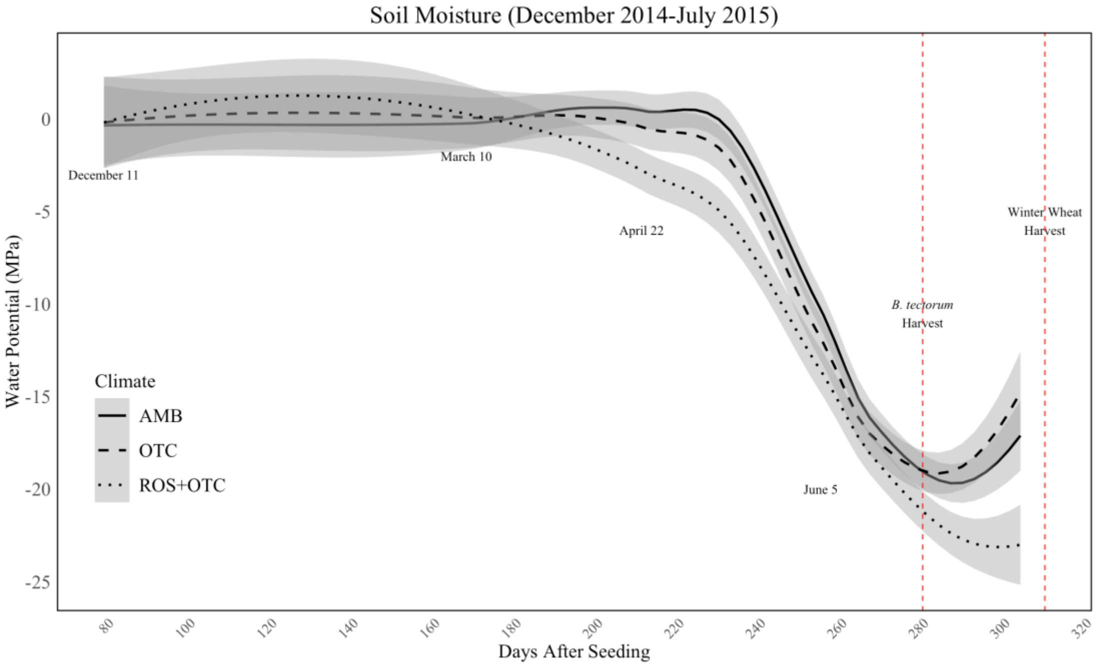
Feb.-May	2	Mean ± SEM	$5.96 \pm 0.07_{a}$	$6.60 \pm 0.09_{b}$	$7.71 \pm 0.10_{c}$
		Min	3.75_{d}	3.99_{d}	4.69_{e}
		Max	8.92_{g}	10.24_{h}	11.76_{i}
June-July	2	Mean ± SEM	$19.01 \pm 0.12_{a}$	$19.17 \pm 0.13_{a}$	$20.90 \pm 0.13_{b}$
		Min	15.27_{d}	15.14_{d}	16.06_{e}
		Max	23.74_{g}	24.4_{h}	27.23_{i}
Oct.-Nov.	3	Mean ± SEM	$5.41 \pm 0.09_{a}$	$6.10 \pm 0.08_{b}$	$6.86 \pm 0.09_{c}$
		Min	3.19_{d}	4.03_{e}	4.32_{f}
		Max	8.66_{g}	9.07_{h}	10.51_{i}
Feb.-May	3	Mean ± SEM	$5.29 \pm 0.08_{a}$	$5.28 \pm 0.08_{a}$	$5.77 \pm 0.08_{b}$
		Min	2.77_{d}	3.16_{e}	3.39_{e}
		Max	8.72_{g}	8.18_{h}	9.1_{g}
June-July	3	Mean ± SEM	$18.11 \pm 0.09_{a}$	$17.46 \pm 0.08_{b}$	$18.38 \pm 0.09_{a}$
		Min	13.88_{d}	13.89_{d}	14.71_{e}
		Max	23.61_{g}	21.94_{h}	22.81_{i}

Soil Moisture

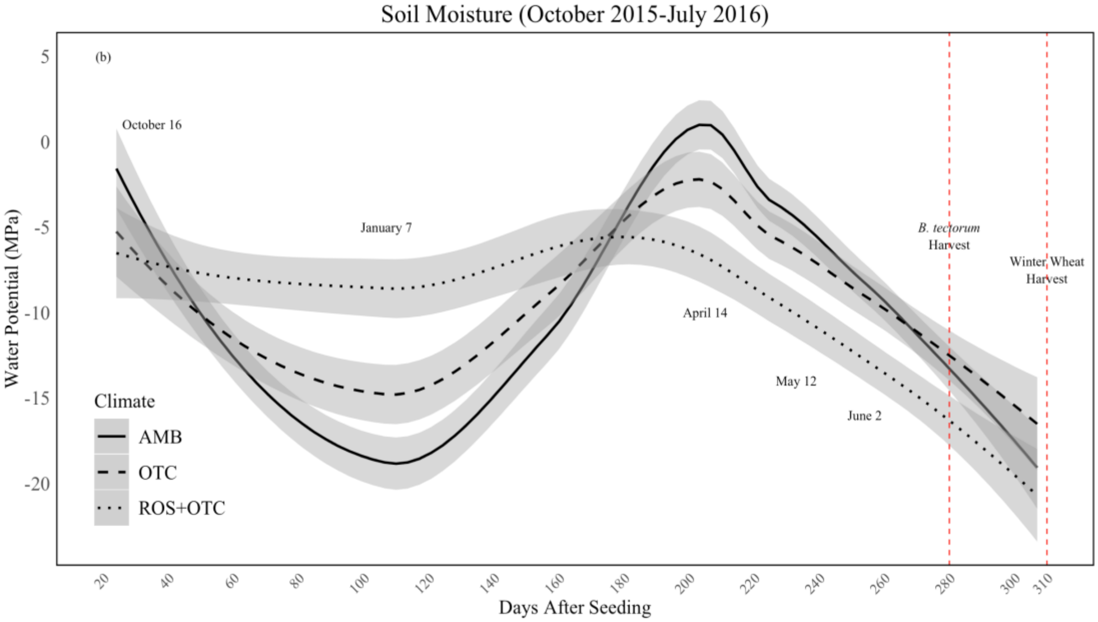
Averaged over the months of March to July, ROS's significantly reduced soil water potential compared to both ambient and OTC plots in all three trials (Table 3.5, Figures 3.5 a, b, and c.

Table 3.5. Results of pairwise comparisons of the estimated marginal means of soil moisture data collected for all three trials between March and July.

Trial	Contrast	Estimate	SE	df	t.ratio	p.value
1	Ambient-OTC	0.433	0.523	997	0.829	>0.05
1	Ambient-ROS+OTC	2.657	0.523	997	5.083	<0.0001
1	OTC-ROS+OTC	2.224	0.522	997	4.257	0.0001
2	Ambient-OTC	0.580	0.615	1045	0.943	>0.05
2	Ambient-ROS+OTC	3.920	0.615	1045	6.385	<0.0001
2	OTC-ROS+OTC	3.340	0.615	1045	5.438	<0.0001
3	Ambient-OTC	-0.477	0.400	1186	-1.192	>0.05
3	Ambient-ROS+OTC	0.946	0.400	1186	2.366	<0.05
3	OTC-ROS+OTC	1.423	0.400	1186	3.559	<0.005



Soil Moisture (December 2014-July 2015)



Soil Moisture (October 2015-July 2016)

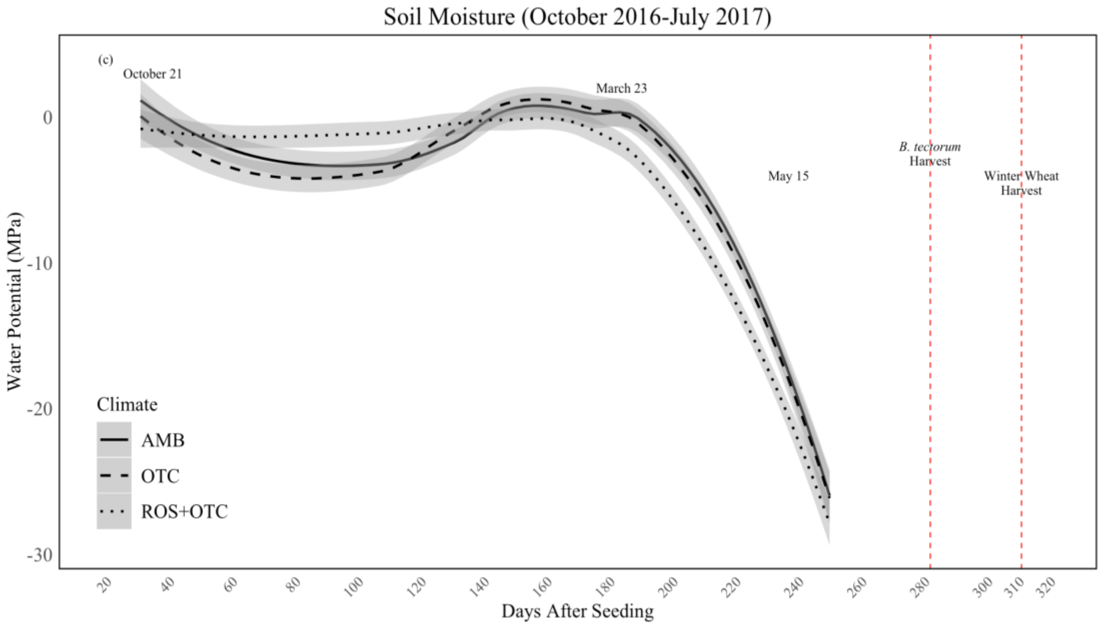


Figure 3.3. Mean soil water potential response to climate treatments at the Arthur H. Post Agronomy Farm during the (a) 2014-2015, (b) 2015-2016, (c) 2016-2017 growing seasons with associated 95% confidence interval.

Winter Wheat and *B. tectorum* Responses to Climate Treatments

Winter wheat grown in the OTC treatment as a monoculture did not differ in yield compared to the ambient treatment ($P > 0.5$) for all three trials. Rain out shelters reduced monoculture winter wheat yield compared to both ambient ($P < 0.005$) and OTC ($P < 0.0005$) climate conditions (Fig. 3.6).

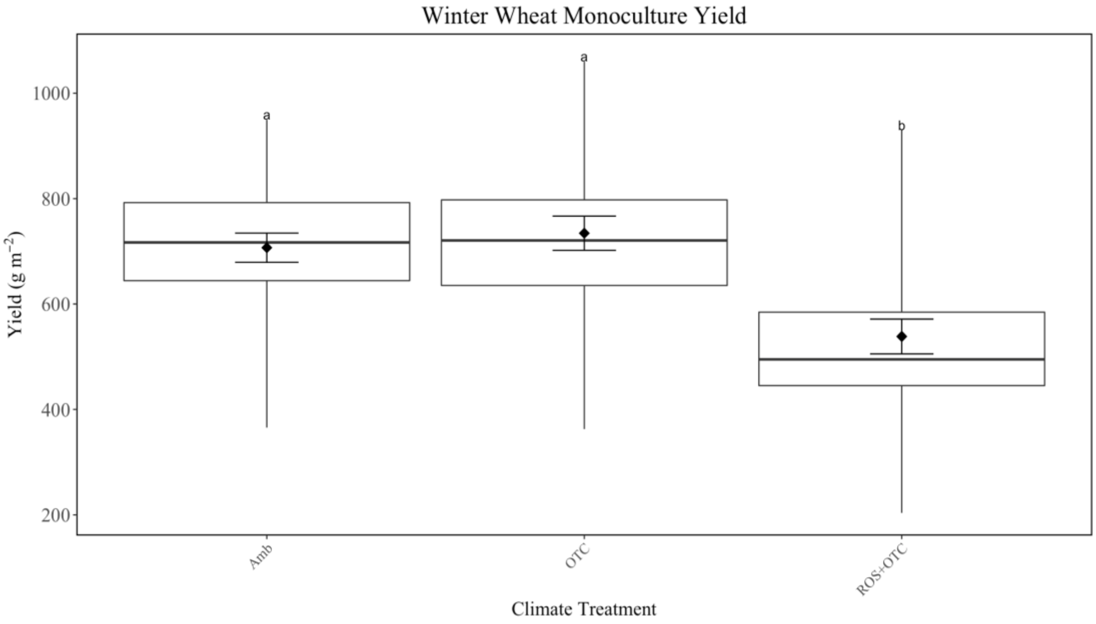


Fig. 3.4. Mean ± SEM (diamond and error bars) and boxplots of monoculture winter wheat yield for ambient (Amb), increased temperature (OTC), and increased temperatures and reduced moisture (ROS) climate simulations. Treatments with different letters are significant at the 0.05 level.

Bromus tectorum grown in monoculture did not produce different amounts of biomass in ambient versus OTC plots ($P > 0.05$). Rain out shelters with OTC reduced *B. tectorum* biomass production compared to both ambient ($P < 0.001$) and OTC ($P < 0.005$) climate treatments (Fig. 3.7).

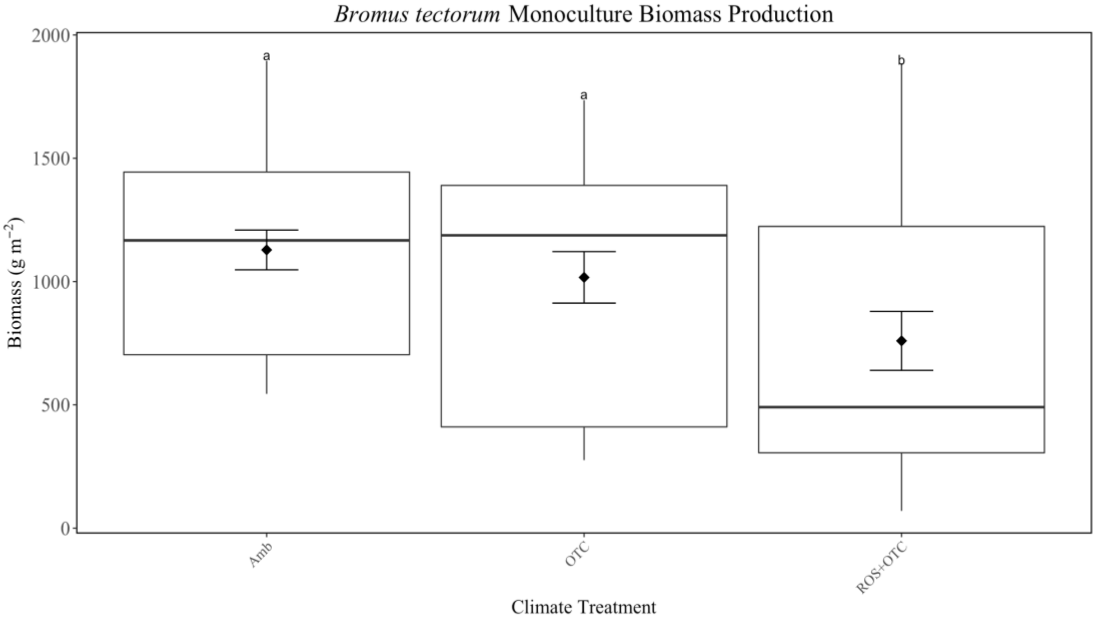


Fig. 3.5. Mean ± SEM (diamond and error bars) and boxplots of monoculture *B. tectorum* biomass production for ambient (Amb), increased temperature (OTC), and increased temperatures and reduced moisture (ROS) climate simulations. Treatments with different letters are significant at the 0.05 level.

Effect of Climate Treatment on Winter Wheat

Seed Protein

Climate treatment did not impact winter wheat seed protein content ($P > 0.05$), however, wheat grown in competition with *B. tectorum* had greater seed protein content compared to wheat grown in monoculture ($P < 0.005$) (Fig. 3.8) (Table 3.6).

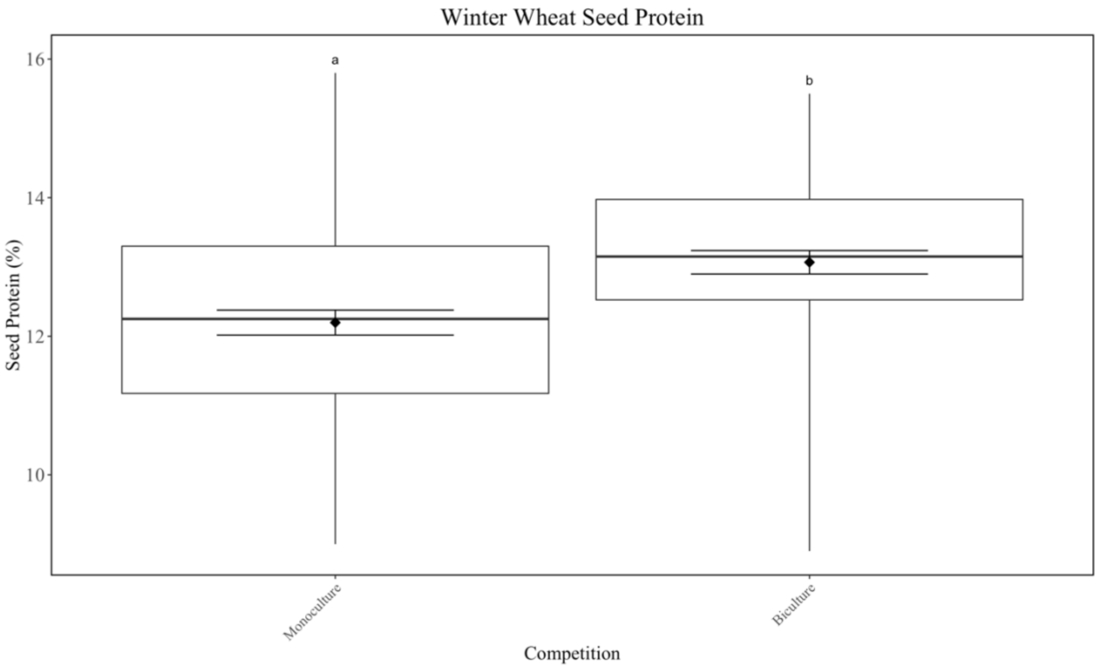


Fig.3.6. Mean ± SEM (diamond and error bars) and boxplots of winter wheat seed protein content (%) for monoculture (winter wheat only) and biculture (winter wheat + *B. tectorum*) across trials. $P < 0.005$. Treatments with different letters are significant at the 0.05 level.

Table 3.6 Mean ± SEM of winter wheat seed protein level by climate, competition and trial.

Climate	Competition	Trial	Mean ± SEM
Ambient	Monoculture	1	13.6±0.63
Ambient	Bi-culture	1	13.5±0.46
Warmer	Monoculture	1	13.3±0.26
Warmer	Bi-culture	1	13.6±0.35
Warmer & Drier	Monoculture	1	13.7±0.19
Warmer & Drier	Bi-culture	1	13.7 ± 0.25
Ambient	Monoculture	2	12.3±0.40
Ambient	Bi-culture	2	13.0±0.25
Warmer	Monoculture	2	12.8±0.33
Warmer	Bi-culture	2	12.8±0.44
Warmer & Drier	Monoculture	2	10.8±0.48
Warmer & Drier	Bi-culture	2	11.5 ± 0.63
Ambient	Monoculture	3	10.4±0.27

Ambient	Bi-culture	3	12.9±0.77
Warmer	Monoculture	3	11.9±0.18
Warmer & Drier	Monoculture	3	11.0±0.30
Warmer & Drier	Bi-culture	3	13.5 ± 0.25

Effect of Climate Treatment on Winter Wheat Yield Loss as a Function of *Bromus tectorum* Biomass

Results from the ANOVA indicate that there is a very strong evidence ($F_{4,63} = 4.2140$, $P < 0.005$) that the quadratic interaction terms are important predictors of winter wheat yield. This provided evidence of a difference in the relationship between *B. tectorum* biomass and winter wheat yield for the three climate treatments. Due to the other model parameters being dependent on the inclusion of β_6 (square of OTC cheatgrass biomass) and β_7 (square of ROS+OTC cheatgrass biomass), only the strength of evidence for the interaction between climate treatment and the square of *B. tectorum* biomass can be assessed, and interpretation of the main effects is not appropriate. However, verification of an interaction means that there is evidence of a relationship between the parameters included in the interaction and response.

Three climate treatments are different, but their confidence intervals frequently overlap (where the grey bands overlap in Fig. 3.9). Winter wheat yield in the OTC plots compared to that of the ambient plots was similarly impacted by *B. tectorum* biomass.

Although the OTC curve is above the ambient curve until *B. tectorum* biomass reaches roughly 1,250 g m^{-2}, their confidence intervals overlap continuously. Confidence intervals for winter wheat yield in the ROS+OTC plots did not overlap with that of ambient plots when *B. tectorum* biomass was low to moderate; roughly 80-200 g m^{-2}, and the ROS+OTC curve is below that of ambient. When *B. tectorum* biomass ranged between 50-400 g m^{-2}, the confidence intervals for ROS+OTC and OTC did not overlap, and the ROS+OTC curve is below that of OTC. Again, due to the quadratic interaction terms in this model, there are no meaningful interpretations of the estimated main effects. However, this figure displays a negative trend between winter wheat yield and *B. tectorum* biomass for all three climate treatments. There is a tendency for the yield trend in ROS+OTC plots to be less than those of ambient and OTC until very high levels of *B. tectorum* biomass, and a trend where winter wheat yield in each climate treatment became more similar as *B. tectorum* biomass increased.

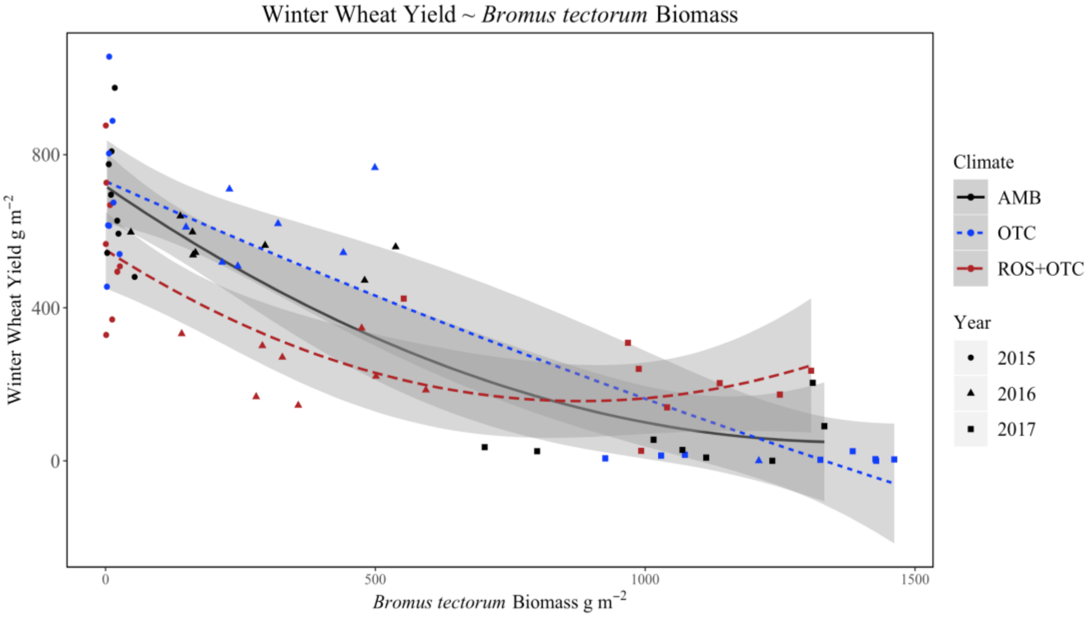


Figure 3.7. The effect of *B. tectorum* biomass on winter wheat yield for the three climate treatments. The shadows represent 95% confidence intervals.

Discussion

This study provided valuable information on the impact of *B. tectorum* on wheat yield under current and predicted climate conditions. This information is required to develop climate-smart cropping systems (Lipper et al., 2014). Using non-linear regressions to assess wheat yield as a function of *B. tectorum* biomass provided us with the required information to develop predictive models of the impact of climate conditions on *B. tectorum* and disease incidence (Cummins et al., 2020), even though our data fell mostly between 0 and 500 g m2 and above 1000 g m2. Our results show that OTC's successfully increased mean, minimum and maximum soil temperatures compared to ambient plots between October and May. ROS+OTC's further increased soil temperatures during the entire growing season. In June and July, OTC soil temperatures were equal to or less than those of ambient, which was likely due to the similar, if not greater, amount of plant biomass produced in OTC's that therefore shaded the soil surface. Rain out shelters successfully reduced incoming precipitation and soil moisture, compared to ambient and OTC plots.

In winter wheat and *B. tectorum* monocultures, reduced precipitation with elevated temperature (ROS+OTC) resulted in yield and biomass reduction. Ambient and OTC plots produced similar amounts of *B. tectorum* biomass and winter wheat yield. Slightly warmer temperatures with normal precipitation (OTC) did not significantly increase *B. tectorum* biomass or winter wheat yield, compared to ambient conditions. We did not find evidence of an interaction between reduced precipitation and increased temperature. These results suggest that soil water availability was the most limiting environmental factor determining wheat and *B. tectorum* growth. While previous research evaluating the impact of drought stress and temperature on wheat growth and yield has shown similar results (Mahrookashani et al., 2017), others suggest the negative effects of temperature variability is underestimated (Asseng et al., 2011). Further, research has shown that the impacts of drought and temperature stress on wheat is influenced by many other factors, such as the timing of stressors, cultivar, genotype, and the extent of stress (i.e. degree and length of time) (Asseng et al., 2011; Ferris et al., 1998; Mahrookashani et al., 2017; Sionit et al., 1980; Urban et al., 2018; Wienhold et al., 2017).

Winter wheat seed protein levels were not significantly impacted by climate treatment, but it increased when winter wheat was grown in biculture with *B. tectorum*. Resource competition with *B. tectorum* likely caused stress on the winter wheat, especially for available soil water, which could have resulted in higher grain protein levels.

The quadratic interaction model used to assess the impact of climate treatments and *B. tectorum* biomass on winter wheat yield proved to be a useful tool to gain insight and add data to this area of study. Although we cannot draw conclusions on the direct treatment effects, and the confidence intervals overlap, the model shows a couple insightful trends. First, warmer plots (OTC) had slightly greater mean winter wheat yield compared to ambient plots when *B. tectorum* biomass was low to moderate. Second, warmer and drier (ROS+OTC) plots had noticeably lower mean winter wheat yield compared to ambient when *B. tectorum* biomass was low-moderate. These results indicate that warmer temperatures may provide a small yield benefit compared to ambient conditions, even when in competition with *B. tectorum* but inadequate precipitation may limit the yield benefit from a slightly warmer environment. Furthermore, *B. tectorum* at even low densities reduces winter wheat yield regardless of climate treatment.

For major wheat production areas such as Montana, it is crucial to understand how climate change impacts wheat and associated pests. Our research shows *B. tectorum* will continue reduces winter wheat biomass and yield under current as well as warmer and drier climate conditions. In addition, our findings suggest that winter wheat production could benefit from slightly warmer temperatures, as long as precipitation is adequate, the timing of precipitation is conducive with the winter wheat growing season, and control of weeds such as *B. tectorum* is successful.

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CHAPTER IV

SUMMARY OF FINDINGS AND FUTURE RESEARCH

Sustainability of dryland winter wheat production in Montana heavily depends on how producers manage crop-pest interactions in future climate conditions. In order to adapt and implement ecologically based integrated pest management in these agroecosystems, further understanding of how multitrophic relations are altered due to climate change is crucial (Castex et al., 2018). This research sought to improve data and understanding of how a warmer, and a warmer and drier climate would impact winter wheat growth and yield. In addition, we explored how climate change impacts *B. tectorum* and *F. pseudograminearum* individually and interactively. To our knowledge *B. tectorum* has not been identified as a host to *F. pseudograminearum* until now. This weed and fungus are both prominent pests in winter wheat systems in Montana, therefore it is important to understand how these crop-pest interactions are impacted by a warmer, drier, higher atmospheric CO_2 climate.

My first objective was to evaluate how elevated CO_2, nitrogen availability, and *F. pseudograminearum* impacted *B. tectorum* growth and primary physiology, in a growth chamber environment. I found that *B. tectorum* is very susceptible to this fungus, which reduced *B. tectorum* root, shoot, and total biomass, relative growth rate, and primary physiology. *Fusarium pseudograminearum* had the most influence on plant health compared to the other treatments. I did not find that *F. pseudograminearum* was impacted by either nitrogen or CO_2 level. Low nitrogen improved emergence and early root production, while higher nitrogen enhanced shoot production later on. This suggests that *B. tectorum* could be sensitive to higher rates of applied nitrogen. Elevated CO_2 had overall positive impact on *B. tectorum* biomass production, namely shoot production throughout the growth period. One interaction was found when plants subject to ambient CO_2 and low nitrogen had significantly greater relative growth rate between the first and second harvest. Overall these findings confirm that *B. tectorum* is a very susceptible host to *F. pseudograminearum*, elevated CO_2 is likely to enhance *B. tectorum* biomass production, and applied nitrogen level is very influential at all *B. tectorum* growth stages.

My second objective was to evaluate how a warmer, and a warmer and drier environment would impact winter wheat growth and yield, growth and reproduction of *B. tectorum*, and crop-weed competition and interaction in a dryland, no-till field setting. Results showed that for this area in southwest Montana, winter wheat subject to no weed competition and a slightly warmer environment had very similar yield to winter wheat grown in ambient conditions. However, winter wheat subject to a warmer and drier environment had significantly smaller yield, on average roughly 200 g m^{-2} less than winter wheat grown in the ambient and warmer environments. *Bromus tectorum* monocultures had similar results, where the weed biomass was similar between ambient and warmer environments, but significantly reduced in warmer and drier conditions. Furthermore, winter wheat seed protein was slightly higher for plants in competition with *B. tectorum*. These results suggest that for winter wheat grown in this area using no-till, rain-fed practices, a warmer environment is not detrimental, and potentially beneficial to the crop, as long as precipitation is adequate. Precipitation, not temperature, was found to be the driving force behind biomass and yield variability for both crop and weed, when grown in monocultures.

Due to the nature of the quadratic interaction model used, no conclusions could be drawn about the direct climate treatment effects on winter wheat yield as a function of *B. tectorum* biomass. However, the observed trends suggested that a warmer environment improved winter wheat yield, while warmer and drier conditions were detrimental, compared to the ambient climate. It is possible that a warmer environment with ambient precipitation could bolster winter wheat competitive abilities, resulting in ambient or above-ambient yield. Overall, this study suggests that precipitation, not temperature, was the driving force behind winter wheat reproductive success.

Future research should seek to continue the work that my research has started. As climate change progresses, agricultural production will benefit greatly from research that addresses crop-pest interactions that are specific to a regions environmental and projected climate conditions. Going forward, it would be ideal to combine the ideas of my two studies into one field project. Little to nothing is known about how *F. pseudograminearum* interacts with *B. tectorum* in a winter wheat field operation, let alone in a warmer, drier, higher CO_2 environment. Research in this area of interest should investigate the possibility of both of these pests becoming more aggressive due to climate change, and the potential to use *F. pseudograminearum* as a biocontrol for *B. tectorum*.

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