

THE ROLE OF CHEMICAL ECOLOGY AND AGROECOLOGICAL IMPORTANCE OF
SMOOTH BROME IN BIOLOGICAL CONTROL OF THE WHEAT STEM SAWFLY BY
NATIVE PARASITIDS

by

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DEDICATION

To my wife and family, for their unwavering support and encouragement throughout my personal and academic journey. I am deeply grateful.

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TABLE OF CONTENTS

1. LITERATURE REVIEW	1
History and Distribution of the Wheat Stem Sawfly	1
Host Plants	1
Smooth Brome	2
Biology of the Wheat Stem Sawfly.....	3
Adult	3
Oviposition.....	4
Eggs.....	5
Larvae	5
Pupae.....	6
Damage Caused by Wheat Stem Sawfly.....	7
Management of Wheat Stem Sawfly	7
Chemical Control.....	7
Cultural Control	8
Host Plant Resistance.....	8
Tillage	9
Trap Crops	10
Delayed Planting & Swathing.....	11
Biological Control Methods.....	12
Soil Fungal Pathogens and Nematodes.....	12
Predatory Beetle.....	12
Parasitoids of the Wheat Stem Sawfly	13
Biology of <i>Bracon cephi</i> and <i>Bracon lissogaster</i>	14
Adult	14
Eggs.....	14
Larvae	15
WSS and Parasitoid Interactions with Smooth Brome	15
Plant Volatile Organic Compounds	16
Semiochemicals in Plant-Insect Systems.....	16
Research Questions	17
References.....	20
2. SENSORY AND BEHAVIORAL RESPONSES OF BRACONID PARASITIDS TO CHANGES IN VOLATILE EMISSIONS INDUCED BY WHEAT STEM SAWFLY (HYMENOPTERA: CEPHIDAE) LARVAL FEEDING IN WINTER WHEAT AND SMOOTH BROME	31
Contribution of Authors and Co-Authors	31
Manuscript Information	32
Abstract.....	34
Introduction.....	35

TABLE OF CONTENTS CONTINUED

Materials and Methods.....	37
Plant Culture	37
Insects	38
Greenhouse Infestation and Volatile Collection.....	39
Volatile Organic Compound Collection	40
Electrophysiology	42
Electroantennography & Gas Chromatography - Flame	
Ionization Detection.....	42
Electroantennography using Synthetic Volatiles.....	43
Behavioral Trials.....	44
Y-Tube Olfactometer Bioassay	44
Wind Tunnel Behavior Bioassay.....	45
Statistical Analysis	46
Comparative Analysis of Volatile Collections	46
Synthetic Volatile Electrophysiology.....	47
Behavioral Experiments.....	47
Results.....	47
Collected Volatile Profiles	47
Electrophysiology of <i>Bracon</i> spp. Parasitoids	48
EAD-GC-FID.....	48
Synthetic Volatile Electrophysiology.....	48
Behavioral Olfactory Experiments	49
Smooth Brome and Winter Wheat Blends	49
Synthetic Compounds	49
Discussion.....	49
Figures.....	53
Tables	58
References.....	62
3. AGROECOLOGICAL IMPORTANCE OF SMOOTH BROME IN MANAGING WHEAT STEM SAWFLY (HYMENOPTERA: CEPHIDAE) VIA ASSOCIATED BRACONID PARASITOIDS	68
Contribution of Authors and Co-Authors	68
Manuscript Information	69
Abstract.....	71
Introduction.....	72
Materials and Methods.....	76
WSS-Inclusion Infestation of Smooth Brome	76
Montana Field Survey.....	77
Statistical Analysis	79
Results.....	80

TABLE OF CONTENTS CONTINUED

WSS-Inclusion Infestation of Smooth Brome	80
Montana Field Sites	80
Discussion	82
WSS-Inclusion Infestation of Smooth Brome	82
Montana Field Sites	83
Broader Implications	86
Figures.....	87
References.....	97
4. CONCLUSION.....	103
CUMULATIVE REFERENCES	105

LIST OF TABLES

Table	Page
1. Table ST2.1. Concentrations of volatiles used for electrophysiological trials on <i>B. cephi</i> and <i>B. lissogaster</i> . Volatiles match those found in samples collected from WSS infested smooth brome (<i>Bromus inermis</i> Leyss, ‘Manchar’) and winter wheat (<i>Triticum aestivum</i> , ‘Yellowstone).	58
2. Table ST2.2. Electrophysiological dose-response ratios and t-test results from adult female <i>B. lissogaster</i> parasitoids. All trials use isolated, synthetic compounds that match those produced by wheat stem sawfly infested wheat plants. *significant behavioral activity at $\alpha = 0.05$	59
3. Table ST2.3. Electrophysiological dose-response ratios and t-test results from adult female <i>B. cephi</i> parasitoids. All trials use isolated, synthetic compounds that match those produced by wheat stem sawfly infested wheat plants. *significant behavioral activity at $\alpha = 0.05$	60
4. Table ST2.4. Behavioral wind-tunnel response counts and t-test results from female <i>B. cephi</i> parasitoids. All trials use isolated, synthetic compounds that match those produced by sawfly infested wheat plants. Blank columns indicate where no statistics were generated due to low N counts. *significant behavioral activity at $\alpha = 0.05$	61
5. Table ST2.5. Behavioral wind-tunnel response counts and t-test results from female <i>B. lissogaster</i> parasitoids. All compounds are isolated, synthetic compounds that match those produced by sawfly infested wheat plants. Blank columns indicate where no statistics were generated due to low N counts. *significant behavioral activity at $\alpha = 0.05$	61

LIST OF FIGURES

Figure	Page
1. Fig. 2.1. Comparison of volatile concentrations between WSS infested and uninfested smooth brome (<i>Bromus inermis</i> Leyss, ‘Manchar’) and winter wheat (<i>Triticum aestivum</i> , ‘Yellowstone’).	53
2. Fig. 2.2. EAD-FID: Electrophysiological depolarization response from adult female <i>B. cephi</i> to volatiles blends from smooth brome (<i>Bromus inermis</i> Leyss, ‘Manchar’) sample. Electroantennographic detection and flame ionization detection (EAD- FID) run using volatile blend of 15 collected samples. Lower, GC-MS plot showing infested smooth brome and winter wheat (<i>Triticum aestivum</i> L., ‘Yellowstone’) chromatograms to show volatile locations and identifications.	54
3. Fig. 2.3. Behavioral preferences from Y-tube olfactometer bioassay tests for both <i>B. cephi</i> and <i>B. lissogaster</i> females when choosing between “Pure air”, smooth brome (<i>Bromus inermis</i> Leyss, ‘Manchar’) and winter wheat (<i>Triticum aestivum</i> , ‘Yellowstone’) volatile blends. The volatile blends for each plant type were combined volatiles samples from 15 infested plants. Left side bar graphs show the number of non-responders from each set of related trials. *represents $P \leq 0.05$, ** < 0.01	55
4. Fig. S2.1. Antennal response of adult female <i>Bracon cephi</i> and <i>B. lissogaster</i> to synthetic volatiles matching those produced by wheat stem sawfly infested plants. mV response represents the averaged response between 0.01, 100, and 10000 volatile concentrations. *significance at $\alpha = 0.05$	56
5. Fig. S2.2. Electrophysiological response ratios of adult female <i>B. cephi</i> and <i>B. lissogaster</i> to varying concentrations of synthetic volatiles matching those produced by WSS infested plants.	57
6. Fig. S2.3. Behavioral preferences of adult female <i>Bracon cephi</i> and <i>B. lissogaster</i> during wind-tunnel olfactory trials. Insects chose between “Pure air” (white) and the tested volatile (blue). Volatiles match those found in samples collected from WSS infested smooth brome (<i>Bromus inermis</i> Leyss, ‘Manchar’) and winter wheat (<i>Triticum aestivum</i> , ‘Yellowstone’). **represents $P \leq 0.01$, *** < 0.005	58

LIST OF FIGURES CONTINUED

Figure	Page
7. Fig. 3.1. Comparison of year and treatment group for WSS-inclusion infestation of smooth brome. Three treatment groups - high, low, and control (zero, not shown) - were used. The control trials showed no visible sign of WSS stem damage. *** represents $P < 0.05$ on ANOVA.	87
8. Fig 3.2. Proportion of infested smooth brome internodes exhibiting visible WSS damage within WSS-inclusion infestation plots in Bozeman, MT. High treatments had 600 ‘stubs’ (WSS pupae) added to each cage, while low had 200. We found that 57.1% of stems in 2022 and 62.3% in 2023 exhibited more than four nodes of WSS boring damage.	88
9. Fig 3.3. Five-year seasonal change in precipitation for Big Sandy and Moccasin, MT, USA. Averaged from data between 2018 and 2023 from Weather Underground. There was a noticeable change in average precipitation after mid-July with little precipitation after July 15. A) Boxplot showing average weekly rainfall during each time period. B) <i>Line plot</i> showing seasonal trend of average rainfall.	89
10. Fig 3.4. Normalized difference vegetation index (NDVI) of smooth brome and adjacent spring wheat field from April 2023 in Big Sandy, MT. Orange boxes in (A) indicate from where NDVI data was gathered using Google Earth Engine. Dotted black line on (B) indicates when spring wheat was harvested.	90
11. Fig 3.5. Proportion of infested smooth brome internodes exhibiting visible WSS damage within WSS-inclusion infestation plots in Big Sandy and Moccasin, MT. We found that 19.5% of stems in Big Sandy and 27.1% of stems in Moccasin had four or more nodes exhibiting WSS damage.	91
12. Fig 3.6. Ratio of stems found to be parasitized by WSS parasitoids to stems cut by WSS. Stems collected from field sites in Moccasin and Big Sandy, MT. Dotted horizontal line represents ratio of 1 where the number of parasitized stems are equal to WSS-cut stems. All ratios are greater than one for smooth brome while all ratios are less than one for adjacent wheat fields.	92
13. Fig 3.7. Proportion of parasitism within infested field-collected smooth brome stems. Fall samplings consistently revealed higher rates of parasitism when compared to summer collections from the same location.	93

LIST OF FIGURES CONTINUED

Figure	Page
14. Supp Fig S3.1. Location of Montana, USA field sites. The WSS-inclusion smooth brome infestation site was in Bozeman, while field sites were located in centrally located Moccasin and in more northern Big Sandy.....	94
15. Fig. S3.2. Fifty-year trend of yearly mean temperature for Big Sandy and Moccasin, MT. We observed a significant average increase of 0.03 °C per when both data sets were combined.....	95
16. Figure S3.3. A) Moccasin, MT, September 22, 2021. Green smooth brome seen in the foreground growing in the ditch next to harvested winter wheat and early winter wheat. B) Moccasin, MT, September 20, 2023. Green smooth brome stems within the coulee adjacent to a harvested wheat field.....	96

ABSTRACT

The wheat stem sawfly (WSS), *Cephus cinctus* Norton (Hymenoptera: Cephidae), poses a serious threat to cereal crops across the Northern Great Plains of North America. Effective management of WSS relies on native parasitoids *Bracon cephi* (Gahan) and *B. lissogaster* Muesebeck (Hymenoptera: Braconidae), which play a crucial role in suppressing WSS populations. Smooth brome grass (*Bromus inermis* Leyss.), when grown adjacent to wheat (*Triticum aestivum* L.) fields, serves as a potential trap crop that can both reduce WSS larvae and provide refuge for parasitoids. However, the agroecological benefits of smooth brome in providing second-generation hosts to *B. cephi* and *B. lissogaster* are not well understood. Therefore, our study explores the ecological dynamics involving WSS, smooth brome, winter wheat, emitted volatile compounds, and the associated parasitoids. We analyzed volatile organic compounds (VOCs) emitted by WSS-infested smooth brome and winter wheat using EAD-GC-FID techniques. Smooth brome under WSS infestation produced higher concentrations of (*Z*)-3-hexenyl acetate, 6-methyl-5-hepten-2-one, and (*E*)-2-hexenal. Both *B. cephi* and *B. lissogaster* were more attracted to WSS-induced volatile blends from smooth brome when given the choice against winter wheat. Field observations were conducted in central and northern Montana to assess the efficacy of smooth brome as a host refuge. We recorded WSS infestation rates and parasitoid prevalence in smooth brome and adjacent wheat fields. Infestation rates were notably high in both crop and adjacent brome fields (e.g., 64.5% in smooth brome and 65.7% in adjacent wheat in Big Sandy, Montana). Smooth brome had a maximum WSS larval survival of 5.7% and a 43.6% greater larval mortality rate compared to adjacent wheat. With similar parasitoid numbers in infested stems, smooth brome effectively reduced WSS survival and provided a sustainable habitat for crucial second-generation parasitoids. Based on our findings, we suggest the strategic conservation and maintenance of smooth brome in areas located adjacent to cultivated wheat fields to better manage populations of WSS.

CHAPTER ONE

LITERATURE REVIEW

History and Distribution of the Wheat Stem Sawfly

The wheat stem sawfly (WSS), *Cephus cinctus* Norton (Hymenoptera: Cephidae), is a native species ([Ainslie 1920](#), [Weiss and Morrill 1992](#), [Beres et al. 2011b](#), [Lesieur et al. 2016](#)) widely distributed across North America ([Olfert et al. 2019](#)) and the most destructive pests of wheat (*Triticum aestivum* L.) in the Northern Great Plains of North America ([Bekkerman and Weaver 2018](#)). Originally known as the ‘western grass-stem sawfly’ ([Ainslie 1920](#)), the WSS was originally discovered within native, hollow-stem, wild grasses ([Criddle 1917](#)). First found mining through *Agropyron* and *Elymus* in Colorado in 1872 ([Norton 1872](#)), it was later identified within wheat in Manitoba, Canada in 1895 ([Fletcher 1896](#), [Ainslie 1929](#)). As human settlement rapidly increased west in the late 1800s, native prairies in the United States and Canada were replaced with a large-scale monoculture of wheat fields ([Fletcher 1904](#), [Ainslie 1929](#)), with reports of WSS following the westward expansion of wheat cultivation. Subsequent surveys found WSS larvae in wheat in fields throughout North and South Dakota, Minnesota, Iowa, and Nebraska. Although WSS was first reported in native grasses Colorado in 1872, the first report of infestation of winter wheat grown in the state was not detected until 2010 ([Irell and Peairs 2014](#)).

Host Plants

With the diminishment of its natural hosts on the landscape, WSS adapted to infest the large tracts of exotic, non-cultivated and cultivated grasses now grown throughout much of the

Northern Great Plains of North America ([Criddle 1923](#), [Rand et al. 2024](#)). In Montana, WSS is found within cultivated crops such as wheat (*Triticum aestivum*), barley (*Hordeum vulgare*) and rye (*Secale cereale*), as well as native Montana grasses including western wheatgrass (*Pascopyrum smithii*), slender wheat grass (*Elymus trachycaulus*), and bluebunch wheatgrass (*Pseudoroegneria spicata*) ([Ainslie 1920](#), [Wallace and McNeal 1966](#), [Cockrell et al. 2017](#), [Rand et al. 2024](#)). In addition, non-native grasses such as downy brome (*Bromus tectorum*), smooth brome (*Bromus inermis*), intermediate wheatgrass (*Thinopyrum intermedium*), and crested wheat grass (*Agropyron cristatum*) are common hosts for WSS ([Criddle 1922](#), [Perez-Mendoza et al. 2006](#), [Rand et al. 2024](#)). Wheat is grown extensively throughout the Northern Great Plains, having been cultivated west of the Mississippi since the late 1800s ([Brigham 1910](#)). Historically, spring wheat was the most susceptible to WSS among wheat classes. However, WSS has progressively adapted to make winter wheat equally as vulnerable in many parts of its cultivated area, beginning in the 1970s in Montana ([Morrill and Kushnak 1996](#), [Portman et al. 2018](#)).

Smooth Brome (*Bromus inermis* Leyss.) is a Eurasian, cool-season grass introduced to the United States in 1884 from Hungary and Russia for soil conservation and use as livestock feed ([Hitchcock and chase 1950](#), [Thomsen and Salesman 2011](#)). Throughout the early 19th and 20th century, it was planted in much of the upper half of North America. A perennial and rhizomatous grass, it is more drought tolerant than other exotic grasses ([Mapfumo et al. 2002](#)). Due to its sod-forming nature and large root system, it is used extensively to promote soil retention along highways ([USDA-NRCS 2002](#)). Several cultivars such as ‘Polar’, ‘Carlton’, and ‘Manchar’ are now agriculturally maintained for use as hay, silage, or pasture grazing due to their high protein and relatively low crude fiber content, although are no longer recommended as

forage crops ([Burger et al. 1958](#), [Dillemuth et al. 2008](#)). Historically, smooth brome was thought of as a potentially useful trap crop due to its WSS antibiosis properties ([Seamans 1928](#), [Hokkanen and Jokioinen 1991](#)). Although feasible as a feed crop, it holds considerably less economic value compared to wheat or other high value cash and forage crops ([Criddle 1922](#)). Due to its propensity to form monocultures and outcompete many native grasses, smooth brome is labeled by conservationists as having invasive capability ([Carlson and Newell 1985](#), [Willson and Stubbendieck 2000](#), [Dillemuth et al. 2008](#)).

As the natural, historic host for WSS, wild grasses play a sizable role in the population dynamics of the pest ([Criddle 1917](#), [Sing 2002](#), [Rand et al. 2024](#)). When suitable host crops, such as cultivated wheat, are abundant, populations of WSS increase significantly ([Rand et al. 2014](#)). This increase in population leads to a higher infestation rate, making cultivated wheat a more crucial source habitat for WSS compared to grassland cover at broad, landscape levels. serving as a crucial source habitat for this pest compared to grassland cover at broad, landscape levels. In contrast, natural or semi-natural habitats offer important resources, including refuges, nectar, and alternate hosts for natural enemies ([Bianchi et al. 2006](#), [Peirce et al. 2021](#)). Understanding the population dynamics of WSS and its natural enemies in both wild and cultivated hosts is crucial for developing effective management tactics, especially when wild hosts and susceptible cereal crops have co-existed in the same field areas for many years.

Biology of the Wheat Stem Sawfly

Adult

Adults are relatively small (8-13 mm) with a narrow elongated and slightly compressed black body, yellow legs, and three characteristic black bands across the abdomen. Females are

larger than males and have a long, dark, ovipositor. Both male and female adults are weak fliers, rarely flying long distances at one time ([Criddle 1923](#)). Wheat stem sawfly are univoltine, having only one generation per year. Males are haploid (9 chromosomes), while females are diploid. Females that do not find a mate will produce male offspring, while those that find mates produce female progeny ([Holmes 1978](#)). Fully mature adults hatch in the spring once it has sufficiently warmed and the moisture levels in the soil reach threshold levels ([Holmes 1978](#), [Perez-Mendoza et al. 2006](#)). In Montana, this period begins in mid- to late-May and ends early in July ([Somsen and Luginbill 1956](#), [Weaver et al. 2005](#)). Their lifespan usually lasts about 5-8 days, emerging asynchronously from May until June. Males emerge before the females, ensuring that many of the early females to hatch will find a mate and deposit eggs that will be female ([Mackay 2011](#)). Copulation lasts less than one minute with the male holding the back of the female with their abdomen curved down under the female ovipositor. Fertilized females lay eggs several hours after copulation ([Holmes 1978](#)).

Oviposition

Each female WSS can carry as many as 50 eggs, which are typically uniform in size and maturity ([Ainslie 1920](#)). After locating a suitable host stem, female WSS oviposit a single egg inside the host plant lumen ([Holmes 1977](#), [Beres et al. 2011b](#)). WSS larvae hatch inside the stem and immediately begin feeding on the stem's parenchyma tissue, reducing the photosynthetic capacity of the plant ([Macedo et al. 2005](#)). As stem senescence progresses, the larvae move to the base of the stem and makes a V-shaped groove ([Ainslie 1929](#)) above a constructed protective hibernaculum where they will overwinter ([Holmes and Peterson 1960](#)). In ripening crops, the weakened stem usually lodges, causing the head of the infested plant to fall to the ground, where

recovery is challenging even with specialized equipment ([Nansen et al. 2005a](#); [2005b](#), [McCullough et al. 2020](#), [Weaver 2023](#)).

Eggs

Newly laid eggs are crescent shaped, milky white, and range between 1- to 1.25-mm long and 0.33- to 0.42-mm wide ([Ainslie 1920](#)). After oviposition, the egg lies freely within the lumen of the host stem or in a hollow created by the female WSS ovipositor ([Fulbright et al. 2017](#)). Laval development occurs rapidly with the recognizable shape becoming apparent at day three. By day five, the mandibles turn brown as the eye spots begin to appear and darken. By day six or seven, the larva begins to hatch using a series of convulsive movements and emerges into the stem cavity, with full functionality achieved by the seventh day ([Ainslie 1920](#)).

Larvae

After hatching and before feeding, the larvae are transparent and colorless ([Ainslie 1920](#), [Criddle 1923](#)). WSS larvae are distinguishable from other larvae feeding in wheat and grasses by their highly sclerotized head capsule and large body size ([Nelson and Farstad 1953](#)). As the larvae chew their way through the parenchyma and vascular tissues of the host stem, the larvae become yellow-green and begin to excrete frass. Frass includes the digested plant tissue as well as metabolic breakdown products from WSS ([Holmes 1978](#)). If multiple eggs are laid within the same stem, the largest (usually the first egg laid and hatched) will typically remain after a few weeks due to larval cannibalization ([Criddle 1923](#), [Seamans et al. 1944](#), [Buteler et al. 2015](#)). It remains unknown whether the consumption of other eggs and larvae is the result of intentional cannibalism or the indirect result of indiscriminate feeding ([Buteler et al. 2015](#)). As the host plant physiologically matures, and the larvae reaches its fifth stadium, the insect is cued to travel

to the base of stem and prepare for obligatory diapause ([Nelson and Farstad 1953](#)). The descending movement of larvae and development of the hibernaculum are triggered by the host plant senescence. As the stem walls becoming increasingly transparent, they allow increased amounts of visible and infrared radiation into the stem ([Holmes 1977](#)). Once the larvae reach the base of the stem, they construct an interior V-shaped groove, making the stem weak enough to lodge due to gravity or wind ([Criddle 1923](#)). The larvae then plug the remaining stub with frass to insulate the hibernaculum during diapause ([Holmes and Peterson 1960](#)). The larval stage of development can be as short as 30 days before entering diapause. Obligatory diapause lasts a minimum of 90 days ([Salt and Hollick 1947](#)). After the larvae are exposed to temperatures less than 10 °C for 90 days, diapause is complete, and pupation can begin. Larvae can reenter diapause if temperatures approach 35 °C ([Salt and Hollick 1947](#)) or if conditions are abnormally dry ([Holmes 1978](#)) shortly after termination of diapause.

Pupae

Once diapause is complete, pupal development begins. Pupation lasts for 21 days, beginning in early- to mid-May ([Criddle 1923](#)). Initially, the pupa is milky white ([Ainslie 1920](#)), gradually changing to bright white as the wings develop ([Fulbright et al. 2017](#)). Additionally, as development continues, characteristic brown and black eye spots appear on the surface of the pupae. Once pupation is complete, the adult will chew through either the frass plug or the side of the stub, and emerge ready for flight ([Ainslie 1920](#), [Holmes and Peterson 1960](#)).

Damage Caused by Wheat Stem Sawfly

Wheat stem sawfly stem girdling weakens the stem, typically leading to lodging, with many of the infested heads on the ground. Stem lodging, which is readily apparent to growers in their wheat fields, disrupts the standing row structure ([Weaver 2023](#)) and results in stems that are not challenging for growers to harvest ([Criddle 1921](#), [Ainslie 1929](#)). In addition, WSS-infested stems exhibit decreased kernel yield ([Ainslie 1920](#), [Criddle 1922](#), [Holmes 1977](#)) due to parenchymal tissue feeding by larvae. Estimates of yield loss from unrecoverable heads range from 6% to 20% ([Morrill et al. 1994](#), [Beres et al. 2007](#)), depending on the cultivated variety and infestation severity. Combined reductions in photosynthetic capacity and exposure to abiotic stress can decrease head weight by as much as 30% ([Macedo et al. 2005](#), [Macedo et al. 2006](#), [Macedo et al. 2007](#), [Delaney et al. 2010](#)). It remains uncertain whether physiological yield loss is caused by the loss of parenchyma or the loss of vascular integrity, as both occur ([Weaver 2023](#)). In addition to yield losses in the harvest year, the reduction in stem residue structure due to low-cut stubble further affects yields in future years. Larval WSS stem-cutting decreases stem residues, which increases soil erosion from wind, reduces snow retention, and lowers soil moisture content ([Keren et al. 2015](#)).

Management of Wheat Stem Sawfly

Chemical Control

Because of a combination of factors, including a cryptic life cycle and an emergence period that lasts between several weeks to more than a month ([Perez-Mendoza et al. 2006](#)), the use of traditional insecticides against WSS are ineffective. The extended adult flight period

makes management with contact insecticides challenging, as it necessitates frequent applications, which are neither effective nor cost-efficient ([Knodel et al. 2009](#)). Chemical control methods were first tested on WSS as early as 1949 ([Wallace 1962](#)). After using six different organochlorine and organophosphate insecticidal dust applied via a powder duster, [Munro et al. \(1949\)](#) found “unsatisfactory results that did not control” WSS populations or limit infestations. [Wallace \(1962\)](#) reported that a 73% control of WSS infestation could be achieved via granular heptachlor applied in the furrow with the wheat seed. However, these findings were not able to be replicated ([Holmes et al. 1963](#)). Similar results were found when testing with foliar insecticides, with few differences in their effect when compared to controls ([Blodgett et al. 1996](#)). Although the Montana Department of Agriculture permitted the use of systemic organophosphate insecticide phorate (Thimet 20-G[®]) for managing WSS larval infestation in winter and spring wheat ([Montana Department of Agriculture 2015](#)), its use was not environmentally friendly due to its toxicity to mammals, fish, and birds ([Weaver 2023](#)). Additionally, a preharvest interval of 85 days complicated harvest scheduling ([Ginsberg 2003](#), [Mahajan et al. 2006](#)), and the high toxicity may have additional adverse toxicity impacts on beneficial parasitoid populations ([Varella 2016](#)).

Cultural Control

Host Plant Resistance Planting rotational crops that are poor or non-hosts of WSS is essential for effective WSS management ([Weiss and Morrill 1992](#)). Regularly rotating dryland crops, such as oats, legumes, and oilseeds, helps curtail the year-over-year cycle of WSS population increase ([Miller et al. 2002](#)). No broadleaf plants, including those commonly grown in Montana like chickpeas (*Cicer arietinum* L.), flax (*Linum usitatissimum* L.), and camelina

(*Camelina sativa* (L.) Crantz), can host WSS ([Farstad and Jacobson 1945](#), [Weaver 2023](#)).

Although WSS will oviposit into both wild and domesticated oat, the plants are lethal to WSS eggs and larvae ([Criddle 1923](#), [Ainslie 1929](#), [Sing 2002](#), [Weaver et al. 2004](#)).

Much of the research done on WSS-resistant wheat cultivars focuses on solid stem trait and pith expression ([Platt and Farstad 1949](#), [Beres et al. 2012](#), [Varella 2016](#)). Increased pith expression in solid stem wheat cultivars enhances resistance to WSS through several mechanisms: it strengthens the stem, which reduces lodging ([Delaney et al. 2010](#), [Bathini et al. 2023](#)); it disrupts the movement of WSS larvae ([Wallace and McNeal 1966](#), [Cárcamo et al. 2005](#)); and it leads to higher egg mortality and lower oviposition rates ([Holmes and Peterson 1961](#)). The solid-stem trait has been developed in numerous spring and some winter wheat cultivars ([Morrill et al. 2001](#), [Varella et al. 2015](#), [Bathini et al. 2023](#)). While the use of solid-stem cultivars is most often recommended for WSS management, hollow-stem cultivars were found to exhibit greater parasitism when compared to solid-stem varieties ([Holmes et al. 1963](#)). Rand et al. ([2012](#)) suggested that the thicker pith in solid-stem cultivars impair the ability of female parasitoids to sense vibrations from WSS larvae ([Mankin et al. 2004](#)), leading to less effective parasitism due to difficulties in locating WSS hosts.

Tillage Larvae WSS are protected against both water loss and freezing temperatures by the soil surrounding the wheat stubble where immatures overwinter. Tilling the soil can both expose wheat stubble to the soil surface or bury stubble underground, conditions which either kill the hibernating larvae or impede adult emergence ([Callenbach and Hansmeier 1944](#)). Tilling the crop residue where WSS reside is effective in decreasing the pest's populations in both spring and winter wheat cultivars. As much as 90% mortality occurs in North Dakota after fall

tillage ([Weiss et al. 1987](#)). Many factors influence the effectiveness of tilling, including adequate exposure of wheat stubs on the soil surface and appropriate timing ([Holmes and Farstad 1956](#), [Morrill et al. 1992](#), [Weiss and Morrill 1992](#)). While the variability in effectiveness exists, some growers consider it a crucial management tool ([Lesieur et al. 2016](#)).

Although tilling can be effective in killing WSS larvae, it has several negative consequences. Tilling increases water loss, soil compaction, and erosion ([Phillips et al. 1980](#), [Lal 1991](#)). Additionally, tilling adversely affects beneficial parasitoids that target WSS larvae. Unlike WSS, which overwinter at the base of the plant, WSS parasitoids overwinter higher up in the stem ([Morrill et al. 1998](#), [Runyon et al. 2002](#)). Tilling displaces soil, burying the upper portion of the plant and preventing adult parasitoids from emerging in the spring ([Weaver et al. 2004](#)). Runyon et al. ([2002](#)) found that reduced tillage led to higher rates of parasitism and fewer instances of stem cutting compared to fields with intensive tillage. Weaver et al. ([2004](#)) reported that employing solid-stemmed cultivars in zero-tillage systems helped conserve parasitoid populations and decrease WSS populations.

Trap Crops Trap cropping uses non-economically important plantings to help reduce pest populations or block their movement into valuable crop areas ([Hokkanen and Jokioinen 1991](#)). Effective trap crops of WSS should have appealing characteristics to attract the pest to the trap planting, and away from the wheat ([Farstad 1940](#)). The earliest trap crop used in WSS management was rye grass, *Lolium perenne* L. (Poaceae), planted in ditches and headlands of wheat fields. This strategy aimed to encourage WSS to deposit most of their eggs in the rye grass stems, which subsequently were destroyed by mowing in July ([Criddle 1922](#)). Criddle ([1922](#)) noted that smooth brome could be a more effective trap crop, as larvae generally did not survive,

eliminating the need for mowing. Additionally, smooth brome elongates earlier in the spring than wheat, making it the primary host for early emerging WSS if planted adjacent a wheat field ([Criddle 1923](#), [Seamans 1928](#)). Criddle ([1922](#)) also noted that parasitism rates were generally higher in adjacent native and non-native grassland, thus advising against mowing these areas.

An alternative strategy for trap strips involves managing the borders of the field by sowing a pest-resistant crop along the perimeter and planting a hollow-stem wheat cultivar in the interior. This method aims to intercept incoming WSS from adjacent infested stubble, concentrating the infestation within the trap perimeter ([Morrill et al. 2001](#), [Beres et al. 2009](#)). This approach also succeeds in conserving beneficial insects as the exterior trap crop and interior protected crop are both harvested, rather than destroyed.

Delayed Planting & Swathing Because adult female WSS require hosts that have undergone stem elongation, wheat planted later in the growing season may avoid oviposition due to delayed elongation ([Criddle 1922](#), [Farstad and Jacobson 1945](#), [Jacobson and Farstad 1952](#)). Unfortunately, delayed planting makes less efficient use of early season soil moisture ([Morrill and Kushnak 1996](#)). Reductions in infestation levels are only realized with planting dates after June 1, seriously reducing potential crop yields ([McNeal et al. 1955](#), [Morrill and Kushnak 1999](#)). To mitigate losses in areas with a history of severe infestation, growers must continuously weigh the trade-offs of delayed planting against the risk of reduced crop yields. This balancing act requires careful consideration of local conditions and historical infestation patterns to optimize both pest management and crop productivity.

Swathing, also known as windrowing, is the practice of cutting the wheat to accelerate the drying process and decrease the losses caused by WSS cutting ([McCullough et al. 2020](#)). By

cutting heavily-infested wheat and allowing it to dry before WSS cutting, swathing works by reducing losses due to lodging ([Ainslie 1920](#)). However, swathing generally does not affect WSS survival because larvae move to the base of plants to overwinter ([Beres et al. 2011a](#)). Swathing too early can decrease yield and grain weight, with significant losses occurring when kernel moisture is at 58% ([Molberg 1963, Holmes and Peterson 1965](#)). Swathing longer stems to reduce stubble height can enhance effectiveness, with early swathing recommended mainly for field edges or heavily infested areas ([Holmes and Peterson 1965](#)).

Biological Control Methods

The use of biocontrol in managing WSS populations has been well studied with variable results. There are several types of organisms that have been reported as biocontrol agents of WSS in wheat fields. These include soil fungal pathogens, nematodes, and insect predators.

Soil Fungal Pathogens and Nematodes Among potentially useful fungal pathogens are a facultative *Fusarium* species ([Wenda-Piesik et al. 2009](#)), as well as commercially marketed strains of *Beauveria* and *Metarhizium* species ([Tangtrakulwanich et al. 2014, Portman et al. 2018](#)). Their effectiveness is limited by their dual pathogenicity to both wheat and larvae, as well as the arid conditions of wheat cultivation, which necessitates their application to the external surfaces of infested plants. Portman et al. ([2016](#)) demonstrated that entomopathogenic nematodes were successful in killing WSS larvae in stubs under laboratory conditions. However, translating these results to field settings has not yielded reliable efficacy.

Predatory Beetle Morrill et al. ([2001](#)) observed *Phyllobaenus dubius* (Wolcott) emerging from wheat stubble and within dissected wheat stems in Montana. Further research is required

for this coleopteran to determine its prospects going forward as an effective WSS management tool.

Parasitoids of the Wheat Stem Sawfly

Two native parasitoid wasps target WSS larvae. The congeneric parasitoids, *Bracon cephi* (Gahan) and *B. lissogaster* Muesebeck, provide significant biological control of WSS ([Buteler et al. 2015](#), [Rand et al. 2017](#), [Rand et al. 2020](#)). First described in 1918 ([Gahan 1918](#)) and 1953 ([Muesebeck 1953](#)), *B. cephi* and *B. lissogaster*, are easily distinguished using the key described in Runyon et al. ([2001](#)). Initially, both species were limited in their ability to parasitize WSS larvae within wheat stems. Historically, WSS was found only within native grasses throughout North America where it coexisted with *B. cephi* and *B. lissogaster* ([Ainslie 1920](#), [Criddle 1922](#), [Cárcamo et al. 2012](#)). As agriculture expanded and native grasses were replaced by large monoculture landscapes, WSS spread to wheat ([Farstad 1940](#), [Davis et al. 1955](#), [Holmes 1978](#)). In contrast, *B. cephi* and *B. lissogaster* were slower to adapt ([Morrill et al. 1998](#)). In Manitoba, Criddle ([1922](#)) reported more than 80% mortality of larval WSS in grasses but observed no parasitism in nearby wheat heavily infested with WSS. The first reports of *B. cephi* attacking WSS larvae in wheat were not until 1923, over 25 years after the first observation of WSS damaging wheat in 1895 ([Ainslie 1920](#), [Criddle 1923](#)). At present, WSS populations are efficiently suppressed by these parasitoids in various regions, with reported parasitism rates exceeding 90% in some instances ([Holmes et al. 1963](#), [Morrill et al. 1998](#), [Runyon et al. 2002](#), [Weaver et al. 2004](#), [Wu et al. 2011](#), [Buteler et al. 2015](#), [Cárcamo et al. 2016](#)).

Biology of *Bracon cephi* and *Bracon lissogaster*

Adult

Both *B. cephi* and *B. lissogaster* are protelean host-specific parasitoids with two generations per year (bivoltine) ([Nelson and Farstad 1953](#), [Somsen and Luginbill 1956](#), [Holmes et al. 1963](#)). They are ectoparasitoids and idiobionts, immediately paralyzing their hosts and living on the integument of their hosts ([Nelson and Farstad 1953](#), [Runyon et al. 2002](#), [Weaver et al. 2004](#)). Adult male parasitoids are approximately 3.5 mm in length, while females are 4.1 mm. They are dark red, with black antennae, eyes, ovipositor, and ocelli ([Gahan 1918](#)). *Bracon lissogaster* and *B. cephi* are distinguishable by their head color and unique metasoma surface texture ([Runyon et al. 2001](#)). Adults emerge after completing a pupal stage within the host stem by chewing a hole through the stem wall.

In Montana, the first generation of both species emerges at approximately the same time as adult WSS ([Nelson and Farstad 1953](#), [Somsen and Luginbill 1956](#)) – late June to late July. The second generation emerges beginning in late July and individuals are active in August and September ([Somsen and Luginbill 1956](#), [Holmes et al. 1963](#)). Adult females locate a potential host stem using a combination of olfactory and volatile cues. The wasps will then locate a host WSS larva using acoustic cues ([Mankin et al. 2004](#), [Perez 2009](#)) and use their ovipositor to first paralyze, then deposit one (*B. cephi*) to four (*B. lissogaster*) eggs next to the paralyzed larva.

Eggs

B. cephi and *B. lissogaster* eggs are on average 0.86 mm in length, exhibiting an elongated shape and pale-yellow color ([Nelson and Farstad 1953](#)). Females lay one to three eggs

on WSS larval integument or adjacent to the larva. The eggs develop for 1-3 days before hatching ([Somsen and Luginbill 1956](#)).

Larvae

After hatching, the larva attaches itself to the integument of the host larva and immediately begins feeding ([Somsen and Luginbill 1956](#)). Parasitoid larvae are 1 mm in length, with a translucent hue that turns increasingly brown as the larva progresses through five stadia ([Nelson and Farstad 1953](#)). The newly hatched larvae have no appendages, save for antennae, and have highly sclerotized mouthparts and well-developed mandibles. Following feeding, the larva spins a light brown cocoon over the course of several days and attaches to the inside wall of the host plant stem. The larval stage takes an average of 10 days between initial hatch and cocoon completion. Because there are two generations per year, the early summer pupae hatch and emerge from the host stem. Second generation pupae overwinter within the cocoon and emerge in the spring ([Nelson and Farstad 1953](#)).

WSS and Parasitoid Interactions with Smooth Brome

Second-generation parasitoids of both species may struggle to reproduce effectively in wheat due to asynchrony, likely driven by early crop ripening and harvest dates that are common in drought-affected dryland cropping systems ([Holmes et al. 1963](#), [Holmes 1979](#), [Rand et al. 2014](#), [Peirce et al. 2021](#)). During landscape-level drought events in such areas, late-ripening grass species such as smooth brome may harbor WSS larvae as reservoir hosts for parasitoids. While a poor host for WSS larvae, surviving immature WSS found within the stems may be parasitized by second generation *B. cephi* and *B. lissogaster*. This combination of factors may indicate that smooth brome can function as a WSS sink and a parasitoid source, with very few

WSS emerging from smooth brome patches, while also supporting populations of parasitoids that can then parasitize WSS in adjacent wheat fields.

Plant Volatile Organic Compounds

Semiochemicals in Plant-Insect Systems

Plants interact with other organisms through a complex system of chemical signals known as volatile organic compounds (VOCs). These compounds or mixtures of compounds are released from one organism and evoke a physiological or behavior response in another organism ([Agelopoulos et al. 1999](#)). VOCs play a large role in both insect-insect and plant-insect interactions and are essential in insects locating feeding sites, mating sites, egg-laying sites, and refugia ([Xu and Turlings 2018](#)). For instance, female *Bagrada hilaris* are attracted to (*E*)-2-octenyl acetate, a compound produced at higher amounts by male *Bagrada hilaris* ([Guarino et al. 2008](#)). (2*E*,4*Z*)-2,4-heptadienal (1) and (2*E*,4*Z*)-2,4-heptadien-1-ol (2) are known aggregation pheromones for the weed biocontrol agent *Diorhabda elongata* ([Cossé et al. 2005](#)). While it is known that these chemicals play an important role in communication between plants, insects, and other organisms, there is still debate about the function of many of them ([Reddy and Guerrero 2004](#), [Voelckel and Jander 2018](#)).

Both the passive ([Hamilton-Kemp and Andersen 1984](#), [Hamilton-Kemp and Andersen 1986](#), [Gianoli and Niemeyer 1997](#), [Wenda-Piesik et al. 2009](#)) and induced ([Perez 2009](#), [Delaney et al. 2013](#), [Castelyn et al. 2015](#)) volatile chemicals of wheat have been extensively researched. As more was learned about these volatiles, researchers investigated the behavioral and electrophysiological responses of insects like WSS ([Cossé et al. 2001](#), [Wenda-Piesik et al. 2009](#)) and their associated specialist braconid parasitoids ([Perez 2009](#), [Bhandari 2020](#)) to volatiles from

wheat and other host plants. Adult female WSS are behaviorally attracted to (*Z*)-3-hexenyl acetate and β -ocimene, while being repelled by 6-methyl-5-hepten-2-one ([Piesik et al. 2008](#)), and *B. cephi* and *B. lissogaster* are attracted to (*Z*)-3-hexenyl acetate, 6-methyl-5-hepten-2-one, hexahydrofarnesyl acetone, (*E*)-2-hexenyl acetate, and (*E*)-2-hexenal with no response from β -ocimene ([Perez 2009](#)).

Research Questions

Given the substantial economic impact of the WSS and the challenges in managing its populations, it is essential to invest in effective integrated pest management strategies. Research supports the effectiveness of conservation biological control methods, highlighting the importance of conserving and promoting *B. cephi* and *B. lissogaster* as natural enemies to manage WSS populations. However, the benefits of smooth brome in aiding parasitoid populations are not fully understood. Therefore, I intend to investigate the complex chemical-ecological interactions between WSS, parasitoids, and smooth brome, and evaluate the ecological benefits of smooth brome for the biological control conservation of *B. cephi* and *B. lissogaster*. The primary goals of this research are as follows:

- i. Evaluate and compare the electrophysiological and behavioral response of *B. cephi* and *B. lissogaster* to WSS induced volatiles from smooth brome and winter wheat (Chapter 2). This portion builds substantially on the earlier findings of Perez (2009), who is a co-first author of the paper presented in this chapter.

- ii. Examine the agroecological impacts of smooth brome in the conservation of *B. cephi* and *B. lissogaster* by assessing the abundance and survival rates of WSS and parasitoid larvae within smooth brome found in areas adjacent to wheat fields in Montana ([Chapter 3](#)).
- iii. Summarize our findings and discuss the application and future direction of this research ([Chapter 4](#)).

Previous research from our lab demonstrated that smooth brome and spring wheat produce similar volatile blends both in the presence and absence of WSS infestation ([Bhandari 2020](#)). In addition, Bhandari ([2020](#)) observed that *B. cephi* and *B. lissogaster* favored WSS-induced blends from smooth brome over those from spring wheat. Here, we hypothesize that *B. cephi* and *B. lissogaster* will exhibit similar behaviors when given the choice between WSS induced volatile blends from smooth brome and winter wheat.

In this research, we will also conduct a field survey assessing the potential ecological benefits of smooth brome adjacent to wheat fields. Previous research has observed smooth brome's unique WSS antibiosis properties ([Seamans 1928](#), [Bhandari 2020](#)), however it is uncertain when WSS larvae are available and the extent to which *B. cephi* and *B. lissogaster* benefit from their late-season presence within smooth brome. We hypothesize that, post-harvest, there will be greater WSS mortality and a greater number of *B. cephi* and *B. lissogaster* pupae within the smooth brome compared to adjacent wheat.

Conserving beneficial populations of *B. cephi* and *B. lissogaster* should greatly benefit wheat growers across Montana and the Northern Great Plains. Our investigations into the behavioral and ecological interactions of *B. cephi* and *B. lissogaster* with smooth brome

represent a step forward in advocating for conservation biological control of WSS and the sustainable cultivation of wheat across the region.

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CHAPTER TWO

SENSORY AND BEHAVIORAL RESPONSES OF BRACONID
PARASITOIDS TO CHANGES IN VOLATILE EMISSIONS
INDUCED BY WHEAT STEM SAWFLY (HYMENOPTERA:
CEPHIDAE) LARVAL FEEDING IN WINTER WHEAT AND
SMOOTH BROME

Contribution of Authors and Co-Authors

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Sensory and behavioral responses of braconid parasitoids to changes in volatile emissions induced by wheat stem sawfly (Hymenoptera: Cephidae) larval feeding in winter wheat and smooth brome

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Abstract

The wheat stem sawfly (WSS), *Cephus cinctus* Norton, is a major pest of cultivated wheat (*Triticum aestivum* L.) and other cereals in North America. The native congeneric parasitoids *Bracon cephi* and *B. lissogaster* are important biocontrol agents and play a crucial role in managing WSS outbreaks and damage. Smooth brome (*Bromus inermis* Leyss) has been found to be an effective WSS sink and parasitoid source, when grown in areas neighboring wheat fields in Montana. To better understand the ecology of the system, we investigated both the WSS induced volatile organic chemicals (VOCs) produced by smooth brome and winter wheat, and the electrophysiological and behavioral response of *B. cephi* and *B. lissogaster* to the collected volatiles via EAD-GC-FID. Volatile concentration analysis indicated increased production of (*Z*)-3-hexenyl acetate, 6-methyl-5-hepten-2-one, and (*E*)-2-hexenal in WSS infested smooth brome, and elevated production of 6-methyl-5-hepten-2-one in infested smooth brome and winter wheat when compared to their uninfested counterparts. Both *B. cephi* and *B. lissogaster* exhibited significant electrophysiological and behavioral response to (*Z*)-3-hexenyl acetate, 6-methyl-5-hepten-2-one, and hexahydrofarnesyl acetone. Our results provide important evidence supporting habitat management recommendations that will enhance the effectiveness of biological control, contributing to more sustainable agricultural practices and the preservation of vital ecological functions.

Introduction

The wheat stem sawfly (WSS), *Cephus cinctus* Norton (Hymenoptera: Cephidae), is a grass-mining sawfly native to North America ([Criddle 1922](#), [Ainslie 1929](#), [Wallace and McNeal 1966](#), [Lesieur et al. 2016](#), [Weaver 2023](#)). Adult female WSS use their saw-like ovipositor to deposit their eggs within the lumen of stems, where the hatched larvae feed on parenchymal tissue ([Roemhild 1954](#), [Holmes and Farstad 1956](#)). Economic damage is caused by reduction of kernel weight reduction due to larval feeding ([Beres et al. 2011a](#); [2011b](#), [Delaney et al. 2010](#)), and stem toppling caused by larval girdling during overwinter chamber preparation that results in unrecovered wheat heads ([Holmes and Peterson 1960](#), [Nansen et al. 2005](#), [McCullough et al. 2020](#)).

Bracon cephi (Gahan) and *Bracon lissogaster* Muesebeck (Hymenoptera: Braconidae) target WSS larvae feeding within wheat stems ([Nelson and Farstad 1953](#), [Morrill et al. 1998](#), [Runyon et al. 2001](#)). These two highly host-specific ectoparasitoids, native to North America, provide biological control by causing significant and irreplaceable mortality in WSS populations ([Peterson et al. 2011](#), [Buteler et al. 2015](#)) and can significantly reduce WSS damage and impact on crop yields ([Buteler et al. 2008](#), [Bekkerman and Weaver 2018](#), [Adhikari et al. 2019](#), [Rand et al. 2020](#)). Wheat stem sawfly is the only known host ([Runyon et al. 2001](#)), although hyperparasitism can occur between congeners as well as intraspecifically ([Nelson and Farstad 1953](#), [Davis et al. 1955](#)).

Smooth brome (*Bromus inermis* Leyss) is a Eurasian cool-season, non-native, rhizomatous grass that was originally thought of as potentially useful trap crop to manage WSS ([Criddle 1922](#), [Seamans 1928](#), [Farstad and Jacobson 1945](#), [Beres et al. 2011](#)). The grass is found

along roadways and within coulees that border much of Montana's 'Golden Triangle', an area of central and northern Montana with intense cereal grain production. Due to its relatively low agricultural value and propensity to form monocultures that outcompete many native grasses, smooth brome is considered problematic in some habitats ([Carlson and Newell 1985](#), [Willson and Stubbendieck 2000](#), [Dilleuth et al. 2008](#)). Yet, it still holds considerable ecological and economic value due to its prolonged growing season and late senescence, as well as WSS larvae antibiosis properties ([Otfinowski et al. 2006](#), [Rand et al. 2024](#), [Strand et al. 2024](#)).

Parasitoids of insect herbivores operate within a complex ecological framework. Consequently, their physiology and behavior are shaped by interactions across multiple trophic levels, including their herbivorous hosts and the plants those hosts consume ([Price et al. 1980](#)). Natural enemies rely on information from these trophic levels to make foraging decisions, with chemical cues playing a crucial role. The foraging behavior of parasitoids typically involves several distinct stages: host habitat location, host location, host recognition, and host acceptance ([Vinson 1998](#)), with host and habitat location often involving the use of non-volatile and volatile chemicals from the host or host plant ([Vet and Dicke 1992](#), [Steidle 2000](#)). Numerous studies have demonstrated that herbivore-injured plants produce specific blends of odors which can be attractive to certain insect predators and parasitoids ([Vet and Dicke 1992](#), [Bernasconi et al. 1998](#)). In agricultural settings, internally feeding grain beetles and their associated parasitoids were a major focus of research into understanding parasitoid host locating behavior on species feeding within the host plant material, via chemical cues ([Steidle et al. 2001](#)), as well as the previously mentioned studies from foliar feeding species.

Volatile organic compounds (VOCs) in plants are a diverse group of organic chemicals that plants produce and release into the atmosphere to communicate with other organisms in their environment. These compounds can volatilize easily at room temperature due to their high vapor pressure. Research has been conducted on the production of both passive ([Hamilton-Kemp and Andersen 1984](#), [Hamilton-Kemp and Andersen 1986](#), [Gianoli and Niemeyer 1997](#), [Piesik et al. 2008](#)) and induced volatile chemicals ([Perez 2009](#), [Delaney et al. 2013](#), [Castelyn et al. 2015](#)) by wheat. As more was learned about these volatiles, researchers began to investigate the electrophysiological and behavioral responses of internal plant-feeding insects like WSS ([Cossé et al. 2001](#), [Piesik et al. 2008](#)) and its two associated specialist braconid parasitoids ([Perez 2009](#), [Bhandari 2020](#)) to volatiles from uninfested and infested wheat and other host plants.

A better understanding of the benefits that un-maintained, semi-natural environments offer to agroecosystems is crucial for enhancing conservation biocontrol in intensified monocultures. Part of this is understanding the molecular mechanisms that govern these processes – at the level of sensory responses and subsequent elicited behaviors. Hence, we aimed to characterize and compare the VOC profiles of both winter wheat and smooth brome, and to analyze the electrophysiological and behavioral responses of WSS parasitoids to these volatile blends. Our findings may help inform future consideration of the ecosystem services provided by parasitoids in smooth brome in dry-land wheat production settings that are challenged by WSS.

Materials and Methods

Plant Culture

Smooth brome ('Manchar') was grown from transplanted plants harvested from the Arthur H. Post Agronomy Farm (43°38'19.39" N, 116°14'28.86" W). Immediately following

collection, plants were transplanted into 7 x 35 cm lightweight dee pot cells (Stuewe & Sons Inc®, Tangent, OR) and moved into greenhouse space at the Montana State University Plant Growth Center. Winter wheat ('Yellowstone') was grown in 2 x 20 cm conical pots. The soil used consisted of MSU Plant Growth Center soil mix (equal parts sterilized Bozeman silt loam soil and washed concrete sand with Canadian sphagnum peat moss incorporated) and Sunshine Mix 1 (Canadian sphagnum peat moss, vermiculite, perlite, and Dolomite lime) in a 1:1 ratio. Fertilization was once weekly using Jack's Professional® Water-Soluble Fertilizer (20-20-20) (J.R. Peters Inc., Allentown, PA). Supplemental light from model MVR1000/C/U GE Multi-Vapor Lamps (GE Lighting, General Electric Company, Cleveland, OH) under photoperiod of 16:8 (L:D) h at 22 °C and 20 – 40% RH. After the wheat plants reached Zadoks 12, they were moved into vernalization storage (8:16 (L:D) h at 4 °C and 20 - 40% RH) for 6 wks to experience the length of dormancy needed for successful flower development. After the 6-wk period, stems were transplanted into 7 x 35 cm conical pots.

Insects

Wheat stubble collected the year before each experiment was used to rear adult WSS. Wheat stubble was collected from Big Sandy (48°10'39.14" N, 110°6'50.62" W) and Three Forks (45°59'33.38" N, 111°37'7.42" W), MT. 'Stubble', or the basal root and stem remaining after WSS cutting, was collected from fields that experienced high levels of WSS infestation and cutting the year before. The stubble, which contained WSS larvae in diapause, was kept in a refrigerator between 0-4 °C for >100 d as required to complete obligatory larval diapause. After diapause completion, stubble was kept at room temperature between 22-27 °C for 4-5 wks in sealed 70 cm x 35 cm x 20 cm plastic Tupperware® bins to allow for larval pupation and adult

emergence. Once emergence began, adults were collected daily and sorted in 2-L glass mason jars sealed with filter paper to allow for airflow. Jars containing adults were refrigerated at 6-10 °C until they were needed for experiments. Unused adults were discarded after 48 hr of refrigeration.

Wheat-stem residue containing parasitoids *B. cephi* and *B. lissogaster* were collected from wheat fields in Three Forks, MT (46°1'12.78" N, 111°35'11.70" W) that experienced high levels of WSS infestation the year before. Stem residue was collected and stored inside 170-L plastic barrel liners and stored in a cold storage room at 4 °C until mid or late spring of the following year to provide enough time for the insects to complete obligatory diapause. Plastic barrel liners were then removed from cold storage and the residue was placed inside 170-L trash barrels at room temperature and watered to encourage larval development and emergence. Parasitoids were collected daily as they emerged and kept at 6-10 °C until used.

Greenhouse Infestation and Volatile Collection

Winter wheat and smooth brome plants of similar heights were infested simultaneously to ensure consistent WSS-induced volatiles. Once the first node was detected in the winter wheat (typically around Zadoks node 32 ([Zadoks et al. 1974](#))), smooth brome plants were paired. Methods for infestation were adopted from Biyiklioglu et al. ([2018](#)). Briefly, plants were infested by placing a transparent plastic cylinder (60 x 3.8 cm) over the main stem of the plant. A 55-60 cm bamboo stick was added to the soil within each tube to help prevent toppling of the cylinder. Each cage had three holes, as well as an open top, covered with fine 530-µM mesh cloth to allow for air circulation. Four females and two male WSS, newly emerged, were introduced into each tube via a small 1-cm opening. The hole was then plugged using a cotton ball covered in mesh

cloth. Damp '50-50 mix' soil was mounded around the base of each tube to prevent insect escape. Adult WSS were left within infestation tubes for 3 d, during which the plants were not watered or fertilized. The tubes were then removed, and any surviving insects, as well as cadavers, were removed. The plants were then returned to normal water and fertilization schedules. For the overall experiment, infestation was undertaken 3 d/wk, for 5 wks. Each replicate included 6 winter wheat plants and 6 smooth brome. For each replicate, 4 wheat and 4 smooth brome plants were infested, with 2 of each left uninfested as controls. Infestation tubes were placed around all 12 plants for each replicate.

Volatile Organic Compound Collection Volatile collection and successive GC-MS analysis were conducted following methods of Weaver et al. (2009). Intact and healthy smooth brome and winter wheat were used for volatile collection. Collections were conducted at Zadoks stage 49 - approximately 6 wks after infestation, for a period of 6 hr from 0900 to 1500. Collection trials were performed 3/wk on 12 plants at a time. Volatiles were collected using glass volatile collection chambers (VCC) that were 80-cm long and 4 cm in diameter. The top end of each VCC funneled into a threaded port that was 10 cm in diameter. Threaded onto the top of each VCC was an 8-port manifold adapter. Two glass filters (traps) (6.35 mm diameter x 76 mm length; Analytical Research Systems, Gainesville, FL) with 30 mg of Super-Q absorbent (Alltech Associates, Deerfield, IL) were inserted into 2 of the adapter ports. The remaining 6 collection ports were sealed to prevent ambient air exchange and pressure loss. One of the traps was used to collect extraneous volatiles from the initial experiment set up for the first 10 min, whereas the other trap was used to collect volatile compounds emanating from plants beginning 10 min after the system was turned on. A 24/210 threaded glass joint at the base of each VCC was connected

to Teflon[®] tubing that pumped in charcoal-filtered and humidified air pressure regulated by a diaphragm air pump, delivering air at a rate of 0.2 L L/min. A vacuum pump was connected via teflon tubing to each of the traps to maintain air pressure and flow rate (humidified air at 1.0 L/min) within the collection system. A Teflon[®] guillotine was used at the base of each plant to tightly seal the base of the system and prevent external air from entering. Each plant stem was wrapped with a small piece of cotton prior to the application of the guillotine to further seal the base of the collection system and prevent contamination by ambient and soil derived volatiles.

After the completion of volatile collection, VOCs were eluted from the glass traps using 200- μ L aliquot dichloromethane. Trapped volatiles were eluted slowly by adding dichloromethane and further clearing by using a slow release of nitrogen gas. The eluted samples were collected in a glass insert held within a 1.5-mL crimped top glass vial. 10 μ L of nonyl acetate was then added to the eluted samples as internal standard to allow for quantification of compound concentrations. The samples were processed using gas chromatography (GC) on a HP - 5MS; 30 m x 0.25 mm, 0.25- μ m film thickness column (J and W Scientific, Folsom, CA). To analyze, the GC instrument (Agilent 6890; Agilent Technologies, Inc., Santa Clara, CA) was coupled to a mass spectrometer (MS, Agilent 5973 instrument). Each sample was injected using the automated system in pulse splitless mode, with the initial pressure set to 82.7 kPa/min. The inlet temperature of the GC was set to 250 °C while the column temperature was 50 °C for 4 min. The temperature was set to increase at a rate of 5 °C/min until it reached 160 °C, after which it increased to a rate of 25 °C/min until it reached 280 °C. The temperature of the transfer line leading to the mass selective detector (MSD) was set at 300 °C. Helium was used as a carrier gas to maintain the flow rate of samples within the column at 1.2 mL/min. The MSD was set in

'SCAN' mode running from 50 – 300 m/z. The compounds collected from both the smooth brome and wheat samples were identified by comparing mass spectra and retention times using the National Institute of Standard and Technology (NIST) library. Peaks and volatiles were analyzed using MSD ChemStation (Agilent Technologies, Inc., Santa Clara, CA).

Electrophysiology

Electroantennography & Gas Chromatography - Flame Ionization Detection To test for response to compounds in smooth brome and winter wheat, we coupled electroantennographic detection with a flame ionization detector (EAD-GC-FID). Adult female *B. cephi* and *B. lissogaster* parasitoids were prepared by excising the head from the body using fine microdissection scissors. For each specimen, the parasitoid head was mounted on a flat electrode supplemented with a small amount of electrode gel (Spectra 360, Parker Laboratories, Inc., Fairfield, NJ) to facilitate electrical conductivity. The electrode was connected to a Type INR-5 micromanipulator (Narishige MN-151, Narishige International USA, Inc., Amityville, NY). The second electrode was also coated with electrode gel and connected to the second manipulator insertion point. Before connection, one insect antenna was cut down to remove 3 segments. The cut end was then manipulated to make contact with the second electrode, completing the circuit. This apparatus and method has been consistently used previously in assessing insect volatile response ([Agelopoulos et al. 1999](#), [Perez 2009](#)). Purified, humidified air (20 mL/s) was supplied consistently onto the antennae. The amplifier transferred the information to a computer interface with an EAG version 2.7 software (Syntech NL 2001, Hilversum, Netherlands).

EAD equipment was coupled to a flame ionization detector (FID, Agilent) to test for electroantennal response to volatile stimuli. Volatile samples were run through FID (6890N,

Agilent Technologies, Inc., Santa Clara, CA) using a 30 m, 250- μ m Agilent J&W column (Agilent Technologies, Inc., Santa Clara, CA). Each sample was injected using the automated system in pulsed splitless mode, with the internal pressure set to 11.8 kPa. The initial oven temperature of the FID was held at 50 °C for 4 min, after which it was increased by 15 °C/min until the final temperature of 160 °C was reached. The inlet temperature of the FID was set to 250 °C with hydrogen flow set to 35 ml/min. Nitrogen was used as the makeup gas and set to a flow rate of 40 ml/min and a pressure of 400 kPa. Air flow was set to 450 ml/min with a pressure of 550 kPa. Once a run was triggered, both FID output and EAD responses were recorded using EAD Plus (EAD, Santa Clara, CA).

Electroantennography using Synthetic Volatiles Adult female parasitoid preparation was similar to that described above. Notably different, a single antenna was used for each antennogram, instead of an entire head. Opposite ends of the antennae were connected to the electrodes. For each trial, 10 μ L of the test compound was applied to filter paper inserted into a glass pipette connected to controlled air flow (Birkett et al. 2004), which then released an airborne stimulus onto the antennae. A release parameter of 0.4 s was set for the delivery, mixed into the constant flow of air (20 ml/s). The antenna's electrical response detected, amplified, and recorded by the Syntech EAD Pro software. Five synthetic compounds were used, (*Z*)-3-hexenyl acetate, hexahydrofarnesyl acetone, 6-methyl-5-hepten-2-one (99%), β -ocimene (70%), (*E*)-2-hexenal (99%), and (*E*)-2-hexenyl acetate (98%). All compounds were sourced from Aldrich Chemical Company (Milwaukee, WI). A single puff of a compound was delivered in every trial, with a new parasitoid used each time. The concentrations of each volatile before dilution can be found in [Supplemental Table ST2.1](#). We tested parasitoid responses to 3 dilutions of each

compound: 0.01, 100, and 10000 ng. Compounds and dilutions were selected randomly for each trial.

Behavioral Trials

Y-Tube Olfactometer Bioassay Bioassays were conducted to assess variation in behavioral responses of naive female parasitoids to both winter wheat and smooth brome volatiles. Volatiles were a combined mixture of 15 collected volatile samples from our volatile collection experiment. We combined volatiles from infested plants and used them to mimic the volatile signature of infested plants in the Y-tube airstream.

We used a Y-Tube system (Analytical Research Systems, Micanopy, FL) similar to those used by Piesik et al. (2008) and adapted for parasitoids in Cavallini et al. (2023). Y-tubes consisted of Corning glass tube (28-mm diameter x 300-mm long) that branched at 20 cm along a 120° angle to form the arm of each tube. Each arm extended 3 cm from the junction before becoming parallel, with a total length of 10 cm for each parallel section. Each arm was connected to a diaphragm air pump that delivered charcoal-filtered and humidified air at a rate of 0.2 l/min. Then, 50 µl of extracted volatile mixture was pipetted onto a small piece of filter paper and placed inside a 46-cm Corning tube with a ground-glass joint at one end to connect to the Y-Tube, and a threaded-glass joint to receive the air supply. Two of these tubes were used for each trial. Y-tubes were used for a single trial before being exchanged for a fresh, clean tube. After each assay, glassware was cleaned using a non-foaming anionic Liquinox detergent (Alconox Inc., White Plains, NY) in warm water, rinsed with water, and rinsed with the solvents acetone and hexane. Glassware was then placed in a 110 °C oven and baked for a minimum of 2 hr before the next use.

For each assay, a single naive female *B. cephi* or *B. lissogaster* parasitoid was introduced 1 cm into the unbranched end of the Y-tube ([Cavallini et al. 2023](#)). To facilitate female parasitoid movement toward the Y-tube junction, black box containing Y-tube was angled at a 10° angle with the ‘Y’ end elevated. In addition, a 28-cm long metal wire was placed on the unbranched portion of the Y-tube, spanning the length from the introduction point to the branch). Females were placed inside the Y-tube on the top of the wire, 3 cm from the introduction point. Individuals were randomly assigned to each assay and discarded after assay completion. Females were observed for 2 min, with the trial ending when a choice was made, or when no response was observed (recorded as non-responders). We used a total of 58 *B. cephi* and 68 *B. lissogaster* during these trials.

Due to the inconsistent nature of parasitoid emergence and the short lifespan of their excised heads and antennae, data for both electrophysiological and behavioral experiments were collected over an extended period of several months.

Wind Tunnel Behavior Bioassay To test parasitoid behavioral response to independent synthetic volatiles, we used a 150 cm x 50 cm x 50 cm (L x W x H) acrylic box with airflow rates set to 0.2 l/m. Set up was similar to that of Miller and Roelofs ([1978](#)). Briefly, at the end of the wind tunnel, 2 plastic Petri dishes (Fisher Scientific, Pittsburgh, Pennsylvania) were positioned, each featuring a 2 x 2 cm square opening in the center and coated with Tanglefoot® on the outer surface. These dishes were mounted 20-cm high and 30-cm apart ([Supplemental Figure S2.3](#)). Each dish was equipped with a rubber septum, treated and secured by a paper clip, and positioned in the center of the opening. The septum released the compound into the air stream. To attract parasitoids, a 12-V light bulb was placed behind each opening to exploit positive

phototaxis. The entire setup was situated in a dark room maintained at a constant temperature of ~27 °C.

Behavioral trials were conducted using pure synthetic compounds that represent those produced by WSS host plants. The tested compounds were diluted using hexane to obtain the concentrations used for each trial. Compound concentrations can be viewed in [Supplemental Table ST2.2](#).

Statistical Analysis

All statistical analyses were conducted using R ([R Core Team 2024](#)) and RStudio (version 4.2.764).

Comparative Analysis of Volatile Collections Volatiles from all plant samples were analyzed using PERMANOVA. The amount of volatile compound present in each sample was calculated ng/g/hr after correcting for plant biomass. Untransformed data were used for concentration analysis, while all other analyses used data transformed using a center log-ratio (CLR) transformation, a technique commonly used when analyzing multivariate compositional data ([Brückner and Heathoff 2017](#)). VOC compositions were compared between samples and treatments using a permutational multivariate analysis of variance (PERMANOVA, Canberra distance, 999 iterations) test within the vegan package (v 2.6-4) ([Oksanen et al. 2011](#)). Potential compounds that might contrast volatiles between wheat and smooth brome were further analyzed using ANOVA after fitting a linear mixed model. Each compound was assessed as a response variable fitting plant type as a treatment and replication as a random effect.

Synthetic Volatile Electrophysiology Response ratios for each trial were calculated using the control responses as a base line. The data was transformed via a log10 before being analyzed using a t-test. To determine the relationship between antennal response and concentration of each compound, we used a simple linear regression analysis.

Behavioral Experiments A Pearson's chi-square test was used to identify differences in parasitoid responses tests to smooth brome and winter wheat volatiles. An alpha level of 0.05 was used for test significance differences in female choices for both *B. cephi* and *B. lissogaster*.

Results

Collected Volatile Profiles

Seventeen peaks were identified between samples of smooth brome and winter wheat. Overall, smooth brome and winter wheat emit similar volatiles, but vary in the quantity produced. Compounds for analysis were selected based on MS-identification quality and consistency across volatile collection trials. We used previously defined systemically active volatiles from Piesik et al. (2008) and Perez (2009) to inform our analysis further based on both WSS and *Bracon* spp. electrophysiological and behavioral activity.

When comparing smooth brome against winter wheat, irrespective of infestation status, quantities of (*E*)-2-hexenal ($P = 0.03$), (*E*)-2-hexenyl acetate ($P < 0.005$), (*Z*)-3-hexenyl acetate ($P = 0.02$) and β -ocimene ($P < 0.005$) differed significantly (Fig. 2.1). Concentrations of 6-methyl-5-hepten-2-one ($P = 0.82$) and hexahydrofarnesyl acetone ($P = 0.51$) were not significantly different across plant types.

Quantities of 6-methyl-5-hepten-2-one were significantly greater in both smooth brome ($P = 0.003$) and winter wheat ($P < 0.005$) when comparing infested plants against their

uninfested counterparts ([Fig. 2.1](#)). Infested smooth brome yielded significantly greater concentrations of (*E*)-2-hexenal ($P = 0.02$) and (*Z*)-3-hexenyl acetate ($P = 0.001$) when compared to uninfested smooth brome.

Electrophysiology of *Bracon* spp. Parasitoids

EAD-GC-FID To determine which volatile compounds elucidated antennal response from WSS parasitoids, we used EAD-GC-FID to look for electrical depolarization when stimulated by smooth brome and winter wheat volatiles. Significant depolarization from *B. cephi* and *B. lissogaster* were induced at (*E*)-2-hexenal (mV \pm SD, 0.23 ± 0.05 mV, $P < 0.005$), (*E*)-2-hexenyl acetate (0.37 ± 0.06 mV, $P = 0.001$), (*Z*)-3-hexenyl acetate (0.83 ± 0.07 mV, $P < 0.005$), 6-methyl-5-hepten-2-one (0.41 ± 0.05 mV, $P < 0.005$), and hexahydrofarnesyl acetone (0.44 ± 0.05 mV, $P < 0.005$). We consistently saw responses at these locations across all trials, plant types, and parasitoid species ([Fig. 2.2](#)).

Synthetic Volatile Electrophysiology We used three dilutions (0.01, 100, 10000 ng) of synthetic volatiles to individually induce depolarization in *B. cephi* and *B. lissogaster*. Consistent and significant dose-dependent depolarization responses of both species of parasitoid antennae were observed to (*Z*)-3-hexenyl acetate, 6-methyl-5-hepten-2-one, (*E*)-2-hexenal, (*E*)-2-hexenyl acetate, and hexahydrofarnesyl acetone. We calculated response ratios using the formula $Ratio = R_{stimulus}/R_{control}$ for each compound to understand how increased volatile concentration impacted insect electrophysiological response. (*Z*)-3-hexenyl acetate and 6-methyl-5-hepten-2-one produced positive response ratios (i.e. stronger responses at higher volatile concentrations), while (*E*)-2-hexenal, (*E*)-2-hexenyl acetate, and hexahydrofarnesyl acetone had negative response ratios ([Fig. S2.2](#), [Table S2.2](#), [Table S2.3](#)).

Behavioral Olfactory Experiments

Smooth Brome and Winter Wheat Blends Adult females responded positively toward air streams containing infested winter wheat volatile blends for both *B. cephi* ($\chi^2 = 7.35$, $df = 1$, $P = 0.006$) and *B. lissogaster* ($\chi^2 = 7.76$, $df = 1$, $P = 0.005$), when compared to “Pure air” ([Fig. 2.3](#)). Likewise, both species of parasitoids responded positively to air streams containing infested smooth brome (*B. cephi*: $\chi^2 = 3.86$, $df = 1$, $P = 0.049$; *B. lissogaster*: $\chi^2 = 9.85$, $df = 1$, $P = 0.002$), when given the choice versus pure air ([Fig. 2.3](#)). Adult female parasitoids from both species preferred air streams containing infested smooth brome volatiles (*B. cephi*: $\chi^2 = 4.23$, $df = 1$, $P = 0.45$; *B. lissogaster*: $\chi^2 = 5.45$, $df = 1$, $P = 0.835$) when given the choice against infested winter wheat ([Fig. 2.3](#)).

Synthetic Compounds Behavioral experiments showed that adult females from both species were significantly attracted to (*Z*)-3-hexenyl acetate and 6-methyl-5-hepten-2-one ([Fig. S2.3](#)). Hexahydrofarnesyl acetone generated a more significant behavioral response in both parasitoid species at low concentrations (0.3 μg , *B. cephi*: $P = 0.005$, *B. lissogaster*: $P = 0.002$) when compared to high concentrations (9 μg , *B. cephi*: $P = 0.033$, *B. lissogaster*: $P = 0.019$). We found no significant behavioral response at any concentration for (*E*)-2-hexenal or (*E*)-2-hexenyl acetate for either species. No male parasitoids exhibited significant behavioral response to any of the tested compounds ([Fig. S2.3](#), [Table S2.4](#), [Table S2.5](#)).

Discussion

Understanding host-seeking behaviors via volatile chemicals is crucial for understanding the benefits of conserving WSS parasitoid host plants in semi-natural, unmanaged environments

in Montana ([Strand et al. 2024](#)). Our study builds on previous research showing that host-plant selection by adult female WSS parasitoids is influenced by olfactory cues ([Miller and Roelofs 1978](#), [Buteler et al. 2009](#)). Bhandari ([2020](#)) found that adult female WSS parasitoids preferred WSS infested smooth brome over spring wheat ('Vida') when given the choice. Consistent with these findings, our results showed a clear preference for infested smooth brome over winter wheat ('Yellowstone'), despite the differences in wheat biology.

Previous studies have identified 6-methyl-5-hepten-2-one and (Z)-3-hexenyl acetate to be potential chemical cues for parasitoid host finding ([Du et al. 1998](#), [Reddy et al. 2002](#)). (Z)-3-hexenyl acetate mediates host and oviposition preference in fall armyworm (*S. frugiperda*) on maize (*Zea mays* L.) ([Wang et al. 2023](#)) and is attractive to both generalist and specialized parasitic wasps that target the fall armyworm ([Turlings et al. 1993](#)). Our study found that adult female *B. cephi* and *B. lissogaster* exhibit strong electrophysiological and positive behavioral responses to both compounds. Volatiles from both host plants include likely induced responses to WSS-feeding stress that helps to attract both species of parasitoids. Although Piesik ([2008](#)) identified 6-methyl-5-hepten-2-one to be a repellent to the WSS, our behavioral trials show it to be an attractant for both *B. cephi* and *B. lissogaster*. Notably, smooth brome did not show increased levels of this compound when compared to winter wheat after a similar duration of infestation, a unique distinction, as we found smooth brome produces greater quantities of many of the other electrophysiologically active volatiles. This distinction may be advantageous as gravid WSS females are not deterred from ovipositing while still attracting parasitoids that use later instar larvae.

Although β -ocimene was not electrophysiologically or behaviorally active in *B. cephi* or *B. lissogaster*, it was present in greater quantities in smooth brome compared to winter wheat. Previously found attractive to adult female WSS by Piesik (2008), β -ocimene may play a role similar to (*Z*)-3-hexenyl acetate and 6-methyl-5-hepten-2-one in explaining why adult female WSS prefer smooth brome over winter wheat.

Both *B. cephi* and *B. lissogaster* responded behaviorally to hexahydrofarnesyl acetone, a compound expressed during wheat ripening (Peck 2004, Miyazawa et al. 2008, Perez 2009). This compound was found in higher concentrations in uninfested plants compared to infested plants. Perez (2009) found lower concentrations of the compound in still green and developing plants and higher concentrations in plants beginning to senescence. Wheat experiences decreased photosynthetic activity while experiencing WSS tunneling damage (Macedo et al. 2005, Macedo et al. 2007, Delaney et al. 2010). This time frame aligns with the behavior of WSS parasitoids, which search for sufficiently sized hosts during a period that extends through plant senescence. During this time, WSS are in late instars, also making them both larger and more damaging to the wheat plant, and a better food source for parasitoid larvae in general (Turlings and Wäckers 2004). Our results showed electrophysiological response and behavioral preference to hexahydrofarnesyl acetone, with significantly stronger responses at lower concentrations. These findings suggest that *B. cephi* and *B. lissogaster* may prefer plants emitting relatively lower concentrations of this compound. This ability to sense minute differences in hexahydrofarnesyl acetone concentrations may help female parasitoids locate high-quality plants infested with WSS larvae, particularly if this preference is part of a specific blend of compounds signaling WSS stem presence.

Our study provides compelling evidence that volatile chemicals significantly influence the host-seeking behaviors of WSS parasitoids to two host plants similar in volatile blend profiles. This understanding of plant volatile profiles and insect behavioral response may inform conservation strategies aimed at preserving and managing semi-natural habitats that support effective biological control. Additionally, insights into VOCs that are behaviorally active may guide future breeding efforts to produce successful resistant wheat cultivars. Lines that produce elevated concentrations of compounds attractive to WSS parasitoids may increase parasitism, especially in fields adjacent to semi-natural grassland habitats. Understanding host-seeking behaviors via volatile chemicals is important in understanding how to effectively communicate the benefits of conserving WSS parasitoid host plants in semi-natural, unmanaged environments in Montana ([Strand et al. 2024](#)). Previous studies have shown the ecological benefits of smooth brome grown next to wheat fields in providing seasonal refuge for WSS parasitoids ([Peirce et al. 2021](#), [Rand et al. 2024](#), [Strand et al. 2024](#)). Our study further supports the strategic conservation and management of semi-natural habitats to maximize biological control. By identifying the specific volatile compounds that attract WSS parasitoids, we provide evidence that can strongly support habitat management recommendations. Integrating this information into conservation strategies will enhance the effectiveness of biological control by ensuring that parasitoids have access to optimal resources throughout their life cycle, contributing to more sustainable agricultural practices and the preservation of vital ecological functions.

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Figures

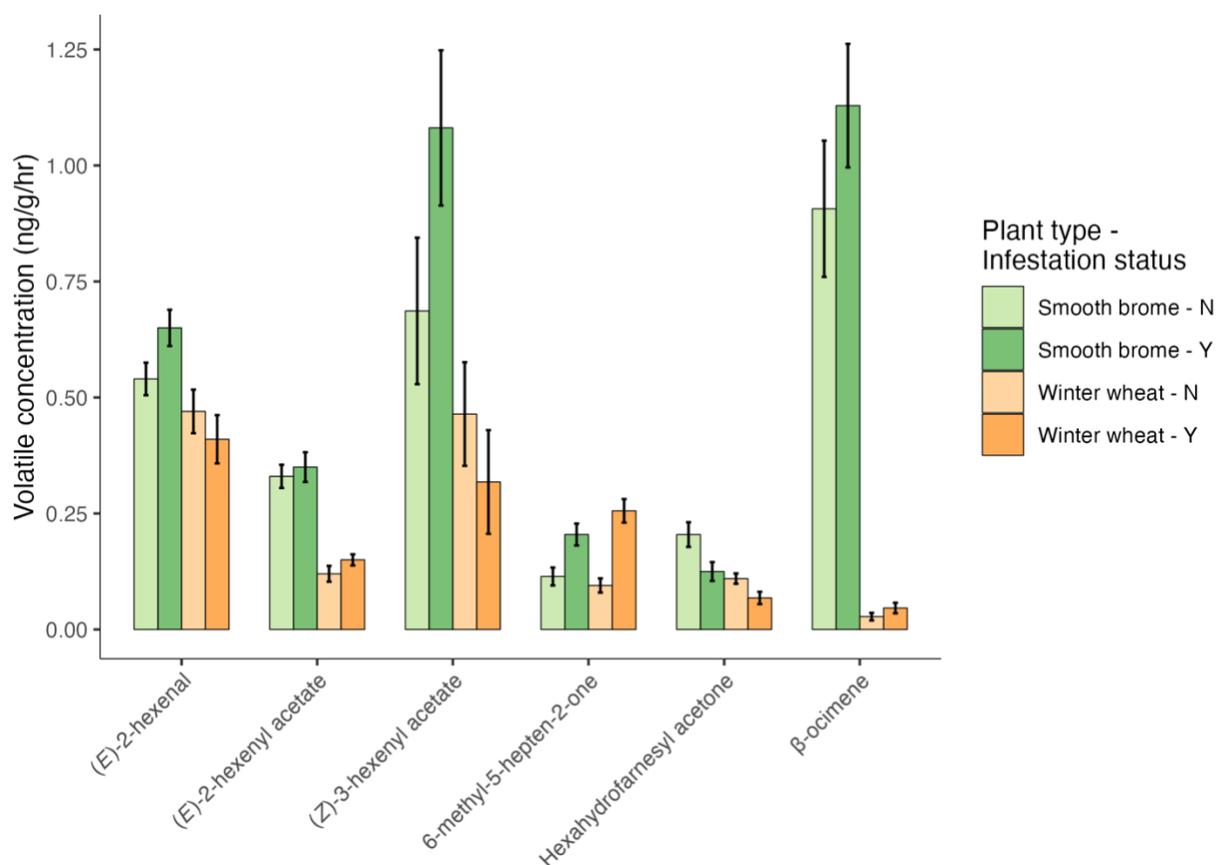


Fig. 2.1. Comparison of volatile concentrations between WSS infested and uninfested smooth brome (*Bromus inermis* Leyss, ‘Manchar’) and winter wheat (*Triticum aestivum*, ‘Yellowstone’).

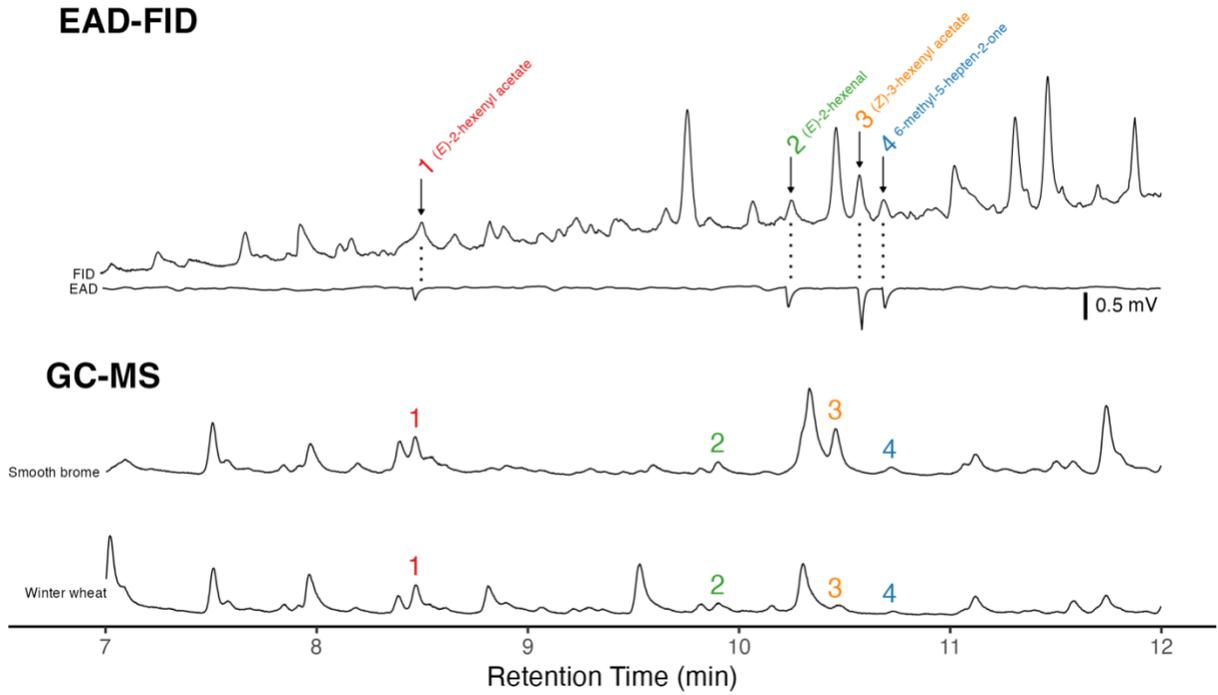


Fig. 2.2. EAD-FID: Electrophysiological depolarization response from adult female *B. cephi* to volatiles blends from smooth brome (*Bromus inermis* Leyss, ‘Manchar’) sample. Electroantennographic detection and flame ionization detection (EAD- FID) run using volatile blend of 15 collected samples. Lower, GC-MS plot showing infested smooth brome and winter wheat (*Triticum aestivum* L., ‘Yellowstone’) chromatograms to show volatile locations and identifications.

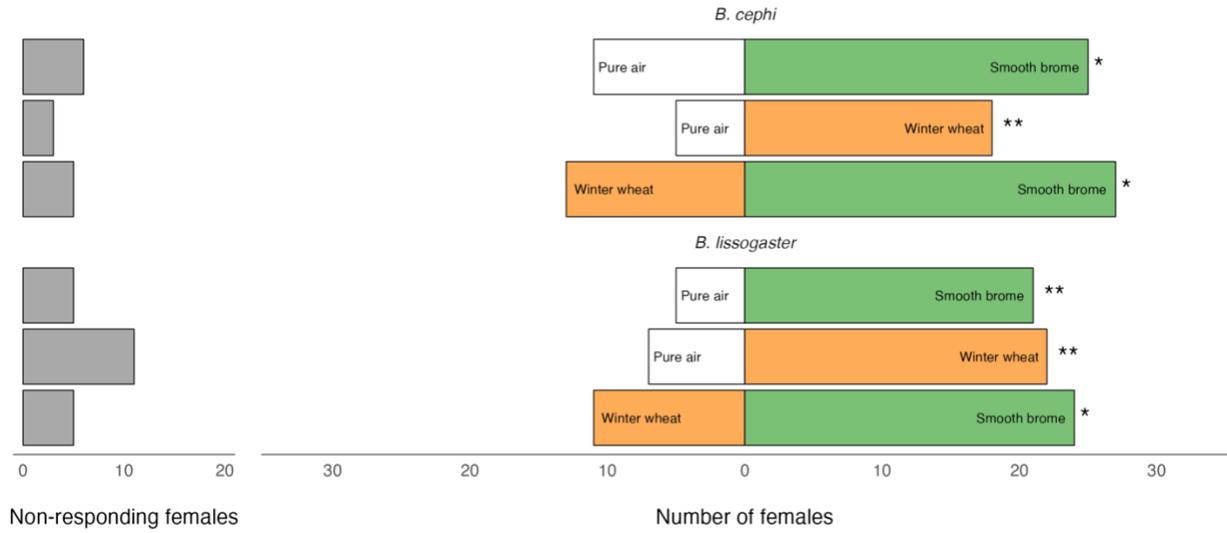


Fig. 2.3. Behavioral preferences from Y-tube olfactometer bioassay tests for both *B. cephi* and *B. lissogaster* females when choosing between “Pure air”, smooth brome (*Bromus inermis* Leys, ‘Manchar’) and winter wheat (*Triticum aestivum*, ‘Yellowstone’) volatile blends. The volatile blends for each plant type were combined volatiles samples from 15 infested plants. Left side bar graphs show the number of non-responders from each set of related trials. *represents $P \leq 0.05$, ** < 0.01 .

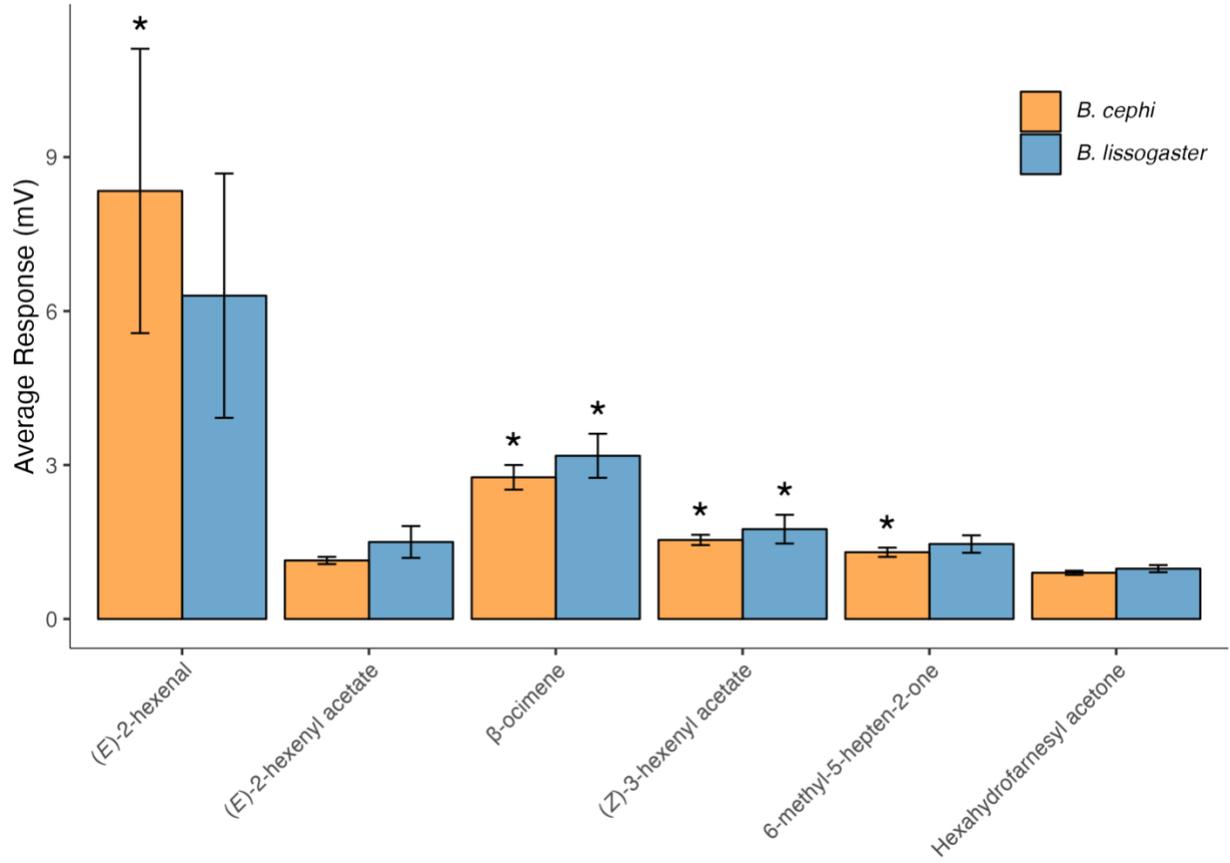


Fig. S2.1. Antennal response of adult female *Bracon cephi* and *B. lissogaster* to synthetic volatiles matching those produced by wheat stem sawfly infested plants. mV response represents the averaged response between 0.01, 100, and 10000 volatile concentrations. *significance at $\alpha = 0.05$.

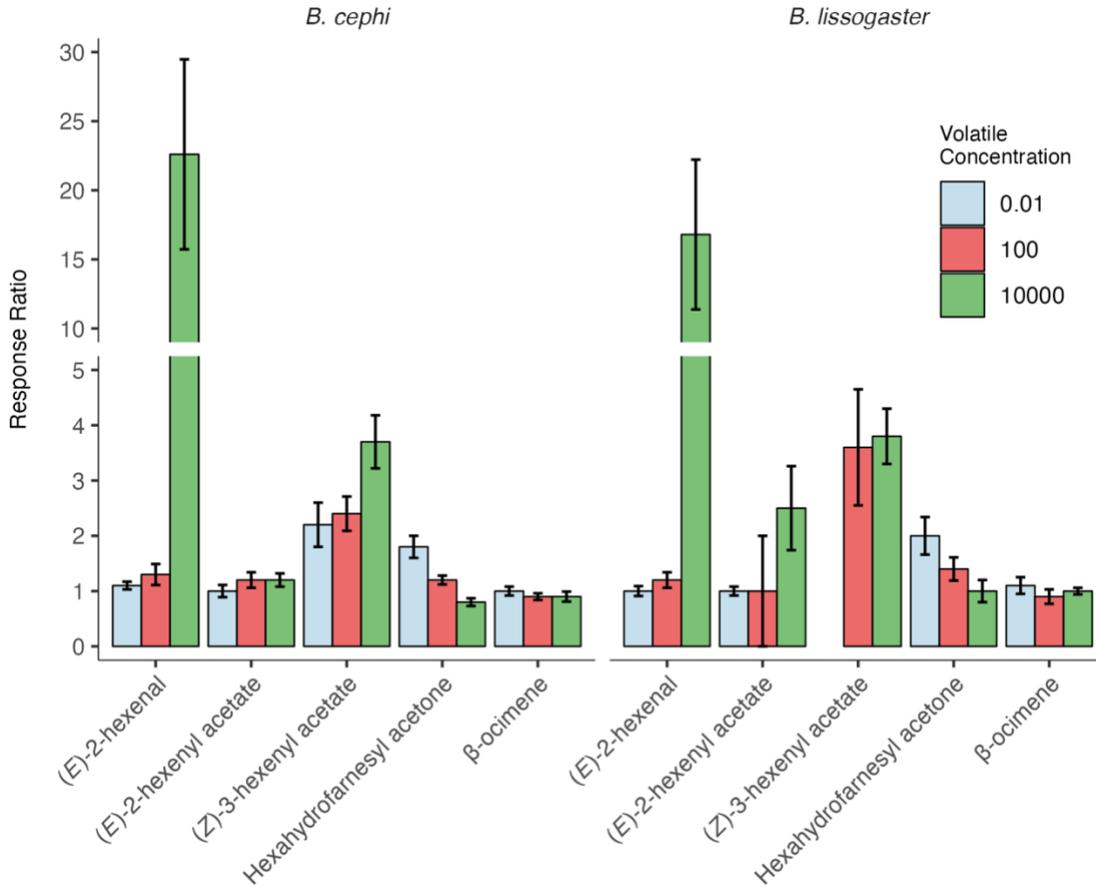


Fig. S2.2. Electrophysiological response ratios of adult female *B. cephi* and *B. lissogaster* to varying concentrations of synthetic volatiles matching those produced by WSS infested plants.

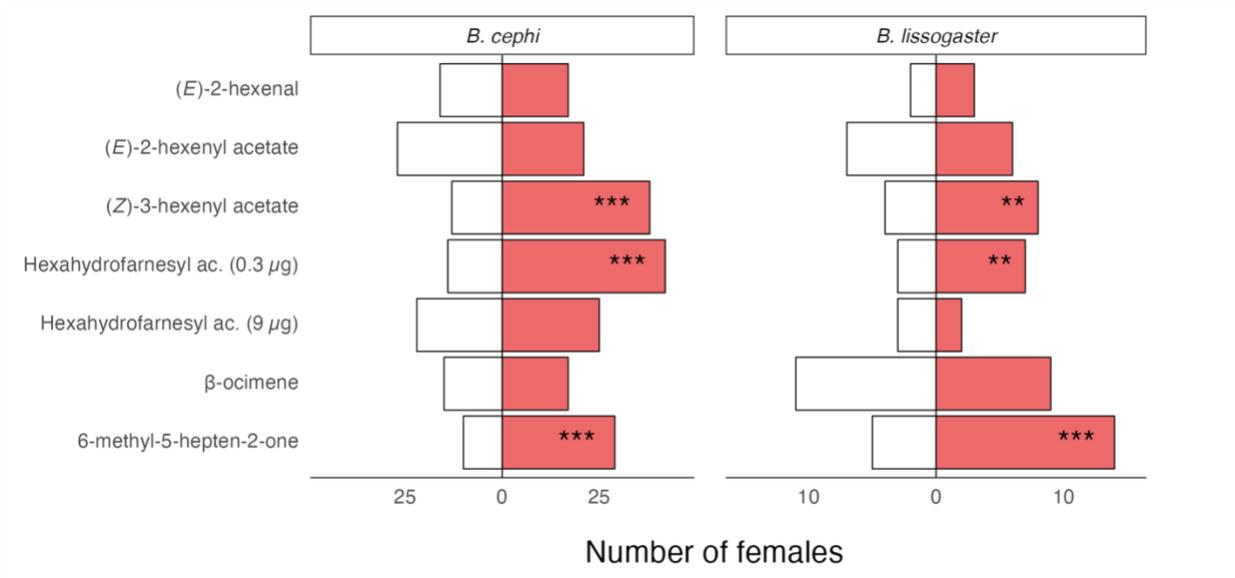


Fig. S2.3. Behavioral preferences of adult female *Bracon cephi* and *B. lissogaster* during wind-tunnel olfactory trials. Insects chose between “Pure air” (white) and the tested volatile (blue). Volatiles match those found in samples collected from WSS infested smooth brome (*Bromus inermis* Leyss, ‘Manchar’) and winter wheat (*Triticum aestivum*, ‘Yellowstone). **represents $P \leq 0.01$, *** < 0.005 .

Tables

Table ST2.1. Concentrations of volatiles used for electrophysiological trials on *B. cephi* and *B. lissogaster*. Volatiles match those found in samples collected from WSS infested smooth brome (*Bromus inermis* Leyss, ‘Manchar’) and winter wheat (*Triticum aestivum*, ‘Yellowstone).

Compound	Concentration (µg/mL)
(Z)-3 hexenyl acetate	90
6-methyl-5-hepten-2-one	35
Hexahydrofarnesyl acetone (low)	0.3
Hexahydrofarnesyl acetone (high)	9
(E)-2-hexenyl acetate	1.4
(E)-2-hexenal	423
β-ocimene	215

Table ST2.2. Electrophysiological dose-response ratios and t-test results from adult female *B. lissogaster* parasitoids. All trials use isolated, synthetic compounds that match those produced by wheat stem sawfly infested wheat plants. *significant behavioral activity at $\alpha = 0.05$.

Compound	N	Concentration (μg)	Ratio	SE	t	df	P
(Z)-3 hexenyl acetate	9	0.01	2.1	0.51	2.84	8	0.02*
		100	3.6	1.05	4.68	8	0.002*
		10000	3.8	0.5	6.46	8	0.0002*
(E)-2-hexenyl acetate	4	0.01	1	0.08	-0.3	3	0.78
		100	1	1	0.38	3	0.73
		10000	2.5	0.76	2.17	3	0.12
β -ocimene	7	0.01	1.1	0.15	0.14	6	0.9
		100	0.9	0.13	-1.39	6	0.21
		10000	1	0.06	0	6	1
Hexahydrofarnesyl acetone	6	0.01	2	0.34	3.58	5	0.02*
		100	1.4	0.21	1.75	5	0.14
		10000	1	0.2	-0.53	5	0.62
(E)-2-hexenal	7	0.01	1	0.09	-0.58	6	0.58
		100	1.2	0.14	1.11	6	31
		10000	16.8	5.42	6.48	6	0.0006*
6-methyl-5-hepten-2-one	5	0.01	1.1	0.06	1.12	4	0.32
		100	1.6	0.29	1.61	4	0.18
		10000	2.3	0.76	2.81	4	0.04

Table ST2.3. Electrophysiological dose-response ratios and t-test results from adult female *B. cephi* parasitoids. All trials use isolated, synthetic compounds that match those produced by wheat stem sawfly infested wheat plants. *significant behavioral activity at $\alpha = 0.05$.

Compound	N	Concentration (μg)	Ratio	SE	t	df	P
(Z)-3 hexenyl acetate	9	0.01	2.2	0.4	3.22	20	0.114
		100	2.4	0.31	6.32	20	0.0001*
		10000	3.7	0.48	9.28	20	0.0001*
(E)-2-hexenyl acetate	4	0.01	1	0.11	-0.69	12	0.5
		100	1.2	0.14	0.62	12	0.55
		10000	1.2	0.12	2.44	12	0.03*
β -ocimene	7	0.01	1	0.08	-1.84	11	0.09
		100	0.9	0.06	-1.43	11	0.18
		10000	0.9	0.09	-1.83	11	0.09
Hexahydrofarnesyl acetone	6	0.01	1	0.08	-1.38	11	0.2
		100	0.9	0.07	-1.3	11	0.22
		10000	1.1	0.19	-0.06	11	0.96
(E)-2-hexenal	7	0.01	1.8	0.2	5.01	21	0.0001*
		100	1.2	0.08	2.91	21	0.008*
		10000	0.8	0.07	2.51	21	0.02*
6-methyl-5-hepten-2-one	5	0.01	1.1	0.07	1.12	12	0.29
		100	1.3	0.19	0.72	12	0.49
		10000	22.6	6.87	6.97	12	0.0001*

Table ST2.4. Behavioral wind-tunnel response counts and t-test results from female *B. cephi* parasitoids. All trials use isolated, synthetic compounds that match those produced by sawfly infested wheat plants. Blank columns indicate where no statistics were generated due to low N counts. *significant behavioral activity at $\alpha = 0.05$.

Compound	Test compound		Control		t	df	P
	N	%	N	%			
(Z)-3-hexenyl acetate	38	63	13	22	-7.9	10	< 0.0001*
6-methyl-5-hepten-2-one	29	58	10	20	-30.96	4	< 0.0001*
Hexahydrofarnesyl ac. (0.3 μ g)	42	60	14	20	-22.38	12	< 0.0001*
Hexahydrofarnesyl ac. (9 μ g)	25	36	22	31	-0.79	12	0.44
(E)-2-hexenyl acetate	21	35	27	45	-2.06	10	0.07
(Z)-3-hexanol	16	32	14	28	-0.68	8	0.52
(E)-2-hexenal	17	34	16	32	-0.31	8	0.76
β -ocimene	17	34	15	30	-0.74	8	0.38

Table ST2.5. Behavioral wind-tunnel response counts and t-test results from female *B. lissogaster* parasitoids. All compounds are isolated, synthetic compounds that match those produced by sawfly infested wheat plants. Blank columns indicate where no statistics were generated due to low N counts. *significant behavioral activity at $\alpha = 0.05$.

Compound	Test compound		Control		t	df	P
	N	%	N	%			
(Z)-3-hexenyl acetate	8	53	4	27	-2.32	6	0.05*
6-methyl-5-hepten-2-one	14	61	5	22	-8.07	8	< 0.0001*
Hexahydrofarnesyl ac. (0.3 μ g)	7	64	3	27	-4.34	6	0.006*
Hexahydrofarnesyl ac. (9 μ g)	2	29	3	43	-	-	-
(E)-2-hexenyl acetate	6	32	7	37	-1.46	6	0.19
(E)-2-hexenal	3	25	2	17	-	-	-
β -ocimene	9	33	11	41	-1.78	8	0.1

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CHAPTER THREE

AGROECOLOGICAL IMPORTANCE OF SMOOTH BROME IN
MANAGING WHEAT STEM SAWFLY (HYMENOPTERA:
CEPHIDAE) VIA ASSOCIATED BRACONID PARASITOIDS

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**Agroecological Importance of Smooth Brome in Managing Wheat Stem Sawfly
(Hymenoptera: Cephidae) via Associated Braconid Parasitoids**

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Abstract

Wheat stem sawfly (WSS), *Cephus cinctus* Norton (Hymenoptera: Cephidae), causes significant damage to cereal crops throughout the Northern Great Plains of North America. *Bracon cephi* (Gahan) and *B. lissogaster* Muesebeck (Hymenoptera: Braconidae) are native WSS parasitoids important in suppressing WSS populations and limiting associated damage. Smooth brome (*Bromus inermis* Leyss.) serves as a potential trap crop for WSS when grown in areas surrounding wheat (*Triticum aestivum* L.) fields in Montana. Its unique biology allows it to be both heavily infested by WSS larvae that will experience considerable mortality throughout the growing season; while any late summer survivors are available to serve as hosts for WSS parasitoids. Our study examines the use of smooth brome in providing host refuge for WSS parasitoids. We measured the WSS larval infestation and survival rate within parasitoid-excluded smooth brome plots, observing a maximum infestation of 66.5% and a maximum end-of-year WSS survival of 5.7%. We also collected stems from sites in central and northern Montana where we measured the WSS infestation and parasitoid prevalence within cultivated wheat fields and adjacent smooth brome populations. Wheat stem sawfly infestation within both smooth brome and adjacent wheat crop fields was high in both Big Sandy (64.5% smooth brome, 65.7% adjacent wheat) and Moccasin, MT (50.6%, 38.6%). Year-end WSS larval mortality in infested stems was 43.6% greater in smooth brome compared to adjacent wheat at both field sites. However, infested smooth brome stems hosted similar numbers of WSS parasitoids. This research underscores the importance of smooth brome in providing a sustainable host refuge for WSS parasitoids and highlights its significant role in supporting the economics of wheat cultivation.

Introduction

Ecologists and agricultural producers may hold different views about the importance of semi-natural, unmanaged habitats within agricultural landscapes, a distinction often overlooked in ecological and conservation discourse ([Tscharntke et al. 2016](#)). Although ecologists recognize the role of more natural habitats such as field-border vegetation in supporting biodiversity and providing ecosystem services like biological control ([Duff et al. 2024](#)), many producers perceive these habitat remnants as occupying valuable cropland or even as sources of pests. As such, documenting how natural enemy and pest populations interact with agricultural landscapes alongside unmanaged habitat buffers on the crop periphery are important to determine the degree of the services provided.

Many insect herbivores and their natural enemies rely on a variety of resources found across diverse habitat types within their environment. Depending on the quality of the resource, different habitat types can provide resources for increased pest or natural enemy populations. Similarly, these habitat types can be sinks that decrease pest populations ([Kennedy and Storer 2000](#)). Altering the presence of these resources may affect either pest or natural enemy populations and communities – or both. For example, diversifying the edge cropping of organic *Brassica* using fava beans, fennel, and marigolds results in a diversified beneficial arthropod community that helps reduce herbivory ([Morais et al. 2023](#)). Understanding the ways in which landscape habitat diversity impacts the relationship between pest and enemy is crucial for effectively managing pest species in large-scale cropping systems. Similarly, understanding how herbivore plant-hosts act as reservoirs for pests or beneficial natural enemies can potentially play a role in stabilizing year-to-year agricultural impact from these pests ([Cano et al. 2022](#)).

The wheat stem sawfly (WSS), *Cephus cinctus* Norton (Hymenoptera: Cephidae), is a grass-mining sawfly native to North America ([Criddle 1922](#), [Ainslie 1929](#), [Wallace and McNeal 1966](#); [Lesieur et al. 2016](#)). Originally adept at using wild grass hosts, the species became a major pest of cultivated cereals as these resources became more prevalent following European settlement, becoming a notable pest of winter wheat in 1990 in Montana ([Morrill and Kushnak 1996](#)), and more recently in Colorado ([Cockrell et al. 2021](#)). Climate warming has the potential to further expand the range of this pest both northward and southward ([Olfert et al. 2019](#), [Weaver 2023](#)). Adult female WSS use their saw-like ovipositor to lay their eggs in the lumen of stems, where the eggs hatch, leading to larval feeding on parenchyma tissue ([Roemhild 1954](#), [Holmes and Farstad 1956](#)). Economic damage manifests in the form of both kernel weight reduction caused by tissue damage ([Beres et al. 2011a](#); [2011b](#), [Delaney et al. 2010](#)) and stem toppling due to late-season larval girdling to create an overwintering chamber that is made below the cut stem ([Holmes and Peterson 1960](#), [Nansen et al. 2005](#), [McCullough et al. 2020](#)). The host plant triggers for WSS larvae to descend to the base of the stem to girdle it are ripening and desiccation ([Criddle 1923](#), [Ainslie 1929](#)), coupled with increased light transmission through the ripened stem ([Villacorta et al. 1971](#), [Holmes 1975](#)).

Several parasitoid and predatory species attack WSS larvae within wild grass hosts ([Morrill et al. 2001](#)), however, two species, *Bracon cephi* (Gahan) and *Bracon lissogaster* Muesebeck (Hymenoptera: Braconidae), have been consistently observed targeting WSS within cultivated cereals ([Nelson and Farstad 1953](#), [Morrill et al. 1998](#), [Runyon et al. 2001](#)). These two host-specific ectoparasitoids are native to North America. Both parasitoids are bivoltine, with the first generation present in Montana from late-June to late-July, while the second generation is

active from mid-July to September ([Gahan 1918](#), [Somsen and Luginbill 1956](#), [Davis 2013](#)). Adult female *B. cephi* and *B. lissogaster* inject a paralytic toxin into a WSS larvae within the host stem, paralyzing the host larvae, and depositing from a single (*B. cephi*) to one to three (*B. lissogaster*) eggs. WSS parasitoids provide biological control of WSS via irreplaceable mortality ([Peterson et al. 2011](#), [Buteler et al. 2015](#)) and can significantly reduce WSS damage to crop yields ([Buteler et al. 2008](#), [Bekkerman and Weaver 2018](#), [Adhikari et al. 2019](#), [Rand et al. 2020](#)). While WSS has a wide range of viable host plants, including native and non-native grasses and cultivated row-crops such as wheat (*Triticum aestivum* L.) and barley (*Hordeum vulgare* L.) ([Wallace and McNeal 1966](#), [Cockrell et al. 2017](#), [Achhami et al. 2020](#)), infestation levels can vary widely across hosts. Previous research identified a preference for host plants with larger stem diameter ([Ainslie 1920](#), [Buteler et al. 2009](#), [Bhandari 2020](#)).

Populations of non-native grasses such as *Agropyron cristatum*, *Bromus tectorum*, *Bromus inermis*, *Elymus trachycaulus*, and *Thinopyrum intermedium* in unmanaged areas host WSS and most also host the *Bracon* spp. parasitoids that use WSS ([Perez-Mendoza and Weaver 2006](#), [Peirce et al. 2021](#), [Rand et al. 2024](#)). Smooth brome has been shown to be a quality, initially-accepted host for WSS oviposition while also causing high larval mortality later on in the growing season ([Seamans 1928](#), [Farstad and Jacobson 1945](#), [Bhandari 2020](#)). However, there is a lack of data relating to the total infestation, WSS stem cutting, and parasitism within smooth brome at multiple times throughout the growing season. Quantitative assessment of potential ‘reservoir’ characteristics and local spatial information could be useful in more fully understanding the ecological impacts of maintaining smooth brome along roadways and within uncultivated areas.

Smooth brome (*Bromus inermis* Leyss.) is a Eurasian cool-season rhizomatous grass intentionally introduced to the United States in 1884 ([Thomsen and Salesman 2011](#)). Smooth brome was originally thought of as potentially useful as a trap crop to combat the growing WSS problem ([Criddle 1922](#), [Seamans 1928](#), [Farstad and Jacobson 1945](#), [Beres et al. 2011](#)). Due to its relatively low forage value and propensity to form monocultures and outcompete many native grasses, smooth brome is considered problematic in some habitats ([Carlson and Newell 1985](#), [Willson and Stubbendieck 2000](#), [Dillemuth et al. 2008](#)). However, smooth brome still holds considerable ecological and economic value due to its late senescence and WSS antibiosis properties ([Otfinowski et al. 2006](#), [Rand et al. 2024](#)).

Montana's golden triangle, an area of central and northern Montana with intense cereal grain production, is prone to drought and historical burning via wildfire ([Wilson 1923](#), [Adhikari et al. 2019](#)). As both WSS and its host-specific parasitoids are relatively restricted in their annual mobility, environmental extremes can significantly affect the population dynamics and distribution of these pests and their natural enemies ([Weaver et al. 2005](#)). As with many predator-prey interactions, WSS and parasitoid populations fluctuate, with crashes and spikes experienced in close succession and through interaction with drought ([Holmes et al. 1963](#), [Holmes 1982](#)).

In this study, we explored the population dynamics between WSS in Montana and their associated braconid parasitoids in relation to smooth brome host sites. Our goals were to understand 1) the degree to which WSS infested smooth brome stems in relation to neighboring cereal crops, and 2) the way in which WSS parasitoids use WSS hosts available within smooth brome stems. To do so, we conducted two studies. In our first study, we conducted a WSS-inclusion infestation of smooth brome by excluding parasitoids to understand the relative

infestation and survival to cutting within the smooth brome stems in the absence of parasitoids. The second study examined rates of stem cutting and parasitism in wheat crops and their surroundings at field sites in central and northern Montana.

In addition, we examined historical weather data from two field locations (10 sites overall) in central and northern Montana. We used these data to understand how changes in local climate trends may be affecting WSS, *B. cephi*, and *B. lissogaster* interactions with smooth brome populations. In addition, we analyzed normalized difference vegetative index (NDVI) at our field sites to understand how smooth brome senescence patterns compare to adjacent cultivated wheat fields.

Using these studies, we addressed three questions: 1) what is the total WSS-caused stem cutting leading into diapause, and thus the source rate, of the subsequent WSS population within smooth brome? 2) can WSS larvae within smooth brome serve as critical second-generation hosts for *B. cephi* and *B. lissogaster*? and 3) how do annual WSS and parasitoid populations in smooth brome compare with those in the adjacent cultivated wheat fields?

Materials and Methods

WSS-Inclusion Infestation of Smooth Brome

Assessment of WSS infestation and mortality within smooth brome stems were assessed using a 10 x 18 m plot at the Arthur H. Post Agronomy Farm (43°38'19.39" N, 116°14'28.86" W), an experimental farm of Montana State University in Bozeman, MT. There is a negligible population of WSS and associated parasitoids at this location. Experimental cages were built using 25 mm PVC piping with the netting made using 530 μm (BioQuip Products, LLC). Twelve cages were built to dimensions of 2 m x 1 m x 1 m (L x W x H) with cage locations selected

randomly based on the space available within the plot and arranged in sets of three. Each set of three cages was treated as a replicate and contained a high, low, and control. This experiment was repeated in 2022 and 2023.

Wheat stem stubble was collected in Three Forks, MT, USA (43°38'19.39" N, 116°14'28.86" W) from fields that experienced high levels of WSS infestation and stem cutting the year prior, as previously described by Hager et al. (2024). Cut wheat stubble, or stubs, which contained WSS larvae in diapause, were kept refrigerated between -2 °C and 3 °C for >100 days as required to complete obligatory larval diapause. As needed, stubs were removed from refrigeration and kept at 22-27 °C for 4-5 weeks inside of 3-L GladWare® storage containers (Glad®, Oakland, CA). Once smooth brome stems reached approximately 15-cm tall, stub containers with emerging WSS were added to cages to mimic infestation pressure. Treatments were high (600 stubs), low (200 stubs), and control (zero stubs).

In late September, smooth brome stems were collected from each cage. Each stem was dissected using X-Acto® knives to collect data on infestation, dead larvae and live larvae, as well as very rare parasitism events, for each stem internode.

Montana Field Survey

Field sites were chosen across two counties, Choteau and Judith Basin, within the 'Golden Triangle' of Montana (Fig. S3.1), areas that consistently experience high WSS pressure. We assessed the medium- and long-term temperature and precipitation trends of our field sites using weather data from the National Oceanic and Atmospheric Administration (NOAA, Silver Spring, MD). Data for each field site were averaged from three of the closest weather stations to that location. To better understand how precipitation patterns vary throughout the growing

season, we examined local daily precipitation totals from weather stations at our sampling sites in Big Sandy and Moccasin, MT. Data were retrieved from historical weather stations ([Weather Underground 2024](#)). Precipitation readings were divided into three categories: dates before July 15 and after September 15, as well as between July 15 and September 15. These dates were chosen based on typical wheat harvest and historical periods of known WSS parasitoid activity. In the ‘Golden Triangle’, typical spring wheat harvest takes place in mid-July on average ([Wilson 1923](#), [Zhu and Burney 2021](#)).

We used the normalized difference vegetation index (NDVI) to compare the relative greening throughout the growing season between wheat fields and adjacent smooth brome ([Fig. 3.2](#)). NDVI is typically used to assess vegetation health and density and is calculated from the visible and near-infrared light reflected by vegetation ([Pettorelli et al. 2005](#)). NDVI data measurements between April and October 2023 were directly downloaded using Google Earth Engine (Google Inc. 2023, Mountain View, CA).

We conducted a field survey to assess WSS infestation, larval mortality, and *B. cephi* and *B. lissogaster* prevalence within smooth brome and adjacent wheat fields. Samples were collected from wheat fields and adjacent smooth brome sites in Big Sandy and Moccasin in early July and late August in 2022, and 2023. Sampling sites were set up as 100 m² polygons along the edge of adjoining wheat fields, with two polygons set up at each location. Four collection squares of 0.3 m x 0.3 m were randomly selected within each polygon during both collection events each year. All stems within each sampling square were collected using a shovel to remove both stem and root material. Wheat stem collection methods were adapted from Weaver et al. ([2004](#)). Samples were collected in four parallel columns arranged perpendicular to the edge of

the field, with each column spaced 10 m apart. Within each column, two sampling points were established at distances of 5 and 20 m from the field edge. At each sampling point, stems were collected using a 0.3-m measuring tool. All stems within the 0.3 m length were collected.

Wheat and smooth brome stems were stored at 10 °C until dissection. Stems were dissected in the same manner as samples from our WSS-inclusion plots. Per stem, we recorded presence or absence of WSS larval infestation, live eggs, dead eggs, dead larvae, live larvae, and *Bracon* spp. parasitism, in addition to stem cutting. Wheat stem sawfly larvae were identified based on descriptions in Ainslie ([1920](#)) and Wallace and McNeal ([1966](#)).

To better understand the densities of WSS and parasitoids within the wheat and adjacent smooth brome at each sampling site, we converted our units to the ratio of parasitoids to surviving hosts stem per unit area. Densities of stems are different when considering unmanaged, long-standing stands of smooth brome and the adjacent cultivated wheat or barley.

Statistical Analysis

All statistical analyses were done in R ([R Team 2024](#)) using R Studio (version 4.3.2). Data were plotted using R package ‘ggplot’ (version 3.4.4) ([Wickham 2016](#)). We analyzed long- and short-term weather trends using linear modeling and the ‘lm’ command. Weather data were analyzed using either average yearly precipitation (cm) or average yearly temperature (°C) as the response variable and year as the predictor. Like our weather data analysis, NDVI data were linear modeled to discern differences in NDVI measurements over time. Differences in WSS infestation and parasitoid presence were analyzed using ANOVA to compare high and low treatments in our WSS-inclusion experiment and assess differences in seasonal parasitoid presence.

Results

WSS-Inclusion Infestation of Smooth Brome

WSS heavily infested stems of smooth brome in the WSS-inclusion test conditions. Averaged across both years, we observed 66.5% (SEM = 6.5) of stems infested for high WSS density treatments and 47.3% (SEM = 5.2) of stems for low density treatments. We found strong evidence suggesting that there was a significant difference between infestation at high and low treatment levels when holding year constant ($P < 0.05$, [Fig. 3.1](#)).

Stem cutting by mature larvae, leading into winter, was 5.7% for the high WSS density treatments and 3.9% for the low WSS density, which was strong evidence of a difference in cutting between high and low treatment groups ($P < 0.05$). Dissected stems often contained WSS larvae that had mined through multiple nodes. On average, WSS damage in infested stems spanned 3.45 nodes of WSS damage. In the high WSS treatment, 33.2% of these stems exhibited five or more internodes with discernible injury, compared to 21.5% of the stems in the low treatment ([Fig. 3.2](#)). We also observed 24 parasitism events by WSS parasitoids across all treatments and years.

Montana Field Sites

In Big Sandy and Moccasin, we saw a decline in average yearly precipitation and a rise in average yearly temperature of the past 50 years. There was a significant linear relationship between average precipitation and year at both locations during this period ($r = 0.1$, $P = 0.03$, $estimate = -0.15$). This means that for each one-year interval, the average precipitation has decreased by 0.15 cm ([Fig. S3.2](#)). Concurrently, there was a significant positive linear relationship ($r = 0.245$, $P < 0.05$, $estimate = 0.03$) between year and average yearly temperature

for Moccasin and Big Sandy. Thus, each year, the average daily temperature has increased by 0.03 °C.

Local precipitation data from the past five years confirmed that central and northern Montana experience relatively dry conditions during the late summer months compared to the wetter conditions in spring and early summer. In Big Sandy, when accounting for year, the daily rainfall in the weeks before July 15 was greater than the daily rainfall during the ‘late-summer’ period (from July 15 to September 15) and in the weeks after this period ($P < 0.05$, $F = 2.067$, [Fig. 3.3](#)). Analysis of Moccasin precipitation data revealed that there is little evidence ($P = 0.08$, $F = 1.535$) of a difference between date categories, but the visual trend is still present ([Fig. 3.3](#)).

NDVI trends were different when comparing adjacent smooth brome and spring wheat. Smooth brome post-July 15 NDVI ($F = 30.21$, $P < 0.05$) was greater than the post-July 15 NDVI of the adjacent wheat crop. The smooth brome NDVI remained relatively linear in downward slope compared to the wheat field ([Fig. 3.4](#)).

We quantified WSS and parasitoid presence in 5,971 wheat and grass stems across four research sites in 2022 and 2023. Initial infestation of smooth brome by WSS varied between collection sites, with the greatest infestation taking place within our three Big Sandy sampling sites (2022: 86.3%, 2023: 67.7%), while in Moccasin we observed lower rates (2022: 56.2%, 2023: 51.6%). Across all sites and years in Big Sandy and Moccasin, we observed an average infestation of 57.6% within smooth brome and 45.3% within the adjacent wheat. Cutting by WSS was observed at an average rate of 3.72% in smooth brome and 47.1% in the adjacent cultivated wheat.

To generate a relative estimate of the number of potentially available WSS host larvae within smooth brome late in the growing season, we calculated the number of stems that contained at least four or more nodes with mining injury. In Big Sandy, 39.5% of collected stems in the fall exhibited at least four nodes of mining injury at our second sampling date. In Moccasin, the corresponding figure was 53.1% ([Fig. 3.5](#)).

We used the ratio of parasitized stems to WSS-cut stems to better understand the impact of our smooth brome sink/source ecology for pest and natural enemy systems. The greatest ratio was within smooth brome in Big Sandy in the fall of 2022, where we recorded a ratio of 16 parasitoids to a single WSS-cut stem. Consequently, for every square meter of smooth brome, there were 16 stems that produced a parasitoid for every 1 stem that was likely to yield an adult WSS. However, the lowest ratio in our study was in adjacent wheat in Moccasin, 2022, where for every parasitoid, more than nine WSS adults were found. All smooth brome sampling locations exhibited positive ratios of parasitoids to WSS-cut stems, whereas adjacent wheat samples consistently demonstrated negative ratios of parasitoids to stems cut by WSS ([Fig. 3.6](#)). Fall collection parasitism was consistently higher when compared to summer samples from the same sites. There is strong evidence ($P < 0.05$) to suggest that parasitism within our fall collections is greater than parasitism rates from our summer collections when considering sample site and year ([Fig. 3.7](#)).

Discussion

WSS-Inclusion Infestation of Smooth Brome

Assessment of WSS infestation and larval mortality within smooth brome from our WSS-inclusion infestation study showed high levels of infestation coupled with high larval mortality

before overwintering diapause. Even in cases of greater infestation (70%+), larval survival to cutting reached a maximum around 15%, indicating the capacity of smooth brome to serve as a quality sink for WSS larvae. These results confirm the assertions by Criddle ([1923](#)) and Seamans ([1928](#)) that smooth brome could serve as a durable WSS trap crop. In addition to high levels of larval mortality, stem dissection indicated that many stems had more than four nodes damaged (five damaged internodes) by WSS larvae. Larval movement through stems can be quick in the case of WSS-susceptible, cultivated cereal grains ([Criddle 1923](#)). However, smooth brome, given its presumed antibiosis properties and slow late-season senescence, leads to slower larval development and thus less movement through the stem.

Our results build upon other studies that have reported high WSS larval mortality in smooth brome before overwintering diapause ([Shanower and Hoelmer 2004](#), [Perez-Mendoza and Weaver 2006](#), [Bhandari 2020](#)). Of the infested stems, a significant proportion (2022: 57.1%, 2023: 62.3%, [Fig. 3.2](#)) exhibited larval damage in five or more internodes. While the timing of stem collection and dissection in October did not allow for precise measurement of availability of living WSS larvae, stems with at least five mined internodes would likely contain large, living larvae, and thus host viable parasitoid hosts in late July and August of the same year. Additionally, we found several smooth brome stems with living WSS larvae during our October dissections; these larvae may have been unable to cut stems at this late date.

Montana Field Sites

Precipitation and temperature data from our sampling sites underscore the importance of continuing to monitor and conserve areas of semi-natural, unmanaged grassland. Our 50-year trend analysis aligns with [Pederson et al \(2009\)](#), indicating that the dryland agricultural

environments found in central and northern Montana are likely to become hotter and dryer on average. Over the past 50 years in Big Sandy, precipitation has decreased by an average of 0.12 cm per year while temperatures have increased by an average of 0.03 °C per year. If the trend continues, by 2050, the area could receive 3 cm less rainfall and temperatures 0.75 °C warmer annually.

Both average precipitation and temperature vary widely between years as both Moccasin and Big Sandy routinely experience droughts and periods of relative high rainfall ([Pederson et al. 2009](#), [Weather Underground 2024](#)). Precipitation significantly decreases during the period after wheat harvest, July 15 - September 15, a period when second generation WSS parasitoid adults are searching for WSS larval hosts ([Nelson and Farstad 1953](#), [Somsen and Luginbill 1956](#)), often after winter wheat harvest. Mid-season senescence of many WSS host plants can then leave second generation WSS parasitoids with limited host resources for perpetuating the population. Consequently, prolonged drought, like seen in 2021 in Big Sandy can cause a dearth of green host plants in these semi-arid environments that can be problematic for second generation adult parasitoids seeking hosts.

Given this context, our analysis of NDVI at our sampling sites revealed that smooth brome is particularly capable of sustaining late-season greening. This continued greening may provide crucial resources for WSS parasitoids during years of drought or crop failure. In these buffer zones, parasitoids may be able to locate WSS larvae in sufficient numbers to prevent the large population crashes that can lead to substantial, localized increases in WSS populations and subsequent heavy crop damage ([Holmes et al. 1963](#), [Holmes 1982](#)). In addition, annual changes in temperature and precipitation could have significant impacts on the timing of crop production

and harvest ([Zhu and Burney 2021](#)), leading to additional challenges for second generation parasitoid adults.

Smooth brome is a quality host of both WSS initially and parasitoids subsequently ([Criddle 1922](#), [Peirce et al. 2021](#), [Rand et al. 2024](#)), but few data are available on the seasonal fluctuation of both WSS and parasitoid use across time frames. Because we collected stem samples twice during the growing season, we were able to elucidate both host potential and subsequent parasitoid potential at two important time points, the end of the first generation of parasitoid flight ([Davis 2013](#)) and the end of the second.

Parasitoid presence in smooth brome increased significantly at all sites between pre- and post-harvest collections ([Fig. 3.7](#)). Given the sample collection methods, fall collection parasitism reflects a combination of both pre-harvest and post-harvest parasitoid activity. While our methods do not allow us to determine parasitoid preference for host stems from our results, they indicate that parasitoids may use infested smooth brome stems to a lesser degree preharvest compared to postharvest, when WSS is no longer available within the adjacent wheat stems. Concurrently, we observed a high number of smooth brome stems exhibiting five or more internodes of visible WSS damage, suggesting prolonged larval presence within smooth brome stems. Specifically, in Big Sandy (39.5%) and Moccasin (53.1%), stems that exhibited four or more nodes damaged indicate that WSS larvae may remain available within smooth brome stems past wheat harvest, when host WSS availability is otherwise limited. This is particularly important in years of drought or increased temperatures, where wheat senescence and harvest may occur earlier in the summer, resulting in little or no success in the second generation of these parasitoids ([Holmes et al. 1963](#)).

Broader Implications

We used parasitism-to-cut-stem ratios to understand the relative impact of smooth brome host sources on overall field parasitism. Simply assessing the overall number of insects can potentially diminish the apparent importance of smooth brome, as per square meter stem counts in cultivated wheat are denser than smooth brome counts in unmanaged environments such as along roadsides. We found greater ratios of parasitized stems to cut stems within smooth brome compared to adjacent wheat fields ([Fig. 3.6](#)). This result indicates that field-edge areas containing smooth brome typically provide a greater parasitoid source potential, per square meter, than adjacent cultivated fields. These results emphasize the importance of habitat diversity and ecological buffers to sustain parasitoid populations over successive years and highlight the crucial role of edge-row areas in maximizing parasitoid effectiveness in minimizing WSS damage.

Overall, this work suggests that smooth brome may play an important role in WSS damage mitigation and parasitoid conservation, especially in drought years. Smooth brome exhibited low levels of WSS stem cutting while remaining a viable host for second-generation WSS parasitoids. Assessing the comparative abundance of WSS and its associated parasitoids within smooth brome and adjacent cultivated cereal hosts is an important initial step in evaluating whether unmanaged road-side environments serve as sink or source origins of the pest and its beneficial natural adversaries infiltrating agricultural crops. Further research is needed to understand the mechanisms behind the ability of smooth brome to both slow larval development while causing appreciable, but not limiting larval mortality and thus prevent the high level of WSS stem cutting typically seen in native grasses and cultivated cereals at the same time.

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Figures

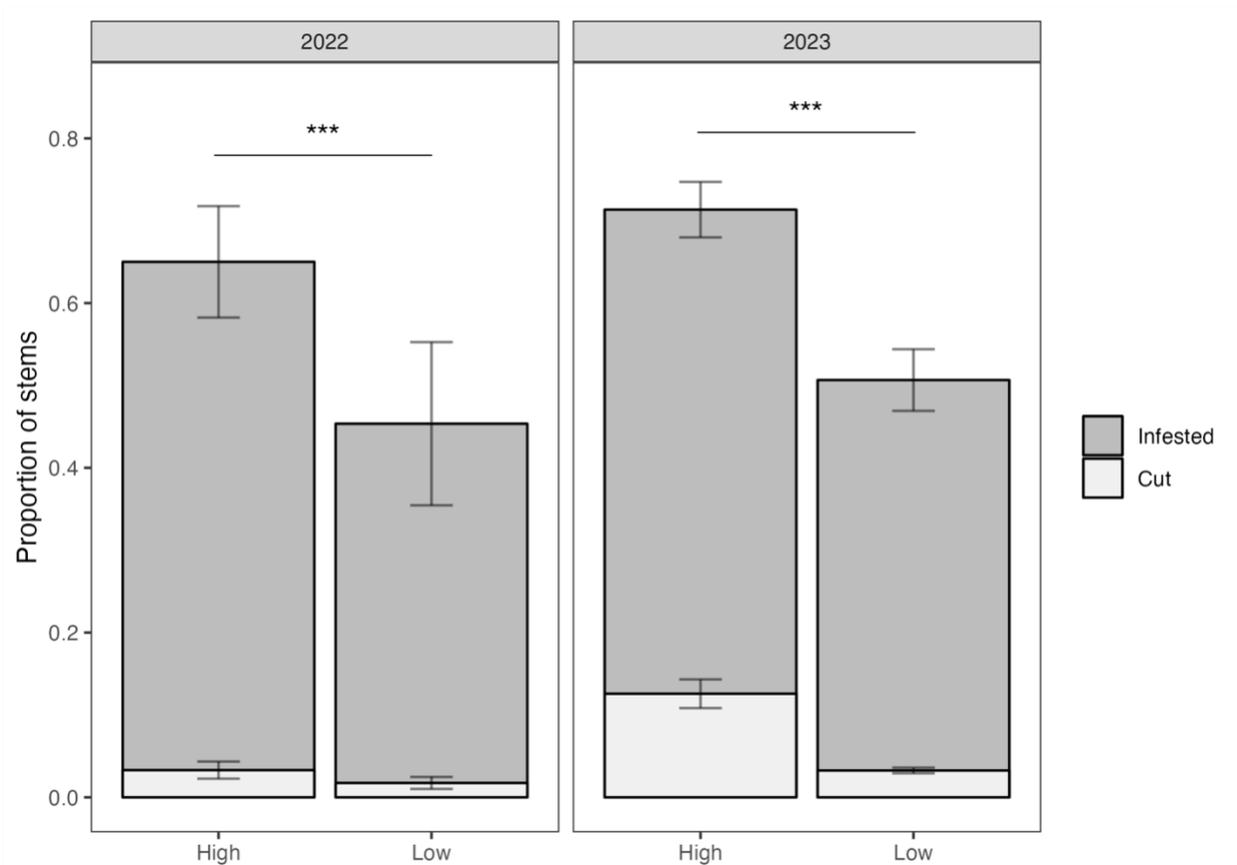


Fig. 3.1. Comparison of year and treatment group for WSS-inclusion infestation of smooth brome. Three treatment groups - high, low, and control (zero, not shown) - were used. The control trials showed no visible sign of WSS stem damage. *** represents $P < 0.05$ on ANOVA.

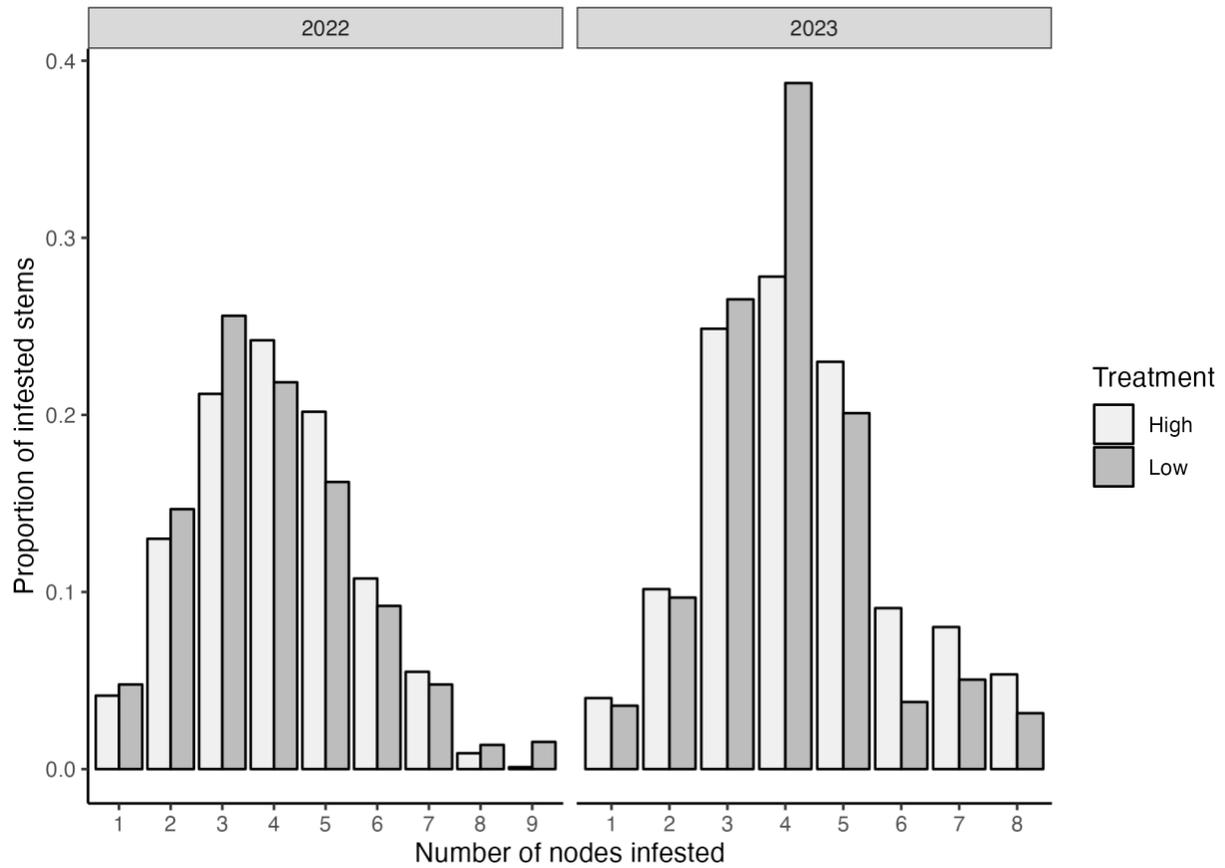


Fig 3.2. Proportion of infested smooth brome internodes exhibiting visible WSS damage within WSS-inclusion infestation plots in Bozeman, MT. High treatments had 600 ‘stubs’ (WSS pupae) added to each cage, while low had 200. We found that 57.1% of stems in 2022 and 62.3% in 2023 exhibited more than four nodes of WSS boring damage.

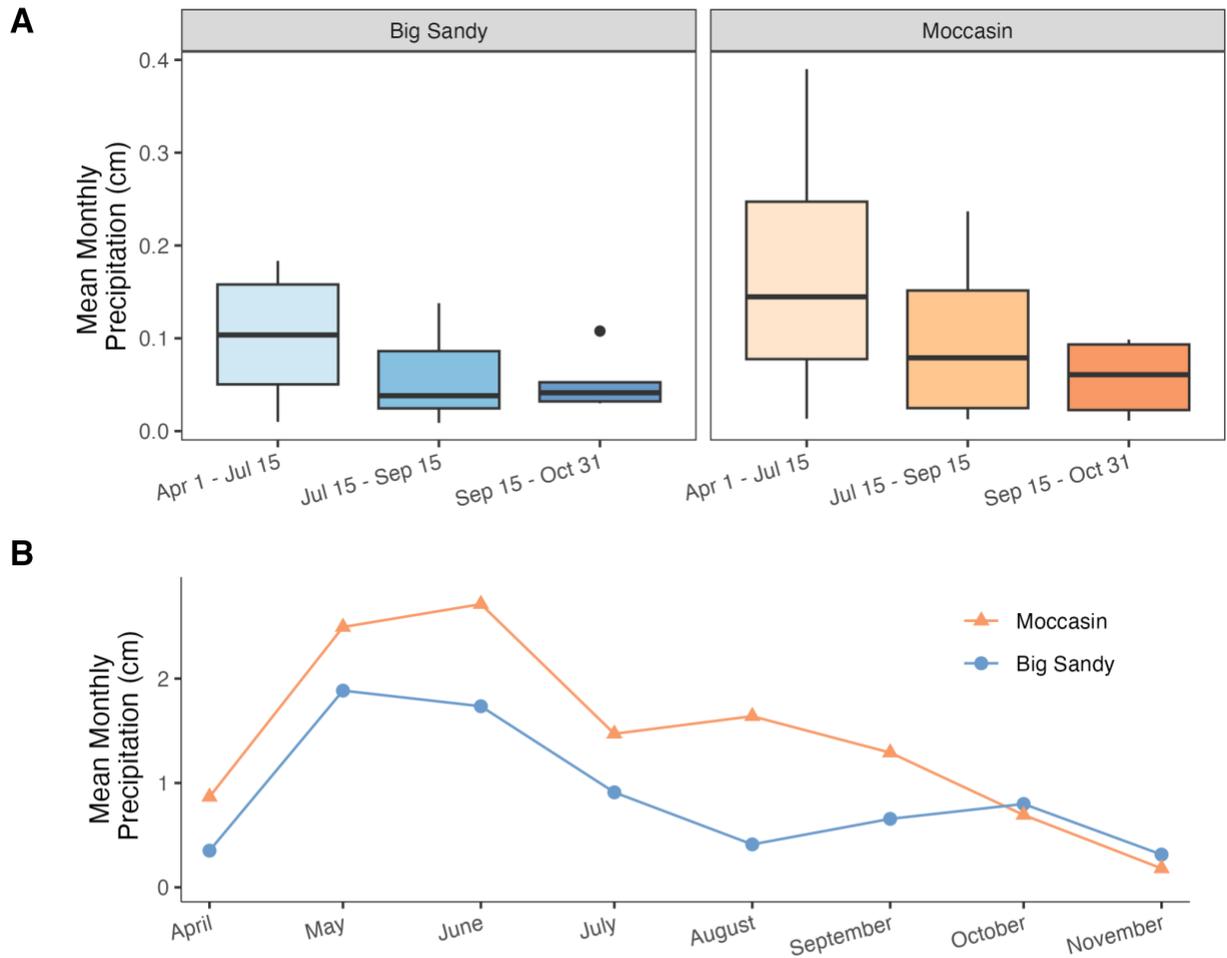


Fig 3.3. Five-year seasonal change in precipitation for Big Sandy and Moccasin, MT, USA. Averaged from data between 2018 and 2023 from Weather Underground. There was a noticeable change in average precipitation after mid-July with little precipitation after July 15. A) Boxplot showing average weekly rainfall during each time period. B) *Line plot* showing seasonal trend of average rainfall.

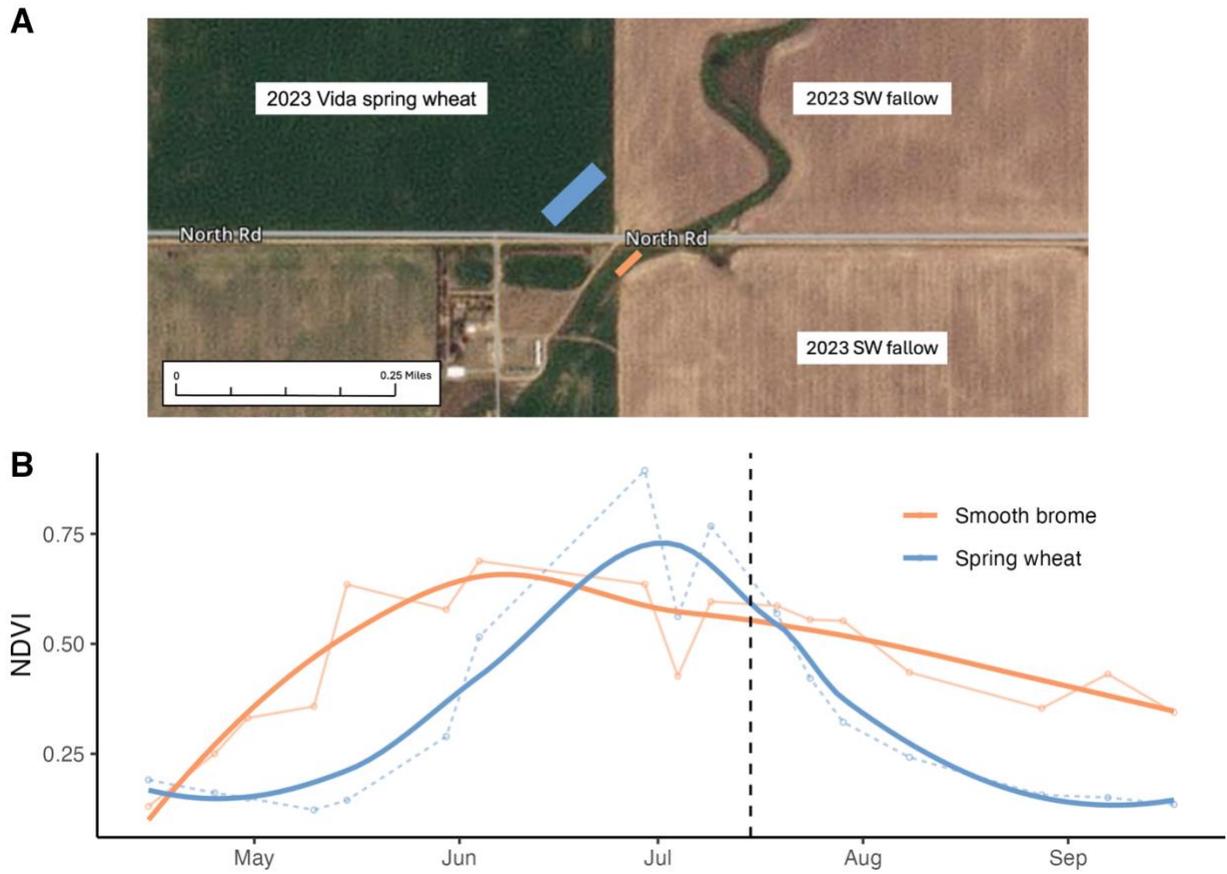


Fig 3.4. Normalized difference vegetation index (NDVI) of smooth brome and adjacent spring wheat field from April 2023 in Big Sandy, MT. Orange boxes in (A) indicate from where NDVI data was gathered using Google Earth Engine. Dotted black line on (B) indicates when spring wheat was harvested.

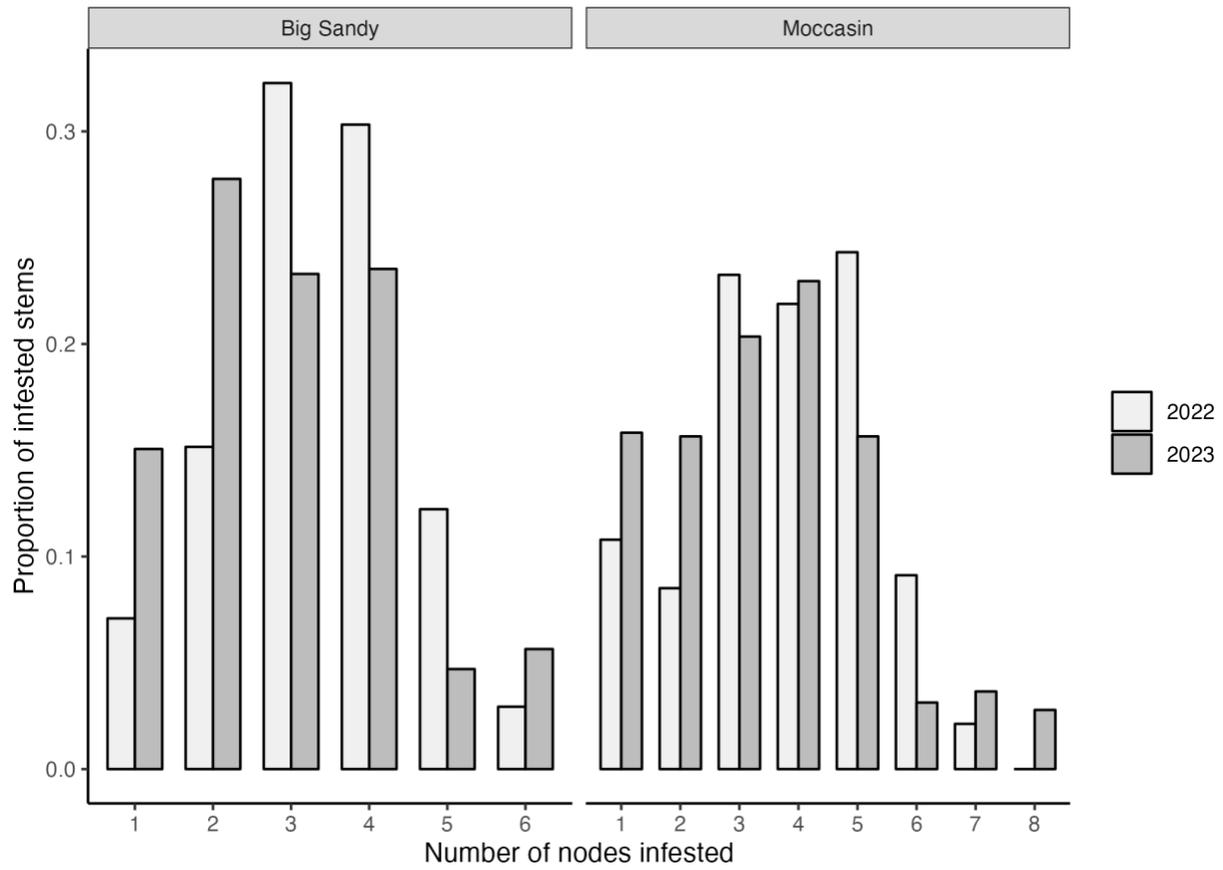


Fig 3.5. Proportion of infested smooth brome internodes exhibiting visible WSS damage within WSS-inclusion infestation plots in Big Sandy and Moccasin, MT. We found that 19.5% of stems in Big Sandy and 27.1% of stems in Moccasin had four or more nodes exhibiting WSS damage.

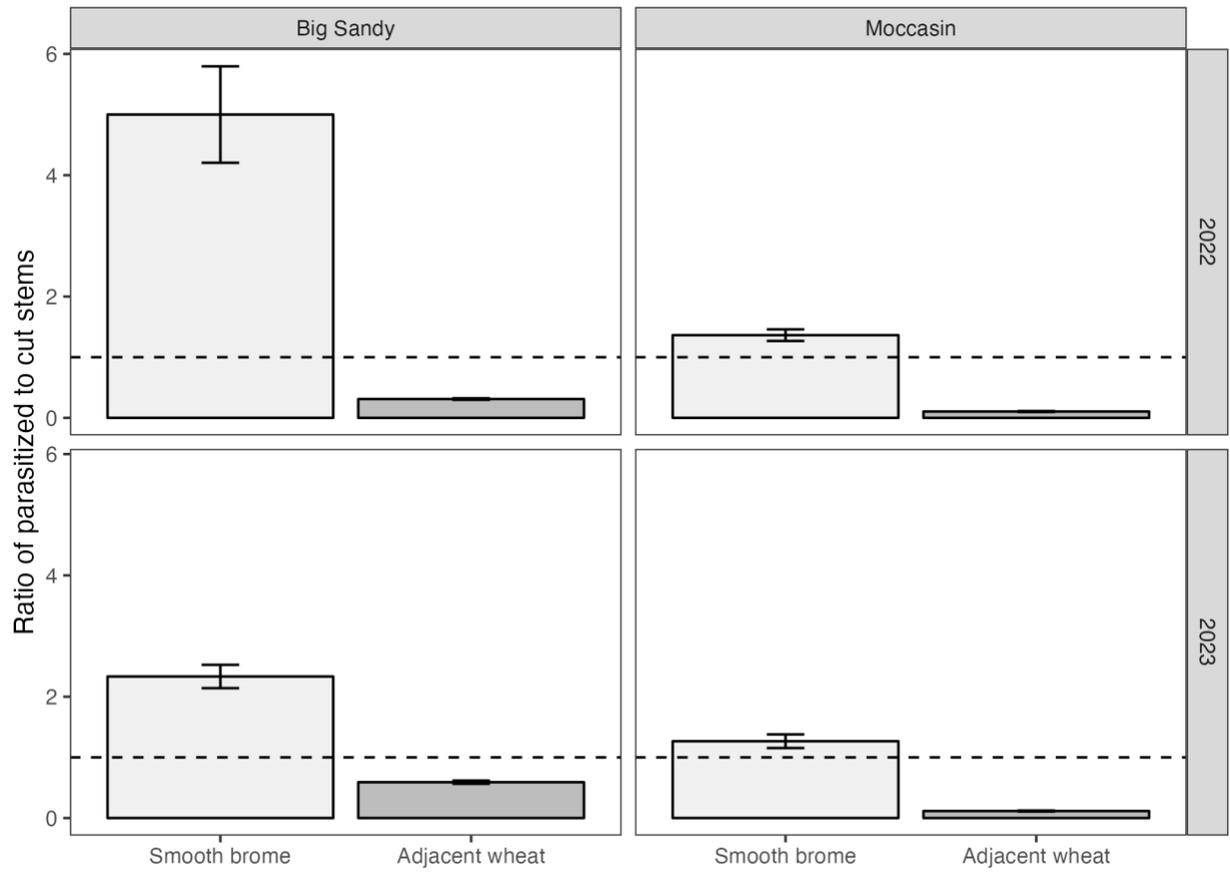


Fig 3.6. Ratio of stems found to be parasitized by WSS parasitoids to stems cut by WSS. Stems collected from field sites in Moccasin and Big Sandy, MT. Dotted horizontal line represents ratio of 1 where the number of parasitized stems are equal to WSS-cut stems. All ratios are greater than one for smooth brome while all ratios are less than one for adjacent wheat fields.

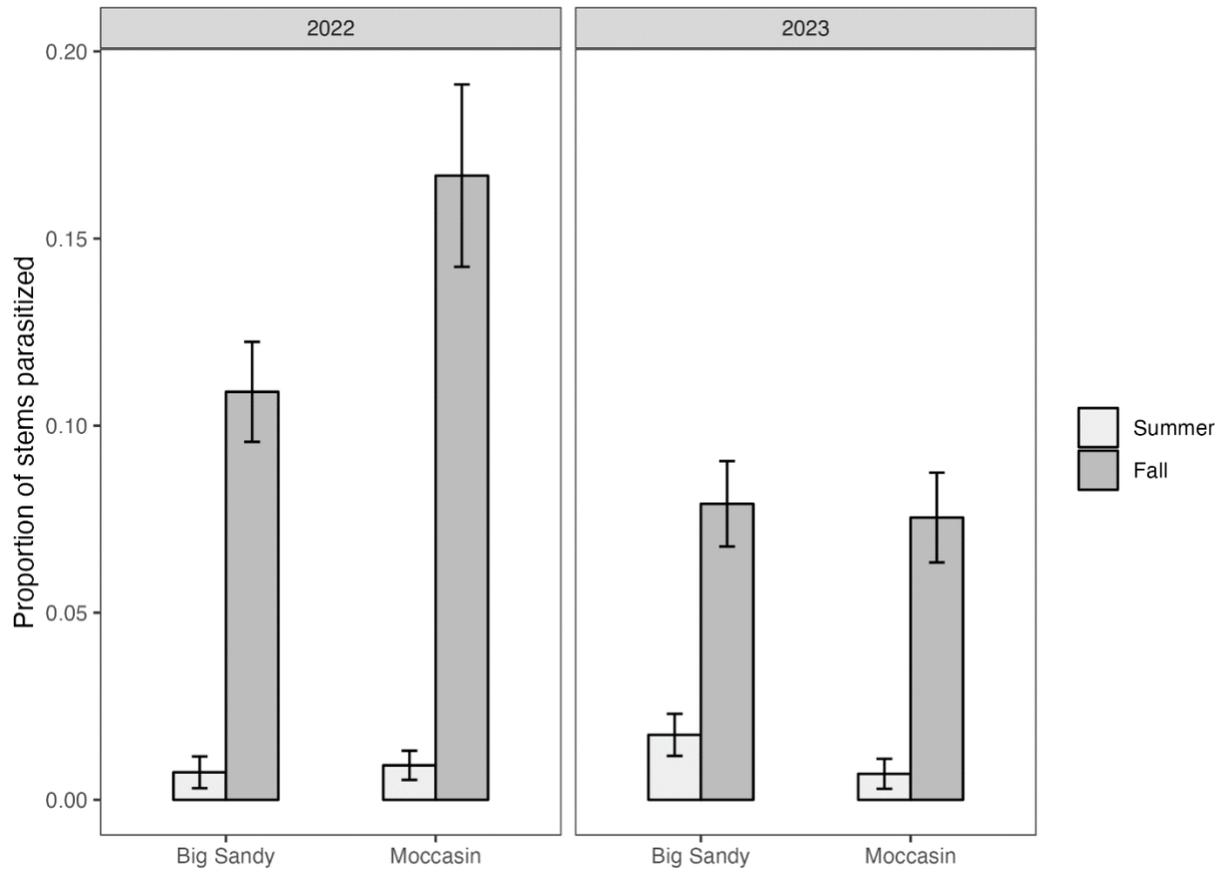
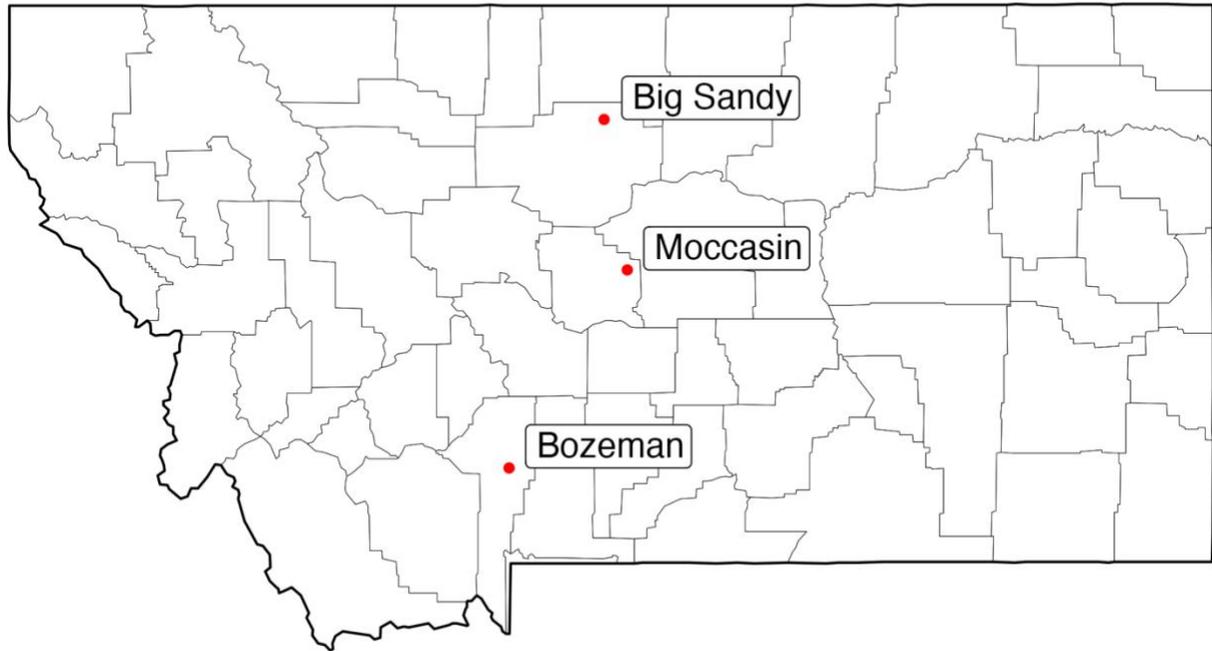


Fig 3.7. Proportion of parasitism within infested field-collected smooth brome stems. Fall samplings consistently revealed higher rates of parasitism when compared to summer collections from the same location.

Montana, USA



Supp Fig S3.1. Location of Montana, USA field sites. The WSS-inclusion smooth brome infestation site was in Bozeman, while field sites were located in centrally located Moccasin and in more northern Big Sandy.

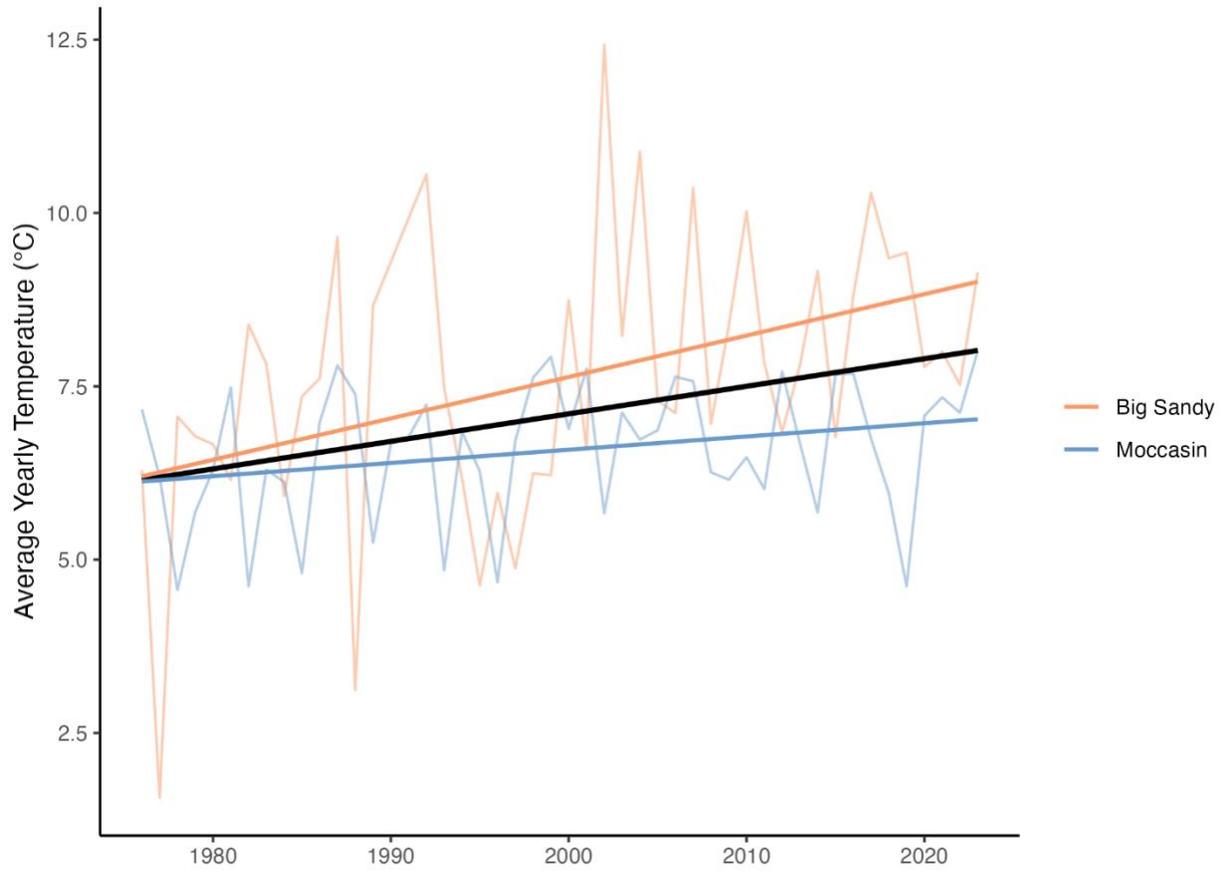


Fig. S3.2. Fifty-year trend of yearly mean temperature for Big Sandy and Moccasin, MT. We observed a significant average increase of 0.03 °C per when both data sets were combined.



Figure S3.3. A) Moccasin, MT, September 22, 2021. Green smooth brome seen in the foreground growing in the ditch next to harvested winter wheat and early winter wheat. B) Moccasin, MT, September 20, 2023. Green smooth brome stems within the coulee adjacent to a harvested wheat field.

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CHAPTER FOUR

CONCLUSION

Given the substantial economic impact of the WSS and the challenges in managing its populations, it is essential to invest in integrated pest management strategies. Our research assessed electrophysiological and behavioral responses of *B. cephi* and *B. lissogaster* to WSS-induced volatiles emitted from smooth brome and winter wheat, as well as the agroecological benefits of smooth brome adjacent to wheat fields. We found that WSS-infested smooth brome is more attractive to host-seeking female *B. cephi* and *B. lissogaster* than WSS-infested winter wheat. In addition, smooth brome provided late-season WSS larval hosts for second-generation parasitoids. These results are an important addition to the improvement of WSS biocontrol programs in winter ([Chapter 3](#)) and spring wheat ([Bhandari 2020](#)).

We evaluated the electrophysiological and behavioral response of *B. cephi* and *B. lissogaster* to WSS-induced volatiles from smooth brome and winter wheat. Both species exhibited positive behavioral response to (*Z*)-3-hexenyl acetate and 6-methyl-5-hepten-2-one, notable for their electrophysiological activity in adult WSS ([Perez 2009](#)). When given the choice between WSS-induced volatiles blends from smooth brome and winter wheat, female *B. cephi* and *B. lissogaster* preferred those from smooth brome ([Chapter 2](#)).

We investigated the potential ecological benefit of smooth brome in providing late-season WSS host refuge for second-generation *B. cephi* and *B. lissogaster*. Our results revealed high overall WSS larval mortality. WSS larvae survived within smooth brome stems after wheat harvest, providing second-generation parasitoids with needed hosts in years of atypically early

harvest or drought. These results suggest that smooth brome can play a critical role in maintaining parasitoid populations and enhancing the biological control of WSS.

By exploring the chemical ecology of smooth brome and its ecological benefits for second-generation parasitoids, we provide a clearer understanding of how smooth brome contributes to managing WSS. Ideally, *B. cephi* and *B. lissogaster* would avoid large annual population fluctuations caused by early harvest, drought, or fires that limit the availability of WSS larval hosts and the reproductive potential of second-generation adults. Smooth brome offers unique advantages due to its delayed senescence and WSS antibiosis properties, both of which were evident in our experiments, while still retaining the volatile signature needed by parasitoids to locate quality WSS host larvae. In regions such as Montana's 'Golden Triangle', the availability of late-season WSS larval hosts is crucial in maintaining consistent parasitoid populations.

We recommend strategically conserving smooth brome already present along roadways and within coulees in areas where wheat is grown. Mowing or otherwise disturbing this beneficial resource could negatively impact WSS larval presence, potential parasitoid emergence, and effective WSS biocontrol. We believe that smooth brome is a strong candidate for further research to decipher its antibiosis properties, whether through genetic or proteomic analysis. This information could be useful in developing more WSS-resistant wheat cultivars or in further advocating for the use of smooth brome as a trap-like reservoir resource. We encourage continued investigation and practical implementation of smooth brome to enhance integrated pest management strategies and sustain dry-land wheat production systems.

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