

EVALUATION OF WHEAT PRODUCTION PRACTICES UNDER WHEAT STREAK
MOSAIC DISEASE RISK AND WHEAT STEM SAWFLY PRESSURE IN MONTANA

by

Uta McKelvy

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ABSTRACT

Wheat (*Triticum aestivum* L.) is an economically important crop for Montana's agricultural industry. Wheat streak mosaic (WSM) is an important viral disease in Montana and the wheat stem sawfly (WSS; *Cephus cinctus* Norton) is a major insect pest in the state. Understanding these disease and pest problems and the factors that promote and suppress disease and pest pressure forms the foundation for a successful integrated pest management program. In this dissertation, we evaluate wheat production practices in Montana and provide information on the effectiveness and implications of cultural and chemical management practices in mitigating WSM disease and WSS pressure. We assessed the tolerance of popular winter wheat, spring wheat, and barley cultivars in Montana to mechanical inoculation with WSMV in field studies. Winter wheat 'Brawl CL Plus' and breeding lines CO12D922 and MTV1681 demonstrated moderate WSMV incidence and minor yield penalties under WSMV inoculation, making them suitable cultivars to be grown in high-risk environments. We investigated the effects of cultivar choice, planting date, and seeding rate on grain yield and quality parameters in field studies. Our results validated current planting date recommendations for Montana. Yield reductions were observed at planting dates later than mid-September and April for winter wheat and spring wheat, respectively. No yield increase was observed when winter wheat was planted before mid-September. No meaningful and reliable economic benefits were associated with an increase in seeding rate beyond the recommended density. We developed a WSM risk prediction model and released it as the online learning tool AWaRe ("Assessment of Wheat streak mosaic Risk"). AWaRe presents the first learning tool that integrates complex information on the dynamics underlying WSM disease and relates them to the user in an interactive way. We expect the adoption of risk assessment based WSM management practices that result in a reduced economic impact through the use of this tool. The potential of different insecticides to manage WSS damage was compared to spring wheat genotypes with varying degrees of WSS resistance. Results showed that application of the systemic insecticide Thimet-20G provided effective protection of susceptible cultivar 'Reeder,' but use of solid-stem cultivars were similarly effective.

CHAPTER ONE

INTRODUCTION

Wheat (*Triticum aestivum* L.) is one of the most important staple crops in the world. In 2017, 773.5 million metric tons of wheat were harvested worldwide from 15.4% of the total cropland area in the world, exceeding maize (*Zea mays*; 13.9%), rice (*Oryza sativa*; 11.7%), and soybean (*Glycine max*, 8.7%) (FAO 2020). The U.S. was the fourth-largest wheat producer in the world in 2017, contributing 6% of the world's wheat production, and was the second largest exporter of wheat grain, trading 27.3 million tons of wheat (FAO 2020). Sixty-eight percent of the wheat hectares in the U.S. were located in the Great Plains states in 2019, two thirds of which were in North Dakota, Kansas, and Montana alone (16%, 15.5%, and 11.3%, respectively) (USDA NASS 2020).

Wheat is the dominant crop produced in Montana. In 2019, 68% of the state's hectares in production were planted in wheat (2.2 million ha total). The approximately 6 million metric tons of wheat harvested amounted to a production value of more than 1 billion USD (USDA NASS 2019).

Wheat is considered an extensive crop (Shtienberg 2013) with a low value per unit area of 603 USD per hectare, compared to cotton and sugar beet with 1,577 USD and 2,655 USD per hectare, respectively (U.S. average; USDA NASS 2020). The low value of newly-harvested wheat provides only a small profit margin to farmers. In addition, wheat production is challenged by abiotic and biotic causes of stress that reduce yield and further decrease the profitability of the crop.

Wheat streak mosaic (WSM) disease is a persistent and economically important viral disease of wheat in the Great Plains region. The disease is caused by a virus complex composed of *Wheat streak mosaic virus* (WSMV), *Triticum mosaic virus* (TriMV), and *High Plains wheat mosaic virus* (HPWMoV; formerly known as High Plains virus and wheat mosaic virus). All three viruses are vectored by the eriophyid wheat curl mite (WCM), *Aceria tosichella* Keifer (Seifers et al. 1997; Seifers et al. 2009; Slykhuis 1955). Average annual yield losses of 1.3% in Kansas were estimated over the past 20 years and yearly yield loss estimates from 2011 to 2019 ranged between 0.05% and 5.6% (Hollandbeck et al. 2019). In Montana, the annual impact of WSM on the state's wheat production has not been systematically measured, but WSM outbreaks with state-wide yield losses of more than 10% occurred in 1964, 1981, 1993, 1994, and 2016 (Burrows et al. 2017).

The wheat stem sawfly (WSS; *Cephus cinctus* Norton) is a major insect pest of winter and spring wheat in the Northern and Central Great Plains of the U.S. and the southern regions of the Canadian provinces (Beres et al. 2011). The economic impact of WSS populations amounts to 350 million USD annually from yield losses in the U.S. and Canada (Beres et al. 2011). In Montana, the economic damage ranges between 44 - 80 million USD each year (Bekkerman and Weaver 2018; Fulbright et al. 2017). Feeding activity of WSS larvae inside stems reduces crop productivity. Moreover, WSS-infested stems are prone to lodging and wheat heads falling to the ground may be impossible to recover during harvest. Unrecovered wheat heads are a likely source of volunteer wheat, which is an important summer host for the WSM disease complex between crop seasons.

The co-occurrence of WSS and WSM across the same geographic region raises the question if interactions between the viral disease and the insect pest exist and how they might affect WSS population dynamics and WSM disease risk?

Both injurious WSS larvae and the virus-transmitting WCMs live in secluded areas on the wheat host and are protected from exposure to pesticides. Moreover, no acaricides exist that have efficacy against WCM (Murphy 2016) and no insecticides with efficacy against WSS larvae are currently registered. Wheat growers rely on cultural management strategies including the use of tolerant or resistant varieties, planting date adjustments, crop rotation and other measures to reduce the impact of the disease and insect on the crop. However, in the light of small profit margins in wheat, certain management practices may not be economically feasible.

Altogether, wheat growers in Montana are confronted with a complex pest management landscape. Knowledge of the disease/pest problems in the production area and the factors that promote and suppress disease/pest pressure, based on accurate and applicable information, forms the foundation for a successful and economic integrated pest management program. This dissertation presents an evaluation of wheat production practices in Montana and provides research-based information on the effectiveness and implications of cultural and chemical management practices in mitigating WSM disease and WSS pressure.

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CHAPTER TWO

LITERATURE REVIEW

Viruses of the WSM Complex

WSM disease complex is composed of three viruses: *Wheat streak mosaic virus* (WSMV), *Triticum mosaic virus* (TriMV), and *High Plains wheat mosaic virus* (HPW, *Aceria tosichella* Keifer (WCM; *Aceria tosichella* Keifer) (Seifers et al. 1997; Seifers et al. 2009; Slykhuis 1955). They infect wheat, other cereal crops and grassy weeds and are widespread across the Great Plains region of the U.S (Tab. 2.1 and 2.2). The WCM vectors a fourth virus, *Brome mosaic virus* (BMV) (Stephan et al. 2008). This virus is known to occur in the U.S. and was frequently detected in wheat fields in Ohio (Hodge et al. 2017), it has thus far been regarded to have minimal economic impact on wheat production (Kao and Sivakumaran 2000; Lane 1974; Scholthof et al. 2011). Little information is available on the distribution and epidemiological potential of BMV in North America.

Wheat Streak Mosaic Virus

Wheat streak mosaic virus was first observed in 1922 by Peltier in winter and spring wheat plants near Lincoln, Nebraska (Haskell and Wood 1923; Staples and Allington 1956). Since then, the virus has been identified in North and South America, Europe, Asia, Africa, and Oceania. A comprehensive summary of all countries in which WSMV has been documented, including associated host plants, is presented in Navia et al. (2013). In North America, the virus has been documented in 30 U.S. states, in four

Canadian provinces (Alberta, Manitoba, Ontario, Saskatchewan) and in Mexico (CABI 2020).

Wheat streak mosaic virus is the type member of the genus *Tritimovirus* in the family Potyviridae (Stenger et al. 1998). It is a filamentous, flexible, rod-shaped virus (Paliwal and Slykhuis 1967) with a positive-sense, single-stranded RNA genome of approximately 9,384 nucleotides (Stenger et al. 1998). The genome encodes a single polyprotein of 3,035 amino acid residues, which is cleaved into eight to ten mature proteins following translation (Choi et al. 2000).

Divergent strains of WSMV occur in the U.S., Mexico, and Eurasia (French and Roy 2003). To date, three WSMV isolates from North America have been sequenced (Choi et al. 2001; Stenger et al. 1998, 2002); Sidney 81, Type, and El Batán. The Type isolate was isolated from Kansas wheat in 1937 and the Sidney 81 isolate was obtained from wheat in western Nebraska in 1981. Both isolates share 97.6% nucleotide sequence identity and produce similar symptoms in wheat (Choi et al. 2001; Hall et al. 2001, Sánchez-Sánchez et al. 2001). El Batán was isolated from wheat in Mexico (Sánchez-Sánchez et al. 2001) and this isolate is more divergent from the two U.S. isolates, sharing 79% nucleotide sequence identity with Sidney 81 and Type (Choi et al. 2001). A high diversity of WSMV genotypes can be found in individual wheat fields (Choi et al. 2001; McNeil et al. 1996) and all strains are vectored by the WCM (Choi et al. 1999, 2001; Sánchez-Sánchez et al. 2001).

Triticum Mosaic Virus

Triticum mosaic virus was first identified in Kansas in 2006 (Seifers et al. 2008). It has since been reported in nine Great Plains states (Burrows et al. 2016). It is the type member of the new genus *Poacevirus* in the Potyviridae family (Tatineni et al. 2009). *Triticum mosaic virus* forms flexuous, rod-shaped virions which contain a single-stranded, positive-sense RNA genome of approximately 10,266 nucleotides encoding a polyprotein of 3,112 amino acids (Fellers et al. 2009; Seifers et al. 2008). The amino acid sequence of the TriMV polyprotein shares 23.2% sequence identity with WSMV (Fellers et al. 2009). *Triticum mosaic virus* has thus far not been reported to occur outside of the U.S. (Navia et al. 2013).

High Plains Wheat Mosaic Virus

High Plains wheat mosaic virus, formerly known as High Plains virus or wheat mosaic virus, was identified in 1993 and 1994 in corn from Colorado, Idaho, Kansas, Nebraska, Texas, and Utah and was also found in wheat (Jensen and Lane 1994; Jensen et al. 1996). It has since been reported in Montana, Wyoming and Ohio, as well (Burrows et al. 2016; Stewart et al. 2013). Moreover, the long-suspected occurrence of HPWMoV in Australia was recently confirmed (Coutts et al. 2014) and the virus's presence was further documented in Argentina (Alemandri et al. 2017). However, HPWMoV has not been documented in Europe or Asia.

High Plains wheat mosaic virus is an *Emaravirus* in the family Fimoviridae (Skare et al. 2006; Tatineni et al. 2014; ICTV 2019). Its genome is composed of eight negative-strand RNAs (Mielke-Ehret and Mühlbach 2012; Tatineni et al. 2014). The

virus is not mechanically transmissible (Seifers et al. 1997) and more complicated to maintain and inoculate. As a result, information on HPWMoV and its interaction with host, vector, and other viruses is limited.

Brome Mosaic Virus

Brome mosaic virus was first detected in 1990 in grass species and sweet corn samples in Ohio (Louie and Knoke 1991). The virus was further detected in wheat fields in Alabama in 2004 at 13% incidence (Srivatasavai 2005) and Ohio in 2012 and 2016 with incidence rates as high as 25% (Hodge et al. 2017). Brome mosaic virus has not yet been reported in Montana.

Brome mosaic virus is the type member of the genus *Bromovirus* in the family Bromoviridae. It has a tripartite, positive-sense RNA genome (Ahlquist et al. 1984). The virus has a remarkably wide host range that includes more than 50 species in the genus *Poaceae*, as well as tobacco (*Nicotiana bentamiana*), soybean (*Glycine max*), and cowpea (*Vigna unguiculata*) (Diaz-Cruz et al. 2017; Haber 1989; Trzmiel et al. 2016). Brome mosaic virus is largely transmitted mechanically in fields (Lane 1974; Mian et al. 2005) although seed transmission can occur (von Wechmar et al. 1984). In addition to the WCM, several other vectors have been described, although with low transmission rates: flea beetle (*Altica foliaceae*), cereal leaf beetle (*Oulema melanopus*), dagger nematode (*Xiphinema* spp.), bird cherry-oat aphid (*Rhopalosiphum padi*), and Russian wheat aphid (*Diuraphis noxia*) (Damsteegt et al. 1992; Gáborjányi and Szabolcs 1987; Rybicki and Wechmar 1982; Srivatsavai 2005).

In summary, this information suggests that BMV could well be prevalent in wheat and other crops across the U.S. and may be considered a part of the WSM disease complex in the future.

Occurrence of WSM Viruses in the Great Plains

All three viruses occur across the Great Plains region, comprised of the major wheat-producing states in the U.S.: Colorado, Kansas, Nebraska, North Dakota, Montana, Oklahoma, South Dakota, Texas, and Wyoming. Two multi-state surveys in 2008 - 2010 and 2010 - 2011 reported that WSMV was the most prevalent virus, followed by TriMV and HPWMoV (Burrows et al. 2016; Byamukama et al. 2013). Moreover, the viruses did not only occur within the same wheat fields but were detected within the same host plants (Burrows et al. 2016; Byamukama et al., 2014; Seifers et al., 2011; De Wolf and Seifers, 2008). Interestingly, TriMV occurs predominantly in co-infections with WSMV; 91% of samples that were infected with TriMV in the survey by Byamukama et al. (2013) also tested positive for WSMV. In contrast, WSMV and HPWMoV were more frequently detected in single infections. Similarly, Burrows et al. (2016) observed that most virus-positive samples carried only one virus, while double- and triple-infection occurred with decreasing frequency.

Symptoms and Damage Caused by WSM Viruses

Plants infected with WSMV show symptoms of subtle, pale green mottling at first, which develop into light colored streaks that run parallel to the leaf veins. With the progression of chlorosis at later stages in disease development, infected leaves develop

patterns of yellow mottling and streaking (Staples and Allington 1956). Infected plants show a stunted growth habit with fewer, poorly producing tillers that sprawl out. Infected plants have reduced root biomass and decreased water use efficiency (Price et al. 2010), which can exacerbate drought stress effects in water-limited environments. Upon superficial examination, WSM disease symptoms may easily be mistaken for nitrogen or iron deficiency. Grain yield of infected plants is reduced, and kernels are shriveled. Under severe infection wheat plants may fail to develop spikes entirely. Timing of infection typically influences the severity of symptoms. Infection in the fall (for fall-planted winter wheat) or before tillering (for all cereals) results in the most severe disease symptoms and yield reductions (Byamukama et al. 2012; Hunger et al. 1992; Wosula et al. 2018).

Symptoms from infection with WSMV, TriMV, or HPWMoV are very similar and difficult to discriminate (Burrows et al. 2009; Mahmood et al. 1998). Infection of susceptible cultivars with TriMV alone elicits milder symptoms than WSMV infection (Byamukama et al. 2012). Symptoms from HPWMoV infection can be much more severe compared to WSMV and result in the rapid death of the host depending on environmental conditions, plant genotype, and time of infection (Mahmood et al. 1998). Co-infection of WSMV with TriMV or HPWMoV typically increases symptom severity (Byamukama et al. 2011; Mahmood et al. 1998; Skare et al. 2006; Tatineni et al. 2010). Tatineni et al. (2010) observed extensive leaf deformation, leaf bleaching and stunting in susceptible cultivars from co-infection with WSMV and TriMV. Similarly, Mahmood et al. (1998) noted severe chlorosis, stunting, and necrosis of wheat plants in the presence of WSMV

and HPWMoV. Consequently, yield loss may be exacerbated under co-infection with two or more viruses (Byamukama et al. 2012, 2014; Tatineni et al. 2010).

Co-infection of wheat with WSMV and TriMV may be mutually beneficial for both viruses in that concentration of both viruses were 2.2 and 7.4-fold increased at 14 dpi over respective single infections (Tatineni et al. 2010). Increased virus titer under co-infection could result in increased vector transmission, as this is typically directly related to virus concentration in the source plant. Increased symptom severity from co-infection with WSMV and TriMV may also have negative consequences for virus and vector; the accelerated decline of the host plant under co-infection may require virus and vector to migrate sooner than new, suitable hosts emerge in the environment.

Impact of Temperature on WSM Viruses and Infection

Temperature affects host resistance to various pathogens like viruses (Garrett et al. 2006), as well as virus development in the host plant, i.e. replication, systemic movement, and symptom development. In greenhouse studies, Wosula et al. (2017) showed that WSMV presence in winter wheat after mechanical infection remained limited to the point of inoculation at 10 °C, while systemic virus movement and mild symptom expression were observed in susceptible plants at 15 °C and symptoms exacerbated at temperatures of 20 °C and above. In resistant winter wheat ‘Mace,’ systemic virus movement was suppressed at temperatures up to 15 °C and no visual symptoms were observed even when systemic movement within the host plant occurred at 20 °C and 25 °C. These results emphasize the critical role that ambient temperatures play in the infection and symptom development process. The presence of resistance genes

in winter wheat cultivars may not prevent WSMV infection from occurring but can prevent or at least delay systemic spread within the host and subsequent symptom development. A delay in symptom development can be critical in protecting crop yield under WSMV-infection as effects are typically worse the sooner systemic infection occurs (Byamukama et al. 2012; Hunger et al. 1992; Wosula et al. 2018).

Price et al. (2014) found that once WSMV-resistance in winter wheat cultivars ‘Mace’ (*Wsm1*) and ‘RonL’ (*Wsm2*) broke down at high ambient temperatures of 28 °C, these winter wheat cultivars were not able to recover from the initial infection with viruliferous WCM, even as temperatures decreased below resistance thresholds. These results suggest that systemic infection, once it occurs, is irreversible. Moreover, WSMV concentration in host tissue declines at temperatures below 7 °C (Price et al. 2014). This indicates reduced virus replication, transmission, and new infections occurring at cool temperatures, which slows the infection process. Consequently, management practices should aim to extend plant development under cool temperatures for as long as possible to delay systemic infection of the crop to later, less vulnerable developmental stages. This can be achieved by postponing winter wheat planting dates until later in the season and planting spring wheat as soon as conditions allow.

The Wheat Curl Mite: Vector of the WSM Complex

Mite Biology

The WCM (superfamily: *Eriophyoidea*) has a white, cigar-shaped body 250 µm long (Keifer 1938). The life cycle of WCM consists of four developmental stages: egg, two nymph stages, and adult (Staples & Allington 1956; Slykhuis 1955). Under optimal

temperatures of 24 to 27 °C, the life cycle is completed in seven days, but is longer at temperatures below or above the optimal range (Boczek and Chyczewski 1975; Sabelis and Bruin 1996; Salome et al. 1964). Reproduction occurs through indirect fertilization, in which male mites deposit spermatophores on plant surfaces, which are picked up by females (Oldfield 1970). Fertilized diploid eggs develop into female mites. Wheat curl mites are capable of arrhenotokous parthenogenesis, where unfertilized haploid eggs develop into male mites (Helle and Wysoki 1983). Female mites lay at least 12 eggs in their lifetime (Staples and Allington 1956) and up to 25 eggs over a 10-day period (Salome et al. 1964). On average, a female produces one egg per day during her lifetime. Over the course of 60 days, a population can expand from one female to three million mites under favorable conditions (Somsen and Sill 1970; Townsend and Johnson 1996). The tremendous colonization and population growth potential characterizes WCM as r-strategists and is seminal to their potential and success as wheat pest and virus vector.

WCM Injury and Virus Transmission

Wheat curl mites feed on the epidermis tissue of host plants. Their feeding results in the collapse of leaf cell walls, which causes leaves to curl, thereby creating a protected environment for the mites (Murugan et al. 2011; Orlob 1966). Mite feeding negatively affects photosynthetic capacity and can cause failure of emergence of leaves and heads (Harvey et al. 2000; Orlob 1966; Royalty and Perring 1996; Somsen and Sill 1970). High WCM population densities can reduce wheat yields and cause yield losses as much as 30% (Styer and Nault 1996; Harvey et al. 2002; Navia et al. 2010).

The economically more impactful damage inflicted by WCMs occurs through their role as vector of the WSM virus complex (Oldfield and Proeseler 1996; Navia et al. 2013; Wegulo et al. 2008). Transmission of WSMV by WCMs has been studied extensively, while many aspects of TriMV and HPWMoV transmission remain unstudied. Wheat curl mites acquire virus through feeding on infected plant material. A minimum feeding time of 15 min is required for WSMV but resulting transmission rates are less than 1% (Orlob et al. 1966). Transmission efficiency increases with longer feeding times and reaches 50% after 16 h (Orlob et al. 1966). Peak transmission rates of TriMV (32%) have been observed after 24 h to 48 h of feeding (Knoell 2008). Wheat curl mite nymphs, but not adults, can acquire TriMV and WSMV and remain infective through molts (Slykhuis 1955; del Rosario and Sill 1965; Orlob 1966; Siriwetwivat 2006). The virus is retained for at least seven days at 23 - 28 °C (Orlob et al. 1966), but transmission efficiency decreases over time and with mite age (del Roasio and Sill 1956; Orlob 1966; Siriwetwivat 2006; Slykhuis 1955). For example, immature WCMs transmit WSMV with 68% efficiency, but efficiency in adult mites decreased to 43% (Siriwetwivat 2006). However, at low temperatures of 3 °C mites can remain infective for as long as two months (Orlob 1966). This suggests that overwintering mites can be a source of virus inoculum in the spring. Wheat curl mites do not pass WSMV to the next generation transovarially (Paliwal 1980). Therefore, each mite generation acquires the virus through feeding on an infected host.

The exact mode of WSMV transmission remains unclear as it seems to share characteristics of both circulative and non-circulative viruses. Both persistent and semi-

persistent modes of transmission have been described in the literature (Bragard et al. 2013; Ng and Perry 2006; Orlob 1966; Paliwal 1980; Stenger et al. 2005). The fact that the virus is retained through molts and for several days after acquisition suggests a persistent mechanism of transmission. At the same time, it has been suggested that the WSMV mode of transmission by WCMs may not conform with any of the mechanisms described for hemipteran-transmitted viruses (Knoell 2018).

Transmission efficiency is influenced by virus characteristics. Wosula et al. (2015) observed that WSMV strain Sidney 81 was transmitted at a higher rate compared to Type strain. Moreover, Oliviera-Hofman et al. (2015) found that co-infection with WSMV and TriMV reduced WSMV transmission from 50% to 36% but increased TriMV transmission from 43% to 57%, compared to transmission rates from respective single infections. The apparent beneficial effect of WSMV on TriMV transmission rates from co-infected source plants may account for the high frequency of TriMV co-infections with WSMV observed in winter wheat fields in Colorado, Kansas, Nebraska, and South Dakota (Byamukama et al. 2013). Similarly, Seifers et al. (2002) reported increased HPWMoV transmission rates from source plants co-infected with HPWMoV and WSMV.

Low levels of seed transmission of WSMV have been observed. Seed transmission rates of 0.1% in maize (*Zea mays*) were reported by Hill et al. (1974), while Jones et al. (2005) documented transmission rates of 0.5 - 1.5% in wheat. Very low seed transmission rates of HPWMoV have been observed in sweet corn by Forster et al. (2001), who found three symptomatic seedlings out of approximately 38,500 seedlings

tested (0.008%). Transmission of HPWMoV or TriMV in wheat seed has not yet been documented. Although such low seed transmission rates are unlikely to contribute significantly to epidemiological dynamics of WSMV and HPWMoV in areas where the viruses are already established, they can have considerable implications for geographic regions where the virus has not yet been introduced, particularly if WCMs are already present.

The WCM is a Cryptic Species Complex

Wheat curl mites occur on five different continents: Europe, Asia, Australia, and North and South America. Navia et al. (2013) compiled a comprehensive table of countries, where WCMs were identified. Although not officially confirmed, WCMs are also suspected to be present on the African continent because WSMV was detected in wheat in Algeria and Zambia (Benmokhtar and Yahia 2009; Kapooria and Ndunguru 2004). Over the past decade, WCMs have been identified as a cryptic species complex of genetically divergent lineages (haplotypes) that differ in host range and specificity, as well as in their virus transmission capabilities (Carew et al. 2009; Skoracka et al. 2012, 2013, 2014, 2018; Hein et al. 2012; Malik 2001; Miller et al. 2013). The extent of this genetic diversity is yet unknown (Skoracka et al. 2015, 2017), but the highest diversity of WCM lineages so far has been observed in Turkey (Szydło et al. 2015). Most lineages have been collected from wild grass species and many demonstrate high host specificity and are unable to colonize wheat (Skoracka et al. 2013). However, two lineages emerged as invasive and demonstrate moderate to high pest potential. These lineages have been found on cereal crops as well as forage grass species, have a global distribution beyond

the Eurasian continent, as well as the ability to vector viruses of the WSM complex (Carew et al. 2009; Hein et al. 2012; McMechan et al. 2014; Schiffer et al. 2009; Seifers et al. 2002; Skoracka et al. 2014). Carew et al. (2009) identified two WCM lineages among mites collected from wheat and grasses in Australia. Corresponding lineages were identified in Europe (Skoracka et al. 2014), North and South America (Hein et al. 2012) and are named MT-1 and MT-8 (Skoracka et al. 2014). In North America, these WCM lineages were originally referred to as Type 2 and Type 1, respectively (Hein et al. 2012).

Lineages MT-1 and MT-8 occur across the U.S. Great Plains (Hein et al. 2012; Malik 2001; McKelvy et al. 2019; Skoracka et al. 2014). MT-1 stands out as a highly pestiferous and invasive lineage with a global distribution and broad host range (Skoracka et al. 2014). MT-1 has been shown to colonize at least 10 plant species in the family *Poaceae* (grass family), as well *Amaryllidaceae* (amaryllis family), and *Liliaceae* (lily family) in bioassays (Skoracka et al. 2014). However, its highest population growth rates were achieved on wheat and triticale. Populations could also be sustained for three months or more on tulips, garlic and onion (Skoracka et al. 2014).

In addition to differences in host colonization between WCM lineages, differences in the lineage's response to resistance genes in wheat have been observed. For example, WCM resistance genes *Cmc1* and *Cmc2* were effective against populations of the MT-8 lineage, but not against populations of the MT-1 lineage (Harvey et al. 1999). Mite lineages further differ in their virus transmission ability and efficiency and show differential interactions with the WSM-viruses. Higher transmission efficiencies of WSMV, TriMV, and HPWMoV have been observed in MT-1 compared to MT-8 in the

Great Plains (McMechan et al. 2014; Oliviera-Hofman et al. 2015; Seifers et al. 2002; Wosula et al. 2016). Among Australian WCM populations, only MT-1 was able to transmit WSMV (Schiffer et al. 2009). Oliviera-Hofman et al. (2015) further observed that transmission rates by lineage MT-1 of TriMV from TriMV and WSMV co-infected source plants were increased by 13% compared to single-infected source plants, suggesting that WSMV presence enhances TriMV transmission. In contrast, WSMV transmission from co-infected source plants was reduced by 14%, indicating a negative effect of TriMV on WSMV transmission. Moreover, only MT-1 was shown to transmit both viruses at the same time. In contrast, lineage MT-8 was not able to transmit TriMV from co-infected source plants and only very low transmission rates of TriMV from single-infected plants were observed (McMechan et al. 2014). Similarly, MT-8 also appears to be less efficient in the transmission of HPWMoV compared to MT-1 mites (Seifers et al. 2002).

Factors Influencing WCM Biology, Dispersal, and Survival

Wheat curl mites tolerate a wide temperature range, which contributes to their widespread distribution and pest potential. Studies in Australia suggested that WCM persist in temperate and semi-arid climates and that heat and drought stress are most limiting to their distribution (Schiffer et al. 2009). Population growth of WCMs is positive at temperatures between 10 and 35 °C and mite activity and reproduction ceases at temperatures below 10 °C (Kuczyński et al. 2016; Staples and Allington 1956). However, WCMs have been shown to survive near-freezing temperatures as low as -18 °C for three months at all developmental stages (Townsend and Johnson 1996),

indicating a substantial temperature tolerance. All mite developmental stages have been found on wheat plants during winter, seeking shelter in the wheat crown and leaf whorls (Jeppson et al. 1975).

Virus presence has been shown to affect mite establishment and population growth on host plants. Increased WCM densities of MT-1 were observed on WSMV-infected wheat plants compared to non-infected or infected, WSMV-resistant plants (Murugan et al. 2011; Siriwetwivat 2006). Similarly, Byamukama et al. (2016) found highest densities of WCMs on field-collected maturing wheat heads that were infected with WSMV. In contrast, lower number of WCMs were found on TriMV-infected wheat plants. In agreement with this, reduced population growth rates in the presence of TriMV were observed in several other studies (Knoell 2018; McMechan et al. 2012; Oliviera-Hofmann et al. 2015). Moreover, population establishment from single-mite transfers was reduced by 20 - 25% on TriMV-infected wheat plants compared to non-infected plants for both MT-1 and MT-8 mites (McMechan et al. 2014).

Wheat curl mite movement and survival are two pivotal factors influencing virus spread (Thomas and Hein 2003). The mites can walk 5 cm in an hour (Salome et al. 1964) and this may be the dominant mode of dispersal on and between adjacent host plants. Wind currents promote mite movement over longer distances, within and between fields (Michalska et al. 2010) and dispersal occurs in the direction of prevailing winds (Slykhuis 1955). The dispersal range by wind is difficult to determine due to the minuscule size of the mites. However, dispersal distances have been approximated by virus spread and subsequent virus expression and distances of over 3 km from a source

plant have been observed (Stilwell et al. 2019). At high wind speeds of more than 9 m/s, WCM spread might cover even further distances (Stilwell et al. 2019). However, as movement on wind currents is passive for wingless WCM, the likelihood of mites reaching an adequate host was estimated to be lower than 10% (Jeppson et al. 1975). Once launched, WCMs cannot control when and where they are going to land. Therefore, the decision when and under what conditions to take-off is of key importance for successful dispersal. Mite population size on the host plant has been identified as important factor in the timing of wind-dispersion (Thomas and Hein 2003). Contrary to earlier perceptions, host plant fitness of un-vernalized winter wheat could not be confirmed as a decisive and direct cue for dispersal (Thomas and Hein 2003). Nevertheless, because healthy plants can sustain larger WCM populations, host plant fitness and deterioration still indirectly contribute to dispersal behavior (Thomas and Hein 2003).

Wheat curl mites are poorly protected against desiccation, but on host plants they find shelter in secluded areas such as whorls, leaf sheaths, glumes, as well as curled and trapped leaves (Nault and Styer 1969; Sabelis and Bruin 1996). However, off-host survival decreases dramatically with increasing temperatures and decreasing humidity. In growth chamber experiments, Wosula et al. (2015) found that WCMs survived away from a host for as long as 168 h (7 d) at low temperatures of 10 °C and high relative humidity of 95%, but only 48 h at low relative humidity of 2%. Moreover, at high temperatures of 30 °C CM survival was considerably reduced under both high and low relative humidity regimes; 36 h compared to less than 8 h at 95% and 2% relative

humidity, respectively. These findings suggest temperature to be the more dominant factor affecting off-host survival compared to relative humidity. In addition, WCM survival away from a host was influenced by virus presence, as well. Survival of WCMs from TriMV-infected host plants was reduced by approximately 20% compared to WSMV- or non-infected host plants at temperatures of 20 °C (Wosula et al. 2015).

Natural Enemies of the WCM

No natural enemies of the WCM have been reported in the literature, but anecdotal evidence suggests a potential role of thrips (order: Thysanoptera, family: Thripidae) as predators of WCM (Stilwell 2009). A correlation between thrips and WCM populations has been reported from greenhouse and field experiments, where WCM populations increased more rapidly on wheat plants in the absence of thrips (Stilwell 2009). In temperate and tropical regions, thrips are known to commonly prey on mites (Lewis 1973; Chazeau 1985) and facultative predation is widespread across thrips genera (Mound 2005). Several thrips species reportedly feed on eriophyid mites. *Leptothrips mali* (Fitch) preys on the tomato russet mite, *Vasates lycopersici* (Masse) (Anderson 1954; Bailey and Keifer 1943) and is common across North America (Bailey 1940). Moreover, *Haplothrips subtilissimus* (Haliday) and *Xylaplothrips fuliginosus* (Schille) are reported to negatively affect populations of eriophyid gall mites in Germany (Schliesske 1992). Stilwell (2009) observed larva and adult thrips of the species *Thrips tabaci* and *Frankliniella occidentalis* actively feeding on WCMs. In surveys of winter wheat fields in western Nebraska in 2007 - 2008, 13 thrips species were collected, many of which are known to be predaceous (Stilwell 2009). *Anaphothrips obscurus* (Muller) was the

predominant species detected in this survey. Moreover, the grain thrips, *Limothrips cerealium* (Haliday), and the barley thrips, *L. denticornis* Haliday, are common pests of small grain crops (Buntin et al. 2007).

Hosts of the WSM Complex

The host range for WCM and WSM-viruses is assessed through field surveys and greenhouse studies. The host potential for WSM-viruses is tested by mechanical inoculation or mite transmission. Host plants for WCMs are typically identified by screening field-collected plant specimen for mite presence or by transferring WCMs to putative host plants and evaluating subsequent survival and population growth.

Wheat streak mosaic virus was detected in more than 40 grass species (Carew et al. 2009; Christian and Willis 1993; Connin 1956; Coutts et al. 2008; Sill and Agusiobo 1955; Sill and Connin 1953; Somsen and Sill 1970) and infects at least eight small grain crops (Seifers et al. 1996; Seifers et al. 2010; Sill and Agusiobo 1955). In addition, WCMs were collected from at least eight crop and 35 wild grass species in North America (Brey et al. 1998, Carew et al. 2009, Connin 1956, Somsen and Sill 1970). Globally, nearly 90 grass species have been associated with the WCM. Navia et al. (2013) published a thorough summary of host plants of the mite-virus complex from various countries.

Epidemiologically important host plants for the WSM-complex must be able to sustain both WCMs and at least one of the WSM-viruses, but this characteristic applies to only a small proportion of host plants. The reproductive success of WCMs on host plants is another determinant of the epidemiological potential, because population size is a key

factor of dispersal (Navia et al. 2013; Thomas and Hein 2003). However, host potential of many plant species is only assessed qualitatively or at a single growth stage (Navia et al. 2013). The plants' life cycle (perennial, summer annual, winter annual) influences host potential and determines whether a plant species is present and susceptible when WCM movement occurs. Susceptibility of plant species to virus infection may further depend on the number of mites infesting a plant, which has been observed in the case of HPWMoV (Seifers et al. 1998). Furthermore, differential results have been obtained depending on the geographic origin and type of virus isolate, WCM lineage, and host plant species tested. This suggests that adaptations of the mite-virus-complex to the conditions in a specific geographic location may occur (Ito et al. 2012), which further limits inferences on the general host range of the WSM complex. This section focuses on plant species that have repeatedly and consistently been identified as host plants to WSM-viruses and WCMs. Moreover, the analysis concentrates on crops and grass species prevalent in the Great Plains region.

Small Grain Crop Hosts of WSM in the U.S.

WCM populations develop on several small grain crops: wheat, oat, barley, pearl millet, maize, rye, triticale, and sorghum (Tab. 2.1). However, population growth on wheat plants, specifically WCM lineage MT-1, consistently exceeds that on barley, triticale, and other cereal crops (Skoracka et al. 2013), marking it as the preferred and most potent host for the virus vector. Wheat, oat, barley, rye, and triticale are further susceptible to all three WSM-viruses (Tab. 2.1). Pearl millet and certain varieties of sorghum are susceptible to some WSMV isolates and TriMV (Seifers et al. 1996). In

contrast, pearl millet appears to be immune to HPWMoV infection, which has not been detected in sorghum either. Maize was reported as a potent host for WSMV and HPWMoV and Knoell (2018) observed higher WCM transmission rates of HPWMoV from maize to wheat compared to WSMV (63% vs 38%, respectively). This suggests that nearby maize fields may be an important source for HPWMoV infection of wheat. In contrast, many maize varieties are immune to TriMV infection, although Knoell (2018) observed low levels of TriMV incidence from WCM transmission studies in the field. Host plants that show differential susceptibility are suitable for isolating individual viruses from mixed infections. For example, certain maize cultivars can be used to obtain pure WSMV isolates from coinfection with WSMV and TriMV. Likewise, pearl millet is suitable to separate WSMV from a mixed infection with HPWMoV.

Mite and Virus Resistance in Wheat. Since the first description of the WSM disease in wheat in the U.S., extensive efforts have been made to explore sources of WCM and WSM-virus resistance in the gene pool of wheat itself, as well as in domesticated and wild relatives. Perennial *Triticeae* have long been important sources for resistances to abiotic and biotic stresses (Jauhar & Peterson 1996; Qi et al. 2007) and several genera, such as *Thinopyrum* and *Aegilops*, have proved to be important sources of resistance to the mite-virus complex.

Four resistance genes against WCMs (*Cmc*) have been identified in various wild grass and crop relatives of wheat. *Cmc1* and *Cmc4* both originate from Tausch's goatgrass (*Aegilops tauschii*) but segregate independently (Malik et al. 2003; Thomas and Conner 1986). *Cmc1* has been bred into Canadian winter wheat line 'Radiant' (Thomas et

al. 2012) and *Cmc4* was incorporated in winter wheat line ‘Yellowstone’ (Hofer et al. 2011). Resistance gene *Cmc2* was identified in tall wheatgrass (*Thinopyrum ponticum*; Whelan and Hart 1988) and bred into Canadian wheat accession PI 525452 (Whelan and Thomas 1989). *Cmc3* originates from rye (*Secale cereale*) and is deployed in winter wheat cultivars ‘Salmon’ and ‘Tam 107’ (Harvey and Livers 1975; Lapitan et al. 1986; Malik et al. 2003; Martin et al. 1984; Schlegel and Kynast 1987). Several other WCM resistance traits were identified in wheat (Harvey and Martin 1992), mosquito grass (*Haynaldia villosa*; Chen et al. 1996), intermediate wheatgrass (*Thinopyrum intermedium*; Chen et al. 1998, 2003), and rye (Martin et al. 1983; Sebesta et al. 1994).

Wheat curl mite resistance traits suppress population growth on host plants, thereby reducing the likelihood of mite dispersal and virus spread. Studies revealed that WSMV incidence was significantly reduced in wheat fields with *Cmc1* and *Cmc3* resistance types (Conner et al. 1991; Harvey et al. 1994; Martin et al. 1984). Moreover, the presence of WCM resistance traits in volunteer wheat would reduce WCM population build-up in this summer host, thereby reducing the risk of virus spread into adjacent crops in the fall. However, effectiveness of WCM resistance is dependent on the source of the resistance gene and the predominant WCM lineages in each location. Harvey et al. (1995, 1999) reported that WCM populations from different geographic origins across the Great Plains states, as well as from across Kansas, respond differentially to the resistance traits. Moreover, reliance on a single resistance gene likely promotes adaptation of WCMs to overcome this resistance. For example, WCM resistance in ‘Tam 107’ (*Cmc3*), which was widely used across the Great Plains, became largely ineffective in the mid 1990’s

against WCMs of the lineage MT-1 (Harvey et al. 1995, 1997). However, other resistance genes remain effective against MT-1, e.g. *Cmc4* (Chuang et al. 2017). Alternation in the use of different resistance traits or the combination of several resistance sources into one genotype present two approaches for preventing the loss of efficacy of available *Cmc* genes.

To date, three WSMV resistance genes have been identified, two of which provide resistance to TriMV infection, as well. *Wsm1* was the first resistance gene to be introduced from intermediate wheatgrass (Wells et al. 1973) and is located on chromosome 4D. Winter wheat ‘Mace’ is the first and to date only commercial cultivar carrying *Wsm1* (Graybosch et al. 2009). The gene confers high levels of resistance to WSMV and TriMV at moderate temperatures under field conditions, but resistance breaks down at temperatures around 24 °C, respectively (Friebe et al. 2009; Seifers et al. 1995). Liu et al. (2011) identified a second source of WSMV resistance from intermediate wheatgrass on chromosome 7B, which was designated *Wsm3*. This gene facilitates resistance to both WSMV and TriMV at 18 °C and even seems to enable WSMV resistance at 24 °C (Seifers et al. 2007). *Wsm3* is not yet established in commercially available germplasm. The first true wheat resistance to WSMV was found in a screening of winter wheat germplasm lines under natural infestation with viruliferous WCMs, where plants of the CO960293-line remained symptomless in field trials and tested negative against antisera to WSMV and TriMV (Seifers et al. 2006). In growth chamber experiments the resistance was shown to be temperature-sensitive, breaking down above 24 °C (Seifers et al. 2006). A homozygous single-plant selection from the

resistant line has subsequently been released as germplasm CO960293-2 (Haley et al. 2002). Lu et al. (2011) were able to attribute the resistance to a single dominant gene on the 3B chromosome through segregation analysis, which was designated *Wsm2*. This wheat-derived resistance has so far been introgressed into cultivars ‘RonL’ (Martin et al. 2007) and ‘Snowmass’ (Haley et al. 2011), ‘Clara CL’ (Martin et al. 2014), and ‘Oakley CL’ (Zhang et al. 2015). In contrast to *Wsm1* and *Wsm3*, *Wsm2* does not confer resistance to TriMV. Another source of wheat-derived resistance was found in the wheat line KS03HW12, which withstood infection with six different isolates of WSMV through mechanical inoculation and concurrently produced negative results in ELISA tests against WSMV and mechanical infectivity back-assays to susceptible wheat plants (Seifers et al. 2007). Similar to germplasm CO960293-2, resistance in KS03HW12 is not effective above 24 °C. In addition, yield reductions were not observed for KS03HW12 selections or CO960293-2 lines in the field (Seifers et al. 2007). This represents a striking advantage of linkage drag-free resistances derived from the primary gene pool of wheat.

Through analysis of the location and movement of fluorescent protein-tagged WSMV and TriMV in resistant wheat cultivars, Tatineni et al. (2016) showed that the viruses are unable to enter the vascular system in the presence of *Wsm1* and *Wsm2* in ‘Mace’ and ‘Snowmass’, respectively. This prevents long-distance movement of viruses throughout the plant and subsequent establishment of a systemic infection at temperatures below 24 °C. The viruses are confined at the point of infection, although virus replication and cell-to-cell movement do not appear to be impaired from *Wsm1*- and *Wsm2*-expression. Although virus resistance presently available in commercial cultivars do not

withstand elevated temperatures above 24 °C, which commonly occur across the Great Plains throughout the summer months, they can still prevent early infection of the wheat crop in the fall or spring. Delaying systemic virus movement until later plant growth stages reduces the impact of WSM infection on crop yield. Moreover, delaying systemic infection of wheat plants through temperature-sensitive resistances can further slow virus spread throughout an infected field. The use of WSMV-resistant cultivars, especially in high WSM-risk years, is an effective approach to protecting crop yield under WSM pressure.

To date, there is no effective resistance to HPWMoV in wheat. The observation that WSMV enhances the transmission of HPWMoV (Seifers et al. 2002) emphasizes the importance of introducing multi-layered resistances into wheat cultivars. Pyramiding resistance genes (Fahim et al. 2012) provides a bigger array of resistance sources and equips the plant for a variety of adverse environmental conditions (biotic and abiotic). The presence of more than one resistance gene presents a more sustainable approach, since it will be harder for viruses to overcome or avoid multiple barriers of resistance. To develop and introduce such lasting multi-resistances, all known resources of resistance need to be thoroughly explored.

Grassy Weeds and Alternate Hosts of the WSM Complex in the U.S.

Of more than 40 grass species that have been documented to host the WSM-complex in the U.S., only five are suitable hosts for WCM and at least two WSM-associated viruses: cheatgrass, field brome, green bristlegrass, jointed goatgrass, and rye brome (Tab. 2.2). These grass species can be considered important alternate hosts, owing

to their potential to host several WSM-viruses and WCMs, as well as their widespread occurrence across the Great Plains. Six additional grass species were documented as hosts of WSMV and WCM: barnyardgrass, Canada wildrye, hairy crabgrass, Italian ryegrass, stinkgrass, and Persian ryegrass. Studies on the grass host range of HPWMoV have been limited due to the virus's inability to be mechanically transmitted. Most confirmed grass hosts are annual species and four of the most potent alternate hosts have a winter annual growth habit (Tab. 2.2). Winter annuals are likely less relevant green bridge hosts for the WSM complex over the summer, because they typically germinate in the fall. They may instead play an important role as overwintering hosts, since these grasses often emerge before the winter wheat crop and can subsequently become exposed to dispersing mites (Ito et al. 2012). The role of winter annuals is of particular importance in the Northern Great Plains, where shorter growing seasons often limit mite dispersal to fall-planted winter wheat. Winter annuals mature in the spring and early summer and can be a source of WCM and virus spread to wheat in the spring (Ito et al. 2012).

One major constraint in the assessment of alternate hosts for WSM is the lack of quantitative data that characterize the grass hosts' potential to promote WCM population growth. This information is however relevant for predicting WCM population densities in the environment and the risk of virus spread. Further research is required to provide this epidemiologically important information and elucidate the role of grassy weeds in the WSM dynamics. In contrast to grassy weeds, the role of volunteer wheat as potent and epidemiologically crucial alternate host for the WSM complex is well-established (Ranabhat et al. 2018; Somsen and Sill 1970; Staples and Allington 1956; Wegulo et al.

2008). Volunteer wheat can host all three WSM viruses and their vector and promotes high WCM densities. Moreover, pre-harvest volunteer wheat often occurs as a result of hail events dislodging mature wheat grain to the ground. Its timely emergence and presence near the maturing wheat crop increases the likelihood of infestation with dispersing WCMs and makes pre-harvest volunteer wheat an important summer host. Volunteer wheat abundance in the agricultural landscape is an important contributor to WSM disease risk. Control of volunteer wheat before planting of the new wheat crop is an important management tool for preventing WSM spread and infection.

The WSM Disease Cycle: Disease Dynamics in the Agricultural Landscape

The WSM disease cycle describes the occurrence and distribution of the mite-virus-complex over space and time in the Great Plains landscape. The interactions between the four corners of the WSM disease tetrahedron (viral pathogen – vector – host – environment) are combined into a coherent story throughout the wheat crop year. In the Great Plains, winter wheat is the most important crop for WCMs and associated viruses because it is present for three quarters of the year and is present in all Great Plains states (Navia et al. 2013). Considerations of the WSM disease cycle revolve around winter wheat. In states such as Montana and North Dakota, spring wheat, durum and barley can be significant hosts of the virus and WCM, but these instances in terms of inoculum perpetuation are largely the exception, although local disease outbreaks can be severe.

WSM epidemiology is inextricable from the fate of WCMs in the environment. The disease cycle can be unlocked and understood by tracking the survival, development,

and movement of WCM in the winter wheat production landscape. For simplification purposes, the WCM cryptic species complex will be considered without differentiation between divergent WCM lineages. Likewise, the WSM virus complex will be considered as a whole, if not indicated differently. These assumptions are considered valid, because all three viruses of the WSM complex occur across the Great Plains states and within the same wheat fields and often the same plants (Burrows et al. 2016; Byamukama et al. 2013). This section aims to highlight differences in WSM disease dynamics between the Central and Northern Great Plains and extract critical factors that contribute to disease risk.

For disease to occur, wind-dispersed, viruliferous WCMs must reach young winter wheat plants in the fall or spring. Mites and WSM typically originate in the highest numbers from volunteer wheat created by hail events near crop maturity. Local dispersal is more likely than long-distance dispersal, but viruliferous WCMs are known to travel miles (Thomas et al. 2004). After landing on a new host plant, WCMs begin to feed and reproduce. Infection of plants in the fall or before tillering stage in the spring typically result in severe disease symptoms and subsequent yield reductions (Byamukama et al. 2012; Hunger et al. 1992; Wegulo et al. 2008; Wosula et al. 2018). Disease severity further depends on temperatures and cultivar susceptibility to WSM and WCMs. Systemic WSMV movement is restricted at temperatures below 20 °C and 15 °C in resistant and susceptible winter wheat cultivars, respectively, and WSMV replication ceases below 7 °C (Price et al. 2014; Wosula et al. 2017). In addition, WCM activity and population growth sharply decreases below 10 °C and stops near 0 °C (Staples and

Allington 1956). WCMs can tolerate sub-freezing temperatures as low as -18 °C for three months at all developmental stages in the crown of their host plant (Jeppson et al. 1975; Townsend and Johnson 1996). Wheat streak mosaic virus overwinters in the living tissue of the host plant.

As temperatures increase in the spring, WCMs resume their feeding and reproductive activity and the virus replicates and moves within the growing host plant. In WSMV-susceptible cultivars, symptoms may become visible at temperatures of 15 °C and above, while resistant cultivars may never develop symptoms or only at much higher temperatures above 24 °C (Wosula et al. 2017). At the field level, WSM symptoms first appear along the edges of the field facing nearby volunteer wheat, spring wheat, maize fields, or grassy pastures, which host virus and vector (Thomas and Hein 2003). If WSM infection originates from infested volunteer wheat or grasses within the field, WSM symptoms may initially occur as scattered infection foci across the field. In severe cases, the pattern of symptoms in the field may be very uniform. As populations grow, WCMs move within and between fields and the virus spread can be observed as expansion of symptomatic plants, typically in the direction of prevailing winds (Stilwell et al. 2019). As a result, disease severity gradients may develop and WSM incidence is correlated with yield reductions (Workneh et al. 2009).

When the wheat crop enters heading stage, WCMs move up their host plant into the wheat heads and population growth is high. Mite densities are typically the highest in maturing wheat (Mahmood et al. 1998; McMechan and Hein 2017). Wheat heads provide secluded sites among developing kernels, which promote WCM feeding and reproduction

(Gillespie et al. 1997). It could be argued that a drastic increase in WCM populations is associated with warm summer temperatures typically occurring at this time of the year, which accelerate WCM development (Boczek and Chyczewski 1975; Sabelis and Bruin 1996; Salome et al. 1964).

Once the wheat crop matures, WCMs must leave the senescing host and seek suitable green host plants on which they can feed and survive. Pre-harvest volunteer wheat represents the highest risk “green bridge” host (Ranabhat et al. 2018; Somsen and Sill 1970; Staples and Allington 1956; Wegulo et al. 2008). It is a suitable host for all three viruses of the WSM complex and supports high reproduction rates of WCMs (Skoracka et al. 2014). The occurrence of pre-harvest volunteer wheat is typically associated with hailstorm events close to wheat maturity knocking grain onto the ground, which germinates readily in the presence of moisture. McMechan and Hein (2017) showed that if wheat kernels at the hard and soft dough stage are dislodged to the ground, WCMs can feed and survive on these kernels and directly infest the emerging seedlings. Wheat stem sawfly (*Cephus cinctus* Norton; WSS) can be another source for volunteer wheat, particularly in the Northern Great Plains. This insect pest has historically been prevalent in Montana and North Dakota as well as Alberta, Saskatchewan, and Manitoba. More recently, WSS has arisen as a serious insect pest in eastern Wyoming and Colorado, as well as western South Dakota and Nebraska (Fulbright et al. 2011; Irell and Peairs 2011; McCullough 2016). The larvae of WSS reside within wheat stems and destabilize the stem’s architecture due to their feeding activity. Infested wheat stems often lodge near maturity under the weight of their heads or as a result of strong winds. This causes seeds

to land on the ground, which is referred to as “biological hail.” Wheat stem sawfly infestation can be another source of volunteer wheat, particularly in years with abundant summer precipitation, which would contribute to the ready germination of pre-harvest wheat seeds on the ground. Other suitable summer hosts for the mite-virus complex are grassy weeds, such as cheatgrass, field brome, green bristlegrass, jointed goatgrass, and rye brome, or nearby fields of spring wheat and maize (Knoell 2018; Wegulo et al. 2008). In the Central Great Plains, maize is abundantly present in the agricultural landscape and presents an important green bridge host, because its growing season typically overlaps with the maturing winter wheat crop and reaches into the early planting season for winter wheat. However, maize is not a common crop in Montana and western North and South Dakota (USDA NASS 2019) and of little relevance to the WSM disease dynamics in the northern parts of the Great Plains.

In the late summer, WCM population size is typically high as a result of growth-promoting summer temperatures, particularly if green bridge hosts are abundant in the environment. Such an environment presents a high risk for newly planted winter wheat to become infested by dispersing WCMs. The occurrence of fall infection is dependent on winter wheat planting dates and the conduciveness of the environment for mite dispersal. The sooner winter wheat is planted and emerges, the longer is the crop exposed to dispersing WCMs, increasing the risk of infection during early plant development. Mild temperatures and a prolonged fall season are conducive for extensive mite movement and WSMV infection. Wind speeds above 9 m/s may further facilitate long-distance dispersal of WCMs for 3 km or farther (Stilwell et al. 2019). Over large areas of the Northern

Great Plains fall temperatures average 13 °C in September and 7 °C in October (30-year Normal 1981-2010; PRISM Climate Group 2015). Wheat curl mite movement is therefore likely to cease in the month of October. In contrast, average temperatures in the Central Great Plains average 11 °C - 14 °C in October allowing for WCM movement to occur longer into the fall. A shorter season length and cooler fall temperatures are likely factors that contribute to a more sporadic occurrence of WSM epidemics in Montana and other parts of the Northern Great Plains.

Dissecting the WSM Disease Cycle: Factors Influencing WSM Disease Risk

Host plants for WCM and WSM viruses are predominantly annual grass species, which necessitates the mite-virus-complex to disperse from host to host at least two times throughout the year (Navia et al. 2013). These periods of dispersal are of crucial importance to WCM ecology and virus epidemiology in wheat. Extracting the factors that influence dispersal success and associated virus spread provides a foundation for the assessment of WSM disease risk and identifies target sites for WSM disease management.

The first period of dispersal occurs when WCMs must leave the maturing winter wheat crop in search for suitable summer hosts. The abundance of summer hosts in the environment, particularly pre-harvest volunteer wheat (Somsen and Sill 1970; Staples and Allington 1956; Wegulo et al. 2008), is an important factor during this period. This is in turn influenced by the occurrence of timely hail events and/or WSS activity in the environment, both of which contribute to the occurrence of volunteer wheat. Precipitation

amounts and drought severity during the summer months influence not only the timely emergence of volunteer wheat but the general abundance of green host plants in the environment. Moreover, the composition of the agricultural landscape with respect to suitable crop hosts for the mite-virus complex, such as spring wheat and maize fields, further determine the likelihood of dispersing WCMs to find a suitable host for over-summering. Although these factors are critical for WCM survival and reproduction between winter wheat crops, little can be done to manipulate or eliminate them at the time of WCM movement. They are however important to keep track of as they can inform about the extent and fitness of WCM populations in the green bridge and WSM disease risk.

The second period of WCM dispersal occurs in the late summer months and early fall, when the mite-virus-complex moves from summer hosts into the newly planted winter wheat crop. Because WCMs have a limited ability to survive without a host, the temporal overlap in hosts is a critical factor of WSM disease risk. Wheat curl mites can survive off-host for as long as seven days at high relative humidity (95%) and cool temperatures (10 °C), but survival time is only a few hours at high temperatures (30 °C) and low relative humidity (2%) (Wosula et al. 2015). Creating a host-free period for at least one week can reduce WSM disease risk for the new crop considerably. Choosing later planting dates for winter wheat reduces the time during which the emerging wheat crop is exposed to dispersing WCMs and will greatly reduce the risk of early infection with WSM (McMechan and Hein 2016; Thomas and Hein 2004). Moreover, late planting

decreases the probability of exposure to temperatures that are conducive for WCM movement and feeding activity.

Risk of infection is further dependent on WCM population size in the green bridge and the proximity of source plants to the new winter wheat. Emphasis should be put on pre-harvest volunteer wheat, as it supports high population densities of WCM and can host all viruses of the WSM complex. Thomas and Hein (2003) showed that the dispersal range increases with increasing WCM population size on source plants. Green bridge hosts near the new wheat crop present a high risk for WSM infection, especially if source plants are located upwind (Stilwell et al. 2019). As a result, green bridge control becomes increasingly important the closer potential WSM sources are located relative to the new winter wheat crop. Timely termination of volunteer wheat and other green bridge hosts several weeks before emergence of the new wheat crop is an effective approach to reducing WCM population numbers and WSM risk. The best method of green bridge control will depend on the planting schedule and environmental conditions. In a greenhouse study, Jiang et al. (2005) showed that WCM populations on glyphosate-treated wheat plants noticeably decreased 10 days after the herbicide application, while WCM numbers increased during the first three days post application. In contrast, paraquat treatment resulted in an immediate decrease in WCM numbers on the plants. Similar results were produced in a field study by Thomas and Hein (2004), who observed that WCM movement from glyphosate-terminated volunteer wheat occurred for up to two weeks post-application. In contrast, significant mite movement from tilled volunteer wheat occurred only for seven days after treatment. Moreover, Brey (1998) noted a flush

of WCM dispersing from vegetative wheat 12 and 36 h after glyphosate treatment in a wind tunnel study, indicating that risk of infection could even increase immediately after herbicide application. Green bridge control should therefore occur several weeks before winter wheat planting to ensure complete death of host plants and a certain decline in WCM numbers on summer hosts.

Wheat Stem Sawfly Biology and Life Cycle

Adult WSS are 12 mm long and black with yellow bands on their abdomen. They have prominent eyes and club-shaped antennae. Wheat stem sawflies have a univoltine life cycle. They spend most of their life inside the host plant and only adults live for an average of seven days outside the host (Criddle 1923). Emergence of WSS occurs in the spring and is dependent on temperature and varies by geographic region (Perez-Mendoza and Weaver 2006). Peak emergence typically occurs after 578 to 595 growing degree days (Beres et al. 2011a). In Montana, WSS flight is typically observed from May to July, lasting between three to four weeks (Fulbright et al. 2011)

Male WSS emerge before females (Holmes 1979) and copulation takes place immediately after emergence. Eggs deposited early during the season are typically fertilized (diploid) and develop into females, while unfertilized eggs, often deposited later, are haploid and produce males (Holmes 1979). Females carry as many as 50 eggs (Ainslie 1920), which they deposit into the stems of host plants. Using their saw-like ovipositor, they cut a small opening in the internode areas of elongating stems and insert the eggs into the stem. Larvae develop inside the eggs, from which they hatch six to

seven days after oviposition (Ainslie 1920). Larvae are transparent and without color at first but are yellow-brown after feeding on plant tissue (Ainslie 1929; Criddle 1923).

Adult WSS females cannot discriminate stems that have been infested already and more than one egg may be deposited into the same stem by different females (Criddle 1923; Buteler et al. 2009). However, only one larva typically survives in the stem due to conspecific cannibalism (Criddle 1923; Holmes 1982; Wallace and McNeal 1966). It is not known whether cannibalism of eggs and larvae occurs intentionally or results from indiscriminate feeding activity (Beres et al. 2011b). However, cannibalism is considered a density-dependent function that minimizes competition for limited resources by reducing population size, thereby increasing the fitness of surviving cannibals (Richardson et al. 2010). Larval survival may further be reduced by pathogens, parasitism, and host plant resistance and ranges between 28% and 84% (Buteler et al. 2015).

Larvae of WSS actively feed for the duration of the growing season, moving up and down the stem. Their development and activity are synchronized with host phenology and transition into obligate diapause is triggered by environmental cues. Infrared light penetrating through the stem wall as the host plant matures, prompts larvae to move towards the base of the plant (Holmes 1979). Once the plant moisture content has declined to 41% - 51%, WSS larvae begin to prepare their hibernaculum (Holmes 1979). Larvae create a imminent breaking point inside the stem by carving a groove around the inside near the ground. This destabilizes the stem architecture and stems become prone to lodging (Ainslie 1929). The larvae seal their hibernaculum with frass

and wrap themselves into a cocoon, which shelters them from the environment and predators (Holmes and Peterson 1960). Protected in this way, diapausal larvae can survive several months immersed in water (Ainslie 1929) and up to 10 days at temperatures as low as -20 °C (Cárcamo and Beres 2006).

Diapause is completed after 90 days at 10 °C or less, after which larvae enter pupation. If unfavorable conditions occur before pupation, such as high temperatures or extreme drought (Holmes 1979; Salt 1947), larvae can continue diapause and remain in this state until the following spring. Pupation is irreversible once entered. Pupation is completed within 21 days, depending on temperature (Criddle 1923), and adults emerge by chewing through the frass plug or the side of the stub (Holmes and Peterson 1960).

Crop Damage Inflicted by WSS

Wheat stem sawfly adults do not feed on host plants and do not injure the crop (Criddle 1923). However, larvae are injurious to the crop and cause yield losses in two ways. Stem-mining activity of larvae reduces the photosynthetic capacity of host plants and damages the vascular tissue, thereby impairing the transport of water and nutrients through the plant (Delaney et al. 2010; Macedo et al. 2005; 2006, 2007). Photosynthetic rates in infested wheat plants were reduced by 12% compared to uninfested stems (Macedo et al. 2007). As a result, plant fitness is reduced and senescence accelerated causing physiological yield losses of 10% to 20% in wheat by reducing grain size and weight (Delaney et al. 2010; Holmes 1977; Macedo et al. 2005, 2006, 2007; Morrill et al. 1992; Seamans et al. 1944).

Little evidence exists externally that could divulge whether stems are infested, but the stem area immediately below nodes may show discoloration from larval activity (Morrill et al. 1992). Infestation at this stage can only be confirmed with certainty by slicing stems open longitudinally to reveal frass and larvae (Holmes 1979). Wheat stem sawfly infestation will become obvious at or near crop maturity when pre-diapause larvae girdle the host stem, which readily falls over in windy conditions (Ainslie 1920). Lodged stems are difficult or impossible to recover during harvest and each wheat head remaining on the ground represents 100% yield loss for that wheat stem. Yield losses at the field level depend on WSS and parasitoid population size, the level of infestation and tolerance and resistance of the host. Infestation rates approaching 100% in winter and spring wheat were reported for some fields in the 1990s (Morrill 1994) and harvest losses of 15.5% from lodging have been estimated (Ainslie 1920; Holmes 1977; Weiss and Morrill 1992).

WSS Hosts

Historic and Recent Host Range

Wheat stem sawflies are native to the American Prairie, where they infect large-stem grasses. Cockrell et al. (2017) presented a list of non-cultivated grass species that have been documented to host WSS. Of the 30 grass species listed, *Agropyron* and *Elymus* species were predominant and many species are of economic relevance as forage for livestock (Cockrell et al. 2017).

With the westward movement of civilization in the 1900s and the expansion of wheat production across the Northern Great Plains, wheat and other cereal crops became

attractive alternative hosts (Ainslie 1920; Fletcher 1896). Infestation of wheat was first reported in Manitoba and Saskatchewan, Canada, in 1895 (Fletcher 1896). Initially, crop damage was limited to spring wheat, while earlier-maturing winter wheat escaped WSS infestation (Davis 1948; Painter 1953; Wallace and McNeal 1966). However, by 1985 widespread infestation of winter wheat was reported in Montana (Morrill 1985), indicating the synchronization of the WSS life cycle with winter wheat phenology (Morrill and Kushnak 1996). The ability of WSS to adapt their life cycle to new hosts is one reason for the expansion of its range southward into the Central Great Plains, which now includes southeastern Wyoming, the Nebraska Panhandle, northeastern Colorado, and northwestern Kansas (Irell and Peairs 2014; Lestina et al. 2016; McCullough et al. 2020; Olfert et al. 2019). Moreover, an increase in WSS infestation of barley has been documented in Montana since 2005 (Varella et al. 2018). Altogether, the known crop host range of WSS to date comprises bread wheat (*Triticum aestivum* ssp. *aestivum*) and other *Triticum* species, common barley (*Hordeum vulgare*), and common rye (*Secale cereale*) (Cockrell et al. 2017; Wallace and McNeal 1966). However, other cereal crop species demonstrate some mechanism of resistance to WSS infestation, including certain durum cultivars (*Triticum durum*), spelt wheat (*Triticum polonicum*), Timopheev wheat (*Triticum timopheevii*), and oats (*Avena sativa*) (Ainslie 1929; Farstad 1944; Holmes and Peterson 1962; Wallace and McNeal 1966). Certain non-cereal crops like flax (*Linum usitatissimum*) and sweetclover (*Melilotus officinalis*) are known to be very infrequently accepted for oviposition but WSS larvae cannot complete development in them (Criddle 1922).

Host Selection

Host selection for oviposition by WSS females is a complex process that involves several plant cues. Host plants must be at the appropriate developmental stage, post tillering and before heading, and succulent stems are preferred (Holmes and Peterson 1960). Taller varieties and less solid stems are more attractive (Buteler et al. 2009; Varella et al. 2018). Stem diameter and plant volatile compounds further influence host selection (Buteler et al. 2010; Buteler and Weaver 2012; Piesik et al. 2008; Weaver et al. 2009). The preference for larger diameter stems is associated with a female-biased sex ratio, i.e. more females emerge from larger-diameter stems, while more males emerge from smaller-diameter stems (Wall 1952; Morrill et al. 2001; Cárcamo et al. 2005).

WSS Resistance in Wheat

Host plant resistance is an effective way to protect crop yield from pest damage without requiring additional inputs. Resistance can be achieved by two mechanisms: antixenosis affects the behavior of the insect pest, while antibiosis affects pest biology (Flint 2012). Stem solidness in wheat is an effective and widely deployed resistance trait for WSS management which operates through both mechanisms of antibiosis, i.e. death of neonates and young larvae, and antixenosis, i.e. nonpreference of solid and other stems for oviposition (Varella et al. 2017a). Yield protection can be achieved through tolerance, if WSS are unable to cut the stems (Flint 2012; Sherman et al. 2010).

Stem solidness is caused by the presence of pith in the wheat stem, which is genetically controlled and dependent on environmental conditions and agricultural practices, such as row spacing and planting density (Berzonsky et al. 2003; Beres et al.

2012; Luginbill and McNeal 1958). Pith impedes egg deposition, larval movement and development in wheat stems, thereby reducing infestation and larval survival (Holmes and Peterson 1962; Wallace and McNeal 1966). Survival rates in solid-stem spring wheat cultivar ‘Choteau’ ranged 40% - 60% compared to 46% - 85% in hollow-stem cultivar ‘McNeal’ (Varella et al. 2018).

Two types of stem solidness are commonly deployed in breeding programs, which are associated with different alleles of the same quantitative trait locus (QTL), *Qss.msub-3BL* (Varella et al. 2016). Consistent stem solidness throughout plant development has been observed in ‘Choteau,’ ‘Duclair’ and other wheat cultivars and traces back to the germplasm of the Portuguese landrace S-615 (Platt et al. 1948). In contrast, stem solidness in spring wheat cultivar ‘Conan’ changes throughout plant development. During stem elongation stem solidness is high, but it decreases during stem maturation. Higher neonatal mortality rates were observed in ‘Conan’ compared to ‘Choteau’ and WSS females appeared to prefer ‘Choteau’ for oviposition (Talbert et al. 2014; Varella et al. 2016). WSS resistance conferred by the ‘Conan’ allele appears due to antibiosis (larval mortality) and antixenosis (non-preference for oviposition limits colonization by WSS) (Varella et al. 2017b).

In search for further sources of resistance to WSS, Varella et al. (2017b) screened over 1,400 spring wheat landrace accessions from diverse geographic regions of the world. Resistance traits other than stem solidness were identified in over 50% of the accessions and were related to both antibiosis and antixenosis. Potential modes of antibiosis in these landraces may be from reduced plant palatability, production of anti-

nutritive substances, hypersensitive plant response, toxic compounds, and physical barriers (Fürstenberg-Hägg et al. 2013; Hilker and Meiners 2006; Michell et al. 2016; Tamiru et al. 2015; Varella et al. 2017a). Potential modes of antixenosis conferring resistance to WSS may be achieved by volatile compounds that manipulate host plant selection and non-volatile compounds that deter probing and oviposition (Tamiru et al. 2015; Varella et al. 2017a; Weaver et al. 2009).

Distribution of WSS in the Field and Implications for Management Strategies

Wheat stem sawfly infestation of a crop field follows spatiotemporal patterns of distribution (Beres et al. 2011b). When WSS adults first emerge from stubble in the spring, they migrate to the nearest suitable host. Most often, these are neighboring wheat fields and early during WSS emergence, density of adults is highest along the field border (Holmes 1982). Consequently, oviposition first occurs on the field margins. Infestation and crop damage are more severe along the field edges compared to the center of the field. Later during WSS flight, adults migrate further into the crop field and patterns of infestation are more uniform (Nansen et al. 2005a). With respect to larval survival, however, densities remain highest along the field edges (Nansen et al. 2005a). Reduced larval survival rates further inside the field may be related to oviposition occurring later during WSS flight so that the larvae may not have enough time to complete their development and prepare for diapause before the host plant matures (Nansen et al. 2005b).

The edge effect during oviposition (Nansen et al. 2005) provides opportunity for management strategies to reduce crop damage and yield loss from WSS. Trap crops may

be planted along the field edges, which absorb the highest WSS pressure (Morrill et al. 2001). Such trap crops could be solid-stem cultivar that are resistant to stem cutting or for which higher larval mortality rates are observed. The interior of the field, where WSS infestation and larval survival is generally lower, may instead be planted to a susceptible, but higher-yielding cultivar. In spring wheat, the margins of a field could alternatively be planted to winter wheat in the fall, which has an earlier phenology attracting WSS females for oviposition. Moreover, other WSS-resistant species may be planted as trap crops. Both oats and flax are unsuitable hosts for WSS, which attract WSS females but do not support larval development.

Salvage harvest is another approach to reduce yield loss from WSS infestation. In this strategy, areas of heavy infestation and stem lodging are swathed to collect stems in windrows before they are cut (Criddle 1915). This strategy has resulted in stem cutting reductions between 23% and 33% depending on the time of swathing (Goosey 1999). However, the effectiveness of this strategy depends on the timing of swathing relative to grain maturity. If the crop is swathed too early, yield reductions may occur from a premature termination of grain filling and maturing, while late swathing may not prevent stem cutting. Moreover, the strategy of salvage harvest does not alter survival rates because larvae will have moved to the base of the stem in preparation for diapause by the time the crop may be swathed (Beres et al. 2011b). In contrast, the use of resistant or unsuitable trap crops would result in reduced larval survival and a likely decrease of the WSS population in the subsequent season.

Parasitism of WSS and Implications for Management Strategies

Parasitism of WSS is an important cause of larval mortality (Buteler et al. 2015; Peterson et al. 2011). Nine different Hymenoptera species are known to parasitize WSS (Morrill et al. 1998; Meers 2005). However, only two species have managed to follow WSS in their transition from grassy hosts to wheat (Morrill et al. 1998; Runyon et al. 2002, Weaver et al. 2005). Parasitism rates by *Bracon cephi* and *Bracon lissogaster* can be as high as 98% (Morrill et al. 1998) but are strongly location-dependent (Holmes et al. 1963).

The life cycle of the parasitoids is synchronized with that of WSS, but the parasitoid species can produce two generations per season (bivoltine). The first generation of parasitoid adults emerges approximately at the same time as WSS in the spring. Parasitoid females locate WSS larvae feeding inside stems, which they paralyze by injecting venom. Eggs are deposited nearby the paralyzed larva and once hatched parasitoid larvae begin feeding on their host. Once the WSS larva is consumed, the parasitoid pupates and enters diapause. The second generation of parasitoid adults emerges in the late summer and repeats the cycle of host location and infestation. The first generation of parasitoids can substantially reduce the larval populations (Buteler et al. 2009, 2015; Peterson et al. 2011). However, the impact of the second generation of parasitoids is more dependent on external factors. In early maturing wheat, the second generation of parasitoids may emerge at a time when WSS larvae have already entered diapause and are protected in their hibernacula (Holmes et al. 1963). In scenarios of delayed crop development parasitoids may still be able to locate WSS larvae feeding in

the stems. Parasitoid larvae produced by the second generation of adults will overwinter inside the wheat stems and emerge as first-generation adults in the following season.

Management strategies that protect and promote parasitoid populations can increase wheat stem sawfly mortality and suppress WSS population growth. Parasitoids overwinter in the upper internodes of the wheat crop and are susceptible to damage from harvest machinery (Holmes 1979). Increasing stubble height at harvest can improve parasitoid survival. Moreover, higher rates of parasitism and less stem cutting have been observed in reduced-tillage fields (Runyon et al. 2002; Weaver et al. 2004). In addition, avoiding insecticide use during the peak flight period of adult parasitoids reduces the risk of harmful side-effects on these beneficial insects (Meers 2005).

Other predators of WSS have been described, but their occurrence may be sporadic, and their life cycle and biology less well understood. The clerid beetle *Phyllobaenus dubius* (Wolcott) (Coleoptera: Cleridae) forages within wheat stems, where it was reported to prey on WSS larvae (Beres et al. 2009; Morrill et al. 2001). Clerid beetle larvae in cocoons have been found overwintering in WSS hibernacula next to dead WSS larvae (Morrill et al. 2001a). Moreover, certain *Fusarium* spp. were reported to act as entomopathogens, infesting WSS larvae inside wheat stems (Wenda-Piesik et al. 2009).

Chemical WSS Management

The concealed lifestyle of WSS larvae prevents the effectiveness of most insecticides because larvae are protected within the host stem. Few studies are published that report on the effectiveness of insecticides in WSS control, leaving considerable

uncertainty around this question. Research in the 1960s reported on the effectiveness of heptachlor (IRAC group 2A), which caused high larval mortality rates of 75% - 86% (Wallace 1962). However, this insecticide has been banned in the U.S. since the late 1980s due to its high environmental toxicity and persistence in the soil for over a decade (Beres et al. 2011b).

Systemic insecticides that translocate throughout the plant could provide efficient control of stem-boring larvae. A special local need registration label for Montana was issued for systemically acting phorate in 2015 (Wanner and Tharp 2015) but expired in 2019. Certain contact insecticides are labeled for the control of adult WSS, but their effectiveness is strongly dependent on careful monitoring of WSS occurrence and timely spray applications (Beres et al. 2011b). In large-scale production systems, typical for Montana, this management approach is difficult to achieve.

Tables and Figures

Table 2.1. Small grain crops reported as host plants for wheat curl mite, *Aceria tosichella*, and viruses of the wheat streak mosaic disease complex in North America.

Common name ^y	Scientific name	Host plant for ^x				Reference
		WCM	WSMV	TriMV	HPV	
Barley	<i>Hordeum vulgare</i>	+	+	+	+	Seifers et al. 1998; Somsen and Sill 1970
Maize	<i>Zea mays</i>	+	+	+	+	Seifers et al. 2010; Sill and Connin 1953; Slykhuis 1955; Orlob 1966; Jensen et al. 1996; Marcon et al. 1997
Oat	<i>Avena sativa</i>	+	+	+	+	Seifers et al. 1998; Somsen and Still 1970
Pearl millet	<i>Pennisetum glaucum</i>	+	+	+	-	Seifers et al. 1996, 1998, 2010
Rye	<i>Secale cereale</i>	+	+	+	+	Seifers et al. 1998, 2010
Sorghum	<i>Sorghum vulgare</i>	+	+	+		Seifers et al. 1996; Somsen and Sill 1970
Triticale	<i>Triticale x Secale</i>	+	+	+	+	Alemandri et al. 2017; Halliday and Knihinicki 2004; Seifers et al. 2010
Wheat	<i>Triticum aestivum</i>	+	+	+	+	Slykhuis 1955; Staples and Allington 1956

^x WCM – wheat curl mite; WSMV – *Wheat streak mosaic virus*; TriMV – *Triticum mosaic virus*; HPV – *High Plains wheat mosaic virus*. Plus (+) indicates confirmed as host; minus (-) indicates confirmed as non-host; blank field indicates no information available/ not tested.

^y Common names were retrieved from the United States Department of Agriculture NRCS Plant database. Alternate common names (synonyms) are indicated in parentheses.

Table 2.2. Grassy weeds reported as host plants for wheat curl mite, *Aceria tosichella*, and viruses of the wheat streak mosaic disease complex in North America.

Common name ^y	Scientific name	Growth habit	Host plant ^x				Reference
			WCM	WSMV	TriMV	HPV	
Barnyardgrass	<i>Echinochloa crus-galli</i>	annual, summer	+	+	-		Christian and Willis 1993; Seifers et al. 2010; Somsen and Sill 1970
Bermudagrass	<i>Cynodon dactylon</i>	perennial	+				Somsen and Sill 1970
Big bluestem	<i>Andropogon gerardii</i>	perennial	+	-		-	Seifers et al. 1998, Seifers et al. 2010; Sill and Connin 1953
Blue grama	<i>Bouteloua gracilis</i>	perennial	+	-		-	Seifers et al. 1998, 2010; Somsen and Sill 1970
Buffalograss	<i>Buchloe dactyloides</i>	perennial	+				Somsen and Sill 1970
Canada wildrye	<i>Elymus canadensis</i>	perennial	+	+			Connin 1956
Cheatgrass (Downy brome)	<i>Bromus tectorum</i>	annual, winter	+	+	+	+	Seifers et al. 1998, 2010; Sill and Connin 1953; Somsen and Sill 1970
Crested Wheatgrass	<i>Agropyron cristatum</i>	perennial	-	-			Ito et al. 2012
Eastern gamagrass	<i>Tripsacum dactyloides</i>	perennial	+	-		-	Seifers et al. 1998; Sill and Connin 1953
Fall panic grass	<i>Panicum dichotomiflorum</i>	annual, summer		+	-		Seifers et al. 2010; Sill and Connin 1953
Field brome (Japanese brome)	<i>Bromus arvensis</i>	annual, winter	+	+	+		Christian and Willis 1993; Seifers et al. 2010
Green bristlegrass (Green foxtail)	<i>Setaria viridis</i>	annual, summer	+	+	+	+	Connin 1956; Seifers et al. 1998; Slykhuis 1955; Somsen and Sill 1970
Hairy crabgrass	<i>Digitaria sanguinalis</i>	annual, summer	+	+	-		Connin 1956; Seifers et al. 2010; Somsen and Sill 1970
Hairy grama	<i>Bouteloua hirsuta</i>	perennial	+				Connin 1956; Somsen and Sill 1970
Indiangrass	<i>Sorghastrum nutans</i>	perennial	+			-	Seifers et al. 1998

Table 2.2. continued

Common name ^y	Scientific name	Growth habit	Host plant ^x				Reference
			WCM	WSMV	TriMV	HPV	
Intermediate wheat grass	<i>Thinopyrum intermedium</i>	perennial	+	+		-	Ito et al. 2012; McKinney et al. 1951; Seifers et al. 1998, 2010; Shannon and Bridgmon 1962
Italian ryegrass	<i>Lolium multiflorum</i>	annual, winter	+	+		-	Seifers et al. 1998
Johnsongrass	<i>Sorghum halepense</i>	perennial	+	-	-	+	Alemandri et al. 2017; Connin 1956; Seifers et al. 2010; Sill and Connin 1953; Sill and Agusiobo 1955; Somsen and Sill 1970
Jointed goatgrass	<i>Aegilops cylindrica</i>	annual, winter	+	+	+		Ito et al. 2012; Seifers et al. 2010; Somsen and Sill 1970
Kentucky bluegrass	<i>Poa pratensis</i>	perennial	+	-	-		Brey et al. 1998; Seifers et al. 2010; Sill and Connin 1953; Slykhuis 1963, 1965; Somsen and Sill 1970
Little bluestem	<i>Schizachyrium scoparium</i>	perennial	+	-		-	Seifers et al. 1998, 2010; Sill and Connin 1953
Mat sandbur	<i>Cenchrus longispinus</i>	?		+	-		Christian and Willis 1993; Connin 1956; Seifers et al. 2010; Somsen and Sill 1970
Orchardgrass	<i>Dactylis glomerata</i>	perennial		-	-	+	Alemandri et al. 2017; Seifers et al. 2010; Sill and Agusiobo 1955; Shannon and Bridgmon 1962
Perennial ryegrass	<i>Lolium perenne</i>	perennial		-	-		Seifers et al. 2010; Slykhuis and Bell 1966
Persian ryegrass	<i>Lolium persicum</i>	annual, winter	+	+			Connin 1956; Somsen and Sill 1970

Table 2.2. continued

Common name ^y	Scientific name	Growth habit	Host plant ^x				Reference
			WCM	WSMV	TriMV	HPV	
Prairie cupgrass	<i>Eriochloa contracta</i>	annual, summer		+	+		Seifers et al. 2010
Quackgrass	<i>Elymus repens</i>	perennial	+	-		-	Seifers et al. 1995, 1998, 2010; Sill and Connin 1953; Somsen and Sill 1970
Rhodes grass	<i>Chloris gayana</i>	perennial			-		Seifers et al. 2010
Russian wildrye	<i>Psathyrostachys juncea</i>	perennial	+			-	Seifers et al. 1998
Rye brome (Cheat)	<i>Bromus secalinus</i>	annual, winter	+	+	+	+	Seifers et al. 1998, 2010; Sill and Connin 1953; Somsen and Sill 1970
Sideoats grama	<i>Bouteloua curtipendula</i>	perennial	+	-		-	Seifers et al. 1998, 2010; Somsen and Sill 1970
Smooth brome	<i>Bromus inermis</i>	perennial	+	-	-		Brey et al. 1998; Connin 1956; Seifers et al. 2010; Ito et al. 2012
Smooth crabgrass	<i>Digitaria ischaemum</i>	annual, summer	+				Connin 1956
Stinkgrass	<i>Eragrostis cilianensis</i>	annual, summer	+	+	-		Connin 1956; Seifers et al. 2010; Sill and Connin 1953
Switchgrass	<i>Panicum virgatum</i>	perennial		-	-		Seifers et al. 2010; Sill and Connin; Sill and Agusiobo 1955; Somsen and Sill 1970
Tall oatgrass	<i>Arrhenatherum elatius</i>	perennial	+				Connin 1956
Tall wheatgrass	<i>Thinopyrum ponticum</i>	perennial	+	-		-	Seifers et al. 1998; Sill and Connin 1953; Somsen and Sill 1970
Tapertip cupgrass	<i>Eriochloa acuminata</i>	annual		+	+		Christian and Willis 1993; Seifers et al. 2010
Virginia wildrye	<i>Elymus submuticus</i>	perennial	+				Somsen and Sill 1970
Western wheatgrass	<i>Pascopyrum smithii</i>	perennial	+	-			Sill and Connin 1953, 1955; Somsen and Sill 1970

Table 2.2. continued

Common name ^y	Scientific name	Growth habit	Host plant ^x				Reference
			WCM	WSMV	TriMV	HPV	
Wild oat	<i>Avena fatua</i>	annual, winter	-	+	+		Ito et al. 2012; Seifers et al. 2010; Somsen and Sill 1970
Witchgrass	<i>Panicum capillare</i>	annual, summer	+				Somsen and Sill 1970
Yellow foxtail	<i>Setaria pumila</i>	annual, summer	+	-	-	+	Seifers et al. 1998, 2010; Sill and Connin 1953; Somsen and Sill 1970

^x WCM – wheat curl mite; WSMV – *Wheat streak mosaic virus*; TriMV – *Triticum mosaic virus*; HPV – *High Plains wheat mosaic virus*. Plus (+) indicates confirmed as host; minus (-) indicates confirmed as non-host; blank field indicates no information available/ not tested.

^y Common names were retrieved from the United States Department of Agriculture NRCS Plant database. Alternate common names (synonyms) are indicated in parentheses.

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CHAPTER THREE

SUSCEPTIBILITY AND TOLERANCE OF WINTER WHEAT, SPRING WHEAT
AND BARLEY CULTIVARS TO MECHANICAL INOCULATION WITH *WHEAT*
STREAK MOSAIC VIRUS

Contribution of Authors and Co-Authors

Manuscript in Chapter 3

Author: Uta McKelvy.

Contributions: Aided in the study, performed data analyses, interpreted results, wrote the manuscript.

Co-Author: Monica Brelsford.

Contributions: Led efforts in conducting the study, provided data sets for analyses, discussed results and implications.

Co-Author: Jamie Sherman.

Contributions: Aided in the study, edited earlier manuscripts.

Co-Author: Mary Burrows.

Contributions: Conceived the study, acquired funding, edited earlier manuscripts.

Manuscript Information

Uta McKelvy, Monica Brelsford, Jamie Sherman and Mary Burrows.

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Abstract

Wheat streak mosaic virus (WSMV) causes sporadic epidemics in Montana which can threaten profitability of wheat production. One challenge for WSMV management efforts in Montana is that commercially available wheat cultivars are largely susceptible to WSMV or their performance under WSMV pressure is unknown. In a three-year study (2017-2019) widely planted winter, spring wheat, and barley cultivars were evaluated for their susceptibility and tolerance to WSMV and yield performance under WSMV pressure. The experiment was conducted under field conditions. Plants were mechanically inoculated and virus incidence was assessed using DAS-ELISA. Winter wheat ‘Brawl CL Plus’ demonstrated moderate WSMV incidence and minor yield penalties under WSMV pressure, making it a suitable cultivar to be grown in high-risk years. Strong and moderate resistance to mechanical infection with WSMV in breeding lines CO12D922 and MTV1681, respectively, highlighted promising efforts in the development of WSMV-resistant winter wheat cultivars suitable for Montana. Although spring wheat cultivars in this study generally demonstrated high susceptibility to WSMV, lower average incidence rates and improved yields under WSMV pressure were unexpectedly observed in two cultivars, ‘O’Neal’ and ‘Alum.’ Although the results require further confirmation, these cultivars may present interesting starting points for breeding efforts. Virus incidence among barley cultivars was considerably lower compared to spring and winter wheat. Only grain barley ‘Haxby’ and forage cultivar ‘Horsford’ had increased levels of WSMV infection. WSMV infection did not significantly affect barley grain yields. This study

presents valuable information for cultivar recommendations for high WSMV pressure environments in Montana.

Introduction

Wheat streak mosaic virus (WSMV) is the most prevalent viral pathogen of wheat in the Great Plains Regions of the U.S. (Burrows et al. 2016). This virus causes wheat streak mosaic (WSM) disease and infects a wide range of cereal crops, most importantly wheat (*Triticum aestivum* L.), barley (*Hordeum vulgare* L.), oats (*Avena sativa* L.), rye (*Secale cereal* L.), and maize (*Zea mays* L.) (Brakke 1971). WSMV is transmitted between host plants via the eriophyid wheat curl mite (WCM, *Aceria tosichella* Keifer), which also vectors two other important cereal viruses, *Triticum mosaic virus* and *High Plains wheat mosaic virus* (Seifers et al. 1997, 2009). Symptoms of WSMV infection are yellow mottling and streaking on leaves that create mosaic-like patterns. Root biomass may be reduced (Price et al. 2010) and plant growth may be stunted with fewer, poorly producing tillers. Under severe infection, wheat plants may fail to develop spikes entirely. Yield loss estimates from WSMV infection in natural settings are difficult to obtain and highly variable. Under experimental conditions, yield losses have been reported to range as high as 75% (Lehnhoff et al. 2015; Sharp et al. 2002).

Wheat is the dominant crop produced in Montana. In 2019, 68% of the state's hectares in production were planted in wheat; 2.2 million ha total, of which 53% were planted to spring wheat and 37% to winter wheat. The approximately 6 million metric tons of wheat harvested amounted to a production value more than 1 billion USD (USDA NASS 2019). Barley is planted on 11% of Montana's hectares in production and produced

0.95 million metric tons of grain in 2019, worth approximately 0.2 million USD. In Montana, wheat is largely grown under no-till dryland conditions in a narrow wheat-fallow rotation, occasionally diversified with pulses, oilseeds, and other crops. Such cereal-focused rotations present a high-risk environment for WSM disease, in which suitable hosts are abundant and epidemics may develop readily under favorable environmental conditions. The most important environmental risk factor is moderate fall temperatures above 10 °C (Ranabhat et al. 2018). Yearly WSMV incidence across the state and associated yield losses have not been systematically measured, but in epidemic years yield losses can be devastating for the livelihood of wheat growers. WSM epidemics causing statewide losses greater than 10% have been observed in 1964, 1981, 1993, 1994, and 2016 (Burrows et al. 2017).

Genetic resistance presents an effective way to protect cereal crops from WSMV infection without requiring additional management inputs. To date, three resistance genes have been identified. *Wsm1* and *Wsm3* both originate from intermediate wheatgrass, *Agropyron intermedium* (Friebe et al. 1996; Lay et al. 1971; Liu et al. 2011; Wells et al. 1973, 1982). *Wsm1* confers high levels of resistance to both WSMV and *Triticum mosaic virus* and has been bred into winter wheat cultivar ‘Mace’ (Graybosch et al. 2009), as well as Montana breeding line MTV1681 (J. Cook and P. Bruckner, *personal communication*). *Wsm3* is not yet established in commercially available germplasm. *Wsm2* has been identified in germplasm of Colorado line CO960293-2 (Haley et al. 2002; Lu et al. 2011; Seifers et al. 2006). It confers resistance to WSMV and is included in winter wheat cultivars ‘RonL’ (Seifers et al. 2006), ‘Snowmass’ (Haley et al. 2011), ‘Clara CL’ (Martin

et al. 2014), ‘Oakley CL’ (Zhang et al. 2015), as well as the breeding line CO12D922 (S. Haley and P. Bruckner, *personal communication*). Other wheat cultivars are described to have varying degrees of resistance or tolerance to WSMV infection, e.g. ‘Yellowstone’ (Bruckner et al. 2007; Miller et al. 2014) and ‘Brawl CL Plus’ (Haley et al. 2012), but the sources of these traits are unknown. Breeding efforts to release WSMV-resistant spring wheat lines have largely been unsuccessful owing to yield penalties. Temperature-sensitivity is a major constraint to current resistance traits limiting their durability and efficacy under field conditions. Numerous growth chamber, greenhouse, and field studies have shown that *Wsm1* resistance to WSMV and *Triticum mosaic virus* breaks down at temperatures above 24 °C and 18 °C, respectively (Friebe et al. 2009; Seifers et al. 1995). *Wsm2* provides effective resistance to WSMV infection only at temperatures below 18 °C (Seifers et al. 2006). This temperature dependency may be most limiting to crop productivity in years where warm fall temperatures lead to an early breakdown of WSMV resistance. Early infection of the newly planted winter wheat crop typically results in severe yield losses (Byamukama et al. 2012; Hunger et al. 1992; Wegulo et al. 2008; Wosula et al. 2018).

One challenge for WSM disease management efforts in Montana is that commercially available wheat cultivars adapted to the Montana environment are largely susceptible to WSMV or their performance under WSMV pressure is unknown. Conversely, wheat lines and cultivars with known WSMV-resistance released in other U.S. states are often poorly adapted to growing conditions in Montana. This situation leaves Montana wheat growers with little information on and limited choices of suitable

wheat cultivars, especially in years with high WSM disease risk. Although barley has been shown to host WSMV (Brakke 1971; Ito et al. 2012; Lehnhoff et al. 2015), little is known about the range of susceptibility of different cultivars to the disease and its impact on yield performance. The objective of this study was to evaluate widely planted winter wheat, spring wheat, and barley varieties in Montana for their susceptibility and tolerance to WSMV and yield performance under WSMV pressure.

Experimental Design

Field experiments were conducted from 2017 through 2019 at the Montana State University (MSU) Arthur H. Post Research Farm, 6 km west of Bozeman, MT (latitude 45°40'N, longitude 111°09'W). Weather data were recorded on site and obtained from the Western Regional Climate Center (Fig. 3.1). Cultivars of winter wheat, spring wheat, and barley evaluated in this study are summarized in Table 1. Winter wheat was planted in late September (2016) or early October (2017, 2018). Spring wheat plots were planted in early May (2018) and mid-May (2017, 2019). Six barley cultivars were evaluated in the experiment. Barley research plots were established in late April (2018) and early May (2017, 2019). Cultivars were assigned to main plots and arranged in a randomized complete block design with four replications. The barley experiment in 2017 had three replications. Winter wheat and barley were planted in six-row and four-row plots, respectively, with 0.3 m spacing. Plot lengths at harvest were approximately 4 m. Spring wheat was planted in three-row plots with 0.3 m spacing and average plot length at harvest was 5 m, 3 m, and 1.5 m in 2017, 2018, 2019, respectively. Individual rows (split plot) within the main plots were inoculated with WSMV (WSMV treatment) or a mock

phosphate-buffered saline (PBS) solution (control treatment). Planting and plot maintenance throughout the season followed standard management practices.

WSMV Inoculation and WSMV Incidence

Wheat streak mosaic virus isolate Conrad I (GeneBank Accession No. HM535796.2; Ito et al., 2012), which was collected from Conrad, MT, in 2007 and maintained at -80 °C, was used for the WSMV treatment. Field inoculum was prepared following protocols of Miller et al. (2014) and Lehnhoff et al. (2015). Crops were sprayed with virus solution from a height of 5 cm from the canopy at a rate of 20 ml per 30 cm² at 80 psi with a Husky siphon feed spray gun (Home Depot, Inc., Atlanta, GA, USA) powered by an air compressor. All crops were inoculated in the spring at the three- to four-leave stage (Zadok's 13-14) or as soon as winter wheat plants resumed growth. Fall inoculation of winter wheat was conducted once in late October 2016.

WSMV incidence was assessed by sampling 30 flag leaves from each treated row (WSMV and control treatment). Samples were collected blindly without giving preference to symptomatic or non-symptomatic leaves, to avoid sample bias and inflation of WSMV incidence. Virus presence was detected using DAS-ELISA, following procedures previously described by Ito et al. (2012). WSMV antibodies were obtained from Agdia (Elkhart, IN, USA). Leaves from WSMV-treated rows were individually subjected to DAS-ELISA. Leaves from PBS rows were pooled into groups of 10 and leaves were only processed individually upon detecting a positive signal for the respective pooled group. Samples were considered positive when their absorbance value was higher than three standard deviations from the mean absorbance value calculated

from six negative controls on each plate. WSMV incidence is expressed in percent (%) and was calculated as follows: (# WSMV positive leaves / # total leaves in sample) x 100.

WSMV incidence in winter wheat under control treatment was absent or very low across all study years, never exceeding 5%. In spring wheat, occasional WSMV infection was detected in PBS-treated rows, averaging $1 \pm 2\%$ and $4 \pm 6\%$ in 2017 and 2018, respectively (raw mean $\pm$ SD). Overall, virus incidence was distinctly lower under control treatment compared to WSMV treatment. Gusty winds during spring inoculation in 2019 caused WSMV inoculum to drift to adjacent PBS-treated rows, resulting in elevated WSMV incidence rates of $11 \pm 12\%$. Incidence and harvest data from an untreated row (no spray treatment) were collected to be compared to WSMV treatment. Infection rates in those control rows averaged $4 \pm 9\%$ and were comparable to PBS-treated rows in 2017 and 2018. In barley, WSMV incidence in PBS-treated rows was negligibly low in all three study years, ranging between 0% in 2018 and 2019 and $0.2 \pm 1\%$ in 2017.

Harvest and Yield Assessments

Row lengths were measured immediately before or after harvest and rows were harvested individually using a Suzue harvest-binder (Suzue Manufacturing, Japan). In 2019, shorter than usual plot lengths and the extreme effect of WSMV treatment on plant height required spring wheat to be harvested by hand. Plant material was processed with a Vogel thresher (custom built by Bill's Welding, Pullman, WA, USA). Grain yield was adjusted to 13% and 14% moisture for wheat and barley, respectively. Relative yield

(RY) was calculated from raw yield data in accordance with Lehnhoff et al. (2015):

$$RY = (\text{WSMV treatment} / \text{control treatment}) \times 100.$$

Statistical Analysis

WSMV incidence was transformed into log odds before analysis. Differences in WSMV incidence and grain yield between study years, cultivars, and treatments were assessed via split-plot analysis of variance using mixed effect models in the R package ‘lme4’ (Bates et al. 2015). Year, cultivar and inoculation treatment were modeled as fixed effects and block was included as random effect nested within year. Tukey’s multiple comparison was used for post-hoc comparisons of means using R package ‘emmeans’ (Lenth 2019). Statistical analyses were conducted in R studio (version 1.1.463; Rstudio 2015) using R version 3.6.1 (R Core Team 2019).

Wsm1 and *Wsm2* Resistance Genes Are Effective against Mechanical Inoculation with

WSMV in the Montana Environment

Average incidence under WSMV treatment was highest in 2018 ($56 \pm 32\%$) and lower in 2017 and 2019 ($24 \pm 27\%$ and $30 \pm 23\%$, respectively) (Table 3.2). Winter wheat yields varied depending on trial year ($P < 0.001$), cultivar ($P < 0.001$), and treatment ($P < 0.001$). Variable growing conditions between study years contributed to yield differences. Very low precipitation amounts from May to August 2017 created severe drought conditions in south-central Montana in the late summer and autumn of 2017 and affected crop productivity. Below-average temperatures in March and April significantly delayed the onset of the 2019 growing season (Fig. 3.1). Average yields

under the control treatment were highest in 2018 ($929 \pm 65 \text{ g m}^{-2}$), followed by 2019 ($816 \pm 57 \text{ g m}^{-2}$) and 2017 ($719 \pm 74 \text{ g m}^{-2}$) (Tab. 3.2).

Montana wheat cultivars showed good yield performance under control treatment, highlighting the advantage of using cultivars that are well adapted to the given environment. ‘Northern’ was the highest-yielding variety under control conditions in 2018 and 2019, yielding $1,024 \pm 64 \text{ g m}^{-2}$ and $920 \pm 56 \text{ g m}^{-2}$, respectively. However, high infection rates in many Montana cultivars demonstrated considerable susceptibility to WSMV. Northern, ‘Warhorse,’ and ‘Decade’ consistently had the highest infection rates indicating a high degree of susceptibility (Fig. 3.2). Those cultivars also displayed some of the most dramatic yield reductions under WSMV treatment as indicated by three-year average RYs of $72 \pm 20\%$, $62 \pm 12\%$, and $60 \pm 13\%$ for Northern, Warhorse, and Decade, respectively (Fig. 3.2; Tab. 3.2).

Efforts towards incorporating WSMV resistance traits into Montana winter wheat lines are currently being undertaken by the MSU breeding program and results are promising. The experimental line MTV1681, carrying the *Wsm1* resistance gene (P. Bruckner, *personal communication*), demonstrated low to moderate WSMV incidence following spring inoculation, which was similar to Mace. Yield performance of MTV1681 was still noticeably affected under WSMV treatment with a three-year average RY of $83 \pm 10\%$. Nevertheless, yield losses were considerably lower compared to highly susceptible cultivars. Altogether, these results suggest that the genetic background of MTV1681 combines two desirable traits focused on in this study: adaptation to Montana growing conditions and resistance to WSMV pressure. Brawl CL Plus exhibited moderate

infection rates similar to MTV1681 and an average RY of $90 \pm 10\%$. These results indicate good resistance to WSMV, which is in accordance with the variety release report where Brawl CL Plus is described to have “moderate susceptibility” to WSMV (Haley et al. 2012).

Another Montana cultivar, ‘Loma,’ displayed low WSMV incidence similar to Mace and MTV1681. Low incidence may indicate some degree of resistance to WSMV infection, although no known resistance gene has been identified (Bruckner et al. 2017). Despite moderate incidence rates, yield losses were consistently high for Loma and RY averaged $61 \pm 13\%$. These results indicate a low tolerance to WSMV infection, making Loma an unsuitable cultivar to be grown in high WSMV pressure environments.

Winter wheat line CO12D922 from Colorado consistently had the lowest WSMV incidence, which can be attributed to the *Wsm2* resistance gene present in this cultivar (S. Haley, *personal communication*). Under control conditions, CO12D922 achieved grain yields comparable to many of the local cultivars, indicating good adaptation to Montana growing conditions. Yield performance of this cultivar under WSMV pressure was the same as under control conditions across all study years and distinctly higher than all other wheat lines under WSMV treatment in 2018 and 2019. These findings demonstrate a high degree of WSMV resistance that would be a desirable trait in high WSMV pressure environments.

WSMV incidence in CO12D922 was very consistent across study years and associated with very low variability. In contrast, average WSMV incidence of Mace in 2017 was increased and associated with high variability ($21 \pm 40\%$), while MTV1681

showed elevated incidence in 2018 ($66 \pm 13\%$). Severe drought conditions in 2017 may have affected virus establishment and spread within treated plants, contributing to increased variability. Moreover, the maximum air temperature of $27.8\text{ }^{\circ}\text{C}$ in the seven-day period following spring inoculation in 2017 exceeded the temperature threshold above which *Wsm1* resistance breaks down (Friebe et al. 2009; Seifers et al. 1995). Increased variability in WSMV incidence in Mace may be due to a temperature-dependent breakdown of WSMV resistance. However, WSMV incidence of MTV1681 was relatively low and more consistent across replicates. Further, *Wsm2* resistance has an even lower temperature threshold (Seifers et al. 2006) and should have lost efficacy under high temperature conditions in 2017. Low WSMV incidence and small variability in CO12D922, however, does not support this hypothesis. Moreover, maximum temperatures in the seven-day period following inoculation in 2018 ($24.4\text{ }^{\circ}\text{C}$) exceeded *Wsm1* and *Wsm2* temperature thresholds, but WSMV incidence in Mace and CO12D922 was very low ($1 \pm 2\%$ for both). A temperature-dependent resistance breakdown does therefore not provide a satisfying explanation for increased variability in some *Wsm1*-carrying genotypes. The observed variability may instead be associated with the method of inoculation. Several publications have indicated that certain crops and cultivars are more susceptible to WSMV infection via viruliferous WCMs compared to mechanical transmission (Ito et al. 2012; Wosula et al. 2018). The observed variability may be caused by a less consistent efficacy of mechanical inoculation. In summary, with the data available it cannot be discerned which factors may have contributed to the increased variability in WSMV incidence in 2017 and in most cultivars compared to CO12D922.

In future studies, the effect of environmental conditions on immediate virus establishment could be discerned by measuring virus presence in the WSMV-treated host tissue a few days after inoculation. Efficacy of the inoculation method itself could be assessed following the method of Wosula et al. 2018. They transferred field-inoculated plants into a controlled greenhouse environment to measure symptom expression and virus presence under conditions favorable for virus replication. Comparing WSMV incidence from mechanical inoculation to infection rates from viruliferous WCMs could confirm WSMV-resistant phenotypes and would provide important information to untangle the contributing effects of environment, inoculation method, and genetic disposition on systemic WSMV incidence.

Fall Inoculation of Winter Wheat Resulted in Low WSMV Incidence and Minor Yield

Losses

In the Southern and Central Great Plains, fall infection with WSMV is associated with high systemic virus incidence and severe effects on plant growth and productivity (Singh et al. 2018; Wosula et al. 2018). However, cooler fall temperatures and an earlier onset of winter create an environment less conducive for fall infection in Montana. Only once over the three-year study period did weather conditions permit fall inoculation of winter wheat. Temperatures in autumn of 2016 exceeded the 50-year average by 2 °C and 4.5 °C in October and November, respectively, extending the growing season considerably (Fig. 3.1.A). Fall infection resulted in low average WSMV incidence of $9 \pm 10\%$ across all cultivars (Tab. 3.3), compared to $24 \pm 27\%$ from spring inoculation (Tab. 3.2). Those cultivars with high susceptibility under spring infection also showed a

trend toward higher WSMV incidence under fall infection of $17 \pm 9\%$, $23 \pm 7\%$, and $15 \pm 17\%$ for cultivars Decade, Northern, and Warhorse, respectively (Fig. 3.3). However, evidence for significant differences in WSMV incidence between fall-inoculated varieties was not convincing ($P = 0.06$). Moreover, no evidence for a correlation between incidence rates from fall and spring inoculation was found (Kendall correlation coefficient $\tau = 0.17$, $P = 0.15$). Only minor effects of fall infection on yield were observed, and RYs were distinctly higher compared to spring inoculation, averaging $92 \pm 13\%$ (Tab. 3.3). Only cultivars Decade, Loma, and Warhorse demonstrated yield losses of 23%, 15%, and 16%, respectively (Fig. 3.3). In contrast, yield penalties close to 40% were observed in response to spring inoculation in the same crop year (Tab. 3.2). Our results agree with Miller et al. (2014), who found a significant impact of timing of inoculation on WSMV incidence and reported similar infection rates from fall inoculation (5 - 7%). Moreover, in the present study, as well as in Miller et al. (2014), yields of fall-infected winter wheat did not differ significantly from the control group.

Assessing WSMV incidence from fall infection in the following summer measures the success rate of establishing a systemic infection rather than the efficacy of fall inoculation itself. Miller et al. (2014) suggested that low systemic infection rates from fall inoculation may be due to increased plant resistance at cool fall temperatures, reduced rates of local infections becoming systemic, or increased rates of loss of infection over the winter. Air temperatures during the seven days following fall inoculation in 2016 (maximum temperature of 25.6 °C) were similar to those observed after spring inoculation in 2017 and 2018. They do not present a convincing argument for the reduced

WSMV incidence rates in this study. However, a limited time window for the establishment of a systemic infection before the onset of winter and loss of WSMV infection over the winter months seem likely factors contributing to the observed low incidence rates.

Having accomplished fall inoculation only once throughout the three-year study suggests how rarely weather conditions in Montana facilitate fall infection. For WSMV epidemics to occur, weather conditions do not only have to permit timely seeding and emergence of the new winter wheat crop and fall infection with WSMV, but must also remain conducive for the virus to establish and sustain in the host before and during winter dormancy. A look at the historic frequency of WSMV epidemics in Montana indicates how sporadic inoculum availability and permissive environmental conditions occur in the state.

High Susceptibility of Spring Wheat Cultivars to Mechanical Inoculation with WSMV

Severe drought conditions in the summer months of 2017 affected the spring wheat crop and resulted in the lowest average grain yields of $296 \pm 23 \text{ g m}^{-2}$ under control treatment across the study period (Tab. 3.4). Favorable growing conditions in 2018 and 2019 produced more than three-times higher grain yields of $709 \pm 89 \text{ g m}^{-2}$ and $782 \pm 71 \text{ g m}^{-2}$ under control conditions, respectively. Incidence rates in spring wheat were distinctly higher than in winter wheat averaging $98 \pm 13\%$, $70 \pm 20\%$, and $80 \pm 31\%$ in 2017 to 2019, respectively (Tab. 3.4). Drift of virus inoculum due to gusty winds during inoculation in 2019 likely contributed to a higher variability in virus incidence that year. High WSMV incidence rates were associated with low average RYs, which were

42 ± 10%, 40 ± 17%, and 25 ± 12% in 2017 to 2019, respectively (Tab. 3.4). ‘Vida’ was among the highest yielding cultivars under control conditions across all study years, averaging 336 ± 4 g m⁻², 846 ± 136 g m⁻², and 930 ± 144 g m⁻² in 2017 to 2019, respectively. However, with RYs ranging between 24% and 35% Vida was also one of the cultivars most severely affected under WSMV pressure (Fig. 3.4). Other cultivars with consistently low tolerance to WSMV infection were ‘Choteau’ and ‘WB9879CLP.’ The consistently high WSMV infection rates and associated yield losses in this study are comparable to those observed by Lehnhoff et al. (2015). The results illustrate a high degree of susceptibility and low tolerance of available spring wheat cultivars to mechanical inoculation with WSMV. Given the lack of WSM resistance in spring wheat germplasm, producers rely solely on cultural management practices that reduce WSMV pressure, such as control of the green bridge, early planting dates for spring wheat, and rotation to non-host crops in high WSMV risk years.

Two cultivars in this study demonstrated an unexpected response to WSMV treatment. Yields of ‘Alum’ were among the least impacted under WSMV pressure, with above-average RYs of 56 ± 8% and 64 ± 6% in 2017 and 2018, respectively (Tab. 3.4). Likewise, RYs of ‘O’Neal’ were 53 ± 10% in 2017 and 67 ± 11% in 2018. The moderate WSMV-associated yield losses in 2018 may be attributable to lower infection rates in these two cultivars, 44 ± 14% and 29 ± 14% for Alum and O’Neal, respectively. Average WSMV incidence in 2017 were comparable to other cultivars in that year (94 ± 56% for Alum and 96 ± 3% for O’Neal), while RYs were still increased. No qualitative resistance trait for WSMV has been identified in spring wheat to date, but the below-average

incidence rates in 2018 and moderately reduced grain yields under WSMV treatment in 2017 and 2018 could suggest some tolerance to WSMV infection and could present an interesting starting point for breeding efforts. However, further experiments are required to confirm the persistence of reduced infection rates following mechanical inoculation and test WSMV incidence and yield performance in response to inoculation via WCMs.

Mechanical Inoculation of Barley Cultivars Resulted in Low WSMV Incidence

Infection rates following WSMV treatment of barley were distinctly lower than in wheat and varied considerably between study years (Tab. 3.5). Average incidence in 2017, 2018, and 2019 was $3 \pm 5\%$, $2 \pm 7\%$, and $14 \pm 20\%$, respectively. This study considered barley cultivars from different market classes; ‘Hays,’ ‘Horsford,’ and ‘Lavina’ represent forage cultivars, while ‘Craft,’ ‘Haxby,’ and ‘Hockett’ are grown for their grain for malting and as feed (Tab. 3.1). Barley cultivars differed in WSMV incidence, but there was no evidence for systematic differences between the barley classes ($P = 0.27$). Haxby and Horsford showed most frequently elevated WSMV incidence, which were as high as $53 \pm 16\%$ and $12 \pm 1\%$ in 2019, respectively (Tab. 3.5). WSMV presence was occasionally detected in Lavina; $1 \pm 2\%$ in 2017 and $11 \pm 5\%$ in 2019. WSMV incidence in Craft and Hockett was detected in only one of three years and was low; $4 \pm 7\%$ in Hockett in 2017 and $3 \pm 3\%$ in Craft in 2019.

Severe lodging, particularly of forage barley cultivars, in 2019 resulted in the overlapping of plot rows, which complicated grain harvest and obscured yield analysis. The 2019 harvest data were excluded from yield analysis. Figure 3.5 shows the two-year average (2017-2018) of RYs and WSMV incidence for each barley cultivar. Although

WSMV incidence was assessed in 2019 (Tab. 3.5), it was not included in the Fig. 3.5. to allow direct comparison between virus incidence and RY. Forage cultivar Hays had the highest grain yields under control treatment in 2018 ($698 \pm 50 \text{ g m}^{-2}$), which was statistically different from grain yields of malt and feed cultivars (Tab. 3.5). Yield losses associated with WSMV-treatment were small and variable even in cultivars with elevated WSMV incidence. RYs were highly variable across replications and could not be associated with WSMV treatment. No evidence was found to suggest differences in RYs between barley cultivars ($P = 0.41$) or classes ($P = 0.92$).

Similar WSMV infection rates of cultivar Haxby have been observed by Lehnhoff et al. (2015), but they observed more consistent and severe WSMV-associated yield losses. Ito et al. (2012) compared WSMV incidence from mechanical inoculation to virus transmission via viruliferous WCMs and found a high susceptibility of barley to WCM-transmitted WSMV, while mechanical inoculation resulted in low incidence. The low incidence rates observed in this study can therefore not be interpreted as proof of resistance of the tested cultivars to WSMV infection. Further inoculation studies using viruliferous WCMs are required to confirm the observed phenotypes. However, moderate and consistent WSMV incidence in Haxby and Horsford across the three-year study period suggests a higher degree of susceptibility to WSMV pressure of those cultivars.

Conclusions and Implications for WSM Disease Management

We evaluated the susceptibility and tolerance of widely grown winter, spring wheat, and barley cultivars to WSMV from mechanical inoculation in Montana. The study results will complement management recommendations for high WSMV pressure

environments and provide valuable information on cultivar choices for preventing and mitigating yield losses due to WSM disease, particularly in winter wheat. In addition to planting tolerant or resistant cultivars, preventive management practices that reduce WCM populations and WSMV pressure in the environment (green bridge control) remain an important means in mitigating the impact of WSM disease on agricultural production.

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This project was accomplished in collaboration with the MSU winter wheat, spring wheat, and barley breeding teams. The authors sincerely thank Everett Owen, Heidi Brelsford, Kyla Crisp, Rebecca King, Bailey Murphy, and Josephine McMahon for their diligent support in the field and lab.

Tables and Figures**Table 3.1.** Summary of cultivars assessed for susceptibility and tolerance to wheat streak mosaic infection.

Cultivar	PI	Registration publication
Winter wheat		
BrawlCLPlus	664255	Haley et al. 2012
CO12D922 ^a		
Decade	660291	Riveland et al. 2011
Judee	665277	Carlson et al. 2013
Loma	680576	Bruckner et al. 2017
Mace	651043	Graybosch et al. 2009
MTV1681 ^b		
Northern	676026	Berg et al. 2016
Warhorse	670157	Berg et al. 2014
Yellowstone	643428	
Spring wheat		
Alum	676289	
Choteau	633974	Lanning et al. 2004
Duclair	660981	Lanning et al. 2011
Egan	671855	Blake et al. 2014
Lanning	676978	Heo et al. 2016
McNeal	574642	Lanning et al. 1994
O'Neal	659480	
Reeder	613586	
Vida	642366	Talbert et al. 2006
WB9879LCP	666046	Blake et al. 2013
Barley		
Craft ^{c/d}	646158	
Haxby ^d	646160	
Hays ^e	not found	
Hockett ^c	not found	
Horsford ^e	not found	
Lavina ^e	not found	

^a Colorado breeding line.^b MSU breeding line.^c Malting barley.^d Feed barley.^e Forage barley.

Table 3.2. Average *Wheat streak mosaic virus* incidence and grain yield responses of winter wheat cultivars following mechanical inoculation in the spring 2017-2019 near Bozeman, MT.

Cultivar	Incidence (%)		Yield (g m ⁻²)				Relative yield (%)	
			Control		WSMV			
2017								
BrawlCLPlus	6 ± 8*	ab	736 ± 107	b	706 ± 47	d	97 ± 11	b
CO12D922	0 ± 0	a	549 ± 149	a	503 ± 159	ac	93 ± 23	b
Decade	56 ± 22	b	701 ± 28	ab	435 ± 49	a	62 ± 9	a
Judee	26 ± 28	ab	702 ± 75	ab	608 ± 33	ad	88 ± 12	ab
Loma	25 ± 2	b	762 ± 053	b	470 ± 172	ab	61 ± 20	a
Mace	21 ± 40	ab	769 ± 82	b	662 ± 37	cd	86 ± 7	ab
MTV1681	11 ± 9	ab	768 ± 45	b	656 ± 66	bcd	86 ± 10	ab
Northern	11 ± 10	ab	708 ± 39	ab	652 ± 15	bcd	92 ± 5	b
Warhorse	57 ± 39	b	674 ± 30	ab	425 ± 61	a	63 ± 12	a
Yellowstone	28 ± 14	b	818 ± 53	b	604 ± 88	ad	74 ± 10	ab
Average	24 ± 27		719 ± 74		572 ± 104		80 ± 17	
2018								
BrawlCLPlus	60 ± 15	bc	798 ± 27	a	649 ± 42	bc	81 ± 6	c
CO12D922	1 ± 2	a	977 ± 51	cd	1051 ± 51	e	108 ± 1	d
Decade	83 ± 11	c	942 ± 56	bcd	508 ± 89	a	54 ± 11	a
Judee	76 ± 8	bc	948 ± 86	bcd	490 ± 43	a	52 ± 4	a
Loma	45 ± 20	bc	945 ± 29	bcd	541 ± 101	ab	57 ± 12	ab
Mace	1 ± 2	a	898 ± 54	ac	900 ± 33	d	100 ± 3	d
MTV1681	66 ± 13	bc	936 ± 62	bcd	719 ± 32	c	77 ± 6	c
Northern	76 ± 13	bc	1024 ± 64	d	520 ± 69	a	51 ± 5	a
Warhorse	87 ± 9	c	853 ± 76	ab	475 ± 23	a	56 ± 5	ab
Yellowstone	72 ± 8	bc	973 ± 49	cd	695 ± 46	c	70 ± 3	bc
Average	57 ± 32		929 ± 65		655 ± 193		70 ± 21	
2019								
BrawlCLPlus	18 ± 7	bc	746 ± 27	a	693 ± 49	ce	93 ± 7	bc
CO12D922	0 ± 0	a	843 ± 38	ac	846 ± 45	e	101 ± 9	c
Decade	39 ± 23	cd	830 ± 77	ac	514 ± 106	ab	63 ± 18	a
Judee	39 ± 16	cd	807 ± 19	ab	689 ± 60	cd	85 ± 9	ac
Loma	15 ± 6	b	844 ± 74	ac	552 ± 31	ac	66 ± 8	a
Mace	8 ± 4	b	740 ± 57	a	769 ± 43	de	104 ± 3	c
MTV1681	18 ± 10	b	815 ± 38	ac	696 ± 88	ce	86 ± 14	ac
Northern	62 ± 18	d	920 ± 56	c	656 ± 115	bcd	72 ± 17	ab
Warhorse	54 ± 20	d	753 ± 41	ab	503 ± 102	a	67 ± 17	a
Yellowstone	38 ± 11	cd	862 ± 82	bc	627 ± 61	acd	73 ± 12	ab
Average	30 ± 23		816 ± 57		655 ± 110		81 ± 19	

* Mean estimates ± standard deviation. Means followed by the same letter in each column within year are not significantly different based on Tukey's multiple comparison ($P \leq 0.05$).

Table 3.3. Average *Wheat streak mosaic virus* incidence and grain yield responses of winter wheat cultivars following mechanical inoculation in the fall 2017 near Bozeman, MT.

Cultivar	Incidence (%)	Yield (g m ⁻²)			Relative yield (%)
		Control	WSMV		
2017					
BrawlCLPlus	4 ± 5*	651 ± 169	631 ± 97	ac	99 ± 13
CO12D922	5 ± 10	656 ± 86	647 ± 114	ac	99 ± 17
Decade	17 ± 9	659 ± 40	503 ± 69	a	77 ± 15
Judee	3 ± 3	659 ± 66	611 ± 48	ac	94 ± 14
Loma	3 ± 3	724 ± 64	614 ± 37	ac	85 ± 10
Mace	3 ± 5	654 ± 60	656 ± 77	ac	100 ± 5
MTV1681	8 ± 10	671 ± 56	671 ± 72	bc	100 ± 8
Northern	23 ± 7	704 ± 51	619 ± 9	ac	88 ± 6
Warhorse	15 ± 17	640 ± 17	537 ± 35	ab	84 ± 8
Yellowstone	12 ± 11	729 ± 52	716 ± 71	c	99 ± 14
Average	9 ± 10	675 ± 32	620 ± 62		92 ± 13

* Mean estimates ± standard deviation. Means followed by the same letter in each column within year are not significantly different based on Tukey's multiple comparison ($P \leq 0.05$).

Table 3.4. Average *Wheat streak mosaic virus* incidence and yield responses of spring wheat cultivars following mechanical inoculation in 2017-2019 near Bozeman, MT.

Cultivar	Incidence (%)	Yield (g m ⁻²)					Relative yield (%)	
		Control		+WSMV				
2017								
Alum	94 ± 56*		288 ± 33		163 ± 37		56 ± 8	d
Choteau	100 ± 0		293 ± 20		105 ± 11		36 ± 4	a
Duclair	98 ± 2		300 ± 32		109 ± 22		36 ± 7	ab
Egan	99 ± 1		293 ± 35		123 ± 19		42 ± 3	ac
Lanning	97 ± 47		299 ± 32		106 ± 14		36 ± 2	a
McNeal	100 ± 0		315 ± 43		154 ± 38		48 ± 8	bcd
O'Neal	96 ± 3		254 ± 26		133 ± 26		53 ± 10	cd
Reeder	98 ± 2		315 ± 58		149 ± 26		48 ± 9	bcd
Vida	97 ± 5		336 ± 4		118 ± 3		35 ± 1	a
WB9879LCP	99 ± 1		272 ± 27		97 ± 21		35 ± 6	a
Average	98 ± 3		296 ± 23		126 ± 23		42 ± 10	
2018								
Alum	44 ± 14	ab	730 ± 42	ac	465 ± 33	e	64 ± 6	cd
Choteau	82 ± 4	cd	645 ± 74	ab	182 ± 85	ab	28 ± 14	a
Duclair	64 ± 9	bc	735 ± 102	ac	319 ± 64	cd	44 ± 12	abc
Egan	76 ± 11	cd	727 ± 97	ac	277 ± 55	abc	39 ± 11	abc
Lanning	76 ± 6	d	661 ± 169	ac	165 ± 45	a	25 ± 5	a
McNeal	89 ± 7	d	571 ± 38	a	293 ± 47	bd	51 ± 6	bd
O'Neal	29 ± 14	ab	608 ± 16	a	409 ± 72	de	67 ± 11	d
Reeder	76 ± 9	cd	826 ± 16	bc	226 ± 39	abc	27 ± 4	a
Vida	78 ± 12	cd	846 ± 136	c	223 ± 37	abc	27 ± 8	a
WB9879LCP	80 ± 7	cd	746 ± 120	ac	204 ± 26	abc	28 ± 8	a
Average	70 ± 20		709 ± 89		276 ± 98		40 ± 17	
2019								
Alum	73 ± 49		820 ± 49 [†]	ab	263 ± 83	a	32 ± 11	ab
Choteau	83 ± 23		768 ± 106	ab	123 ± 27	a	16 ± 5	a
Duclair	90 ± 20		827 ± 59	ab	141 ± 51	a	17 ± 7	a
Egan	97 ± 7		687 ± 90	a	206 ± 85	a	29 ± 10	ab
Lanning	72 ± 48		695 ± 165	a	257 ± 79	a	39 ± 15	b
McNeal	83 ± 34		733 ± 90	ab	230 ± 158	a	44 ± 12	b
O'Neal	75 ± 45		799 ± 105	ab	200 ± 29	a	25 ± 4	ab
Reeder	79 ± 35		792 ± 98	ab	132 ± 28	a	17 ± 4	a
Vida	74 ± 45		930 ± 144	b	227 ± 65	a	24 ± 5	ab
WB9879LCP	80 ± 14		769 ± 97	ab	117 ± 52	a	15 ± 5	a
Average	80 ± 31		782 ± 71		189 ± 56		25 ± 12	

* Mean estimates ± standard deviation. Means followed by the same letter in each column within year are not significantly different based on Tukey's multiple comparison ($P \leq 0.05$).

[†] Grain yield estimates were obtained from untreated (no PBS mock treatment) row in 2019.

Table 3.5. Average *Wheat streak mosaic virus* incidence and grain yield responses of barley cultivars following mechanical inoculation in 2017-2019 near Bozeman, MT.

Cultivar	Incidence (%)		Yield (g m ⁻²)				Relative yield (%)
			Control		+WSMV		
2017							
Craft ^{c/d}	0 ± 0*	a	301 ± 52		240 ± 49		79 ± 2
Haxby ^d	6 ± 5	b	282 ± 62		208 ± 108		80 ± 49
Hays ^e	0 ± 0	a	405 ± 152		335 ± 93		95 ± 54
Hockett ^c	4 ± 7	ab	321 ± 87		344 ± 47		116 ± 51
Horsford ^e	10 ± 3	b	349 ± 23		293 ± 74		83 ± 18
Lavina ^e	1 ± 2	ab	412 ± 46		257 ± 75		62 ± 12
Average	3 ± 5		345 ± 54		280 ± 54		86 ± 36
2018							
Craft ^{c/d}	0 ± 0	a	606 ± 29	bc	540 ± 90	a	89 ± 14
Haxby ^d	19 ± 12	b	650 ± 70	bc	558 ± 88	ab	86 ± 13
Hays ^e	0 ± 0	a	698 ± 50	c	676 ± 16	b	97 ± 8
Hockett ^c	0 ± 0	a	583 ± 22	b	597 ± 42	ab	102 ± 7
Horsford ^e	0 ± 0	a	448 ± 23	ab	483 ± 51	a	108 ± 11
Lavina ^e	0 ± 0	a	580 ± 72	b	593 ± 65	ab	103 ± 15
Average	2 ± 7		594 ± 84		574 ± 65		98 ± 13
2019							
Craft ^{†/‡}	3 ± 3	a					
Haxby [†]	53 ± 16	b					
Hays [¶]	3 ± 5	a					
Hockett [†]	0 ± 0	a					
Horsford [¶]	12 ± 1	b					
Lavina [¶]	11 ± 6	b					
Average	14 ± 20						

* Mean estimates ± standard deviation. Means followed by the same letter in each column within year are not significantly different based on Tukey's multiple comparison ($P \leq 0.05$).

† Malting barley.

‡ Feed barley.

¶ Forage barley.

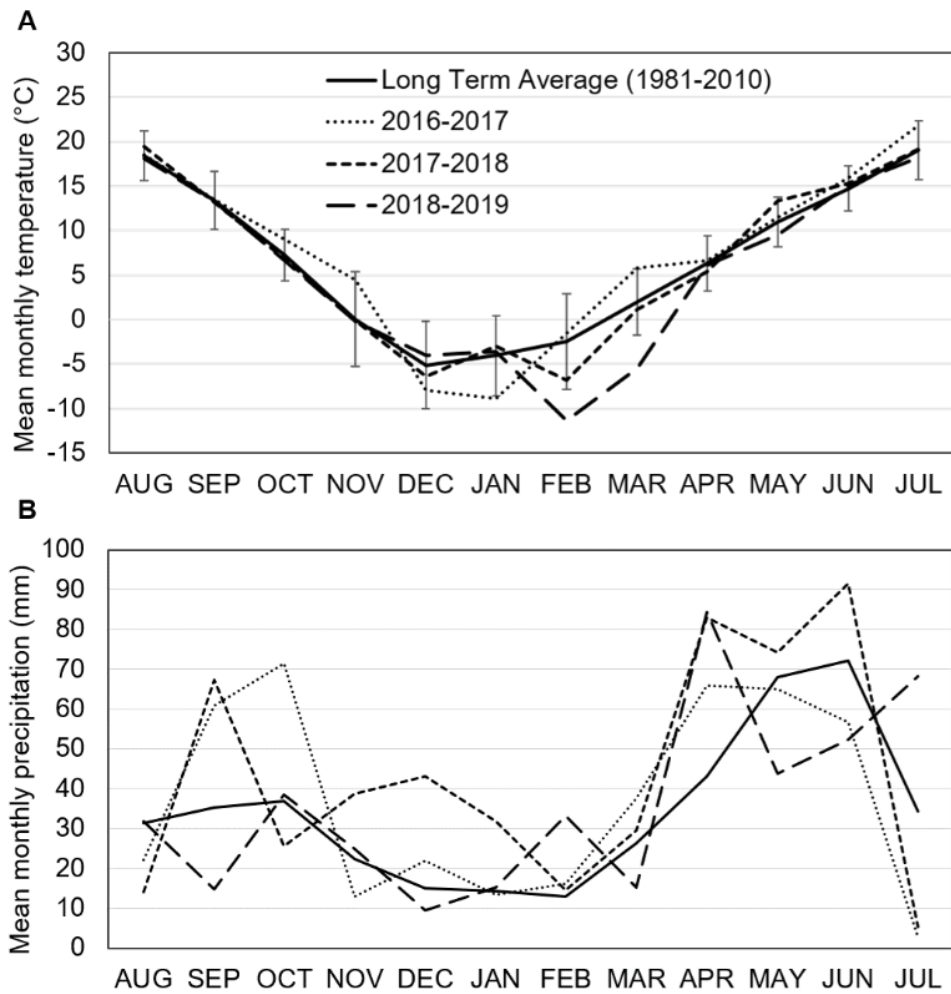


Figure 3.1. Mean monthly (A) temperature and (B) precipitation at the Arthur H. Post Research Farm, Bozeman, MT. Error bars around the long-term temperature average indicate the mean monthly maximum and minimum temperatures. Data source: Bozeman 6 W Exp Farm weather station, Western Regional Climate Center, NOAA.

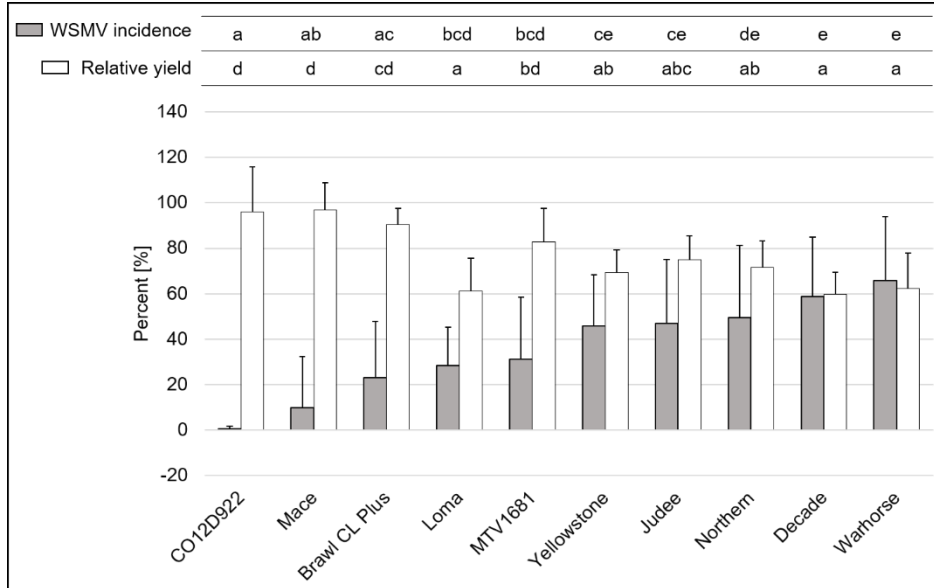


Figure 3.2. Three-year average (2017-2019) *Wheat streak mosaic virus* (WSMV) incidence and relative yield of winter wheat cultivars following mechanical inoculation in the spring. Error bars indicate standard deviation. Same letters within ‘WSMV incidence’ and ‘Relative yield’ rows indicate that corresponding means are not significantly different based on Tukey’s multiple comparison ($P \leq 0.05$) and accounting for year to year variation.

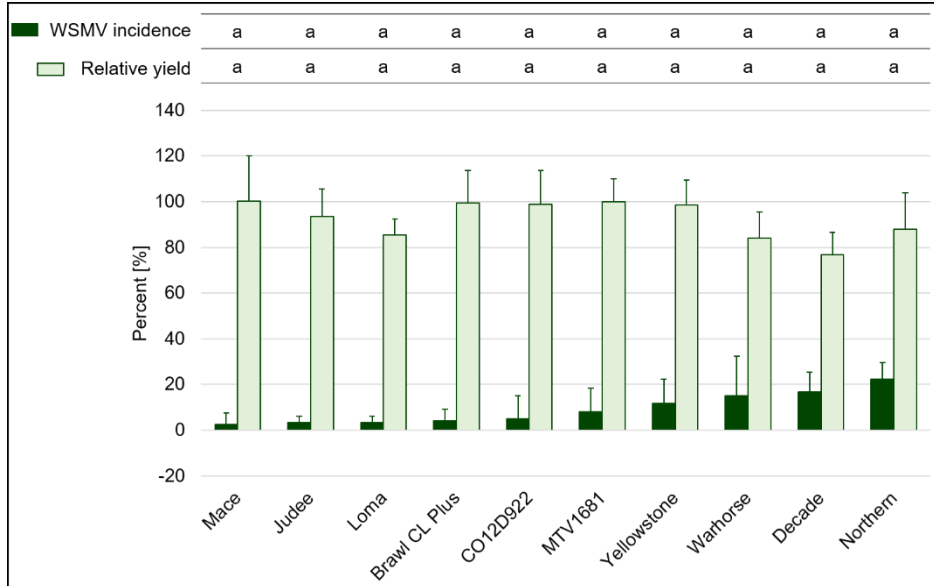


Figure 3.3. 2017 *Wheat streak mosaic virus* (WSMV) incidence and relative yield of winter wheat cultivars following mechanical inoculation in the fall. Error bars indicate standard deviation. Same letters within ‘WSMV incidence’ and ‘Relative yield’ rows indicate that corresponding means are not significantly different based on Tukey’s multiple comparison ($P \leq 0.05$).

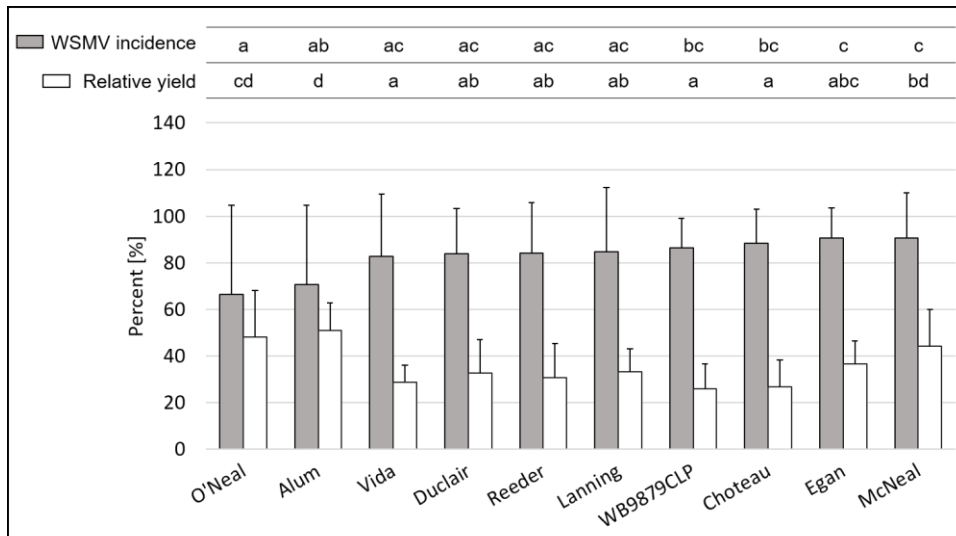


Figure 3.4. Three-year average (2017-2019) *wheat streak mosaic virus* (WSMV) incidence and relative yield of spring wheat cultivars following mechanical inoculation. Error bars indicate standard deviation. Same letters within ‘WSMV incidence’ and ‘Relative yield’ rows indicate that corresponding means are not significantly different based on Tukey’s multiple comparison ($P \leq 0.05$) and accounting for year to year variation.

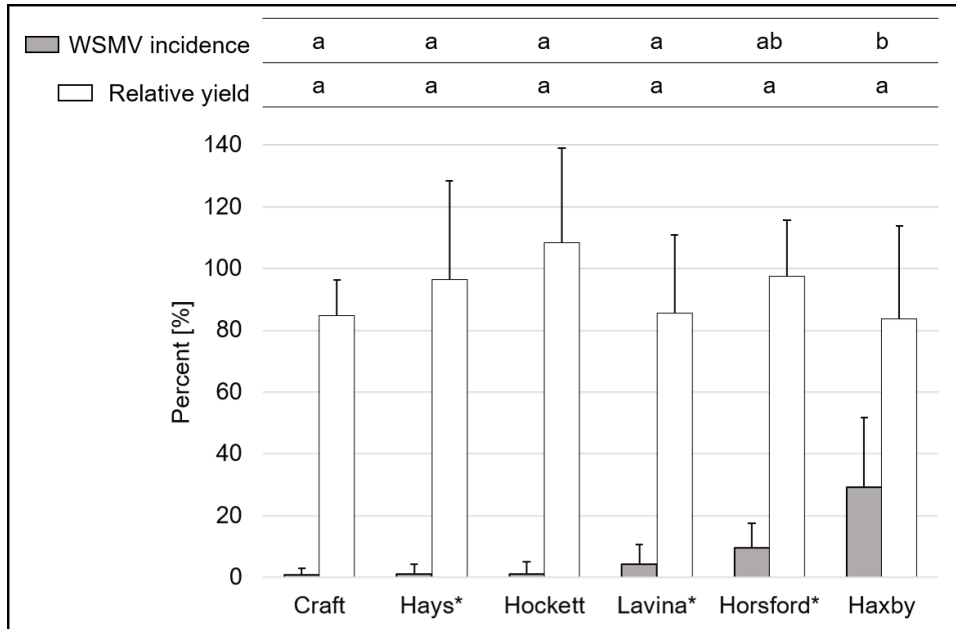


Figure 3.5. Two-year average (2017-2018) *wheat streak mosaic virus* (WSMV) incidence and relative yield of barley cultivars following mechanical inoculation. * indicates forage barley cultivars. Error bars indicate standard deviation. Same letters within 'WSMV incidence' and 'Relative yield' rows indicate that corresponding means are not significantly different based on Tukey's multiple comparison ($P \leq 0.05$), and accounting for year to year variation.

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CHAPTER FOUR

IMPACT OF PLANTING DATE, SEEDING RATE AND CULTIVAR CHOICE ON
SPRING AND WINTER WHEAT PRODUCTIVITY AND PROFITABILITY IN
MONTANA

Contribution of Authors and Co-Authors

Manuscript in Chapter 4

Author: Uta McKelvy.

Contributions: Conceived the study, performed data analyses, interpreted results, wrote the manuscript.

Co-Author: Peggy Lamb.

Contributions: On-station supervision of the study, provided data for analyses, edited earlier manuscripts.

Co-Author: Monica Brelsford.

Contributions: Assistance in conduction of the study, discussed results and implications, edited earlier manuscripts.

Co-Author: Mary Burrows.

Contributions: Conceived the study, acquired funding, discussed results and implications, edited earlier manuscripts.

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Uta McKelvy, Peggy Lamb, Monica Brelsford and Mary Burrows.

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Abstract

Planting date and seeding rate decisions, as well as cultivar selection, are essential management strategies for optimizing yield potential. However, best management practices depend on the specific environmental conditions in a production region. Projected trends of longer growing seasons and an increase in summer temperatures highlight the need for continued evaluation of management alternatives as climate changes. A two-year field study (2016-2018) in spring and winter wheat was conducted near Havre, MT. The objectives were to evaluate the effects of planting date and seeding rate on grain yield and quality parameters in different wheat cultivars. An economic analysis was conducted to assess the impact of these management practices on the profitability of wheat production in Montana. The study validated current planting date recommendations for Montana. Yield reductions were observed at planting dates later than mid-September and April for winter wheat and spring wheat, respectively. No yield increase was observed when winter wheat was planted before mid-September. Later planting dates were associated with higher grain protein content owing to reduced overall grain yields in both spring and winter wheat. Cultivar choices influenced when the wheat crop transitioned to the reproductive growth stage, as well as yield and grain protein content, but planting date decisions were dominant. Seeding rate effects on yield performance were the least dominant and were inconsistent. No meaningful and reliable economic benefits were associated with an increase in seeding rate beyond the recommended density. Only under scenarios of very late planting may an increase in

seeding rate achieve a small increase in revenue, or at least a minor compensation of income losses.

Introduction

Agriculture is the leading industry in Montana (Montana Agricultural Statistics 2018) and wheat (*Triticum aestivum* L.) is an important crop produced in the state. In 2018, 40% of the states' acres in production were planted to wheat (2.2 million ha total, 21.7 % to spring wheat, 12.3 % to winter wheat) and the approximately 5.4 million metric tons (t) of wheat harvested amounted to a production value of over 1 billion USD (USDA NASS 2018). Montana places consistently among the leading wheat producing states in the U.S., ranking third only behind North Dakota and Kansas in 2018 (total wheat produced; USDA NASS 2019).

Wheat prices in the recent past have been volatile and average annual wheat prices have remained below 220.5 USD t^{-1} since 2014, while they had reached historic records of 293.6 USD t^{-1} in 2008 (Macrotrends 2020). Low wheat prices leave growers with very narrow profit margins. To maintain profitable wheat production, growers need to strike a balance between minimal inputs and maximum yields to achieve optimal returns. Many environmental factors impacting wheat yield and quality are outside of the producers' control, but several management practices may modify the effect of limiting environmental factors (Geleta et al. 2002). Cultivar selection, planting date (PD), and seeding rate (SR) are essential management strategies that can be adjusted to optimize yield potential (Otteson et al. 2007).

Wheat is a highly adaptable crop that produces acceptable yields under a wide range of growing conditions (Cook and Veseth 1991). Wheat yield and quality parameters are largely dependent on environmental and genotypic effects and their interaction (Geleta et al. 2002; Peterson 1998; Eskridge 1994; Baenziger 1985; Otteson et al. 2007). Choosing a cultivar with good yield potential and desired grain quality parameters for a given environment is a critical consideration that lays the foundation for profitable production.

Planting date is an important agronomic factor influencing yield performance (McLeod et al. 1992). Early planting allows for a longer vegetative growing period (Green and Ivins 1985), which may result in better stand establishment, increased production of fertile tillers (Gallagher 1984; Frederick and Marshall 1985), more heads (Dahlke et al. 1993), and subsequent higher grain yields (Dahlke et al. 1993; Gallagher 1984). Early planting of spring wheat can also offer the advantage of a longer grain fill period, which is often restricted by high summer temperatures for late planted spring wheat (Lanning et al. 2012; Subedi et al. 2007). The effect of decreasing yields as a result of delayed planting has been demonstrated in many studies (Dahlke et al. 1993; Blue et al. 1990; Lanning et al. 2012), but the optimum time window for planting is strongly location dependent. Blue et al. (1990) observed that winter wheat PDs in southeastern Nebraska that allowed for the accumulation of at least 400 growing degree days (4.4 °C base temperature) before 31 December achieved the highest yields. Dahlke et al. (1993) found that winter wheat yields in Arlington, WI, decreased for PDs later than October 1. Hunt et al. (1996) conducted field studies near Crookston, MN, and obtained highest

yields from spring wheat planted in mid-May, while yields decreased drastically at PDs later than the end of May. Subedi et al. (2007) produced similar results in a spring wheat study in Ottawa, Canada.

The primary motivation for a producer to increase SR is to directly manipulate wheat growth and yield components towards higher productivity. Increasing SR has led to denser plant stands and higher tiller numbers (Otteson et al. 2007). Geleta et al. (2002) observed fewer secondary tillers at SRs of 65 kg ha⁻¹ and 130 kg ha⁻¹ compared to low SRs of 16 kg ha⁻¹ and 33 kg ha⁻¹ in eastern Nebraska. As a result, earlier and more homogeneous maturity and higher grain volume weights were observed at the two higher SRs. Many studies over the past several decades have looked at the effect of various ranges of SRs on spring and winter wheat yields in many different environments with variable outcomes. Otteson et al. (2007) found that increasing SRs from 290 seeds m⁻² to 420 seeds m⁻² did not translate into higher yields in spring wheat trials at Casselton and Carrington, ND. Similarly, Chen et al. (2008) did not observe any yield improvement at SRs of 323 seeds m⁻² and 430 seeds m⁻² compared to 215 seeds m⁻² in spring wheat planted in Moccasin, MT. In contrast, Staggenborg et al. (2003) achieved highest grain yields when winter wheat was seeded at a density of 430 seeds m⁻² in Manhattan, KS, but did not observe further improvement at higher rates. Dahlke et al. (1993) reached maximum yields at 300 seeds m⁻² for winter wheat planted in Arlington, WI. From this array of studies, it can be concluded that SRs can be used as a tool to boost grain yield, but optimum SRs are strongly dependent on location and predominant environmental conditions. It is therefore difficult to extend inferences about SR effects on wheat

productivity across different environments. Instead, such conclusions should be confined to the environment in which the study was conducted. This consequently highlights the need to evaluate optimum SRs within specific environments.

Much research focusing on the effects of agronomic practices on yield and yield components has been done in the past 50 years across the Great Plains region, including Montana. However, current climate models predict a high likelihood of considerable increases in average air temperatures in tropical, subtropical, and temperate regions owing to climate change dynamics by the end of the 21st century (Battisti and Naylor 2009). Lanning et al. (2010) analyzed climatic data associated with 57 years of variety testing trials across the state of Montana (1950 – 2007). They found that over the course of the study period, average monthly temperatures in March increased significantly by 0.08 °C yr⁻¹ and mean annual temperatures increased non-significantly by 0.03 °C yr⁻¹. Increased air temperatures during the growing season are likely to result in increased risk of drought and heat stress conditions for crops (Tebaldi et al. 2006; Lightfoot 2010). Given the looming trend of longer growing seasons and an increase in summer temperatures already observed across the state of Montana, such climatic changes will likely affect wheat production in the state. This highlights the need for continued evaluation of the potential of management strategies in the light of changing climatic conditions. Accurate and up-to-date management recommendations will support growers in maintaining profitable wheat production.

Here we present results from a two-year field study of spring and winter wheat at Northern Agricultural Research Center (NARC) near Havre, MT (2016 - 2018). The

objectives of this study were to evaluate the effects of PD and SR on grain yield and quality parameters in different wheat cultivars.

Materials and Methods

Site Description

Experiments were conducted in 2017 and 2018 under dryland conditions at NARC of Montana State University, near Havre, MT (109.8 W longitude, 48.49 N latitude). The site is in the Northern Great Plains of the U.S. at an altitude of 787 m above sea level. The predominant soil across the trial area is clay loam of the Joplin series (Soil Survey Staff 2019). The area has a semi-arid climate with an average annual precipitation total of 284 mm. The average annual air temperature is 6.3 °C, but temperatures vary greatly throughout the year; from as low as -13.8 °C in January to as high as 29.4 °C in July (30-year temperature normal; Arguez et al. 2010).

Treatment, Experimental Design and Plant Cultivation

Experiments were conducted both in winter wheat and spring wheat. The 2017 winter wheat experiment was set up as a completely randomized design. The 2018 winter wheat experiment, and the 2017 and 2018 spring wheat experiments were organized in a randomized complete block design. Treatments were arranged following a split-plot structure. Planting date was the main plot treatment and SR and cultivar were randomly assigned within the main plots. Every treatment was replicated four times per experiment. Treatments were assigned to six-row plots, 1.83 m wide (30 cm-spacing) and 6.71 m

long. Six-row fill passes were planted along the edges of each experiment area to reduce border effects.

In each experiment, four different cultivars were studied (Tab. 4.1). A total of five hard red winter wheat cultivars, commonly grown in Montana, were used over the course of the two study years: ‘Rampart’ (PI 593889, Bruckner et al. 1997), ‘Judee’ (PI 665277, Carlson et al. 2013), experimental line MTV1681, ‘Warhorse’ (PI 670157, Berg et al. 2014), and ‘Yellowstone’ (PI 643428, Bruckner et al. 2007). Four hard red spring wheat cultivars were used in both study years: ‘Choteau’ (PI 633974, Lanning et al. 2004), ‘WB Gunnison’ (PI 665064), ‘Reeder’ (PI 613586), and ‘Duclair’ (PI 660981, Lanning et al. 2011).

Two SRs, 215 seeds m^{-2} (low/recommended SR) and 430 seeds m^{-2} (high/increased SR) were applied in the experiments. The low SR is based on the upper limit of MSU Agricultural Experiment Stations’ recommendations for spring and winter wheat (Berg et al. 2019; Heo et al. 2019). Seeding depth was 3.5 cm.

Three different PDs were compared in each experiment. In the winter wheat studies, PDs were centered on the recommended PD for the region at approximately one-month intervals (Berg et al. 2019). Actual PDs varied between years due to variable weather conditions and are summarized in Tab. 4.1. The recommended planting time for spring wheat in the study region is as soon as conditions allow past April 1st (Heo et al. 2019). For this study, the first PD occurred as soon as conditions allowed with subsequent PDs at approximately two-week intervals. The dates of the spring wheat planting events are detailed in Tab. 4.1.

The trial area in both study years was in chemical fallow during the preceding crop season and was planted to oilseeds and peas in the two years prior. Fertilizer (125-20-10-10) was side banded at seeding at 380 kg ha⁻¹ for the winter wheat, based on soil sample analyses before planting. Spring wheat was side banded at seeding with 100-20-10-10 fertilizer at 316 kg ha⁻¹. Post-emergence weeds were controlled through application of bromoxynil octanoic acid ester (3,5-dibromo-4-hydroxybenzonitrile) at 0.355 kg a.i. ha⁻¹ and isooctyl ester of 2-methyl-chlorophenoxyacetic acid (MCPA) at 0.38 kg a.i. ha⁻¹, respectively. At later plant growth stages, trails were maintained weed-free by hand, as needed.

Data Collection

Daily climatic data were obtained from a weather station located at NARC. Monthly temperature averages and precipitation totals are summarized in Fig. 4.1.A and 4.1.B. Seasonal weather observations are summarized in Tab. S4.1.

The accumulated drought severity and coverage index (ADSCI) is an experimental tool that summarizes drought information, for a defined geographic area and aggregated over time, in a single numeric value (Akyuz 2017). ADSCI data for Hill County were obtained from United States Drought Monitor website as an approach to quantify and compare drought severity over the course of the study period (<https://droughtmonitor.unl.edu/>). ADSCI are summarized in Fig. 4.1.A.

Data on statewide planting activity were obtained from weekly Montana Crop Progress reports (USDA NASS 2020) for Montana. The accumulated percent of crop

acreage planted by the end of each calendar week (CW) during the 2016/2017 and 2017/2018 crop years and the five-year averages are summarized in Fig. 4.2.A and 4.2.B.

Information on heading date and plant height were collected for each plot in the study. Heading date was determined by counting the numbers of days from planting until 50% of the spikes per plot had fully emerged past the flag leaf collar (Zadoks growth stage 59). Plant height was recorded at Zadoks growth stage 87 by measuring the distance from the soil surface to the tip of spikes excluding the awns.

Grain samples were harvested at wheat maturity using a plot combine (Wintersteiger Inc., Salt Lake City, UT, USA). Grain samples were cleaned using a Clipper office tester A7512 (A.T. Ferrel Company, Bluffton, IN, USA) and weighed to determine grain yield (kg ha^{-1}). Grain yield was adjusted to 13% moisture. Grain protein content (GPC, g kg^{-1}) was measured on a whole grain basis for each plot sample using an Infratec 1241 Grain Analyzer (Foss, Eden Prairie, MN, USA). Test weight (kg m^{-3}) was determined for a representative sample from each plot based on a standardized volume.

Statistical Analysis

Data analysis was conducted in R studio (version 1.1.463; Rstudio 2015) using R version 3.6.1 (R Core Team 2019). Preliminary analysis indicated a strong year effect on all response variables considered in the experiment, as well as complex three- and four-way interactions between study year and other treatment variables. To simplify statistical analysis and effect interpretation, winter and spring wheat experiments were analyzed individually for each year. The split-plot design structure was accounted for in the statistical analysis by using a linear mixed effects models in the lme4 package (Bates et

al. 2015). The independent variables PD, SR, and cultivar were considered fixed effects, while block and pass nested within block, to which the PD main effect was randomly assigned, were considered random effects. The annual data for the winter and spring wheat studies were individually subjected to analysis of variance (ANOVA) using the car package (Fox and Weisberg 2011) and P - values based on χ^2 -tests were extracted. Conditional R^2 values based on fixed and random effects were estimated for each model using the MuMIn package (Barton 2018). Tukey's multiple comparison tests were conducted to identify groups that were different from each other when the ANOVA results indicated significant treatment effects using the multcomp package (Hothorn et al. 2008) and emmeans package (Lenth 2019). Statistical significance was evaluated at $P = 0.05$.

Economic Analysis

Average yield, GPC, and test weight were estimated based on study results for the six PD by SR treatment combinations per year in winter and spring wheat. To simplify the analysis, cultivars were not considered individually. The cash value of wheat grain was determined based on average market price for the respective harvest year as recorded in the Montana Annual Crop Bulletin (Montana Department of Agriculture 2019). Protein premiums and test weight discounts (Bekkerman 2018) were added to and subtracted from the wheat market value, respectively. Revenue was estimated by subtracting direct and indirect production costs, which were approximated by production cost estimates for the northwest region of North Dakota for the respective years (NDSU 2019). Wheat seed prices were inquired from local Montana seed vendors. Average prices for certified,

treated wheat seed were considered in the production cost estimates and adjusted according to SR treatment. Revenue estimations assumed that production costs (fertilizer and fungicide applications, machinery, etc.) do not differ between recommended and increased SR treatment with the exception of increased seed costs at high SR. It was further assumed that all standard management practices considered in the wheat production budget would be performed independent of the market value of wheat and that the wheat grain harvested would be sold the same year at the current market prices.

Results and Discussion

Weather Summary and Environmental Effects

Extreme climatic and environmental conditions characterized the two-year period during which field experiments were conducted. The 2016/2017 crop year was marked by an unusually long growing period in the fall of 2016. September and October of 2016 were characterized by monthly precipitation totals that were 1.6 and 2.7 times higher than the 30-year normal (1981 - 2010) recorded at NARC (Fig. 4.1.A). Average daily temperatures in November 2016 were 4.7 °C warmer than the 30-year normal (Fig. 4.1.B). The onset of winter in 2016 was observed in early December and winter conditions lasted until mid-March of 2017 (Tab. S4.1). The spring and summer months of 2017 were dominated by exacerbating drought conditions. March through July 2017 were characterized by below average monthly precipitation totals that were 12%, 26%, 21%, 60%, and 8% of the 30-year normal for those months, respectively. Sustained below-average precipitation amounts resulted in the buildup of severe drought conditions in northcentral Montana. Drought conditions are reflected in the ADSCI for Hill County,

MT, which increased from 0 to 479 ADSCI between May through July of 2017 (Fig. 4.1.A). The 2017/2018 crop year began under severe drought conditions with the ADSCI peaking at 1621 in October 2017. The winter period of 2017/2018 was approximately two months longer than in the previous season, beginning in early November 2017 and ending in mid-April 2018 (Tab. S4.1). Above-average precipitation amounts in November 2017 through March 2018 recharged the soil water and alleviated drought severity (Fig. 4.1.A). Drought conditions in the summer of 2018 began to rise in June but drought severity was lower compared to the previous year, peaking at 441 ADSCI in August 2018. The observed differences in fall precipitation and drought conditions, as well as the onset and length of the winter period across just two years in this study, illustrate how variable growing conditions between seasons can be in the Northern Great Plains.

Comparison between Study and State-Wide Planting Dates

Winter wheat planting depends on the timely coordination with harvest of the summer crop. Water availability plays an important role in winter wheat planting as sufficient soil moisture is necessary to induce germination. State-wide winter wheat planting in 2016 and 2017 was delayed by one to two weeks compared to the five-year average (2011 - 2015) (Fig. 4.2.A). The late start of planting in 2017 reflects the severe drought conditions in the fall. Moreover, the earliest planting date in this study (PD1) occurred well before winter wheat planting across the state, during CW 32 in both years. Even the recommended planting (PD2) during CW 37 was ahead of state-wide trends. On the other hand, the late planting (PD3) during CW 43 and 42 in 2017 and 2018,

respectively, marked the tail end of the planting activity across the state. Planting dates in this study capture the extremes of planting activities in the state.

Planting in the spring is dependent on the snow melt and accessibility of fields with farming equipment. Spring wheat planting in Montana has traditionally fallen in the month of April, but global warming trends have resulted in shorter winter periods and an earlier beginning of the growing season in the temperate regions. Lanning et al. (2010) estimated a significant advance of spring wheat planting dates by approximately 13 d between 1950 to 2007 across Montana. The five-year average of cumulative spring wheat acreage planted in Montana (Fig. 4.2.B) shows that planting activity in the recent past has begun during the first and second week of April, CW 14 and 15. Across the five-year period and in 2017, 50% of the states' spring wheat acreage were planted by the end of April (CW 18). The impact of the long winter in 2017/2018 is reflected in noticeably delayed spring wheat planting activity in 2018, which began approximately three weeks later than in 2017. Spring wheat PDs in this study captured the window of planting activity in the state in both study years well.

Planting Date Effects on Crop Performance

Grain yield and quality parameters of winter and spring wheat were consistently affected by the interaction between PD and cultivar (Tab. S4.2). The decision of when to plant can have large effects on crop establishment and productivity. Growers typically choose PDs with the intention to maximize yields. For winter wheat, earlier planting allows for a longer plant growth period in the fall, which is beneficial for stand

establishment and productivity of the crop. The limiting effect of late planting on crop development in this study was observed in distinctly shorter heading heights of late-planted winter wheat, which was 12% and 8% shorter compared to winter wheat planted at PD1 in 2017 and 2018, respectively (Tab. S4.3). Winter wheat planted in mid-September, which is the recommended planting time for Montana (Berg et al. 2019), achieved higher grain yields compared to winter wheat planted in mid-October. Grain yield of late planted wheat in 2017 was reduced by 37% compared to PD1 (Tab. 4.2). Similarly, in 2018, a yield reduction of 20% was observed at PD3 relative to PD1 for wheat line MTV1681 and cultivar Yellowstone at recommended SR. These findings match observations by Gallagher (1984), who noted that fall-produced tillers are more synchronized in their development and achieve higher yields. In contrast, no additional yield gain was observed when winter wheat was planted in mid-August, before the recommended PD in mid-September. Winter wheat planted at the early two PDs achieved very similar yields in both study years.

Differences in yield potential between cultivars in this study were most expressed at PD1 and PD2, while yield differences diminished at PD3. At PD1, solid-stem Judee and Rampart achieved yields that were 28% and 19% lower than that of the hollow-stem wheat line MTV1681 at recommended SR in 2017, respectively (Tab. 4.2). Similarly, Judee and Rampart yields were 14% and 16% lower than MTV1681 yields, and 18% and 20% lower than hollow-stem Yellowstone at recommended SR in 2018. Yield performance of solid-stem Warhorse in 2017 was similar to MTV1681 and noticeably higher than the other solid-stem winter wheat cultivars in this study. This was expected,

since Warhorse is described to have a higher yield potential than Rampart (Berg et al. 2014).

The yield benefit of extended fall establishment was also illustrated by higher winter wheat yields harvested in 2017 compared to 2018. Despite limiting drought conditions in the summer of 2017, winter wheat yields averaged $4,230 \pm 1,040 \text{ kg ha}^{-1}$ compared to $3,130 \pm 532 \text{ kg ha}^{-1}$ in 2018. Ample soil moisture and mild air temperatures extended the late growing season in 2016 and facilitated resource accumulation and crop establishment. In contrast, the lack of soil moisture due to sustained drought conditions over the summer and fall of 2017 impaired timely crop establishment and limited resource accumulation. Winter conditions commenced approximately one month earlier than in 2016 (Tab. S4.1), shortening the period for fall establishment considerably.

Terminal drought describes drought stress during grain fill and is an important yield-limiting factor (Porter and Gawith 1999; Wheeler et al. 2000). Avoiding terminal drought protects and increases crop productivity. For spring wheat, this can be achieved by preponing PDs. Results in this study demonstrated a gradual decline in spring wheat yields associated with delayed planting. For example, late-planted spring wheat in 2017 yielded 57% less than spring wheat planted at PD1 of the same year (Tab. 4.3). Moreover, Reeder showed a decrease in yield by 13% from PD1 to PD2 ($P = 0.004$) and 26% from PD2 to PD3 ($P < 0.0001$) in 2018. In both study years, early- and second-planted spring wheat headed in mid- to late June, while late-planted spring wheat headed in early July (Tab. S4.4). While the heading event is not equivalent to flowering, it is indicative of the time window within which the flowering and subsequent grain fill

occurs. The heading dates in this study indicated that flowering and grain fill of late-planted spring wheat occurred approximately 20 days later than early-planted spring wheat, occurring during mid- to late July in both study years. At the same time, drought conditions in 2017 and 2018 began to increase over the course of July (Fig. 4.1.A). Late-planted spring wheat was therefore exposed to more severe drought conditions than the earlier two PDs, resulting in lower yields.

Spring wheat heading dates were not only dependent on PD but were also influenced by cultivar choice in 2018 (PD x C interaction, Tab. S4.2). Across all PDs, Duclair headed significantly earlier than the other cultivars, but the difference in heading date depended on PD (Tab. S4.4). Early-planted Duclair headed 3 d earlier than Choteau ($P < 0.0001$) and 2 d earlier than WB Gunnison ($P < 0.0001$) and Reeder ($P < 0.0001$), while late planted Duclair still headed on average 1.5 d earlier than the other three cultivars. These findings agree with the cultivar release information (Lanning et al. 2011), where Duclair is described as heading one day earlier than its parent Choteau. Earlier heading dates of 1.5 - 3 d may present a noticeable advantage to this spring wheat cultivar, enabling it to escape yield-limiting drought conditions during grain fill. Indeed, yield performance of Duclair in 2018 was improved over Choteau and similar to high-performing WB Gunnison and Reeder at PD1 and PD2 (Tab. 4.3).

The limiting effect of drought conditions on spring wheat yields are also illustrated by substantial yield differences between 2017 and 2018. Spring wheat yields in 2017 averaged $936 \pm 479 \text{ kg ha}^{-1}$ compared to $2,330 \pm 408 \text{ kg ha}^{-1}$ in 2018 (Tab. 4.3). Moreover, early-planted spring wheat in 2018 yielded 2.1 times more than in 2017 and

late-planted spring wheat in 2018 yielded 3.5 times more than in the previous year. ADSCI for Hill County indicated similar drought severity in early June in both study years (Fig. 4.1.A). However, drought severity increased faster and more dramatically during 2017. These conditions caused more limiting effects for spring wheat in 2017, resulting in substantially lower yields that year.

Results from this study illustrate that PD management and cultivar choice influence GPC through a two-way interaction in both winter and spring wheat (Tab. S4.2). The only exception to this was the spring wheat trial in 2017, when extremely low grain yields of late-planted spring wheat did not provide enough material for protein analysis. With only two PDs to analyze in 2017, no PD or PD x cultivar interaction effect on GPC was detected.

Spring wheat WB Gunnison had noticeably and consistently lower GPC compared to all other spring wheat cultivars in the study, averaging $162 \pm 4 \text{ g kg}^{-1}$ and $159 \pm 3 \text{ g kg}^{-1}$ across PDs in 2017 and 2018, respectively. In contrast, Choteau achieved an average GPC of $171 \pm 6 \text{ g kg}^{-1}$ in both study years. These results are in agreement with data from variety performance evaluations conducted at NARC (Heo et al. 2019), in which WB Gunnison had among the lowest GPC of 24 cultivars considered in the study, between 150 and 156 g kg^{-1} . These results indicate a genetic disposition of WB Gunnison towards lower GPC compared to other spring wheat cultivars and this genetic effect appears to dominate over environment-related influences, such as PD.

Overall, an inverse relationship between yield and GPC was observed. At the cultivar level, lower-yielding cultivars typically had higher GPC and vice versa. For

example, winter wheat Judee, which had consistently lower yields compared to wheat line MTV1681 in both study years, had significantly higher GPC which were 7 g kg^{-1} ($P = 0.0006$) and 8 g kg^{-1} ($P = 0.0005$) higher than MTV1681 at PD2 and PD3 in 2017, respectively (Tab. 2). In 2018, GPC of Judee was 6 g kg^{-1} ($P = 0.0003$) to 14 g kg^{-1} ($P < 0.0001$) higher than MTV1681 at PD3 and PD1, respectively. Similarly, GPC of the lower-yielding spring wheat Choteau was 6 g kg^{-1} ($P = 0.0001$) to 11 g kg^{-1} ($P < 0.0001$) higher than high-yielding Reeder at PD2 and PD1 in 2018, respectively (Tab. 4.3).

The relationship between grain yield and GPC was also observed in the between-year comparison of winter wheat. While average winter wheat yields in 2018 were reduced due to limiting drought conditions in the fall of 2017, average GPC of winter wheat grain that year was $148 \pm 8 \text{ g kg}^{-1}$ and thereby 8% higher compared to the average of $135 \pm 9 \text{ g kg}^{-1}$ in 2017. Subedi et al. (2007) observed that late-planted spring wheat had 6% to 17% higher GPC than earlier PDs. They hypothesized that higher GPC was associated with lower yields, resulting in the same amount of nitrogen being translocated to fewer grain at later PDs. Although Subedi et al. (2007) could not gather convincing evidence in support of this hypothesis from their observations, results from this study still suggest an association between grain yield and GPC.

As an alternative explanation for their observations, Subedi et al. (2007) suggested that late-planted wheat accumulated more nitrogen in grain compared to early-planted wheat. Supported by observations from Selles and Zentner (2001) and Pannozzo and Eagles (1999), this shift in nitrogen versus carbohydrate accumulation in wheat grain was hypothesized to be related to water stress conditions, which are often

more severe for a late-planted crop. Indeed, drought stress conditions very likely account for yield differences between 2017 and 2018 and may have impacted GPC, as well. Moreover, late PDs in this study were associated with reduced yields and increased GPC, as well, paralleling Subedi et al.'s observations. Within a study year, GPC of late-planted winter wheat was significantly elevated compared to PD1. In 2017, average GPC at PD1 was $133 \pm 5 \text{ g kg}^{-1}$, while GPC at PD3 was increased by 10% to $146 \pm 5 \text{ g kg}^{-1}$ (Tab. 4.2). Similarly, in 2018, a 6% increase in GPC was observed from $143 \pm 8 \text{ g kg}^{-1}$ at PD1 to $152 \pm 6 \text{ g kg}^{-1}$ at PD3. Spring wheat GPC varied depending on PD as well, but differences between PDs were less pronounced as overall spring wheat GPC was very high, averaging $168 \pm 6 \text{ g kg}^{-1}$ and $165 \pm 6 \text{ g kg}^{-1}$ in 2017 and 2018, respectively (excluding PD3, Tab. 4.3).

Results from this study highlight that PD presents an influential management tool that can be used to control crop exposure to constraining environmental conditions through avoidance, thereby affecting yield and GPC outcomes. Existing PD recommendations for Montana, particularly for winter wheat, are based on empirical observations and long-term averages. Results from this study demonstrate that winter wheat PD recommendations remain valid because no yield increase was observed when planting occurred before mid-September, while yield reductions were observed at PDs later than September. Likewise, spring wheat yields were highest when the crop was planted as soon as conditions in April permitted, while delays in planting past the end of April were associated with considerable yield penalties. Later PDs were associated with higher GPC in both spring and winter wheat. Yield and GPC were consistently impacted

by cultivar choice, which influences how soon the wheat crop transitions from vegetative to reproductive growth stage. However, the effect of PD decisions appeared to dominate cultivar choices.

Seeding Rate Effects on Crop Performance

Adjusting SR at planting can be a useful tool for boosting yields. A consistent effect of SR on heading date was detected in both winter wheat and spring wheat (Tab. S4.2). Wheat planted at recommended SR headed later than at increased SR. However, heading date differences were less than 1 d in 2017 and no more than 1.5 d in 2018. Planting wheat at high density reduces the proportion of secondary tillers. Plant stands dominated by primary tillers mature more homogeneously and earlier (Geleta et al. 2002). The observed earlier heading dates are likely associated with fewer secondary tillers at increased SR. While a heading date difference of 1 d to 1.5 d may seem negligible, advancing the grain fill period by that time may have a beneficial impact on crop productivity under the limiting conditions of drought stress and high temperatures during this critical period.

Apart from the heading date response, SR rarely had noticeable impacts by itself. Rather, SR was influential through interaction with PD and/or cultivar (Tab. S4.2). Seeding rate influenced wheat yield, but effects were inconsistent within and between study years. In 2017, SR impacted yield production of both spring and winter wheat by modifying the effect of PD and cultivar in three-way interactions. Occasional evidence suggested higher yields at increased SR. In winter wheat, early-planted Warhorse and late-planted Judee had higher yields at increased SR compared to recommended SR, 13%

($P = 0.005$) and 16% ($P = 0.04$) respectively (Tab. 4.2). In spring wheat, yields of double-seeded Choteau at PD2 and WB Gunnison at PD3 were 1.5-times ($P = 0.01$) and 2-times ($P = 0.01$) higher compared to the respective recommended SRs (Tab. 4.3). Moreover, non-significant increases in yield associated with high SR treatments were most consistent across cultivars in late-planted spring and winter wheat. Increasing SR has been found to moderate yield reductions due to late planting (Darwinkel et al. 1977; Joseph et al. 1985; Pittman and Andrews 1961; Smid and Jenkinson 1979). This compensatory effect can be linked to the above-mentioned lower proportion of secondary tillers in high density wheat, which results in earlier and more homogeneous crop maturity (Geleta et al. 2002). In late-planted wheat, where limited water availability and high summer temperatures create stress conditions that shorten the grain fill period and accelerate maturity, a lower proportion of secondary tillers could provide a yield advantage by moderating the impact of terminal drought stress. In addition, a lower proportion of secondary tillers at increased SR is also associated with higher grain test weights (Geleta et al. 2002; Wilson and Swanson 1962; Sahs 1970; Samuel 1990). In this study, SR affected test weights of winter and spring wheat, as well, which was usually through interaction with PD and/or cultivar (Tab. S4.2). When significant differences in test weight were detected between the two SR treatment levels, an increase in SR was usually associated with an increase in test weight (Tab. S4.3 and S4.4).

In contrast, increased SRs had negative impacts on crop productivity under conditions that created resource limitations early during plant development. In 2018, an average yield loss of 200 kg ha^{-1} was observed in winter wheat under high SR treatment

compared to the recommended SR. Increasing SR can intensify intra-species competition and likely exacerbate constraints in a resource-limited environment (Geleta et al. 2002). Winter wheat planted at PD1 and PD2 in the fall of 2017 was affected by severe drought conditions. In this environment a denser plant stand has increased competition, especially for limited water resources, impairing plant growth and agronomic performance.

Chen et al. (2008) considered different SR treatments in a spring wheat study in central Montana and observed that GPC either decreased when SR was increased or did not differ between SR treatments. Results from this study demonstrated a significant SR effect on GPC in spring wheat, as well. In contrast to Chen et al. (2008), the increase from recommended to doubled SR resulted in an average additive increase in GPC by 3 g kg^{-1} and 5 g kg^{-1} in 2017 and 2018, respectively. Under severe drought conditions in the summer of 2017, the SR effect on GPC was observed at both PD1 and PD2, for which GPC content could be measured. In 2018, which was governed by more moderate drought conditions, the SR-dependent increase in GPC was more explicit the later spring wheat was planted (Tab. 4.3). Terminal drought affected spring wheat productivity in both study years and water stress during grain fill is known to result in higher protein content (Chen et al. 2008). Drought conditions may have been exacerbated under high SR treatment due to intra-species competition, resulting in increased GPC at high spring wheat SR. In contrast to spring wheat, weak or no SR effects on GPC were observed in winter wheat, further supporting the notion that SR influences GPC by exacerbating the impact of late season drought stress during grain fill, which is more severe for later-maturing spring wheat.

Of the three management tools considered in this study, relevant effects associated with SR treatment were least dominant and consistent. The limited influence of SR may be in part explained by the choice of seeding density levels considered in this study. The lower SR in this study, 215 seeds m^{-2} , was based on recommendations for wheat production in Montana (e.g. Berg et al. 2019). Based on the results in this study, a blanket increase in SR beyond this recommended density does not appear advisable for dryland wheat production in Montana, since no consistent yield gains were observed at the increased SR of 430 seeds m^{-2} . Results from this study have shown that an increase in SR may compensate for the negative effects of late planting and provide a small yield advantage under terminal drought conditions. However, increasing SR was also associated with a decrease in winter wheat yield under conditions of early season drought stress. The time of occurrence of environmental constraints appears to be critical in determining the direction of SR effects on crop productivity. Since these factors are challenging to predict, SR should be considered a less effective and rather unreliable management tool compared to PD decisions and cultivar choice.

Economic Implications of Planting Date and Seeding Rate Management Decisions

The economic analysis revealed narrow profit margins for winter wheat production. Average winter wheat grain prices in Montana were 175 USD t^{-1} and 189 USD t^{-1} in 2017 and 2018, respectively. Average GPCs ranging from 128 g kg^{-1} at PD2 in 2017 to 152 g kg^{-1} at PD3 in 2018 qualified for protein premiums of 11 USD t^{-1} to 43 USD t^{-1} , respectively. Based on the average winter wheat seed costs of 0.48 USD kg^{-1} and production costs of 491 USD ha^{-1} and 506 USD ha^{-1} in 2017 and 2018, respectively,

the revenue for winter wheat grain was highest in early-planted winter wheat at recommended SR in 2017, 399 USD ha⁻¹ (Fig. 4.3). In the same year, cost returns diminished to a small profit margin of 96.2 USD ha⁻¹ at PD3 at recommended SR. Winter wheat revenues were lower in 2018 due to lower winter wheat productivity. Profit margins ranged from 219 USD ha⁻¹ at recommended SR at PD2 to 83 USD ha⁻¹ at increased SR at PD1.

Potential profitability of spring wheat across the two study years was less than winter wheat. Average spring wheat grain prices were 228 USD t⁻¹ and 202 USD t⁻¹ in 2017 and 2018, respectively. Grain protein content in spring wheat was very high in both study years, but protein premiums for spring wheat grain were lower compared to winter wheat. Premiums were 22 USD t⁻¹ across all PDs and SRs in 2017 and varied between 18 USD t⁻¹ and 22 USD t⁻¹ in 2018. Based on the average spring wheat seed costs of 0.54 USD kg⁻¹ and production costs of 472 USD ha⁻¹ and 482 USD ha⁻¹ in 2017 and 2018, respectively, only small profit margins were observed in 2018, which were at the most 85 USD ha⁻¹ for early-planted spring wheat at recommended SR (Fig. 4.3). The narrow profit margin at recommended SR faded with later PDs and became negative at PD3, -111 USD ha⁻¹. No profits were estimated for spring wheat produced in 2017. Very low yields resulted in small cash returns, which were further reduced by occasional discounts due low test weights. Ultimately, income from spring wheat yields could not compensate for production costs, resulting in negative balances across all PDs that ranged from -183 USD ha⁻¹ at PD1 to -403 USD ha⁻¹ at PD3.

There were no economic benefits associated with increased SRs in winter or spring wheat in either study year. In 2017, differences in winter and spring wheat revenue between recommended and increased SR were negligible across all three PDs. In 2018, winter wheat profit margins at increased SR were lower compared to recommended SR across all PDs. For winter wheat, the biggest financial loss was observed at PD1 in 2018, where the economic return at increased SR was 130 USD ha⁻¹ lower than at the recommended SR. Similar to winter wheat, differences in profit margins between recommended and increased SR were observed in spring wheat in 2018. Doubling the SR at PD1 and PD2 was associated with a decrease in revenue to no or negative income. Revenues of late-planted spring wheat in 2018 were negative for both recommended and increased SR.

Overall, results from this analysis demonstrate that there are no meaningful and reliable economic benefits associated with an increase in SR beyond the recommended density of 215 seeds m⁻² for Montana. On the contrary, increased production costs due to increased seed investment reduced profit margins and raised the risk of financial loss. The results suggest that highest profit margins can be observed when adhering to current PD recommendations for Montana. Earlier planting of winter wheat was not associated with a meaningful increase in profit. On the other hand, considerable revenue losses were observed when spring and winter wheat were planted several weeks after the recommended PD. Only under scenarios of very late planting may an increase in SR achieve a small increase in revenue, or at least a minor compensation of income losses. However, since the possible benefit of increased SRs is highly dependent on

environmental factors that are outside a growers' control and difficult to predict, this management strategy is also associated with the risk of further exacerbating financial losses. Increasing planting density is not a reliable management practice that can be recommended.

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Tables and Figures**Table 4.1.** Planting dates, harvest dates and wheat genotypes used in the two-year field experiment to assess the impact of planting date, cultivar selection, and seeding rate on grain yield and yield components.

Crop	Year	Planting Date		Harvest Date	Genotype	
Winter Wheat	2017	PD1 [†]	15 Aug.	12 July	Judee, MTV1681,	
		PD2	15 Sept.	12 July	Rampart,	
		PD3	28 Oct.	21 July	Warhorse	
	2018	PD1	15 Aug.	11 July	Judee, MTV1681,	
		PD2	13 Sept.	20 July	Rampart,	
		PD3	18 Oct.	26 July	Yellowstone	
	Spring wheat	2017	PD1	7 Apr.	4 Aug.	Choteau, Duclair,
			PD2	29 Apr.	4 Aug.	WB Gunnison,
			PD3	19 May	18 Aug.	Reeder
2018		PD1	28 Apr.	9 Aug.	Choteau, Duclair,	
		PD2	9 May	14 Aug.	WB Gunnison,	
		PD3	21 May	23 Aug.	Reeder	

[†]PD1 - PD3 indicate treatment levels of planting date main plot treatment.

Table 4.2. Winter wheat grain yield, protein content, and test weight averages affected by planting date, genotype, and seeding rate.

Planting Date	Genotype	Seeding Rate	Yield		Grain Protein Content	
			2017	2018	2017	2018
			-----kg ha ⁻¹ -----		-----g kg ⁻¹ -----	
PD1	Judee	1x*	3,983 ± 354cde [†]	3,141 ± 260ab	135 ± 5bc	150 ± 2cd
		2x**	3,891 ± 465bd	2,697 ± 288 [‡]	129 ± 9	149 ± 4
	MTV1681	1x	5,516 ±499h	3,626 ± 548bc	133 ± 1cd	137 ± 4a
		2x	5,301 ± 284gh	3,337 ± 254	136 ± 2	135 ± 2
	Rampart	1x	4,457 ± 402df	3,043 ± 360a	133 ± 5ac	151 ± 3ce
		2x	4,378 ± 440df	2,322 ± 204	130 ± 5	152 ± 4
	Warhorse/ Yellowstone [¶]	1x	5,251 ± 403fh	3,802 ± 680c	135 ± 3bc	134 ± 2a
	2x	5,930 ± 313h	3,481 ± 393	134 ± 3	136 ± 6	
PD2	Judee	1x	4,268 ± 361df	3,407 ± 437ac	129 ± 4bc	153 ± 3def
		2x	4,295 ± 277df	2,935 ± 275	133 ± 2	153 ± 2
	MTV1681	1x	5,357 ± 353h	3,363 ± 290bc	125 ± 2a	141 ± 1b
		2x	5,459 ± 588h	3,710 ±764	123 ± 7	143 ± 1
	Rampart	1x	4,434 ± 173dfg	2,904 ± 284a	129 ± 2ac	156 ± 3fg
		2x	4,471 ± 357dfg	2,543 ± 106	127 ± 5	156 ± 1
	Warhorse/ Yellowstone	1x	5,047 ± 384fh	3,675 ± 556c	127 ± 2ab	143 ± 3b
	2x	5,033 ± 614efh	3,710 ± 579	128 ± 4	139 ± 2	
PD3	Judee	1x	3,003 ± 232ab	2,975 ± 301ab	152 ± 6f	155 ± 6eg
		2x	3,469 ± 380ad	2,915 ± 267	147 ± 3	154 ± 5
	MTV1681	1x	2,943 ± 425ab	2,866 ± 555ab	144 ± 3de	148 ± 6c
		2x	3,301 ± 588abc	2,940 ± 588	140 ± 1	149 ± 2
	Rampart	1x	2,951 ± 430ab	2,960 ± 199ab	146 ± 6ef	157 ± 4g
		2x	3,069 ± 493abc	2,853 ± 433	143 ± 4	158 ± 1
	Warhorse/ Yellowstone	1x	2,993 ± 454ab	3,110 ± 263ab	146 ± 3ef	148 ± 2c
	2x	2,717 ± 336a	2,804 ± 141	148 ± 7	147 ± 4	

* 1x; Recommended seeding rate (SR): 215 seeds m⁻².** 2x; Doubled SR: 430 seeds m⁻².[†] Numbers followed by the same letters within a column are not statistically different based on Tukey's multiple comparison at the 0.05 probability level.[‡] No letter code associated with 2x SR within a column indicates no significant interaction effect.[¶] Warhorse was grown in 2017. Yellowstone was grown in 2018.

Table 4.3. Spring wheat grain yield, protein content, and test weight averages affected by planting date, genotype, and seeding rate.

Planting Date	Genotype	Seeding Rate	Yield		Grain Protein Content	
			2017	2018	2017	2018
			-----kg ha ⁻¹ -----		-----g kg ⁻¹ -----	
PD1	Choteau	1x*	1,538 ± 389g [†]	2,410 ± 266b	169 ± 7cd	173 ± 3gi
		2x**	1,266 ± 395cg	2,350 ± 268 [‡]	173 ± 6d	174 ± 3hi
	Duclair	1x	1,382 ± 345eg	2,792 ± 243cd	167 ± 3bc	164 ± 3acef
		2x	1,142 ± 268deg	2,655 ± 198	171 ± 6cd	164 ± 1acef
	WB Gunnison	1x	1,253 ± 252cg	2,724 ± 385bd	159 ± 5a	158 ± 3a
		2x	1,032 ± 337cg	2,501 ± 234	165 ± 1b	160 ± 1a
	Reeder	1x	997 ± 197bceg	2,906 ± 171d	172 ± 2bd	162 ± 1ac
		2x	1,318 ± 636fg	2,791 ± 158	169 ± 7bd	163 ± 2ace
PD2	Choteau	1x	760 ± 110acef	2,484 ± 345b	173 ± 5cd	172 ± 4gi
		2x	1,265 ± 737cg	2,234 ± 243	175 ± 3d	176 ± 1i
	Duclair	1x	920 ± 436aceg	2,657 ± 228bd	168 ± 4bc	164 ± 3ace
		2x	915 ± 548aceg	2,568 ± 52	173 ± 7cd	170 ± 2fgi
	WB Gunnison	1x	1,109 ± 278cg	2,420 ± 194b	159 ± 4a	158 ± 5a
		2x	1,049 ± 597aceg	2,394 ± 184	166 ± 1b	162 ± 3acd
	Reeder	1x	1,028 ± 448cg	2,563 ± 146bc	165 ± 3bd	167 ± 1cegh
		2x	1,281 ± 489eg	2,499 ± 177	169 ± 4bd	169 ± 2egh
PD3	Choteau	1x	337 ± 281a	1,911 ± 166a	- [¶]	164 ± 4acef
		2x	526 ± 233ac	1,807 ± 241	-	169 ± 5degh
	Duclair	1x	417 ± 326ab	1,906 ± 53a	-	160 ± 2ab
		2x	608 ± 283ace	1,894 ± 312	-	167 ± 3bcg
	WB Gunnison	1x	374 ± 146a	1,662 ± 145a	-	158 ± 4a
		2x	759 ± 207acef	1,911 ± 69	-	161 ± 2ac
	Reeder	1x	558 ± 398acd	1,910 ± 241a	-	162 ± 3ace
		2x	645 ± 130acef	1,961 ± 144	-	168 ± 2cegh

* 1x; Recommended seeding rate (SR): 215 seeds m⁻².** 2x; Doubled SR: 430 seeds m⁻².[†] Numbers followed by the same letters within a column are not statistically different based on Tukey's multiple comparison at the 0.05 probability level.[‡] No letter code associated with 2x SR within a column indicates no significant interaction effect.[¶] No information available.

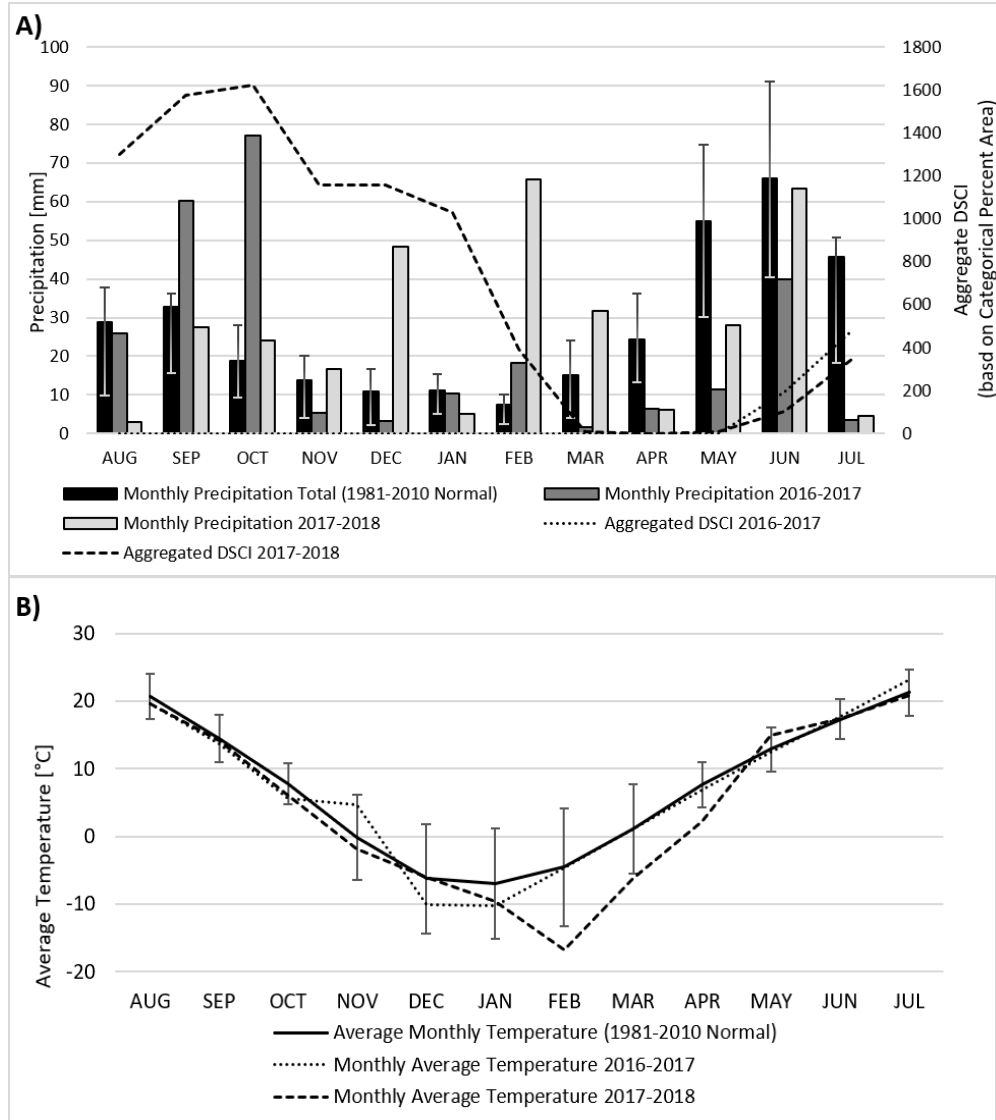


Figure 4.1. Climatic summary of the 2016/2017 and 2017/2018 growing seasons at Northern Agricultural Research Center in Havre, MT. **A)** Monthly accumulated precipitation totals and aggregate drought severity and coverage index (ADSCI). Error bars associated with the 30-year precipitation normals indicate the 25th and 75th percentiles. **B)** Monthly average temperatures. Error bars associated with the 30-year temperature normal indicate the standard deviation of the long-term average.

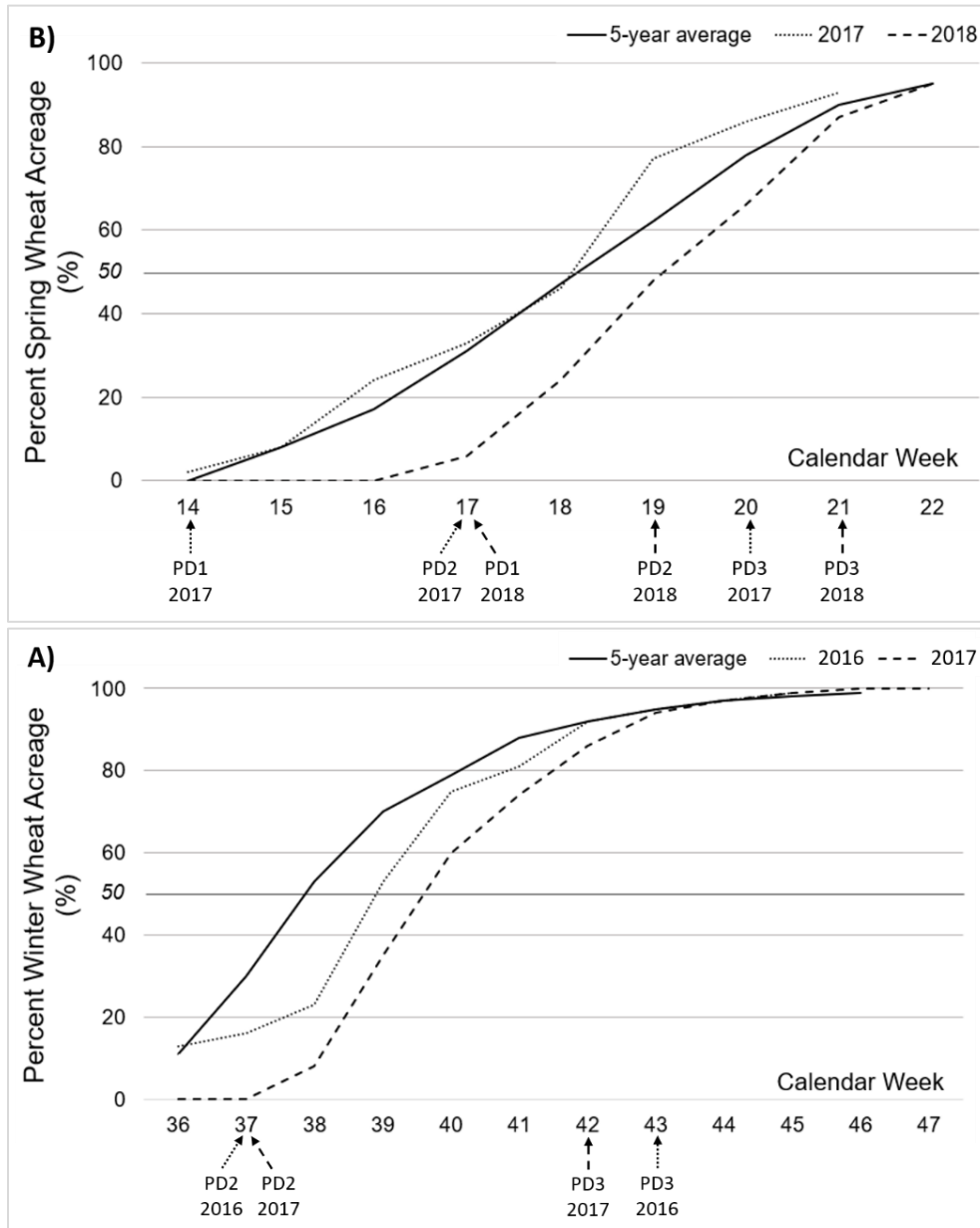


Figure 4.2. Progression of state-wide wheat planting activity across Montana and planting dates (PD) implemented in the two-year field study (2017 – 2018) at Northern Agricultural Research Center, Havre, MT. **A)** Winter wheat planting of the 2016/2017 and 2017/2018 crop and five-year average (2011-2015). Early planting (PD1) occurred during calendar week 32 in 2017 and 2018. **B)** Spring wheat planting of the 2017 and 2018 crop and five-year average (2012-2016).

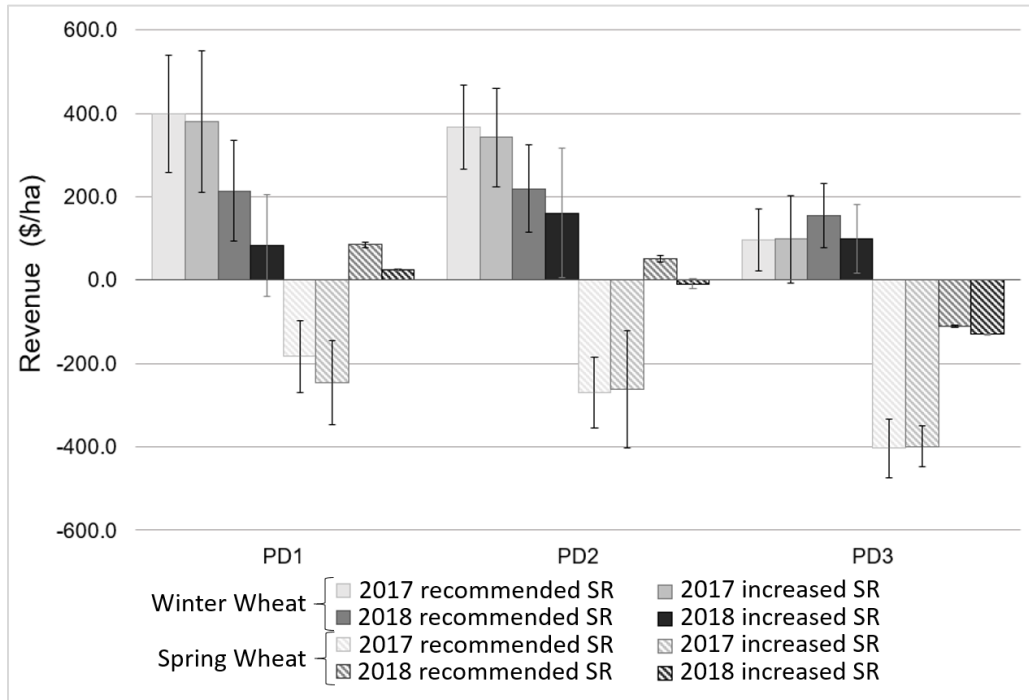


Figure 4.3. Winter and spring wheat revenue estimates based on yield data from the two-year field experiment (2017 – 2018) at Northern Agricultural Research Center, Havre, MT. Columns represent revenue estimates based on mean yield estimates for each planting date (PD) by seeding rate (SR) combination. Error bars indicate the minimum and maximum revenue and are based on the standard deviation of the underlying yield estimates. Recommended SR: 215 seeds m⁻²; Increased SR: 430 seeds m⁻².

Table S4.1. Crop year summary, including precipitation totals and mean temperatures recorded at the Northern Agricultural Research Center in Havre, MT.

Crop Year	Onset of Winter [†]	Beginning of Spring [‡]	Precipitation Total [¶]		Mean Temperature	
			Aug. - Oct. [¶]	Apr. - July	Aug. - Oct.	Apr. - July
			----- mm -----		----- °C -----	
2016/2017	5 Dec.	15 Mar.	163.3	61.2	12.8	15.1
2017/2018	2 Nov.	11 Apr.	54.6	102.1	13.3	13.9

[†] The onset of winter was defined the first period of continued below-freezing average daily temperatures for seven days or more.

[‡] Beginning of spring was defined as the first period of continued above-freezing average daily temperatures for seven days or more.

[¶] Precipitation totals are summarized by fall and spring/summer season: Aug. – Oct. indicates fall precipitation received by winter wheat only; Apr. – Jul. indicates spring/summer precipitation received by both winter and spring wheat.

Table S4.2. Dependence of winter and spring wheat yield, grain quality parameters, heading date and plant height on planting date, genotype, and seeding rate assessed by ANOVA for each year and crop separately.

Genotype, and seeding rate assessed by ANOVA for each year and crop separately.															
Source of Variation	df	Yield		df	Grain Protein		df	Test Weight		df	Plant Height		df	Heading Date	
		2017	2018		2017	2018		2017	2018		2017	2018		2017	2018
		-----g m ⁻² -----			-----g kg ⁻¹ -----			-----kg m ⁻³ -----			-----cm-----			-----JCD [¶] -----	
Winter Wheat															
Planting date (PD)	2	***	**	2	***	***	2	***	***	2	***	**	2	***	***
Genotype (G)	3	***	***	3	***	***	3	***	***	3	***	**	3	NS [†]	**
Seeding rate (SR)	1	NS	**	1	*	NS	1	NS	*	1	NS	NS	1	*	**
PD x G	6	***	**	6	**	***	6	***	***	6	NS	*	6	**	NS
PD x SR	2	NS	NS	2	NS	NS	2	NS	NS	2	NS	NS	2	NS	NS
G x SR	3	NS	NS	3	NS	NS	3	*	*	3	NS	NS	3	NS	NS
PD x G x SR	6	*	NS	6	NS	NS	6	*	NS	6	NS	NS	6	NS	NS
R ² ‡		0.87	0.46		0.84	0.9		0.82	0.91		0.51	0.43		0.91	0.84
Spring Wheat															
Planting date (PD)	2	***	***	1	NS	***	2	***	***	2	***	***	2	***	***
Genotype (G)	3	NS	***	3	***	***	3	***	***	3	NS	***	3	NS	***
Seeding rate (SR)	1	NS	NS	1	***	***	1	***	NS	1	NS	NS	1	*	***
PD x G	6	NS	*	3	NS	***	6	NS	***	6	NS	NS	6	NS	*
PD x SR	2	NS	NS	1	NS	**	2	NS	***	2	NS	NS	2	NS	NS
G x SR	3	NS	NS	3	*	NS	3	NS	NS	3	NS	NS	3	NS	NS
PD x G x SR	6	*	NS	3	NS	NS	6	NS	**	6	NS	NS	6	NS	NS
R ²		0.81	0.83		0.76	0.80		0.86	0.87		0.48	0.70		0.99	0.99

[¶]JCD, Julian calendar days.

* Significant at the 0.05 probability level.

** Significant at the 0.01 probability level.

*** Significant at the 0.001 probability level

[†] NS, nonsignificant.

[‡] Coefficient of multiple determination conditional on all significant main effects and random effects in the model.

Table S4.3. Test weight, plant height and heading date averages of winter wheat affected by planting date, genotype, and seeding rate.

Planting Date	Genotype	Seeding Rate	Test Weight		Plant Height		Heading Date	
			2017	2018	2017	2018	2017	2018
			-----kg m ⁻³ -----		-----cm-----		-----JCD [†] -----	
PD1	Judee	1x*	816 ± 5hj	816 ± 3fg	61 ± 7abc [‡]	62 ± 5bc	151 ± 1ab	158 ± 1a
		2x**	814 ± 10fghj	819 ± 3g	63 ± 11 ^{‡‡}	64 ± 3	150 ± 1	157 ± 1
	MTV1681	1x	804 ± 1cg	796 ± 1ce	64 ± 2bc	61 ± 4bc	151 ± 1ab	158 ± 2ab
		2x	806 ± 3ceghi	797 ± 4e	65 ± 6	66 ± 7	150 ± 1	157 ± 1
	Rampart	1x	801 ± 4bce	789 ± 5ace	65 ± 3bc	63 ± 4ac	151 ± 1ac	159 ± 1ac
		2x	799 ± 2bce	789 ± 1ace	65 ± 3	62 ± 6	151 ± 1	158 ± 1
	Warhorse/ Yellowstone [¶]	1x	806 ± 2ceghi	795 ± 3bce	71 ± 5d	70 ± 3c	150 ± 1a	158 ± 1ac
		2x	802 ± 3bceg	795 ± 4bce	73 ± 1	67 ± 3	150 ± 0	158 ± 1
PD2	Judee	1x	815 ± 9ghj	811 ± 3fg	60 ± 1ab	60 ± 3ac	152 ± 1bc	158 ± 1ac
		2x	823 ± 4j	814 ± 2fg	62 ± 3	64 ± 7	152 ± 1	158 ± 2
	MTV1681	1x	811 ± 1eghi	796 ± 4de	67 ± 4bc	63 ± 4ac	152 ± 1c	160 ± 1c
		2x	809 ± 4deghi	793 ± 4bce	63 ± 5	60 ± 3	153 ± 1	160 ± 1
	Rampart	1x	802 ± 4bcef	791 ± 6bce	67 ± 3bd	64 ± 6bc	152 ± 1bc	159 ± 1ac
		2x	798 ± 8acd	787 ± 6acd	62 ± 5	63 ± 2	152 ± 1	158 ± 1
	Warhorse/ Yellowstone	1x	809 ± 2deghi	788 ± 6acd	66 ± 3cd	65 ± 3bc	152 ± 1ac	159 ± 0bc
		2x	810 ± 2eghi	791 ± 4bce	70 ± 5	65 ± 4	152 ± 1	159 ± 1
PD3	Judee	1x	813 ± 4egj	807 ± 3f	56 ± 5ab	63 ± 5ab	158 ± 1d	164 ± 2d
		2x	817 ± 3ij	811 ± 3fg	58 ± 4	59 ± 6	156 ± 1	162 ± 1
	MTV1681	1x	794 ± 8ac	780 ± 8a	54 ± 6a	57 ± 1a	158 ± 1de	163 ± 2d
		2x	804 ± 2ceh	787 ± 6ac	58 ± 2	54 ± 1	157 ± 1	162 ± 1
	Rampart	1x	802 ± 2bceg	789 ± 4ace	61 ± 3ab	63 ± 6bc	158 ± 1d	163 ± 1d
		2x	802 ± 4bcef	787 ± 1ab	57 ± 3	63 ± 5	156 ± 1	163 ± 1
	Warhorse/ Yellowstone	1x	792 ± 4ab	782 ± 3a	63 ± 3ab	63 ± 8ab	158 ± 1e	164 ± 1d
		2x	786 ± 11a	785 ± 5ab	57 ± 4	59 ± 5	159 ± 2	164 ± 1

* 1x; Recommended seeding rate (SR): 215 seeds m⁻².** 2x; Doubled SR: 430 seeds m⁻².

† JCD; Julian Calendar Day.

‡ Numbers followed by the same letters within a column are not statistically different based on Tukey's multiple comparison at the 0.05 probability level.

‡‡ No letter code associated with 2x SR within a column indicates no significant interaction effect.

¶ Warhorse was grown in 2017. Yellowstone was grown in 2018.

Table S4.4. Test weight, plant height and heading date averages of spring wheat affected by planting date, genotype, and seeding rate.

Planting Date	Genotype	Seeding Rate	Test Weight		Plant Height		Heading Date	
			2017	2018	2017	2018	2017	2018
			----- $kg\ m^{-3}$ -----		----- cm -----		----- JCD [†] -----	
PD1	Choteau	1x*	763 ± 8ef	777 ± 2gjk	66 ± 1	59 ± 2bd	163 ± 1	173 ± 1b
		2x**	774 ± 6	783 ± 5hil	65 ± 2	62 ± 6 ^{‡‡}	162 ± 2	171 ± 1
	Duclair	1x	760 ± 13de	772 ± 5eghi	65 ± 2	63 ± 3cde	162 ± 2	169 ± 1a
		2x	765 ± 8	784 ± 3ijl	64 ± 2	65 ± 4	161 ± 2	169 ± 1
	WB Gunnison	1x	775 ± 12f	791 ± 5kl	64 ± 3	69 ± 2ef	161 ± 3	171 ± 1b
		2x	779 ± 9	790 ± 6jl	65 ± 2	67 ± 3	162 ± 2	170 ± 1
	Reeder	1x	766 ± 12f	789 ± 3jl	66 ± 1	66 ± 2df	163 ± 1	171 ± 1b
		2x	784 ± 3	800 ± 2l	65 ± 1	65 ± 1	162 ± 1	170 ± 1
					b		b	
PD2	Choteau	1x	748 ± 5de	758 ± 11bceg	52 ± 0	67 ± 6df	171 ± 0	180 ± 1b
		2x	757 ± 5	763 ± 3bceg	52 ± 1	65 ± 3	171 ± 1	179 ± 1
	Duclair	1x	736 ± 6bc	756 ± 14ade	53 ± 1	68 ± 5ef	172 ± 1	179 ± 1c
		2x	753 ± 20	744 ± 13a	52 ± 1	71 ± 3	171 ± 1	177 ± 2
	WB Gunnison	1x	753 ± 12de	774 ± 7fgjk	53 ± 3	66 ± 4ef	172 ± 3	180 ± 0d
		2x	765 ± 8	774 ± 7egj	52 ± 2	68 ± 2	171 ± 2	179 ± 2
	Reeder	1x	741 ± 4cd	764 ± 10bceg	53 ± 1	70 ± 6f	172 ± 1	180 ± 1d
		2x	761 ± 11	773 ± 5dfgj	53 ± 1	69 ± 2	172 ± 1	179 ± 1
					a		c	
PD3	Choteau	1x	722 ± 24a	764 ± 6bceg	47 ± 1	54 ± 4a	186 ± 1	190 ± 1f
		2x	728 ± 12	757 ± 9aef	46 ± 1	57 ± 3	185 ± 1	188 ± 1
	Duclair	1x	711 ± 15a	757 ± 2ae	47 ± 1	61 ± 6abc	186 ± 1	188 ± 1e
		2x	726 ± 5	751 ± 10ab	46 ± 2	59 ± 6	185 ± 2	188 ± 1
	WB Gunnison	1x	739 ± 4bc	757 ± 8ae	46 ± 1	55 ± 2ab	185 ± 1	190 ± 1f
		2x	739 ± 10	751 ± 7ac	46 ± 1	58 ± 6	185 ± 1	189 ± 0
	Reeder	1x	727 ± 9ab	765 ± 10begh	46 ± 1	58 ± 4ab	185 ± 1	190 ± 1f
		2x	737 ± 14	761 ± 6bceg	47 ± 1	60 ± 7	186 ± 1	189 ± 0

* 1x; Recommended seeding rate (SR): 215 seeds m⁻².** 2x; Doubled SR: 430 seeds m⁻².

† JCD; Julian Calendar Day

‡ Numbers followed by the same letters within a column are not statistically different based on Tukey's multiple comparison at the 0.05 probability level.

‡‡ No letter code associated with 2x SR within a column indicates no significant interaction effect.

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CHAPTER FIVE

EVALUATION OF CHEMICAL AND CULTURAL MANAGEMENT PRACTICES
FOR WHEAT STEM SAWFLY CONTROL AND EFFECTS ON BENEFICIAL
INSECTS IN SPRING WHEAT IN MONTANA

Contribution of Authors and Co-Authors

Manuscript in Chapter 5

Author: Uta McKelvy

Contributions: Conceived the study, performed data analyses, interpreted results, wrote the manuscript.

Co-Author: David Weaver

Contributions: Conceived the study, discussed results and implications.

Co-Author: Mary Burrows

Contributions: Conceived the study, acquired funding, discussed results and implications.

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Uta McKelvy, David Weaver and Mary Burrows.

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Abstract

Wheat stem sawfly (WSS; *Cephus cinctus* Norton) is a major insect pest of winter and spring wheat in the Northern and Central Great Plains of the U.S. It causes damage through the feeding activity of larvae inside wheat stems and through stem lodging. Control of WSS populations using insecticides is difficult owing to the secluded lifestyle of larvae within host stems and little information is available on the effectiveness of different products. The use of resistant cultivars is currently the most effective approach to mitigating WSS damage. In this study, we evaluated the potential of different insecticides in controlling WSS infestation and damage and compared them to different spring wheat genotypes with varying degrees of WSS resistance at two different seeding rates. Our results showed that contact insecticides in IRAC groups 1B and 3A do not reduce stem infestation or increase mortality of injurious larvae. In contrast, application of the systemic organophosphate phorate (Thimet-20G) provided effective protection of susceptible cultivar 'Reeder' by inducing high larval mortality rates, which resulted in reduced stem lodging and protected grain yield. The use of solid-stem cultivars like 'Choteau' and 'WB Gunnison' provided equally effective protection from WSS infestation. Moreover, 'WB Gunnison' produced yields that were as high as those achieved by hollow-stem cultivar 'Reeder' under the Thimet treatment. Seeding rate effects on WSS infestation and cultivar resistance were inconsistent across study years. No effects of insecticide applications on WSS parasitism or on thrips density in treated spring wheat were observed in this study, but insect numbers were highly variable across study sites and years. Further research is needed to investigate the role of insecticides on non-target and beneficial insect populations. This study is one of few that reports on the

efficacy of insecticide products in controlling WSS infestation and assess their effect on the larger agroecosystem.

Introduction

Wheat stem sawfly (WSS; *Cephus cinctus* Norton) is a major insect pest of winter and spring wheat in the Northern and Central Great Plains of the U.S. and the southern regions of the Canadian provinces (Beres et al. 2011a). The economic impact of WSS populations amounts to 350 million USD annually from yield losses in the U.S. and Canada (Beres et al. 2011a). Economic damage in Montana ranges between 44 - 80 million USD each year (Bekkerman and Weaver 2018; Fulbright et al. 2017).

Wheat stem sawfly have an univoltine life cycle. Larvae overwinter in wheat stubble and adults emerge in the spring after pupation. Wheat stem sawfly flight occurs between May and July and females deposit eggs into wheat stems. Larvae develop inside the stem, where they feed on the parenchyma. As the host plant matures, WSS larvae move downward to the base of the stem, where they create an imminent breaking point by girdling the inside of the stem, making it prone to lodging. The larvae seal their hibernaculum with frass and undergo obligate diapause in the below-ground portion of the wheat stub.

Wheat stem sawflies induce yield loss in two ways: Larval feeding activity within wheat stems reduces the photosynthetic capacity of the host plants and damages the vascular tissue, thereby impairing the transport of water and nutrients through the plant. As a result, plant fitness is reduced and senescence accelerated (Delaney et al. 2010; Macedo et al. 2005, 2006, 2007; Morrill et al. 1992) causing yield losses of 10% to 30% in wheat heads (Delaney et al. 2010; Seamans et al. 1944). In addition, lodged stems are

difficult or impossible to recover during harvest and each wheat head remaining on the ground represents 100% yield loss for that wheat stem.

Unrecovered wheat heads are a source of volunteer wheat, which is an important alternate host for the wheat curl mite (WCM; *Aceria tosichella* Keifer) and viruses of the wheat streak mosaic (WSM) disease complex, which it vectors (Wegulo et al. 2008).

Wheat streak mosaic is an important viral disease affecting wheat and other cereal crops across the Great Plains. Annual yield losses are estimated at 1% across the region (Appel et al. 2015) but can be much higher in epidemic years. Wheat is a mutual host of the WSS and the WSM disease complex and both co-occur in the same geographic region. This raises the question if interactions between the viral disease and the insect pest exist and how they might affect population dynamics and epidemic risk? However, no studies investigating such interactions have been reported in the literature to date.

Several management approaches are employed to control WSS populations and mitigate yield losses. Cultural management strategies involving the use of solid-stem wheat cultivars are most effective. Stem solidness is caused by the presence of pith in the wheat stem, which is genetically controlled and dependent on environmental conditions and agricultural practices, such as row spacing and planting density (Berzonsky et al. 2003; Beres et al. 2012; Luginbill and McNeal 1958). Pith impedes egg deposition, larval movement and development in wheat stems, thereby reducing infestation and larval survival (Holmes and Peterson 1962; Wallace and McNeal 1966). Survival rates in solid-stem spring wheat cultivar ‘Choteau’ ranged between 40 - 60% compared to 46 - 85% in hollow-stem cultivar ‘McNeal’ (Varella et al. 2018). Two types of stem solidness are commonly deployed in breeding programs, which are associated with different alleles of

the same QTL, *Qss.msub-3BL* (Varella et al. 2016). Consistent stem solidness throughout plant development has been observed in ‘Choteau,’ ‘Duclair’ and other wheat cultivars originating from germplasm of the Portuguese landrace S-615 (Platt et al. 1948). In contrast, stem solidness in spring wheat cultivar ‘Conan’ changes throughout plant development. During stem elongation, stem solidness is high, but it decreases during stem maturation. Higher neonatal mortality rates have been observed in ‘Conan’ compared to ‘Choteau’ and WSS females appeared to prefer ‘Choteau’ for oviposition (Talbert et al. 2014; Varella et al. 2016). The ‘Conan’ allele has since been deployed in other spring wheat cultivars, one of which is ‘WB Gunnison’ (Heo et al. 2019).

Life table studies of pre-diapause WSS larvae revealed that parasitism is an important contributor to larval mortality and can be effective at reducing damaging populations of WSS (Peterson et al. 2011). Two hymenopteran species are known to parasitize larvae in wheat production systems, *Bracon cephi* (Gahan) and *Bracon lissogaster* (Muesebeck) (Morrill 1998, Runyon et al. 2002, Weaver et al. 2005). The parasitoid females locate feeding WSS larvae within stems and deposit their eggs next to the larvae, which they paralyze. Parasitoid larvae then feed on the WSS larvae, thereby killing them. Parasitism rates by *B. cephi* and *B. lissogaster* can be as high as 98% (Morrill 1998), but are variable dependent on environmental conditions, agricultural practices, and WSS abundance (Holmes et al. 1963).

Only systemic insecticides that translocate throughout the plant have potential to provide efficient control of stem-boring larvae due to their secluded lifestyle. A special local need registration label for Montana was issued for the systemic-acting organophosphate product Thimet-20G in 2015 (Wanner and Tharp 2015) but expired in

2019. Some contact insecticides are labeled for the control of adult WSS, but their effectiveness is strongly dependent on careful monitoring of WSS occurrence and timely spray applications (Beres et al. 2011b). In large-scale production systems, typical for Montana and other Great Plains states, this management approach is difficult to accomplish with satisfying results. Moreover, insecticide applications may negatively affect beneficial insect populations. For example, an unintended reduction in *Bracon* spp. parasitoids could exacerbate yield loss from WSS. Thrips (Thysanoptera) have been reported to suppress WCM population growth, possibly due to predatory behavior (Stilwell 2009). Application of insecticides with efficacy against thrips could result in increased WCM populations and subsequent WSM disease risk.

In this study, we evaluated the potential of three different insecticides in controlling WSS infestation and damage in the susceptible spring wheat cultivar ‘Reeder’ and assessed the impact on beneficial insect populations in wheat at two location in north and southcentral Montana. In addition, we assessed four spring wheat cultivars for their resistance to WSS infestation and yield under WSS pressure at two seeding rates. The objectives of this study were to compare cultural and chemical management approaches in high WSS-pressure environments and to assess their effect on the larger agroecosystem.

Materials and Methods

Site Description, Experimental Design and Plant Cultivation.

To assess the impact and efficacy of chemical and cultural management practices on WSS infestation and population development in spring wheat, three different

experiments were conducted in two locations over two years, in 2017 and 2018. An extended insecticide study was conducted in northcentral Montana in Choteau County, near Big Sandy. Study sites in 2017 (48°15'42.1" N, 110°22'19.1" W) and 2018 (48°14'04.1"N, 110°20'45.1" W) were located 4 km from each other. A reduced insecticide study and a variety study were conducted in southcentral Montana in Gallatin County, near Amsterdam. Study sites in 2017 (45°45'33.2" N, 111°23'50.0" W) and 2018 (45°45'24.8"N, 111°24'11.4" W) were located at a 0.5 km distance from each other. Both sites were located on conventional, rain-fed farmland in no-till, chemical fallow - cereal crop rotation. Both locations have long-established WSS populations with varying degrees of parasitism.

Insecticide Study. The extended insecticide study included six treatments (Tab. 5.1) and was established near Big Sandy, MT. A reduced insecticide study with four treatments (Tab. 5.1) was established near Amsterdam, MT. The experiments were organized in a randomized complete block design (RCBD) with four replications in 2017 and six replications in 2018. Treatments were assigned at the plot level. In Big Sandy, six-row plots were established, 1.8 m wide (30 cm-spacing) and 4.9 m long, with 1.5 m alleys between blocks. In Amsterdam, seven-row plots were 1.8 m wide (25 cm-spacing) and 7 m in length with 1 m alleys between blocks. Plots were seeded at 2.5 cm depth to a density of 215 seeds m⁻². Six-row fill passes of WSS-resistant spring wheat cultivar 'WB Gunnison' were planted along the edges of each experimental site to reduce border effects. The Big Sandy sites were planted on 20 April 2017 and 4 May 2018. The Amsterdam sites were planted on 13 April 2017 and 28 April 2018.

Cultivar Study. The variety study was conducted near Amsterdam, MT, adjacent to the reduced insecticide study. Four spring wheat cultivars (Tab. 5.2) were compared at two seeding rates, 215 seeds m⁻² (recommended) and 430 seeds m⁻² (increased), amounting to eight different treatment combinations. The study design was a RCBD with four replications in 2017 and six replications in 2018. Seven-row plots were 1.8 m wide (25 cm-spacing) and 7 m in length with 1 m alleys between blocks. Plots were seeded at 2.5 cm depth on 13 April 2017 and 28 April 2018 and surrounded by a six-row border pass of ‘WB Gunnison.’

Insecticide Treatments.

Research plots were planted to WSS-susceptible spring wheat cultivar ‘Reeder.’ Untreated ‘Reeder’ plots were used as control. Wheat stem sawfly-resistant cultivar ‘Choteau’ was included in the insecticide study at Big Sandy as a second control for the insecticide treatments.

Thimet-20G (Tab. 5.3) was applied using a six-row double-disk plot seeder. The granules were pre-weighed and packaged into envelopes on a per-plot basis, dispersed through the seed cone and drilled into the soil at 3.8 cm depth adjacent to the emerged spring wheat rows. For the full rate, Thimet was applied at 5.6 kg ha⁻¹, incorporating the granules parallel to each row in a plot. For the half rate application, Thimet was applied at 2.8 kg ha⁻¹, incorporating granules next to every other row in the plot (total of three rows). The insecticide was applied after crop emergence and just before WSS adults emerged; on 22 May 2017 and 30 May 2018 at Amsterdam, and on 23 May 2017 and 30 May 2018 at Big Sandy.

Mustang Maxx and Lorsban-4E insecticides (Tab. 5.3) were applied to wheat foliage at early jointing, during peak WSS flight, using a backpack sprayer with six-inch boom width and flat spray tip nozzles (XR8002VS; TeeJet Technologies, Wheaton, IL, USA) at 1.7 bar (25 psi). Mustang Maxx was applied at 0.29 L ha⁻¹ and Lorsban-4E at 1.17 L ha⁻¹. Application dates were 31 May 2017 and 5 June 2018 at Big Sandy, 2 June 2017 and 9 June 2018 at Amsterdam.

In the Big Sandy study in 2017, one plot received an incorrect insecticide treatment ('Choteau' + Lorsban-4E) and was excluded from the study. As a result, only three replications of 'Choteau' control and Lorsban-4E treatment were considered in the study, while the 'Reeder' control treatment had five replications.

Grain Harvest and Post-Harvest Assessment of Research Plots.

Research plots were harvested at wheat maturity using a plot combine (Wintersteiger Inc., Salt Lake City, UT, USA). Grain samples were cleaned and weighed to determine grain yield (kg ha⁻¹). Grain yield was adjusted to 13% moisture. Plots at the Big Sandy site were harvested on 9 August 2017 and 23 August 2018. Harvest at the Amsterdam site was completed on 22 August 2017 and 19 September 2018.

After harvest, research plots were assessed for the number of wheat heads remaining unharvested in the plot as a result of stem lodging. For the assessment, a metal ring with 35 cm diameter (area of 0.1 m²) was randomly thrown into the plot. The number of wheat heads and stems that were attached to a head and located to at least one-half of their length in the circular area were counted. The procedure was repeated three times for each plot.

Assessment of Wheat Stem Sawfly Infestation
and Impact on Grain Yield Components.

Infestation with WSS larvae and survival status was determined at crop maturity and sampling occurred one to three days before harvest. Within each plot, three 0.3 m row sections were randomly selected by tossing a wooden measuring stick (30 x 2.5 x 2.5 cm) into the plot. Wheat stems in the marked row section were carefully dug up, placed in labeled paper bags and transferred to the laboratory. Outer rows and a 0.3 m-wide section at the top and bottom of each plot were excluded from sampling to reduce border effects.

In the laboratory, wheat stems were dissected along the length of the stem. Dissected stems were assigned to one of four categories based on visual examination (Tab. 5.4): uninfested stems, infested stems with dead immatures, infested stems with parasitized immatures, and infested stems with pre-diapause larvae. The number of stems in each category and the total number of stems per sample were recorded.

To determine the impact of WSS infestation and larval survival on yield quality parameters, wheat heads from dissected stems were grouped according to infestation status of the corresponding stem. The wheat heads were individually threshed, the cleaned grain was weighed, and kernels counted using a Contador Electronic Seed Counter (Pfeuffer, Kitzingen, Germany). The average number of kernels per head was estimated by dividing kernel count by the number of heads sorted into the respective category for each sample. Thousand kernel weight (TKW) was estimated by dividing the weight of the cleaned grain sample by the number of kernels in the sample and multiplying it by 1,000.

Assessment of Arthropod Populations in Insecticide-Treated Plots.

To determine the impact of insecticide treatments on non-target arthropod populations, ten wheat plants were randomly collected from each research plot, excluding the outer rows and the top and bottom 0.3 m of the plot to reduce border effects. The first sampling occurred one day before the application of foliar insecticides, when spring wheat plants were at late tillering (Feekes 5) or early jointing stage (Feekes 6). Post-application sampling at Big Sandy was done 7 and 21 days post application (dpa) of insecticide (Feekes 9 and Feekes 10.5, respectively) in 2017, and 12 dpa (Feekes 9) in 2018. At Amsterdam, post-application sampling occurred 12 dpa (Feekes 10) and 24 dpa (Feekes 10.5) in 2017, and 12 dpa (Feekes 9) in 2018. Collected plants were placed in labeled paper bags, which were stored in plastic trash bags for transportation, and transferred to the Arthur H. Post Farm in Bozeman, MT. Samples from the Big Sandy site were sometimes stored over-night in an air-conditioned storage room (approximately 10 °C) before transportation to Bozeman.

The number of tillers per sample was recorded and each sample was placed in a Berlese funnel. Wide-mouthed mason jars (86 mm diameter, 473 ml volume) were filled with 150 ml 70% (v/v) ethanol, labeled according to the sample, and placed under the funnel tube. After 48 h, the dried plant samples were removed from the Berlese funnels. The mason jars were sealed and transferred to the laboratory for further analysis.

For sample analysis, the content of a mason jar was poured into 100 mm diameter polystyrene petri dishes (Fisher Scientific, Hampton, NH, USA) with a 10 x 10 mm square grid drawn underneath the bottom. The petri dish was placed under a stereo microscope and its content screened for arthropod specimen, which were sorted in one of

four categories: thrips (Thysanoptera: Thripidae), aphids (Hemiptera: Aphididae), mites (Acari), and “other.” The latter group summarized flies (Diptera: Muscidae), mosquitos (Diptera: Culicidae), and spiders (Araneae) and specimens that could not be identified. Sorted specimen were preserved in 70 % (v/v) ethanol in 1.5 ml centrifuge tubes for potential later identification to genus and species. Arthropod numbers were normalized to the numbers of spring wheat tillers per sample and extrapolated to number of specimens per 100 spring wheat tillers to obtain integer estimates.

Collection of Weather Data.

Average daily temperature and precipitation amount for the time period from planting to harvest were retrieved from an online database (<https://www.wunderground.com/>). Station KMTBIGSA (Edwards Farm) was located at 2 km distance from the Big Sandy experimental sites and station KBZN (Bozeman Yellowstone International Airport) was located at 22 km distance from the Amsterdam sites. Average daily temperature was used to estimate growing degree days (GDD) for wheat (0 °C base). Growing degree days and precipitation were summarized by calendar week and are presented in Fig. 5.1.

Statistical Analysis.

Preliminary analysis indicated a strong location and year effects on WSS infestation and crop yield. To simplify statistical analysis and effect interpretation, data were analyzed for each study site and year separately.

To assess the impact of insecticide, variety and seeding rate on the likelihood of stem infestation, the number of infested stems was considered relative to the total number of stems per sample. The likelihood of larval death, parasitism, and larvae reaching pre-

diapause stage depending on treatment variables was assessed by comparing the number of stems in each of the three categories to the total number of infested stems per sample (Tab. 5.4). Generalized linear mixed effect models with a binomial distribution on the logit scale were fit using ‘glmer’ (Bates et al. 2015). Insecticide treatment, variety, and seeding rate were considered fixed effects in the corresponding studies. Plot identity was fit as random effect to account for repeated measures. Evidence for a treatment effect was assessed using the ‘Anova’ function (Fox and Weisberg 2011). R-squared values were estimated using ‘r.squaredGLMM.’ Effect sizes were estimated using the ‘emmeans’ (Lenth 2019). Differences between treatments were tested with Tukey’s multiple comparison at the 0.05 significance level (Hothorn et al. 2008).

The impact of insecticide treatment, cultivar and seeding rate on grain yield and the average number of wheat heads remaining in the plot were analyzed by fitting linear mixed effect models using ‘lmer’ (Bates et al. 2015). Fixed effects were the same as above and a random effect was included to account for variation between treatment blocks. ANOVA and post-hoc tests were conducted as described above. Correlations between the proportion of stem infestation and wheat heads remaining in the field after harvest were assessed using the Kendall correlation method in ‘ggscatter’ and ‘cor.test’ (R Core Team 2019).

To assess the impact of WSS infestation and larval fate on grain yield components (kernels per head, TKW) linear mixed effects models were fit using ‘lmer’ (Bates et al. 2015). Infestation status (Tab. 5.4) was modeled as fixed effect and plot identity was considered as random effect. Category “infested - larva parasitized” was excluded from

the statistical analysis due to the infrequent occurrence of parasitism resulting in low sample sizes. ANOVA and post-hoc tests were conducted as described above.

The impact on insecticide treatment on arthropod populations over time was assessed by fitting a repeated measures mixed effects model using ‘lmer’ (Bates et al. 2015). Sampling time and insecticide treatment were modeled as fixed effects and repeated measures were accounted for by incorporating a plot random effect. The number of thrips per wheat tiller was the dependent variable. ANOVA and post-hoc tests were conducted as described above.

The following packages were used throughout the analysis: lme4 (Bates et al. 2015), car (Fox and Weisberg 2018), MuMIn (Barton 2018), emmeans (Lenth 2019), multcomp (Hothorn et al. 2008), ggpubr (Kassambara 2018). All statistical analyses were conducted in R studio (version 1.1.463; Rstudio 2015) using R version 3.6.1 (R Core Team 2019).

Results

Weather Summary of the 2017 and 2018 Growing Seasons.

Spring wheat in 2017 was planted approximately two weeks earlier than in 2018 at both research sites, indicating an earlier beginning of the 2017 growing season. 2017 was further characterized by severe drought conditions in the latter half of the growing season, which were particularly severe in northern Montana. Precipitation amounts from planting to harvest in 2017 accumulated to 90 mm at Big Sandy and 130 mm at Amsterdam in 2017, which was approximately 50 mm and 40 mm less than in 2018, respectively (Fig. 5.1). In addition to precipitation differences, the Big Sandy research

site was further characterized by higher average temperatures past calendar week 24 (mid-June) resulting in a more rapid increase of accumulated GDD compared to the Amsterdam site (Fig. 5.1). Crop harvest at the Amsterdam site occurred in late September (calendar week 39) in 2018, due to a slow drying of the spring wheat crop, as a result of continued precipitation events near crop maturity.

Wheat Stem Sawfly Infestation and Survival.

The number of WSS infested stems, regardless of larval fate within the stem, was calculated relative to the number of uninfested stems in each sample, to estimate the probability of infestation in response to insecticide or cultivar and seeding rate treatments. The probability of WSS infestation was higher in 2017 than in 2018 across study sites and trials. At Big Sandy, no differences in the probability of stem infestation between treatment groups were observed in either year (2017: $\chi^2 = 3.4$; $P = 0.63$; 2018: $\chi^2 = 3.1$; $P = 0.69$), indicating that insecticide applications did not affect WSS oviposition behavior (Tab. 5.5). Probability of infestation averaged 0.55 (95% CI: 0.50 - 0.60) and 0.33 (95% CI: 0.29 - 0.37) across treatments in 2017 and 2018, respectively.

Probability of infestation was generally higher at the Amsterdam site compared to Big Sandy (Tab. 5.5), indicating higher WSS pressure at Amsterdam. The probability of stem infestation differed between insecticide treatments at Amsterdam in 2017 ($\chi^2 = 13.5$; $P = 0.004$) and 2018 ($\chi^2 = 57.4$; $P < 0.001$). Thimet treatment was associated with a significantly lower probability of stem infestation compared to the other treatment groups (Tab. 5.5). In the cultivar study, spring wheat genotype influenced the probability of stem infestation in 2017 ($\chi^2 = 26.7$; $P < 0.001$) and 2018 ($\chi^2 = 143.9$; $P < 0.001$). The probability of infestation was consistently lower for 'WB Gunnison,' particularly

compared to ‘Reeder’ (Tab. 5.6). The increase in seeding rate from 215 seeds m⁻² to 430 seeds m⁻² in 2017 was associated with insignificant increases in the probability of infestation across all cultivars. In 2018, infestation in response to seeding rate was more variable between cultivars, but a significant increase in the likelihood of infestation was observed for ‘Choteau’ (Tab. 5.6).

Insecticide treatment significantly affected the probability of larval death across both study years and locations. The likelihood of immatures dying was lowest for untreated ‘Reeder’ and applications of the foliar insecticide Mustang Maxx did not increase the probability of larval death compared to the susceptible control (Tab. 5.7 and Tab. 5.8). However, treatment with systemic insecticide Thimet resulted in a significant increase in the probability of larval death ranging as high as 0.95 (95% CI: 0.92 - 0.97) at full rate in 2017 at Amsterdam (Tab. 5.8). The probability of larval death in ‘Choteau’ control plots at Big Sandy was as high as in the Thimet treatment group in both study years (Tab. 5.7). Lorsban-4E treatment at Big Sandy increased larval mortality to intermediate levels between ‘Reeder’ control and Thimet treatment in 2017 and 2018.

The probability of parasitism was generally higher at Amsterdam, suggesting a larger population of parasitoids at this location. Moreover, probability of parasitism was higher in 2017 compared to 2018 across both study sites. Moderate evidence for an impact of insecticide treatment on the likelihood of parasitism was detected at Big Sandy in 2017 ($\chi^2 = 13.5$; $P = 0.02$) but did not hold under post-hoc multiple comparison at $P = 0.05$ probability level (Tab. 5.7). Thimet treatment significantly decreased the probability of parasitism events at Amsterdam in 2017 (Treatment effect: $\chi^2 = 43.3$;

$P < 0.001$) (Tab. 5.8). No evidence for a treatment effect on the probability of parasitism was detected in 2018 in either location.

The likelihood of larval survival at crop maturity (pre-diapause) was significantly reduced under Thimet treatment compared to the foliar insecticides and ‘Reeder’ control at Amsterdam in both years (Tab. 5.8). Results from the Big Sandy trials indicated similar trends, although less pronounced (Tab. 5.7). The probability of larval survival at crop maturity was somewhat reduced under Lorsban-4E treatment compared to ‘Reeder’ control and Mustang Maxx at Big Sandy, but differences were not statistically significant (Tab. 5.7). Moreover, the likelihood of survival at crop maturity in solid-stem ‘Choteau’ was as low as under Thimet treatment at Big Sandy.

Cultivar choices significantly influenced larval mortality within wheat stems. The probability of larval death was significantly increased in ‘WB Gunnison,’ ‘Duclair,’ and ‘Choteau’ compared to ‘Reeder’ in 2017 (Tab. 5.9). No seeding rate effect on the likelihood of larval death was observed in 2017 ($\chi^2 = 1.3$; $P = 0.25$), but seeding rate influenced larval mortality depending on cultivar choice in 2018 ($\chi^2 = 8.9$; $P = 0.03$). In 2018, an increase in seeding rate was associated with an increase in probability of larval death in cultivars ‘Reeder’ and ‘WB Gunnison’ (Tab. 5.7).

Cultivar choice further influenced parasitism of WSS larvae in 2017 ($\chi^2 = 28.1$; $P < 0.0001$), which was highest in hollow-stem ‘Reeder’ and lowest in solid-stem ‘Choteau’ (Tab. 5.9). Evidence for a cultivar effect on parasitism was observed in 2018, as well ($\chi^2 = 8.6$; $P = 0.03$), but specific differences did not hold under adjustment for post-hoc multiple comparison at $P = 0.05$ probability level. However, trends indicated a higher probability of parasitism in ‘Reeder’ compared to the other cultivars.

Larval survival at crop maturity was higher in 2017 compared to 2018 across all cultivars (Tab. 5.9). The probability of survival was highest for ‘Reeder’ and significantly lower in all other cultivars. No seeding rate effects on parasitism or pre-diapause survival were detected in either study year.

Grain Yield and Stem Lodging in Response to Insecticide Treatments, Cultivar and Seeding Rate Choices.

Grain yields were distinctly lower in 2017 compared to 2018 across studies and location, owing to severe drought conditions in the summer months of 2017 (Fig. 5.1). Insecticide treatment influenced grain yield across study sites. At Big Sandy in 2017, highest yields were observed in Thimet-treated plots at full rate, which were significantly higher than under Lorsban-4E and Mustang Maxx treatment (Tab. 5.7). The lowest yields were observed in ‘Choteau’ control plots, despite high larval mortality and low survival at crop maturity in 2017. In 2018, grain yield of untreated ‘Reeder’ was significantly lower than all other treatment groups at Big Sandy (Tab. 5.7). Highest yields were again observed in Thimet treated plots (full rate), but no statistically significant differences between Thimet and other treatments groups occurred. At the Amsterdam site, Thimet treatment was associated with the highest yields in 2017, which were significantly higher than under Mustang Maxx treatment (Tab. 5.8). However, differences between treatment groups were less pronounced and average yield was lower compared to Big Sandy in 2017. No evidence for differences in grain yield between insecticide treatment groups were observed in 2018 at Amsterdam ($\chi^2 = 0.7$; $P = 0.88$). A very low conditional R^2 -value of 0.06 indicated a high degree of variability in the data that could not be accounted for by the model variables and likely confounded estimation of treatment effects.

Cultivar choice affected grain yield in 2017 ($\chi^2 = 4.6$; $P = 0.009$), while no evidence for a significant seeding rate effect was detected ($\chi^2 = 0.2$; $P = 0.62$). ‘WB Gunnison’ achieved higher yields than all other cultivars in the Amsterdam study (Tab. 5.9). However, no evidence for cultivar- or seeding rate-dependent differences in grain yield were found in 2018 (cultivar: $\chi^2 = 5.7$; $P = 0.12$; seeding rate: $\chi^2 = 2.5$; $P = 0.11$) and the conditional R^2 value of 0.14 indicated a high degree of unexplained variability in the data.

Estimates of the average number of wheat heads remaining in the plot after harvest are indicative of the degree of stem lodging due to WSS activity. A higher number of wheat heads remaining in harvested plots were observed in 2017 compared to 2018 across both study sites and stem lodging was more severe at Big Sandy in 2017 than at Amsterdam (Tab. 5.7 and Tab. 5.8). At Big Sandy, trends suggested a low occurrence of stem lodging in ‘Choteau’ control plots, compared to a high number of unharvested wheat heads remaining in ‘Reeder’ control plots in 2017 (Tab. 5.7). However, variation in head counts between replications was high and no evidence for statistically significant differences between treatment groups was found in 2017 ($\chi^2 = 9.9$; $P = 0.08$) or 2018 ($\chi^2 = 5.4$; $P = 0.36$). Regardless of insecticide treatment, the average number of wheat heads per m^{-2} remaining in the field after harvest was negatively correlated with the average proportion of uninfested stems in 2017 (kendall correlation coefficient $\tau = -0.56$, $P = 0.005$). No evidence for such a correlation was found in 2018.

Significant differences between insecticide treatment groups were observed in Amsterdam in 2017 ($\chi^2 = 7.8$; $P = 0.05$) and 2018 ($\chi^2 = 8.3$; $P = 0.001$). The lowest numbers of unharvested wheat heads were counted in Thimet-treated plots (Tab. 5.8).

The average count of wheat heads was negatively correlated with the proportion of uninfested wheat stems in 2018 ($\tau = -0.34$; $P = 0.02$). In the cultivar study, stem lodging was dependent on spring wheat genotype in 2017 ($\chi^2 = 29.4$; $P < 0.0001$) and 2018 ($\chi^2 = 12.8$; $P < 0.0001$) and significantly more wheat heads were counted in ‘Reeder’ plots than in all other cultivars in both study years (Tab. 5.9). A negative correlation between the average proportion of uninfested stems and wheat heads remaining in the field after harvest was found in 2017 ($\tau = -0.27$; $P = 0.03$) and 2018 ($\tau = -0.41$; $P < 0.0001$).

Wheat heads obtained from infested and uninfested stems were analyzed for average kernel count per head and TKW. Across all study sites and years, uninfested wheat stems were associated with a lower number of kernels per spike, while infested stems had consistently and significantly more kernels per spike, regardless of WSS survival (Tab. 5.10). Although more variable across years and study sites, TKW was generally higher in infested stems where WSS immatures had died and reduced in stems where larvae survived to crop maturity (Tab. 5.10).

Impact of Insecticide Treatments on Arthropod Densities in Spring Wheat.

Arthropod incidence and diversity were monitored in response to insecticide treatments at the Big Sandy and Amsterdam site. Across research sites and years, the total number of specimens collected per sampling time ranged between 10 and 96 (Fig. 5.2). Thrips were the most abundant arthropod group detected in samples, except for Amsterdam 2018. Aphids were somewhat abundant at Big Sandy in 2018. Mites were rarely detected in samples and were identified as predatory mites. Wheat curl mites were never detected in samples. Flies (Diptera: Muscidae), mosquitoes (Diptera: Culicidae),

and spiders (Araneae) were occasionally detected. Arthropod incidence in samples was extremely low at Amsterdam in 2018, which was excluded from subsequent analysis.

Due to the dominant abundance of thrips across site-years, the impact of insecticide treatments over time was assessed specifically on thrips density, excluding other taxonomic groups that were detected infrequently or were heterogeneous. Variability in thrips density between replications was high and no evidence for an impact of insecticide treatment was detected in the Big Sandy and Amsterdam trial in 2017 (Tab. 5.11). Thrips density varied depending on sampling time in both locations in 2017 (Tab. 5.11), but no consistent trend over time could be observed between locations (Tab. 5.12). At Big Sandy, average thrips density 21 dpa was significantly higher than the day before application ($P = 0.02$) and 7 dpa ($P = 0.01$) (Tab. 5.12). In contrast, average thrips density continuously decreased from 23 ± 2.3 thrips per 100 tillers the day before insecticide application to 3 ± 2.3 thrips per tiller 24 dpa ($P < 0.001$) at Amsterdam in 2017.

In 2018, evidence for significant differences in thrips density between treatment groups was found for the Big Sandy data, but no evidence for an effect of sampling time (Tab. 5.11). Across both sampling times, average thrips density was highest in ‘Choteau’ control plots and significantly different from Thimet full rate ($P = 0.01$), Thimet half rate ($P = 0.03$), and Lorsban-4E treatment groups ($P = 0.02$) (Tab. 5.12). However, no differences in thrips densities between insecticide-treated and ‘Reeder’ control plots were found. ‘Reeder’ control plots were not statistically different from ‘Choteau’ control plots.

The conditional R^2 -value of 0.27 for Big Sandy 2018 indicated a considerable amount of variability in the data that was not accounted for by insecticide treatment and

sampling time, while R^2 -values in 2017 suggested a lower degree of unexplained variation in the Big Sandy ($R^2 = 0.51$) and Amsterdam ($R^2 = 0.48$) data.

Discussion

Sawfly Infestation and Survival under Chemical and Cultural Management.

The probability of WSS infestation of spring wheat was higher in 2017 than in 2018. Later planting dates by approximately two weeks in 2018 delayed spring wheat development that year and were hypothesized to have caused lower infestation rates that year due to spring wheat plants not having reached the stem elongation stage at the time of WSS emergence. Peak emergence of adult WSS can be predicted by GDD and occurs from 578 to 595 GDD (Beres et al. 2011a). Based on the estimated GDD for the Big Sandy and Amsterdam locations starting at the beginning of April (data not shown), peak WSS flight would have occurred during early and late calendar week 22 in 2017 and 2018, respectively. Stem elongation of spring wheat plants typically occurs at approximately 400 GDD (Cook and Veseth 1991), which were reached during the middle of calendar week 21 in 2017 and early calendar week 22 in 2018 (Fig. 5.1). Thus, the spring wheat crop would have been at a suitable developmental stage for WSS oviposition in both years. A later start of the growing season in 2018 does not convincingly explain differences in infestation rates between years. Instead, it is possible that the harsher and longer winter in 2017/2018 may have caused higher mortality during diapause, resulting in fewer adults emerging in the subsequent spring. Cárcamo and Beres (2006) reported that survivorship of hibernating WSS larvae decreased drastically when exposed to temperatures of $-20\text{ }^{\circ}\text{C}$ for more than 10 consecutive days. Monthly average

temperatures in February 2018 averaged -15 °C and -8 °C with minimum temperatures as low as -37 °C and -18 °C as recorded by the Big Sandy and Amsterdam weather stations, respectively. Moreover, minimum temperatures in March were still as low as -22 °C at the Big Sandy site. The determination of the exact factors contributing to lower infestation rates in 2018 were beyond the scope of this study and can't be known with certainty. Overall, higher infestation rates in 2017 coincided with higher larval survival rates at crop maturity and increased numbers of wheat heads remaining in the research plots after harvest, suggesting a greater incidence of WSS-associated stem lodging in 2017. Taken together, these results indicate greater WSS pressure on spring wheat in 2017.

Insecticide treatment did not affect the probability of stem infestation at Big Sandy (Tab. 5.7), which agreed with our expectations that insecticide treatment would not affect WSS oviposition behavior. However, at the Amsterdam site Thimet application was associated with a lower probability of stem infestation (Tab. 5.8). It is possible that these results are due to mischaracterization of a portion of wheat stems as uninfested, when they were infested but the larva had died from ingestion of phorate-contaminated plant tissue at an early developmental stage. Since samples were collected at crop maturity and processed over a period of several months, dead neonates would have desiccated in wheat stems and could have been more difficult to detect, resulting in false positive identification of uninfested stems.

Larval mortality at the Amsterdam site was higher in 2018 compared to 2017 (Tab. 5.8, Tab. 5.9), while no such differences between study years were observed at Big Sandy. This suggests a location-dependent cause for increased mortality rates. The 2018

experiment site near Amsterdam was located at the foot of a hill to the west and was bordered by winter wheat to the east. Water running off the hill would have accumulated at this location and contributed to nutrients washing out of the topsoil, which could have caused nutrient deficiencies and reduced plant vigor. Indeed, plant stands in 2018 had thin stems and plant height was shorter than in 2017. However, the reason for this appearance could not be determined with certainty and possible herbicide injury from spray drift from the adjacent winter wheat field was suspected, as well. This host phenotype may account for lower infestation rates at the experiment site in 2018, since WSS females prefer taller plants and wider stems for oviposition (Buteler et al. 2010; Buteler and Weaver 2012). The impact of location-dependent factors on plant fitness was further noted in relatively low grain yields in 2018, which were independent of insecticide, seeding rate and cultivar treatments. A high amount of variability in yield data could not be accounted for by the treatment variables in the study. Regardless of its cause, reduced plant fitness and thinner wheat stems could have caused higher larval mortality in 2018. Reduced survival rates due to a lack of nutrients essential for larval development may be considered (Achhami et al. 2020). Stem infestation and larval mortality was assessed at crop maturity and no notes were taken on the likely cause of death and developmental stage of larvae when death occurred. Based on multiple decrement life table analysis, Buteler et al. (2015) found that host plant resistance and parasitism by *Bracon* spp. are dominant causes of death of injurious larvae over the summer. Since death from parasitism was recorded separately in this study, the observed increased larval mortality may be more likely related to location- and year-specific interaction with the wheat host. However, due to a lack of information on host-related

parameters, such as stem solidness and diameter, it is not possible to determine a more specific cause of increased mortality rates in 2018 in this study.

Of the three insecticide treatments compared in this study, Thimet applications were consistently associated with increased larval mortality rates and reduced survival at crop maturity. The highest yields in 2017 and reduced numbers of wheat heads remaining in the plot after harvest were observed in Thimet-treated plots at both study sites, suggesting that this insecticide provides effective yield protection by suppressing WSS development in wheat stems. Application of Thimet into the soil and its systemic activity enables the absorption of the phorate active ingredient by the plant roots and translocation throughout the plant, including the stem lining tissue that larvae feed on (Wanner and Tharp 2015). Two application rates of Thimet were compared in the Big Sandy study and mortality rates were slightly lower at Thimet half-rate (2.8 kg ha^{-1}) compared to full-rate (5.6 kg ha^{-1}), although not statistically different. These results suggest that the lower application rate of Thimet may provide satisfying efficacy in WSS control, but further studies should be conducted to confirm this trend in different locations and under a broader range of conditions.

This study produced convincing evidence that the application of insecticide Mustang Maxx does not increase the likelihood of larval death in wheat stems or decrease larval survival at crop maturity. Grain yield from Mustang Maxx-treated plots were similarly low as those from untreated 'Reeder' control plots and a high incidence of wheat heads remaining in the research plots after harvest suggested a considerable degree of stem lodging. These results were expected owing to the foliar application of Mustang Maxx and its activity on the plant surface, where WSS larva would not encounter the

insecticide. Mustang Maxx is labeled to aid in the control of adult WSS (FMC 2018), suggesting that it could reduce stem infestation, but such an effect was not observed in this study.

Spring wheat treatment with foliar insecticide Lorsban-4E did not result in increased larval mortality rates compared to untreated ‘Reeder’ control in the Amsterdam study (Tab. 5.8). However, a consistent but statistically insignificant trend of increased larval mortality and decreased survival at crop maturity was observed in the Big Sandy study (Tab. 5.7). Lorsban-4E is an organophosphate insecticide with the same mode of action as Thimet, which may account for the increased probability of larval death. However, Lorsban-4E is applied as foliar spray and does not have systemic activity (Tab. 5.3), leaving to question how and where the active ingredient would come into contact with WSS larvae. Ultimately, stem lodging under Lorsban-4E treatment was as high as in untreated ‘Reeder’ control plots and grain yield was not different from the control treatment, at Big Sandy or Amsterdam. These findings suggest that Lorsban-4E does not protect wheat yield from WSS damage and should be considered unsuitable for the management of WSS.

Our study results demonstrated a high likelihood of larval death and a low probability of larval survival at crop maturity in untreated ‘Choteau,’ which was comparable to rates observed in response to Thimet treatment (Tab. 5.7). A low average number of wheat heads remaining in plots after harvest in 2017 suggest a reduced rate of stem lodging. Similar rates of larval mortality, survival at crop maturity, and stem lodging were observed for ‘Duclair’ in the Amsterdam cultivar study. Both ‘Choteau’ and ‘Duclair’ are WSS resistant owing to their solid-stem trait. Findings from this study agree

with previous observations that highlight the role of stem solidness in larval mortality (Buteler et al. 2015). Increased rates of larval mortality and reduced survival at crop maturity were observed in cultivar ‘WB Gunnison,’ as well. A significantly lower probability of stem infestation was estimated for ‘WB Gunnison,’ suggesting that this cultivar is less attractive for WSS oviposition. ‘WB Gunnison’ carries the ‘Conan’ allele at QTL *Qss.msub-3BL*, which has a dominant impact on stem solidness (Beres et al. 2011b; Heo et al. 2019). The ‘Conan’ allele is associated with temporal pith expression that causes high stem solidness during early plant development and reduced stem solidness during stem maturation (Talbert et al. 2014; Varella et al. 2016). As a result, mortality of WSS neonates and larvae is high in ‘Conan’-type stems. Moreover, WSS females showed reduced preference for ‘Conan’ plants compared to ‘Choteau’ in choice experiments (Varella et al. 2016). Results from this study highlight the effectiveness of resistant cultivars in mitigating WSS pressure, and stem solidness is a good alternative to chemical pest management.

There is an agronomic disadvantage of solid-stem cultivars, which have a lower yield potential in the absence of WSS. In 2017, despite high larval mortality rates and reduced stem lodging at Big Sandy and in the cultivar study at Amsterdam, grain yields of ‘Choteau’ were as low as ‘Reeder,’ which was severely affected by WSS infestation. Particularly in resource-limited environments such as the 2017 drought, there is a yield penalty to the solid-stem trait. While competitive yields from susceptible cultivars may be attractive, the long-term implications of the use of susceptible cultivars for WSS population development are important to consider. Pre-diapause larvae at the end of the feeding period are the source of adult WSS emerging in the following season (Achhami

et al. 2020; Peterson et al. 2011). High infestation and survival rates in susceptible cultivars may increase the risk of infestation and damage in the subsequent crop, perpetuating and increasing WSS populations. Increases in infestation rates from 10% - 15% in one year to as high as 80% in the following crop year have been reported (Farstad et al. 1945; Holmes 1982). Solid-stem cultivars reduce survival of pre-diapause larvae and negatively affect fecundity of sawflies, because smaller larvae tend to develop into smaller females that lay fewer eggs (Cárcamo et al. 2005; Morrill et al. 1994). Over time, the widespread use of solid-stem cultivars could reduce WSS populations. Larval survival probability in susceptible cultivar ‘Reeder’ at Amsterdam was more than twice as high compared to ‘Choteau’ and ‘Duclair’ in 2017, highlighting the different roles that these cultivars may play in WSS population growth. Interestingly, ‘WB Gunnison’ produced yields that exceeded those of all other cultivars. Our study results do not only demonstrate the effectiveness of ‘WB Gunnison’ in mitigating WSS pressure, but also highlight its competitive yield potential, making this cultivar particularly suited for high WSS pressure environments.

The increase in seeding density from 215 seeds m^{-2} to 430 seeds m^{-2} was associated with a moderate increase in the probability of stem infestation across cultivars in 2017 (Tab. 5.9). In 2018, the effect of seeding rate was dependent on cultivar and an increase in stem infestation was only observed for ‘Choteau.’ These observations stand in contrast to those reported by Luginbill and McNeal (1958), who observed a decrease in stem infestation and cutting at increased seeding densities of solid-stem and hollow-stem spring wheat cultivars. Instead, the observed increases in infestation rates may be associated with a higher number of primary tillers occurring in denser plant stands

(Geleta et al. 2002), which have a wider stem diameter and are preferred by WSS females for oviposition (Buteler and Weaver 2012). Our study results suggest that seeding rate may have a moderate influence on infestation and mortality rates, but the inconsistent and weak trends limit inferences at this point. More detailed studies are necessary to test a more nuanced range of seeding rates across a wider range of environmental scenarios. In addition, further parameters, such as number of tillers per area, stem diameter, and stem solidness should be considered to elucidate interaction between seeding rates and WSS infestation.

The number of kernels per head and kernel weight are two components that determine grain yield (Chen et al. 2008). In this study, we evaluated how infestation status and larval survival may affect these yield components. Our results showed that the average number of kernels per head was higher in infested stems than uninfested stems. Higher kernel count in infested stems may be associated with the WSS's preference for the main stem and larger diameter tillers (Morrill et al. 1992), which typically produce more kernels per head (Cook and Veseth 1991). Our results indicate that stem infestation with WSS larvae does not reduce the number of kernels per spike. However, TKW across year-sites was more frequently decreased in infested wheat stems, where pre-diapause larvae were detected. Decreased kernel weights are likely associated with continued feeding activity of larvae, which damages the vascular tissue in the stems, impedes water and nutrient transport and drains carbohydrates that would otherwise be translocated to the grain (Delaney et al. 2010; Macedo et al. 2007; Morrill et al. 1992). In contrast, no such larval sink exists in uninfested stems or ceases at some point during plant development, due to larval death. In our study, reductions in TKW in infested stems with

pre-diapause larvae ranged between 4% and 11% compared to infested stems with dead larvae. Seamans et al. (1944) reported yield loss in wheat heads of 10% due to stem mining activity of WSS larvae. Our results suggest that the reduction in head weight is at least in part due to a reduction in grain weight.

Two parasitoids of WSS larvae are known to occur in Montana, *B. cephi* and *B. lissogaster* (Morrill 1998, Runyon et al. 2002, Weaver et al. 2005) and parasitism has been shown to be an important contributor to larval mortality (Peterson et al. 2011). Parasitism rates in this study were higher in 2017 compared to 2018 across all study sites. Increased parasitism is likely related to higher infestation rates in 2017, increasing the likelihood of parasitoids finding WSS larvae within wheat stems. Parasitism rates were higher at the Amsterdam site compared to Big Sandy, suggesting a larger population of parasitoids established at Amsterdam. These findings further highlight that the potential of parasitoid complementing WSS control is dependent on the local presence and size of parasitoid populations, as well as environmental conditions and WSS abundance (Holmes et al. 1963). Across study sites and years, parasitism rates were distinctly lower than larval death occurring from other causes, suggesting that WSS control through parasitoids is less effective than the use of resistant cultivars. Overall, parasitism rates were increased where larval mortality due to other reasons was low. In Amsterdam in 2017, evidence for an insecticide effect on the probability of parasitism was found. It seems likely that this effect is related to increased larval death rates under Thimet treatment resulting in fewer alive WSS larvae that have grown large enough to be a suitable host for parasitoids, rather than insecticide applications negatively affecting adult parasitoids. If the latter was the case, decreased rates of parasitism would have been expected under

Mustang Maxx and Lorsban-4E treatment, as well. Parasitism rates were also dependent on cultivar choice and there was a similar trend of increased parasitism where larval mortality was low. Parasitism occurred most frequently in hollow-stem cultivar ‘Reeder’ and was less frequent in solid-stem wheat cultivars. Similar findings were reported by Buteler et al. (2015), who compared parasitism rates of injurious larvae between cultivars ‘Reeder’ and ‘Choteau.’ Overall, results from this study do not suggest a negative effect of insecticide treatments on parasitoids. This assessment is based on indirect observations. Therefore, inferences are limited, and our results cannot rule out a negative effect of insecticide applications on parasitoid populations. Further studies are needed to directly evaluate real-time effects of insecticide application on parasitoid presence and parasitism incidence in wheat stems.

Insecticide Impact on Beneficial Insect Species.

Mites, thrips, and aphids are common in small grain crops (Buntin et al. 2007). The detection of WCM was of particular interest due to their role as vector of viruses in the WSM complex and our interest in assessing the relationship between WSS damage, volunteer wheat emergence, and WSM disease risk.

Mites were occasionally detected in samples, but they were identified as predatory mites that typically inhabit the soil. No WCMs were found in any of the samples. It is likely that Berlese funnels are not well suited for collecting WCM. This specific extraction method is based on alive arthropods crawling away from a heat source that is placed above the plant material, thereby falling into a collection jar. However, WCMs are extremely susceptible to desiccation (Nault and Styer 1969; Sabelis 1996) and can crawl only a few centimeters per hour (Salome et al. 1964). It is likely that the WCMs would

have desiccated faster than they could have moved away from the heat source. Moreover, their small size and white color makes it difficult to detect WCMs among debris and other specimen at the magnification of a stereomicroscope. To assess the potential impact of insecticide applications on WCM populations, wheat tillers should be screened directly under the stereomicroscope.

Across site-years, thrips were the most abundant taxonomic group detected in samples. Thrips larvae were detected most commonly, while adult thrips were rare. This was expected since adult thrips can fly and are therefore more mobile. Thrips density was low and less than 10 specimens per 100 tillers were detected across most samples. The highest thrips density observed in our study was 25 thrips per 100 tillers at Amsterdam in 2017 (Tab. 5.12). In comparison, larval thrips densities in a Nebraska field survey of winter wheat ranged from 0.25 to 113.7 thrips per 25 tillers. Differences in thrips densities between our study and those reported from the Nebraska survey may be associated with differences in crop development, environmental and agroecosystem-related factors.

On average, thrips densities at the Amsterdam site were higher than at Big Sandy. These differences may be explained by the timeliness with which samples from the Big Sandy site could be prepared for extraction in Berlese funnels. It is likely, that some portion of thrips on the sampled plants may have escaped or expired during transportation and could not be extracted. Difference in thrips densities between treatment groups were detected at Big Sandy in 2018, when thrips incidence in ‘Choteau’ control plots was significantly higher than in Thimet- and Lorsban-4E-treated plots (Tab. 5.12). However, these differences occurred even before foliar insecticides were applied, suggesting that it

may be related to other factors that were not accounted for in the analysis. No further evidence for an effect of insecticide treatment on thrips incidence in spring wheat was detected in this study. A significant effect of sampling time on thrips incidence was observed at both study sites in 2017, suggesting crop developmental stage or environment may be more influential for thrips incidence than insecticide treatment.

Our results do not warrant the conclusion that insecticide applications do not affect thrips populations. Experiments were conducted in an open agricultural system. Potential arthropod movement in and out of the experimental system could not be controlled and confounding factors may have influenced response variables. Moreover, intervals between sampling times ranged between seven and 24 dpa. The life cycle of the grain thrips, *Limothrips cerealium* (Haliday), which is a common species occurring in small grain crops, is completed within 30 to 50 days, depending on environmental conditions, and this species can have two generations per year (Buntin et al 2007). It is possible that the sampling period encompassed two generations, which could have contributed to the fluctuation in thrips densities over time. The efficacy of contact insecticides like Lorsban-4E and Mustang Maxx would be expected to decline over time and pre-harvest interval information for both products suggest a loss of efficacy within 14 dpa (Dow Agrosience 2014; FMC Corporation 2018). A one-time application of foliar insecticides is therefore unlikely to result in the sustained suppression of thrips populations over several weeks. Stilwell (2009) reported variation in thrips densities between sampling in mid-May to mid-June and noted a general trend of declining larval populations when wheat began to senesce. The latest sampling times in our study coincided with spring wheat entering the flowering stage and it is likely that plant

development influenced thrips densities. Further research efforts addressing the implications of insecticide treatment for non-target organisms should consider shorter sampling intervals, focusing on specific crop growth stages and different sampling techniques. Alternatively, studies focused on a specific taxonomic group of interest may better be conducted in controlled environments, such as greenhouse or growth chamber settings.

Our results demonstrate that resistant cultivars are effective in mitigating WSS damage to spring wheat and are comparable to the use of the systemic insecticide phorate (Thimet-20G), without posing a potential risk to human and environmental health associated with organophosphate insecticides. Moreover, ‘WB Gunnison’ produces competitive yields under WSS pressure that compare to those of hollow-stem cultivar ‘Reeder,’ making it an attractive cultivar to be grown in high WSS pressure environments. Cultural management approaches should be given preference over chemical strategies and are currently the single most effective management option.

Wheat stem sawfly parasitism can complement mortality rates associated with stem solidness, but the relative contribution of parasitism is strongly dependent on the size and condition of local parasitoid populations and environmental conditions (Holmes et al. 1963). Cultural practices should be implemented to conserve and promote parasitoid populations. Increasing stubble height during harvest by cutting stems approximately 20 cm above ground protects the first generation of parasitoids, which overwinter in wheat stubble between seasons. Reduced tillage practices are further associated with higher parasitism rates and reduced stem cutting (Runyon et al. 2002). Moreover,

avoiding insecticide use during the peak flight period of adult parasitoids reduces the risk of potentially harmful side-effects on these beneficial insects (Meers 2005).

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Tables and Figures

Table 5.1. Summary of insecticide and control treatments included in the insecticide field studies at the Big Sandy and Amsterdam trial sites, MT, in 2017 and 2018.

Treatment	Big Sandy	Amsterdam
Reeder control	+	+
Reeder + Thimet Full	+	+
Reeder + Thimet Half	+	
Reeder + Lorsban 4E	+	+
Reeder + Mustang Maxx	+	+
Choteau control	+	

Table 5.2. Spring wheat cultivars and their attributes considered in the wheat stem sawfly variety study near Amsterdam, MT, in 2017 and 2018.

Cultivar	PI	WSS- related characteristics ^a
Choteau	633974	Solid-stem; resistant to WSS.
Duclair	660981	Less solid-stem than Choteau; resistant to WSS.
WB Gunnison	665064	Intermediate stem solidness; resistant to WSS.
Reeder	613586	Hollow-stem; susceptible to WSS.

^a Information on cultivar traits were obtained from Heo et al. (2019).

Table 5.3. Characterization of insecticides compared in field studies at Big Sandy and Amsterdam, MT, in 2017 and 2018 for their efficacy in wheat stem sawfly (WSS) control.

Trade name	Active ingredient	IRAC	Control of WSS	Mode of action
Lorsban 4E	Chlorpyrifos	1B	Not labeled for WSS control	Organophosphate; non-systemic; contact and stomach poison.
Mustang Maxx	Zeta-Cypermethrin	3A	WSS adult ^a	Pyrethroid; non-systemic; contact and stomach poison.
Thimet 20G	Phorate	1B	WSS larva ^b	Organophosphate; systemic; contact and stomach poison.

^a “Aids in control”, according to product label.

^b Montana Department of Agriculture issued a 24 (C) special local needs registration label for control of WSS in spring and winter wheat crops in May 2015, which was valid until 31 Dec. 2019 (Wanner and Tharp 2015).

Table 5.4. Overview and description of wheat stem sawfly (WSS) infestation categories used to assess the effect of chemical and cultural control measures in WSS management.

Infestation	WSS larva fate	Description
Uninfested		No trace of infestation within wheat stem.
Infested	Larva dead	Some traces of infestation; larva died at early stages of development.
	Larva parasitized	Traces of infestation; larva died as a result of parasitism.
	Pre-diapause larva	Heavy traces of infestation; larva in (pre-)diapause stage in the base of stem; chamber formed; stem lodged or still attached.

Table 5.5. Impact of insecticide treatments on the probability of wheat stem sawfly infestation of spring wheat stems based on the field trials at Big Sandy and Amsterdam in 2017 and 2018.

Treatment	Probability *					
	Big Sandy site			Amsterdam site		
	2017	2018	2017		2018	
Reeder control	0.52 (0.42 – 0.62)	0.37 (0.28 – 0.48)	0.90 (0.84 – 0.94)	a	0.49 (0.37 – 0.62)	a
Thimet Half	0.45 (0.35 – 0.55)	0.32 (0.23 – 0.42)				
Thimet Full	0.44 (0.34 – 0.54)	0.26 (0.19 – 0.36)	0.78 (0.69 – 0.85)	b	0.19 (0.14 – 0.26)	b
Lorsban 4E	0.41 (0.30 – 0.53)	0.35 (0.26 – 0.45)	0.91 (0.86 – 0.94)	a	0.58 (0.49 – 0.67)	a
Mustang Maxx	0.46 (0.36 – 0.56)	0.32 (0.24 – 0.42)	0.85 (0.78 – 0.90)	ab	0.65 (0.56 – 0.72)	a
Choteau control	0.39 (0.28 – 0.51)	0.34 (0.25 – 0.45)				

* Data in parenthesis represent the 95% confidence interval. Estimates followed by the same letters within a column and year are not statistically different based on Tukey's multiple comparison at the 0.05 probability level.

Table 5.6. Impact of cultivar and seeding rate on the probability of wheat stem sawfly infestation of spring wheat stems based on the Amsterdam trial in 2017 and 2018.

		Probability*			
Seeding Rate [†]	Cultivar	2017		2018	
Recommended	Reeder	0.92 (0.83 – 0.96)	ab	0.64 (0.50 – 0.76)	a
	Duclair	0.86 (0.74 – 0.93)	ab	0.34 (0.22 – 0.48)	bc
	Choteau	0.83 (0.70 – 0.91)	bc	0.34 (0.22 – 0.48)	bc
	Gunnison	0.69 (0.52 – 0.83)	c	0.10 (0.06 – 0.17)	d
Increased	Reeder	0.95 (0.89 – 0.98)	a	0.54 (0.40 – 0.68)	ab
	Duclair	0.91 (0.82 – 0.95)	ac	0.30 (0.19 – 0.43)	c
	Choteau	0.89 (0.79 – 0.94)	ab	0.58 (0.43 – 0.71)	a
	Gunnison	0.79 (0.64 – 0.89)	bc	0.11 (0.06 – 0.19)	d

* Data in parenthesis represent the 95% confidence interval. Estimates followed by the same letters within a column and year are not statistically different based on Tukey's multiple comparison at the 0.05 probability level.

† Recommended seeding rate: 215 seeds m⁻²; Increased seeding rate: 430 seeds m⁻².

Table 5.7. Impact of insecticide treatments on wheat stem sawfly larval fate in spring wheat stems and effects on grain yield and stem lodging based on the Big Sandy trial in 2017 and 2018.

Probability *										
Year	Treatment	Larva dead		Larva parasitized		Pre-diapause larva		Grain yield	Heads m ⁻²	
-----g m ⁻² -----										
2017										
	Reeder control	0.30 (0.21 – 0.42)	a	0.08 (0.05 – 0.14)	a	0.65 (0.62 – 0.76)	c	215.2 ± 14.6†	ac	96 ± 14†
	Thimet Half	0.44 (0.31 – 0.58)	ab	0.12 (0.07 – 0.19)	a	0.43 (0.35 – 0.51)	ab	232.7 ± 15.4	bc	69 ± 15
	Thimet Full	0.59 (0.45 – 0.72)	b	0.06 (0.03 – 0.12)	a	0.37 (0.29 – 0.45)	a	246.8 ± 15.4	c	60 ± 15
	Lorsban 4E	0.36 (0.22 – 0.52)	ab	0.19 (0.11 – 0.30)	a	0.44 (0.34 – 0.54)	ab	190.8 ± 17.0	ab	82 ± 17
	Mustang Maxx	0.25 (0.16 – 0.38)	a	0.16 (0.10 – 0.25)	a	0.54 (0.49 – 0.65)	bc	190.0 ± 15.4	ab	88 ± 15
	Choteau control	0.62 (0.46 – 0.77)	b	0.05 (0.02 – 0.12)	a	0.34 (0.24 – 0.44)	a	171.0 ± 17.0	a	38 ± 17
2018										
	Reeder control	0.41 (0.28 – 0.54)	ab	0.04 (0.02 – 0.09)		0.54 (0.40 – 0.68)	bc	325.7 ± 12.3	a	13 ± 3
	Thimet Half	0.53 (0.41 – 0.64)	bcd	0.04 (0.01 – 0.09)		0.42 (0.31 – 0.55)	ac	394.6 ± 12.3	b	19 ± 3
	Thimet Full	0.65 (0.54 – 0.75)	cd	0.02 (0.01 – 0.05)		0.32 (0.22 – 0.44)	ab	412.6 ± 12.3	b	14 ± 3
	Lorsban 4E	0.51 (0.40 – 0.62)	ad	0.06 (0.02 – 0.12)		0.41 (0.30 – 0.53)	bc	395.5 ± 12.3	b	12 ± 3
	Mustang Maxx	0.30 (0.21 – 0.41)	a	0.04 (0.01 – 0.10)		0.64 (0.52 – 0.74)	c	379.5 ± 12.3	b	11 ± 3
	Choteau control	0.65 (0.54 – 0.74)	c	0.06 (0.02 – 0.13)		0.25 (0.17 – 0.36)	a	375.6 ± 12.3	b	12 ± 3

* Data in parenthesis represent the 95% confidence interval. Estimates followed by the same letters within a column and year are not statistically different based on Tukey's multiple comparison at the 0.05 probability level.

† Mean estimate ± SE.

Table 5.8. Impact of insecticide treatments on wheat stem sawfly larval fate in spring wheat stems and effects on grain yield and stem lodging based on the Amsterdam trial in 2017 and 2018.

Foliar feeding based on the Amsterdam trial in 2017 and 2018:											
Year	Treatment	Probability *						Grain yield	Heads m ⁻²		
		Larva dead		Larva parasitized		Pre-diapause larva					
-----g m ⁻² -----											
2017											
	Reeder control	0.31 (0.24 – 0.39)	a	0.30 (0.19 – 0.43)	b	0.37 (0.30 – 0.45)	b	151.7 ± 13.8†	ab	37 ± 8†	ab
	Thimet Full	0.95 (0.92 – 0.97)	b	0.03 (0.02 – 0.06)	a	0.02 (0.01 – 0.04)	a	172.6 ± 13.1	a	24 ± 8	a
	Lorsban 4E	0.32 (0.26 – 0.39)	a	0.31 (0.22 – 0.40)	b	0.36 (0.30 – 0.44)	b	157.5 ± 13.1	ab	48 ± 8	b
	Mustang Maxx	0.30 (0.24 – 0.37)	a	0.29 (0.21 – 0.38)	b	0.40 (0.33 – 0.47)	b	142.3 ± 13.1	b	44 ± 8	ab
2018											
	Reeder control	0.75 (0.45 – 0.96)	a	0.18 (0.11 – 0.29)		0.21 (0.14 – 0.31)	b	244.7 ± 16.9		38 ± 5	b
	Thimet Full	0.90 (0.83 – 0.95)	b	0.07 (0.03 – 0.15)		0.02 (0.01 – 0.07)	a	246.7 ± 16.9		13 ± 5	a
	Lorsban 4E	0.63 (0.56 – 0.69)	a	0.11 (0.07 – 0.16)		0.26 (0.21 – 0.31)	b	247.5 ± 16.9		35 ± 5	b
	Mustang Maxx	0.68 (0.63 – 0.74)	a	0.12 (0.08 – 0.18)		0.18 (0.14 – 0.23)	b	261.4 ± 16.9		44 ± 5	b

* Data in parenthesis represent the 95% confidence interval. Estimates followed by the same letters within a column and year are not statistically different based on Tukey's multiple comparison at the 0.05 probability level.

† Mean estimate ± SE.

Table 5.9. Impact of cultivar and seeding rate on wheat stem sawfly larval fate in spring wheat stems and effects on grain yield and stem lodging based on the Amsterdam trial in 2017 and 2018.

Stem rodding based on the Amsterdam trial in 2017 and 2018.												
Year	Treatment		Probability *						Grain yield -----g m ⁻² -----	Heads m ⁻²		
	Seeding Rate†	Cultivar	Larva dead		Larva parasitized		Pre-diapause larva					
2017												
	Recommended											
		Reeder	0.38 (0.32 – 0.45)	a	0.22 (0.18 – 0.26)	c	0.38 (0.29 – 0.49)	b	220.6 ± 17.3‡	a	41 ± 5‡	b
		Duclair	0.69 (0.63 – 0.74)	bc	0.14 (0.12 – 0.18)	ab	0.15 (0.10 – 0.22)	a	220.8 ± 17.3	a	22 ± 5	a
		Choteau	0.76 (0.71 – 0.81)	c	0.10 (0.08 – 0.13)	a	0.13 (0.09 – 0.19)	a	220.0 ± 17.3	a	20 ± 5	a
		Gunnison	0.60 (0.54 – 0.67)	b	0.19 (0.15 – 0.23)	bc	0.19 (0.13 – 0.27)	a	295.1 ± 17.3	b	22 ± 5	a
2018												
	Recommended											
		Reeder	0.64 (0.53 – 0.74)	a	0.16 (0.12 – 0.21)		0.14 (0.11 – 0.18)	b	259.4 ± 16.1		31 ± 3	b
		Duclair	0.86 (0.78 – 0.92)	bc	0.09 (0.06 – 0.13)		0.04 (0.03 – 0.07)	a	255.0 ± 16.1		16 ± 3	a
		Choteau	0.86 (0.78 – 0.92)	bc	0.09 (0.06 – 0.13)		0.07 (0.05 – 0.10)	a	270.8 ± 16.1		15 ± 3	a
		Gunnison	0.79 (0.63 – 0.89)	ab	0.07 (0.04 – 0.14)		0.05 (0.02 – 0.10)	a	302.4 ± 16.1		10 ± 3	a
	Increased											
		Reeder	0.75 (0.65 – 0.83)	ac								
		Duclair	0.85 (0.76 – 0.91)	bc								
		Choteau	0.81 (0.69 – 0.88)	ab								
		Gunnison	0.94 (0.85 – 0.98)	bc								

* Data in parenthesis represent the 95% confidence interval. Estimates followed by the same letters within a column and year are not statistically different based on Tukey's multiple comparison at the 0.05 probability level.

† Estimates shown only for recommended seeding rate present averages across both seeding rates, due to a lack of evidence for a significant seeding rate effect. Recommended seeding rate: 215 seeds m⁻²; Increased seeding rate: 430 seeds m⁻².

‡ Mean estimate ± SE.

Table 5.10. Impact of stem infestation and wheat stem sawfly survival on spring wheat yield components*.

Stem infestation	Kernels per head											
	Insecticide Big Sandy				Insecticide Amsterdam				Cultivar Amsterdam†			
	2017		2018		2017		2018		2017		2018	
Not infested	19 ± 1	a	22 ± 1	a	16 ± 1	a	20 ± 1	a	18 ± 1	a	17 ± 1	a
Larva dead	29 ± 1	b	27 ± 1	b	26 ± 1	b	25 ± 1	b	25 ± 1	b	20 ± 1	b
Pre-diapause larva	28 ± 1	b	27 ± 1	b	27 ± 1	b	26 ± 1	b	23 ± 1	b	21 ± 1	b

Stem infestation	Thousand kernel weight											
	g											
	2017		2018		2017		2018		2017		2018	
Not infested	20.0 ± 0.6	a	18.9 ± 0.5	ab	17.2 ± 0.8	a	31.6 ± 0.3	b	21.4 ± 0.6		34.4 ± 0.3	b
Larva dead	22.8 ± 0.6	c	19.6 ± 0.5	b	20.3 ± 0.7	b	32.3 ± 0.3	b	23.6 ± 0.6		34.1 ± 0.3	b
Pre-diapause larva	21.8 ± 0.6	b	18.4 ± 0.5	a	18.0 ± 0.8	a	28.6 ± 0.4	a	20.4 ± 0.6		31.1 ± 0.4	a

* Mean estimate ± SE. Estimates followed by the same letters within a column and year are not statistically different based on Tukey's multiple comparison at the 0.05 probability level.

† Estimates account for cultivar and seeding rate effects.

Table 5.11. Evidence for sampling time and insecticide treatment effects on thrips density (the number of thrips per spring wheat tiller) at Big Sandy and Amsterdam, MT, in 2017 and 2018 based on ANOVA, accounting for repeated measures.

Variable	Big Sandy site						Amsterdam site		
	2017			2018			2017		
	χ^2	df	Pr ($>\chi^2$)	χ^2	df	Pr ($>\chi^2$)	χ^2	df	Pr ($>\chi^2$)
Sampling time (A)	48.3	2	< 0.001	1.7	1	0.21	38.4	2	< 0.001
Treatment (B)	7.3	5	0.20	17.3	5	0.004	2.0	3	0.57
A x B	14.5	10	0.15	6.3	5	0.28	3.0	6	0.81
R ² (conditional)	0.51			0.27			0.48		

Table 5.12. Impact of insecticide applications on the number of thrips per 100 tillers of spring wheat at Big Sandy and Amsterdam, MT, in 2017 and 2018.

2017, in 2017 and 2018.

		Number of thrips per 100 tillers*					
Year	Treatment	Big Sandy site			Amsterdam site		
		- 1 dpa†	7 dpa	21 dpa	-1 dpa	12 dpa	24 dpa
2017							
	Reeder control	2 ± 1.4	1 ± 1.4	7 ± 1.4	19 ± 4.5	11 ± 4.5	5 ± 4.5
	Thimet Half	3 ± 1.6	1 ± 1.6	7 ± 1.6			
	Thimet Full	3 ± 1.6	0 ± 1.6	6 ± 1.6	25 ± 4.5	7 ± 4.5	4 ± 4.5
	Lorsban 4E	3 ± 1.8	0 ± 1.8	12 ± 1.8	19 ± 4.5	1 ± 4.5	2 ± 4.5
	Mustang Maxx	5 ± 1.6	2 ± 1.8	4 ± 1.6	24 ± 4.5	4 ± 4.5	3 ± 4.5
	Choteau control	4 ± 1.8	4 ± 1.8	11 ± 1.8			
	Average	3 ± 0.7	1 ± 0.7	8 ± 0.7	23 ± 2.3	6 ± 2.3	3 ± 2.3
2018							
		-1 dpa	12 dpa				
	Reeder control	3 ± 1.7	8 ± 1.7				
	Thimet Half	2 ± 1.7	3 ± 1.7				
	Thimet Full	1 ± 1.7	5 ± 1.7				
	Lorsban 4E	2 ± 1.7	2 ± 1.7				
	Mustang Maxx	4 ± 1.7	3 ± 1.7				
	Choteau control	9 ± 1.7	7 ± 1.7				
	Average	3 ± 0.7	5 ± 0.7				

* Mean estimate ± SE.

† Days post foliar insecticide application.

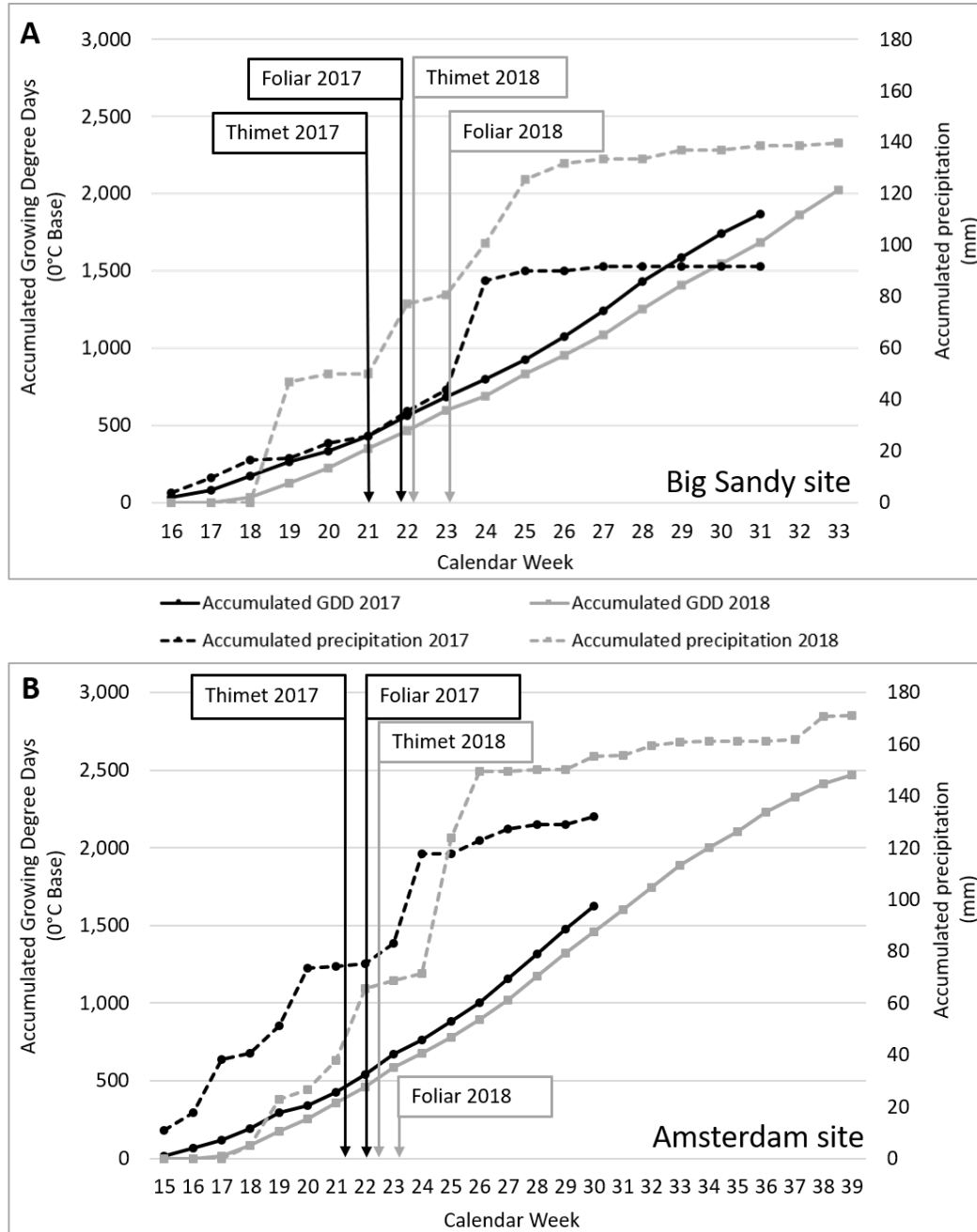


Figure 5.1. Accumulated growing degree days (GDD) and precipitation from planting to harvest in 2017 and 2018 at the Big Sandy and Amsterdam research sites. Daily temperature and precipitation amount were retrieved from an online database (<https://www.wunderground.com/>). “Thimet” and “Foliar” boxes indicate application time of Thimet-20G systemic insecticide and Lorsban 4E and Mustang Maxx foliar insecticides in the respective years. **A)** Weather data for Big Sandy site from station KMTBIGSA. **B)** Weather data for Amsterdam site from station KBZN.

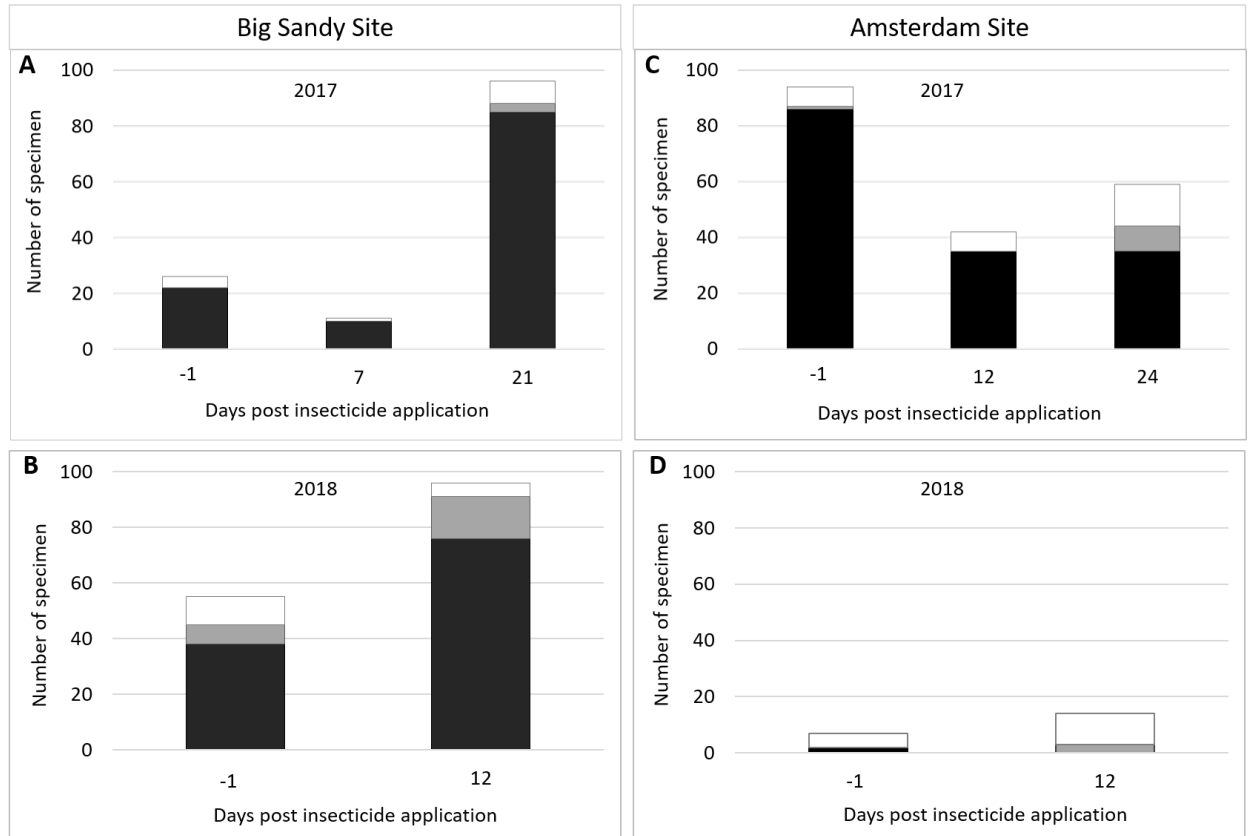


Figure 5.2. Total number of arthropods and relative abundance of taxonomic groups collected from spring wheat plants before and after foliar insecticide application at Big Sandy and Amsterdam, MT, in 2017 and 2018. For each sampling time, the total number of specimens across all treatment plots and replications is summarized. Black column – thrips; gray – aphids; white – other.

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CHAPTER SIX

AWaRe: AN ONLINE LEARNING TOOL FOR THE ASSessment OF WHEAT
STREAK MOSAIC RISK

Wheat streak mosaic is an economically important disease of cereal crops in Montana. Its management relies on preventive strategies that reduce the risk of infection. Here we present the online learning tool “AWaRe” that identifies some of the most important factors contributing to WSM disease risk in Montana.

Wheat streak mosaic (WSM) is a viral disease affecting spring and winter wheat, barley, durum, and other cereal grain crops and grassy weeds in Montana and across the Great Plains region. There are at least three viruses known to cause WSM, of which *Wheat streak mosaic virus* is most prevalent. Viruses of the WSM complex are transmitted by the wheat curl mite (WCM; *Aceria tosichella* Keifer). The disease causes yellow streaking and mosaic-like patterns on leaves and infected plants may be stunted. The younger plants are at the time of infection, the more severe disease symptoms and yield losses will be. The WSM disease cycle is shown in Fig. 6.1. Refer to the Extension MontGuide “Cereal Viruses of Importance in Montana” for more information on WSM disease in Montana.

There are no pesticides registered for the control of WCM or WSM viruses. Management of WSM disease is dependent on the use of tolerant varieties and agricultural practices that reduce the risk of the crop becoming infected. Preventive

management strategies become more important the higher the risk of WSM disease.

AWaRe is an online learning tool that assists users in identifying and evaluating the most important factors contributing to WSM disease risk in Montana and the Northern Great Plains. This publication introduces the AWaRe tool and describes 1) when and how the tool can be used, 2) what factors are most influential for WSM risk in Montana, and 3) some constraints of the AWaRe tool. AWaRe can be accessed online at [https://tim-msu-ecol.shinyapps.io/Wheat Streak Mosaic Risk MT](https://tim-msu-ecol.shinyapps.io/Wheat_Streak_Mosaic_Risk_MT).

When and How Should AWaRe Be Used?

AWaRe is designed to help users understand which factors are influential for WSM disease risk. The factors are presented through five interactive questions, which are associated with numeric scores that demonstrate the relative importance of each factor to the overall disease risk. AWaRe can be used to assess the specific conditions in a field of interest or to analyze WSM disease risk in hypothetical scenarios. AWaRe focuses primarily on WSM disease in winter wheat. Winter wheat is the most important crop for the disease complex due to its high risk as host to both WCM and WSM viruses and its presence in the agricultural landscape for three quarters of the year. However, the tool can also be applied to spring wheat and other host crops of WSM disease. Moreover, AWaRe focuses on those components of WSM risk that can be assessed before winter wheat planting. Evaluation of WSM-promoting factors during late summer provides an opportunity to implement management strategies to mitigate disease risk before planting of the new crop.

How Does AWaRe Work?

AWaRe was developed to simplify an exhaustive review of the scientific literature on the WSM disease complex. In simple terms, WSM disease occurs if a susceptible host, the viral pathogen, and the WCM vector are present and environmental conditions are conducive for disease development. Moreover, virus spread is tightly associated with WCM movement, which is in turn dependent on conditions that promote WCM population growth, dispersal, and survival. The likelihood of WSM disease spreading from one crop season to the next is strongly influenced by the time of occurrence and abundance of summer hosts for mites and virus. The five questions in the AWaRe tool assess WSM presence, WCM dispersal success, and survival of the mite-virus complex between wheat crops. A screenshot of the AWaRe tool appearance is shown in Fig. 6.2.

Question 1: In the previous season, did you observe wheat streak mosaic symptoms in the field to be planted?

This question assesses whether mites and virus were present in the location of interest during the previous season. The more widespread WSM symptoms were, the higher the WSM risk score will be (Fig. 6.1). In Montana, severe WSM infections occur sporadically over time and tend to be a local, not statewide, problem when they do occur. A high incidence of symptomatic plants locally, where a susceptible crop is to be planted, increases the likelihood of WSM. It is less likely the disease will blow in from outside the local area and cause extensive losses in the same year. This question highlights that the WSM disease cycle is spread over successive crop seasons.

Question 2: What proportion of fields within five miles of your field are wheat?

This question takes into consideration what proportion of susceptible crops are near the location of interest. If there is a high proportion of susceptible crops nearby, there is a greater likelihood they will host the virus and WCMs that spread disease. This question focuses specifically on wheat because it is the best host for mites and virus. Wheat supports large WCM populations and is susceptible to all viruses of the WSM disease complex. The more abundant wheat fields are in the vicinity, the higher the WSM risk score will be. However, even if wheat fields are rare in the environment ($< 5\%$), a minimal risk score will still occur. This is because we assume that WCMs and virus are always present in the environment. Wheat curl mites are wind-dispersed and can travel distances of 2 miles and possible farther if wind speeds are high (> 20 mph). For a conservative estimate that errs on the side of overestimating WSM disease risk, a range of five miles is considered in this question.

Question 3: Did you observe volunteer wheat emerging as a result of hail damage and/or wheat stem sawfly infestation?

This question emphasizes the important role of volunteer wheat in the WSM disease cycle and highlights how hail events and wheat stem sawfly infestation can increase volunteer wheat abundance. The more volunteer wheat there is present in the environment, the higher the resulting WSM risk score will be.

Volunteer wheat that emerges as the wheat crop is maturing (pre-harvest volunteer wheat) is an important summer hosts for WCMs and viruses. The more volunteer wheat present in the immediate vicinity of WCM source plants, the more likely

dispersing WCMs are to reach a suitable host on which they can survive between crops. Moreover, research shows that volunteer wheat seedlings can be directly infested by WCMs, which feed on maturing wheat kernels as they dislodge during hail events. Direct colonization is most likely if grain is dislodged at the soft and hard dough stage. The timing of hail events occurring in relation to crop stage is important for volunteer wheat establishment and disease risk. Wheat stem sawfly infestation is another cause for mature wheat seeds landing on the ground and may therefore contribute to WSM risk. In contrast to hailstorms, wheat stem sawfly-associated lodging does not necessarily coincide with precipitation. Wheat stem sawfly infestation during crop years with below-average precipitation in the summer months may not contribute to WSM risk, while it may have a significant impact on pre-harvest volunteer wheat emergence and resulting WSM risk during a wet harvest season.

Question 4: How did precipitation throughout the season impact grassy weeds in and around your field?

Grassy weeds can serve as summer hosts for the mite-virus complex. Cheatgrass (downy brome), field brome, green foxtail (green bristlegrass), jointed goatgrass, and rye brome can host both WCMs and viruses. The most significant of these in Montana is cheatgrass. Although it is not as good of a host of the virus or mite as wheat, it is highly prevalent. Since cheatgrass emerges over the entire growing season, it can serve as a green host plant at any time. The more abundant grassy hosts are, the more likely WCM survival is.

Question 5: Are volunteer wheat and grassy weeds in your field managed so they are dead prior to planting?

This question focuses on the importance of managing volunteer wheat and other summer hosts of the WSM complex ('green bridge') before planting of the new crop. Managing the green bridge is of crucial importance for interrupting the WSM disease cycle and reducing WSM disease risk. Research shows that even low initial WCM numbers in a wheat field can cause high infection rates of 95% under favorable conditions. The goal of green bridge termination is to eliminate all potential source plants of WCMs and virus to reduce WCM population size and minimize the number of dispersing mites in the environment.

The optimal method for managing the green bridge depends on environmental conditions and the time until planting of the new wheat crop. Mechanical forms of volunteer wheat and weed control by tillage (blading, disking, rod-weeding) or swathing can be very effective. Particularly when conditions are dry and hot, tilling will rapidly kill host plants within a few days and eliminate WCM populations. In contrast, under cool and wet conditions, plant death may not occur as rapidly and WCM populations will likely decline at a slower pace. Chemical control of the green bridge is most commonly achieved by glyphosate. In contrast to tillage, cool and wet conditions are ideal for the rapid termination of plants with glyphosate. However, hot and dry conditions reduce the effectiveness of glyphosate, slowing plant death. In addition, WCM survival apart from a host needs to be considered. Under cool and humid conditions, mites have been shown to survive for as long as seven days without a host, while high temperatures and low relative humidity decreases WCM survival to less than a day.

In conclusion, a minimum time window of at least two weeks between green bridge termination and planting of the new wheat crop should be implemented to plant new crops into bare ground. Therefore, the WSM risk score in AWaRe increases as the plant termination window is decreased.

From the AWaRe Questions to Overall WSM Risk.

The individual risk scores associated with selected answers are presented in a summary table (see Fig. 6.2) in the AWaRe user interface. Total WSM risk is calculated by summation of the individual scores and termed “Your Risk Total.” It is contrasted with the highest risk score achievable (“Max Risk Total” = 22). “Your WSM risk” is further presented as a percentage relative to the maximum achievable risk score and visualized in a color-coded risk gauge, ranging from low to high. Volunteer wheat plays a pivotal role in the perpetuation of WSM disease between wheat crops and green bridge control will be increasingly important, the more abundant volunteer wheat is. The risk score associated with question 3 is therefore weighted higher in the total risk calculation. Moreover, the contribution of question 5 towards total risk is dependent on volunteer wheat presence and increases the more abundant volunteer wheat is in the environment.

What Other Factors Are Important for WSM Disease Risk?

The AWaRe tool focuses on those factors influencing WSM disease risk, which can be assessed before planting of the new wheat crop. However, several other factors are similarly important for disease spread and development. **Season length and fall temperatures** are important factors that influence WCM activity and symptom

development. Wheat curl mite dispersal typically stops when temperatures decrease below 10 °C. A long fall season with mild temperatures can greatly increase WSM disease risk. **Planting date** is an important consideration for WSM disease management. The earlier winter wheat is planted, the longer it may be exposed to dispersing WCMs. Infection early during plant development results in severe symptoms and yield loss. Postponing winter wheat planting to later in the fall will become more important if host plants, such as infected summer cereal crops, are upwind of the wheat field. Moreover, planting dates should be coordinated with **green bridge management efforts**. For summer cereal crops, later planting dates may increase WSM disease risk because the plants are younger when infested with WCMs. More well established, older plants are more tolerant to WSMV infection.

How Reliable Is the AWaRe Tool?

AWaRe is first and foremost a learning tool that demonstrates important factors of WSM disease risk through interactive questions. AWaRe was developed based on the review of scientific literature and empirical observations. The WSM risk indicated in AWaRe is an expression of the estimated risk score relative to the highest possible score within the AWaRe framework. The accuracy of AWaRe has not yet been tested against experimental data and the use of the tool cannot replace careful monitoring of the crop.

Where Can I find More Information about WSM Disease and Management?

Please refer to the Extension MontGuide “Cereal Viruses of Importance in Montana” for more information on WSM disease in Montana and management recommendations.

Figures

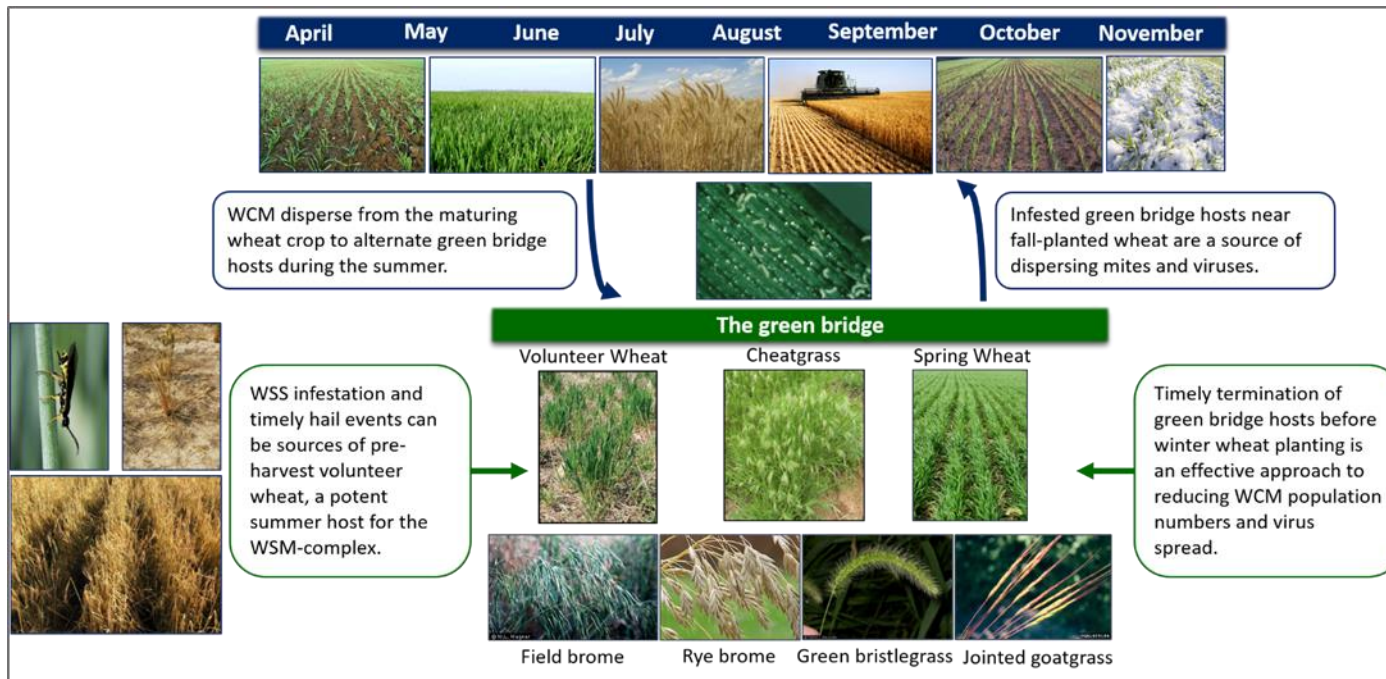


Figure 6.1. Illustration of the wheat streak mosaic disease cycle in the Northern Great Plains region of the U.S. WCM – wheat curl mite; WSM – wheat streak mosaic; WSS – wheat stem sawfly.

AWaRe: Assessment tool for Wheat streak mosaic Risk

Q 1. In the previous season, did you observe wheat streak mosaic symptoms in the field to be planted?

No ▼

Minimal: 1% - 5% Minimal: 1% - 5%

Considerable: 5% - 25%

Severe: > 25%

Q 2. What proportion of fields within a five mile radius of your field are wheat?

Few: < 5% ▼

Moderate: 5% - 25% Moderate: 5% - 25%

Considerable: 25% - 50%

Abundant: > 50%

Q 3. Did you observe volunteer wheat emerging as a result of hail damage and/or wheat stem sawfly infestation?

No volunteer ▼

There were only a few volunteer plants

There was some volunteer growth There was some volunteer growth

Volunteer wheat was abundant

Q 4. How did precipitation throughout the season impact grassy weeds in and around your field?

Severe drought – there were no green weeds ▼

Below normal precipitation – there were few green weeds

Normal precipitation – there were some green weeds Normal precipitation – there were some green weeds

Above normal precipitation – green grassy weeds were abundant

Q 5. Are volunteer wheat and grassy weeds in your field managed so they're dead prior to planting?

Yes, they'll be dead for at least 2 weeks before planting ▼

Yes, but they will have been dead for less than two weeks prior to planting

They may not die before planting

No

Risk_Factor	Risk_Score
WSM History	2
Environment	2
Green Bridge 1	2
Green Bridge 2	2
Green Bridge Control	0

Max_Risk_Total	Your_Risk_Total
22	11

You have MODERATE risk for wheat streak mosaic disease



Wheat streak management

Montana IPM

Figure 6.2. Screenshot of the AWaRe online learning tool. Question windows are expanded to show all answer options. Grey bars highlight the preset answers selected, which are associated with a numeric risk score in the right-hand table. Overall wheat streak mosaic (WSM) risk in percent expresses the risk total relative to the maximum risk score possible. “Wheat streak management” and “Montana IPM” fields redirect the user to the MSU Extension MontGuide on “Cereal viruses of importance in Montana” (Burrows et al. 2017) and to the Montana IPM website. The AWaRe application is available online: https://tim-msu-ecol.shinyapps.io/Wheat_Streak_Mosaic_Risk_MT/.

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CHAPTER SEVEN

SUMMARY AND FUTURE DIRECTIONS OF RESEARCH

Wheat growers in Montana must navigate a complex wheat production landscape that is complicated by biotic and abiotic causes of disease and insect pests. Wheat streak mosaic (WSM) disease and wheat stem sawfly (WSS) are two widespread and economically important disease/pest problems in Montana. Wheat growers must balance disease/pest management decisions with economic considerations to maintain profitability. This dissertation presented an evaluation of wheat production practices in Montana focusing on the effectiveness and implications of cultural and chemical management practices in mitigating WSM disease and WSS pressure.

The tolerance of popular winter wheat, spring wheat, and barley cultivars to mechanical inoculation with *Wheat streak mosaic virus* (WSMV) was assessed in field studies and provided valuable information for cultivar recommendations for high WSM pressure environments in Montana. Moreover, this study highlighted promising efforts in the development of WSMV-resistant winter wheat cultivars that are adapted to production conditions in the state. Resistant cultivars that emerged from this study should be evaluated under natural conditions of infection using viruliferous wheat curl mites (WCM) to confirm the resistance phenotype in future studies. This will be particularly important for barley cultivars, which have demonstrated low, variable infection rates under mechanical inoculation, but are known to be susceptible to WSMV infection from WCM.

The effects of cultivar selection, planting date, and seeding rate on grain yield and quality parameters were evaluated for spring and winter wheat in a two-year field study in northern Montana. An economic analysis was conducted to assess the impact of these management practices on the profitability of wheat production in Montana. The study validated current planting date recommendations for Montana and concluded that no meaningful and reliable economic benefits were associated with an increase in seeding rate beyond the recommended density of 215 seeds m⁻². Only under scenarios of very late planting did an increase in seeding rate achieve a small increase in revenue, or at least a minor compensation of income losses. Future research should evaluate the implications of these management practices under increased WSM disease pressure. Particularly planting date studies in the presence of WSM disease could provide quantitative information on WSM disease risk and associated yield losses in Montana. This information would be valuable for the development of a quantitative prediction model for WSM disease risk.

A framework for a WSM risk prediction model was developed and released as the online learning tool AWaRe (“Assessment of Wheat streak mosaic Risk”). The objective of AWaRe was to develop an application that assists users in identifying and evaluating crucial components contributing to WSM disease risk. Due to lack of quantitative data, the accuracy and precision of AWaRe has not yet been validated. AWaRe is primarily a learning tool. Through interaction with AWaRe, users can explore the individual and combined impact of different factors on the overall WSM risk. To our knowledge, AWaRe presents the first and only learning tool that integrates complex information on

the dynamics underlying WSM disease and relates them in an interactive way. We expect AWaRe to support growers' decision processes on the location-specific necessity of green bridge management, planting date adjustment, and appropriate cultivar selection. Long-term, we expect an adoption of targeted and risk assessment-based WSM management practices that result in a reduced economic impact of WSM disease on wheat production in Montana. Further developmental stages of AWaRe should target the testing of AWaRe's predictive quality and integration of quantitative data towards a probabilistic risk assessment method for WSM disease risk.

The potential of different insecticides in controlling WSS infestation and damage was evaluated in field studies and compared to different spring wheat genotypes with varying degrees of WSS resistance. Results showed that contact insecticides do not reduce stem infestation or increase mortality of injurious larvae, but application of the systemic insecticide Thimet-20G provided effective protection of susceptible cultivar 'Reeder.' The use of solid-stem cultivars provided equally effective protection from WSS infestation and cultivar 'WB Gunnison' produced yields that were as high as those achieved by hollow-stem cultivar 'Reeder' under Thimet treatment without the economic and ecological burden that is associated with the use of insecticides. This study is one of few that reports on the efficacy of different insecticide products in controlling WSS infestation and assess their effect on the larger agroecosystem. Future work should focus on potential interaction between WSS and WSM disease in Montana. By causing wheat stems to lodge, WSS likely contributes volunteer wheat to the green bridge, which is a crucial factor for WSM disease risk. Specifically, the presence and density of WCM

populations and virus incidence in volunteer wheat resulting from WSS-infestation should be assessed to identify potential correlations between WSS infestation and WSM disease risk. The impact of Thimet insecticide on WCM populations should be investigated to see if such treatments might increase WCM populations due to a lack of predators (Stilwell 2009). A further question that should be explored is whether WSM infection affects WSS preference of wheat stems for oviposition. Wheat streak mosaic-infected wheat plants frequently show stunted growth with straddling tillers (Wegulo et al. 2008). Since stem characteristics, such as solidness, diameter, and length, are important cues for stem selection by WSS females (Holmes and Peterson 1960; Buteler et al. 2009), changes in oviposition preference may be expected. Moreover, potential changes in the composition of volatile compounds resulting from WCM feeding and/or virus infection may also influence WSS oviposition behavior.

Knowledge of disease and pest problems in a production area and the factors that promote and suppress disease/pest pressure forms the foundation of successful and economic integrated pest management programs. The research presented here provides information that confirms and expands management recommendations for WSS and WSM disease. The consideration of potential interactions between different pest and disease problems and implications of management practices on the larger-scale agroecosystem are important aspects of the development of sustainable and profitable agricultural production practices.

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APPENDICES

APPENDIX A

EFFECT OF CROP ROTATION SEQUENCES ON THRIPS POPULATION SIZE IN
WINTER WHEAT FIELDS IN MONTANA

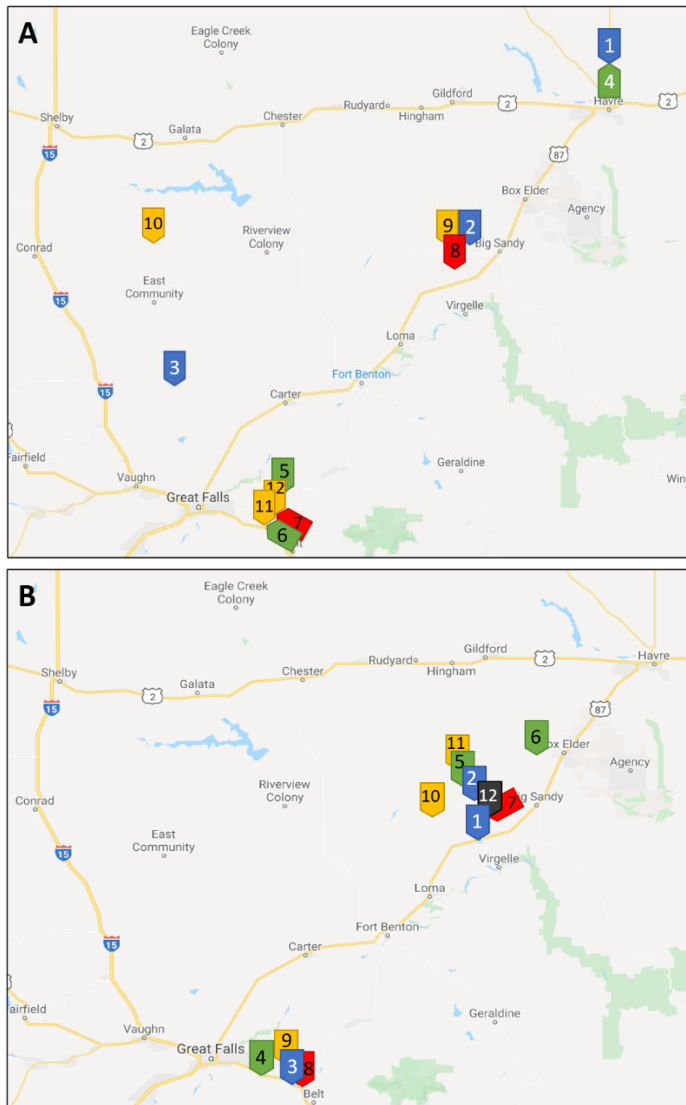


Figure A.1. Field sampling locations in central and northern Montana in (A) 2017 and (B) 2018. Numbers in flags indicate field ID. Colors indicate crop planted in the previous season: blue – lentil; green – pea; red – barley; yellow – fallow; black – winter wheat.

Table A.1. 2017 Summary statistic of thrips population sizes in winter wheat fields dependent on crop sequence as assessed by Berlese funnel extraction.

Field ID	Crop Rotation†	Sample size*	Number of thrips per 10 tillers			
			Min.	Max.	Mean	SD
1	Lentil	5	2.7	6.5	4.4	1.9
2	Lentil	5	0.4	2.9	1.5	1.1
3	Lentil	7	0	2.4	1.1	1.0
4	Pea	4	1.3	4.4	2.3	1.8
5	Pea	9	0.2	6.5	2.0	2.5
6	Pea	8	0.3	1.5	0.9	0.6
7	Barley	8	0	9.7	3.6	4.0
8	Barley	7	0.4	4.6	2.1	1.5
9	Fallow	8	0.2	6.3	2.6	2.3
10	Fallow	8	0	2.1	0.7	0.8
11	Fallow	11	0.5	4.3	1.4	1.1
12	Fallow	9	0	1.2	0.4	0.4

† Crop planted in the previous crop season.

* Number of subsamples processed in Berlese funnels. 50 plants were sampled in each field, following a W-shaped pattern of 75' and 25' length. Plants were summarized in 4 sampling bags (on per leg of the "W" sampling pattern) and later split into smaller sub-samples for processing in Berlese funnels if necessary due to sample volume.

Table A.2. 2018 Summary statistic of thrips population sizes in winter wheat fields dependent on crop sequence as assessed by Berlese funnel extraction.

Field ID	Crop Rotation†	Sample size*	Number of thrips per 10 tillers			
			Min.	Max.	Mean	SD
1	Lentil	6	0.2	2.4	1.6	0.8
2	Lentil	4	2.0	4.9	3.2	1.2
3	Lentil	5	1.2	2.9	1.8	0.7
4	Pea	6	0.7	3.7	1.8	1.1
5	Pea	6	1.2	5	2.8	1.7
6	Pea	4	1.3	2.6	1.8	0.6
7	Barley	4	0.6	2.8	1.9	0.9
8	Barley	5	2.6	18.8	9.3	6.1
9	Fallow	6	0.9	3.8	2.1	1.0
10	Fallow	4	0.6	3.1	1.9	1.0
11	Fallow	6	0.3	1.5	0.9	0.5
12	Fallow	5	1.2	2.4	1.7	0.5

† Crop planted in the previous crop season.

* Number of subsamples processed in Berlese funnels. 50 plants were sampled in each field, following a W-shaped pattern of 75' and 25' length. Plants were summarized in 4 sampling bags (on per leg of the "W" sampling pattern) and later split into smaller sub-samples for processing in Berlese funnels if necessary due to sample volume.