ASSESSMENT OF HOST SELECTION BEHAVIORS AND OVIPOSITION PREFERENCES OF *Cephus cinctus* Norton (HYMENOPTERA: CEPHIDAE) USING WHEAT AND SMOOTH BROME

by

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DEDICATION

To my entire family for their tangible and intangible support as well as their constant encouragement throughout my personal and academic journey.

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TABLE OF CONTENTS

TABLE OF CONTENTS CONTINUED

LIST OF TABLES

Table Page

LIST OF TABLES CONTINUED

LIST OF FIGURES

LIST OF FIGURES CONTINUED

Figure Page

LIST OF FIGURES CONTINUED

LIST OF FIGURES CONTINUED

ABBREVIATION

SB - crop: Smooth brome transect bordering crop

SB - fallow: Smooth brome transect bordering fallow

WSS: Wheat Stem Sawfly

ABSTRACT

Wheat stem sawfly, *Cephus cinctus* Norton (WSS), is an important pest of cereal crops in Northern Great Plains. Smooth brome has historically been suggested as a potential trap crop around wheat fields in Montana. The objective of this study was to compare oviposition preference and selection behaviors of female WSS and measure subsequent larval survival in wheat and smooth brome stems. We compared infestation, parasitism and larval development of WSS using field transects in smooth brome and adjacent wheat fields. We found no clear difference in infestation between the two host plants. There was greater larval mortality and less tunneling in smooth brome stems compared to wheat at a site near Big Sandy, Montana. At a second site near Big Sandy, there was greater infestation in smooth brome compared to wheat, but there were more dead larvae and greater parasitism in smooth brome. In Y-tube olfactometer studies, WSS females were more attracted to volatiles emitted by smooth brome than wheat. In greenhouse trials, the observation of specific behaviors leading to oviposition indicated differences in duration of ovipositor insertion and in number of ovipositor insertions that favored greater oviposition in smooth brome, but only by emergence of the first awn of the inflorescence (Zadoks 49 growth stage). There were different numbers of eggs in smooth brome stems relative to wheat, with no difference in the proportion of infested stems in choice tests conducted for two days at Zadoks 49. In no-choice tests, there were differences in both infested stems and in the number of eggs in stems at Zadoks 49. We found significantly greater amounts of key behaviorally active compounds used by female WSS, like (*Z*)-3-hexenyl acetate and β-ocimene, that were among the few differences in the amounts of volatile compounds collected from two plant species. The greater amount of these compounds leads to more eggs that subsequently experience greater larval mortality in young plants, resulting in fewer cut stems in mature plants. Our findings support the consideration of smooth brome for use in trap crops to improve integrated pest management strategies for WSS.

WHEAT STEM SAWFLY HOST PLANT ASSESSMENT IN SMOOTH BROME AND WHEAT

Introduction

Wheat stem sawfly (WSS) *Cephus cinctus* Norton (Hymenoptera: Cephidae), is an economically important pest of cereal crops in the Northern Great Plains of North America (Bekkerman and Weaver 2018). Historically, WSS infested large stemmed native grasses in the northern prairies of Canada (Ainslie 1929, Criddle 1923). Gradually, WSS adapted to exotic, non-cultivated and cultivated grasses as a result of the relative scarcity of its historical hosts (Criddle 1922, Ainslie 1929, Lesieur et al. 2016, Shanower et al. 2004, Beres et al. 2009, Beres et al. 2011a). Small grain cereal crops significantly contribute to agricultural output of these regions, but the annual losses caused by WSS are approximately $350 million, primarily in wheat (*Triticum aestivum* L.) production (Beres et al. 2011a). Meanwhile, losses attributed to WSS infestation were reported to be $52.2-$80.0 million annually from 2011-2016 in Montana (Fulbright et al. 2017). Female WSS oviposit in succulent stems of favored host plants, depositing an egg in the stem lumen. After hatching, WSS larvae continue to tunnel and feed on parenchyma tissues of stems (Beres et al. 2011a). As harvest approaches, these larvae descend towards the base of the stem, make a V-shaped groove (Criddle 1922) above a protective hibernaculum constructed for overwintering (Holmes and Peterson 1960). As a result, the grooved stem weakens and eventually topples. The recovery of these lodged stems is challenging and both harvest efficiency and yield are decreased (Ainslie 1929, Holmes 1977, Morrill et al.

1992, Beres et al. 2007). Although the use of solid-stemmed cultivars and biological control tactics are reported to sometimes be effective for managing WSS, the adoption of different management tactics in an integrated manner is the most reliable strategy to manage this pest (Beres et al. 2011b).

A cultural management approach that is complemented by an understanding of chemical ecology calls for the proper utilization of attractive plants that can be used for trap cropping (Khan and Pickett 2004). For instance, Khan et al. (2006) reported that a border of Napier grass (*Pennisetum purpureum* Schumach.) causes obvious disruption of moths foraging near maize (*Zea mays* L.) crops. Females of *Chilo partellus* Swinhoe. (Lepidoptera: Crambidae) selectively prefer this grass and will approach, alight on plants and deposit eggs due to volatile attractants (Van den Berg et al. 2001, Khan et al. 2006, Finch and Collier 2012). Due to increased plantings of wheat that result in edge effects in WSS infestations (Morrill et al. 2001a, Weaver et al. 2005) near fallow crop fields, studies exploring the potential use of trap cropping have become important (Weaver et al. 2009, Buteler et al. 2010).

Fundamentally, insect herbivores choose their potential host plants through discriminating and non-random selection during oviposition (Hanski and Singer 2001). The pre-alighting and post-alighting behaviors of many herbivores are impacted by their detection of volatiles emitted by a prospective host plants. For instance, while foraging, many insect herbivores alight on hosts as well as non-hosts, but most species are adapted to further assess suitability for oviposition prior to alighting through visual, morphological and volatile cues (Bernays and Chapman 1994). The arrays of different plant secondary metabolites that govern the preference of herbivores for specific host plants do so by providing signals that can influence correct selection of rewards or a rapid assessment of defensive compounds (Eisner and Grant 1981, Heard 1999, Wright and Schiestl 2009, Cooney et al. 2012). Previous studies on oviposition behaviors of WSS suggests that their host selection behavior involves a catenary process influenced by volatile cues and contact cues from host plants (Piesik et al. 2008, Buteler et al. 2009, Weaver et al. 2009, Varella et al. 2017). In an olfactometer study by Piesik et al. (2008), female WSS were attracted to wheat volatile compounds like *β*-ocimene, (*Z*)-3-hexenyl acetate, and (*Z*)-3-hexen-1-ol, whereas they were repelled by compounds like 6-methyl-5 hepten-2-one and were indifferent to less abundant (*E*)-2-hexenal and (*E*)-2-hexenyl acetate. Wheat stem sawfly females detect hosts using volatiles and show preference towards 'Reeder', a hollow stemmed cultivar that emits more (*Z*)–3 hexenyl acetate than 'Conan', a semi-solid stemmed cultivar that is less suitable (Weaver et al. 2009). For further host assessment, females use a sequence of behaviors including abdominal tapping, walking, antennating and quiescence that are elicited prior to ovipositor insertion after alighting on wheat plants (Buteler et al. 2009).

Physical characteristics like stem height, diameter, and phenology of host plants also influence the discrimination and selection of oviposition sites (Holmes and Peterson 1960, Morrill et al. 2000, Perez-Mendoza et al. 2006, Holmes and Peterson 1960, Buteler et al. 2009). Buteler et al. (2009) reported the influence of stem height on infestation, where WSS laid more eggs in taller plants irrespective of presence or absence of cryptic conspecifics in the stem. Morrill et al (2001a) reported that an earlier maturing winter wheat strip planted along the border of spring wheat acts as a trap strip for WSS. This is the result of edge effects and greater attractiveness of the earlier maturing winter wheat cultivar.

Within the natural environment, pests modulate their behavior in response to nutritional availability, survival, genetics, and environment. The selection of the host plant includes fitness consequences. According to the ‘maternal preference hypothesis’, herbivores select and prefer hosts conferring greater fitness to their progeny. Behaviors of WSS were not found to comply with the ‘preference performance hypothesis’ because females did not discriminate between previously infested stems that pose a serious risk of cannibalism and similar, but uninfested, stems in wheat plants (Buteler et al. 2009). However, the quantitative trait loci on chromosome 3B that characterizes stem solidness and larval antibiosis in wheat was found to influence WSS oviposition behavior, stem preferences and field infestation, resulting in lower infestation in stems that cause greater larval mortality (Varella et al. 2017). Thus, the preference of WSS was found to be influenced by overall favorability of hosts (Varella et al. 2017) rather than individual triggering cues. However, there is dearth of comprehensive information about how this pest selects and prefers potential hosts across grasses of different genera.

Smooth brome, *Bromus inermis* Leyss., an exotic perennial grass that is established near many wheat fields in many counties of Montana (Lesica et al. 2012), is also listed as an exotic host of WSS in Cockrell et al. (2017) and was also reported to attract greater numbers of parasitoids of WSS (Wallace and McNeal 1966). Despite the apparent attractiveness of smooth brome to foraging and ovipositing females, it was not found to be a highly suitable host for developing immatures (Criddle 1922). After three years of evaluation, Seamans et al. (1928) recommended brome as a permanent trap around wheat fields. However, it is still not clear whether the infestation of female WSS in smooth brome is merely due to a ‘border effect’ of encounter during immigration towards wheat fields, or whether ovipositing females actually make choices among wheat and smooth brome.

Investigation of the infestation, larval development and parasitism of WSS in smooth brome and two types of wheat, winter wheat and spring wheat, is important to understand actual population dynamics of WSS in field conditions. Specifically, it is necessary to understand the underlying mechanisms for preferences of WSS and relative attractiveness of smooth brome over wheat by evaluating behaviors using smooth brome and wheat grown under controlled conditions.

This study provides preliminary information on the population dynamics of WSS in wheat and smooth brome in Montana, where both grasses have co-existed at field sites for many years. This study will also play an important role in further elucidating the underlying mechanisms for host preferences of female WSS for wheat and smooth brome, which might provide insights for developing integrated pest management strategies targeting WSS.

Research Objective

The overall objective of this study was to understand the host selection behavior, oviposition preferences and larval development of WSS in two exotic grasses, smooth brome (*Bromus inermis* L.) and wheat (*Triticum aestivum* L.) in the field and under laboratory conditions. The major goal of this study was to understand how female WSS evaluate and choose among highly susceptible wheat cultivars and smooth brome for oviposition at two growth stages under controlled conditions.

To accomplish this, we first surveyed incidence of WSS, development of WSS larvae and parasitism of WSS larvae in wheat and smooth brome around wheat fields in Montana using sampling transects. Next, we observed behavior of adult females in a Y-tube olfactometer to evaluate preference for volatiles emitted by smooth brome plants and a susceptible wheat cultivar. After studying the pre-alighting behavior when provided with a choice of hosts, we compared post-alighting behaviors key in the further evaluation of hosts for oviposition, including duration of walking time on leaves and stems and number of abdominal taps on stems and leaf surfaces. We also quantified triggering events like ovipositor insertions in stems that could lead to actual egg deposition. We conducted choice bioassays in cages to determine infestation and measured the number of eggs when exposed to both plant species for two days. Similarly, we compared oviposition under no-choice conditions to determine if it would be different when only one plant was exposed; in the absence of any kind of exploration between two host plants. We accounted for physical parameters like stem length and diameter that could influence oviposition. Subsequently, a survival study was conducted under no-choice conditions to further contrast WSS mortality in experimental host plants in a greenhouse. This is an important follow up on assessing infestation and survival from field transects. Eventually we collected volatiles to determine qualitative and quantitative differences in volatile compounds between the plant species that could trigger differences in WSS behavior.

Literature Review

Origin and Distribution of Host Plants

Wheat stem sawfly, *Cephus cinctus* Norton (Hymenoptera: Cephidae), is an opportunistic native species (Lesieur et al. 2016) that has evolved to become one of the economically most important pests of wheat (*Triticum aestivum* L.) in the Northern Great Plains of North America (Bekkerman and Weaver 2018). In Montana, it caused overall losses of \$52.2-\$80.0 million annually from 2011 – 2016 (Fulbright et al. 2017).

Wheat stem sawfly was originally detected in hollow-stemmed native wild grasses and was first reported from *Agropyron* and *Elymus* in Colorado in 1872 and was subsequently found in wheat in Manitoba, Canada, in 1895 (Ainslie 1920). In the early 1900s, the territorial distribution of WSS was surveyed and found to extend to different parts of the northern United States like North and South Dakota, Minnesota, Iowa, and Nebraska. It was found first foraging on grasses like *Agropyron*, *Elymus*, *Phleum* and *Bromus spp*., and this is why WSS was first known as the “western-grass stem sawfly”(Ainslie 1920). Quite rapidly, farmers displaced the native and feral grasses by cultivating succulent small grain cereal crops that covered a large area of the habitat used by WSS (Ainslie 1929). A prediction reported in Riley and Marlatt (1891), that WSS would broaden its host range to more succulent small grain cereal crops and non-native grass species, was confirmed after the pest was found invading small grain cereal crops like wheat and exotic grasses like smooth brome. In 1895, the pest was found damaging spring wheat for the first time in Manitoba and Saskatchewan (Wallace and McNeal 1966). Although, it was first reported from a native grass in Colorado in 1872, infestation in cultivated winter wheat grown in Colorado was first detected in 2010 (Irell and Peairs 2014).

Solid stemmed cultivars of wheat were first reported to be resistant to WSS at varying degrees in the 1930s (Farstad 1940). Initially, WSS adapted to spring wheat crops only. Gradually, after adaptation to early maturing winter wheat in Montana in the 1970s (Morrill and Kushnak 1996), WSS distribution expanded to many winter wheat cultivating areas like Nebraska, southeastern Colorado, and eastern Wyoming (Lesieur et al. 2016). A large amount of genetic variation is expected among the disparate WSS sawfly populations in Montana, North Dakota, and Wyoming, suggesting the existence of potential biotypes (Lou et al. 1998), which was supported by Lesieur et al. (2016). There are twenty-five to thirty members of the genus *Cephus* worldwide and two species are found in North America (Ivie 2001). The native *Cephus cinctus* Norton is found in the western United States and Canada and the introduced *Cephus pygmaeus* (L.) has established in the eastern U.S. and Canada (Weiss and Morrill 1992), and are pests of small grain crops (Shanower 2006).

Host plants

In the Northern Great Plains, WSS has numerous potential hosts. Among cultivated crops, it attacks wheat, rye, triticale and some varieties of barley; wheat being most preferred. Wheat, *Triticum aestivum* L., is an exotic species grown on large amounts of land in Northern Great Plains of America. Although introduced along with the settlement by European settlers, it has been intensely cultivated in the region west of Mississippi since the late 1800s (Brigham 1910).

Among wheat crops, spring wheat was most susceptible to WSS in the past, but now, winter wheat has become equally susceptible in many parts of the United States (Portman et al. 2018). Durum wheat is also a susceptible host of WSS (Beres et al. 2011a). Barley is comparatively susceptible to oviposition, but larval survival and development is poor and rarely causes yield losses, although the incidence is certainly increasing (Farstad and Platt 1946, O'Keeffe et al. 1960, Varella et al. 2018). Beyond cultivated hosts, native grasses have been reported as hosts of WSS that permit successful development. The historical inventory of native North American grass hosts includes many *Agropyron* spp., *Bromus* spp., *Calamagrotis* spp. *Calamovilfa longifolia* (Hook.) Scribn, *Elymus* spp., *Festuca* spp., *Hordeum* spp., *Phleum pretense* L., *Stipa viridula* Trin. and *Beckmannia syzigachne* (Steud.) Fern. (Wallace and McNeal 1966) and has been recently been updated (Cockrell et al. 2017).

Among the grass hosts, *Festuca* spp. and *Bouteloua* spp. are reported as less susceptible to infestation by female WSS (Mills 1942), possibly due to slender stems as reported in many studies (Holmes and Peterson 1960, Morrill et al. 2000, Perez-Mendoza et al. 2006). Cockrell et al. (2017) found lower infestation in relatively common grasses like *Bouteloua gracilis* (9%), *Bromus arvensis* (12%), and *Koeleria macrantha* (33%). However, beyond stem diameter, other potential factors limiting infestation including physical host plant resistance (solid stem traits, cuticular wax content), diverse chemical defenses of host plants and the host plant phenology during the WSS flight period, have not been studied thoroughly enough to fully understand factors determining host suitability.

In agricultural systems, pest and natural enemy diversity and abundance is influenced by landscape structure suggesting the need for landscape perspectives for effective management (Tscharntke et al., 2007). While some herbivores showed increased abundance with increasing complexity of landscapes, for instance, host-alternating aphids like soybean aphids and cereal aphids (Thies et al. 2005, Bahlai et al. 2010, Ragsdale et al. 2011), other herbivores have greater abundance with the increase in area of suitable crops at landscape scale, for example, abundance of northern and western corn rootworm in corn (Beckler et al. 2004, O’Rourke et al. 2011). Therefore, incidence, abundance and density in response to landscape complexity requires understanding of the response of target species to various facets of landscape simplification (Thies et al. 2005, Bahlai et al. 2010, Ragsdale et al. 2011). This understanding helps to effectively manage the herbivores using IPM tactics that focus on habitat manipulation (Brewer and Goodell, 2012).

Early literature suggested that wild grasses were serving as hosts of WSS (Criddle 1917). A few studies have been conducted to understand pest population dynamics on these cultivated and wild hosts that would assist management tactics for WSS (Sing 2002, Perez-Mendoza et al. 2006, Keren et al. 2015). Rand et al. (2014) found that abundance of a suitable host crop like wheat augments the population of WSS and its infestation, acting as an important source habitat for this pest compared to grassland cover at the landscape level. While the landscape-scale natural or semi-natural habitat provides important resources like refuges, nectars and alternate hosts (Landis et al. 2000, Bianchi et al. 2006) for natural enemies, Rand et al. (2014), in the same paper, did not find an influence on local and landscape abundance of WSS natural enemy population of the abundance of natural grassland cover or wheat cover. The knowledge of population dynamics of WSS in wild and cultivated hosts is useful for developing management tactics and would be particularly relevant when wild hosts and susceptible cereal crops like wheat have co-existed in the same field areas for many years.

Downy brome, *Bromus tectorum* L., is an invasive weed that causes yield loss of wheat due to competition for resources in fields (Keren et al. 2015). A pre-alighting behavioral study, as well as bioassays for oviposition preference and survival at different stages was carried out in downy brome adjacent to winter wheat (Altilmisani 2016), where WSS infestation was less in downy brome than in wheat, but larval mortality was greater in downy brome. In spring wheat fields infested with downy brome in Montana, Perez-Mendoza et al. (2006) found that infestation was greater in downy brome than in spring wheat, but very few larvae survived in downy brome relative to wheat. An understanding of the preferential selection of downy brome over wheat for oviposition coupled with the less likely development of larvae within stems of downy brome found more emphasis on yield loss caused by downy brome relative to its role in WSS population dynamics in wheat fields (Keren et al. 2015). However, the presence of downy brome grass in most wheat areas in the northern Great Plans (Morrow and Stahlman

1984) may negatively impact population dynamics because of lower immature survival (Perez-Mendoza et al. 2006).

Smooth brome (*Bromus inermis* L.), is a cool-season grass introduced into the United States in 1884 from Hungary and Russia for soil conservation (Hitchcock and Chase 1971) and as a fodder supplement for animals (Larson et al. 2001). It was widely used in upper half of the North America during late 19th and early 20th century. It is a rhizomatous perennial grass that is more drought resistant than other exotic grasses.(Mapfumo et al. 2002). Smooth brome cultivars like ‘Superior’, ‘Manchar’, ‘Carlton’, ‘Jubilee’, ‘Saratoga’, ‘Polar’, and ‘Bravo’ are selected and improved northern type cultivars of smooth brome. Their seeds are viable for 2-10 years (USDA-NRCS 2002) and are good sources of protein that also contain relatively low amounts of crude fibers. Thus, these can be used as hay or silage and also be maintained for pasture grazing. Additionally, due to its sod forming nature and massive root system, smooth brome is also used for managing soil erosion (USDA-NRCS 2002) along roadways. It is found growing in headlands and road easements as a perennial fodder grass.

Emphasizing the importance of cultural control practices for mitigating WSS damage, the “War-Time Production Series” report published by several regional Agricultural supply boards presented the potential of smooth brome as a trap crop to decrease WSS populations (Farstad et al. 1945). Due to a suggested invasive capability, smooth brome was reported to inflict adverse effects over native grasses. Smooth brome populations have a significant role in modifying population dynamics and movement of native herbivores on the North American prairies (Haynes and Cronin 2003, Baum et al. 2004, Cronin and Haynes 2004, Cronin et al. 2004, Cronin 2007)

Factors Affecting Host Plant Selection

Even though WSS infests many native, cultivated and non-cultivated grasses of Poaceae family (Criddle 1923), WSS does select suitable hosts and exhibit preferences for certain hosts when options are available (Holmes and Peterson 1960, Weaver et al. 2009). Wheat stem sawfly, in general, does not select its host plants randomly, nor do most insect species. It is a sequential encountering of sensory information from plants that elicits either positive or negative responses (Heard 1999, Finch and Collier 2002). There are gustatory, olfactory, mechanical or visual cues that pests perceive from chemosensory and mechanosensory modalities. These plant related cues help herbivores to either reject or accept host plants depending on perceived suitability (Miller and Strickler 1984, Jackson 1990, Kogan 1994, Piesik et al. 2008, Gress 2014, Lavergne et al. 2018).

The physical characteristics of plants like phenology, size, color, shape, trichome density and chemical features of plants like cuticular chemistry, volatile compounds and non-volatile compounds also influence pest behavior and assist in discriminating hosts (Braccini et al. 2015, Holmes and Peterson 1960, Piesik et al. 2008, Tamiru et al. 2015, Lavergne et al. 2018). Studies suggest that host finding and selection behavior in insects is a catenary process that includes host finding and host acceptance cues (Ramaswamy 1988), and is not a one step process, because, first, they search and select a host from the distance, then accept the host as they establish contact with the plant surface. The plants on which they land after being perceived as favorable host might not be suitable for adult feeding or oviposition due to unfavorable associated physical and chemical contact cues (Braccini et al. 2015, Tamiru et al. 2015, Lavergne et al. 2018). Thus, insects further examine host plant surfaces after they alight. For example, WSS assesses the host stem through antennal and abdominal tapping before ovipositor insertion, which could allow them to access information on host suitability for oviposition (Buteler et al. 2009, Varella et al. 2017).

Farstad (1940) reported that moisture, as well as succulence and maturity of host plants affect the development of WSS larvae. Even though late maturing varieties produce larger larvae and adults, this condition was not expected to be a useful index for host suitability due to potentially greater larval mortality in such plants.

The host suitability, preference, growth and survival of WSS depends upon many host attributes like physical and chemical parameters (Holmes and Peterson 1960, Youtie and Johnson 1988, Morrill et al. 1992, Perez-Mendoza et al. 2006, Weaver et al. 2009). However, researchers reported that larger stems are more susceptible to successful mining by WSS larvae and ensures sawfly fitness (Ainslie 1929, Morrill et al. 2000, Carcamo et al. 2005). Further, it has been suggested that even slender stemmed but typically vigorous grasses like *Hordeum jubatum* can be susceptible enough for attack by *Cephus cinctus* (Ainslie 1929). In the same article, Ainslie (1929) suggested that the diameter of host plant should not be too large that it becomes difficult for female WSS to grasp the stems and oviposit. In a study to evaluate host preference between previously infested and non-infested wheat plants, females preferred laying eggs into taller wheat plants irrespective of infestation (Buteler et al. 2009).

The phenology of host plants also determines infestation. WSS prefer to oviposit in a wheat stem once it has more than two nodes (Ainslie 1920). However, WSS females also mostly prefer to oviposit in the lower internodes of later developing stems and in the higher internodes of earlier developing stems, and differences in infestation patterns between two varieties was attributed to difference in growth rates (Holmes and Peterson 1960).

Understanding chemical ecology and insect behavior plays an important role in addressing plant-insect interactions and factors that govern insect behaviors (Hawkes 1974, Kennedy 1977). There are nitrogen and carbon containing defensive compounds in host plants that govern the flight, development and survivorship of herbivores. The behavior of WSS is also influenced by green-leaf volatile compounds including esters like (*Z*)-3-hexenyl acetate, alcohols like (*Z*)-3-hexenol and terpenes like *β*-ocimene, as well as ketones like 6-methyl-5-hepten-2-one (Piesik et al. 2008). Weaver et al. (2009) reported the emission of a greater amount of (*Z*)-3-hexenyl acetate in the highly susceptible wheat cultivar ‘Reeder’ than in the less susceptible cultivar ‘Conan’.

WSS oviposition behavior in host plants

In a behavioral flowchart or ethogram, Buteler et al. (2009) showed an array of behaviors of female WSS on wheat plants. In general, female WSS initially follow a sequence of events begun by walking up the stem with frequent antennal tapping, encircling of stem with legs, and periods of quiescence for examining host suitability.

Reaching the uppermost part of the stem, they subsequently move up and down for repeated host assessment. They usually insert their ovipositor while moving down the stem rather than moving up, accompanied by simultaneous antennal grooming and tapping behaviors. They partially encircle the host stem before ovipositor insertion, which has been described as a behavior for estimating the host size through morphological cues (Buteler et al. 2009). Buteler et al. (2009) further noted that antennal tapping events and abdomen tapping events as behaviors that allow them to perceive and respond to chemical cues from plants that trigger ovipositor insertion in suitable sites. These authors documented no differences in behaviors of WSS that led to differential oviposition in previously infested and non-infested wheat plants.

Similarly, a laboratory note reported in Ainslie (1929) informs on numerous unsuccessful attempts for ovipositor insertion by female WSS in *Elymus* stems; but he reported that, at times, they inserted their ovipositor and then stood motionless after extending it to full length, which was mentioned as reliable indicator that such behavior might lead to actual oviposition.

Biology of WSS

The life cycle of WSS is completed within the host stem except the short adult phase. This species is univoltine and undergoes complete metamorphosis with stages progressing through eggs, larvae, pupae and adults. The adult emerges from stubble remaining from the previous year’s crop in early summer (Beres et al. 2011b)

Eggs. Eggs are translucent or milky white in color, crescent shaped with average size of 1.00-1.25 mm in length (Ainslie 1929). After oviposition, the egg lies freely within the lumen of host stem (Ainslie 1929). Gradually, beginning at three days, eggs hatch and larvae emerge. The larvae become fully functional by sixth or seventh day after oviposition (Fulbright et al. 2017).

Larvae. After hatching, young larvae are colorless and translucent (Criddle 1923, Ainslie 1929). The dark, heavily sclerotized head capsule and larger body size contrast WSS larvae from other larvae that are found in wheat and grasses (Fulbright et al. 2017). Gradually, the larvae start to tunnel by feeding on parenchyma and vascular tissues from inside the stem of host plants (Ainslie 1929, Beres et al. 2011a) and eventually become yellowish brown in color. During this process, the infested stem is filled with frass, which is digested plant tissue that is excreted (Fulbright et al. 2017). Typically, the first larva to emerge has a size advantage that allows it to destroy all others that are deposited in the same stem. This is because there is only one survivor in infested stems within a few weeks due to cannibalism (Criddle 1923, Holmes 1982; Buteler et al. 2015). Once the host plant becomes physiologically mature, the large larvae receive cues to move towards the base of the stem and undergo obligatory diapause (Beres et al. 2011a). Generally, a fifth instar larva prepares for overwintering (Beres et al. 2011a). This descending movement and subsequent formation of a hibernaculum for obligatory diapause is triggered when the host plant becomes sufficiently mature to allow visible and infrared light into the stem, and when moisture content of kernels reduce to 40% - 50% (Holmes 1977). They form a V-shaped groove in the stem interior near the base of stem, making it weak enough to lodge due to gravity or wind (Criddle 1922). As the stem topples, they plug the remaining stub with frass and other solid materials to form a protective hibernaculum for residing underneath throughout the diapause period (Holmes and Peterson 1960). After larvae in stubs are exposed to less than 10° C for 90 days, diapause is completed, and they undergo pupation when temperatures warm (Salt 1947). Larvae can reenter diapause if they are exposed to unexpectedly high temperatures and unfavorably dry conditions shortly after termination of diapause (Salt 1947).

Pupae. After the larva completes overwintering, it develops into pupa at around late May (Holmes 1977), which lasts for about 21 days (Criddle 1922). The pupa is initially pale white in color, which gradually intensifies to bright white, and the development of wings occurs as the life cycle progresses (Fulbright et al. 2017). Under favorable conditions, pupae transform into adult WSS, which chew through the frass plug or side of the stub, and become ready for flight (Holmes and Peterson 1960).

Adult. The adult life span ranges between five to eight days. Typical emergence time for adults from the host stem occurs from mid-May to mid-June and lasts for three to four weeks (Fulbright et al. 2017). Generally, haploid male WSS (from unfertilized eggs) emerge from the previous year’s stubs before diploid females (from fertilized eggs). This allows fertilization of eggs in most of the early emerged females, such that they can oviposit in their early flight period, thus resulting in robust female progeny (Fulbright et al. 2017). Females are sexually mature as soon as they emerge, copulate with males and select suitable host for oviposition. The female WSS, using the saw-like ovipositor, makes a slit on an elongating stem and inserts eggs into the lumen of stem (Beres et al. 2011a). Throughout the life span, one mature female WSS lays about 30 to 50 eggs

(Fulbright et al. 2017). Generally, each female deposits only one egg per stem at a time (Holmes 1977, Beres et al. 2011a).

Damage

Wheat stem sawfly larvae tunnel wheat stems by consuming parenchymal tissue and chewing through the nodes. This causes an impairment in vascular translocation of water and nutrients in plants (Macedo et al. 2007) that ultimately causes reduction in yield and quality of grains (Holmes 1977, Morrill et al. 1992, 1994, Seamans et al. 1945). Additionally, the physical weakening of stem leads to lodging before harvesting, which is exacerbated by girdling of the stem by larvae. This lodged condition reduces harvest efficiency (Ainslie 1929), and yield is lost from unrecovered toppled stems (Ainslie 1920, Beres 2007). Lodging also increases the likelihood of soil erosion, and reduces soil moisture because of reduced stubble residues for retaining snow (Keren et al. 2015).

Management of WSS

Wheat stem sawfly are stem mining pests, so they complete most of their life cycle inside the host stem. This cryptic life cycle makes them less amenable to be managed through direct contact methods such as the use of insecticides, greatly reducing the breadth of possible control measures (Beres et al. 2011a). Before deploying management strategies in the field, it is necessary to develop risk assessment tools for monitoring infestation level and severity of pests in the field. According to the sampling plan described by Nansen et al. (2005), plants can be sampled along the edges of the field, processed and assessed for the presence of larvae to predict the infestation level up to 200 m into the field. The infestation can also be assessed by detecting the presence of dark spots below nodes of the host stem that indicates the presence of larvae. However, the prominence of these black spots depends upon the time of sampling (Morrill et al. 1992). Although more advanced methods like audio recording of WSS larval feeding (Mankin et al. 2004) and hyperspectral imaging (Nansen et al. 2009) can be helpful for detection of infestation and related stresses, use of these techniques is limited, because effective data collection using these techniques requires highly technical skills and sensitive equipment (Mankin et al. 2004, Nansen et al. 2009). There is no specific management practice for WSS that is a silver bullet, but different tactics can be used in an integrated manner to maintain WSS population below the economic injury level (Beres et al. 2011b).

Chemical Control. For large-acreage crops like wheat and other small grain cereal crops, chemical insecticides are not an economic management tool for WSS. The immature stages are protected inside the stem, and adults can also escape from exposure to chemical applications due to a large emergence window, thus management of this pest using insecticides is very challenging (Knodel et al. 2009, Beres et al. 2011a, Knodel et al. 2016). The efficacy of chemically treated seeds in WSS management was found to be limited to certain length of plants only (Holmes and Peterson 1963). Although the Montana Department of Agriculture has given authority for the use of systemic organophosphate insecticide phorate (Thimet 20-G®) for controlling WSS in winter and spring wheat, its use is not environmentally or consumer friendly because of high toxicity to mammals, fish, and birds. The preharvest interval for phorate is 85 days (Mahajan et al. 2006, Lerro et al. 2015, Portman et al. 2018) which complicates harvest scheduling and this toxicity may also adversely affect parasitoid populations that are important in the biological control of WSS (Varella 2016).

Biological Control. Studies suggest that there are several parasitoids that have been detected in feral and native grasses (Neilson 1949, Holmes 1953, Meers et al. 2005, Rand et al. 2016). Two congeneric parasitoids, *Bracon cephi* (Gahan) and *B. lissogaster* Muesebeck (Hymenoptera: Braconidae) are reported as an occasionally effective source of mortality for WSS in wheat fields (Runyon et al. 2001). Typically, these larval ectoparasitoids have two generations per year (Nelson and Farstad 1953) and WSS is their only known host. The first generation of *B. lissogaster* is present from late June to late July in Montana and the second generation is active from August to September (Somsen and Luginbill 1956). Adult females insert their ovipositors inside the infested stem containing WSS larvae (Buteler et al. 2008). After inserting the ovipositor, they lay eggs near or on a WSS larva. Adult females secrete venom that paralyses the WSS larva, assisting their progeny in drawing liquid and nutrients when feeding, thus killing the host within 10 days. Afterwards, the fully developed larva undergoes pupation within a cocoon and emerges as an adult second-generation parasitoid in August (Nelson and Farstad 1953). Although the life cycle of a predatory beetle, *Phyllobaenus dubius* (Wolcott) (Coleoptera: Cleridae) is not entirely clear, it has been found attacking larvae of *C. cinctus* in Montana (Morrill et al. 2001b, Beres et al. 2009). Similarly, *Fusarium spp*. were found on the field collected larval cadavers of WSS that could decrease the larval survival (Wenda-Piesik et al. 2009). However, the dual pathogenicity of *Fusarium* *spp*. to both wheat and larvae limits its usefulness in WSS management (Wenda-Piesik et al. 2009).

Host Plant Resistance. Host plant resistance is generated due to mechanisms like antixenosis, antibiosis and tolerance (Horber 1980, Smith 2005, Smith and Clement 2012). Antixenosis is the mechanism of triggering resistance by inducing non-preference of herbivores when they attempt to feed or oviposit. Similarly, due to antibiosis in plants, improper development of herbivores occurs, mainly negatively affecting survival, longevity and reproduction in more resistant plants when compared to susceptible. Similarly, tolerance is the capacity of plant to withstand the infestation of herbivores and the ability to recover from the injury (Teetes 1996). The genetics of wheat germplasm has been studied with emphasis on the solid stem trait and levels of pith expression (Platt and Farstad 1946, Wallace et al. 1973, Cook et al. 2004, Varella et al. 2015). The solid-stemmed cultivars are more resistant to WSS than hollow stemmed cultivars. This trait in the host plant reduces oviposition and enhances egg mortality (Holmes and Peterson 1961). Pith also disrupts movement within the stem, resulting in lighter and less fecund adults and reduced larval survival due to reduced foraging (Wallace and McNeal 1966) relative to hollow stemmed cultivars (Carcamo et al. 2005). Additionally, the compact pith in solid stemmed cultivars increases stem strength while minimizing lodging and reduced economic loss due to WSS (Delaney et al. 2010). The solid stem trait has been developed in many spring wheat and some winter wheat cultivars from more resistant wheat cultivars (Beres et al. 2011a). The single dominant gene (SSt1) localized at 3B chromosome in “Golden Ball” is responsible for controlling stem solidness in durum wheat (Platt and Farstad 1949, McKenzie 1965, Clarke et al. 1998) and exhibits good pith expression over range of environmental conditions (Platt and Farstad 1949). The solid stem trait from “Golden Ball”, durum wheat (tetraploid wheat cultivar) was transferred to hexaploid wheat cultivar after crossing “Golden Ball” with goat grass, Aegilops .species (Poaceae), and backcrossing the offspring with the hexaploid wheat cultivar (Clarke et al. 1998, Clarke et al. 2002). However, transfer of resistant gene from tall wheat grass *Thinopyrum ponticum (Podp.)* (Poaceae) to common wheat was not very effective due to expression of inferior level of resistance (Platt and Farstad 1949).

The identification of various quantitative trait loci on chromosomes that control stem solidness allows for the transfer of this trait in susceptible cultivars (Beres et al. 2013). Cook et al (2004) reported that solid-stem trait in wheat is mostly controlled by single quantitative trait loci *Qss.msub-3BL*. However, other loci that control stem solidness in different wheat cultivars throughout the growing season have also been discovered (Varella et al. 2015). Although the use of solid-stem wheat cultivars is most often recommended for WSS management, the resistance in wheat cultivars could be confounded by the variation in climatic factors (Morrill et al. 1992). Furthermore, the number of parasitoids in a specific site complicate assessment of cutting because they remove large larvae that have potential for stem cutting, especially when the cut stems are used as index to estimate WSS infestation (Sherman et al. 2010). As plant resistance is dependent upon genetic and environmental factors, photoperiod and light intensity during stem elongation influence the degree of pith expression in specific cultivar, causing inconsistent expression of WSS resistance (Beres at al. 2011b).

Hollow-stemmed cultivars were found to have more parasitism than that of solid stem cultivars (Holmes et al. 1963). Rand et al. (2012), suggested that extra pith in solid stem cultivars hinder the ability of parasitoids to sense the vibration of larvae (Mankin et al. 2004) inside the stem, thus causing ineffective location and parasitism of WSS larvae.

Varella et al (2018), discussed the different form of antibiosis in barley lines, which could otherwise have been expressed due to stem solidness. Although, both antixenosis (infestation) and antibiosis (larval mortality) are involved in the resistance of barley to WSS, antibiosis was found to be more dominant in influencing resistance (Varella et al. 2018).

Cultural control. There is a lack of effective chemical control measures due to the cryptic nature of larvae that reside inside the stem, short flight period of adult WSS and the high investment on the chemicals. Similarly, there are inconsistent results from biocontrol activities (Shanower and Waters, 2006), which may be due to the requirement of long period of time for the establishment of parasitoids. Furthermore, management efforts using resistant varieties are not consistent. The expression of solid stem trait is not consistent throughout the phenology, geography and the environmental conditions. The use of solid stem varieties causes lower tunneling in the stems. However, the economic tradeoff associated with the use of solid stemmed cultivars of wheat results in reduced yields and lower economic returns. Therefore, cultural controls are important and need to be integrated in WSS management strategies. The typical wheat growing system practiced by farmers across most of the Northern Great Plains of United States is an alternate-year, summer fallow production system (Willis et al. 1983, Troeh et al. 1999).

In this scenario, the use of trap strips, a narrow area that borders the crop field, was suggested for managing WSS (Farstad 1942). The early phenological development of trap strips relative to the main crop can be utilized to trap the eggs of WSS in trap strip stems (temporary trap) as the main crop stems will not elongate to a degree required for WSS to oviposit. Similarly, perennial grasses such as smooth brome can be seeded as permanent trap, in which the WSS readily oviposit but the larvae are reported to not be properly developed to achieve maturity (Mills 1944). Some trap strips are generally suggested to cut for hay or disked to destroy stems as the WSS flight period ends and before the larvae move towards the base to form hibernacula and overwinter (Farstad 1942). Not only would trapping the WSS larvae in the trap strips help to manage WSS populations, but the long growth habit of perennial grasses may serve as a resource for second generation parasitoids. Perimeter trap cropping was proposed as sustainable approach to manage WSS populations in the field (Morrill et al. 2001, Buteler et al. 2012), but insufficient economic analysis, inconsistent control and impractical seeding operations limit adoption among farmers (Varella 2016). In this type of system, wheat stubble from the previous year serves as a source of WSS in adjacent fields in the current wheat growing season. Previously, tillage practices were proposed as an effective way to destroy and bury or expose stubs with overwintering WSS larvae (Morrill et al. 1993). However, this practice was found ineffective and also negatively impacted parasitoid populations (Runyon et al. 2002). The specific timing of tillage operations may have other undesirable impacts such as favoring soil erosion, reducing soil moisture and deterioration of soil health and declining parasitoids of WSS (Holmes and Farstad 1956, Morrill et al. 1993, Runyon et al. 2002). Other recommendations like sheep grazing to kill overwintering larvae (Salt and Hollick 1946; Hatfield et al. 2007), mowing grassy borders ; burning; early harvesting via swathing (Ainslie, 1920, Beres et al. 2011a) were found to be less effective due to various economic and environmental considerations (Morrill 1992, Morrill et al. 1993, Holmes, 1977). Crop rotation integrating resistant crops like soybeans (*Glycine max* L.), oats (*Avena sativa L.*), and sunflower (*Helianthus annus L.*) McBride 1996, Callenbach & Hansmeier 1945, Knodel et al. 2010) has also been suggested for managing WSS. Delayed planting in WSS susceptible fields (Beres et al. 2011b) and promotion of organic farming practices that boost plant diversity (Adhikari et al. 2018) may be promising management approaches. However, adoption of such sustainable management approaches is typically initially low due to reluctance of farmers to employ novel approaches that are more labor and cost intensive.

In addition to the use of solid stem wheat and augmentation of biological control agents as effective management tactics for WSS, deployment of push-pull strategies using wheat has been found to be potential approach for this pest's management. Weaver et al (2009) reported that "Reeder" cultivar received more eggs in comparison to "Conan," and this variation was attributed to the greater amount of attractive volatile compound (*Z*)-3 hexenyl acetate released in 'Reeder". This compound was reported as an attractive compound for ovipositing female WSS (Piesik et al. 2008). In an evaluation of wheat varieties: 'Norstar', 'Neeley' and 'Rampart' as potential trap crop, Buteler and Weaver (2012) found Norstar to be the best candidate as it emitted more behaviorally active volatiles like (*E*)- and (*Z*)-β-ocimene.

Hypotheses associated with choice making behaviors

The host plant selection and preferences for oviposition are governed by various factors such as host detection, host phenology, larval physiological adaptation to host plants, and abundance and dynamics of natural enemies in host plants (Crawley 1983, Bernays and Graham 1988, Bernays 2001, Forister et al. 2013, Mayo-Hernández et al. 2018). The choice making behavior of herbivores have been long discussed and various theories have been proposed to address mechanisms used to make host plant choices. Among these, the “preference performance hypothesis” (Jaenike 1978) or “mother-knows-best hypothesis” (Valladares and Lawton 1991) states that herbivores prefer host plants in which their progeny thrive best. As juveniles are often not able to choose the best host for further development, mothers are expected to place eggs on or in a host suitable of ensuring survival of their progeny for fitness benefits (Prager et al. 2014). While results from many studies show positive correlation between female preference and progeny performance (Singer et al. 1988, Gripenberg et al. 2010, Fortuna et al. 2012, Fortuna et al. 2013), there are numerous studies which did not or weakly comply with this relationship (Chew 1977, Rausher 1979, Valladares and Lawton 1991, Ohsaki and Sato 1994, Larsson and Ekbom 1995, Fortuna et al. 2012). In addition, several cases of invasive plant species-herbivore interactions were found to contradict this relationship (Feldman and Haber 1998, Keeler and Chew 2008, Nakajima et al. 2013). This hypothesis is more strongly correlated in the plant-insect interaction in which herbivores lay eggs in clutches than singly because they have to bear more losses due to poor host selection decisions (Mangel 1987). For WSS, the larva is confined to single stem chosen by its mother until it emerges into adult. Only one larva can complete its life cycle within a stem that may contain several immatures due to cannibalism among larvae at different instars (Buteler et al. 2008, 2015), thus perhaps the “preference performance hypothesis” is negatively correlated to this system. There is considerable evidence that helps to refute this hypothesis. In our research, WSS was not found to discriminate previously infested and non-infested host plants of same cultivar and chooses to deposit eggs in host disregarding the risk to progeny (Buteler et al. 2009). However, Weaver et al (2005) suggested multiple larvae in single stem could be beneficial for WSS, because it could reduce parasitism since the parasitized larvae are more prone to cannibalism than unparasitized larvae. Another argument on “preference performance hypothesis” includes the female tendency to choose suitable host for oviposition that increases her own fitness, either for the sake of nutrition or for increasing their own longevity by laying eggs on a given host plant (Nanthagopal and Uthamasamy 1989, Mayhew 1997), also known as “optimal bad motherhood” hypothesis (Mayhew 1997). This condition is mainly expected to incur when there is conflict in the mother’s longevity and progeny’s larval development, growth and survival in different hosts (Jaenike 1986, Mayhew 2001, Scheirs and De Bruyn 2002, Janz 2005). In our system, WSS does not feed on host plants but lays multiple eggs per wheat stem in fields with higher levels of infestation due to sequential oviposition events by different females (Criddle 1923, Perez-Mendoza et al. 2006, Buteler et al. 2009), despite larval development being restricted to within one stem with a threat of cannibalism to their offspring. Furthermore, crops like oat, barley or rye are also acceptable hosts for oviposition by WSS, but larval development is not well supported in their stems (Farstad 1944, Gilbertson 1925). There are several species of cereal grains that were identified as showing some level of resistance to WSS larval development (Cockrell et al. 2017). Such conflicts between mothers and offspring is expected due to the searching behavior of female. In some species, the limited searching time for female to find suitable host for oviposition in terms of host-plant quality and distribution within habitat, potentially correlates with optimal bad motherhood (Tilmon 2008). While WSS is reported as a relatively weak flier, it was found to fly up to 800m distance to find a stem suitable enough for egg-laying (Criddle 1922). Similarly, optimal bad motherhood is expected to incur when herbivores are not restricted by evolutionary or physiological limitations. In evolutionary terms, selecting against the females who are choosing bad hosts requires several generations to show preference to the hosts that ensure fitness of their progeny. For instance, traits in insects may evolve that natural selection for those trait may occur that promote the avoidance of the unfavorable habitat, or physiological traits may evolve that increase survival of progenies in the previously unfavorable habitat (Hanski 2003). Similarly, when insects encounter novel plant species, the "preference performance hypothesis" is negatively correlated (Chew 1977, Thomson 1988).

Relationship between exotic hosts and native herbivores

WSS is a native herbivore to United States whose original hosts were large-stemmed feral grasses. With the conversion of natural grassland into cultivated farms, the scarcity of natural wild grassland caused WSS to adapt to exotic commercial crops like wheat. This adaptation resulted the WSS as a major pest in Northern Great Plains of

North America (Criddle 1915, Criddle 1922, Morrill and Kushnak 1996). They are also found infesting in the introduced invasive and forage grasses (Criddle 1915, Farstad 1940, Perez-Mendoza et al. 2006). Invasive plants may possess many organic volatile compounds and other chemical compounds that may either attract or repel completely, or attract but disrupt the development of native herbivores, thus influencing the plant-insect interactions (Bezemer et al. 2014). So, there is a need for better understanding of plant volatile compounds in uncultivated grasses and the influence of these compounds on WSS behavior among native hosts (Cockrell et al. 2017). Nutritional quality of plant tissues, primary and secondary metabolites, and morphological characteristics are determining factors that affect behavior and development of native herbivores (Awmack and Leather 2002). While wheat is an exotic host of WSS, it is a good host for WSS supporting frequent oviposition and good larval development. On the other hand, oat (*Avena sativa* L.), another exotic crop, is resistant to infestation by WSS, possibly due to the lack of essential nutrient needed for WSS development (Farstad 1940). However, there could be variation in the oviposition behavior and larval performance on different plant species as the herbivore is subjected to selection at variety of spatial scales due to their different host plant species (Thomson 1988).

There are species of brome grasses native to United States like mountain brome (*Bromus marginatus*) that have been reported to be infested by WSS (Ainslie 1929). The 16 haplotypes of WSS were found from the areas where congeneric species of grasses like smooth brome, *Bromus inermis ssp. inermis* (exotic species), mountain brome, *Bromus marginatus* (native species), and Pumpelly’s brome, *Bromus inermis ssp. pumpellianus* (native species) were abundant, addressing that some members of this genus are acting as reservoir of WSS (Lesieur et al. 2016). It has been reported that WSS shows greater infestation and foraging in smooth brome (Criddle 1922). The similarity of traits of plant species (Becerra 1997), or potential shared evolutionary history between native and non-native species (Ehrlich and Raven 1964) are expected to predict the intensity of herbivory on non-native species by native herbivores.

Some circumstances address the attraction of native herbivores to exotic plants, for example, the attraction of pierid butterflies towards exotic hosts like Eurasian crucifers that are closely related to their native host phylogenetically (Chew 1981). Similarly, switching hosts to a closely related exotic invasive host like *Cirsium vulgare* (Savi) Ten. from native thistles like *Cirsium altissimum* (L.) Hill have been discussed as a suppressing strategy against invasive species, provided that they possess similar allelochemicals (Suwa and Louda 2012). Thus, the close phylogenetic and physiological relationship between native and exotic host species can explain the suitability of exotic host for the native herbivores (Chew 1981, Harvey et al. 2012). There is an evolutionary arms race between invasive exotic species and native herbivores. To ward off the suppressing behavior of native herbivores, exotic plants can change morphologically (Strauss et al. 2006, Carroll and Fox 2007). Meanwhile, invasive exotic hosts can act as “evolutionary traps” that attract and accept native herbivores but readily lower their fitness compared to native hosts (Schlaepfer et al. 2005, Keeler and Chew 2008). Similarly, despite the fact that smooth brome, which is an exotic invasive grass, has been reported as suitable for foraging and infestation by WSS, it is also reported as an unsuitable host for complete larval development of WSS (Criddle, 1922). In contrast to this, despite wheat being an exotic host for WSS, wheat fields are now the source habitat for this pest while other grasslands appear to be a relative sink (Rand et al. 2014). To adapt to invasive plants and to shift hosts, native herbivores also develop traits when invasive plants benefit them as high-quality resources (Strauss et al. 2006, Carroll and Fox 2007) leading to morpho-physiological changes in native herbivores as driven by exotic invasive plants. Currently, the pattern of genetic diversity among populations of WSS collected from wheat and grasses (including native and exotic) was found to be similar (Lesieur et al. 2016).

Methodology

Field survey

Infestation and larval survival of WSS *Cephus cinctus* Norton was assessed in cropland near Big Sandy, MT, USA in 2018. To measure WSS infestation, larval mortality and parasitism in either wheat or in adjacent smooth brome, sampling was conducted in three transects in two fields. The selected winter wheat field (Big Sandy 1; 48º14´01.2″N, 110º20´41.8″W) and spring wheat field (Big Sandy 2; 48º13´09.0″N, 110º19´33.1″W) were located at two historically WSS-infested sites near Big Sandy, MT, USA (Fig. 1). Each site was selected to allow sampling of wheat plants in the growing wheat crop, as well as smooth brome plants along the edge of the wheat field. In addition, smooth brome plants were sampled along the edge of an adjacent fallow wheat field that was the source of the immigrating WSS adults. In Big Sandy 1, the winter wheat variety ‘War-horse’ was grown whereas in Big Sandy 2, spring wheat variety ‘Vida’ was grown.

Each site included three transects: the first was 5 m into the growing wheat field and was called ‘crop’, second was in smooth brome adjacent to the growing crop and was called ‘smooth brome-crop (SB-crop)’ and third was in smooth brome growing adjacent to the fallow wheat field that was the source of immigrating adult WSS and was called ‘smooth brome-fallow (SB-fallow)’. Three blocks were imposed across these transects perpendicularly, ensuring that each block included adjacent portions of all three transects. The fallow source was located opposite the growing crop on the other side of a county road between the fields. The distance between blocks was 5 meters (Fig. 2.). The road plus ditch was approximately 5 meters at Big Sandy 1 and 6.5 meters wide at Big Sandy 2. The sampling transects were set up along the field at a length of 80 meters.

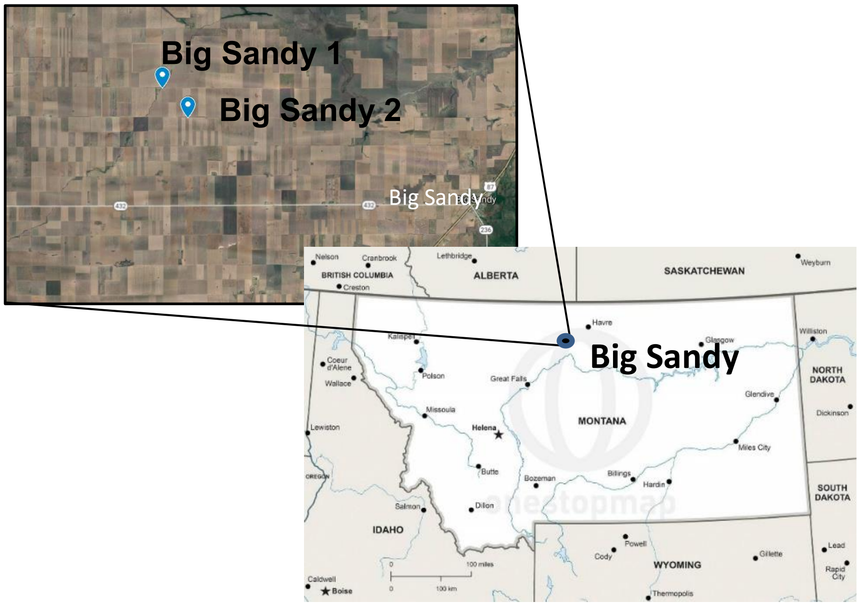

Fig 1. Geographic location of two fields, one cropped with winter wheat (Big Sandy 1) and other with spring wheat (Big Sandy 2) which were selected for sampling in Big Sandy, MT, US in 2018.

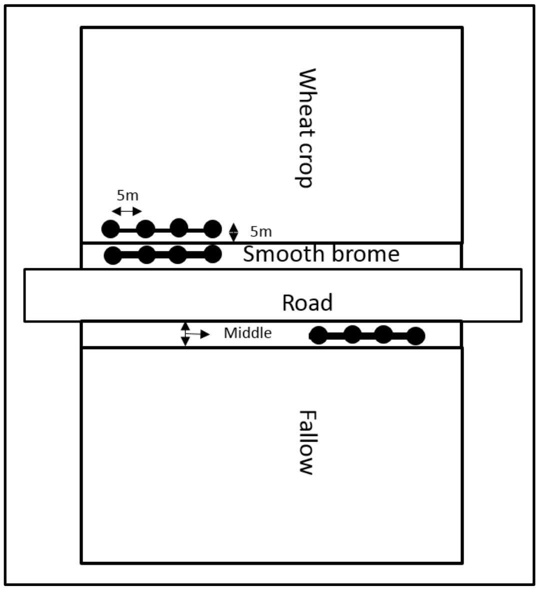

Fig 2. Layout of individual blocks (out of three blocks) for fields showing different transects and sampling points that were taken from an individual 25-meter block length of in both fields.

For each block, four smooth brome samples, consisting of uprooted stems were collected from a $0.1m^2$ area along the smooth brome-fallow and smooth brome-crop transects. Wheat samples consisted of all plants along a 30 cm length of row and were collected at 5 m intervals along the plant transect for each block. There were three sampling dates. The first sampling was conducted 10 July 2018 when winter wheat and spring wheat were headed but grains were immature. Due to phenological differences among winter wheat, spring wheat and smooth brome, both immature smooth brome samples and mature wheat samples were collected before harvest on 9th August 2018, whereas only the dry, mature samples for smooth brome were collected on the final sampling date of 19 September 2018. The samples were processed in the laboratory to assess proportion of infested internodes and proportion of parasitized stems, number of live and dead larvae by internodes, and WSS-cut stems as soon as they were brought into the lab, except the green smooth brome stem samples, which were stored in cold storage for few days while the samples were being dissected. The samples were processed using X-Acto® knives. Data on infestation, live eggs, dead eggs, dead larvae, live larvae and parasitism were recorded for each internode. I also recorded whether stems were vegetative or flowering for smooth brome. The phenology of smooth brome in the field includes vegetative stems that ripen and senesce at the end of the season without flowering and these were recorded as vegetative stems.

Greenhouse Experiments

Insects. Adult WSS were reared from wheat stubble collected in late summer and early fall 2018 from wheat fields near Amsterdam, MT, USA. Stubble contained WSS larvae in diapause, which were kept in a refrigerator at 0-4 °C for >100 days as required to complete obligatory larval diapause. Immature WSS were incubated at room temperature ranging from 22-27 °C for 4-5 weeks in sealed 70 cm x 35 cm x 20 cm plastic Tupperware® boxes to allow pupation and adult eclosion. Once emergence began, adults were collected daily and held in 2-liter glass Mason® jars containing moistened filter paper for humidification. Wooden skewers with attached glass vials (20 ml) containing water-moistened cotton plugs were placed inside jars to allow adults to move, perch and drink until they were used in experiments. The adults were used for the experiments within 24-48 hours of eclosion.

Plant materials. All choice or no choice bioassays were conducted in a greenhouse at the MSU Plant Growth Center in Bozeman, MT, USA. For bioassays, the susceptible spring wheat variety ‘Reeder’ was used and for smooth brome the commercially available ‘Manchar’ variety was used. Previously, we also attempted to grow mountain brome, a native brome, but this species did not reliably produce stems under greenhouse conditions (see Appendix on page 98).

Wheat plants were grown from seed stock and smooth brome was grown using transplants collected from plots maintained at the Post Agronomy farm of Montana State University. Because smooth brome is rhizomatous in growth habit, both plant species were grown in conical pots (top diameter 6.35 cm and depth 25.4 cm) to yield tillers comparable to those of wheat plants for bioassays. The plants were held in a greenhouse with supplemental light from model MVR1000/C/U GE Multi-Vapor Lamps (GE Lighting, General Electric Company, Cleveland, OH) under a photoperiod of 16:8 (L:D) h at 22 ± 2°C and 20 - 40 % RH. Soil used for growing plants consisted of MSU Plant Growth Center soil mix (equal parts of sterilized Bozeman silt loam soil and washed concrete sand with Canadian sphagnum peat moss incorporated) and Sunshine Mix 1 (Canadian sphagnum peat moss, perlite, vermiculite, and Dolomite lime) in a 1:1 ratio. Plants were fertilized twice each week using Peters Professional® General Purpose Fertilizer (J.R. Peters Inc., Allentown, PA) at the rate of 100 ppm in aqueous solution and were watered as needed. All experiments were conducted using plants at either the Zadoks 32 (two detectable nodes in the stem) stage or Zadoks 49 (fully elongated stem prior to flowering) growth stage (Zadoks et al. 1974), because these span the most favorable range for oviposition by WSS before flowering.

Y- Tube Olfactometer Bioassay. Y-tube bioassays were conducted in a chemical ecology and insect behavior laboratory in the Plant Growth Center at Montana State University. These were conducted to determine behavioral responses of individual female WSS to an airstream containing volatiles emanating from ‘Manchar’ smooth brome and ‘Reeder’ spring wheat. Separate bioassays were conducted using two different growth stages, Zadoks 32 and Zadoks 49. The Y- tube system (Analytical Research Systems, Micanopy, FL) used for the experiment was similar to that described in a previous study (Piesik et al. 2008). Briefly, for each growth stage, a single plant of each species in a container was enclosed in a volatile collection chamber (VCC) (outer diameter 100 mm, length 254 mm). Charcoal-filtered and humidified air was pressure regulated by a diaphragm air pump that delivered air at a rate of 0.2 L min^{-1}. Air passed into the VCC through a Teflon tubing connection with a 24/410 threaded glass joint. The lower end of the VCC enclosed each plant and was tightly sealed by a Teflon guillotine (Analytical Research Systems, Micanopy, FL) (diameter 995 mm, center opening 15 mm) that encircled the stem to prevent unpurified air from entering. The olfactometer system used a Y-shaped glass tube that had two arms that was connected to the lower port of each VCC by Teflon tubing (outer diameter 0.64 cm). This delivered the airstream from each enclosed odor source. Each plant housed inside a VCC was illuminated by enhanced spectrum LED grow light (Sunshine Systems Grow UFO Light SS-Gu90w, Led

Lighting4 Less, Paradise, CA) for one hour before the experiment to make plants photosynthetically active.

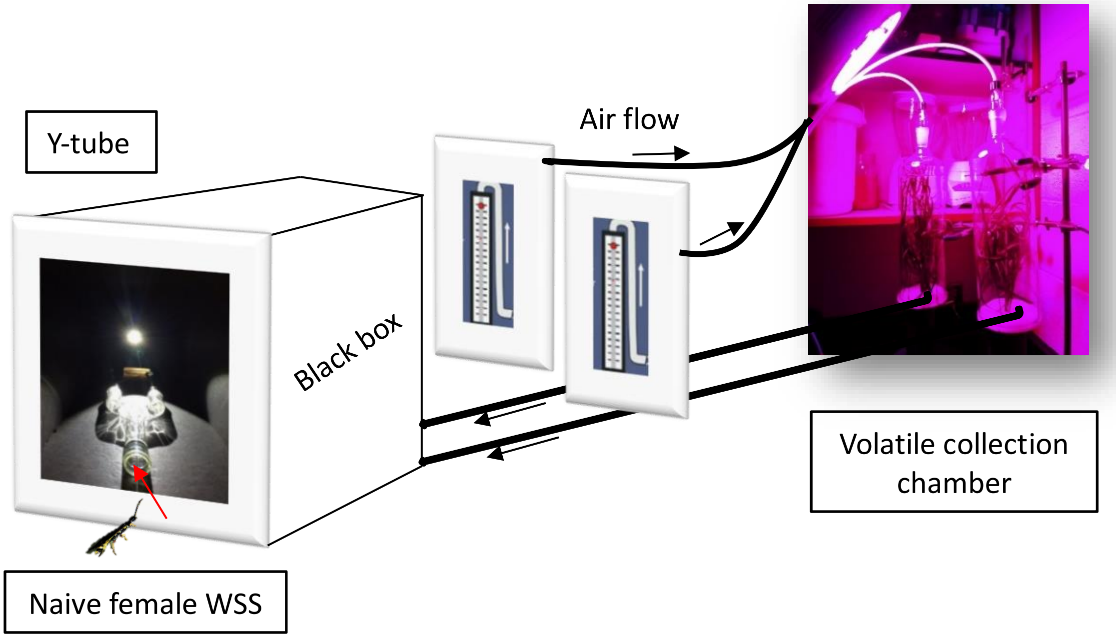

Fig 3. Y-tube olfactometer set-up in the laboratory.

The Y-tube was a 28-mm diameter x 300 mm long bifurcated Corning® glass tube that branched in Y shape at a 120° angle. Each branch served as an arm of the olfactometer. The stem of each Y-tube was 20 cm long. At the bifurcation, each branch extended 4 cm from the junction before ending in 10 cm parallel arms (Fig. 3.) The Y-tube was oriented horizontally inside a black poster board box (46.0 x 32.0 x 101.5 cm) that prevented entry of ambient light. The black box had two holes on the upstream side of the olfactometer, one allowing a fiber optic illuminator (T-Q/FOI-1, Techni Quip Corp, E1 Segundo, CA) to deliver light equally to both arms from center of the bifurcation, while the other hole allowed access for Teflon tubing connecting the VCC to an arm of the Y-tube (Fig. 3). Each arm delivered volatiles from one plant species to the stem of the Y-tube. The movement of adult WSS is positively phototactic and the horizontally placed Y-tube was positioned such that the light distribution towards both arms was balanced to avoid bias. The arms of Y-tube were carefully oriented to minimize directional bias and the position of the plants was alternated between assays.

Individual naive female WSS were introduced 1 cm into the unbranched end of the Y-tube. A 28-cm wire was used to facilitate WSS movement from the unbranched stem of the glass Y-tube to the test junction between the two upper arms. The order of individual test insects from a pool of naive females was randomly assigned for each bioassay, and test plants were also chosen randomly from the greenhouse culture before each experiment. Individual smooth brome and wheat plants at the same growth stage, either Zadoks 32 or Zadoks 49, were used as odor sources. All glassware was thoroughly cleaned using non-foaming Alconox® detergent in warm water, followed by solvent rinses with acetone and hexane. Clean glassware was baked at 110°C in a glassware oven for 24 hours before use. A new set of plants were used for each experiment.

In addition, at the start of experiment the choices of individual WSS were assessed using air from empty VCC chambers at both ends of the Y-tube to ensure that there was no directional bias. Subsequently, air from an empty VCC chamber was used as a control, while air passing over wheat or smooth brome was the treatment. These trials were conducted to assess upwind orientation of female WSS towards the airstream containing volatiles emanating from these host plants. It was expected that both plants would be preferred over purified air, but this trial was a necessary step before assessing choices made when female WSS could respond to volatiles in the airstream from both host plants.

Each individual female WSS was allowed five minutes to respond to either airstream. If the response was positive to either airstream, the trial ended. If no choice was made after five minutes, the trial was ended, and the result was recorded as no response. In the trial conducted to assess preference for the airstream containing volatiles of control (air) and wheat at Zadoks 32 and Zadoks 49, sixty individuals were assessed in each trial separately. Similarly, in the assessment of preference for the airstream containing volatile of control (air) and smooth brome at Zadoks 32, sixty individuals were assessed, and eighty-two individuals were assessed at Zadoks 49. Similarly, eighty-five individuals of female WSS were assessed for preference for airstreams containing volatiles of smooth brome and wheat at Zadoks 32, and ninety-two individuals were assessed at Zadoks 49. The trials that utilized plants at Zadoks 32 were conducted 21 March to 25 April 2018, and all the trials at Zadoks 49 stage were conducted from 26 September to 12 October 2018. Data for individuals that did not respond were not used in the analysis as this could be due to the various other confounding factors like environment and insect condition.

Host Preference and Oviposition Behaviors - Choice Bioassays. This experiment was conducted to determine whether there are differences in foraging and oviposition behaviors of WSS when provided a choice of two host plants that include all visual and tactile cues as well as volatile profiles. Visual observations were made to quantify the differences in a sequence of events that lead to ovipositor insertions and egg deposition when provided with a choice of either wheat or smooth brome. These choice tests were conducted in the greenhouse at the MSU Plant Growth Center in Bozeman, MT during summer 2018. In each cage containing pots planted with both plant species, fifteen female WSS and five male WSS were released. The experiment was only conducted on bright sunny days since WSS are much more active under these conditions. The photosynthetic activity of test plants was also favored on bright days.

The behaviors studied in this experiment allowed me to ultimately quantify the number of ovipositor insertions that resulted in egg deposition in the stem and to also record the overall differences in egg deposition by all fifteen females within a 3.5-hour time frame from 10 am - 1:30 pm. In addition, all specific behavioral events exhibited by each female WSS were recorded, as well as their duration. These behaviors included: walking, abdominal tapping, quiescence, either on the leaf or on the stem, and ovipositor insertion on the stem. These are the behaviors of WSS that lead to oviposition in susceptible and resistant wheat (Buteler et al. 2009, Varella et al. 2017). The location of oviposition insertion in the stem was marked on a recording plant diagram, noting the approximate distance from each node. One smooth brome and one wheat plant were placed inside a screen cage (91 X 67 X 91cm with 530 µm mesh openings) with two replications each day. Replicates in which insects were not active for the first hour in cage after the start of experiments were discarded. After three and a half hours, the pair of plants were removed from cages and stems were dissected to observe location and number of eggs in stems of each host plant. The recording plant diagram helped match the exact location and also correctly score the number of ovipositor insertions that led to egg deposition in the stems. It is important to note that ovipositor insertion into the stem might not lead to actual egg deposition due to various contact cues encountered after they alight on the plant surface or by the ovipositor inside stems (Varella et al. 2017). The number of ovipositor insertions that resulted in eggs in the stem (acceptance of the host stem as an oviposition site) were also quantified. This quantification helped us to better assess the number of oviposition attempts made before depositing eggs in each plant type. Altogether, we used twenty and twelve cage trial bioassays at Zadoks 32 and Zadoks 49, respectively, for analysis.

Choice Tests to Determine Infestation and Oviposition. Oviposition patterns might differ over a longer duration than is possible for direct behavioral observation, so we conducted a second-choice test in the greenhouse. Fifteen female WSS and five male WSS were introduced into a 47 X 47 X 91 cm screen cage with 530-µm mesh openings (BioQuip Products, Rancho Dominguez, CA), containing single plants of each species (wheat and smooth brome) in separate pots. This trial was also conducted in a series using plants at two different growth stages, Zadoks 32 and Zadoks 49. Due to limitations on insect availability these were conducted at different times. Female WSS were allowed to oviposit in their preferred hosts for forty- eight hours. The exposed plants were then dissected to record the total number of eggs in each plant. The egg loads in each plant type was recorded by segregating the type of stem as either ‘main stem’ with all other stems as ‘tillers’. Experiments were conducted in late summer in 2018 using fifteen replicates for bioassays at Zadoks 32 conducted from 27 July to 13 August of 2018, and twenty-one replicates at Zadoks 49 conducted from 27 June to 17 September of 2018.

No-Choice Tests to Determine Infestation and Larval Survival. Ecologically, factors such as proximity to another favorable host plant could influence oviposition and infestation in the choice tests described above (Mayhew 1997, Scheirs et al. 2000, Scheirs and De Bruyn 2002). So, to understand patterns of infestation and development of WSS in the absence of exploration of two plant types, no-choice tests were conducted by enclosing a single plant inside a transparent plastic tube (767 ml volume, 4.5 diameter X 62 cm long) that was drilled for four, circular equally-spaced holes (4 diameter) (each covered with mesh cloth to allow air exchange) along the tube. Two experiments were conducted in series. The first experiment was conducted to evaluate infestation and oviposition of WSS when no alternate host plant choices were provided. The second experiment was conducted to measure differences in larval survival in the two host plant species by allowing infested plants to mature in the greenhouse. No-choice experiments were conducted with a cohort of plants at both Zadoks 32 and Zadoks 49 for the infestation study whereas plants were only assessed at Zadoks 49 for the larval survival study.

For the infestation and oviposition study at Zadoks 32, ten plants grown in individual pots were assessed after exposing with WSS in individual tubes in three trials that were conducted from 21 July to 28 September 2018. Similarly, for infestation and oviposition study at Zadoks 49, three trials were conducted in which fifteen plants that were grown separately in individual pots were exposed to WSS using individual tubes. These were conducted from 19 July to 2 September 2018. Each tube containing either a single wheat or smooth brome plant received five female and three male WSS to allow mating and oviposition for two days. After two days, plants were dissected to record infestation status and number of eggs in each stem. Diameter and length of stems were also measured to quantify impact of phenological parameters on infestation and egg numbers.

The second experiment was very similar but addressed larval survival. Three trials including twelve plants altogether, each grown in individual pots, were infested by enclosing each plant with individual tubes from 19 July to 5 September 2018. All procedures were identical to the oviposition and infestation study described above, but in this case the WSS exposed plants were grown in the greenhouse until they ripened. Due to phenological variation between wheat and smooth brome, the wheat plants matured earlier than smooth brome, so I dissected wheat first and assessed infestation status among the cohort of WSS-exposed plants and recorded the number of cut and uncut stems, as well as live or dead larvae among infested stems in this experiment. Subsequently I did the same for smooth brome stems.

Comparative Analysis of Collections of Volatiles. Volatile compounds were collected from intact smooth brome and wheat at two different stages inside a greenhouse at the MSU Plant Growth Center, Bozeman, Montana. Volatiles were collected from smooth brome and wheat in pairs at either Zadoks 32 or Zadoks 49 separately from six different trials for each growth stage, each trial containing either four to six replicates. For plants at Zadoks 32, volatiles were collected from 21 November 2017 to 1 January 2018 and at Zadoks 49, volatiles were collected from 7 November to 31 December 2018. The volatile organic compounds were collected from undamaged plants for six hours from 1000 to 1600 hr. Each day, I collected volatiles from paired smooth brome plants and wheat plants, enclosing individual plants inside a glass VCC that was 4 cm in diameter by 80 cm long. The volatile collection and GC-MS analysis was conducted following methods initially described in Weaver et al. (2009). The chamber was fitted with a volatile collection port at the upper end and was open at the base to enclose plants. Two glass filters (6.35 mm diameter by 76 mm long; Analytical Research Systems, Gainesville, FL) with 30mg of Super-Q adsorbent (Alltech Associates, Deerfield, IL) were inserted in each volatile collection port. One trap was used to collect extraneous volatile compounds from the initial experimental set up for the first ten minutes, whereas the other trap filter was used to trap volatile compounds emanating from plants beginning ten minutes after the system was switched on. A regulated vacuum pump was used to maintain the pressure and flow rate of purified, humidified air at 1.0 liter/min over the plant inside the collection chamber. A Teflon® guillotine was used at the base of plant to tightly enclose the stem and to prevent entry of external air into the system. Each plant stem was also wrapped with a small piece of absorbent cotton before adjusting the guillotine to further prevent entry of extraneous volatiles from soil and to also prevent wounding from the guillotine. A 200 µl aliquot of dichloromethane was used to elute samples from trap filters containing the volatiles collected from plants. Trapped volatiles were eluted slowly by adding dichloromethane and further cleared by using a slow release of nitrogen gas. The eluted samples were collected in a glass insert held in a 1.5-ml crimp top glass vial. Next, 10µl nonyl acetate was added to eluted samples as internal standard to quantify compounds. The sample solution was subjected to gas chromatography (GC) on a HP - 5MS; 30m × 0.25mm, 0.25 µm film thickness column; (J and W Scientific, Folsom, CA). For analysis, the GC instrument (Agilent 6890; Agilent Technologies, Santa Clara, CA) was coupled to a mass spectrometer (MS, Agilent 5973 instrument). The samples were injected onto the column in pulse splitless mode, with the initial pressure of 82.7 kPa per minute. The inlet temperature of GC was adjusted at 250 °C. Column temperature was 50 ºC for 4 minutes, and temperature was increased at the rate of 5 ºC per minute until it reached 160 ºC, at which time it was further increased at the rate of 25 ºC until it reached the final temperature of 280 ºC. The temperature of the transfer line leading to the mass selective detector (MSD) was set at 300 ºC. The flow rate of samples in the column was maintained at 1.2 mL/min using helium as a carrier gas. The MSD was set in 'Scan' mode running from 50 – 300 m/z.

Compounds collected from wheat and smooth brome were identified by comparing mass spectra and retention time of authentic standards for a similar set up on this instrument, and by using the National Institute of Standards and Technology (NIST) library for comparing the spectra of unknown compounds. The actual quantity of compounds was calculated relative to the internal standard using a detector response of unity.

Data Analysis

Field Survey

The two field sites contained different types of wheat crops, so the analysis of all parameters was conducted separately for two fields. The statistical analysis was performed in R version: 3.4.1 (R Core team, 2017) using linear model after square root transformation to improve the normality and constant variance assumptions. 'Transect type' and 'block' were used as fixed effects (treatments) and mean number of infested stems, parasitized stems, dead larvae, alive larvae, dead eggs, alive eggs in sampling unit were used as the response variable analyzing the differences in parameters among the transects. The levels for the factor 'transect type' were 'smooth brome-crop' (SB-crop), 'smooth brome-fallow' (SB-fallow) and 'crop'. I conducted analysis of variance (ANOVA) that calculated P-values using F- distribution to understand overall significant differences in mean WSS infestation, parasitism, number of live and dead eggs and larvae among transects. Additionally, to further investigate the mean proportion of infestation and average number of dead larvae in various transect by internodes of plants at 'vegetative' and 'flowering stage' (Zadoks 32-Zadoks 69), I fitted responses in linear model for analysis using ANOVA, for each field. The response variables were square root transformed improve the normality and constant variance assumptions. To further assess differences in responses among levels of transects and levels of stage, a post hoc ranked Tukey test was conducted using the 'multcomp' package (Hothorn et al. 2008) in R version 3.4.1. Similarly, based on data collected in stems with larva-tunneled nodes that were accompanied by dead larvae from different transects in the Big Sandy 1, I analyzed the mean proportion of tunneling of stems for each transect type from the first collected samples taken on 10 July 2018. The tunneling data were fitted to a linear model after log transformation to improve normality, followed by ANOVA value and Tukey test using 'multcomp' package (Hothorn et al. 2008) in R version 3.4.1.

Greenhouse Experiments

Y tube Olfactometer Bioassay. The difference in responses to volatiles in the airstream from test plants or pure air were analyzed using a simple Pearson’s chi-square test in R version 3.4.1 (R Core team 2017). Data for observed choices were analyzed using chi-square test of independence with an alpha level of 0.05 to test significant difference in choice of WSS for each odor sources.

Host Preference and Oviposition Behaviors - Choice Bioassays. To contrast the number of each behavioral events, I did a simple Pearson’s Chi-square test whereas, to understand the difference in time interval WSS spent on each behavior at each stage, data were analyzed using linear mixed model using ‘nlme’ package (Pinheiro et al. 2013), which was then analyzed using ANOVA in the ‘car’ package (Fox and Weisberg 2011). Further differences in time duration between plant species for each behavior were differentiated by conducting a post hoc ranked Tukey test using ‘multcomp’ package (Hothorn et al. 2008) in R version 3.4.1. (R Core team 2017). Before conducting analysis individually, the MANOVA test in R version 3.4.1 (R Core team 2017) was carried out to determine overall influence of all behavioral time durations for both Zadoks stages separately after square root transformation. The time duration analysis for individual behavior was square root transformed to improve normality; plant species and location were used as fixed effects and interaction between location and plant species were dropped as they were not significant in either Zadoks stage. Date of the experiment and cage representing individual choice bioassay were used as random variables.

Choice Tests to Determine Infestation and Oviposition. A univariate analysis was used for analyzing choice data in R version 3.4.1 (R Core team 2017). Infestation data were analyzed by fitting to a generalized linear model (GLM) with random variable (glmer) using lme4 package (Bates et al. 2015) to account for variation due to date of infestation, which was then analyzed using ANOVA from ‘car’ package (Fox and Weisberg 2011) with ‘likelihood ratio test’ (chi-squared). The binary response variable recorded as either ‘infested’ or ‘uninfested’ allowed me to analyze responses using binomial distribution with a ‘logit’ link function. Egg counts were analyzed using a Poisson distribution which was then analyzed using ANOVA from ‘car package’ (Fox and Weisberg 2011) with ‘likelihood ratio test’ (chi-squared) in R version 3.4.1 (R Core team 2017). The interaction among date of infestation, plant species and stem types were fitted in the model as explanatory variables. Interactions with no significance were dropped from the model and further analyzed using fixed effects of treatments. The model was refined subsequently with backward selection.

No-Choice Tests to Determine Infestation and Larval Survival. Potted experimental plants contained many tillers, especially at Zadoks 49. Stems were sorted into two groups as ‘main stem’ or ‘tillers’, where primary, secondary and tertiary tillers were pooled together as ‘tillers’ for recording of the proportion of infestation and the oviposition rates (number of eggs) as well as for data from the survival study. Diameters (mm) were averaged for each stem type and average heights (cm) were calculated for all stems and tillers using the length of each internode.

For analyzing data on infestation, a generalized linear model with a binomial distribution was fitted for assessing interactions between the factors stem type, plant species diameter and length. A similar model was fitted to assess the impact of these factors on number of eggs using a generalized linear model with a Poisson distribution. Models were over dispersed and thus were corrected for the ‘quasi-binomial error’ and ‘quasi-Poisson error,’ respectively. Backward selection of the model was conducted by eliminating the insignificant interactions. Analysis of variance was conducted using the ‘car’ package (Fox and Weisberg 2011) with likelihood ratio test (chi squared), and significantly different factors were contrasted further using post hoc ranked Tukey test in ‘multcomp’ package (Hothorn et al. 2008) in R version 3.4.1 (R Core team 2017).

Comparative Analysis of Collections of Volatiles. The amount of volatile compounds was calculated in nanogram per gram per hour ($ng^{-1}g^{-1}hr^{-1}$) after correcting for plant biomass. Data were subjected to factorial multivariate analysis of variance (MANOVA) using R version 3.4.1 (R Core team 2017) to determine differences among identified plant volatile compounds between two plant types at two developmental stages, also assessing its interaction with date of volatile collection. Potential compounds that might contrast volatiles between wheat and smooth brome were further analyzed using univariate ANOVA using ‘car’ package (Fox and Weisberg 2011) after fitting a linear mixed model. The amount of each compound was assessed as a response variable fitting plant types as treatment and replication as a random variable. Volatile collections for the two different growth stages were conducted separately on different days, so I analyzed these separately. Data were transformed using log2 (x+1) transformation to better meet assumptions of normality, but untransformed data are presented for the amounts of compounds.

Results

Field Survey

In Big Sandy 1 field, I found a significant interaction between transect and block (F (4, 27) =6.80, P = 0.00) when assessing proportion of infestation. There was no difference in mean proportion of infested stems within the blocks in crop transects (Fig. 4). The first block was infested less than the second block within SB-crop transect and infestation was greater in third block compare to second block in SB-fallow transect (Fig. 4). Comparing smooth brome adjacent to fallow and smooth brome adjacent to crop, the infestation was greater when adjacent to fallow than when adjacent to crop in the second block (Fig. 4). I did not find any differences in infestation between smooth brome adjacent to fallow or adjacent to wheat in the third block (Fig. 4). Without accounting for blocks, there was no difference in the transect types in Big Sandy 1 field F (2,27) = 0.31, P = 0.73) (Fig. 5).

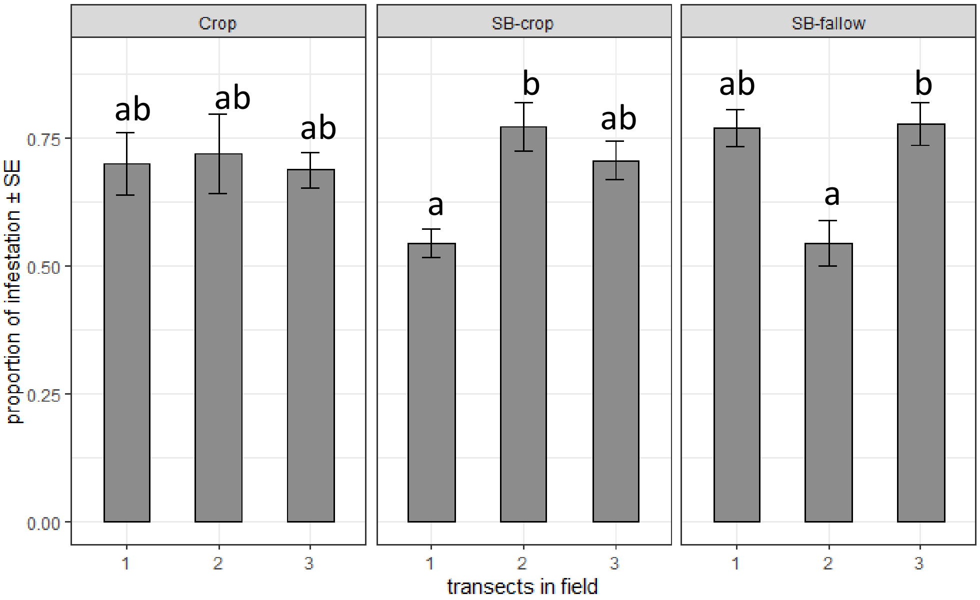

Fig. 4. Mean proportion of wheat stem sawfly infested stem samples taken along transects and blocks in field Big Sandy 1.

[1] The letters indicate significant difference among the blocks transects (P < 0.05) at α = 0.05.

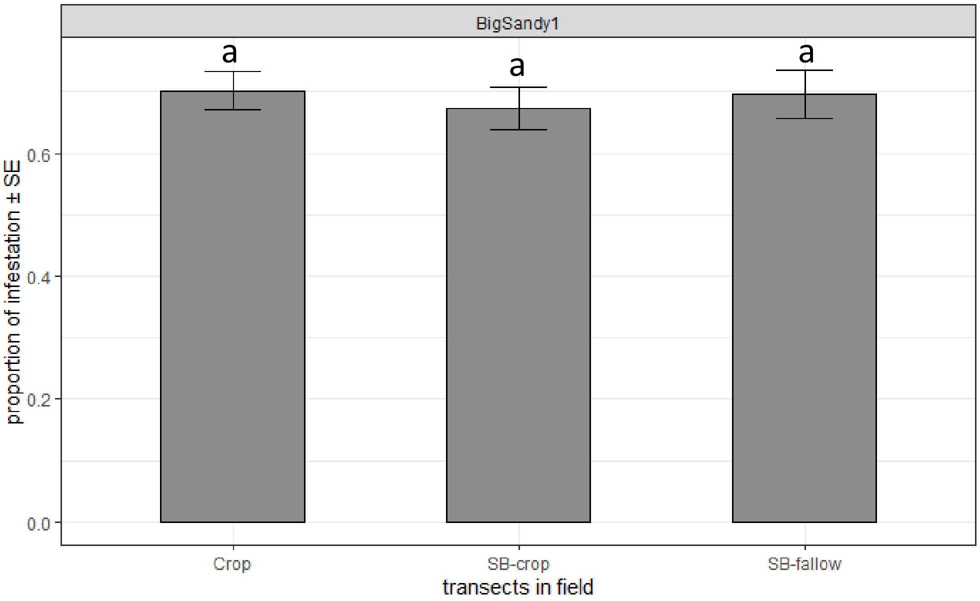

Fig. 5. Mean proportion of wheat stem sawfly infested stem samples taken along transects in field Big Sandy 1.

[2] The letters indicate significant difference (P < 0.05) among transects at α = 0.05

In the Big Sandy 2 field, the mean infestation in the stem samples was different among transects (F (2, 31) = 199.31, P = 0.00). Spring wheat was less infested in crop transect compared to smooth brome in SB-crop transect (Fig. 6). Similarly, I found strong evidence that there was greater infestation in SB-fallow than in crop transect (Fig. 6). However, there were differences in the proportion of stems infested by WSS among the transect types in Big Sandy 2 field.

The proportion of tunneling among transects was different (F (2, 685) = 172.29, P = 0.00). Smooth brome at SB-crop and SB-fallow transects had lower proportions of tunneling than winter wheat in Big Sandy1 (t = -13.49, P = 0.00) and (t = -17.62, P = 0.00) respectively (Figure 7).

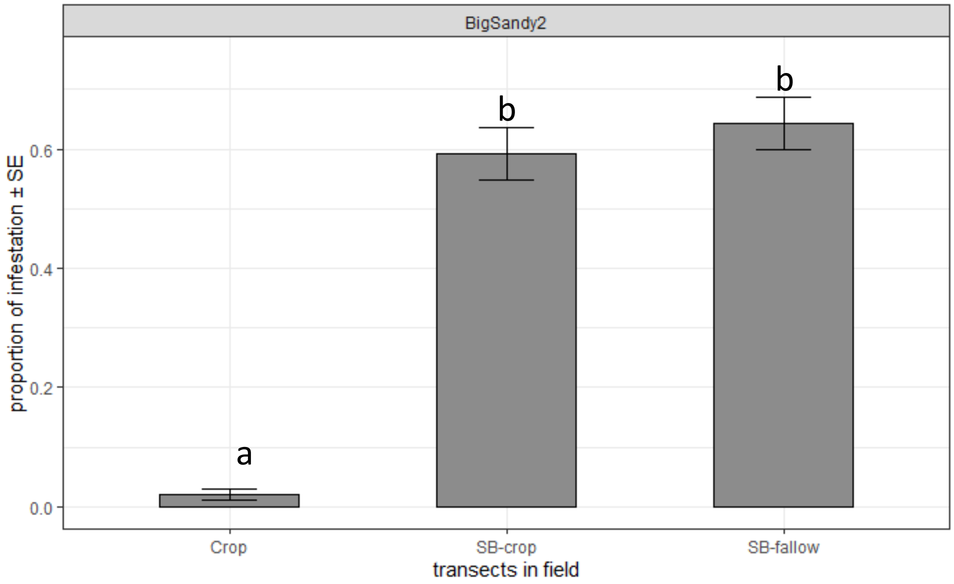

Fig. 6. Mean proportion of wheat stem sawfly infested stem samples taken along transects in field Big Sandy 2.

[3] The letters indicate significant difference ($P < 0.05$) among transects at $\alpha=0.05$

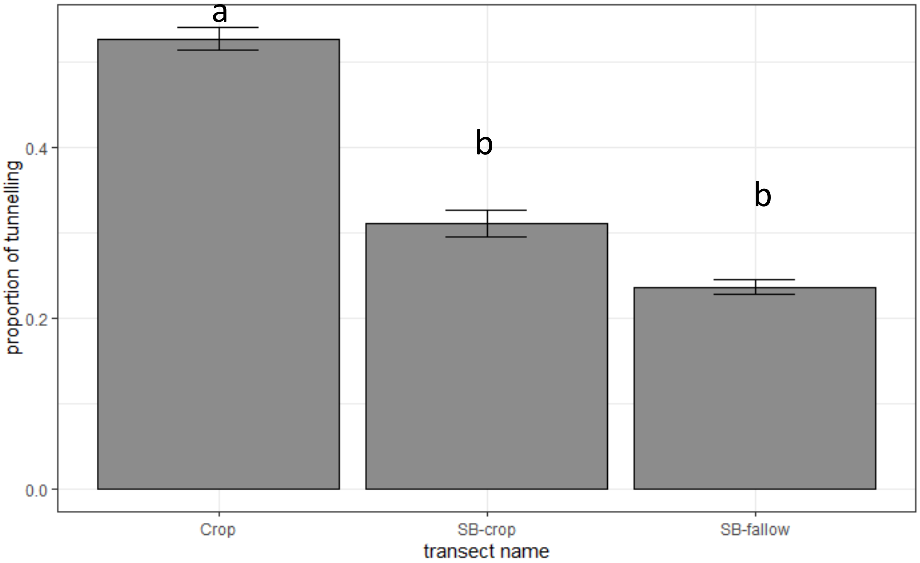

Fig. 7. Mean proportion of nodes tunneled by wheat stem sawfly larvae in stem samples taken along transects in field Big Sandy 1 on first sampling date (10 July 2018).

In Big Sandy 1, when the mean proportion of infested internodes in samples was investigated, this was found to vary depending on the phenological type (vegetative or flowering, i.e. sample contained stems at Zadoks 32 to Zadoks 69)) of stems in samples (F (2, 56) = 77.49, P = 0.00). Using a Tukey test using ‘multcomp’ package (Hothorn et al. 2008) in R version 3.4.1 (R Core team 2017), I found a greater proportion of internodes in the flowering stems than for the vegetative stems in transects (t = 8.80, P = 0.00) (Fig. 8).

In Big Sandy 2, there was a difference in mean proportion of infested internodes in samples among the transect types (F (2, 56) = 177.61, P = 0.00). For all transects, there were differences in infestation depending upon the phenological type (vegetative or flowering) of stems (F (1, 56) = 75.31, P = 0.00). The stems from crop transect were less infested than in smooth brome from the SB-fallow transect (t = -17.81, P = 0.00) or smooth brome from the SB-crop transect (t = -17.04, P = 0.00) (Fig. 9).

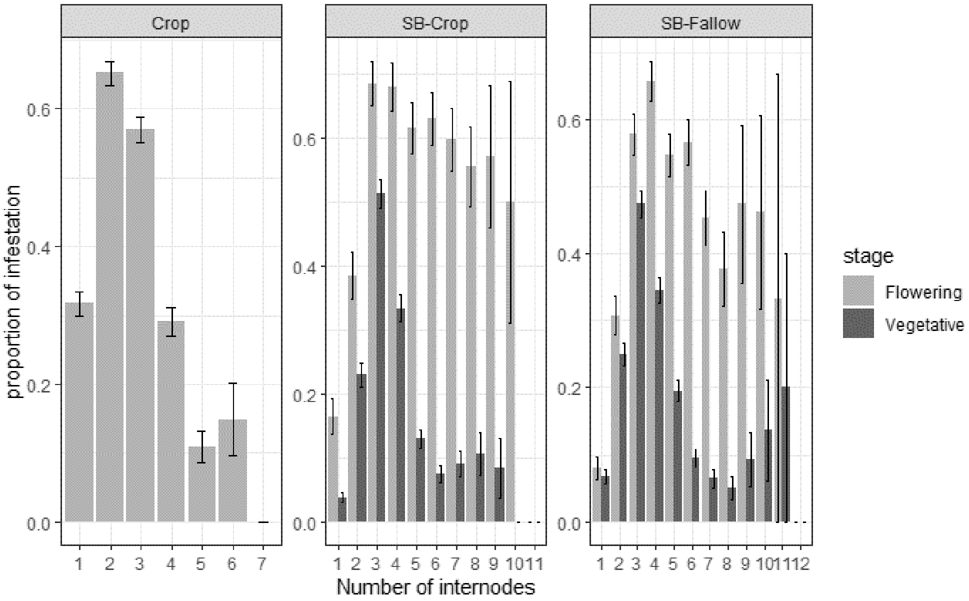

Fig. 8. Mean proportion of infested internodes in stem samples taken along transects in the field Big Sandy 1 for both flowering and vegetative stems.

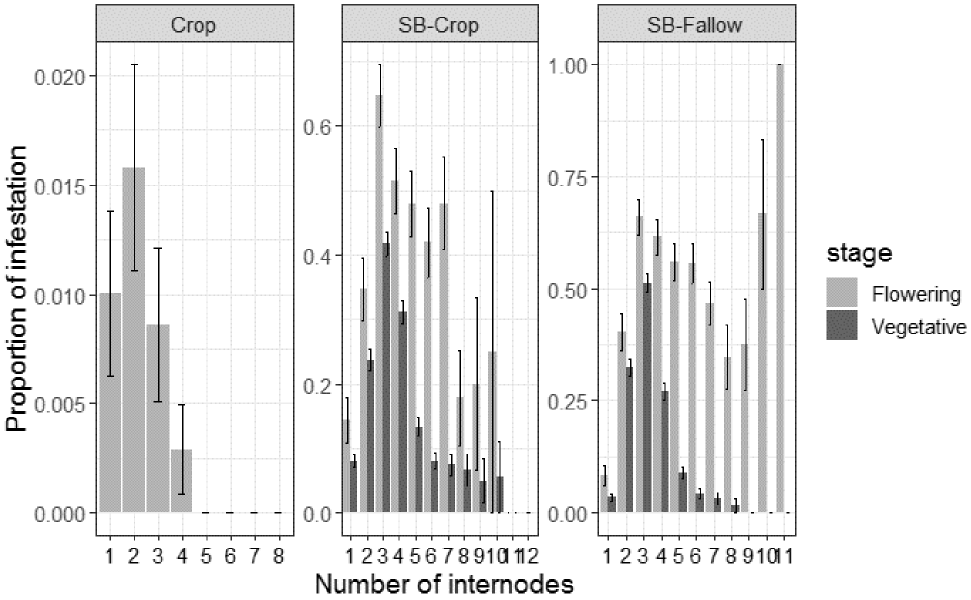

Fig. 9. Mean proportion of infested internodes in stem samples taken along transects in the field Big Sandy 2 for both flowering and vegetative stems.

For the number of dead larvae in the sample stems among transects at Big Sandy 1, I found strong evidence for an effect of transect on the number of dead larvae F (2,31)

= 15.04, P = 0.00 .There were fewer dead larvae in the crop transect than in the SB-crop transect (t= - 4.11, P = 0.00) (Fig. 12) There was no difference in mean number of dead larvae in stems from the SB-fallow transect compared to smooth brome from the SB-crop transect (t= 0.52, P = 0.52) (Fig. 9). Also, smooth brome in SB-fallow transect had more dead larvae in the stems than for those from the crop transect (t = 5.20, P = 0.00) (Fig. 12).

For the Big Sandy 2 field, there was a difference in number of dead larvae in the stems between some transects F (2,31) = 98.62, P = 0.00. I found more dead larvae in the stems from SB-fallow transect than in stems from the crop transect (Fig. 10) and less dead larvae in stems from the crop transect than from SB-crop transect (Fig. 10). There was no difference in the mean number of dead larvae in smooth brome samples taken from the SB-crop and SB-fallow transects.

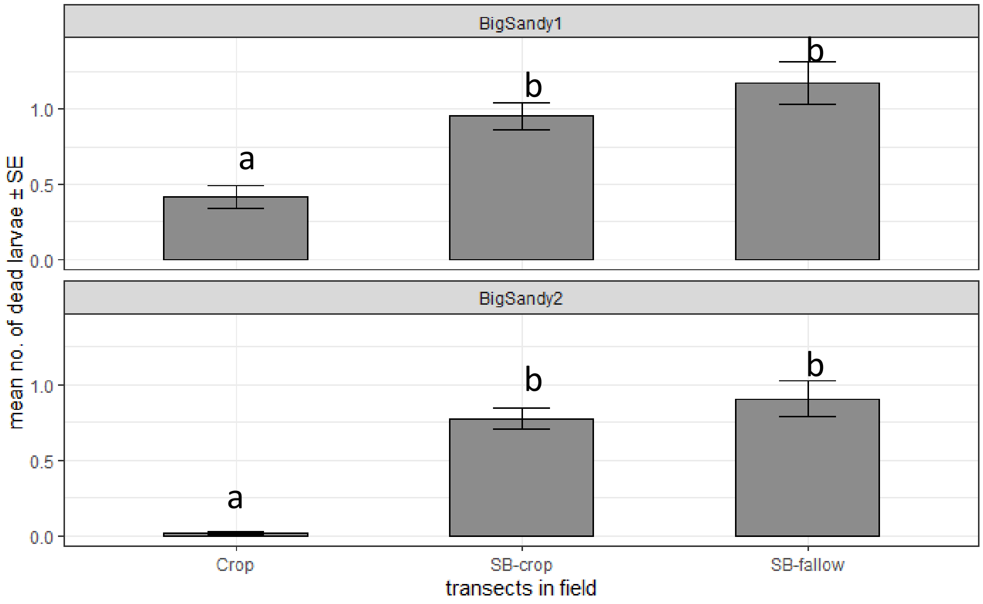

Fig. 10. Mean number of dead larvae of wheat stem sawfly in stem samples taken along transects in two fields.

[4] The letters indicate significant difference ($P < 0.05$) among transects for the individual fields at $\alpha=0.05$

When investigating the mean number of dead larvae by internodes for stems collected along transects at Big Sandy 1, I found significant differences in the number of dead larvae among transects (F (2,56) = 21.06, P = 0.00) and by phenological type (vegetative or flowering) (F (1,56) = 33.81, P = 0.00) with more dead larvae in flowering stems. From the Tukey test, I found fewer dead larvae in the winter wheat transect than in either the SB-crop transect (t = -5.57, P = 0.00) and SB-fallow transects (t = - 6.31, P = 0.00) (Fig. 11). Similarly, at Big Sandy 2, there were differences in the number of dead larvae among transects (F (2,56) = 88.01, P = 0.00) and among phenological type (vegetative or flowering) (F (2,56) = 26.82, P = 0.00). From the Tukey test, I found that spring wheat had fewer dead larvae than smooth brome at the SB-crop transect (t = -12.56, P=0.00) and SB-fallow transect (t = - 11.96, P = 0.00) (Fig. 12).

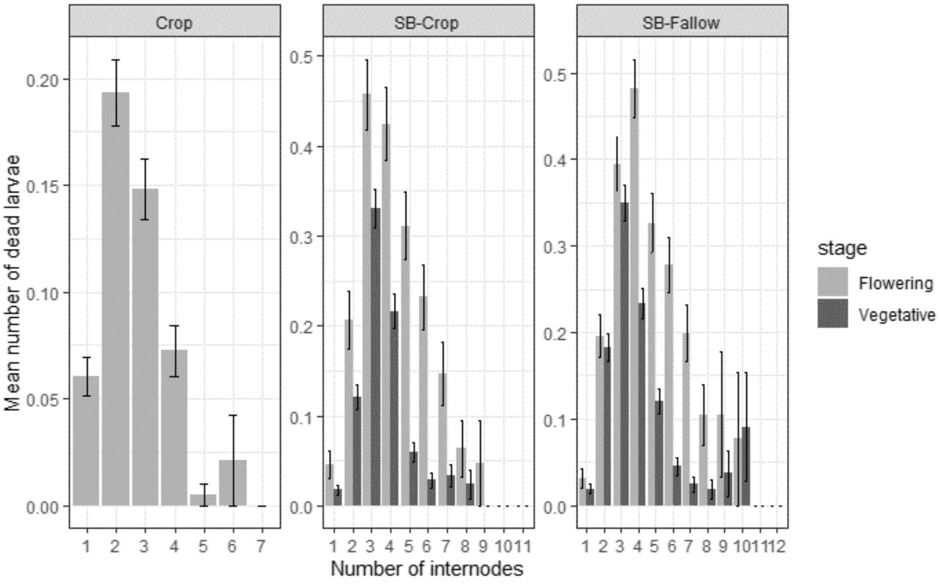

Fig. 11. Mean number of dead larvae of wheat stem sawfly in each internode of stem samples at vegetative and flowering stages taken along transects in field Big Sandy 1.

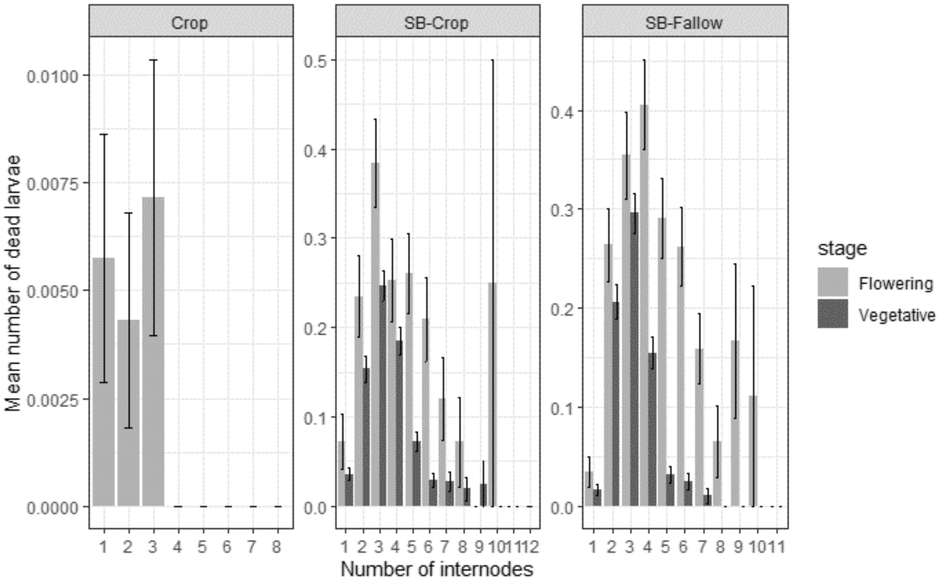

Fig. 12. Mean number of dead larvae of wheat stem sawfly in each internode of stem samples at vegetative and flowering stages taken along transects in field Big Sandy 2.

Overall, I found different mean numbers of live larvae among transects at Big Sandy 1 F (2, 31) = 27.98, P = 0.00. I found differences between the number of live larvae in stems from the crop and SB-crop transect (t = 6.007, P = 0.00) (Table 1). There was strong evidence for fewer live larvae in stems in SB-fallow than in the crop transect (t = - 6.86, P = 0.00) (Table 1). I did not find differences in the number of live eggs among transects at Big Sandy 1 (Table 2). Similarly, I did not find differences in the number of live larvae and live eggs in transects at Big Sandy 2 (Table 1 and Table 2).

Table 1. Mean number of live larvae of wheat stem sawfly in stem samples taken along transects in two fields.

Field	Transects in fields	Test statistics	Mean ± SE
BigSandy1	SB-crop	F (2,31) = 27.98, P = 0.00	0.01 ± 0.00 a
BigSandy1	Crop		0.14 ± 0.04 b
BigSandy1	SB-fallow		0.00 ± 0.00 a
BigSandy2	SB-crop	F (2,31) = 1.70, P = 0.20	0.00 ± 0.00 a
BigSandy2	Crop		0.00 ± 0.00 a
BigSandy2	SB-fallow		0.00 ± 0.00 a

[5] Letters indicate significant difference ($P < 0.05$) among transects from individual fields at $\alpha = 0.05$

Table 2. Mean number of live eggs of wheat stem sawfly in stem samples taken along transects in two fields.

Field	Transects in fields	Test statistics	Mean ± SE
BigSandy1	SB-crop	F (2,31) =7.41, P = 0.00	0.00 ± 0.00 a
BigSandy1	crop		0.02 ± 0.01 b
BigSandy1	SB-fallow		0.00 ± 0.00 a
BigSandy2	SB-crop	F (2,31) = 0.05, P = 0.95	0.00 ± 0.00 a
BigSandy2	Crop		0.00 ± 0.00 a
BigSandy2	SB-fallow		0.00 ± 0.00 a

[6] Letters indicate significant difference ($P < 0.05$) among transects from individual fields at $\alpha=0.05$

Overall, I found different numbers of dead eggs among transects at Big Sandy 1 (F (2,31) = 4.41, P = 0.02). There was strong evidence for fewer dead eggs in SB - fallow transects than in crop transects (t = - 2.94, P = 0.02) (Fig. 13) and no difference in mean number of dead eggs between stems from the SB-fallow transects or SB-crop stems (t = - 1.13, t = 0.50) (Fig. 13). Conversely, at Big Sandy 2, there were differences among transects (F (2,31) = 37.22, P = 0.00). There was evidence for fewer dead eggs in crop transects than in SB-crop transects (t = - 7.35, P = 0.00) (Fig. 13). There were more dead eggs in SB-fallow transects than in crop transects (t = 7.59, P = 0.00) (Fig. 13).

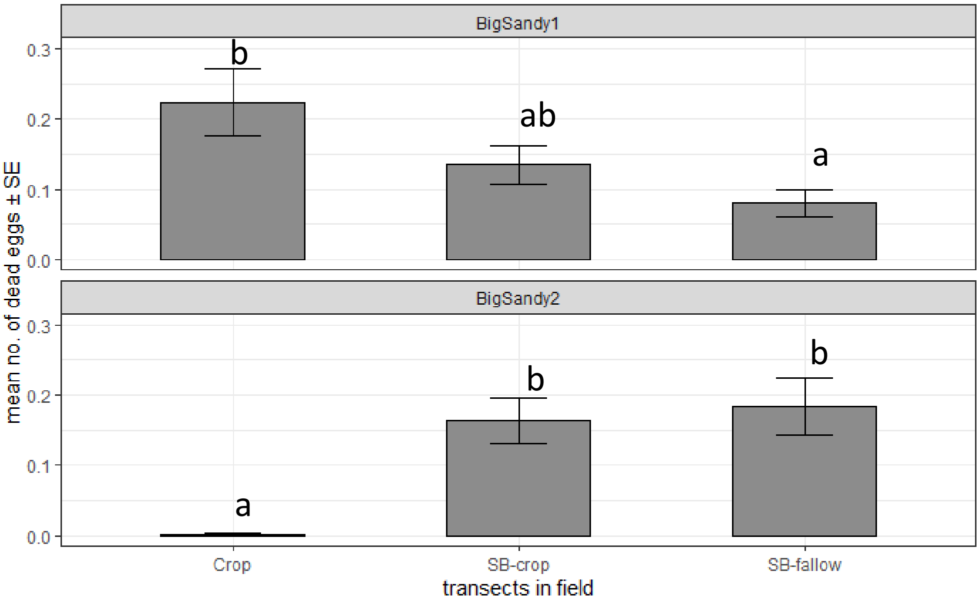

Fig. 13. Mean number of dead eggs of wheat stem sawfly in stem samples taken along transects in two fields.

[7] Letters indicate significant difference ($P < 0.05$) among transects for individual fields at $\alpha=0.05$

There was no difference in the mean proportion of parasitized stems in different transects in the field Big Sandy 1 (F (2, 31) = 0.32, P = 0.83) (Fig. 14). At Big Sandy 2 where spring wheat was cropped, there were differences in parasitism among transects (F (2,31) = 10.19, P = 0.00) with no difference in mean proportion of parasitized stems in SB-fallow transect compared to SB-crop transect (t = 1.62, P = 0.25). (Fig. 14), while there were more parasitized stems in SB-fallow transect compared to crop transect (t = 4.46, P = 0.00) and less parasitized stems in crop transect compared to SB-crop (t = -2.83, P = 0.02).

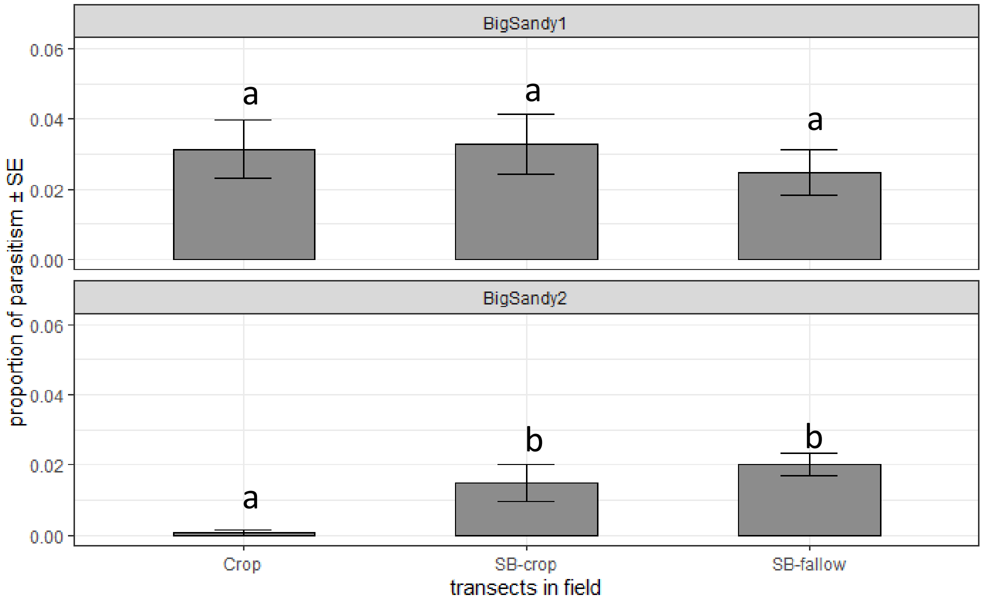

Fig. 14. Mean proportion of wheat stem sawfly parasitized stem samples taken along transects in two fields.

[8] Letters indicate significant difference ($P < 0.05$) among transects for individual fields at $\alpha=0.05$

There were more cut stems (mean ± SE = 0.12 ± 0.00, sum = 33) in winter wheat at Big Sandy 1 because no cut stems were found in the smooth brome transects in that field. I did not find any cut stems in any transects at Big Sandy 2. We did not find any cut stems in any transects in the spring wheat field.

Greenhouse Experiments

Y - Tube Olfactometer Bioassay. The upwind movement and choices of female WSS was assessed for the airstream containing volatiles emitted from wheat versus pure air (control). I found that female WSS preferred airstreams containing volatiles that were emitted from wheat ($P = 0.04$) (Table 3). Similarly, they also chose to move in the direction of the airstream containing volatiles emitted by smooth brome more than pure air ($P = 0.01$) (Table 3). Meanwhile, when airstreams containing volatiles emitted by both smooth brome and wheat plants were assessed, female WSS significantly preferred the airstream from the smooth brome plants over the airstream from wheat at Zadoks 32 growth stage (P = 0.01) (Table 3).

Table 3. Response of female wheat stem sawflies to the airstream containing volatiles emitted from wheat and smooth brome in a Y- tube olfactometer at Zadoks 32.

Stage	**Plant choices**	**Observed**	**Expected**	**Behavioral responses**	
				χ^2	P value
Zadoks 32	Wheat	33	24	4.41	0.04*
	Air	18	24		
Zadoks 32	Smooth brome	30	21	7.71	0.01*
	Air	12	21		
Zadoks 32	Wheat	21	31	6.45	0.01*
	Smooth brome	41	31		

[9] * indicate the significant difference in number of tested female WSS individuals showing preferences towards the airstreams containing volatiles emitted from wheat and smooth brome in each trial.

The response of female WSS in Y-tube experiments using wheat and smooth brome plants at Zadoks 49 stage was similar to the response at Zadoks 32. Female WSS preferred airstreams containing volatiles emitted from wheat more so than pure air (P = 0.04) (Table 4) and smooth brome more so than that of pure air (control) (P = 0.00) (Table 4). When airstreams containing volatiles emitted by smooth brome and wheat plants were assessed, female WSS significantly preferred airstreams from smooth brome over the airstreams from wheat (P = 0.03) (Table 4).

Table 4. Response of female wheat stem sawflies to the airstream containing volatiles emitted from wheat and smooth brome in a Y- tube olfactometer at Zadoks 49.

Stage	**Plant choices**	**Observed**	**Expected**	**Behavioral responses**	
				χ^2	P value
Zadoks 49	Wheat	37	26.5	8.32	0.04*
	Air	16	26.5		
Zadoks 49	Smooth brome	48	33.5	9.33	0.00*
	Air	23	33.5		
Zadoks 49	Wheat	32	41.5	4.35	0.03*
	Smooth brome	51	41.5		

[10] * indicate the significant difference in number of tested female WSS individuals showing preferences towards the airstreams containing volatiles emitted from wheat and smooth brome in each trial.

Host Preference and Oviposition Behaviors - Choice Bioassays. The MANOVA test did not show any differences in duration of any behaviors (Wilk’s lambda = 0.77, F = 0.39, P = 0.63) at Zadoks 32. The number of ovipositor insertions did not differ between wheat and smooth brome (P = 0.33) (Table 5). There were also no differences in the number of eggs deposited into the stems of the two species (P = 0.74) (Table: 5). However, at Zadoks 49 I found differences in the number of ovipositor insertions (P = 0.00) and eggs deposited (P = 0.00) for stems of wheat and smooth brome (Table 5).

Table 5. The number of ovipositor insertions and number of eggs deposited per insertion by female WSS in wheat and smooth brome stems at Zadoks 32 and Zadoks 49.

	Number of ovipositor insertions				**Number of eggs**			
Plant stage	Observed	Expected	χ^2	P value	Observed	Expected	χ^2	P value
Zadoks 32								
Wheat	22	19	0.94	0.33	4	5		
S. brome	16	19			6	5	0.40	0.74
Zadoks 49								
Wheat	14	27.5	13.30		4	9		
S. brome	41	27.5		0.00*	16	9	10.88	0.00*

[11] *indicates a significant difference in number of oviposition insertions by female WSS in the stems of wheat and smooth brome in each trial and also shows a significant difference in number of eggs deposited by female WSS in the stems of wheat and smooth brome for each trial.

Ovipositor insertions and antennal tapping happened each time after female WSS walked on stems of both wheat and smooth brome. At Zadoks 32, time spent walking differed between wheat and smooth brome (χ^2 (1) = 11.88, P = 0.00), and there were also differences in time spent walking that depended on location on the plants (χ^2 (1) = 5.83, P = 0.02). Specifically, wheat (on the stem) $_{\text{walking}}$ = 81 ± 17 seconds, smooth brome (on the stem) $_{\text{walking}}$ = 32 ± 5 seconds; wheat (on the leaf) $_{\text{walking}}$ =103 ± 11 seconds, smooth brome (on the leaf) $_{\text{walking}}$ = 82 ± 10 seconds (Fig. 15). No difference was observed for time in quiescence for female WSS on the two plant species (Fig. 16). However, time in quiescence on leaves was greater than on stems (Fig. 15). No interaction was found between location on plant and plant species. There were no differences in duration of abdominal tapping by WSS on stems of the two species (Table 6). There was also no difference in the time invested for ovipositor insertions in stems of either plant at Zadoks 32 (χ^2 (1) = 1.12, P = 0.29).

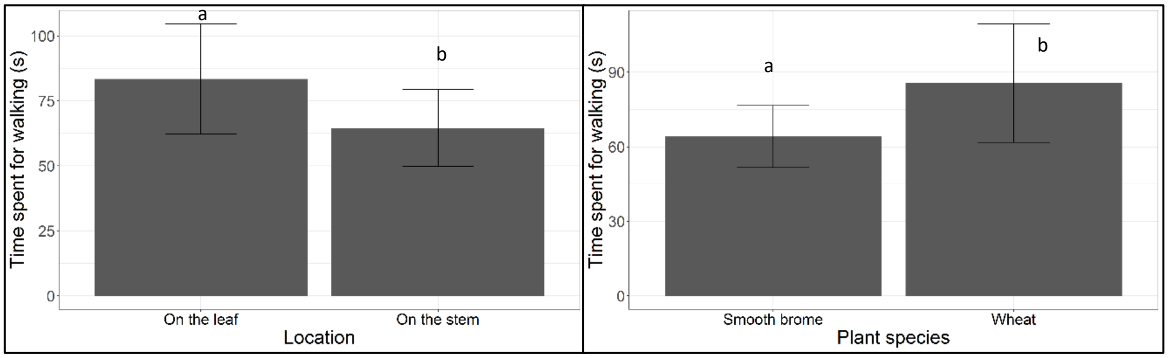

Fig. 15. a) Mean duration (seconds) for female wheat stem sawfly walking on wheat and smooth brome b) Mean duration (seconds) for female WSS walking on leaves and stems of two plant species at Zadoks 32.

Table 6. Mean duration (seconds) of behaviors for female WSS on wheat and smooth brome at Zadoks 32.

Plant Species	Behavior	N	Mean ± SE
Wheat	Abdominal tapping	20	31 ± 7a
Smooth brome	Abdominal tapping	32	22± 6a
Wheat	Ovipositor insertion	16	98± 34 a
Smooth brome	Ovipositor insertion	22	79 ± 10 a
Wheat	Quiescent	168	1194 ± 159 a
Smooth brome	Quiescent	224	1697 ± 174a
Wheat	Walking	266	98 ± 9a
Smooth brome	Walking	314	69 ± 7 b

[l2] Letters indicate significant difference (P < 0.05) between smooth brome and wheat for each behavior of female WSS at α=0.05

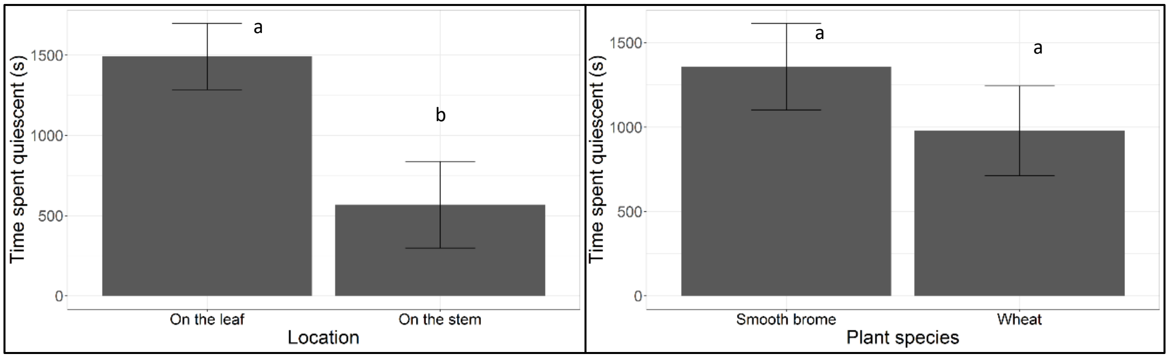

Fig. 16. a) Mean duration (seconds) for female wheat stem sawfly in quiescence on wheat and smooth brome b) Mean duration (seconds) for female wheat stem sawfly in quiescence on leaves and on stems of two plant species at Zadoks 32.

There was no difference in total duration of all behavioral events between wheat and smooth brome at Zadoks 49 (Wilks's lambda = 0.10, F = 6.74, P = 0.07). However, when I analyzed individual behaviors, there were significant differences in duration of time spent on ovipositor insertions per female (χ^2 (1) = 10.68, P < 0.05) (Table 7). Females frequently inserted their ovipositors into stems, which is required before choosing to deposit an egg. There was more observations of ovipositor insertions in smooth brome (N = 49) than in wheat (N = 14), which resulted in more eggs in smooth brome than in wheat (P = 0.00) (Table 5). Time spent abdominal tapping by female WSS was 12.4 ± 1.7 seconds for wheat, whereas, it was 45.3 ± 23.6 seconds for smooth brome (Table 7).

Table 7. Mean duration (seconds) of behaviors for female wheat stem sawfly on wheat and smooth brome at Zadoks 49.

Plant Species	Behavior	N	Mean ± SE
Wheat	Abdominal tapping	18	12 ± 2 a
Smooth brome	Abdominal tapping	22	45 ± 24 a
Wheat	Ovipositor insertion	14	102 ± 7 a
Smooth brome	Ovipositor insertion	41	80 ± 12b
Wheat	Quiescent	89	1456± 204a
Smooth brome	Quiescent	193	1001 ± 120a
Wheat	Walking	129	102± 32 a
Smooth brome	Walking	288	59 ± 6a

[13] Letters indicate significant difference (P < 0.05) between each behavior of female WSS at α=0.05.

Table 8. Overall frequency of behavioral events for female wheat stem sawfly on wheat and smooth brome at Zadoks 32 and Zadoks 49.

Behavior	Location	Smooth brome	Wheat	χ 2	P value
		Zadoks 32 stage			
Quiescent	On the leaf	200	154	5.98	0.00*
Quiescent	On the stem	24	14	2.63	0.10
Walking	On the leaf	232	204	1.80	0.18
Walking	On the stem	82	62	2.78	0.10
Abdominal tapping	On the stem	32	20	2.77	0.09
Ovipositor insertion	On the stem	22	16	0.94	0.40
		Zadoks 49 stage			
Quiescent	On the leaf	81	175	34.50	0.00*
Quiescent	On the stem	8	18	3.85	0.04*
Walking	On the leaf	209	101	37.63	0.00*
Walking	On the stem	79	28	24.30	0.00*
Abdominal tapping	On the stem	22	18	2.77	0.09
Ovipositor insertion	On the stem	41	14	10.88	0.00*

[14] Letters indicate significant difference ($P < 0.05$) between each behavior of female WSS at different locations on plant at α=0.05.

Although walking time on leaf and on stem was greater for wheat (116.20 ± 40.80 s) than for smooth brome (59.60 ± 7.00 seconds) and less on wheat stems (48.30 ± 11.50 seconds) compared to smooth brome stems (57.01 ± 14.20 seconds), respectively, no difference was observed between location on plant (χ^2 (1) = 1.23, P = 0.27) or plant species (χ^2 (1) = 0.87, P = 0.35). Nevertheless, they walked more frequently (N = 288) on wheat (N = 129), but with more frequent abdominal tapping (N = 22) in smooth brome than in wheat (N = 18). Similarly, WSS were more frequently quiescent (N = 193) on smooth brome than on wheat (N = 89) (Table 8). Most of the time walking and antennal tapping events were concurrent. Although differences were not observed for duration of quiescence between plant species, WSS were quiescent longer on wheat (1455.60 ± 203.50 seconds) than on smooth brome (1001.0 ± 120.10 seconds) (Fig. 17). However, they rested on leaves more frequently than on stems on both species (χ^2 (1) = 9.21, P = 0.00) (Table 8).

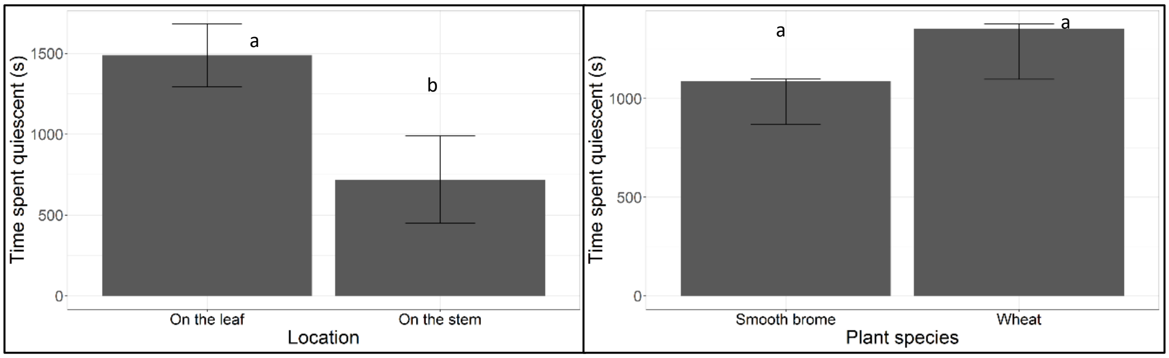

Fig. 17. a) Mean duration (seconds) for female wheat stem sawfly in quiescence on wheat and smooth brome and b) Mean duration (seconds) spent by female WSS in quiescence on the leaves and on the stem of plant species at Zadoks 49.

<u>Choice Tests to Determine Infestation and Oviposition</u>. While assessing differences in proportion of infestation between smooth brome and wheat at Zadoks 32, I found no differences in infestation of wheat and smooth brome (χ^2 (1) = 0.10, P = 0.78). There was no interaction between date of infestation and plant species to influence infestation (χ^2 (3) = 0.67, P = 0.88), so only fixed main effects were accounted for in the ANOVA with likelihood ratio tests. However, there was a difference in infestation among stem types as observed in choice tests at Zadoks 32 (χ^2 (1) = 12.60, P = 0.00). Main stems were significantly more infested than primary tillers at this stage (Fig. 18).

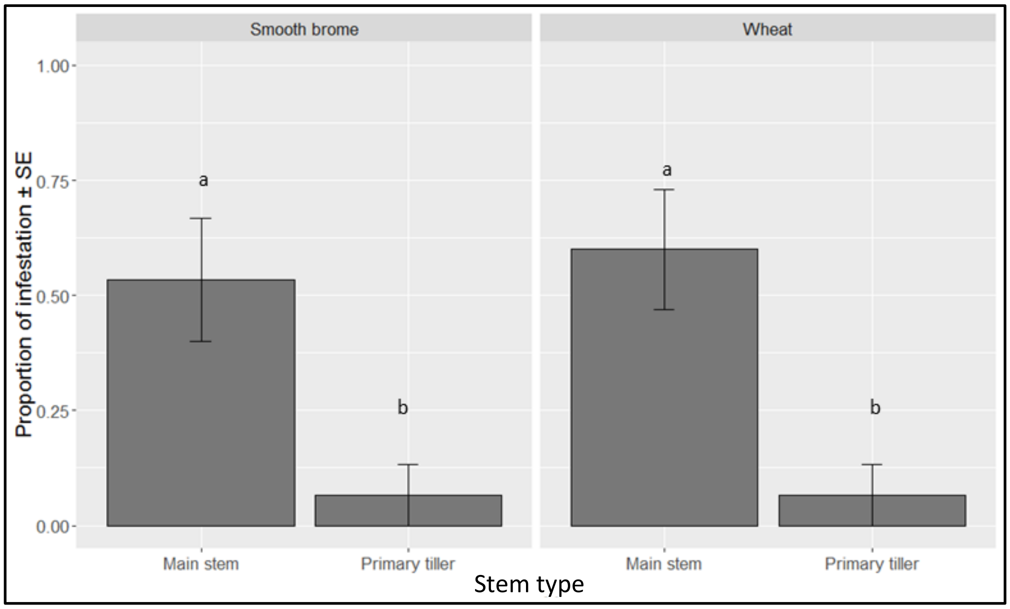

Fig. 18. Mean proportion of WSS infested main stems and primary tillers of smooth brome and wheat in choice trials at Zadoks 32.

[15] Letters indicate significant interactions ($P< 0.05$) between stem types and plant species at $\alpha = 0.05$

Similarly, there was no difference between wheat and smooth brome for the number of eggs deposited in stems ($\chi^2(1) = 0.04$, $P = 0.84$). There was a difference in the number of eggs deposited in different stem types ($\chi^2(1) =10.48$, $P = 0.00$), with more eggs in main stems than in primary tillers (Fig.19).

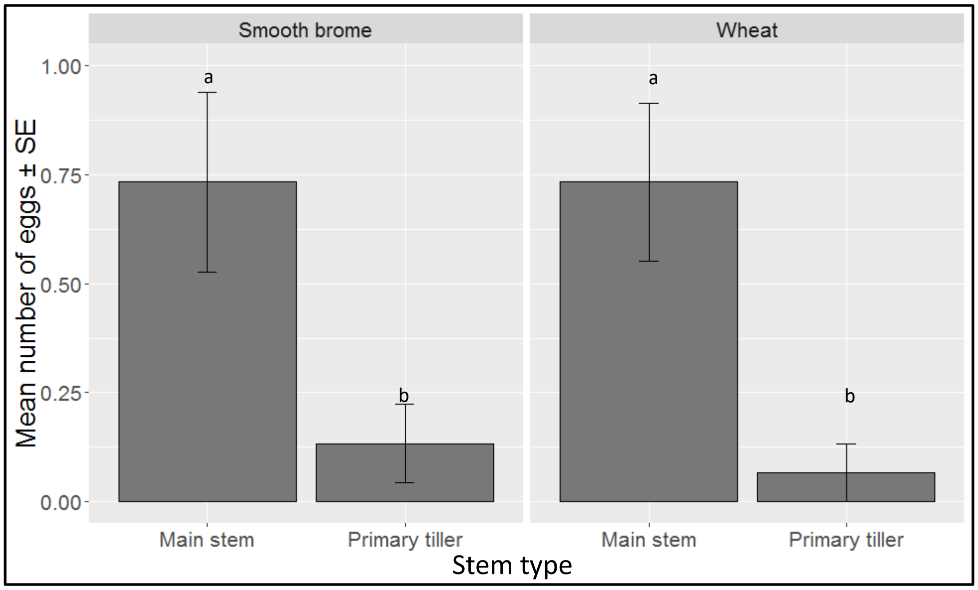

Fig. 19. Mean number of eggs deposited by wheat stem sawfly in main stems and primary tillers of smooth brome and wheat in choice trials at Zadoks 32.
[16] Letters indicate significant interaction ($P< 0.05$) between stem types and plant species at $\alpha=0.05$

In a similar choice test conducted at Zadoks 49, WSS infestation differed between wheat and smooth brome (χ^2 (1) = 3.93, P = 0.04) (Fig. 20). Similarly, a difference was observed in number of eggs deposited in wheat and smooth brome (χ^2 (1) = 26.37, P = 0.00) with more eggs in smooth brome. There was a significant interaction between plant type and stem type (main stem or tiller) (χ^2 (1) = 5.06, P = 0.02) (Fig.21).

Fig. 20. Mean proportion wheat stem sawfly infested stems of smooth brome and wheat in choice trials at Zadoks 49.

[17] Letters indicate significant differences ($P < 0.05$) between smooth brome and wheat at α=0.05

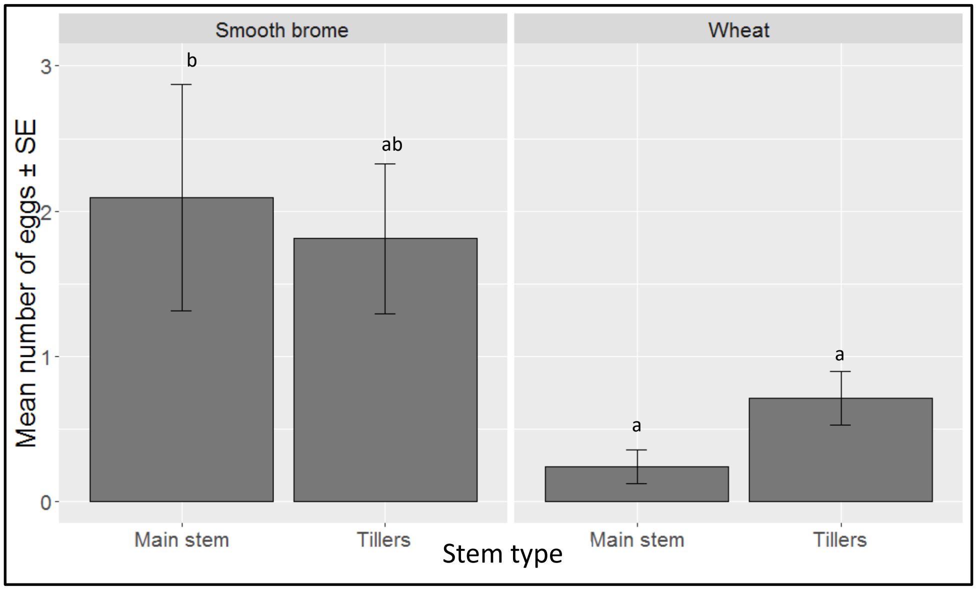

Fig. 21. Mean number of eggs deposited by wheat stem sawfly in main stems and tillers of smooth brome and wheat in choice trials at Zadoks 49.

[18] Letters indicate significant interaction ($P < 0.05$) between stem types and plant species at $\alpha = 0.05$

<u>No-Choice Tests to Determine Infestation and Larval Survival</u>. At Zadoks 32, there was no difference in the proportion of WSS-infested stems for smooth brome and wheat (χ^2 (1) = 3.15, P = 0.08), but there was a difference in the proportion of infestation among the stem types (χ^2 (1) = 21.65 P = 0.00) with greater infestation in main stems than in tillers (Z = 2.97, P = 0.00) (Fig. 22). Furthermore, in this oviposition study, after a suitable backward selection for the model, I found a difference between wheat and smooth brome (χ^2 (1) = 3.81, P = 0.05) (Fig. 23). Also, number of eggs differed between stem types (χ^2 (1) = 34.37, P = 0.00).

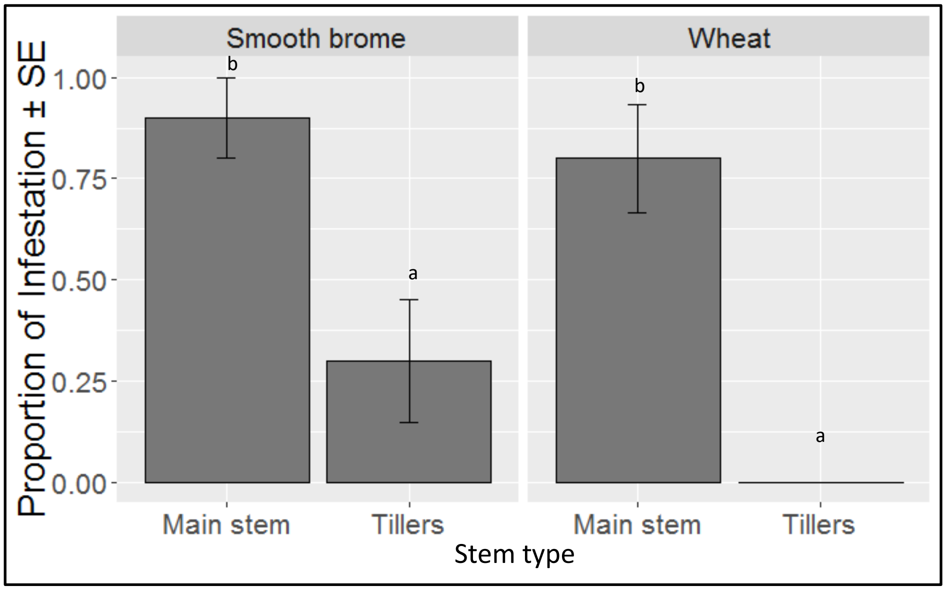

Fig. 22. Mean proportion of wheat stem sawfly infested main stems and tillers of smooth brome and wheat in no-choice trials at Zadoks 32.

[19] Letters indicate significant interaction (P < 0.05) between stem types and plant species at α = 0.05

Fig. 23. Mean number of eggs deposited by wheat stem sawfly in stems of smooth brome and wheat in no-choice trials at Zadoks 32.

[20] Letters indicate significant differences ($P < 0.05$) among smooth brome and wheat at $\alpha = 0.05$.

At Zadoks 49, there was difference in infestation of wheat and smooth brome (χ^2 (1) = 6.22, P = 0.01) (Fig. 24). Similarly, there were interactions among species, stem type and stem length (χ^2 (1) = 6.67, P = 0.00) along with an interaction between species and stem type (χ^2 (1) = 5.38, P = 0.02). The main stems of smooth brome were more infested than the main stems of wheat (Fig.25). Further analysis revealed a significant interaction between main stems and stem length (χ^2 (1) = 4.12, P = 0.04 (Fig. 25).

Fig. 24. Mean proportion of wheat stem sawfly infested stems in smooth brome and wheat in no-choice trials at Zadoks 49.

[21] Letters indicate significant differences ($P < 0.05$) between smooth brome and wheat.

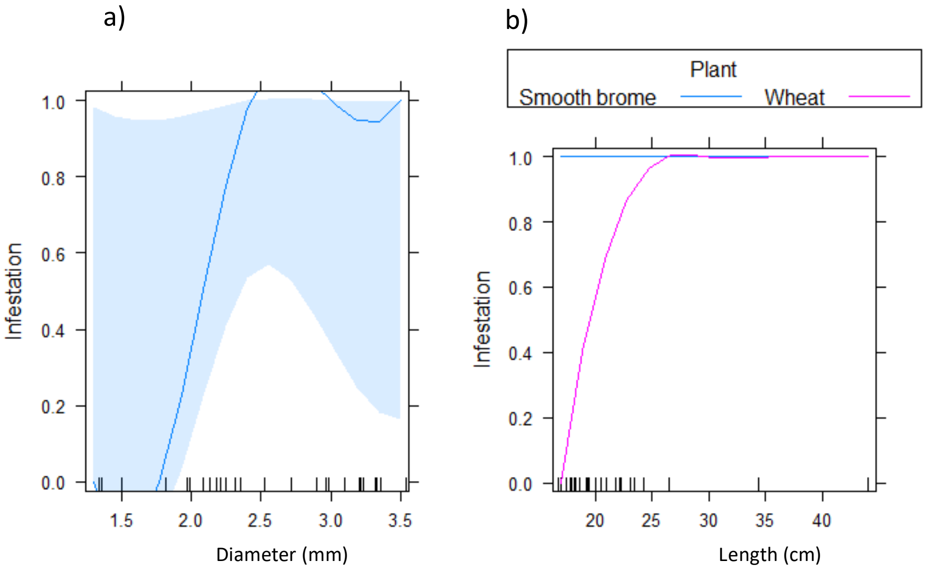

Fig. 25. Effect plot showing a) main effect of diameter on infestation of main stems by wheat stem sawfly b) impact of interaction between lengths of main stems of plant species on infestation of main stems by WSS in no-choice trials at Zadoks 49.

[22] The shaded region in a) shows confidence band for fitted values at $\alpha=0.05$.

Similarly, there were differences in egg numbers for smooth brome and wheat stems at Zadoks 49 (χ^2 (1) =24.91, P = 0.00) (Fig. 26). There were interactions among species, stem type and stem length (χ^2 (1) = 10.51, P = 0.00) along with an interaction between species and type of stem (χ^2 (1) = 5.77, P = 0.02), where main stems of smooth brome were more infested than main stems of wheat (Fig. 27). Further analysis revealed an interaction between main stems and stem length for number of eggs (χ^2 (1) = 6.04, P = 0.01 (Fig. 28).

Fig. 26. Mean number of eggs deposited by wheat stem sawfly in stems of smooth brome and wheat in no-choice trials at Zadoks 49.

[23] Letters indicate significant differences (P < 0.05) between smooth brome and wheat.

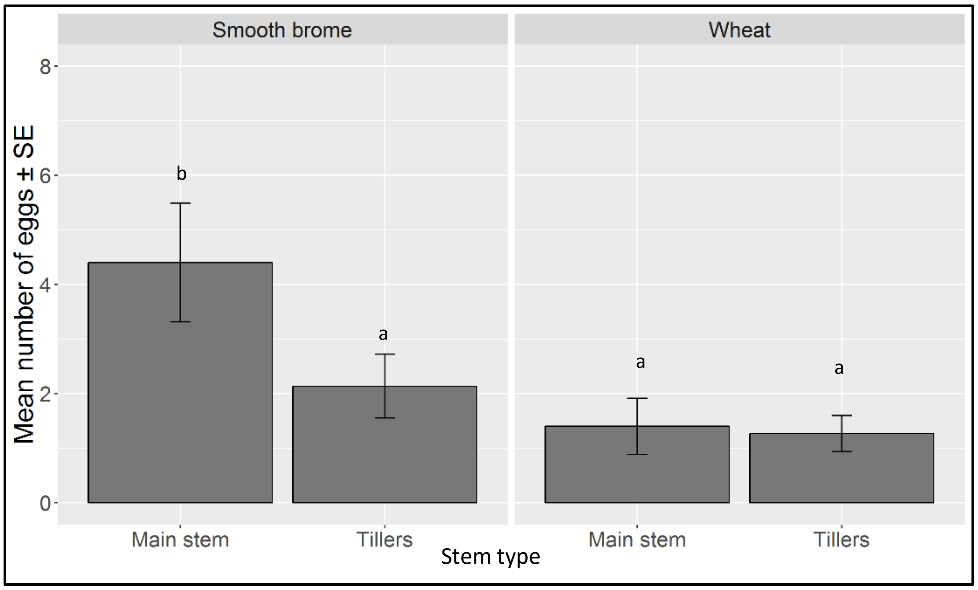

Fig. 27. Mean number of eggs deposited by wheat stem sawfly in main stems and tillers of smooth brome and wheat in no-choice trials at Zadoks 49.

[24] Letters indicate significant interaction (P < 0.05) between stem types and plant species at α=0.05

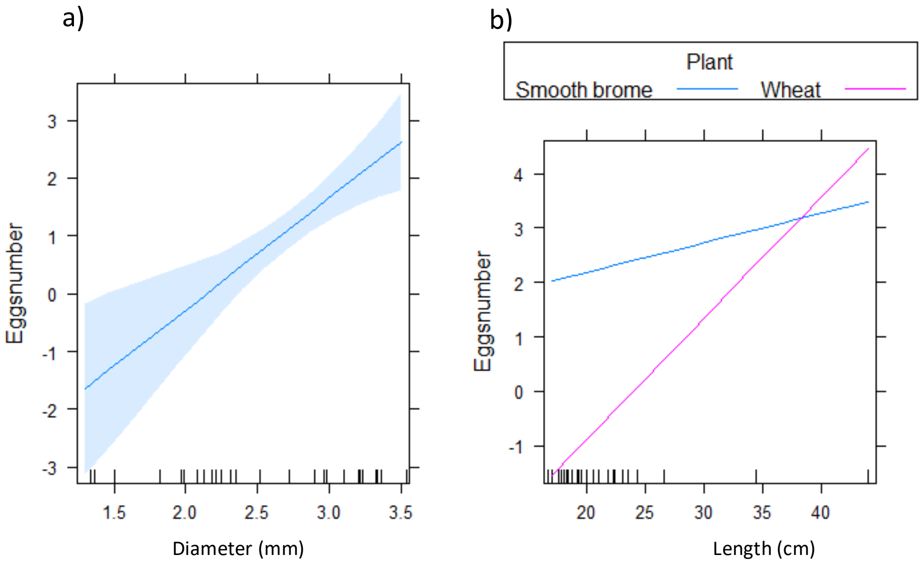

Fig. 28. Effect plot showing a) main effect of diameter of main stems on number of eggs deposited in main stems by wheat stem sawfly b) impact of interaction between lengths of main stems of plant species on number of eggs deposited by WSS in main stems in no-choice trials at Zadoks 49.

[25] The shaded region in a) shows confidence band for fitted values at α=0.05.

Length of main stems of smooth brome was greater than length of the main stem of wheat (t = 2.25, df = 17.30, P = 0.04), but there was no difference in the length of all other tillers in wheat and smooth brome. Diameter was different for main stems (t = -10.40, df = 22.88, P = 0.00) and tillers (t = -5.68, df = 27.99, P = 0.00) of wheat and smooth brome.

For larval survival at Zadoks 49, we found an interaction between date of infestation and plant species that impacted infestation by WSS (χ^2 (3) = 0.02, P = 0.02). From the cohort of plants used in the larval survival study, we found differences between infested wheat and smooth brome stems for WSS survival (χ^2 (1) = 9.68, P = 0.02). For infested stems, there was a difference in number of stems that were WSS cut for smooth brome and wheat (χ^2 (1) = 30.83, P = 0.00) (Table 9).

Table 9 Mean proportion of infested and wheat stem sawfly - cut stems with live larvae.

Plant species (49 stage)	Infested		Larval survival		Cut stem	
	N	Mean ± SE	N	Mean ± SE	N	Mean ± SE
Smooth brome	24	0.75±0.10	18	0.00 ± 0.00 a	18	0.00± 0.00a
Wheat	24	0.58 ± 0.10	14	0.79 ± 0.11b	14	0.71 ± 0.13b

[26] Letters indicate significant difference (P < 0.05) between smooth brome and wheat at α = 0.05 within a column.

Comparative Analysis of Collections of Volatiles. The volatile profiles of wheat and smooth brome contained many chromatogram peaks at Zadoks 32. However, only volatile compounds with prominent peaks in the chromatogram or compounds that were different in overlays of the two species were selected for analysis. There was no interaction between plant species and date of volatile collection (Wilks lambda = 0.07, F = 1.31, P = 0.05), but there was a difference in volatile compounds collected from the two species (Wilks lambda = 0.14, F = 10.97, P = 0.00). The compounds that visually differed in overlays between smooth brome and wheat were myrcene, (*Z*)-3-hexenyl acetate, β-ocimene, linalool, β-cubebene, β-terpineol, limonene, methyl-salicylate, β-cis-farnesene, decanal, nonanal, and octanal. Although additional compounds were evident, they were not different in the chromatograms (Table 10).

There was a significant interaction between plants species at Zadoks 49 stage and date of volatile collection (Wilk's lambda = 0.02, P = 0.00). Similarly, wheat and smooth brome were different (Wilk's lambda = 0.12, P = 0.00) in the quantities of a number of eluted volatile compounds at Zadoks 49. Those compounds included myrcene, (*Z*)-3-hexenyl acetate, β-ocimene, linalool, β-cubebene, limonene, β-terpineol, methyl-salicylate, β-caryophyllene, cis-β-farnescene, and farnesol (Table 11).

Table 10. Mean amounts of plant volatile compounds (ng^{-1} g^{-1} hr^{-1}) collected from wheat and smooth brome plants at Zadoks 32.

Compound	**Smooth brome**	**Wheat**	**F-statistics**	**p-value**
myrcene	0.18 ± 0.03	0.06 ± 0.02	11.56	0.00 *
Z-3-hexenyl acetate	0.20 ± 0.03	0.04 ± 0.01	4.08	0.05 *
β-ocimene	2.86 ± 0.45	0.42 ± 0.20	45.89	0.00 *
Linalool	0.22 ± 0.05	0.54 ± 0.09	8.08	0.00 *
β-cubebene	0.02 ± 0.01	0.00 ± 0.00	3.93	0.05 *
limonene	0.06 ± 0.02	0.01 ± 0.01	7.11	0.01 *
α-terpineol	0.12 ± 0.04	0.02 ± 0.02	5.75	0.02 *
methyl-salicylate	0.73 ± 0.10	0.06 ± 0.02	47.98	0.00 *
cis β-farnesene	0.12 ± 0.05	0.00 ± 0.00	8.44	0.01 *
Decanal	2.69 ± 0.31	1.76 ± 0.15	9.26	0.00 *
Nonanal	2.77 ± 0.33	1.99 ± 0.19	4.81	0.03 *
6-methyl-5 hepten-2-one	0.08 ± 0.02	0.25 ± 0.19	0.08	0.77
Octanal	0.92 ± 0.12	0.68 ± 0.07	4.54	0.04 *

[27] *indicates a difference ($P < 0.05$) in amount of each compound between smooth brome and wheat at $\alpha = 0.05$.
Although statistically insignificant, 6-methyl-5-hepten-2-one was found to produce responses in parasitoid antennae (Pérez 2009) and was reported to cause repellency in female wheat stem sawfly (Piesik et al. 2008).

Table 11. Mean amounts of volatile compounds (ng^{-1} g^{-1} hr^{-1}) collected from wheat and smooth brome plants at Zadoks 49.

Compound	Smooth brome	Wheat	F-statistics	p-value
myrcene	0.31 ± 0.30	0.16 ± 0.04	0.09	0.00 *
Z-3 hexenyl acetate	0.60 ± 0.21	0.07 ± 0.03	11.15	0.00 *
β-ocimene	9.83 ± 2.54	1.23 ± 0.19	25.93	0.00 *
Linalool	1.15 ± 0.70	0.39 ± 0.01	0.79	0.38
β-cubebene	0.85 ± 0.37	0.00 ± 0.00	12.89	0.00 *
limonene	0.20 ± 0.03	0.03 ± 0.01	43.48	0.00 *
α-terpineol	0.31 ± 0.05	0.06 ± 0.02	30.43	0.00 *
methyl-salicylate	0.75 ± 0.36	0.29 ± 0.24	5.44	0.02 *
β-caryophyllene	0.93 ± 0.23	0.15 ± 0.04	23.54	0.00 *
cis β-farnescene	0.88 ± 0.29	0.00 ± 0.00	20.66	0.00 *
Decanal	0.71 ± 0.07	0.77 ± 0.12	0.04	0.84
Nonanal	0.68 ± 0.08	0.84 ± 0.12	1.72	0.20
6-methyl-5 hepten-2-one	0.07 ± 0.02	0.07 ± 0.01	1.34	0.25
Octanal	0.92 ± 0.44	0.43 ± 0.17	0.80	0.37
Farnesol	0.11 ± 0.03	0.04 ± 0.01	5.09	0.03 *

[28] *indicates differences ($P < 0.05$) in amount of each compound between smooth brome and wheat.

Decanal, nonanal, octanal, although statistically insignificant at Zadoks 49, are different at Zadoks 32. Decanal and nonanal were also found to cause electrophysiological responses in adult male and female WSS (Cossé et al. 2002)

A principal component analysis (PCA) biplot was created to elucidate relationships between species and volatile compounds and to simplify the data set into identifiable components. Approximately 89% of total variance was explained by first and second components. Differences in amounts of volatile compounds between wheat and smooth brome at Zadoks 32 and Zadoks 49 are mostly explained by the first component (69.7%) (Fig. 29). Wheat compounds at Zadoks 32 and Zadoks 49 are somewhat clustered together, so they have similar features in the array of volatile compounds, while smooth brome and wheat at the same stages are separated, indicating differences in the amounts of volatile compounds. Decanal, nonanal and 6-methyl-hepten-2-one are not clustered with the remainder of the volatile compounds, while decanal and nonanal are correlated.

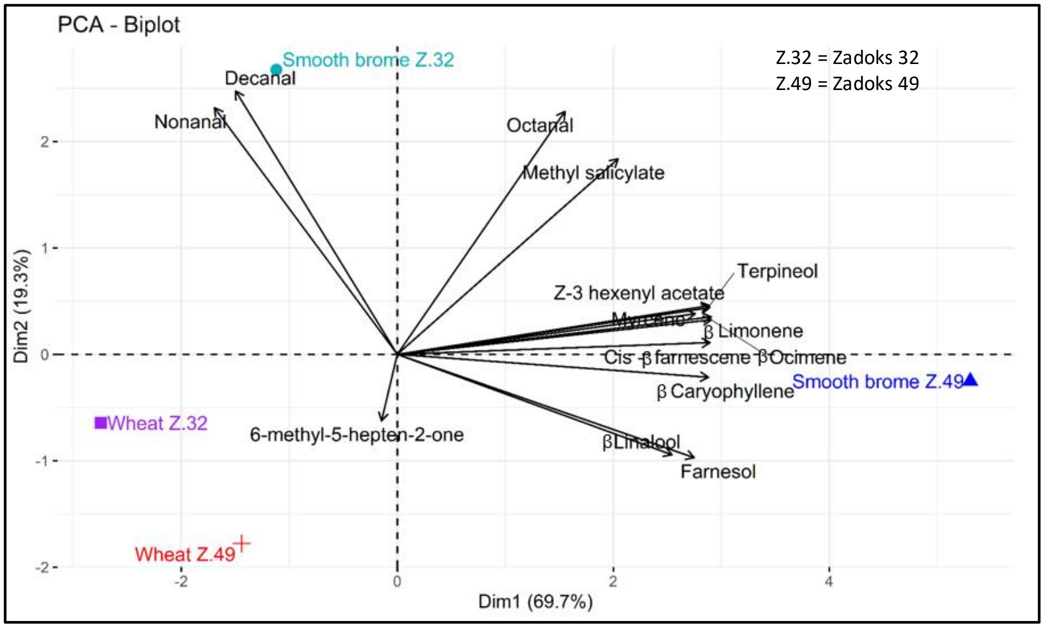

Fig. 29. Biplot showing principal component 1 and principal component 2 from Principal Component Analysis (PCA) using volatile compounds from wheat and smooth brome at Zadoks 32 and Zadoks 49.

Discussion

In this study we first assessed the infestation of smooth brome and wheat in two Montana fields using three transects at locations that have a history of damaging WSS populations. Patterns of infestation of both exotic species reflect maternal oviposition decisions, and we were also able to determine viability of larvae that were conferred by these maternal decisions by sampling throughout the growing season. As a follow up, experiments assessing oviposition preferences and host selection behaviors of WSS were conducted under controlled conditions in a greenhouse using ‘Reeder’, a susceptible spring wheat cultivar and ‘Manchar, a commonly grown smooth brome cultivar. After the behavioral studies, volatiles were collected from both plant species to evaluate quantitative and qualitative differences in emitted volatile compounds.

WSS experienced a series of host shifts in the western portion of the Northern Great Plains of North America. Almost two decades after the first record from native grasses, WSS was documented infesting spring wheat stems and became established as a pest of spring wheat. Later, WSS also adapted to winter wheat cultivars and caused severe infestations in Montana (Irell and Peairs, 2011, Lestina et al., 2016), and most recently, areas farther south are facing WSS outbreaks. In the field study, I found discrepancies in patterns of WSS infestation in wheat based on seasonality that reflected differing phenologies of winter and spring wheat relative to smooth brome. Our field study did not reveal any clear differences in the proportion of infested stems between the crop and SB-crop transect at Big Sandy 1, as both winter wheat and smooth brome had elongated stems at the time WSS flight began. At Big Sandy 1, there were no clear differences in stem infestation among transects. Also, after further assessing the proportion of infested internodes among transects in Big Sandy 1, overall infestation was not different among the transects. However, there was greater tunneling by WSS larvae in the stems of wheat from the crop transect for Big Sandy 1. No differences in infestation by internodes for transects, but greater tunneling in wheat stems compared to smooth brome stems shows that there could actually be greater oviposition in the internodes of stems from smooth brome transects compared to crop transects.

There were more dead larvae, along with fewer live larvae, in stems from samples taken from the SB-crop and SB-fallow transects compared to stems from samples taken from the crop transect for both fields. Cannibalism among WSS larvae and confounding mortality caused by biological control agents (Sherman et al. 2010) makes initial infestation status of a stem difficult to assess when sampling is conducted later in the season, especially when infestation cannot be precisely recorded by the number and location of eggs. However, because the number of dead larvae in smooth brome transects was greater than in wheat, there were fewer tunneled internodes in stems from samples taken from the SB-crop and SB-fallow transects relative to stems from wheat samples taken along the transect in the winter wheat crop at Big Sandy 1.

Survivability of WSS larvae is known to be reduced in resistant, solid stemmed cultivars relative to susceptible, hollow stemmed cultivars (Holmes 1977, Buteler et al. 2015), resulting in less damage and reduced overwintering success (Cárcamo et al. 2005). In comparison to solid-stemmed wheat cultivars, hollow-stemmed cultivars had lower mortality ranging from 5 to 14% in hollow-stemmed wheat, much less than the 34 to 50% reported for solid-stemmed wheat (Buteler et al. 2015). Interestingly, smooth brome has hollow stems, but also had more dead larvae than the ‘Warhorse’ solid-stemmed winter wheat sampled during this project. A similar pattern was found in a recent characterization of barley cultivars for resistance to WSS; all barley cultivars had greater larval mortality than hollow stemmed wheat cultivars surveyed at the same time, and only a few barley lines had larval mortality lower than solid-stemmed wheat lines, even though barley has hollow stems (Varella et al. 2018).

This study did not reveal any differences in mean proportion of parasitized stems at Big Sandy 1 across transects (Fig. 13). Nevertheless, the high percentage of dead larvae in smooth brome and no overall difference in parasitoids provide the basis for further study of mortality factors in life tables, especially antibiosis. In contrast, at Big Sandy 2, there were very large differences in both infestation and number of dead larvae in stems from susceptible ‘Vida’ spring wheat compared to stems from both adjacent transects of the smooth brome, with greater parasitism of WSS larvae in smooth brome adjacent to the fallow field compared to smooth brome adjacent to spring wheat (Fig. 13). Lower infestation in spring wheat could be the result of planting delayed by weather that limited the number of developing stems available during the WSS flight period. Adhikari et al. (2018) found that WSS infestation and parasitism were influenced by farming system and seasonality of wheat crops in another study conducted several years earlier near Big Sandy, Montana. Winter wheat is seeded by October, and after vernalization the stems were sufficiently elongated for egg deposition by WSS before adult WSS flight began in late May to early June. In comparison, spring wheat that is seeded from March through May could not attain stem elongation required for WSS infestation. This causes an innate preference for infestation of winter wheat by WSS (Morrill and Kushnak 1999).

Smooth brome is a perennial grass that has fully elongated stems when WSS adults emerge, making smooth brome susceptible enough for WSS infestation. In addition, the hollow stems of smooth brome may play a vital role in greater infestation because hollow stems were suggested as an important trait of host plants vulnerable to WSS (Holmes and Peterson 1961, Cárcamo et al 2005). In addition, Morrill et al (2001a) suggested that border effects, in combination with attractive features of earlier maturing winter wheat cultivars, can be used to create a trap crop area around the perimeter of spring wheat. There was a greater proportion of infested internodes in flowering smooth brome stems in both transects than in wheat, but larval mortality was also high in flowering stems of smooth brome transects in both fields compared to crop stems (Fig.10, Fig11).

Overall, dead larvae were more common in internodes from SB-crop and SB-fallow transects than in crop transect (Fig. 10, Fig. 11), which is due in part to greater infestation of smooth brome. There was a lower chance of larval mortality due to cannibalism in smooth brome, as indicated by less frass and reduced tunneling, both within and across internodes. This study showed a greater proportion of infested internodes in stems taken from the smooth brome transect next to fallow compared to those taken next to the growing crop (Fig. 7). Smooth brome stands often have inconsistent flowering patterns at maturity, which could be the reason for greater interception of WSS females in mature plants bordering the fallow field, which contained a greater proportion of vegetative elongating stems than flowering stems. This information can be useful to further develop the idea of conserving smooth brome as a lethal trap border. Smooth brome remained green longer than wheat, which favored greater infestation and parasitism of WSS. Larval survival, easily scored from cut stems in wheat, was assessed from mature and dry smooth brome samples one month after wheat was harvested. Only three mature larvae were found alive in stems from smooth brome samples collected in September. These may have survived to cut the stems eventually, but had yet to do so, even at that late date in the growing season. In the field study, I did not find any cut stems of smooth brome, but extensive sample collections early the next year would likely have resulted in the discovery of a few cut stems, as indicated by stubs, because smooth brome can support complete WSS development (Cockrell et al. 2018). However, this result from the field was corroborated by our greenhouse larval survival study, in which no larvae were found alive and no stems were cut in infested, fully mature smooth brome plants (Table 9).

Morrill et al. (2001a) discussed the synchrony of host phenology to flight period of WSS as a key factor impacting host selection. In this field study, the proportion of infested internodes was greater in flowering stems of smooth brome transects than in non-flowering stems, which could be due to better synchrony of early flowering stems with the flight period of WSS. The less frequently infested internodes of vegetative stems might have developed later in the season allowing some stems to escape infestation. A more intense sequential sampling from the start of the WSS flight period could provide a more accurate assessment of overall infestation status, which would allow for more rigorous comparison of survival in both flowering and vegetative stems.

There is a specific host range for many herbivores, but they also express preferences within that range (Bernays et al.1994). These studies suggest that choices of host tissue for oviposition by female WSS is influenced by several host finding cues, including physical characteristics such as stem diameter, length, cuticular waxes, stem solidness and attractive volatile compounds (Holmes and Peterson 1960, Piesik et al. 2008, Youtie and Johnson 1988, Morrill at al. 1992, Weaver et al. 2009). In the current study, a hierarchical analysis of preferences of WSS was attempted to tease apart differences in pre-alighting behavior when WSS were exposed to an airstream containing volatiles emitted from hollow-stemmed susceptible wheat and smooth brome. Female WSS preferred volatiles emitted by smooth brome relative to wheat at both growth stages.

The quantification and characterization of volatile compounds at Zadoks 32 and Zadoks 49 growth stages provided further insights on the attractive nature of smooth brome. In these experiments, smooth brome produced significantly greater amounts of volatile compounds that were previously reported as attractive to WSS. Weaver et al (2009) suggested that greater susceptibility of the wheat cultivar ‘Reeder’ to WSS infestation was due, at least in part, to a greater amount of the attractive compound (*Z*)-3-hexenyl acetate (Piesik et al. 2008) in its volatile profiles compared to that of the more resistant cultivar ‘Conan’. Consistent with this pattern, the current study also suggested that smooth brome produces a different amount of β-ocimene, as well as (*Z*)-3-hexenyl acetate, which are both behaviorally significant volatile compounds for female WSS, first isolated from wheat (Piesik et al. 2008). These differences further support results from our Y-tube bioassays, where smooth brome was more attractive to female WSS compared to wheat at both Zadoks 32 and Zadoks 49. While foraging on the surface of a host plant, female WSS exhibit behavioral activities key in the evaluation of a host for oviposition (Buteler et al, 2009, Varella et al. 2017). Buteler et al. (2009) reported that female WSS were not able to discern whether a stem was already infested and subsequently deposited more eggs, despite potential competition among conspecifics that could lead to cannibalism. In the same study, they did not find any difference in frequency of specific behaviors or behavioral transitions associated with oviposition of female WSS foraging on either infested or uninfested stems of ‘Reeder’ spring wheat.

However, Varella et al. (2017), when assessing whether female WSS discriminates among plant cues from near isogenic lines containing quantitative trait loci associated with stem solidness and larval antibiosis, found that allelic variations at Qwss.msub-2D and Qss.msub.3BL influenced foraging behavior, stem probing behavior, and ultimately, egg deposition. Near isoline pairs developed from a Scholar/Conan cross influenced differential attraction of female WSS, but the near isoline pairs developed from a Reeder/Conan cross did not differ in attraction, despite differing susceptibility to WSS oviposition in the parents (Varella et al. 2017).

Conversely, in this study, I observed clear upwind preference for airstreams of volatiles emitted by smooth brome over those of wheat at both growth stages. Smooth brome was clearly preferred over wheat at Zadoks 49, with more foraging behavior after alighting on the surface smooth brome, resulting in more eggs in the stems. From our post-alighting behavioral study, walking time was significantly greater on wheat compared to smooth brome at Zadoks 32, whereas duration of walking events and frequency of other key behaviors was not different. No clear difference in most of these behaviors suggests that WSS might not receive sufficiently different contact cues for wheat and smooth brome at Zadoks 32. There was no difference in the duration of WSS oviposition behaviors, and females exhibited behaviors that are key in selection of smooth brome over wheat more frequently at Zadoks 49. Similarly, duration of ovipositor insertions was longer in wheat compared to smooth brome at Zadoks 49, with more eggs in stems of smooth brome compared to wheat.

Even though very few instances of movement of WSS from wheat to smooth brome were observed at Zadoks 49 stage in choice trials, this information is important in assessing WSS behavioral activity. Female WSS walked, tapped their abdomens, underwent quiescence and inserted ovipositors more frequently in smooth brome than in wheat at Zadoks 49. The ovipositor of WSS contains sensory receptors similar to many other insect systems (Buteler et al. 2009). Active assessment of contact cues inside the stem lumen made by frequently inserting their ovipositor might help female WSS choose to deposit eggs in smooth brome more quickly than in wheat, as has been reported for maize stalk borer, *Busseola fusca* (Haile and Hofsvang 2002), and potato psyllid, *Bactericera cockerelli* (Prager et al. 2014). Gravid females of the Indian meal moth, *Plodia interpunctella*, had similar foraging activities such as periods of rest with antennal movements, combined with brief episodes of active oviposition (Sambaraju et al. 2016). Theoretically, an insect selects a host more quickly and spends more time on more preferred plant species while tending to disperse more quickly from less preferred species (Thompson and Pellmyr 1991). Our pre-alighting study suggests that volatile compounds emitted by smooth brome attract WSS. Similarly, the study of post alighting behaviors suggests that the arresting nature of smooth brome might influence more foraging or oviposition behavior compared to wheat. These preferential behaviors to smooth brome suggest that they might influence host acceptance and subsequent oviposition. This result is consistent with the attracting and arresting nature of potato plants infected with potato leaf curl virus for its vector insects like potato aphid, *Myzus persicae* (Eigenbrode et al. 2002).

When WSS were exposed to both plant species for a greater number of days, the rate of infestation in stems was not different, but the numbers of eggs deposited were greater in smooth brome than in wheat (Fig. 19). At Zadoks 49, the main stem of smooth brome had more eggs than that of wheat (Fig. 20). This could also be due to a greater number of internodes at the same growth stage in smooth brome, which may trigger more key behavioral activity and perhaps trigger more egg deposition per stem. While host parameters like stem length and stem diameter are reported to influence infestation and egg numbers (Holmes and Peterson 1960, Buteler et al. 2009, Morrill et al. 1992, Perez-Mendoza et al. 2006), these did not differ between smooth brome and wheat at Zadoks 49 (Fig. 24, 27).

There was a trend towards an overall increase in infestation and for greater numbers of eggs in stems with greater diameters (Fig. 24, 27). While the diameter of smooth brome stems was significantly less than that of wheat in bioassays in the greenhouse, smooth brome was more infested and received more eggs relative to wheat. So, it can be determined that physical parameters like stem length and diameter do not have a significant impact in determining infestation in smooth brome compared to wheat as was observed in foxtail barley, *Hordeum jubatum*, in which despite of slender stems, WSS preferred to lay eggs in them (Ainslie 1929). Belonging to a different genus than wheat, smooth brome might have different contact cues that also trigger oviposition (Iason et al. 2012).

The results from the greenhouse choice bioassays provide more evidence supporting more eggs per stem in smooth brome than in wheat at Zadoks 49 (Fig. 20), but the subsequent survival of larvae was very low (Table 9). This provides further justification for smooth brome to be used as trap crops (Shelton 2004, Van den Berg 2006), as mentioned in the 'Wartime Production Series' described in Farstad et al. (1945). Similar results for oviposition preference and survival of *Plutella xylostella* (L.) was observed where they foraged among glossy-type *Barbarea vulgaris*, *Brassica oleracea var. italic*, and *Brassica oleracea var. capitata* (Lu et al. 2004). Female *P. xylostella* (L.) preferentially oviposited on *Barbarea vulgaris,* but larval development was poor, suggesting its potential use as dead end trap for *P. xylostella* (L.) management. However, the rate of movement and preference responses of herbivores are relative and depend on the hierarchy of available hosts as determined by the quality of the current environment (Thompson 1988). For instance, Van den Berg (2002) found sorghum as an effective trap crop for stem borer (*Chilo partellus*) when surrounding a maize field. Although acceptable for oviposition, the sorghum trap crop did not maintain the density of pests sufficiently to prevent subsequent emigration of larvae to maize, resulting in higher damage to maize (Van den Berg 2002). A very high density of WSS larvae in stems along the crop border might be expected to alter the preference of later ovipositing WSS for these smooth brome and wheat plants, resulting in a pest population moving further into the wheat field after density of infested stems increase along crop edges (Mills 1944, Mumb 1945, Pesho et al. 1971, Holmes 1982, Morrill et al. 2001, Weaver et al. 2005). This might not hold true for WSS infestation since Buteler et al. (2009)

reported that ovipositing WSS does not discriminate between infested and uninfested wheat plants, and larvae cannot leave the stems. In this study, oviposition patterns indicate similar behavior was exhibited by WSS females foraging among infested and uninfested smooth brome stems, thus maintaining the potential of smooth brome for receipt of more eggs irrespective of infestation status. However, the underlying mechanisms for selection and preference for ovipositing female WSS when provided with infested stems of both wheat and smooth brome, and also when provided infested smooth brome and uninfested wheat stems, should be experimentally assessed to fully elucidate efficacy of smooth brome as a trap crop.

The 'preference performance hypothesis' states that herbivores prefer to lay eggs on host plant species that maximize their larval fitness (Singer et al. 1988, Gripenberg et al. 2010, Fortuna et al. 2012, Fortuna et al. 2013). The correlation between preference and performance has been observed in a host preference study for *Earias clorana* L., native to Europe, where *Earias clorana* L. was found to prefer laying eggs on *Spiraea tomentosa* L. (an alien and invasive shrub species in Central Europe), but is more adapted to native *Salix viminalis* L. as a host (Wiatrowska et al. 2017). However, WSS selection behaviors and preferences are relative and depend upon type of choices that are possible. For instance, Varella et al. (2016) found that wheat near isogenic lines that possessed alleles for stem solidness and greater larval mortality were less preferred than lines that did not possess those alleles, which is in accordance to preference performance hypothesis. In contrast to this, Buteler et al. (2009) reported that WSS does not discriminate between previously infested and uninfested plants and undergo a greater risk of cannibalism with frequent oviposition in infested wheat, which does not support the preference performance hypothesis. However, in this study, WSS chose smooth brome for oviposition over that of the highly susceptible wheat cultivar ‘Reeder’, even though smooth brome did not support survival of progeny, thus refuting the preference performance hypothesis. This could be due to maternal mistakes (Nanthagopal and Uthamasamy 1989, Mayhew 1997) or to variation in phenology among available plants, other plant attributes, and arresting effects (Chew 1977, Rausher 1979, Fortuna et al. 2012, Braccini et al. 2015, Lavergne et al. 2018). The optimal bad motherhood hypothesis (Mayhew 1997) could, in part, be discussed from an evolutionary perspective for WSS. The herbivorous WSS, being native in origin, is adapted to native, wild grasses such as mountain brome (*Bromus marginatus* Nees ex Steud.) and other wheat grasses of the large historical genus *Agropyron spp.* (Ainslie 1929). Slowly, WSS started to adapt to exotic cereal crops which covered the huge land mass of the Northern Great Plains, and eventually wheat became a major target of infestation when the native population of hosts decreased in the area (Ainslie 1929, Lesieur et al. 2016). Lesieur et al. (2016) discussed similar patterns of genetic diversity in WSS collected from wheat and grass habitats and suggested local adaptations of ambient WSS populations to wheat from nearby feral grasses. However, from the current study we can only surmise that smooth brome must sufficiently resemble other native host(s) in terms of features such as volatile profiles or contact cues, which makes stems highly attractive to WSS despite being an unsuitable host for larval survival as has been discussed in Pearse and Hipp (2009). Due to similar genetic diversity of WSS populations in wheat and grasses (Lesieur et al. 2016) and the dominance of wheat fields in the surrounding area, WSS might not experience sufficient selection pressure to allow them to evolve recognition that will deter them from bad hosts. Or, from an evolutionary perspective, this might require many generations (Chew 1977, Thomson 1988) and wheat and smooth brome are both recent exotics. A similar finding was made in study by Prager et al. (2014), where they found that potato psyllid *Bactericera cockerelli* from California reared on pepper leaves will lay eggs on potato leaves, despite poor development of nymphs. This poor performance was attributed to maternal mistakes that might be due to the low cost associated with laying eggs in the poor host or due to their adaptation from wild species (Prager et al. 2014). The adaptation of good performance of herbivores occur more quickly to plants which are more frequently used (Fellowes 2005). Similarly, with wheat being the predominant crop in fields across the Northern Great Plains and covering a huge land mass, perhaps, WSS might have adapted more to wheat, although it is exotic - correlating preference and performance. Although smooth brome, another exotic grass, is preferred for infestation by WSS, the performance of larvae is poor. This poor performance in smooth brome, in part, could be due to slow adaptation to perform well in less frequently used plants as mentioned by Fellowes (2005). Thus, further investigation of WSS selection behaviors and preferences among native and exotic hosts might provide additional insights on the ecological and evolutionary aspects that govern preference for smooth brome despite it being a bad host choice (Lesieur et al. 2016).

Conclusion

This study has investigated and revealed patterns of WSS infestation in exotic smooth brome and cereal crops in the alternate year crop-fallow system predominant in on the Northern Great Plains of North America. Additionally, this study focused on the mechanisms involving preference and selection of hosts for oviposition by female WSS when offered by smooth brome and wheat plants. Overall, the findings from this study show that smooth brome is a preferred host for WSS oviposition, despite high levels of larval mortality, suggesting a weak association of the preference of ovipositing WSS with performance of the stems.

The field study did not show a clear difference in infestation between smooth brome and wheat but tunneling pattern and average number of dead larvae per stem suggest a greater preference of WSS for smooth brome relative to wheat from one of our sites. The late planting of spring wheat in Big Sandy 2 might have resulted in less infestation of spring wheat, even if smooth brome might have been absent in the area. However, the probability of lower infestation in spring wheat samples might also be due to attraction of and arrest of newly emerged WSS to smooth brome transects next to crop and fallow.

While experimentally assessing the mechanisms of host preference of WSS, it was evident that WSS preferred volatiles emanating from smooth brome at both stages tested. There was a greater amount of volatile compounds like β-ocimene and (*Z*)-3-hexenyl acetate which have been recorded as being behaviorally important for WSS

(Buteler 2008, Weaver et al. 2009). Similarly, there were differences in the amount of other terpenes, aldehydes, and alcohol compounds that might also induce differences in behavior of WSS between the two species. Future research should emphasize developing an understanding of the behavioral importance of quantitatively varying compounds and blends of compounds in specific ratios using gas chromatography coupled with electroantennographic detection methods.

In the study of post-alighting behaviors, the overall number of times different behaviors were observed more in smooth brome than in wheat happened mainly during the initial emergence of inflorescence (Zadoks 49), although the duration of most behaviors was not different. However, the duration of ovipositor insertion was less in smooth brome at Zadoks 49 and was accompanied by more frequent foraging behaviors, which led to more eggs deposited relative to wheat.

In choice tests at both stages, egg numbers were higher in smooth brome than wheat, and, in a no-choice test WSS infested more stems and laid more eggs per stem in isolated smooth brome than isolated wheat. The results for larval survival in our no-choice tests showed much greater mortality with no stems cut by WSS larvae in smooth brome.

The greater infestation and higher mortality in smooth brome located along crop edges could perhaps be initially attributed to ‘border effects. Based on our field layout, it could be possible that WSS emerged and could first oviposit in smooth brome near fallow and near crops. However, the greenhouse study clarifies that oviposition in smooth brome is not just due to interception of females in the adjacent smooth brome nor is it by associational susceptibility (Wahl and Hay 1995). Rather, WSS prefers smooth brome for oviposition due to favored features such as the emission of attractive volatiles and subsequent arrest on the plant that increase the chances of egg deposition. Thus, despite variation in infestation in the two growth stages, WSS showed greater preference towards volatiles of smooth brome that influence pre-alighting behavior and exhibited more behavioral events that arrest females, which led to a greater number of eggs in stems. Low survival resulted in many dead larvae with rare instances of cut stems.

The preference of WSS to smooth brome over wheat could also suggest the adaptability of WSS to native close relatives of smooth brome like *Bromus inermis spp. pumpellianus*. It can be surmised that WSS could be disguised by traits of smooth brome, some of which might be similar to that of native hosts of WSS, where they are expected to be able to survive to cut stems (See Appendix at page 98)

Thus, this study describes the underlying mechanisms that further support the use of smooth brome in integrated pest management strategies like perimeter trap cropping or other behavioral displacement of WSS. Information obtained from this field study can also be used in managing WSS in wheat fields by further manipulating the field layout. Specifically, by utilizing smooth brome in permanent trap strips perpendicular to the flight direction of immigrating WSS. Similarly, applications of synthetic volatile blends in smooth brome in traps can be explored to further manipulate WSS behaviors. Furthermore, other potential trap crops might be genetically improved by introducing similar traits that attract WSS and especially in those that cause greater larval mortality. In addition, from the mechanistic understanding of oviposition and larval survival at different stages, smooth brome can be used for behavioral manipulation of WSS and serve as sink for eggs in a dead-end trap for WSS. Overall, the information provided in this study would help to develop innovative cultural tactics for managing WSS through understanding of preference for smooth brome over wheat.

APPENDIX A

INITIAL RESEARCH EFFORTS ON WSS IN NATIVE AND EXOTIC GRASSES AND CROPS

WSS is a native species in North America whose original hosts were reported as large stemmed native feral grasses. It is believed that WSS adapted to wheat crops from the surrounding wild grasses (Ainslie 1929). From specimens collected from Montana, similar genetic diversity was found between WSS individuals collected from wheat or grasses (Lesieur et al. 2016). The grasses were sampled from the sites with canopies of exotic subspecies of *Bromus inermis* (*Bromus inermis* Leyss. ssp. *inermis*), or smooth brome; possibly the native subspecies of *Bromus inermis* (*Bromus inermis* Leyss. ssp. *pumpellianus* (Scribn.) Wagnon), or Pumpelly's brome; and the native species *Bromus marginatus* Nees ex Steud., or mountain brome. Despite the reported attractiveness of smooth brome to WSS ovipositing adults (Criddle 1922), smooth brome was also suggested as an unsuitable host for WSS in the same report. Thus, corroborating the WSS haplotype results among the hosts in grass canopies, Lesieur et al. (2016) suggested that native *Bromus* species could be suitable hosts of WSS, fully supporting their development within the stem. WSS has also been reported to survive on several wild grasses, including species of *Agropyron, Bromus, Elymus* (Ainslie 1929, Criddle 1922), which speculates on the role of wild grasses in local WSS perpetuation (Criddle 1917).

However, there is no comparative assessment of WSS oviposition and survival among exotic wheat crops, exotic grasses, and native grasses that could provide further information about the population dynamics of WSS among native and exotic grasses, including exotic crops. The initial research approach was to evaluate the differences in volatile profiles of these native and exotic species, as well as oviposition preference plus survival of WSS in these species under greenhouse and laboratory conditions. This study could have added the understanding on possible host shift of WSS to wheat crops from native grasses that could further aid in developing integrated pest management approaches for WSS.

There were very few locations reported for Pumpelly's brome in Montana that could be accessed or confirmed (Montana Field Guide, 2019). We could not find any populations of Pumpelly’s brome to further consider for research. Thus, we initially selected mountain brome as one of the native host grasses of WSS, and wheat crop as well as smooth brome as exotic hosts of WSS for this study.

In the summer of 2017, mountain brome was transplanted from a cultivated field at the Bruce Seed Farm, near Townsend, Montana using 2 to 3 shoots per square pot using MSU Plant Growth Center soil mix (equal parts of sterilized Bozeman silt loam soil and washed concrete sand with Canadian sphagnum peat moss incorporated) and Sunshine Mix 1 (Canadian sphagnum peat moss, perlite, vermiculite, and Dolomite lime) in a 1:1 ratio. The transplanted plants were grown in greenhouse providing supplemental light from model MVR1000/C/U GE Multi-Vapor Lamps (GE Lighting, General Electric Company, Cleveland, OH) under a photoperiod of 16:8 (L:D) h at 22 ± 2°C and 20 - 40 % RH. Plants were fertilized twice each week using Peters Professional® General Purpose Fertilizer (J.R. Peters Inc., Allentown, PA) at the rate of 100 ppm in aqueous solution and were watered as needed.

After the successful establishment of plants in pots, plants were first cultured under optimal conditions, and subsequently were stressed by holding in a vernalization chamber at 4 °C and further stressed by restricting the biomass in long conical narrow pots to trigger stem initiation and elongation. Stem initiation by mountain brome, which is an essential requirement for assessing the behavior of WSS, did not occur satisfactorily under any greenhouse conditions. Therefore, our study then progressed to using only smooth brome and wheat, both exotic species, for WSS oviposition, survival, and plant volatile profile studies in controlled experiments under greenhouse and laboratory conditions.

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