THE EFFECTS OF INCREASING CROP DIVERSITY ON POPULATIONS OF WHEAT STEM SAWFLY (*CEPHUS CINCTUS*) AND ASSOCIATED BRACONID PARASITOIDS

by

Benjamin Vernon Fischer

A thesis submitted in partial fulfillment
of the requirements for the degree

of

Master of Science

in

Entomology

MONTANA STATE UNIVERSITY
Bozeman, Montana

April 2019

TABLE OF CONTENTS

TABLE OF CONTENTS CONTINUED

LIST OF TABLES

LIST OF FIGURES

ABSTRACT

Wheat stem sawfly, *Cephus cinctus* (Norton) (WSS) is the most damaging pest of wheat in the Northern Great Plains. Insecticides are not widely used to control this insect, and cultural control methods provide inconsistent management of this pest. However, biological control by the parasitoids *Bracon cephi* (Gahan) and *Bracon lissogaster* Muesebeck has been shown to reduce damage caused by WSS. In addition, increased agroecosystem diversity has benefitted biological control agents in many other systems. Therefore, this study assessed the effect on populations of WSS and associated parasitoids by the inclusion of pulse and cover crops near wheat fields. Field trapping, dissection of postharvest crop residue, and rearing of insects out of crop residue were used to survey WSS and parasitoid populations in pairs of wheat fields throughout the major wheat producing regions of Montana. One wheat field in each pair was seeded next to a fallow field, and the other was seeded next to a field of either pulse or cover crop. Postharvest stem dissection samples show that wheat fields next to pulse or cover crops had a mean increase of 51 parasitoids per m^2 than wheat fields next to fallow. A corresponding 3% reduction in stem cutting was also observed in postharvest samples from wheat fields adjacent to flowering pulse or cover crops. Land-use data from CropScape™ were used as well to evaluate other land-use impacts around each wheat field such as wheat, fallow, grassland/pasture, flowering crops, and developed space. The regression equation $Y = 18.96X + 6.08,$ where X = proportion of fallow land within 2 km of the wheat field and Y = square root of WSS abundance in a 7.5 m sample of crop residue from rows of wheat, can be used to predict WSS abundance in wheat fields. Replacing fallow fields with flowering pulse or cover crops in the Northern Great Plains may be an important integrated pest management tactic to reduce WSS damage. Cultural practices such as crop diversification are key to developing consistent biological control for WSS.

LITERATURE REVIEW

Overview

The wheat stem sawfly (WSS), *Cephus cinctus* (Norton), is an insect native to the northern Great Plains of North America. The species was first described in 1872 by E. Norton, from adults collected in Colorado grasslands (Norton 1872; Beres et al. 2011c). Albert Koebele later found larvae of *C. cinctus* feeding in stems of grass near Alameda, California, and reared them to adults in 1909 (Ainslie 1920). Wheat stem sawfly was first reported as a pest of spring wheat in Saskatchewan and Manitoba by J. Fletcher in 1895 (Beres et al. 2011c).

The cultivation of historic grassland into farmland gave WSS an excellent opportunity to expand its host range from native grasses such as western wheatgrass, *Pascopyrum smithii* (Rydb.) Á. Löve, bluebunch wheatgrass, *Pseudoroegneria spicata* (Pursh) Á. Löve, and basin wildrye, *Leymus cinereus* (Scribn. & Merr.) Á. Löve (Ainslie 1920; Criddle 1922; Wallace and McNeal 1966; Cockrell et al. 2017), to introduced forage species such as timothy, *Phleum pratense* L., smooth brome, *Bromus inermis* Leyss., and crested wheat grass, *Agropyron cristatum* (L.) Gaertn (Ainslie 1920; Criddle 1922; Cockrell et al. 2017). Cultivated cereals such as rye, *Secale cereal* L., barley, *Hordeum vulgare* L., and especially spring wheat, *Triticum aestivum* L. also became widely used host plants (Criddle 1922; Wallace and McNeal 1966; Cockrell et al. 2017). There were 258,000 acres of cultivated farmland in Montana in 1909 and by 1919 there were 3,400,000 acres (Morrill 1983). As wheat continued to spread across the landscape, populations of WSS (Lesieur et al. 2016) continued to adapt to this new host. The range of damaging populations of WSS increased, as did overall abundance in wheat fields over the next three decades, and by 1948 WSS was regarded as the most serious pestiferous threat to wheat in Montana (Morrill 1983). Wheat stem sawfly continues to be the most serious pest of wheat in Montana and was responsible for annual crop losses that exceeded $80 million in 2012 alone (Table 1).

Table 1: Annual damage to wheat caused by WSS across Montana from 2008-2012 (excerpted from Bekkerman 2014).

	2012	2013	2014	2015	2016	2017
	Spring Wheat					
Acres harvested (mil.)	2.666	2.592	2.980	2.540	2.060	2.290
Estimated Infested acres (mil.)	0.710	0.690	0.794	0.677	0.549	0.610
Estimated Yield	34	34	34	34	34	34
Estimated Forgone yield (mil. bu)	4.231	4.122	4.675	3.985	3.232	3.593
Estimated Forgone yield %	4.61	4.61	4.61	4.61	4.61	4.61
Estimated Forgone yield per acre	1.6	1.6	1.6	1.6	1.6	1.6
Market price	8.52	6.70	6.08	4.80	4.76	6.21
Estimated Forgone revenues ($ mil.)	36.04	27.62	28.43	19.13	15.38	22.31
	Winter Wheat					
Acres harvested (mil.)	1.815	1.607	2.980	2.220	2.060	1.590
Estimated Infested acres (mil.)	0.702	0.621	0.794	0.858	0.831	0.615
Estimated Yield	48	49	49	49	49	49
Estimated Forgone yield (mil. bu)	5.467	5.006	6.923	6.861	6.644	4.914
Estimated Forgone yield %	6.31	6.31	6.31	6.31	6.31	6.31
Estimated Forgone yield per acre	3.0	3.1	3.1	3.1	3.1	3.1
Market price	8.05	7.05	5.86	4.59	3.88	4.76
Estimated Forgone revenues ($ mil.)	44.04	35.29	40.57	31.49	25.78	23.39
Total (mil.)	80.08	62.91	68.99	50.62	41.16	45.70

Other factors that contributed to the proliferation of WSS were rust resistant wheat varieties (McGinnis 1950), the drought of the 1930s (Morrill 1983), and soil conservation efforts including the use of the Noble blade (Beres et al. 2011a; 2011c). In the early 20th century, WSS outbreaks were often stifled by wheat rust epidemics (Platt and Farstad 1949; Holmes 1982; Beres et al 2011c). The pathogenic rust would kill the wheat, leaving WSS unable to complete its life cycle. The development of rust resistant cultivars, in tandem with the drought of the 1930s, allowed new populations of WSS to thrive (Morrill 1983).

Intense soil erosion due to tillage during drought years prompted farmers to adopt low disturbance tillage practices (Shanower and Hoelmer 2004; Beres et al. 2011c) and narrow strip cropping (McGinnis 1950; Morrill 2001; Weaver et al. 2004). This allowed for excellent overwinter survival of WSS and a greater area of crop edge to infest, which in turn led to greater populations. Wheat stem sawfly are most devastating on field edges because they are primarily moving from a field of wheat in the previous season to an adjacent field in wheat the current season (Beres et al. 2011; Weiss and Morrill 1992; Holmes 1982).

Historically, winter wheat was not a suitable host for WSS. However, by 1985, heavy losses due to WSS infestation were evident in Montana winter wheat fields (Morrill 1985; Morrill and Kushnak 1996). This was primarily due to changes in annual emergence, effectively 1 month earlier, by WSS adults. There was a significant decrease in spring wheat acreage between 1921 and 1945. Winter wheat replaced spring wheat on many of the acres, so WSS benefitted from adapting the completion of the life cycle to the earlier maturation of winter wheat (Morrill and Kushnak 1996). Another adaptation that played a role in the switch to earlier adult emergence and oviposition was within-stem cannibalism by larvae. In high competition situations due to dense populations, several WSS may lay an egg in a single wheat stem (Buteler et al. 2009). The larva that hatches first typically is the individual that survives because it will consume competing eggs or larva that it encounters. This internecine competition, coupled with the increasing acreage of winter wheat, selected for earlier emergence of adults, and allowed WSS to take advantage of abundant winter wheat as a host (Morrill and Kushnak 1996; Buteler et al. 2009).

The Wheat Stem Sawfly

Biology

Post-diapause development of WSS begins as temperature approaches 10° C and relative humidity approaches 43% in the early spring. Ideal conditions for post-diapause development are from 20°-25° C and 60-75% RH (Perez-Mendoza and Weaver 2006a). Under these conditions, larvae break diapause and begin to pupate. The pupal stage usually lasts about 20 days (Fulbright et al. 2017). Adult WSS emerge as temperature and humidity rise in the spring. Emergence usually begins in mid- to late May in Montana and may last through mid-July (Fulbright et al. 2017). Wheat stem sawfly adults usually live only 5-8 days (Fulbright et al. 2017), which is adequate for mating and oviposition. Males generally appear first, emerging 2-4 days before females (Cárcamo et al. 2005). Wheat stem sawfly are arrhenotokous (Mackay 1956), so mated females can choose to fertilize their eggs, leading to female, diploid offspring, or can oviposit unfertilized eggs which will be haploid males (Fulbright 2017). The earlier emergence of males allows female eggs to be deposited earlier in the season, providing more time for development (Fulbright 2017).

Wheat stem sawfly lay eggs in the lumen of wheat plants, generally the uppermost internode in northern spring wheat (Holmes and Peterson 1960) or they use the lower internodes in late-seeded southern spring wheat (Sing 2002). Female WSS commonly lay one egg per host stem, but if there is a large WSS population or limited hosts, several individuals may lay eggs in a single stem. However, only one individual will survive due to cannibalism (Buteler et al. 2009, 2015; Holmes 1982).

Mated females, with fertilized eggs, prefer to deposit these in larger, more vigorous stems, while male eggs tend to be deposited in smaller stems (Morrill et al. 2000a, 2000b). Females are larger than males, so a larger, more nutritious host is necessary for female development (Cárcamo et al. 2005). In addition, females laid in larger stems tend to live longer and lay more eggs than those laid in relatively smaller stems (Morrill et al. 2000b; Holmes and Peterson 1960; Wall 1952; Cárcamo et al. 2005). Females usually lay 30 -50 eggs throughout their life (Criddle 1922; Perez-Mendoza et al. 2006b; Fulbright et al. 2011; Holmes et al. 1982), but stem diameter and cultivar have a large effect on female egg load (Cárcamo et al. 2005). Abiotic conditions that affect the health of the host wheat plant also can reduce the fitness of emerging WSS by reducing egg load, weight, and longevity (Platt and Farstad 1949; Holmes 1982; Morrill 1983; Cárcamo et al. 2005; Perez-Mendoza and Weaver 2006a; Beres et al. 2011c).

Larvae hatch 5-7 days after oviposition and begin to feed as soon as their mouthparts are sclerotized. The larvae feed within the stem, burrowing their way up and down for about a month and the later instars breach the nodes when feeding (Holmes 1954). Multiple eggs may be laid within the same stem, but cannibalism allows only one larva to survive, which occurs because large larvae feed in more than one internode (Holmes 1954; Buteler et al. 2009; 2015). As the wheat matures and dries to 41-51% moisture, the larvae make their way to the bottom of the stem. Once there they girdle the stem by cutting a v-shaped notch around it and plugging the stem with frass (Fulbright 2017). This causes lodging, which leads to the bulk of yield loss due to harvest inefficiency (Beres et al. 2007). Ainslie (1920) reported yield losses of more than 60% in some fields. The plugged stub provides an excellent, protected environment for the larvae to overwinter. A "stub" is the area of the stem just above the crown in which the WSS overwinters. Securely located within this structure near the crown of the stem, the larva creates a thin hibernaculum and enters diapause in order to overwinter. The following spring the larva will pupate and emerge from the stub as an adult (Beres et al. 2011; Fulbright et al. 2011; Weiss and Morrill 1992).

Crop Damage

WSS is the most injurious pest of wheat in the northern Great Plains, causing more than $80 million of damage annually in Montana (Bekkerman 2014; Blodgett et al. 1997) and $350 million annually across the northern Great Plains and Canadian Prairies (Beres et al. 2011a; 2011c; 2012). Stem mining by WSS larvae can cause a 3-30% (Morrill et al. 1992; Wallace and McNeal 1966) reduction in seed head size and weight

(Munro 1945; McNeal et al. 1955; Holmes 1977; 1982; Weiss and Morrill 1992), as well as a 0.6-1.2% reduction in protein (Weiss and Morrill 1992). This is caused by reductions in photosynthesis and nutrient transport within the host plant from larvae feeding on the vascular bundles. Photosynthetic capacity can be reduced 10-20% due to larval feeding on vascular tissue altering source-sink relationships (Macedo et al. 2005; Delaney et al. 2010; Beres et al. 2011).

Injury due to larval feeding may begin reducing flag leaf photosynthetic activity as soon as 28 days post infestation, and by 40-42 days after oviposition there is a significant reduction, leading to further yield loss (Delaney et al. 2010, Macedo et al. 2005; 2006; 2007). The flag leaf and head supply the bulk of carbon needed during the grain fill stage (Evans et al. 1975). Delaney et al. (2010) suggest that the leaf photosynthetic reduction is caused by a combination of reduced stomatal conductance and increased intercellular leaf CO_2, leading to reductions in chlorophyll fluorescence parameters. Stem mining alone will only cause a 10% reduction in photosynthetic rate, however additional drought or nutrient stress will have a synergistic effect with herbivory leading to photosynthetic reductions as high as 25-30% (Macedo et al. 2005; 2006; 2007; Delaney et al. 2010).

When the plants are under stress due to feeding by WSS, their metabolic homeostasis is altered, rendering them incapable of tolerating injury (Macedo et al. 2005). In addition, under ideal conditions, some cultivars can receive 10 to 76% of the grain weight from resources contributed by the wheat head (Evans et al. 1975). Without drought or nutrient stress, the plant can use photosynthetic resources from the head to overcome those lost from the flag leaf (Macedo et al. 2006). However, if the WSS larva dies, there will be no reduction of photosynthetic rate at all (Delaney et al. 2010). Plant genetic background i.e. solid vs hollow stem also makes a difference in the magnitude of this photosynthetic reduction (Macedo et al. 2006; Delaney et al. 2010). Bekkerman and Weaver (2018) show 67.92 and 388.71 kg/ha yield loss from WSS infestation in solid and hollow stemmed winter wheat respectively.

The relationship in yield between infested and uninfested stems is extremely hard to quantify because uninfested stems tend to be smaller with lighter kernels. This makes it difficult to make a valid comparison of yield between infested and uninfested stems, because the plants that are preferred for oviposition are also the ones that will yield the highest (Seamans et al. 1944; McNeal et al. 1955; Holmes 1977; Buteler and Weaver 2012; Bekkerman and Weaver 2018). Buteler (2008) observed that WSS infested stems where the larva did not complete development were often the highest yielding stems. Infested stems often have the highest yield potential, and yield loss is stopped immediately after mortality of the larvae, allowing these plants to yield close to their potential. Bekkerman and Weaver (2018) use a copula function to examine a large data set to calculate loss parameters that can, in part, account for this. This makes it possible to have a more accurate comparison of lost yield across infestation parameters, ranging from uninfested (generally low yield potential) to infested but parasitized (usually high yielding). They found that a 1% increase in the proportion of infested stems that are cut results in an 8% reduction in seed weight. In contrast, a 1% increase in the proportion of infested stems in which the WSS does not live to cut the stem will lead to an 11% increase in seed weight.

The main source of yield loss is the lodging of cut stems. Thin stands, high wind, and precipitation can all exacerbate crop loss by causing a higher proportion of cut stems to fall over (Wallace and McNeal 1966; Weiss and Morrill 1992; Beres et al. 2007; 2011c). Once on the ground, stems are very difficult to collect, and there is a large loss of grain. Ainslie (1920) reported grain losses of greater than 60% due to the cutting and subsequent lodging caused by WSS.

Control

Control of WSS relies on using several cultural methods in conjunction. There is no “silver bullet” that will keep damage from this pest at acceptable levels. When used together, crop rotation, trap crops, resistant cultivars, and improving habitat for natural enemies may be able to lessen the damage done by WSS.

Tillage. Most early methods used in attempts to control WSS involved destroying the stub, because WSS spend most of their life within the stem and the larvae are in the stub from harvest through spring growth the following season (Criddle 1917; 1922). Tillage was the most widely adopted method, which does cause measurable mortality of WSS larvae (Ainslie 1920). If soil is removed from the stubs, the larvae are exposed to ambient conditions without insulation from desiccation or very cold winter conditions, which causes high mortality (Weiss and Morrill 1992; Criddle 1917; 1922; Wallace and McNeal 1966). Unfortunately, regular tillage can result in severe soil erosion and this practice has not been widely used since the adoption of no-till weed control through herbicide applications (Long et al. 2014a; Beres et al. 2011; Shanower and Hoelmer 2004). Another drawback of using tillage to manage WSS is that it also kills beneficial insects. Wheat stem sawfly can dig themselves out of the soil if buried, but parasitoids cannot. This means that while tillage has a limited effect on WSS survival, it does significantly increase mortality of the parasitoid population (Runyon et al. 2002).

Trap Crops. Trap crops are another early method of WSS management. Criddle (1919; 1922) suggested a narrow strip of rye, wheat, or brome grass be sown between the previous season's stubble and the current cereal crop. This trap crop should be seeded as early in the season as possible so the trap crop will be more advanced than the cereal crop. At the beginning of WSS flight, when plants are small, WSS will prefer to oviposit in larger, more developed stems. Therefore, WSS will preferentially oviposit in the earlier seeded trap crop (Ainslie 1920; Criddle 1919; 1922; Holmes and Peterson 1960). It was also recommended to mow or till trap crops before larvae can reach the bottom of the stem and cut in order to reduce survival into the next season (Criddle 1919; 1922). However, this should not be done in smooth brome because this grass attracts many parasitoids that should be conserved (Criddle 1922).

A more recent strategy for trap cropping has been planting cultivars that are more attractive or resistant to WSS around the border of a more susceptible, higher yielding variety (Beres et al. 2009; Buteler et al. 2010; 2012). Morrill et al. (2001) show that an earlier maturing winter wheat border protecting spring wheat was effective at limiting WSS infestation of the crop. It was also found that higher yielding hollow-stemmed cultivars can be protected by planting a border of a semi-resistant solid-stemmed cultivar. Beres et al. (2009) also investigated the effect of planting solid-stemmed varieties as trap crops with less significant results. Climatic conditions resulted in the solid-stemmed variety not consistently achieving adequate pith expression for resistance. This, combined with increased WSS infestation, limited the retention of adult WSS in the solid-stemmed wheat. A slight increase of yield was observed in wheat protected by the trap crop.

Buteler et al. (2010; 2012) investigate the role of semiochemicals in WSS oviposition preference, and the impact on trap crop selection. They found that cultivars have a large range in the amount of volatile chemicals produced and released. (*Z*)-3-hexenyl acetate is a compound of particular interest because WSS prefer cultivars that emit higher amounts (Weaver et al. 2009). Stem height and diameter are also factors in host plant preference by WSS (Holmes and Peterson 1960; Buteler et al. 2010; 2012). At earlier growth stages (Zadoks 33) stem height is the only significant variable of host preference. However, later in development (Zadoks 49) there is no relationship between stem height or diameter and oviposition preference. Once plants exceed an acceptable size, other factors such as the amount and combination of semiochemicals released play a larger role in host preference (Buteler and Weaver 2012). More research on the impact of plant volatile cues on WSS host preference is vital to developing more effective trap crop strategies. Buteler et al. (2009) have identified several wheat cultivars which have potential to be excellent trap crops, but more research is needed on WSS preference of these cultivars as well as cultivar semiochemical production in order to use trap crops more effectively in the field.

Plant Resistance. One of the most effective, albeit variable, methods to control WSS is seeding entire fields of solid-stemmed cultivars of wheat rather than limiting this trait to a trap crop (Szczepaniec et al. 2015; Buteler et al. 2015; Bekkerman and Weaver 2018). Wheat stems expressing greater amounts of pith show mechanical resistance against feeding and boring of WSS larvae (Wallace and McNeal 1966). Pith dries early in plant maturity, and probably contributes to desiccation and death of C. cinctus larvae (Holmes and Peterson 1962; Holmes 1960). As the stem matures, the moisture and nitrogen content is reduced much more quickly in the upper internodes. This leads to the downward movement of WSS larvae as the season progresses (Holmes 1960). The amount of light received by the plant drives pith development in the lumen. Narrow row spacing and overcast weather can greatly reduce the amount of pith in the stem, limiting the plant's resistance (Beres et al. 2017; Holmes et al. 1960; Holmes 1984; Holmes and Peterson 1962; Platt 1941; Shanower and Hoelmer 2004).

Morrill et al. (1994) demonstrated that larval tunnels are shorter and fewer nodes are tunneled in solid stems relative to hollow stems. This is significant because node damage greatly decreases plant efficiency in transporting carbohydrates and other materials to the developing kernels, resulting in greater yield loss (Macedo et al. 2005). This claim was also supported by data showing that head weight was significantly less for infested hollow-stemmed varieties when compared to infested stems from solid-stem varieties (Morrill et al. 1994). A multi-decrement life table also showed that solid-stem cultivars may provide around 34% irreplaceable mortality in the presence of other factors (Buteler et al. 2015).

The first solid stemmed cultivar, “Rescue” was released in the late 1940’s, reducing *C. cinctus* infestation by an average of 59% (Platt and Farstad 1946; Platt et al. 1948). Solid-stemmed wheat cultivars were developed with improved milling quality, yield, and disease resistance, however there is still gap in quality between solid and hollow stemmed wheat that makes some producers hesitant to plant solid-stemmed cultivars (McNeal et al. 1959; Luginbill and Knipling 1969; Weiss and Morrill 1992; Beckerman and Weaver 2018). However, Sherman et al. (2015) demonstrate that solid-stem cultivars could have the same potential yield as hollow stemmed cultivars with additional breeding. Yield studies over multiple years and locations showed that differences in the gene *Qss.msub-3BL*, which controls 75% of stem-solidness, were not sufficient to reduce yield. The historically used S-615 allele for stem solidness can also be replaced with the ‘Conan’ allele instead, which only shows intermediate solidity at harvest, yet a high level of resistance that doesn’t necessarily have to limit yield potential (Varella et al. 2016; Sherman et al. 2015; Talbert et al. 2014).

The ‘Conan’ allele at *Qss.msub-3BL* has improved resistance and greater potential yield than the S-615 allele in ‘Rescue’ and other solid-stemmed varieties for several reasons. The first is that the timing of pith development is critical for WSS resistance. Wheat plants containing the ‘Conan’ allele rapidly develop robust pith early in the growing season and have greater pith moisture as well. The advanced timing of stem solidness increases the rate of neonate WSS mortality in contrast to wheat with the S-615 allele (Talbert et al. 2014; Varella et al. 2016). More pith moisture early in development also decreases WSS egg hatch (Holmes and Peterson 1964).

Plants with the 'Conan' allele lose pith moisture at a greater rate than those with the S-615 allele. The timing of this moisture reduction also coincides with the timing of increased larval tunneling. Dry pith has more mechanical resistance to tunneling than moist pith, therefore higher rates of larval mortality are evident in stems with less moisture during this time period (Varella et al. 2016). Stems with the 'Conan' allele are said to have an intermediate level of solidness in relation to stems with the S-615 allele, because solidness was normally evaluated post-anthesis. However, this is probably a benefit because the 'Conan' allele causes rapid pith retraction during stem maturation. This allows the plant to convert resources used in pith maintenance back into seed development at grain fill, thereby increasing the yield potential of these plants over those with the S-615 gene while losing little resistance to WSS (Varella et al. 2016).

<u>Cultural Control</u> Seeding at a higher density around field borders has been recommended to prevent lodging and increase oviposition at the field border relative to the interior (Wallace and McNeal 1966). Higher rates of parasitism have also been observed in densely sown fields of hollow-stemmed wheat (Beres et al. 2011b). However, this practice can have detrimental effects in drought years, and does not adequately manage the WSS population (Wallace and McNeal 1966; Beres et al. 2011b). Solid stemmed cultivars are detrimentally affected by higher seeding density even in years with adequate rainfall. Beres et al. (2011b) found that pith expression and stem diameter decrease at sowing densities over 150 seeds m^{-2}. However, these solid stemmed cultivars have optimal yield and retain enough pith expression at 250 seeds m^{-2}.

Swathing before stem cutting can limit the loss of stems to lodging, but this is not an ideal management practice. An extra field operation is needed, increasing costs for producers. The combine header must be at a low height to pick up swathed grain, which increases wear and tear on equipment in addition to reducing numbers of natural enemies (Nansen et al. 2005; Bekkerman and Weaver 2018). The 5-30% yield reduction due to decreased head weight as a result of stem mining is also not recovered. Swathing does not reduce infestation and has a negligible effect on the survival of WSS. This practice may also lead to increasing WSS infestation in subsequent years due to the destruction of parasitoid cocoons during the swathing and harvesting operations (Holmes and Peterson 1965; Wallace and McNeal 1966; Bekkerman and Weaver 2018).

Swathing is a good strategy for recovering fallen stems in wheat fields with densely distributed WSS populations but should not be the main management tool. It is popular with producers because it enables them to plant hollow-stemmed wheat with higher potential yield, while still recovering stems that would be cut by WSS at harvest. However, this strategy does not reduce WSS losses in the long run. Bekkerman and Weaver (2018) demonstrate that, in a 10-year period beginning with first year cutting at ≥10%, planting hollow-stem cultivars and swathing nets less income per hectare relative to utilizing solid-stem cultivars. In the first three years, this swathing-based strategy will earn the producer more money, however over the 10-year period planting solid-stem cultivars nets ~$56.79/hectare more. Additionally, solid-stemmed wheat fields will average 12% cutting over the 10-year period, corresponding to a 67.25 kg/hectare yield reduction. When planting hollow-stemmed cultivars the cutting rate will be 74% with an associated yield loss of 269.0-403.5 kg/hectare.

Chemical Control. Research has been conducted on the use of insecticides to control WSS, but their life history makes the effective use of insecticides difficult. The continual emergence of adults for up to 6 weeks makes contact insecticides ineffective, because many applications would have to be made in order to reduce the number of eggs laid (Wallace 1962). In addition, adults do not feed on plant tissue rendering insecticides requiring ingestion inoperative. Furthermore, the entire juvenile life cycle is completed within the stem of the wheat plant, making systemic insecticides the only viable option (Wallace 1962; Holmes and Peterson 1963). Wallace (1962) found that an in-furrow application of heptachlor applied at seeding provided control against WSS. However, subsequent research found that this treatment is only effective against relatively lesser WSS populations, and that heptachlor only reached the lower internodes (Wallace and McNeal 1966; Holmes and Peterson 1963). Heptachlor also persists in the environment for long periods and poses a significant human health risk, causing the EPA to ban its use in 1988 (Anonymous 1997).

More recently, the Montana Department of Agriculture has issued a special local need pesticide registration (Section 24(c)) for phorate (Thimet®20-G) an organophosphate soil and systemic insecticide to control WSS larva. Recent data have shown that the use of Thimet®20-G caused 64-100% reduction of stem cutting, and a 363.2 and 410.2 kg/hectare yield increase for spring and winter wheat respectively (Wanner and Tharp 2015; Montana Department of Agriculture 2015). However, due to its high toxicity to fish, birds, and mammals, Thimet®20-G cannot be applied more than once per crop per season, and it must be incorporated into the soil and applied 85 days before harvest (Montana Department of Agriculture 2015). These label requirements, plus an application rate of 5.6 kgha^{-1}, have constrained adoption by Montana wheat producers. Thus, the Section 24(c) registration for the use of granular phorate will probably not be renewed when it ends in 2019.

Biological Control. In addition to host plant resistance, biocontrol from braconid wasp parasitoids is the most promising method of suppression of damaging WSS populations (Holmes et al. 1963). Nine species of parasitoid use larval WSS in feral grasses, but only two, Bracon cephi (Gahan) and B. lissogaster Muesebeck have made the switch to wheat (Nelson and Farstad 1953; Somsen and Luginbill 1956). Both species are protelean host-specific idiobionts with two generations, however the second generation generally has much lower reproductive success (Ainslie 1920; Nelson and Farstad 1953; Somsen and Luginbill 1956).

Criddle (1923) reported that parasitism of larval WSS in uncultivated grasses frequently approached 100%, but parasitism in wheat was usually less than 2%. Parasitoids have become more successful in wheat since then, ranging 15-98% parasitism across the state of Montana (Morrill et al. 1998; Runyon et al. 2002; Weaver et al. 2002; Peterson et al. 2011), however parasitoids have not provided consistent control across the cereal growing regions of the northern Great Plains (Morrill et al. 1998; Weaver et al. 2004, Peterson et al. 2011, Buteler et al. 2015). Although, in areas where parasitoids are present in high numbers, adequate WSS control may be achieved (Morrill et al. 1998; Runyon et al. 2002; Buteler et al. 2008)

Rates of parasitism are greatly enhanced in cool, wet growing seasons, due to the wheat plant remaining green and succulent for a longer period (Holmes et al. 1963). As the plant begins senescence and desiccation at ripening, it becomes difficult for parasitoids to locate and oviposit on mature WSS larvae (Morrill et al. 1998; Shanower and Hoelmer 2004; Holmes et al. 1963). Wheat plants emit parasitoid attracting, volatile, semiochemicals when being fed on by WSS larvae (Perez 2009). Younger plants emit higher levels of these volatiles, making them more noticeable to female parasitoids looking for a host on which to lay eggs. These younger plants may produce more volatiles because they can put more resources toward secondary metabolites, while more mature plants are using their resources for reproduction (Piesik et al. 2006a; 2006b; Peck 2004). In addition to increased amounts of plant volatiles, cool, wet periods soften the wheat stem, making it easier for the parasitoid ovipositor to penetrate the lumen and locate large WSS larvae (Holmes et al. 1963). In fact, parasitism has been seen to increase by 50% shortly after rain showers (Nelson and Farstad 1953).

Parasitism is an invaluable form of WSS suppression for farmers because of the amount of irreplaceable mortality. Because these are native species, they are present throughout the majority of the state, further increasing their value as biological control agents. Peterson et al. (2011) reported that irreplaceable mortality due to parasitism ranges from 22-35%. Buteler et al. (2015) found a slightly lower percentage of parasitism, but this was attributed to much greater WSS infestation. Greater numbers of

WSS infested stems cause parasitoids to become less efficient in host location, and if more than one larva has infested a stem, vulnerable immature parasitoids may be consumed by WSS larvae (Holmes et al. 1963; Weaver et al. 2005; Buteler et al. 2015).

Releasing adult parasitoids to establish or augment the population in fields with heavy infestations increases WSS mortality (Morrill et al. 1998). However, mass rearing these insects is difficult because WSS develop within the wheat stem, which greatly complicates the process of rearing large quantities of parasitoids (Pallipparambil 2006; Rand et al. 2016). However mass production could be more successful with additional research on sequential rearing of these parasitoids under controlled conditions such as an environment chamber or greenhouse (Portman et al. 2018).

There are also cultural practices that can help conserve parasitoids. Runyon et al. (2002) show that adopting no-till management is beneficial to braconid parasitoids because heavy tillage will often kill more parasitoids than WSS. Harvesting with the combine header no lower than 15 cm can also help conserve parasitoids by minimizing their destruction during harvest (Holmes et al. 1963; Meers 2005; Beres et al. 2011a). Delayed seeding or planting late maturing varieties may increase the second-generation success of parasitoids (Holmes et al. 1963). Later crop maturity allows more time for the second generation of parasitoids to locate and parasitize WSS larvae before the stem is too dry and oviposition is more difficult (Morrill and Kushnak 1996). Larval WSS descend into stubs and form hibernacula sooner when the host plant matures rapidly, making it more difficult for the later parasitoids to find hosts for their offspring (Holmes et al. 1963), while a later maturing crop may make this less likely.

Bracon cephi (Gahan) and
Bracon lissogaster Muesebeck

Bracon cephi is an external larval parasitoid which lives on the integument of its host, a WSS larva. Yellow, oblong eggs are laid on or near the host, with only one egg laid per host. Eggs hatch after one to two days, and there are 5 instars in *B. cephi*, with the first three instars being delicate and translucent with measurable head capsules. The later stage larvae have button-like disc heads and are a light, brownish color. The larvae have well-developed, strongly sclerotized mouthparts (Nelson and Farstad 1953).

After hatch, the mobile first instar immediately locates and attaches to the integument of its host, where it begins to feed. When feeding is complete, only the integument of the host is left (Runyon 2001; Nelson and Farstad 1953). Fully grown larvae then spin a cocoon inside of the wheat stem, fastened to the lumen wall with a disc-like plate at each end. This process takes 1-2 days. First generation larval cocoons are usually flimsy and misshapen, as they don't need to survive in them long. Offspring of the first generation are often smaller, with atypical body development. This may be because their host was too small to provide sufficient food to fuel their development. The larval stage lasts around ten days (Nelson and Farstad 1953).

Overwintering individuals stay in their cocoon as fifth instars, and do not pupate until the following spring. *B. cephi* larvae overwinter much higher up the stem than WSS, making them more vulnerable to freezing and cold weather (Holmes et al. 1963). The larvae tolerate colder temperature with large concentration of glycerol in their hemolymph, which lower their supercooling point, as well as allowing them to live if they do freeze (Salt 1959). The main cause of mortality between generations spanning the winter is being destroyed by harvesting equipment (Holmes et al. 1963; Meers 2005) or by tillage on organic fields (Runyon et al. 2002; Adhikari et al. 2018). As temperature and humidity increase in the spring, the larva becomes more active inside its cocoon, becoming a prepupae with a constriction behind the third thoracic segment. Two days later, the larva becomes a delicate, white pupae with pink eyes. This stage generally lasts six days at 25º C and 70% relative humidity (Nelson and Farstad 1953).

It takes a few hours for pupae to transform into adults. Once in the adult stage, *B. cephi* are inactive in the cocoon to allow the cuticle to harden. Usually, the adult escapes the stem by chewing a small, circular exit hole through the cocoon and wheat stem. Sometimes, the adult exits the end of the cocoon into the stem lumen, escaping from the stem at another point. This tactic sometimes results in the parasitoid becoming trapped in the lumen, and it is unable to escape and dies (Nelson and Farstad 1953).

Female parasitoids are usually longer lived than males. Males usually live from 10-14 days, while females can live more than 4 weeks and are often still alive when the second generation emerges. Adult *B. cephi* feed on moisture droplets as well as the nectar of nearby flowers, which probably increases their longevity (Nelson and Farstad 1953). Nelson and Farstad (1953) suggested that females have a preoviposition period of three weeks in the first generation to allow eggs to mature, however Holmes et al. (1963) claims that this period may be less than 12 days.

Female *B. cephi* locate potential hosts from volatile semiochemicals released by the wheat plant (Piesik et al. 2006; Peck 2004). Once the stem is located, the female parasitoid walks up and down the stem, using her antennae to sense vibrations of the feeding WSS larva (Mankin et al. 2000; Mankin et al. 2004). The female inserts her ovipositor when the host is located and stings the larva. The venom injected during the sting paralyses the host larva, and an egg is laid on or near the immobilized larva. Oviposition can last longer than an hour, making it unlikely that females lay more than 4 eggs per day. Adult *B. cephi* do not develop their full complement of eggs at once, instead opting to mature eggs in batches of 6-10 (Nelson and Farstad 1953; Reis 2018). There are generally two generations of *B. cephi* each season, but the second is often incomplete. Completion of the second generation depends on the length of the growing season as well as how late into the season the first generation continued to oviposit (Holmes et al. 1963).

The biology of *Bracon lissogaster* Muesebeck is very similar to that of *B. cephi*. One key difference however is that *B. lissogaster* can be gregarious. Somsen and Luginbill (1956) recorded as many as four larvae on a single WSS host. The method of oviposition also differs, with the female locating the host larva and stinging it multiple times with a pumping motion. After the venom is injected, the female lays 1 to 4 sticky eggs that will adhere to the immature host if it is still moving slightly. The eggs require approximately two and a half days to hatch and the early instars do not have sclerotized mouthparts. *B. lissogaster* adults are slightly shorter lived than *B. cephi*, living a maximum of 35 days in the lab on a diet of sugar water (Somsen and Luginbill 1956; Reis 2018).

Impact of Body Size on Parasitoid Fitness

Body size is often very important to individual parasitoids (Godfray 1994) and can affect everything from physiological processes such as metabolism, to fitness traits such as mate selection and fecundity (Shine 1988; Honek 1993; Godfray 1994; Blanckenhorn 2000; Blanckenhorn and Demont 2004; Roff 1980). Larger bodied organisms have smaller surface area to volume ratios as well, boasting a better ability to conserve heat in colder climates such as the northern Great Plains where unseasonal freezes and periods of colder than average weather are not uncommon (Lamb 1992). Extra food resources such as larger hosts or nectar from nearby flowering plants can increase fat reserves in parasitoids, thereby increasing longevity and fecundity (Salt 1941; Landis et al. 2000; Gurr et al. 2017; Reis 2018).

Locations at greater altitudes and latitudes have shorter seasons with less time to forage, grow, and develop, resulting in smaller body size (Blanckenhorn and Demont 2004). However, *B. cephi and B. lissogaster* are multivoltine species with much shorter generation turnaround enabling them to grow more quickly, despite the constraints of a short season. The short generation time of multivoltine species gives an advantage over species with only one generation in areas with short growing seasons because it allows for more rapid population growth in a short amount of time (Roff 1980; Rowe and Ludwig 1991). Body size which increases with available growth time within a single species, and reproductive success, are closely tied (Godfray 1994). In addition, the probability of survival to adulthood increases when time to maturity decreases. Balancing body size with time to maturity is imperative to species in areas with short growing seasons such as the northern Great Plains (Chown and Gaston 1999; 2010; Blanckenhorn and Demont 2004).

The size of adult parasitoids is driven by the quality of the host an individual was reared on (Nicol and Mackauer 2003). Host choice and, for *B. lissogaster*, clutch size by the ovipositing parent have large impacts on the size and fitness of an individual (Godfray 1994). Longevity, egg reserves, and host searching efficiency are all positively correlated with body size (West et al. 1996; Visser 1994). In addition, Salt (1941) found that larger body size helps females oviposit on hosts that have a protective covering. Overall, parasitoid female fitness increases with adult size (Godfray 1994; Visser 1994).

Charnov's theory of conditional sex allocation is an important factor in female parasitoid fitness. The theory states that parasitoid wasps oviposit male eggs in relatively small hosts, and female eggs into larger hosts (Charnov 1979; Charnov et al. 1981) because the female larvae require more resources to develop and are more important to reproduction. Larval resources of parasitoids are restricted, and strongly influenced by the size and quality of their host, especially in solitary parasitoids. It has been shown in laboratory experiments that female parasitoids receive a larger benefit than males from increased body size (van den Assem et al. 1989; Heinz 1991; Harvey et al. 1994). Larger females lay more eggs, and more body mass also allows parasitoids to live longer, increasing their overall reproductive success (King 1987; Godfray 1994; Visser 1994; Ellers et al. 1998). In addition, increased body size leads to increased fat reserves. Fat is used for body maintenance, as a flight energy source, and as fuel for oogenesis (Ellers et al. 1998; Ellers and van Alphen 1997; Ellers 1996; Cockbain 1961; Beenakkers 1969;

King and Richards 1969). In general, larger female parasitoids should be more effective as biological control agents of WSS.

Importance of Biodiversity to Biological Control

Recent trends in world agriculture have been resulting in expansion of field size and an increase in monocultures (Key 2018; Rada and Fuglie 2018). The simplification of agricultural landscape, loss of natural habitats, and increase in agrochemical inputs has led to a sharp decrease of biodiversity within these agroecosystems (Bianchi et al. 2006; Robinson and Sutherland 2002; Benton et al. 2003; Landis 2017; Gurr et al. 2016). Within field intensification of management (i.e. increased inputs and simplified crop rotations) has also led to a decrease in biodiversity in agro-ecosystems (Benton et al. 2003; Concepción et al. 2008). Biodiversity has been linked with natural pest control, and farmers have lost many sources of beneficial insects by reducing plant diversity within their agroecosystems (Ives et al. 2000; Wilby and Thomas 2002; Bianchi et al. 2006; Gurr et al. 2003). Multiple studies have also shown that herbivorous pests are often better controlled by diverse predator and parasitoid communities (Landis 2017; Quispe et al. 2017; Gurr 2016; Cardinale et al. 2003; Losey and Denno 1998). Snyder and Ives (2003) found that more complex communities of predators and parasitoids provide better control of pea aphids and Schmidt et al. (2003) have shown that cereal aphids are better controlled when both ground-dwelling and flying predators are feeding on them.

Montana farms have historically used a wheat-fallow cropping system. In the last couple of decades, farmers have begun to switch to more diverse systems, which utilize pulse and cover crops in their rotation. While the trend in worldwide agriculture is cropland simplification, the trend in Montana has actually been adding diversity (Long et al. 2014a; b). In 2017, Montana became the nation's leading producer of pulse crops with 1,535,905 acres seeded. This was a 256% increase since 2013, another landmark year in which Montana became the nation's top producer of peas (Montana Department of Agriculture 2018). Most of these extra pulse crop acres replaced fields that would have otherwise been fallow, increasing landscape cover and complexity (Long et al. 2014a; b). This shift in cropping systems may have a beneficial effect on WSS biological control, as natural enemies tend to be more susceptible to the negative effects of low habitat diversity than herbivores (Rand and Tscharntke 2007; Perović 2018). Another shift in Montana cropping systems that may have a beneficial effect on WSS management is the transition from continuous wheat-fallow strip cropping to block managed wheat-fallow or wheat-pulse rotations (Fig. 1). Wheat stem sawfly infestation has a very distinct edge effect and this management change greatly reduces the edge area of fields (Criddle 1922; Holmes 1982; Weiss and Morrill 1992; Long et al. 2014a; b).

MT agricultural production 2001-

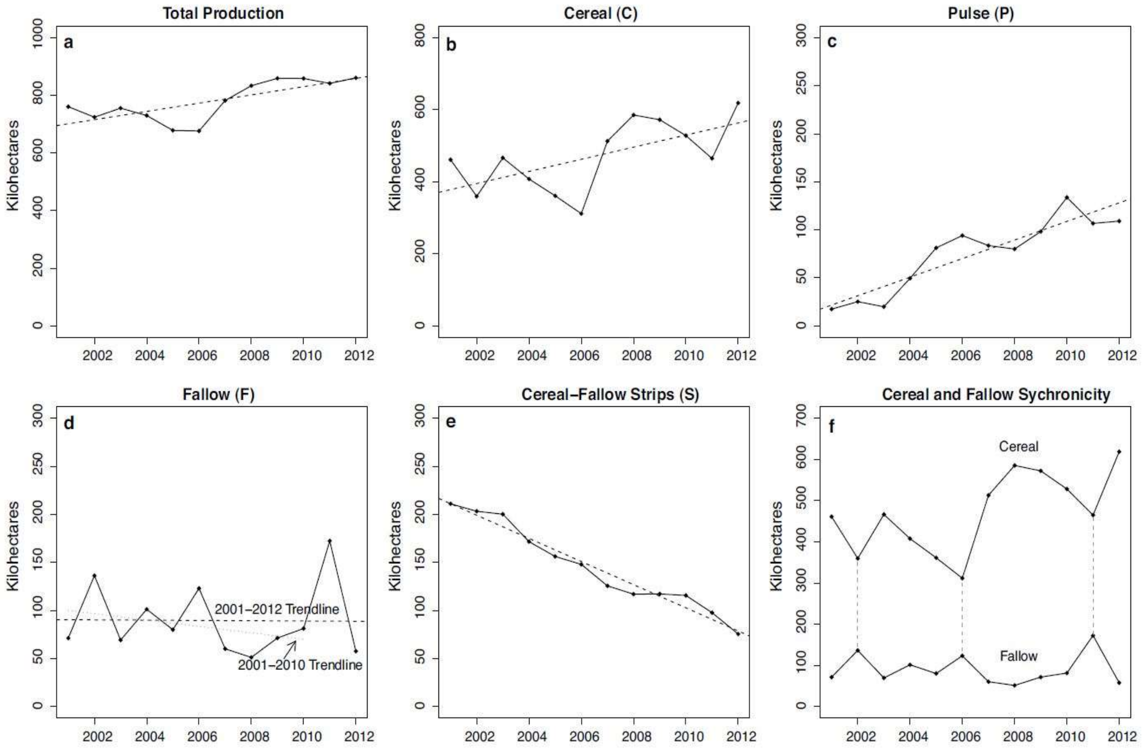


Figure 1: Kilohectares of a) total agricultural production, b) cereals, c) pulses, d) fallow, e) strip cropping, and f) cereal and fallow synchronicity in Montana from 2001-2012. The sharp decline in cereal acres (b) and increase in fallow acres (d) in 2011 was due to an exceptionally wet spring which made some fields impossible to plant. (adapted from Long et al. 2014a).

Crop plants are generally more desirable to herbivorous pests than non-cultivated plants, which cause herbivores to congregate in the crop (Root 1973). Low diversity plant communities generally give an advantage to feeding specialist herbivores, which tend to perform better in highly disturbed environments (Gurr et al. 2017). In contrast, natural enemy populations tend to be disrupted by disturbance events such as insecticide applications and tillage, forcing these populations to keep recolonizing crop fields from source populations in a less disturbed area. If there are no source populations close enough to recolonize the field, then disturbance events can eradicate natural enemies from the field (Root 1973; Wissenger 1997; Tscharntke et al. 2012; 2016; Letourneau et al. 2012; McCabe et al. 2017; Wilson et al. 2017; Perović et al. 2018).

Diversity at the first trophic level also benefits natural enemies, providing shelter, nectar, alternate prey, and pollen, which would assist natural enemies in surviving the frequent disturbances in agroecosystems (Gurr et al. 2017). Indeed, Adhikari et al. (2018) found that the rate of parasitism of WSS in organic winter wheat was higher than in conventional winter wheat, leading to a significant reduction in infestation and cutting. This was attributed to greater crop diversity and weed abundance within the organic cropping systems.

Non-crop habitat gives natural enemies a place to escape disturbance events such as insecticide applications, tillage, or harvest (Landis et al. 2000; Chakraborty et al. 2017; Gurr et al. 2017). Negative effects of these events on natural enemies will be reduced if they can simply leave the field and return when it is safe for them. Alternate habitat also may provide natural enemies with alternative prey for subsistence if they successfully eliminate crop pests, or when pest numbers are low such as after insecticide treatment (Chakraborty et al. 2017; Gurr et al. 2017; Landis et al. 2000; Adhikari et al. 2018). However, this is not the case for the two braconid parasitoids of WSS, *B. cephi and B. lissogaster*. They are specialist parasitoids and cannot use any hosts other than larval WSS. Pulses and most species grown in cover crops are not hosts of WSS, the parasitoids' main food source, so increased acreage of these crops in the landscape will not provide alternative prey, and probably will directly reduce the amount of prey available.

Although they reduce host availability, increases in the acreage of flowering pulse crops, as well as the slow adoption of cover crops increase parasitoid access to the ephemeral nutritive resource of plant nectar. In addition, increased plant biodiversity within the system may also provide additional shelter, protection, and food resources for the parasitoids (Landis et al. 2000; Gurr et al. 2017; Perović et al. 2018; Adhikari et al. 2018). In general, it is recognized that spatial surroundings of habitat patches can have a large effect on local diversity and abundance of organisms (Clough et al. 2005). As acreage of flowering pulse and cover crops increases, parasitoids will have shorter distances to travel between hosts and floral resources, facilitating more efficient biological control (Wäckers 2008; Perović et al. 2018). Laboratory experiments performed by Wäckers (1994) showed that starved wasps had reduced flight activity relative to satiated wasps, so greater amounts of floral resources on the landscape may increase the time parasitoids are able to search for hosts. While decreased amounts of grass hosts in the landscape may reduce the amount of available prey for parasitoids, the influx of extra floral resources may increase the efficiency of these parasitoids in suppressing WSS. Improving habitat for better biological control of WSS by parasitoids is of paramount importance to wheat production in Montana. Due to the life history of WSS, generalist predators do not often prey upon them, making specialist parasitoids their most effective enemy.

Benefits of Floral Resources to Adult Parasitoids

Predators and parasitoids often benefit from non-host food sources such as pollen, nectar and honeydew (Balzan and Wäckers 2013; Jamont et al. 2013; Géneau et al. 2013; Landis et al. 2000). Non-crop habitats often have alternative sources of food such as nectar and pollen. Increasing the amount of this habitat near agricultural lands may benefit parasitoid populations (Maier 1981; Bianchi et al. 2006) through increased longevity and fecundity (Baggen and Gurr 1998; Siekmann et al. 2001; Wäckers 2001; Costamagna and Landis 2004; Lee et al. 2004; Gurr et al. 2017; Portman et al. 2018), as well as a higher ratio of female parasitoids (Gurr et al. 2017). Increased rates of egg maturation have also been noted in parasitoids with access to floral resources (Coombs 1997; Leius 1961; Schmale et al. 2001; Syme 1975). In addition, parasitoids have been found to be more active in areas with blooming flowers than in nearby areas without flowers (Van Emden 1962; McCabe et al. 2017; Quispe et al. 2017). Parasitoids use these non-crop resources, then spread into nearby crop fields and provide pest control (Tylianakis et al. 2004; Bianchi et al. 2006).

However, not all flowers give the same benefit to natural enemies. Parasitoid morphology, floral architecture, flower color, floral area, flowering time, and nectar chemistry all impact how much, if at all, natural enemies will benefit from additional flowers on the landscape (Landis et al. 2000; Gurr et al. 2017; McCabe et al. 2017). Plants that have extrafloral nectaries can be even more beneficial than those with flowers only. While flowers are an ephemeral source of nectar, extrafloral nectaries provide nectar over a longer period (Quispe et al. 2017). Natural enemies are also more likely to access extrafloral nectar than nectar from deep, or narrow flowers. Quispe et al. (2017) found that refuge plants with extrafloral nectaries attracted more predators and parasitoids than other refuges next to maize crops. Herbivorous insects may also benefit from non-crop resources, so producers must be aware of the composition of flora in their system and any associated risks (Baggen et al. 1999; Wäckers 2004; McCabe et al. 2017; Perez-Alvarez et al. 2018).

The flowering pulse and cover crops work differently in the Montana wheat-fallow agroecosystem that favors WSS than a typical field border or flower strip deployed in crop fields, which aim to benefit generalist predators. One of the benefits of increased plant diversity in most agroecosystems is the addition of alternate prey for natural enemies to survive on when pest populations are low. But, the two species of specialist braconid parasitoids can only utilize WSS as a host, so alternative prey is not a factor in this system. The effect of adjacent pulse and cover crops that this research is most focused on is the addition of nectar and pollen into the system. Nectar is scarce in the wheat-fallow cropping system, as flowers are restricted to non-crop habitat and are rare even in these areas. The addition of flowering pulse and cover crops could greatly increase the amount of nutrients available to adult parasitoids.

While pulse and cover crops will hopefully benefit populations of braconids, another benefit is the presence of more non-host plants on the landscape for WSS. This has potential to disrupt WSS populations through increased fragmentation of their habitat, making it more difficult to locate hosts for oviposition, while also benefitting natural enemies through nectar provisioning and additional shelter. Increased areas of these pulse and cover crops on the landscape will increase fragmentation or the dominant wheat-fallow areas and reduce the distance parasitoids must travel between foraging for nectar and searching for WSS larval hosts by adding more foraging locations on the landscape. Wheat drives this agroecosystem, and the objective of this study is to measure the indirect effects of the addition of flowering forb species to the environment on WSS and its natural enemies.

Habitat Fragmentation and Complexity

Crop rotation has been shown to increase yield and reduce pest pressure within agroecosystems (Bullock 1992; Miller et al. 2002; Kirkegaard et al. 2008). These effects can be particularly pronounced when the main insect pest, like WSS, is highly specialized with a low dispersal ability (Flint and Roberts 1988). Crop rotations increase diversity as well as the distance insect pests must travel to locate host crops. Increasing the distance insect herbivores must search lessens energy reserves and survival rate of the insects once they locate the crop (Vankosky et al. 2017).

Indeed, Banks (1998) found that herbivores with low dispersal ability have difficulty locating and reaching host plants in highly fragmented habitats. However, the effects of increased crop diversity may also impact the parasitoids of WSS. Reducing host availability for WSS will indirectly reduce host availability for their braconid parasitoids. Feral and natural grass populations may help conserve parasitoid populations with increasing crop diversity by providing hosts for small populations of WSS (Gurr et al. 2017). More species of hymenoptera parasitize WSS in feral and native grasses, and *B.*

cephi and *B. lissogaster* are more successful in these grasses than in cultivated crops (Shanower and Hoelmer 2004).

The cropping systems within the wheat growing regions of Montana have been diversifying in recent years. However, instead of reducing wheat on the landscape, the acres being replaced by pulse crops have primarily been fallow (Long et al. 2014a; b). A reduction in fallow acres surrounding wheat may also reduce WSS populations through a decrease in host apparency. The specialist aphid *Therioaphis trifolii* (Monell) with low-dispersal ability was found at very high densities on red clover (*Trifolium pretense* L.) surrounded by bare ground (Haynes and Crist 2009). The authors posited that the aphids' reluctance to move over bare ground may have played a part, but the relatively high dispersing clover leaf hopper (*Ceratagallia agricola* Hamilton) was also present at much higher densities in clover surrounded by bare ground than when surrounded by alternate vegetation (Schroeder 2007).

Prokelisia crocea (van Duzee) is a planthopper that is monophagous to prairie cordgrass (*Spartina pectinata* Bosc). Patches of cordgrass surrounded by mudflats have much higher densities of *P. crocea* than patches surrounded by smooth brome (Cronin 2007; Reeve et al. 2008). The absence of vegetation around these host patches may make them more apparent to herbivores. Herbivorous insects with low dispersal ability, such as WSS, are greatly affected by habitat fragmentation (Banks 1998). An increase in the acreage of non-host crops in Montana should result in a reduction of WSS populations by decreasing host availability, increasing search distance, and reducing host apparency.

Using Pheromone Traps to Estimate Larval Density

Pheromone trapping is an oft used tool for monitoring pest populations in agriculture (Riedl and Croft 1974; McNeil 1991) and forestry (Shepherd et al. 1985; Ramaswamy et al. 2012). Weslien et al. (1989) found strong correlations between trap capture of adult spruce bark beetles (*Ips typographus* (L.)) and tree damage and mortality caused by larval beetles. Additionally, Silvain and Ti-A-Hing (1985) found extremely strong correlations between adults captured in pheromone traps and relative larval abundance of fall armyworm (*Spodoptera frugiperda*) in pasture grasses. Pheromone traps may be able to be used in a similar fashion to monitor WSS outbreaks at a field level. 9-acetyloxynonanal is a promising semiochemical attractant for trapping adult WSS, however no field studies have been performed to evaluate the ability of these traps to estimate subsequent larval infestation (Bartelt et al. 2001; Cossé et al. 2002). We will attempt to correlate trap capture data to stem dissections of postharvest crop residue to evaluate the efficacy of field trapping for surveying WSS and braconid parasitoid populations.

Research Objectives

Bracon cephi and *B. lissogaster* are effective natural enemies of WSS populations. Practices that can improve the ability of these parasitoids to suppress WSS populations are of paramount importance to wheat farmers in the northern Great Plains. Therefore, the main objective of this research was to observe whether pulse or cover crops grown adjacent to wheat provide any benefits to the populations of these two specialist braconid species. This may be through increases in adult longevity, fecundity, or by increased access to hosts for their offspring, made possible through the increased nutrition provided by the floral or extrafloral nectar of pulse or cover crops. The populations of WSS and these braconid parasitoids found in paired wheat fields grown next to fallow and grown next to pulse or cover crop were compared. Field pairs were managed similarly to those in Runyon et al. (2002) to control for climatic differences. Differences in wheat cultivar and management were minimized between paired fields. Size and relative abundance of WSS and braconid populations were evaluated for each field comparison in an attempt to answer key research questions.

1. Do wheat fields adjacent to pulse or cover crops have more abundant WSS parasitoids compared to wheat fields grown adjacent to fallow wheat?
2. Do WSS parasitoids emerging from wheat that was grown next to flowering pulse or cover crops have increased body size compared to WSS parasitoids emerging from wheat that was grown next to fallow wheat?
3. Can trap capture reflect actual larval WSS and parasitoid abundance in the field?
4. Do different compositions of land cover types around wheat fields influence WSS and parasitoid populations?

Several recent studies have used paired fields to understand and characterize the effects of landscape management on farmland biodiversity. These studies have primarily focused on two land management strategies in paired fields (Concepción et al. 2008; Kishinevsky et al. 2017; Kleijn et al. 2006) or examined the effect of a landscape heterogeneity gradient on paired fields with different management schemes (Concepción et al. 2008; Clough et al. 2005; Holzschuh et al. 2007; Kleijn et al. 2004; Puech et al. 2015; Schmidt et al. 2005; Wilson et al. 2017).

Kishinevsky et al. (2017) used paired pomegranate orchards to study the effects of planting companion plants on natural enemy populations. Each pair of orchards had one with the companion plants and one without. Concepción et al. (2008) used field pairs to study the effects of agroenvironmental schemes on the diversity and abundance of vascular plants, birds, bees, spiders, grasshoppers, and crickets at both local and landscape levels. Seven field pairs were selected in each of three agricultural regions in Spain. Within each pair, one field had had an agroenvironmental schemes implemented for at least 5 years and the other had been conventionally managed. Differences between field pairs were analyzed to discern the effect of agroenvironmental schemes at a local level. Additionally, the landscape diversity within each of the three regions was added to the analysis to provide insight on the effect of agroenvironmental schemes at different levels of landscape diversity.

The best way to measure the effects of natural enemy conservation management strategies would be to survey identical field pairs with and without the application of the management strategy in question (Head et al. 2005; Kleijn et al. 2006; Concepción et al. 2008; Kishinevsky et al 2017). However, comparisons of fields with and without conservation measures can have many confounding variables. Therefore, all variables other than the conservation or land management strategy must be as consistent as possible between fields. This includes factors such as landscape heterogeneity

(Concepción et al. 2008), regional species pools, and land-use history (Kleijn and Sutherland 2003); as well as agricultural inputs and abiotic factors (Head et al. 2005). Thus, as study area increases, so does environmental heterogeneity which makes separation of effects of confounding variables difficult to distinguish from the effects of the conservation measure (Holzschuh et al. 2007; Kleijn et al. 2004; Kleijn et al. 2006). However, Adhikari et al. (2018) have conducted a study in Montana using paired wheat fields assessing the difference between WSS and braconid parasitoid populations in neighboring conventional and organic fields. Obviously, these fields are not managed in the same manner, but they controlled for differences in climate, local insect species pools, and land-use history by having paired fields close together. Runyon et al. (2002) studied the effect of tillage on WSS and parasitoid survival by looking at matched field pairs which were managed identically except for the difference in tillage. This study used similar methods to discern the effects of crop and landscape diversity on populations of WSS and their parasitoids. Using paired fields, differences in insect population, management, climate, and abiotic factors can be reasonably controlled.

MATERIALS AND METHODS

Sites

Sites were chosen throughout the main wheat growing regions of Montana (Fig. 2). Each site had a pair of wheat fields, one next to fallow and one next to either a pulse or cover crop. Both wheat fields were managed similarly by the producer and were as close as possible to reduce confounding factors. There were 5 wheat next to cover crop or fallow comparisons and 5 wheat next to pulse or fallow comparisons (Table 2, 3). All wheat fields were farmed under dryland conditions except for the wheat field next to fallow at the Conrad 3 site in 2017, which was irrigated.

Table 2: Site descriptions for wheat fields next to fallow. WW=winter wheat, SW=spring wheat.

Site	County	Wheat Variety	Seeding Date	Herbicides
Moccasin 2016	Judith Basin	Wolf WW	Oct. 20, 2015	Carnivore, Class Act, Interlock
Moccasin 2017	Judith Basin	Wolf WW	Oct. 25, 2016	Carnivore, Class Act, Interlock
Conrad 3 2016	Pondera	Corbin SW	May 3, 2016	2-4D
Conrad 3 2017	Pondera	Warhorse WW	Sep. 15, 2016	2-4D
Dutton 2016	Pondera	Keldin WW	Sep. 11, 2015	Class Act, RT3, Edition Tank Mix, Olympus, Preference
Dutton 2017	Teton	Keldin WW	Sep. 13, 2016	Edition Tank Mix, Olympus, Preference, Class Act
Conrad 4 2016	Pondera	Warhorse WW	Sep. 14, 2015	Goldsky, LV6, Ally
Conrad 4 2017	Pondera	Warhorse WW	Sep. 12, 2016	2-4D, Goldsky, Ally
Brady 2016	Pondera	Judee WW	Sep. 15, 2015	Goldsky, 2-4D, Ally
Brady 2017	Pondera	Judee WW	Sep. 18, 2016	Goldsky, 2-4D, Ally
Conrad 1 2016	Pondera	Judee WW	Sep. 20, 2015	Ally
Conrad 1 2017	Pondera	Judee WW	Sep. 17, 2016	Powerflex
Conrad 2 2016	Pondera	Judee WW	Sep. 26, 2015	Huskie
Conrad 2 2017	Pondera	Judee WW	Sep 28, 2016	Huskie

Table 2 Continued

Joplin 2016	Continued Liberty	Corbin SW	Apr. 22, 2016	Glyphosate, Bromac Advanced
Joplin 2017	Liberty	Vida SW	May 4, 2017	Glyphosate, Bromac Advanced
Box Elder 2016	Hill	Judee WW	Sep. 12, 2015	Bronate, 2-4D
Box Elder 2017	Hill	Judee WW	Sep. 18, 2016	Bronate, 2-4D
Chester 2016	Liberty	Vida SW	Apr. 20, 2016	2-4D
Chester 2017	Liberty	Vida SW	May 1, 2017	2-4D

Table 3: Site description information for wheat fields next to pulse or cover crops. WW= winter wheat, SW= spring wheat, D= Durum Wheat.

Site	County	Wheat Variety	Seeding Date	Herbicides	Pulse or Cover Crop Mix	Seeding Date
Moccasin 2016	Judith Basin	Wolf WW	Oct. 20, 2015	Carnivore, Class Act, Interlock	Peas, Triticale, Collards, Radish, Sorghum, Pearl Millet, Buckwheat	Apr. 26, 2016
Moccasin 2017	Judith Basin	Wolf WW	Oct. 25, 2016	Carnivore, Class Act, Interlock	Peas, Collards, Radish, Sorghum, Pearl Millet, Buckwheat	May 26, 2017
Conrad 3 2016	Pondera	Corbin SW	May 3, 2016	2-4D	Lentils	May 2, 2016
Conrad 3 2017	Pondera	Warhorse WW	Sep. 15, 2016	2-4D	Hyline Pea	Apr. 28, 2017
Dutton 2016	Pondera	Keldin WW	Sep. 11, 2015	Class Act, RT3, Edition Tank Mix, Olympus, Preference	CDC Greenland	Apr. 5, 2016
Dutton 2017	Teton	Keldin WW	Sep. 13, 2016	Edition Tank Mix, Olympus,	Sawyers	Apr. 9, 2017

Table 3 Continued

				Preference, Class Act		
Conrad 4 2016	Pondera	Warhorse WW	Sep. 14, 2015	Goldsky, LV6, Ally	Canola, Camelina, Flax, Oats, Radish, Daikon, Safflower, Purple Top Turnip	Apr. 6, 2016
Conrad 4 2017	Pondera	Warhorse WW	Sep. 12, 2016	2-4D, Goldsky, Ally	Canola, Camelina, Flax, Oats, Radish, Daikon, Safflower, Purple Top Turnip, Sunflower	Apr. 10, 2017
Brady 2016	Pondera	Alzada D	Apr. 18, 2016	Goldsky, 2-4D, Ally	Camelina, Flax, Oats, Forage Pea, Purple Top Turnip	Apr. 13, 2016
Brady 2017	Pondera	Judee WW	Sep. 15, 2016	Goldsky, 2-4D, Ally	Camelina, Flax, Oat, Forage Pea, Purple Top Turnip	May 5, 2017
Conrad 1 2016	Pondera	Corbin SW	Apr. 22, 2016	2-4D	Oat, VNS Common Vetch, Clover, Flax,	May 4, 2016

Table 3 Continued

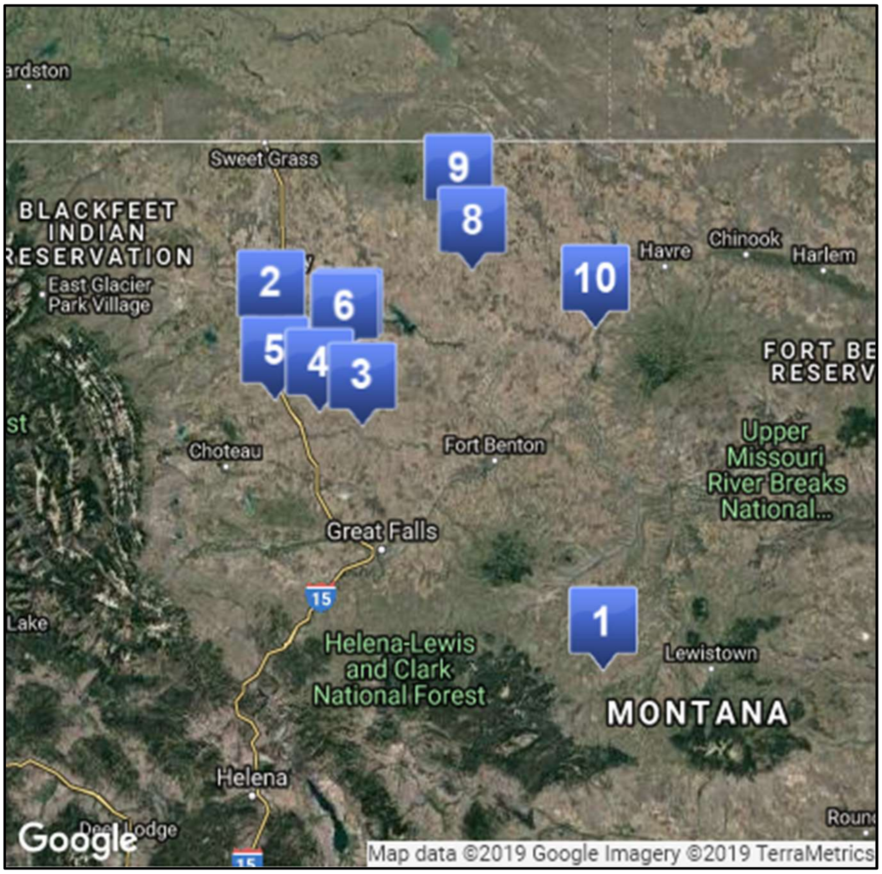
					Lupin, Forage Pea	
Conrad 1 2017	Pondera	Judee WW	Sep. 17, 2016	Powerflex	Oat, VNS Common Vetch, Clover, Flax, Lupin, Forage Pea	May 2, 2017
Conrad 2 2016	Pondera	Judee WW	Sep. 26, 2015	Huskie	Flax, Tillage Radish, Oats, Feed Barley, Turnip, Rye	May 20, 2016
Conrad 2 2017	Pondera	Judee WW	Sep. 28, 2016	Huskie	Flax, Tillage Radish, Oats, Feed Barley, Turnip, Rye	May 17, 2017
Joplin 2016	Liberty	Corbin SW	Apr. 19, 2016	Glyphosate, Bromac Advanced	Yellow Peas	Apr. 21, 2016
Joplin 2017	Liberty	Vida SW	May 3, 2017	Glyphosate, Dicamba, 2-4D	Yellow Peas	May 2, 2017
Box Elder 2016	Hill	Judee WW	Sep. 12, 2015	Bronate, 2-4D	Hampton	Apr. 10, 2016
Box Elder 2017	Hill	Judee WW	Sep. 18, 2016	Bronate, 2-4D	Hampton	Apr. 5, 2017

Table 3 Continued

Chester 2016	Liberty	Vida SW	Apr. 20, 2016	2-4D	CDC Richlea	Apr. 3, 2016
Chester 2017	Liberty	Vida SW	May 1, 2017	2-4D	CDC Richlea	Apr. 21, 2017

Emergence Barrels

Emergence barrels were used to evaluate the parasitoid and WSS abundance of each field. The first year, post-harvest stubble samples were collected from each field in May of 2016, as soon as fields had dried enough to allow access. Post-harvest stubble samples for the second year were collected in September 2016 and placed in cold storage for the duration of winter. Twenty-five 30 cm samples of stubble were collected from each field for the emergence barrel experiments. The 30 cm stubble samples were taken while walking a large "W" pattern through the first 20 m of wheat from the field edge (Fig. 3).



Site Locations:
1: Moccasin
2: Conrad 3
3: Dutton
4: Conrad 4
5: Brady
6: Conrad 1
7: Conrad 2
8: Joplin
9: Chester
10: Box Elder

Figure 3: Site locations. The marker for Site 7 is behind Site 6.

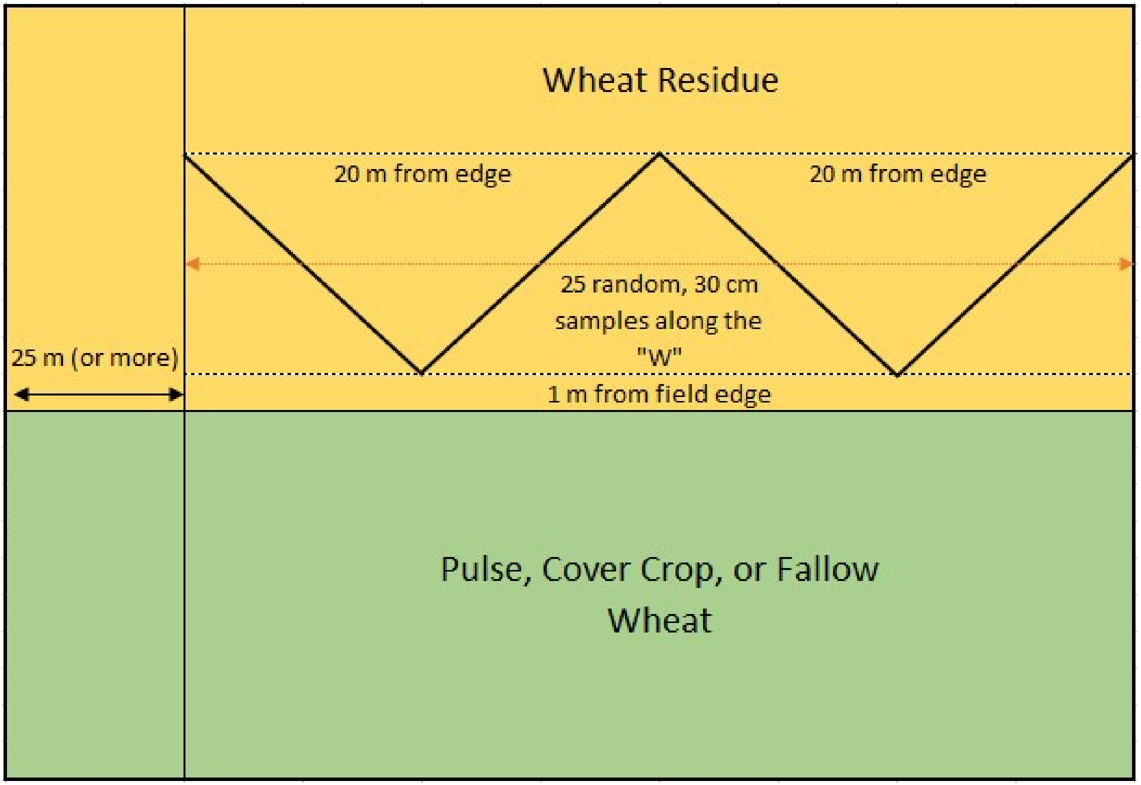


Figure 4: Sampling schematic for crop residue collected for use in wheat stem sawfly and parasitoid emergence barrels and postharvest stem samples.

Emergence barrels were constructed using 57 x 86 cm 208-liter plastic barrel liners (Uline, Pleasant Prairie, WI, S-12589) with a cylinder of wire fencing (15-cm squares) inside for structure. The 7.5 m of stubble were placed inside the barrel and a lid was fastened to the top with caulk. The lid was made of two pieces of poster board taped together and cut to the width of the barrel liner opening (58 cm). An 8.5 cm diameter circle was cut out of the lid and a plastic jar cap, also with a hole cut out, was caulked, top down, over the opening. A cone was made by folding a plastic sheet into a cone and stapling it together. A string was taped to the cone and hung through the barrel opening to assist insects in getting out of the barrel. Wheat stem sawfly are not strong fliers, so the string helps insects reach the jar. Finally, an 11 cm plastic jar (Uline, Pleasant Prairie, WI, S-9937) was screwed in to the lid to capture any emerging insects from within the barrel. Contractor bags. (208-liter) covered the entire barrel other than the jar to block light from entering anywhere except the opening in the barrel lid.

Once the barrels were constructed, the 7.5 m of wheat stubble was placed in the container and sprayed with approximately 4.8 ml of water to increase humidity and facilitate insect emergence. Insects began to emerge around 3 weeks after removal from the soil or cold storage. Once emerged the insects sensed the light coming from the top of the barrel and flew towards it. After they passed through the plastic cone around the jar lid, insects became trapped in the jar.

Barrels were checked daily, and insects from each barrel were collected in a 50 ml centrifuge tube (Falcon™, Syringa Lab Supplies, Boise, ID). Centrifuge tubes were then placed in a -30° C freezer overnight to kill the insects. Wheat stem sawfly were sexed and counted then put in 1.5 ml safe-lock tubes with 95% ethanol. Parasitoids were sexed, weighed on a microbalance (Explorer, Ohaus, Parsippany, NJ), and the hind tibia was measured using a digital micrometer (Digital Micrometer H-2780, Mitutoyo®, Kawasaki, Japan).

Postharvest Samples

Postharvest abundance of WSS and parasitoids was evaluated by collecting crop residue from each field and splitting the stems in the lab. The samples were collected in September, shortly after harvest of the crop. Crop residue collection was done using the same procedure as for emergence barrels (Fig. 3). Samples were placed in cold storage the same day they were collected. The samples were processed by splitting each stem or stem fragment with an X-ACTO (High Point, NC) knife with a #4 blade and recording whether WSS or parasitoid cocoons were present in the stem. Other factors such as stem solidness, cutting, WSS larval tunneling, presence of fungal hyphae, and parasitoid exit holes were also recorded. Cocoons and hibernacula were also saved in covered petri dishes and stored at -30º C.

Field Trapping

Yellow sticky cards (Rebell Yellow Trap, Great Lakes IPM, Vestaburg, MI) were used to capture WSS and braconid parasitoid adults throughout the growing season. Yellow sticky cards were clamped to 0.6 m sections of 2 cm rebar with two #4 Bulldog clips (X-ACTO, High Point, NC), and coated in Tangle-Trap® (Grand Rapids, MI). Two traps per site in 2016 and 4 traps per site in 2017 used pheromone bubble lures (ChemTica International, Santo Domingo, Costa Rica) with 9-acetyloxynonanal to attract WSS. The remaining traps were unbaited to provide a control to compare the baited traps to. The yellow sticky cards were fastened to the rebar 25 cm above the ground in order to intercept flying insects as they traveled into the wheat canopy.

2016

During the 2016 field season, there were 10 traps placed along the wheat fields bordering pulse or cover crops and 6 traps along the wheat fields next to fallow. Traps were put out to coincide with WSS and parasitoid emergence (13-17 June). The first trap was placed a minimum of 75 m from the field edge for both field types. After the first trap, the remaining traps were placed every 25 m along the field border. A WSS pheromone lure was placed on the traps on either end of the trap line, and these two traps were both placed 1 m into the wheat crop. The remaining 8 traps were randomly assigned to 1 m inside the wheat crop or 1 m inside the pulse or cover crop.

Six traps were placed in the border between wheat and fallow fields. The two traps on either end of the trap line were fitted with a WSS lure and placed 1 m into the wheat field. Two traps were randomly assigned to be 1 m into the fallow and two were 1 m into the wheat crop. The traps were spaced every 25 m. Wheat stem sawfly lures were replaced every other week, and the traps were checked weekly. The number of WSS and parasitoids were recorded for each trap and the insects were removed from the trap surface. Traps were replaced every 2-3 weeks as the Tangle-Trap® lost effectiveness.

2017

In 2017, a similar design was used with a few changes. Both wheat bordering fallow and wheat bordering pulse or cover crop fields received 8 traps, and all traps were placed 1 m into the wheat because of low trap capture outside of wheat the previous season. A WSS lure was placed on each odd numbered trap in both field types. Insects caught in the traps were counted and WSS lures were changed each week. The traps were replaced when the Tangle-Trap® began to lose efficacy. If large numbers of WSS or parasitoids were captured, the sticky cards were replaced, wrapped in wax paper to preserve sample integrity, and brought back to the lab where insects were removed and counted.

Figure 5: Example of a trap in the field

Land-Use Data

The land surrounding each research site was categorized and analyzed to determine the effects of alternate habitat on WSS and parasitoid populations. The Cropland Data Layers for these areas in 2016 and 2017 were downloaded from CropScape© (2018). Crop diversity and amount of cropland vs non-crop land were analyzed within concentric circles of 0.5, 1, 2, 3, and 4 km radii around the interface of each wheat crop and the alternate field. These values were correlated to relative WSS and parasitoid abundance within postharvest samples from the corresponding wheat field.

The 0.5 and 1 km radii were selected because it is unlikely that WSS can travel further due to their weak flight abilities (Criddle 1923). These radii lengths were useful in determining the distance that WSS parasitoids travel to forage. The 2, 3, and 4 km radii were added to this because parasitoids may travel greater distances to locate additional resources. Another reason for using these larger areas was that many fields in this study were very large and the 500 m radius may not have reached outside the field area. Linear regression models were fit to interpret the extent to which different land uses surrounding wheat fields explain WSS and parasitoid numbers within the fields. Fallow, winter wheat, spring wheat, durum wheat, grassland/pasture, and flowering crops were land use types of particular interest due to their potential to affect WSS and parasitoid populations.

Statistical Analysis

Although wheat fields on the same farm were comparable, comparisons among farms are difficult due to differences in climate, cultivar, management, existing insect population, and soil type. These factors are important unfixed variables that make conducting an ANOVA among fields impossible. Therefore, paired t-tests were conducted using “R” (R Core Team 2016) to assess the differences in WSS and parasitoid abundance between wheat bordering fallow and wheat bordering pulse or cover crop fields. Because there were a different number of traps in the wheat bordering fallow fields and the wheat bordering pulse or cover crop fields in 2016, the trap captures were averaged for each field and used for analysis. In 2017 both wheat fields at each site were sampled with the same number of traps and the total trap capture for each field was used for analysis. In both years a log base 2 (x+1) transformation was performed to reduce the variation in insect abundance between sites. Two sample t-tests were also conducted to test for differences in adult parasitoid weight and parasitoid size between insects collected in emergence barrels with residue from wheat fields bordering fallow and wheat fields bordering pulse or cover crop fields using the t.test package (R Core Team 2016). A Welch’s two sample t-test was used when the sample data failed to meet the assumption of equal standard deviations.

RESULTS

Emergence Barrel Results

Data from the emergence barrel experiments show no difference in WSS or parasitoid numbers between wheat next to fallow and wheat next to alternate pulse or cover crops (Table 4, 5). In 2016, about half of the sites comparing WSS and parasitoid abundance in wheat next to fallow and cover crops had large populations and half did not. Brady, Great Falls, and Conrad 1 had large WSS and parasitoid populations. The wheat field next to cover crop at the Conrad 2 site also had a high WSS population, but only 0.9 parasitoids per m^2. Dutton was the only site where we compared wheat bordering fallow to wheat bordering pulse crops that had a moderately high population of WSS and parasitoids. The 6 remaining sites had very low numbers of WSS and parasitoids emerge from the barrels (Table 4).

In 2017, there were relatively few WSS in the residue from any of the fields. The Dutton site had the most WSS with seven in each field (Table 5). Parasitoid abundance was more consistent throughout the sites than in 2016, but the Moccasin and Conrad 2 sites each still had fewer than 2 parasitoids per m^2 (Table 5). In both years, WSS abundance in the emergence barrels was lower than what may be expected from data collected through trapping or stem dissection of the same fields.

There was no difference in parasitoid body size in the parasitoids from fields next to pulse or cover crops compared to fields next to fallow. In 2016, there was no difference in parasitoid tibia length between fields at any of the sites ($p > 0.10$) (Table 6). At the Conrad 1 site in 2016, the male parasitoids weighed 8 μg less in wheat fields bordering the cover crop than in those next to fallow ($t = 3.78$, $p < 0.01$) (Table 7). However, the female parasitoids at the Dutton site followed the opposite trend and weighed 7 μg more in the fields bordering lentils ($t = -2.40$, $p < 0.05$) (Table 7). In 2017, male parasitoids had significantly longer tibias in the wheat field bordering chickpeas than in those next to fallow at the Dutton site ($t = -1.94$, $p < 0.1$) (Table 6). At Conrad 1 the female parasitoids had longer tibias in the wheat adjacent to fallow ($t = 2.44$, $p < 0.05$). At all other sites there was no difference in parasitoid tibia length between fields ($p > 0.10$) (Table 6). No overall effect of pulse or cover crops was observed on parasitoid body size.

Table 4: The number of adult wheat stem sawfly and adult braconid parasitoids per m^2 that emerged from emergence barrels in spring 2016. Stubble was collected from 2015 wheat crop. Parasitoid sex and species information in supplemental table 1.

	WSS		WSS Parasitoids	
Site (Emergence Dates)	Wheat next to fallow wheat	Wheat next to growing crop	Wheat next to fallow wheat	Wheat next to growing crop
Cover Crops				
Brady (May 29-July 5)	6.7	16.0	22.7	4.4
Great Falls (May 30-July 5)	17.3	38.7	3.1	35.1
Conrad 1 (May 31-July 9)	12.0	0.9	13.3	8.4
Denton (June 6-21)	0.0	0.0	0.0	3.1
Conrad 2 (June 4-19)	0.0	18.2	0.0	0.4
Chester (June 7-25)	0.4	0.0	0.4	1.3
Pulse Crops				
Denton (June 6-16)	0.0	0.0	0.0	2.7
Chester (June 20)	0.4	0.0	0.4	0.4
Dutton (June 1-July 8)	5.3	5.8	1.8	14.2
Conrad 3 (June 5)	0.0	0.0	0.0	0.9
Box Elder (June 7-20)	0.4	0.0	3.6	1.3
Joplin (June 14-18)	0.0	0.0	0.9	0.4

Table 5: The number of adult wheat stem sawfly and adult braconid parasitoids per m^2 that emerged from emergence barrels in spring 2017. Stubble was collected from 2016 wheat crop. Parasitoid sex and species information in supplemental table 2.

	WSS		WSS Parasitoids	
Site (Emergence Dates)	Wheat next to fallow wheat	Wheat next to growing crop	Wheat next to fallow wheat	Wheat next to growing crop
Cover Crops				
Conrad 4 (July 7-Aug. 18)	0.4	0.0	7.6	12.4
Brady (July 10-Aug. 4)	0.0	0.0	5.8	3.1
Conrad 1 (July 5-Aug. 14)	2.2	0.0	4.9	8.9
Conrad 2 (July 24-29)	0.0	0.0	0.0	1.8
Moccasin (July 19-20)	0.0	0.0	0.9	0.4
Pulse Crops				
Chester (July 5-Aug. 3)	0.0	0.0	6.2	0.0
Dutton (July 6-Aug. 15)	3.1	3.1	0.9	8.4
Conrad 3 (July 17-22)	0.0	0.0	0.0	4
Box Elder (July 3-Aug. 15)	0.9	0.0	5.8	1.3
Joplin (July 13-Aug. 11)	0.0	0.0	0.0	5.3

Table 6: Average tibia length of male and female *B. cephi* which emerged from barrels for sites where each field had at least one parasitoid of the same sex. Also displays results of two sample t-tests measuring the difference in parasitoid tibia length between wheat bordering fallow and wheat bordering pulse or cover crop for each site. Statistical difference ($p < 0.1$) marked by *.

Emergence Barrel Parasitoid Tibia Length

Site	Year	M/F	Average Parasitoid Tibia Length in Wheat Bordering Pulse or Cover Crop (mm)	n	Average Parasitoid Tibia Length in Wheat Bordering Fallow (mm)	n	t-stat	p-value
Brady	2016	F	1.38	5	1.34	29	-0.58	0.57
Brady	2016	M	1.11	5	1.13	22	0.38	0.71
Conrad 1	2016	F	1.32	14	1.33	14	0.14	0.89
Conrad 1	2016	M	1.14	10	1.26	9	0.39	0.19
Dutton	2016	F	1.39	14	1.41	3	0.30	0.77
Great Falls	2016	F	1.33	50	1.36	6	0.53	0.60
Brady	2017	M	0.79	5	0.81	7	0.25	0.81
Conrad 1	2017	M	0.83	15	0.88	3	0.65	0.53
Conrad 1	2017	F	0.87	5	1.03	7	2.44	0.04*
Dutton	2017	M	0.83	11	0.73	3	-1.94	0.09*

Table 7: Average weight of male and female *B. cephi* which emerged from barrels for sites where each field had at least one parasitoid of the same sex. Also displays results of two sample t-tests measuring the difference in parasitoid weight between wheat bordering fallow and wheat bordering pulse or cover crop for each site. Statistical difference (p < 0.1) marked by *.

Emergence Barrel Parasitoid Weight

Comparison	Year	M/F	Average Parasitoid Weight in Wheat Bordering Pulse or Cover Crop (µg)	n	Average Parasitoid Weight in Wheat Bordering Fallow (µg)	n	t-stat	p-value
Brady	2016	F	27	5	26	29	-0.55	0.60
Brady	2016	M	10	5	13	22	1.17	0.29
Conrad 1	2016	F	18	14	20	14	0.79	0.44
Conrad 1	2016	M	8	10	16	9	3.78	0.00*
Dutton	2016	F	29	14	22	3	-2.40	0.03*
Great Falls	2016	F	23	50	24	6	0.20	0.85
Brady	2017	M	9	5	11	7	0.71	0.50
Conrad 1	2017	M	13	15	9	3	-1.70	0.11
Conrad 1	2017	F	25	5	27	7	0.68	0.53
Dutton	2017	M	14	11	12	3	-0.55	0.59

Field Trapping Results

Field trapping data show differences between years in the effect of pulse and cover crops on WSS infestation (unreported data). In 2016, every site, with the exceptions of Moccasin and Box Elder, had significantly more WSS in the wheat fields next to flowering crops than wheat next to fallow ($t = -2.86$, $p < 0.05$) (Table 8, 9). However, the opposite trend was apparent at the cover crop sites in 2017, as all wheat fields next to a cover crop (except at Conrad 2) had fewer WSS captured than wheat fields adjacent to fallow (Table 10). No difference in WSS numbers was observed between wheat next to fallow and next to pulse ($t = -1.06$, $p > 0.10$) (Table 10, 11).

There were significantly more parasitoids captured in the wheat fields next to a pulse or cover crop in 2016 ($t = -1.85$, $p < 0.10$) (Table 9). One exception was the Brady site, but it was discovered that a parasitoid release (approximately 500 females of both braconid species) was made by MSU County Extension staff the previous year on the fallow field. This inoculation of parasitoids on the landscape may have impacted results. Thus, a new wheat field adjacent to fallow was selected for the Brady site in 2017, and the results were different, with more parasitoids trapped in the wheat field bordering cover crop (Table 10). Along with the Brady site, the Conrad 1 and Conrad 2 sites had more parasitoids caught in wheat bordering a cover crop than in wheat bordering fallow in 2017. However, no overall difference was observed in parasitoid numbers (Paired t-test, $t = 1.06$, $p > 0.10$) or proportion of parasitoids (Paired t-test, $t = 1.23$, $p > 0.10$) between wheat fields next to fallow and next to a pulse or cover crop in 2017 ($t = 1.06$, $p > 0.10$) (Table 11).

To assess if field trapping adult WSS and parasitoids is an effective monitoring technique, the log2 (x+1) transformed values for WSS and parasitoid numbers in trap catch and postharvest abundance for each wheat field were displayed on a scatterplot for both years (Figure 5, 6, 7, 8). A linear best fit and R^2 value were calculated for each correlation. In 2016, the R^2 value for the correlation between WSS trap capture and abundance in postharvest samples was 0.26. The parasitoid abundance in trap captures and postharvest samples was loosely correlated in 2016, with an R^2 of 0.11. The trap captures in 2017 were more strongly correlated to the insect abundance in postharvest samples ($R^2 = 0.59$). Likewise, the correlation between parasitoid trap capture and abundance in postharvest samples in 2017 is much stronger than in 2016 ($R^2 = 0.52$). The postharvest sampling is certainly a more robust data source that is more likely to represent the true population, however it takes many more resources than field trapping. If monitoring WSS and parasitoids with limited resources, field trapping may be an acceptable alternative.

Table 8: Average capture of one trap for wheat stem sawfly and parasitoids in each field in the 2016 season, as well as the percentage of total trap capture that were parasitoids.

2016 Average Trap Catch

Site	WSS in wheat next to fallow	WSS in wheat next to alternate crop	Parasitoids in wheat next to fallow	Parasitoids in wheat next to alternate crop	Percent parasitoids in wheat next to fallow	Percent parasitoids in wheat next to alternate crop
Cover Crop Sites						
Brady	7.2	17.7	6.1	3.2	45.8	15
Conrad 1	3.8	35.3	0.6	12.3	13.6	26
Conrad 2	4.4	7.6	0.3	0.1	6.4	1
Conrad 4	8.3	34.1	16.3	22.7	66.3	40
Moccasin	0.4	0.3	0	0.7	0.0	70
Pulse Sites						
Chester	0	0.9	0.2	0.7	100.0	44
Dutton	33.6	48.6	1.5	1.4	4.3	3
Conrad 3	0.2	3	0.3	0.3	60.0	9
Box Elder	0.7	0.6	0	0.1	0.0	14
Joplin	3.5	2.5	0.2	1.4	5.4	36

Table 9: Comparisons of log2 average total trap captures for the 2016 field season. The wheat bordering fallow and wheat bordering crop columns report the untransformed wheat stem sawfly and parasitoid abundance for each group of fields. Parasitoid percentage is calculated as the percent of total wheat stem sawfly and parasitoids captured that are parasitoids for each field. Paired t-tests were done for each comparison. Brady was left out of the analysis due to a parasitoid release near the fallow field in the previous season, which skewed results. Statistical difference ($p < 0.1$) marked by *.

Comparison	Wheat bordering fallow	Wheat bordering alternate crop	t-stat	p-value
WSS all sites	5.66	13.73	-2.86	0.02*
WSS pulse sites	6.37	9.33	-1.59	0.17
WSS cover crop sites	4.23	19.33	-2.54	0.06*
Parasitoid all sites	2.34	3.92	-1.85	0.10*
Parasitoid pulse sites	0.40	0.68	-1.56	0.18
Parasitoid cover crop sites	4.66	7.80	-1.41	0.25
Percentage parasitoids all sites	30.6%	27.6%	0.25	0.81
Percentage parasitoids pulse sites	36.6%	23.2%	0.94	0.39
Percentage parasitoids cover crop sites	21.6%	34.3%	-0.62	0.58

Table 10: Average capture of one trap for wheat stem sawfly and parasitoids in each field in the 2017 season, as well as the percentage of total trap capture that were parasitoids.

2017 Trap Catch

Site	WSS in wheat next to fallow	WSS in wheat next to alternate crop	Parasitoids in wheat next to fallow	Parasitoids in wheat next to alternate crop	Percent parasitoids in wheat next to fallow	Percent parasitoids in wheat next to alternate crop
Cover Crop Sites						
Brady	15.5	7.5	0.4	0.7	2.3	8
Conrad 1	9.6	7.9	1.1	1.5	10.3	16
Conrad 2	4.4	4.3	0.5	0.6	9.7	12
Conrad 4	47.4	27.7	22.9	7.2	32.5	21
Moccasin	0.4	0.2	0.0	0.0	7.1	0
Pulse Sites						
Chester	0.4	0.4	0.1	0	15.2	0
Dutton	19.9	18.0	8.1	8.1	29.0	31
Conrad 3	1.8	2.5	0.2	0.1	11.1	2
Box Elder	2.3	2.3	0.1	0.1	3.3	3
Joplin	1.3	1.9	0.1	0.1	4.8	3

Table 11: Comparisons of log2 total trap captures for the 2017 field season. The wheat bordering fallow and wheat bordering crop columns report the untransformed wheat stem sawfly and parasitoid abundance for each group of fields. Parasitoid percentage is calculated as the percent of total wheat stem sawfly and parasitoids captured that are parasitoids for each field. Paired t-tests were done for each comparison. Statistical difference ($p < 0.1$) marked by *.

Comparison	Wheat bordering fallow	Wheat bordering alternate crop	t-stat	p-value
WSS all sites	10.3	7.3	1.29	0.23
WSS pulse sites	5.1	5.0	-1.06	0.35
WSS cover crop sites	15.5	9.5	3.08	0.04*
Parasitoid all sites	3.4	1.9	1.06	0.32
Parasitoid pulse sites	1.8	1.6	1.77	0.15
Parasitoid cover crop sites	5.0	2.0	0.27	0.80
Percent parasitoids all sites	12.5%	9.6%	1.23	0.25
Percent parasitoids pulse sites	12.7%	7.7%	1.54	0.20
Percent parasitoids cover crop sites	12.4%	11.4%	0.26	0.81

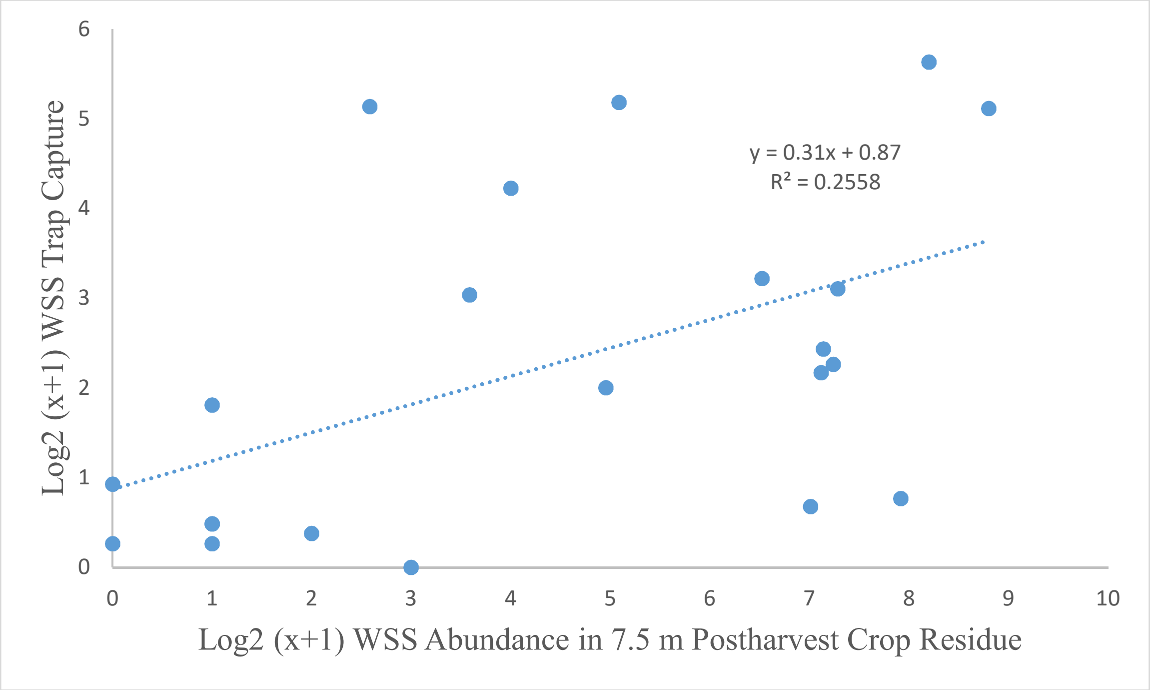


Figure 5: Average wheat stem sawfly trap capture per trap and postharvest sampling regression for 2016. Values underwent a Log2 (x+1) transformation.

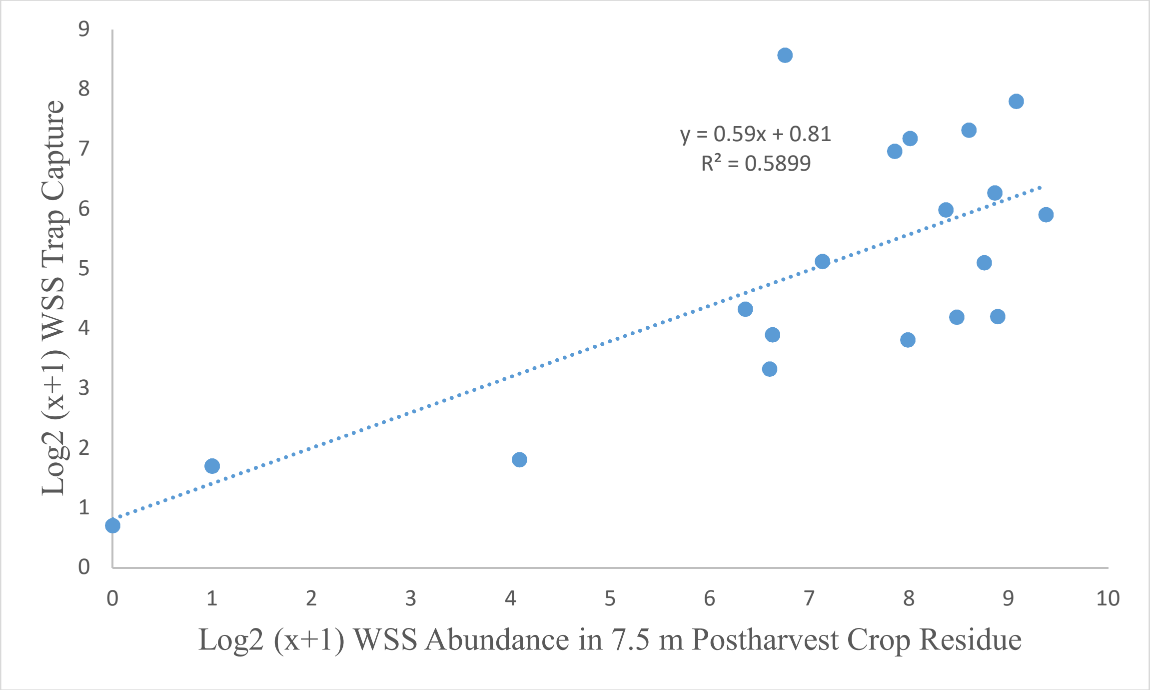


Figure 6: Average wheat stem sawfly trap capture per trap and postharvest sampling regression for 2017. Values underwent a Log2 (x+1) transformation.

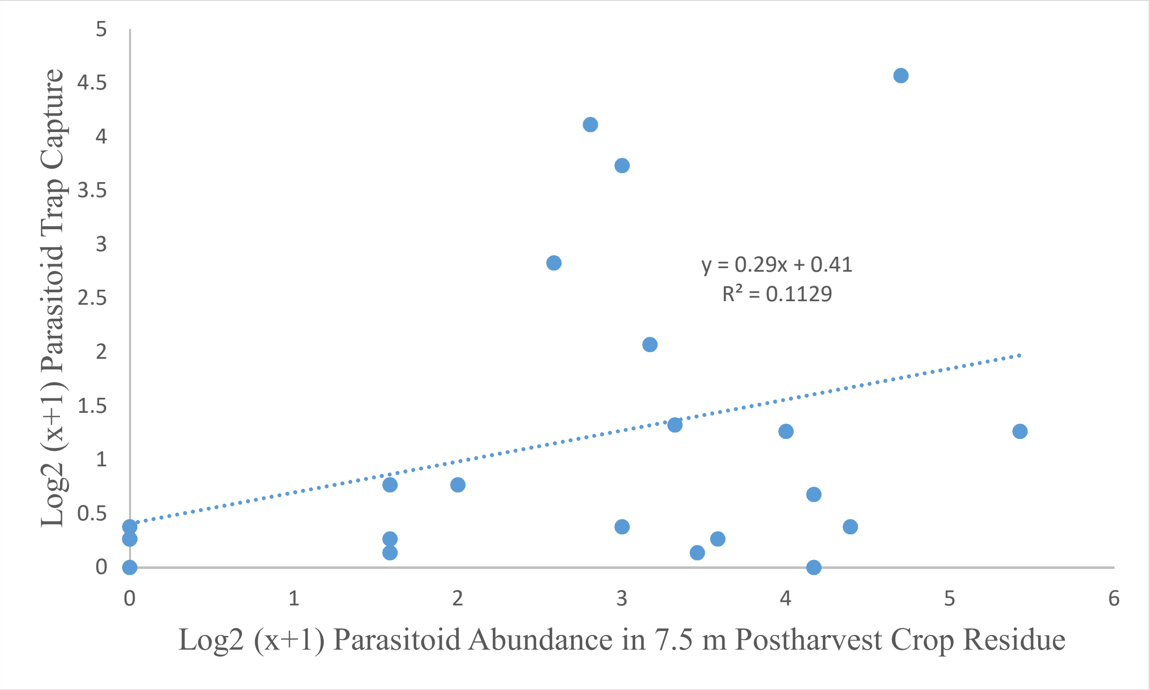


Figure 7: Average parasitoid trap capture per trap and postharvest sampling regression for 2016. Values underwent a Log2 (x+1) transformation.

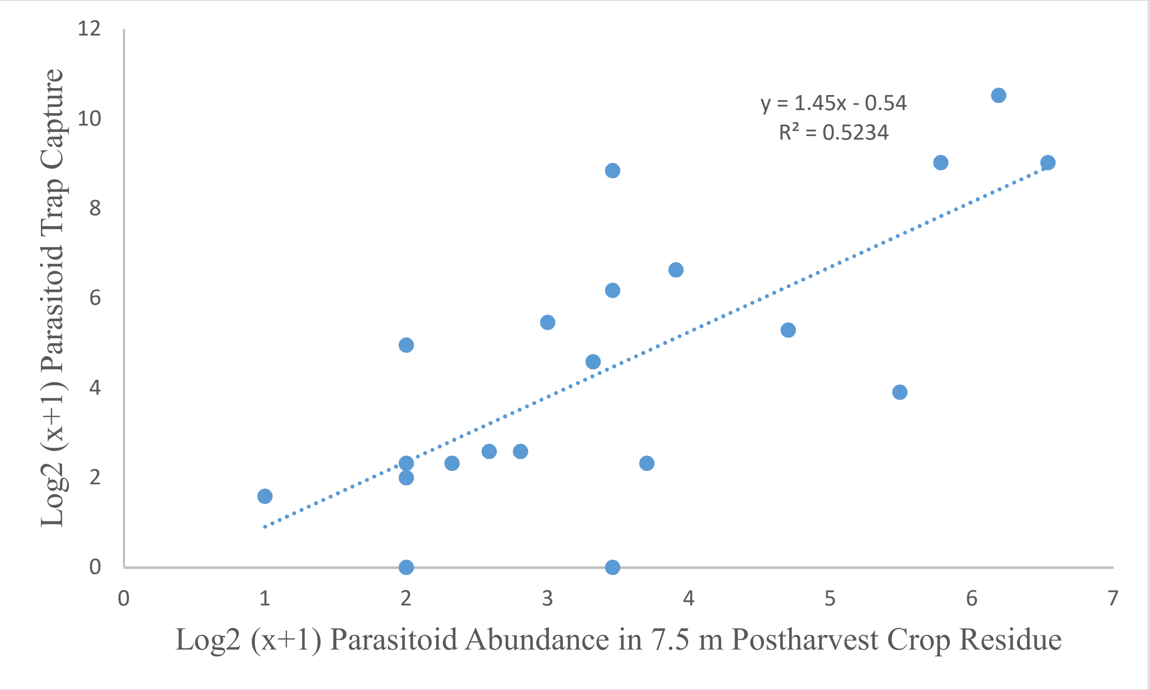


Figure 8: Average parasitoid trap capture per trap and postharvest sampling regression for 2017. Values underwent a Log2 (x+1) transformation.

Postharvest Stem Samples

In 2016, comparison of data obtained from postharvest dissection indicated that WSS numbers in wheat next to a cover crop or pulse were reduced by 1.5 (Paired t-test, $t = 2.44$, $p < 0.01$) and 2.9 (Paired t-test, $t = 3.83$, $p < 0.01$) WSS per 7.5 m wheat row respectively. The largest differences came at the Conrad 4 and Conrad 1 sites with reductions of 3.5 (Paired t-test, $t = 2.74$, $p < 0.05$) and 4.7 (Paired t-test, $t = 3.10$, $p < 0.05$) WSS per 7.5 m wheat row. The only site with significantly more WSS next to the alternate crop was Conrad 3 with 1.2 more WSS in the wheat next to pulse (Paired t-test, $t = -2.94$, $p < 0.05$) (Table 14).

The data for parasitoid abundance in 2016 postharvest stem dissection samples were less conclusive. The only cover crop site which had a significant increase in parasitoid abundance in the samples from the field of wheat next to cover crop than the one next to fallow was Conrad 4 (Paired t-test, $t = -3.07$, $p < 0.05$). There was no difference between parasitoid abundance in stem dissections from wheat fields next to cover crop and wheat fields next to fallow (Paired t-test, $t = -1.06$, $p > 0.10$). On average, no difference was observed in parasitoid numbers between wheat next to pulse and next to fallow (Paired t-test, $t = -0.44$, $p > 0.10$). More parasitoids were recorded in postharvest samples from the wheat field next to pulse at Dutton (Paired t-test, $t = -3.65$, $p < 0.01$), Conrad 3 (Paired t-test, $t = -3.46$, $p < 0.01$), and Joplin (Paired t-test, $t = -3.12$, $p < 0.05$). But the opposite trend was observed at both Box Elder (Paired t-test, t = 1.88, $p < 0.10$) and Chester (Paired t-test, t = 2.01, $p < 0.10$) (Table 15).

Table 12: Abundance of wheat stem sawfly and parasitoids per m^2 in 25, 30 cm postharvest crop residue samples in 2016. Percent parasitoid is the percentage of parasitoids in the total number of WSS and parasitoids in each wheat field. Percent stem cutting is the percentage of wheat stems sampled that were cut by a WSS larva.

	WSS Abundance		Parasitoid Abundance		Percent Parasitoid		Percent Stem Cutting	
Site	Wheat next to fallow	Wheat next to alternate crop	Wheat next to fallow	Wheat next to alternate crop	Wheat next to fallow	Wheat next to alternate crop	Wheat next to fallow	Wheat next to alternate crop
Cover Crop Sites								
Brady	4.9	6.7	2.2	3.6	31	35	2	2
Conrad 1	66.7	14.7	7.6	3.1	10	18	9	2
Conrad 4	40.4	2.2	2.7	11.1	6	83	7	0
Conrad 2	62.2	68.9	3.1	0.9	5	1	9	10
Moccasin	0.4	1.3	0.0	0.9	0	40	0	0
Pulse Sites								
Conrad 3	0.0	13.3	0.0	8.9	0	40	0	5
Dutton	197.8	130.2	4	18.7	2	13	20	17
Joplin	61.3	0.4	0.9	6.7	1	94	8	0
Box Elder	107.1	56.9	7.6	4.4	7	7	9	7
Chester	3.1	0.0	4.9	1.3	61	100	1	0

Table 13: Abundance of WSS and parasitoids in 25, 30 cm postharvest crop residue samples in 2017. Percent parasitoid is the percentage of parasitoids in the total number of WSS and parasitoids in each wheat field. Percent stem cutting is the percentage of wheat stems sampled that were cut by a WSS larva.

	WSS Abundance		Parasitoid Abundance		Percent Parasitoid		Percent Stem Cutting	
Site	Wheat next to fallow	Wheat next to alternate crop	Wheat next to fallow	Wheat next to alternate crop	Wheat next to fallow	Wheat next to alternate crop	Wheat next to fallow	Wheat next to alternate crop
Cover Crop Sites								
Brady	295.6	103.1	3.1	4	1	4	30	12
Conrad 1	206.7	147.1	4.4	6.2	2	4	38	23
Conrad 4	240.0	48	4.4	32	2	40	39	6
Conrad 2	62.2	192	1.3	11.1	2	6	11	34
Moccasin	0.9	0.4	0.4	1.3	33	75	0	0
Pulse Sites								
Conrad 3	36.4	112.9	1.3	19.6	4	15	10	20
Dutton	114.7	172.9	24	40.9	17	19	28	37
Joplin	43.1	44	1.8	5.3	4	11	11	7
Box Elder	211.1	158.7	2.7	1.3	1	1	63	52
Chester	7.6	0.9	2.2	4.4	23	83	2	0

Table 14: Results of paired t-tests performed on the difference in wheat stem sawfly numbers from the 25 paired 30 cm postharvest wheat residue samples from the wheat field next to fallow and the wheat field next to an alternate crop for each site in 2016. Columns reporting wheat stem sawfly abundance show the average number of wheat stem sawfly larvae in the 25 paired crop residue samples for each wheat field. Statistical difference (p < 0.1) marked by *.

2016 Postharvest WSS Abundance

Site	Mean WSS abundance in wheat next to fallow	Mean WSS abundance in wheat next to alternate crop	WSS abundance t-stat	p-value	Number of paired samples analyzed
Cover Crop Sites					
Brady	0.4	0.6	-0.78	0.45	25
Conrad 1	6.0	1.3	3.10	0.01*	25
Conrad 4	3.7	0.2	2.74	0.01*	25
Conrad 2	5.6	6.2	-0.29	0.78	25
Moccasin	0.0	0.1	-1.00	0.33	25
All cover crop sites	3.2	1.7	2.44	0.02*	125
Pulse Sites					
Conrad 3	0.0	1.2	-2.94	0.01*	25
Dutton	17.1	11.9	1.82	0.08*	25
Joplin	5.56	0.0	5.00	0.00*	25
Box Elder	9.6	5.1	2.51	0.02*	25
Chester	0.3	0.0	2.59	0.02*	25
All pulse sites	6.5	3.6	3.83	0.00*	125

Table 15: Results of paired t-tests performed on parasitoid numbers from the 25, 30 cm postharvest wheat residue samples from the wheat field next to fallow and the wheat field next to an alternate crop for each site in 2016. Columns reporting WSS abundance show the average number of parasitoids in the 25 crop residue samples for each wheat field. Statistical difference ($p < 0.1$) marked by *.

2016 Postharvest Parasitoid Abundance

Site	Mean parasitoid abundance in wheat next to fallow	Mean parasitoid abundance in wheat next to alternate crop	Parasitoid abundance t-stat	p-value	Number of paired samples analyzed
Cover Crop Sites					
Brady	0.2	0.3	-0.57	0.57	25
Conrad 1	0.6	0.2	1.30	0.21	25
Conrad 4	0.2	1.0	-3.07	0.01*	25
Conrad 2	0.2	0.1	1.00	0.33	25
Moccasin	0.0	0.1	-1.45	0.16	25
All CC Sites	0.2	0.3	-1.06	0.29	125
Pulse Sites					
Conrad 3	0.0	0.8	-3.46	0.00*	25
Dutton	0.3	1.4	-3.65	0.00*	25
Joplin	0.0	0.5	-3.12	0.01*	25
Box Elder	0.6	0.3	1.88	0.07*	25
Chester	0.4	0.1	2.01	0.06*	25
All Pulse Sites	0.4	0.5	-0.44	0.66	125

Table 16: Results of paired t-tests performed on wheat stem sawfly numbers from the 25, 30 cm postharvest wheat residue samples from the wheat field next to fallow and the wheat field next to an alternate crop for each site in 2017. Columns reporting wheat stem sawfly abundance show the average number of wheat stem sawfly larvae in the 25 crop residue samples for each wheat field. Statistical difference ($p < 0.1$) marked by *.

2017 Postharvest WSS Abundance

Site	Mean WSS abundance in wheat next to fallow	Mean WSS abundance in wheat next to alternate crop	WSS abundance t-stat	p-value	Number of paired samples analyzed
Cover Crop Sites					
Brady	26.6	9.3	6.42	0.00*	25
Conrad 1	18.6	13.2	2.67	0.01*	25
Conrad 4	21.6	4.3	12.8	0.00*	25
Conrad 2	5.6	17.3	-7.81	0.00*	25
Moccasin	0.1	0.0	0.57	0.57	25
All CC Sites	14.5	8.8	4.52	0.00*	125
Pulse Sites					
Conrad 3	3.3	10.2	-4.70	0.00*	25
Dutton	10.3	15.6	-3.71	0.00*	25
Joplin	3.9	4.0	-0.12	0.91	25
Box Elder	19.0	14.3	1.56	0.13	25
Chester	0.7	0.1	3.46	0.00*	25
All Pulse Sites	7.4	8.8	-1.68	0.10*	125

Table 17: Results of paired t-tests performed on parasitoid numbers from the 25, 30 cm postharvest wheat residue samples from the wheat field next to fallow and the wheat field next to an alternate crop for each site in 2017. Columns reporting WSS abundance show the average number of parasitoids in the 25 crop residue samples for each wheat field. Statistical difference (p < 0.1) marked by *.

2017 Postharvest Parasitoid Abundance

Site	Mean parasitoid abundance in wheat next to fallow	Mean parasitoid abundance in wheat next to alternate crop	Parasitoid abundance t-stat	p-value	Number of paired samples analyzed
Cover Crop Sites					
Brady	0.3	0.4	-0.40	0.69	25
Conrad 1	0.4	0.6	-0.70	0.49	25
Conrad 4	0.4	2.9	-5.06	0.00*	25
Conrad 2	0.1	1.0	-3.56	0.00*	25
Moccasin	0.0	0.1	-0.81	0.43	25
All CC Sites	0.2	1.0	-4.91	0.00*	125
Pulse Sites					
Conrad 3	0.1	1.8	-4.06	0.00*	25
Dutton	2.2	3.7	-1.64	0.11	25
Joplin	0.2	0.5	-1.55	0.13	25
Box Elder	0.2	0.1	1.37	0.19	25
Chester	0.2	0.4	-0.93	0.36	25
All Pulse Sites	0.6	1.3	-3.27	0.00*	125

In 2017, WSS abundance in postharvest samples from the cover crop sites followed the same trend as in 2016; more WSS in the wheat fields grown next to fallow than next to a cover crop (Paired t-test, $t = 4.52$, $p < 0.01$). This was true of all cover crop sites except for Conrad 2. The postharvest stem dissection results were more variable for WSS abundance at pulse sites. Stem dissections yielded 6.9 and 5.3 more WSS per sample in the wheat fields next to pulse crops than those next to fallow at Conrad 3 (Paired t-test, $t = -4.70$, $p < 0.01$) and Dutton

(Paired t-test, $t = -3.71$, $p < 0.01$) respectively. The only pulse site with more WSS in the wheat field next to fallow was Chester (Paired t-test, $t = 3.27$, $p < 0.01$). Overall, postharvest stem dissections yielded 1.4 more WSS in wheat fields next to pulse than in those next to fallow in 2017 (Paired t-test, $t = -1.68$, $p < 0.10$) (Table 16).

Dissection of 2017 postharvest wheat residue from cover crop sites had increased parasitoids in wheat fields next to cover crop compared to those next to fallow by 2.5 at Conrad 4 (Paired t-test, $t = -5.06$, $p < 0.01$) and 0.9 at Conrad 2 (Paired t-test, $t = -3.56$, $p < 0.01$). Overall, there was a 0.8 parasitoid reduction per 7.5 m wheat residue from fields next to cover crop (Paired t-test, $t = -4.91$, $p < 0.01$). Parasitoids were more abundant in the postharvest samples from wheat fields next to a pulse crop at all pulse sites other than Box Elder. However, the only site with statistically greater parasitoid abundance in the wheat field next to pulse was Conrad 3 (Paired t-test, $t = -4.06$, $p < 0.01$). When paired fields at all pulse sites were considered, there were significantly more parasitoids in the wheat next to pulse (Paired t-test, $t = -3.27$, $p < 0.01$) (Table 17).

During stem dissection of postharvest crop residue samples, the percentage of wheat stems that were cut by WSS larvae was also recorded. The wheat field seeded next to cover crop had an 8 percentage point reduction in WSS stem cutting at Conrad 1 (Paired t-test, $t = 3.05$, $p < 0.05$) and a 6 percentage point reduction at Conrad 4 (Paired t-test, $t = 2.88$, $p < 0.05$) in 2016. Stem cutting by WSS was reduced by 2 percentage points on average across all cover crop sites in

2016 (Paired t-test, $t = 2.52$, $p < 0.05$). Postharvest stem dissection data also suggest that wheat fields next to a pulse crop had a stem cutting rate of 6% compared to 8% in fields next to fallow in 2016 (Paired t-test, $t = 1.95$, $p < 0.10$). The only pulse site with a significantly lesser rate of cut stems in the wheat next to pulse on its own was Joplin (Paired t-test, $t = 5.07$, $p < 0.01$) (Table 18).

Wheat stems were cut at a rate of 24% in wheat next to fallow compared to 15% in fields next to cover crop in 2017 (Paired t-test, $t = 4.28$, $p < 0.01$). The only contradiction was at the Conrad 2 site, where stem cutting rate was 23 percentage points higher in the wheat next to cover crop (Paired t-test, $t = -8.48$, $p < 0.01$). No overall trend was observed for the difference in stem cutting rate between wheat fields next to pulse crops and next to fallow in 2017 (Paired t-test, $t = -0.15$, $p > 0.10$). There was a greater percentage of WSS cut stems next to fallow than in the field next to pulse at the Chester (Paired t-test, $t = 4.76$, $p < 0.01$), Box Elder (Paired t-test, $t = 3.26$, $p < 0.01$), and Joplin sites (Paired t-test, $t = 1.82$, $p < 0.10$). But these results were contradicted when more stem cutting was observed in the field next to pulse at the Conrad 3 (Paired t-test, $t = -3.74$, $p < 0.01$) and Dutton sites (Paired t-test, $t = -3.19$, $p < 0.01$) (Table 19).

Table 18: Table of the proportion of wheat stem sawfly cut stems in each wheat field in 2016. The final 2 columns are the results of paired t-tests of the difference between the percentage of cut stems in the wheat field next to fallow and the wheat field next to an alternate crop at each site. Statistical difference ($p < 0.1$) marked by *.

2016 Proportion of WSS Cut Stems

Site	Mean percentage of cut stems in wheat next to fallow	Mean percentage of cut stems in wheat next to alternate crop	t-stat	p-value	Number of paired samples analyzed
Cover Crop Sites					
Brady	2	2	0.01	0.99	25
Conrad 1	9	2	3.05	0.01*	25
Conrad 4	7	0	2.88	0.01*	25
Conrad 2	9	10	-0.23	0.82	25
Moccasin	0	0	0.97	0.34	25
All Cover Crop Sites	6	3	2.52	0.01*	125
Pulse Crop Sites					
Conrad 3	0	5	-3.35	0.00*	25
Dutton	20	17	0.81	0.43	25
Joplin	8	0	5.07	0.00*	25
Box Elder	9	7	1.27	0.22	25
Chester	1	0	1.88	0.07*	25
All Pulse Crop Sites	8	6	1.95	0.05*	125

Table 19: Table of the percentage of stems cut by wheat stem sawfly in each wheat field. The final 2 columns are the results of paired t-tests of the difference between the percentage of cut stems in the wheat field next to fallow and the wheat field next to an alternate crop at each site. Statistical difference ($p < 0.1$) marked by *.

2017 Proportion of WSS Cut Stems

Site	Mean percentage of cut stems in wheat next to fallow	Mean percentage of cut stems in wheat next to alternate crop	t-stat	p-value	Number of paired samples analyzed
Cover Crop Sites					
Brady	30	12	8.73	0.00*	25
Conrad 1	38	23	4.63	0.00*	25
Conrad 4	39	6	13.33	0.00*	25
Conrad 2	11	34	-8.48	0.00*	25
Moccasin	0	0	0.27	0.79	25
All Cover Crop Sites	24	15	4.28	0.00*	125
Pulse Crop Sites					
Conrad 3	10	20	-3.74	0.00*	25
Dutton	28	37	-3.19	0.00*	25
Joplin	11	7	1.82	0.08*	25
Box Elder	63	52	3.26	0.00*	25
Chester	2	0	4.76	0.00*	25
All Pulse Crop Sites	23	23	-0.15	0.88	125

WSS and parasitoid abundances in the postharvest crop residue samples were also used in the analysis of the land-use data. Multiple linear regression was used to analyze which land-use types had the largest impact on WSS and parasitoid abundance in wheat fields. Land-use types from the CropScape data layers were broken into the following groups; fallow wheat, winter wheat, spring wheat, durum wheat, grassland/pasture, flowering crops, and developed space. We found that the most impactful factor on WSS abundance in wheat fields was the proportion of fallow wheat on the landscape within a 2 km radius of the field (Fig. 9). According to our model, the regression equation of square root transformed WSS abundance on the proportion of fallow land on the landscape within a 2 km radius is $Y = 18.96X + 6.08$ (F: 3.93, $p < 0.05$) where Y is square root WSS abundance and X is the proportion of fallow within 2 km (Supplemental Table 3). No land-use factors had any significant correlation with parasitoid numbers.

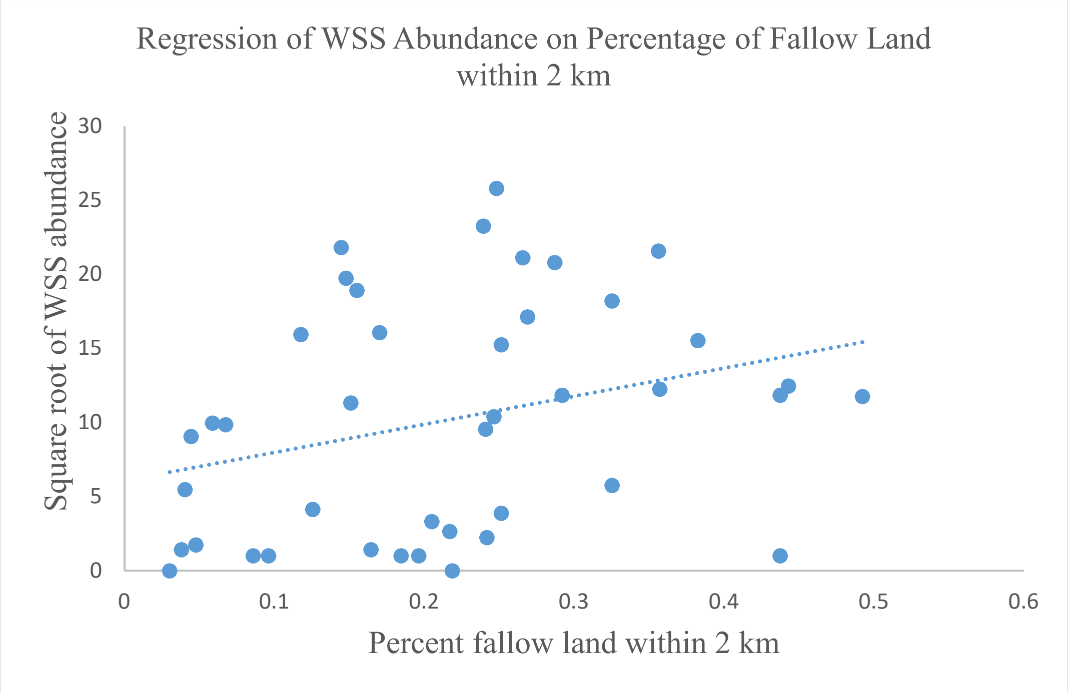


Figure 9: The square root of WSS abundance in postharvest crop residue from each wheat field regressed on the percentage of land within 2 km which is fallow.

DISCUSSION

Study Objectives

The first objective of this study was to determine if parasitoid abundance increased (or decreased) in wheat fields when flowering pulse or cover crops were seeded on the wheat residue from the previous crop, as opposed to fallowing the previous season's wheat residue. Data from the emergence barrels do not show a clear difference in parasitoid abundance between residue from wheat fields grown next to a pulse or cover crop and wheat fields grown next to fallow (Table 4, 5).

Trap captures of adult parasitoids throughout the growing season indicate that there were 1.6 more parasitoids caught per trap in wheat fields seeded next to a pulse or cover crop in 2016 (Paired t-test, $t = -1.84$, $p < 0.10$) (Table 9), but no difference was detected in 2017 (Paired t-test, $t = 1.06$, $p > 0.10$) (Table 11). Data gathered from field trapping did not show a consistent difference in parasitoid numbers between wheat next to fallow and wheat next to pulse or cover crops.

Our parasitoid abundance data from postharvest stem dissection provided differing results depending on year. In 2016 there was no evidence of a difference in parasitoid abundance between wheat fields next to fallow or next to a flowering cover crop (Paired t-test, $t = -1.06$, $p > 0.10$) or pulse crop (Paired t-test, $t = -0.44$, $p > 0.10$) (Table 15). The only site with significantly greater parasitoid abundance in the wheat field next to an alternate crop versus next to fallow was Conrad 4 (Paired t-test, $t = -3.07$, $p < 0.05$). In 2017, 0.8 additional parasitoids were observed per 30 cm crop residue in wheat grown next to cover crops (Paired t-test, $t = -4.91$, $p < 0.01$) and a 0.7 parasitoid increase next to pulse crops (Paired t-test, $t = -3.27$, $p < 0.01$) in the dissected postharvest samples (Table 17). These data show that, contrary to numbers provided by emergence barrels and traps, there was an increase in parasitoid abundance in wheat fields next to flowering crops.

There were 1.5 more WSS on average in 30 cm crop residue from fields next to fallow than those next to cover crop (Paired t-test, $t = 2.44$, $p < 0.05$), and 2.9 additional WSS were observed per 30 cm crop residue in the field next to fallow than next to pulse (Paired t-test, $t = 3.83$, $p < 0.01$). Although no difference in parasitoid abundance between wheat next to fallow and wheat next to flowering crops was observed in 2016, a greater proportion of parasitoids to WSS was evident in wheat fields next to flowering crops (Table 14, 15). An interesting result of the 2017 postharvest WSS abundance analysis was that overall, wheat fields next to pulse crops had 1.4 additional WSS per 30 cm row than their fallow pairs (Paired t-test, $t = -1.68$, $p < 0.10$), but wheat next to cover crops had 5.7 less WSS per 30 cm row (Paired t-test, $t = 4.52$, $p < 0.01$) (Table 16). Regardless, wheat next to pulse and cover crops had 0.7 (Paired t-test, $t = -3.27$, $p < 0.01$) and 0.8 (Paired t-test, $t = -4.91$, $p < 0.01$) additional parasitoids per 7.5 m of crop residue respectively than paired fields adjacent to fallow (Table 17).

Wheat stem sawfly trap captures in 2016, like parasitoid trap captures, were greater in wheat fields adjacent to a pulse or cover crop (Paired t-test, $t = -2.63$, $p < 0.05$) (Table 9). Because the numbers of both WSS and parasitoids were greater in the wheat fields next to pulse or cover crops in 2016, the proportion of parasitoids within total insect capture was not different between wheat fields grown next to fallow and wheat fields grown next to pulse or cover crop (Paired t-test, $t = 0.25$, $p > 0.10$) (Table 9). However, the trapping data that suggest WSS were more abundant in wheat fields next to pulse or cover crops than in wheat next to fallow were contradicted by the postharvest WSS abundance data.

In 2017 there was no statistical difference between number of WSS trapped in wheat fields next to pulse crops versus those next to fallow (Paired t-test, $t = -1.06$, $p > 0.10$), and 6 fewer WSS per trap were caught in wheat fields next to cover crops compared to wheat next to fallow (Paired t-test, $t = 3.08$, $p < 0.05$) (Table 11). This was corroborated by the postharvest stem dissection data, which suggest an increase of only 1.4 WSS per 30 cm crop residue in wheat fields next to pulse crops than wheat next to fallow (Paired t-test, $t = -1.68$, $p < 0.10$), and a decrease of 5.7 parasitoids per 30 cm crop residue (Paired t-test, $t = 4.52$, $p < 0.01$) (Table 16).

However, in 2016 the field trapping results did not match the data from postharvest samples as well as in 2017. An additional 3 WSS per trap were captured in fields next to pulse than in those next to fallow, and an increase of 15.1 WSS was observed in fields next to cover crop. Data from postharvest stem samples however show a 2.5 and 1.5 WSS decrease in pulse and cover crops respectively.

We believe that the change in the field trapping study design between 2016 and 2017 was responsible for trapping data matching the postharvest stem dissections more closely in 2017. In 2016, the design of putting half of the traps in either the alternate growing crop or fallow wheat did not provide accurate data. The traps in the pulse or cover crops caught many more WSS than those in the fallow field. A possible explanation is that the yellow, sticky traps were more attractive to WSS adults in the absence of alternate crops than when the pulse or cover crop was present. Criddle (1923) recorded instances of adult WSS visiting yellow flowers. The yellow traps may attract WSS traveling into the wheat crop from fallow, but not be as evident to WSS leaving a pulse or cover crop. While pulse and cover crops do not attract WSS, they provide shelter from rain, wind, and avian predation. They also make it more difficult for WSS adults emerging from wheat residue in the pulse or cover crop fields to locate and move into the wheat crop, thus increasing the time adult WSS spend on the interface between the two fields and in proximity to the traps.

In 2017, all traps were placed 1 m into the wheat field to limit any confounding effects of comparing trap catch from a fallow field to trap catch from a field of pulse or cover crop. These changes caused trap data to more closely

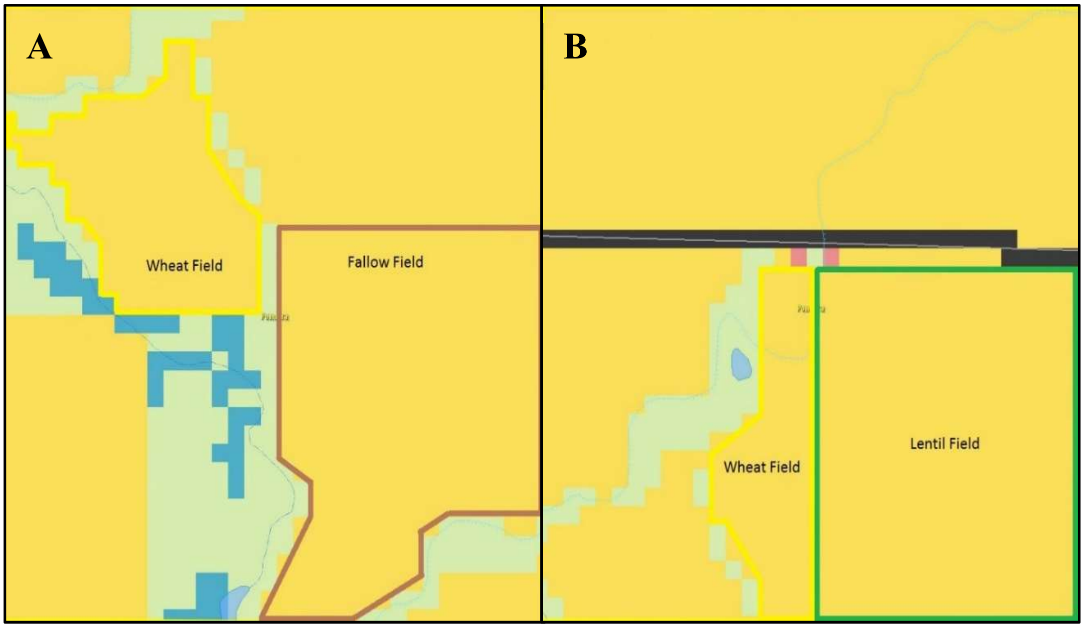


Figure 10: Field maps for the Conrad 3 site in 2016. Light blue represents areas of prairie grasses and dark blue represent areas of riparian grasses. Map created from Montana Natural Heritage Map Viewer, http://mtnhp.org/mapviewer/.

resemble postharvest results in 2017 (Linear Regression, $R^2 = 0.59$) than in 2016 (Linear Regression, $R^2 = 0.26$) (Fig. 5, 6). Although data correlated more closely in 2017, the stem dissection data were still better. The more intensive sampling yielded more analytical power to show differences in WSS and parasitoid abundance between fields. In addition, more information can be gathered from stem dissections than field trapping such as rate of WSS larval mortality, fungal mortality, and stem cutting rate.

Analysis of stem cutting rate provides a good indicator of the potential crop damage due to WSS. In 2016, the rate of stem cutting was reduced by 2 percentage points in both wheat next to pulse (Paired t-test, $t = 1.95$, $p < 0.10$) and cover crop (Paired t-test, $t = 2.52$, $p < 0.05$) when compared to paired fields next to fallow (Table 18). The only site to have more stems cut next to pulse in 2016 was Conrad 3, which is consistent with the postharvest estimate of WSS abundance (Table 14). A large area of riparian and prairie grasses between the wheat and fallow fields may have been why stem cutting and WSS abundance were reduced in wheat next to fallow compared to wheat next to lentils (Figure 10). This grass may have intercepted WSS as they searched for hosts after emerging from the fallow field, preventing WSS from infesting the wheat. The riparian grasses are more of a sink than regular grassland because the additional moisture in the riparian area causes the grass to be more vigorous and desirable to WSS.

The difference in stem cutting between wheat fields did not match the difference in WSS abundance at the Dutton site in 2016. There were significantly more abundant WSS in the wheat field next to fallow (Table 14), but there was no difference in the rate of stem cutting (Table 18). This may have been due to a difference in the density of the wheat stand between the two fields (unreported data). In the wheat field next to fallow, the denser stand of wheat with more stems reduced the percentage of cut wheat stems. Even though there were more WSS in the wheat field next to fallow, the proportion of WSS to available wheat stems did not differ.

There was a much greater rate of stem cutting in the wheat field next to cover crop at the Moccasin site in 2017. This is probably due to natural differences in WSS populations between the two wheat fields, and the fact that the cover crop emerged late. There were more cut stems in the wheat next to the pea field at Conrad 3 in 2017 as well. However, irrigation was a confounding factor at this site, because the wheat field next to fallow was irrigated while the field adjacent to peas was not. Additionally, more WSS mortality was attributed to fungal pathogens in the irrigated wheat field adjacent to fallow (unreported data). There were more cut stems in samples collected from the wheat field next to chickpeas than in samples from the field next to fallow at the Dutton site. There were more abundant parasitoids in samples taken adjacent to the chickpea crop, but more WSS infestation as well.

Stem cutting rate was higher in 2017 than 2016 (Table 18, 19). Rate of stem cutting was reduced by 8 percentage points in wheat next to cover crop compared to paired fields (Paired t-test, $t = 4.28$, $p < 0.01$). However, no difference was observed between stem cutting rates in wheat next to pulse and wheat next to fallow (Paired t-test, $t = -0.15$, $p > 0.10$). WSS and parasitoid abundance data match this result. There were more WSS in the fields next to pulse, but more parasitoids were there as well.

Parasitoids were observed aggregating on the flowers of lamb’s quarters (*Chenopodium album*) growing in the field margins at both fields, but primarily at the edge of the fallow field next to wheat. The presence of lamb’s quarters in the margin of the fallow field may have attracted enough parasitoids to mute the effect of the chickpea crop on the other wheat field. Considering that there were many less WSS in the wheat field next to fallow to begin with, the extra parasitoids brought in by the lamb's quarters may have reduced the damage done by WSS in that field. There were significant reductions of WSS cut stems in the wheat adjacent to pulse in Joplin, Box Elder, and Chester. The wheat fields next to cover crops had 8 percentage points less cutting compared to wheat next to fallow in 2017 (Paired t-test, $t = 4.28$, $p < 0.01$) (Table 19).

Postharvest data show large differences in WSS abundance, parasitoid abundance, and stem cutting in favor of wheat next to cover crop at the Conrad 4 site in both years (Table 14, 15, 16, 17, 18, 19). In 2017, the field next to fallow had 39% cut stems while the one adjacent to cover crop had only 6% cutting (Table 19). This may be attributed to a difference in WSS population size between the two fields (Table 12, 14), but this cover crop was also beneficial to the rate of parasitism.

Aggregations of parasitoids were seen on the leaves of sunflowers (*Helianthus annuus*) seeded in the cover crop (Figure 11). Sunflowers have bracteal extrafloral nectaries which attract more parasitoids than other nectary morphologies (Quispe 2017). Extrafloral nectaries improve parasitoid fitness through increased host seeking ability, longevity, and resources for oogenesis. Extrafloral nectaries are also present in the field for longer periods than inflorescences (Géneau et al. 2012; 2013; Pemberton and Lee 1996; Stapel et al.

1997; Wäckers 2004). The aggregation of parasitoids on sunflower was observed over a three-week period and could have increased parasitoid success.

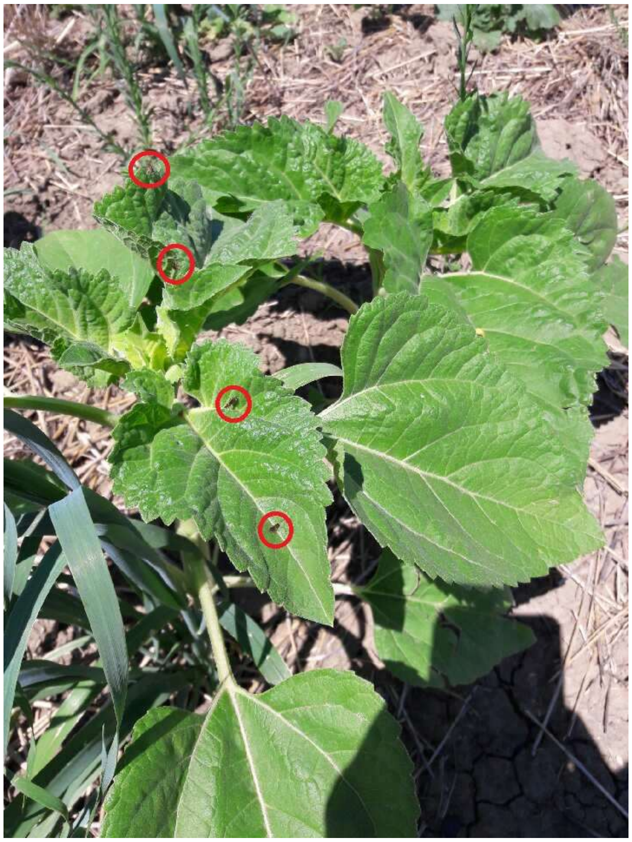


Figure 11: Parasitoid aggregation on sunflower (*Helianthus annuus*) in the cover crop field at the Conrad 4 site in 2017.

Safflower was another plant unique to this cover crop that may provide a benefit to parasitoids. Reis (2018) found that access to safflower increases the longevity of female *B. cephi* parasitoids. Oats (*Avena sativa*) may have been another beneficial component of this cover crop mix. Wheat stem sawfly preferentially oviposit in oats but cannot complete their life cycle within the oat stem (Holmes and Peterson 1961). This creates a biological ‘dead end’ and prevented some WSS from infesting the wheat, as described by Sing (2002). The Conrad 4 cover crop mix with sunflower, safflower, and oats was the best cover crop for attracting parasitoids (Table 15, 17) and reducing stem cutting (Table 18, 19).

Overall, the rest of the sites had a lower rate of stem cutting in samples collected from wheat fields next to pulse or cover crops than wheat next to fallow, except for one. Although the Conrad 2 site had a cover crop, it was late to emerge both years and remained essentially fallow throughout most of the WSS and first-generation parasitoid flight. The more abundant population of WSS was then able to infest the wheat field next to cover crop without the added predation that the cover crop field may have provided through an increased parasitoid population. This combination of factors caused the wheat field next to cover crop to have a greater rate of stem cutting than the wheat field next to fallow at the Conrad 2 site in 2016 and 2017.

The second objective of this study was to determine if parasitoids emerging from wheat beside a pulse or cover crop had larger bodies than parasitoids emerging from wheat grown adjacent to fallow. No trend for an effect of pulse or cover crops on parasitoid size was evident (Table 6, 7). This suggests no direct benefit is provided to the next generation by increased availability of sugar resources to the parents. Comparisons were made using newly emerged adult parasitoids with no access to food, so the only source of nutrition was the

WSS host. Differences in quality of the host larva, and indirectly host plant quality, were responsible for any difference in parasitoid size rather than additional nectar availability. Increased nectar resources may increase adult female body size and fecundity, yet any increase in carbohydrate reserves probably will not pass to their offspring. However, it is likely that access to nectar allows female parasitoids to develop more eggs and locate more hosts, thereby increasing WSS control provided by individual parasitoids (Salt 1941; Landis et al. 2000; Gurr et al. 2017; Reis 2018).

Another goal of this study was to determine whether field trapping is an acceptable alternative to postharvest stem dissection for surveying populations of WSS and braconid parasitoids. Postharvest stem dissections have the drawback of being time consuming and labor intensive compared to trapping WSS and parasitoid adults in the field. But stem dissections also have many advantages over field trapping. There are a lot of data gained from stem dissections that cannot be discerned from trap captures, such as parasitism rate, WSS and parasitoid mortality, and wheat stem solidness.

Stem dissections also sample the larval WSS which are causing damage to the wheat crop as opposed to adults caught in traps which are the parents of the generation causing damage. This makes stem dissections ideal for studies that require intensive WSS and parasitoid sampling. Trapping is much less time consuming, making it an ideal method for gathering data in real time about WSS and parasitoid adult populations. However, trapping does not capture as many insects in the sampled area as stem dissections. This makes trapping less suitable for areas with low abundances of WSS and parasitoid adults.

Trap placement is critical to the success of a trapping survey, as we saw in the difference in the correlation of trap captures and stem dissections between 2016 and 2017 (Figure 5, 6, 7, 8). In 2016, half of the traps were in the field adjacent to wheat, which made trap catches inconsistent. Having a differing number of traps on the interface of wheat and fallow fields and wheat and cover or pulse crop fields also caused discrepancies in WSS (R^2: 0.25) and parasitoid (R^2: 0.11) abundances between field trapping and postharvest stem dissections. In 2017 all traps were placed 1 m inside the wheat crop, and 8 traps were placed on each wheat field. This methodology performed better and had much higher correlation of WSS (0.59) and parasitoid (0.52) abundances between trapping and stem dissection.

Effects of Landscape Composition

Many papers show that herbivore abundance may increase with increasing landscape diversity (Jonsen and Fahrig 1997; Ragsdale et al. 2011). Perez-Alvarez et al. (2018) reported that increased meadow habitat around cabbage fields in New York state increased aphid and flea beetle abundance while decreasing lepidopteran pest abundance. Aphids and flea beetles benefitted from the undisturbed non-crop habitat, while lepidopteran pests suffered an increased number of parasitoids coming from the meadows. Semi-natural and natural grasslands may provide a role similar to meadow habitat and provide a source of parasitoids to attack WSS in the wheat crop but are most likely not a significant sink to WSS because wheat is usually a more desirable host than native grasses. However, there is a major difference between the two systems. While lepidopteran parasitoids are specialized on lepidopteran hosts, they can still take multiple species as hosts. The braconid parasitoids of WSS are not known to attack any other species. So, while grasslands may provide a source of parasitoids, they can only do so if there are WSS there as well.

Increasing crop diversity throughout the landscape is a benefit because it reduces host availability for WSS. Rand et al. (2014) claim that in this system, damage caused by WSS is not driven by landscape complexity so much as the amount of wheat on the landscape. As wheat cover decreases, so does WSS infestation, but no relationship was observed with the amount of natural grasslands in the area. One exception was the area of riparian grass between the wheat and fallow fields at Conrad 3 in 2016. This grass likely acted as a trap that intercepted WSS as they searched for hosts after emerging from the fallow field. Because of the available moisture, these grasses were green and vigorous throughout WSS flight. However, this is unlikely to happen at a significant scale on the landscape because the wet, riparian habitat is relatively uncommon in the region.

All sites in this study had relatively similar proportions of wheat and fallow wheat in the surrounding area, except for Moccasin in central Montana and

Chester in north central Montana which had limited infestation of WSS (Table 12, 13). The site in central Montana had significantly less wheat and fallow on the landscape than the other sites in the study, and the Chester site had less winter wheat on the surrounding landscape than sites with more WSS infestation (Supplemental Table 4). This corresponds with the results of our analysis on the response of WSS abundance to different land cover compositions in which we found that fallow acreage within a 2 km radius is the main driver of WSS abundance (Fig. 9). The proportion of fallow wheat on the landscape positively correlates with WSS numbers because it is a measure of the amount of habitat available to the previous generation. It is also a source of adult WSS which infest the current wheat crop.

The specialization of WSS as it adapted to wheat contributed to this effect. Wheat matures much more quickly than grasses native to the northern Great Plains. Wheat stem sawfly, a univoltine species, has quickly adapted its life cycle to synchronize with the winter wheat system that is prevalent in the study area. Meanwhile, bivoltine parasitoids are often unable to complete their second generation in the more rapidly maturing wheat (Holmes et al. 1963). When the crop matures too quickly, such as in a drought, it can cause the parasitoid population to crash, greatly reducing available biocontrol in the following season (Holmes et al. 1963). More natural grassland in the vicinity of the field may act as a source for parasitoids after these drought events and help maintain a constant parasitoid population. Natural or semi-natural grassland also increases parasitoid success leading to a reduction in WSS survival in grass relative to wheat (Rand et al. 2014).

Increased wheat acreage on the landscape provides more abundant, healthy hosts for WSS. Studies of other systems have shown that increasing acreage of a highly suitable host crop throughout the landscape greatly increases insect pest abundance (Beckler et al. 2004; O'Rourke et al. 2011; Carrière et al. 2012). Additionally, increased acreage of a crop in the landscape is correlated with host plant connectivity (Fahrig 2013), which allows WSS to easily locate nearby crops to infest when they emerge in the spring.

Carriere et al. (2012) found a similar increase in *Lygus* spp. density in cotton in areas with greater amounts of cotton, uncultivated habitats, and seed alfalfa on the surrounding landscape. *Lygus* spp. overwinter in uncultivated habitats then move into seed alfalfa crops in the spring. As the population develops, adult *Lygus* spp. migrate to cotton and cause severe damage. O'Rourke et al. (2011) found that *Diabrotica virgifera* abundance was highly correlated with corn field connectivity and it is likely that a similar reaction to the wheat dominated landscape is happening with WSS. The number of WSS hosts per acre is increased by an order of magnitude in wheat crops versus natural grasslands (Rand et al. 2014).

In addition, the increased stem diameter and vigor of wheat compared to natural grasses greatly improves the availability and quality of food resources within the stem (Criddle 1922; Perez-Mendoza et al. 2006b). The plant vigor hypothesis proposed by Price (1991) states that plants growing more vigorously and of a greater size than other plants within their population are favorable to insect herbivores, particularly endophytic herbivores such as WSS. In addition, chances of larval survival are increased on larger hosts (Price 1991; De Bruyn et al. 2001). High-quality hosts also allow for larger bodied WSS with more carbohydrate reserves allowing greater dispersal and the ability to create more eggs (Morrill et al. 2000b; Cárcamo et al. 2005). The increased acreage of monoculture wheat, a high-quality WSS host, has compounding effects over multiple years and allows WSS populations to increase rapidly while still retaining enough hosts to support the population (Risch et al. 1983). Replacing fallow and wheat acres with a non-host crop reduces the connectivity and availability of high-quality hosts for WSS, thus depressing the population.

The wheat crop can be a sink for parasitoids as well (Rand et al. 2014). Tillage operations (Runyon et al. 2002), poor life history synchronization (Holmes 1963), and low cutting height at harvest (Beres et al. 2011a) all reduce parasitoid success in wheat relative to native grasses. In contrast, reducing crop connectivity limits the ability of WSS to locate suitable hosts due to their relatively low mobility (Hanski, 1998; van Nouhuys 2005; Carriere et al. 2012).

Criddle (1923) proposed that WSS are weak fliers and cannot disperse more than 800 m. Since then average field sizes have drastically increased with mechanization and are sometimes greater than 1 km in length. It is likely that WSS have adapted to fly further than 800 m since 1923, but still most likely cannot disperse more than 2 km. Female parasitoids however, are able to disperse further than WSS. Egg resorption gives female parasitoids the ability to use egg resources to fuel their host searching and increases reproductive success at low host densities. Additional crop diversity may also provide foraging parasitoids with additional resources; increasing longevity, dispersal range, egg volume, and egg load (Reis 2018). This would allow parasitoids to adapt more readily than WSS to an environment with a more complex mosaic of habitat.

The type of habitat surrounding each field was analyzed as well. Regression models with km^2 fallow wheat, winter wheat, spring wheat, durum wheat, grassland/pasture, flowering crops, and developed space used as the explanatory variables were applied to WSS and parasitoid abundance data from postharvest stem dissections. Wheat fields with more fallow within a 2 km radius tended to have increased WSS infestation (Figure 9).

This was the result of increased host availability for the previous generation leading to larger WSS populations in the current growing season. When the current wheat crop was surrounded by vast amounts of fallowed wheat, it connected emerging adult WSS to habitat for their offspring, which allowed for rapid growth of source populations which led to severe infestation of wheat in subsequent growing seasons. No land-use variables other than fallow had a significant impact on the WSS abundance model and were left out. Rand et al. (2014) performed a less intensive survey of WSS abundance over a much larger area and found that wheat cover on the landscape was the most important driver of WSS abundance as well.

The relationship between surrounding land-use and parasitoid abundance was also analyzed but no significant effects were observed. It was hypothesized at the beginning of this study, that increased areas of natural grassland surrounding wheat fields may increase parasitoid populations. However, analysis of our data show this is not the case. Rand et al. (2014) found no correlation between landscape variables and parasitism rates.

These results make sense as braconid parasitoids of WSS are not known to take any other host. Natural grassland is ideal habitat for parasitoids of WSS, but is not advantageous to the parasitoid population outside of this habitat. Wheat stem sawfly abundance is the driving factor in parasitoid abundance. No matter how much grassland there is, the parasitoids must go where the WSS host is available. This research, as well as that of Rand (2014), likely found no correlation between land cover composition and parasitism rate because the rate of parasitism was not affected, only the abundance of WSS, which allowed the parasitoid population to increase as well.

Conclusions

This study shows that pulse and cover crops next to wheat certainly do not increase WSS damage to the crop and may benefit the wheat crop in some situations. However, more information is needed about the landscape interactions within the surrounding area of study sites. Getting sufficient landscape data to create a model of how different crop and grassland species interact with WSS and their natural enemies may provide insight into the effects of host connectivity, floral resources, and alternate plant hosts on WSS and associated parasitoids.

The sunflower, safflower, and oat combination within the cover crop mix at the Conrad 4 site was highly beneficial to parasitoids and reduced cutting by WSS from 39% next to fallow to 6% next to the cover crop in 2017. Cover crop mixes in general tended to be more effective than pulses in aiding parasitoid success and reduced cutting from 6 to 3% on average in 2016. In 2017, the difference was more pronounced with an average of 32% cut stems next to fallow and only 15% cut stems next to the cover crop.

This is likely due to increased nectar availability in mixed species cover crops that flower at different times and may possess extrafloral nectaries. Increased crop diversity may be a powerful tool to combat WSS when used in conjunction with other control methods such as seeding resistant wheat cultivars, increasing harvest height, and adopting no-till. All these practices benefit parasitoids of WSS, allowing them to become a more consistent and effective component of the agroecosystem. Reducing habitat connectivity may decrease WSS's ability to locate and infest crops, while also reducing the availability of hosts on the landscape.

WORKS CITED

Adhikari, S., T. Seipel, F. D. Menalled, and D. K. Weaver (2018) Farming System and Wheat Cultivar Affect Infestation of and Parasitism on *Cephus cinctus* in the Northern Great Plains. *Pest Management Science*, 74(11): 2480-2487.

Ainslie C. N. (1920) The western grass-stem sawfly (No. 841). *US Department of Agriculture*.

Ainslie C. N. (1929) The western grass-stem sawfly - a pest of small grains. *U.S. Department of Agriculture Technical Bulletin 157.*

Anonymous (1997) Wheat stem sawfly. Montana Crop Health Report. Special Edition. Montana Extension Service 10: 1-7.

van den Assem, J., J. A. van Iersel, and R. L. Los-den Hartogh (1989) Is Being Large More Important for Female Than Male Parasitic Wasps? *Behavior*, 108: 160-195.

Baggen, L. R., G. M. Gurr, and A. Meats. (1999) Flowers in Tri-Trophic Systems: Mechanisms Allowing Selective Exploitation by Insect Natural Enemies for Conservation Biological Control. *Entomologia Experimentalis et Applicata*, 91(1): 155-161.

Baggen, L. R. and G. M. Gurr. (1998) The Influence of Food on *Copidosoma koehleri* (Hymenoptera: Encyrtidae), and the Use of Flowering Plants as a Habitat Management Tool to Enhance Biological Control of Potato Moth, *Phthorimaea operculella* (Lepidoptera: Gelechiidae). *Biological Control*, 11: 9-17.

Balzan, M.V. and F.L. Wäckers. (2013) Flowers to Selectively Enhance the Fitness of a Host-Feeding Parasitoid: Adult Feeding by *Tuta absoluta* and its parasitoid *Necremnus artynes*. *Biological Control*, 67: 21-31.

Banks, J.E. (1998) The Scale of Landscape Fragmentation Affects Herbivore Response to Vegetation Heterogeneity. *Oecologia*, 117: 239-246.

Bartelt, R.J., A.A. Cossé, R.J. Petroski, D.K. Weaver (2001) Cuticular Hydrocarbons and Novel Alkenediol Diacetates from Wheat Stem Sawfly (*Cephus cinctus*): Natural Oxidation to Pheromone Components. *Journal of Chemical Ecology*, 28(2): 385-405.

Beckler, A.A., B.W. French, L.D. Chandler (2004) Characterization of Western Corn Rootworm (Coleoptera: Chrysomelidae) Population Dynamics in Relation to Landscape Attributes. *Agricultural and Forest Entomology*, 6(2): 129-139.

Beenakkers, A.M.T. (1969) Carbohydrate and Fat as a Fuel for Insect Flight: A Comparative Study. *Journal of Insect Physiology*, 15: 353-361.

Bekkerman, A. (2014) *Economic impacts of the Wheat Stem Sawfly and an Assessment of Risk Management Strategies*. Accessed 5/9/18 http://antonbekkerman.com/docs/sawfly_economics_final.pdf.

Beres, B.L. (2011) *Integrating the building blocks of agronomy into an integrated pest management system for wheat stem sawfly* (doctorate dissertation). University of Alberta, Edmonton, Alberta, Canada.

Beres, B. L., B.D. Hill, H.A. Cárcamo, J.J. Knodel, D.K. Weaver and R.D. Cuthbert (2017) An Artificial Neural Network Model to Predict Wheat Stem Sawfly Cutting in Solid-Stemmed Wheat Cultivars. *Canadian Journal of Plant Science*, 97(2): 329-339.

Beres, B. L., H. A. Cárcamo, and J. R. Byers (2007) Effect of Wheat Stem Sawfly Damage on Yield and Quality of Selected Canadian Spring Wheat. *Journal of Economic Entomology*, 100(1): 79-87.

Beres, B.L., H.A. Cárcamo, D.K. Weaver, L.M. Dosdall, M.L. Evenden, B.D. Hill, R.H. McKenzie, R.-C. Yang, and D.M. Spaner (2011a) Integrating the Building Blocks of Agronomy and Biocontrol into an IPM Strategy for Wheat Stem Sawfly. *Prairie Soils & Crops*, 4: 54-65.

Beres, B.L., H.A. Cárcamo, and E. Bremer (2009) Evaluation of Alternative Planting Strategies to Reduce Wheat Stem Sawfly (Hymenoptera: Cephidae) Damage to Spring Wheat in the Northern Great Plains. *Journal of Economic Entomology*, 102(6): 2137-2145.

Beres, B.L., H.A. Cárcamo, R.-C. Yang, and D.M. Spaner (2011b) Integrating Spring Wheat Sowing Density with Variety Selection to Manage Wheat Stem Sawfly. *Agronomy Journal*, 103(6): 1755-1764.

Beres, B. L., L.M. Dosdall, D.K. Weaver, H.A. Cárcamo, and D.M. Spaner (2011c) Biology and Integrated Management of Wheat Stem Sawfly and the Need for Continuing Research. *The Canadian Entomologist*, 143(2): 105-125.

Beres, B.L., R.H. McKenzie, H.A. Cárcamo, L.M. Dosdall, M.L. Evenden, R.-C. Yang, and D.M. Spaner (2012) Influence of Seeding Rate, Nitrogen Management, and Micronutrient Blend Applications on Pith Expression in Solid-Stemmed Spring Wheat. *Crop Science* 52: 1316-1329.

Benton, T.G., J.A. Vickery, and J.D. Wilson. (2003) Farmland Biodiversity: Is Habitat Heterogeneity the Key? *Trends in Ecological Evolution*, 18: 182-188.

Bianchi, F.J.J.A., C.J.H. Booij, and T. Tscharntke (2006) Sustainable Pest Regulation in Agricultural Landscapes: A Review on Landscape Composition, Biodiversity and Natural Pest Control. *Proceedings of the Royal Society of Biological Sciences*, 273(1595): 1715-1727.

Blanckenhorn, W. U. (2000) Temperature Effects On Egg Size and Their Fitness Consequences in the Yellow Dung Fly. *Evolutionary Ecology*, 14:627–643.

Blanckenhorn, W. U., and M. Demont. (2004) Bergmann and Converse Bergmann Latitudinal Clines in Arthropods: Two Ends of a Continuum? *Integrated Complete Biology*, 44: 413-424.

Bullock, D.G. (1992) Crop Rotation. *Critical Reviews in Plant Sciences*, 11: 309-326.

Buteler, M. and D.K. Weaver (2012) Host Selection by the Wheat Stem Sawfly in Winter Wheat and the Role of Semiochemicals Mediating Oviposition Preference. *Entomologia Experimentalis et Applicata*, 143(2): 138-147.

Buteler, M., D.K. Weaver, P.L. Bruckner, G.R. Carlson, J.E. Berg, P.F. Lamb (2010) Using Agronomic Traits and Semiochemical Production in Winter Wheat Cultivars to Identify Suitable Trap Crops for the Wheat Stem Sawfly. *The Canadian Entomologist*, 142(3): 222-233.

Buteler, M., D.K. Weaver, P.R. Miller (2008) Wheat Stem Sawfly-Infested Plants Benefit from Parasitism of the Herbivorous Larvae. *Agricultural and Forest Entomology*, 10(4): 347-354.

Buteler, M., D. K. Weaver, R. K. D. Peterson (2009) Oviposition Behavior of the Wheat Stem Sawfly When Encountering Plants Infested With Cryptic Conspecifics. *Environmental Entomology*, 38(6): 1707-1715.

Buteler, M., R. K. D. Peterson, M. L. Hofland, and D. K. Weaver (2015) A Multi-Decrement Life Table Reveals That Host Plant Resistance and Parasitism Are Major Causes of Mortality for the Wheat Stem Sawfly. *Environmental Entomology*, 44(6): 1571-1580.

Cárcamo, H. A., B. L. Beres, F. Clarke, R. J. Byers, H.-H. Mündel, K. May, and R. DePauw (2005) Influence of Plant Host Quality on Fitness and Sex Ratio of the Wheat Stem Sawfly (Hymenoptera: Cephidae). *Environmental Entomology*, 34(6): 1579-1592.

Cardinale, B. J., C. T. Harvey, K. Gross, and A. R. Ives. (2003) Biodiversity and Biocontrol: Emergent Impacts of a Multi-Enemy Assemblage on Pest Suppression and Crop Yield in an Agroecosystem. *Ecol. Lett*. 6: 857-865.

Carrière Y., P.B. Goodell, C. Ellers-Kirk, G. Larocque, P. Dutilleul, S.E. Naranjo, P.C. Ellsworth (2012) Effects of Local and Landscape Factors on Population Dynamics of a Cotton Pest. *PLoS one*, 7(6): e39862.

Chakraborty, S., P. K. Tiwari, S. K. Sasmal, S. Biswas, S. Bhattacharya, J. Chattopadhyay. (2017) Interactive Effects of Prey Refuge and Additional Food for Predator in a Diffusive Predator-Prey System. *Applied Mathematical Modeling*, *47*: 128-140.

Charnov, E.L. (1979) The General Evolution of Patterns of Sexuality: Darwinian Fitness. *American Naturalist*, 113: 465-480.

Charnov, E.L., Los-den Hartogh, R.L. Jones, W.T. & van den Assem. (1981) Sex Ratio Evolution in a Variable Environment. *Nature*, 289: 27-33.

Chisolm, P.J., M.M. Gardiner, E.G. Moon, D.W. Crowder (2014) Tools and Techniques for Investigating Impacts of Habitat Complexity on Biological Control. *Biological Control*, 75: 48-57.

Chown, S. L. and K. J. Gaston. (1999) Exploring Links Between Physiology and Ecology at Macro-Scales: The Role of Respiratory Metabolism in Insects. *Biology Review*, 74: 87–120.

Chown, S.L. and K.J. Gaston (2010) Body Size Variation in Insects: A Macroecological Perspective. *Biological Reviews*, 85: 139-169.

Chown, S. L. and C. J. Klok. (2003) Altitudinal Body Size Clines: Latitudinal Effects Associated with Changing Seasonality. *Ecography*, 26:445–455.

Clough, Y., A. Kruess, D. Kleijn, T. Tscharntke (2005) Spider Diversity in Cereal Fields: Comparing Factors at Local, Landscape and Regional Scales. *Journal of Biogeography*, 32: 2007-2014.

Cockbain, A.J. (1961) Fuel Utilization and Duration of Tethered Flight in *Aphis facae* Scop. *Journal of Experimental Biology*, 38: 163-174.

Cockrell, D. M., R. J. Griffin-Nolan, T. A. Rand, N. Altilmisani, P. J. Ode, and F. Peairs (2017) Host Plants of the Wheat Stem Sawfly (Hymenoptera: Cephidae). *Environmental Entomology,* 46(4): 847-854.

Concepción, E. D., M. Díaz, R. A. Baquero (2008) Effects of Landscape Complexity on the Ecological Effectiveness of Agri-Environment Schemes. *Landscape Ecology*, 23: 135-148.

Conover, D. O. and T. M. C. Present. (1990) Countergradient Variation in Growth Rate: Compensation for Length of the Growing Season Among Atlantic Silversides from Different Latitudes. *Oecologia,* 83: 316–324.

Coombs, M.T. (1997) Influence of Adult Food Deprivation and Body Size on Fecundity and Longevity of *Trichopoda giacomellii*: A South American Parasitoid of *Nezara viridula*. *Biological Control*, 8(2): 119–123.

Cossé A.A., R.J. Bartelt, D.K. Weaver, B.W. Zilkowski (2002) Pheromone Components of the Wheat Stem Sawfly: Identification, Electrophysiology, and Field Bioassay. *Journal of Chemical Ecology*, 28(2): 407-423.

Costamagna, A. C. and D. A. Landis. (2004) Effect of Food Resources on Adult *Glyptapameles militaris* and *Meteorus commums* (Hymenoptera: Braconidae), Parasitoids of *Pseudaletia unipuncta* (Lepidoptera: Noctuidae). *Environmental Entomology*, 33: 128-137.

Criddle, N. (1917) Further Observations upon the Habits of the Western Wheat Stem Sawfly in Manitoba and Saskatchewan. *The Agricultural Gazette of Canada*, 4(3): 176-177.

Criddle, N. (1922) The Western Wheat-Stem Sawfly and its Control. *Dominion of Canada Department of Agriculture*, Pamphlet No. 6.

Criddle, N. (1923) The Life Habits of *Cephus cinctus* Nort. In Manitoba. *The Canadian Entomologist*, 55:1-4.

Cronin, J.T. (2007) From Population Sources to Sieves: The Matrix Alters Host-Parasitoid Source-Sink Structure. *Ecology*, 88(12): 2966-2976.

(2018) Cropscape. *USDA National Agricultural Statistics Service*. Accessed 5/15/18, https://nassgeodata.gmu.edu/CropScape/.

Davis, E.G., C. Benton, and H.W. Somsen. (1955) Natural Enemies of the Wheat Stem Sawfly in North Dakota and Montana. *Bimonthly Bulletin*, 18(2): 63-65.

De Bruyn, L., J. Scheirs, R. Verhagen (2002) Nutrient Stress, Host Plant Quality and Herbivore Performance of a Leaf-Mining Fly on Grass. *Oecologia*, 130(4): 594-599.

Delaney, K.J., D.K. Weaver, and R.K.D. Peterson (2010) Photosynthesis and Yield Reductions from Wheat Stem Sawfly (Hymenoptera: Cephidae): Interactions with Wheat Solidness, Water Stress, and Phosphorous Deficiency. *Journal of Economic Entomology*, 103(2): 516-524.

Ellers, J. (1996) Fat and Eggs: An Alternative Method to Measure the Trade-Off Between Survival and Reproduction in Insect Parasitoids. *Netherlands Journal of Zoology*, 46, 227-235.

Ellers, J. and van Alphen, J.J.M. (1997) Life History Evaluation in *Asobara tabida*: Plasticity in the Allocation of Fat Reserves to Survival and Reproduction. *Journal of Evolutionary Biology*, 10: 771-785.

Ellers, J., J.J.M. van Alphen, and J.G. Sevenster. (1998) A Field Study of Size-Fitness Relationships in the Parasitoid *Asobara tabida*. *Journal of Animal Ecology*, 67: 318-324.

Evans, L. T., I. F. Wadlaw, and R. A. Fischer (1975) Wheat. In *Crop Physiologies: Some Case Histories* (pp. 101-150). London, UK: Cambridge University Press.

Fahrig, L. (2013) Rethinking Patch Size and Isolation Effects: The Habitat Amount Hypothesis. *Journal of Biogeography*, 40: 1649-1663.

Flint, M.L. and P.A. Roberts (1988) Using Crop Diversity to Manage Pest Problems: Some California Examples. *American Journal of Alternative Agriculture*, 3: 163-167.

Fulbright, J., K. Wanner, A. Bekkerman, and D. Weaver (2017) Wheat Stem Sawfly Biology. *Montana State University Extension*, MT201107AG.

Géneau, C.E, F.L. Wäckers, H. Luka, C. Daniel, O. Balmer (2012) Selective Flowers to Enhance Biological Control of Cabbage Pests by Parasitoids. *Basic Applied Ecology*, 13:85-93.

Géneau, C. E., F. L. Wäckers, H. Luka, O. Balmer (2013) Effects of Extrafloral and Floral Nectar of *Centaurea cyanus* on the Parasitoid Wasp *Microplitis mediator*: Olfactory Attractiveness and Parasitization Rates. *Biological Control*: 66(1): 16-20.

Godfray, H.C.J. (1994) *Parasitoids: Behavioral and Evolutionary Ecology*. Princeton University Press, Princeton, New Jersey.

Gurr, G. M., S. D. Wratten, and J. M. Luna. (2003) Multi-Function Agricultural Biodiversity: Pest Management and Other Benefits. *Basic Applied Ecology*, 4: 107-116.

Gurr, G.M., Z. Lu, X. Zheng, H. Xu, P. Zhu, G. Chen, X. Yao, J Cheng, Z. Zhu, J.L. Catindig, S. Villareal, H.V. Chien, L.Q. Cuong, C. Channoo, N. Chengwattana, L.P. Lan, L.H. Hai, J. Chaiwong, H.I. Nicol, D.J. Perovic , S.D. Wratten, and K.L. Heong. (2016) Multi-country evidence that crop diversification promotes ecological intensification of agriculture. *Nature Plants*, 2: 1-4.

Gurr, G. M., S. D. Wratten, D. A. Landis, & M. You. (2017). Habitat management to suppress pest populations: progress and prospects. *Annual Review of Entomology*, 62: 91–109.

Hanski, I. (1998) Metapopulation Dynamics. *Nature*, 396:41-49.

Harvey, J.A., I.F. Harvey, and D.J. Thompson. (1994) Flexible Larval Growth Allows Use of a Range of Host Sizes by a Parasitoid Wasp. *Ecology*, 75: 1420-1428.

van der Have, T. M. and G. de Jong. (1996) Adult Size in Ectotherms: Temperature Effects on Growth and Differentiation. *Journal of Theoretical Biology*, 18: 329–340.

Haynes K.J., and T.O. Crist (2009) Insect Herbivory in an Experimental Agroecosystem: The Relative Importance of Habitat Area, Fragmentation, and the Matrix. *Oikos*, 118(10): 1477-1486.

Head, G., W. Moar, M. Eubanks, B. Freeman, J. Ruberson, A. Hagerty, and S. Turnipseed (2005) A Multiyear, Large-Scale Comparison of Arthropod Populations on Commercially Managed *Bt* and non-*Bt* Cotton Fields. *Environmental Entomology*, 34(5): 1257-1266.

Heinz, K.M. (1991) Sex-Specific Reproductive Consequences of Body Size in the Solitary Ectoparasitoid *Diglyphus begini*. *Evolution*, 45: 1511-1515.

Holmes, N.D. (1954) Food Relations of the Wheat Stem Sawfly, *Cephus cinctus* Nort. (Hymenoptera: Cephidae). *The Canadian Entomologist*, 86(4): 159-167.

Holmes, N.D. (1960) Resistance of Host Varieties to the Wheat Stem Sawfly, *Cephus cinctus* Nort. (Hymenoptera: Cephidae). *Report of the 7th Commonwealth Entomological Conference*.

Holmes, N.D. (1977) The Effect of the Wheat Stem Sawfly, *Cephus cinctus* (Hymenoptera: Cephidae), on the Yield and Quality of Wheat. *The Canadian Entomologist*, 109: 1591-1598.

Holmes, N.D. (1982) Population Dynamics of the Wheat Stem Sawfly, *Cephus cinctus* (Hymenoptera: Cephidae), in Wheat. *Can. Entomologist*, 114: 775-788.

Holmes, N.D. and Peterson, L.K. (1960) Influence of the Host on Oviposition by the Wheat Stem Sawfly, *Cephus cinctus* Nort. (Hymenoptera: Cephidae). *Canadian Journal of Plant Science*, 40: 29-46.

Holmes, N.D. and Peterson, L.K. (1961) Resistance of Spring Wheats to the Wheat Stem Sawfly, *Cephus cinctus* Nort. (Hymenoptera: Cephidae): I. Resistance to the Egg. *The Canadian Entomologist*, 93(4): 250-260.

Holmes, N.D. and Peterson L.K. (1963) Heptachlor as a Systemic Insecticide Against the Wheat Stem Sawfly, *Cephus cinctus* Nort. *The Canadian Entomologist*, 95(8): 792-796.

Holmes, N.D. and Peterson L.K. (1965) Swathing Wheat and Survival of Wheat Stem Sawfly. *Canadian Journal of Plant Science*, 45: 579-581.

Holmes, N.D., W.A. Nelson, L.K. Peterson, and C.W. Farstad. (1963) Causes of Variations in Effectiveness of *Bracon cephi* (Gahan) (Hymenoptera: Braconidae) as a Parasite of the Wheat Stem Sawfly. *The Canadian Entomologist*, 95(2): 113-126.

Holzschuh, A., I. Steffan-Dewenter, D. Kleijn, & T. Tscharntke (2007) Diversity of Flower-Visiting Bees in Cereal Fields: Effects of Farming System, Landscape Composition, and Regional Context. *Journal of Applied Ecology*, 44(1): 41-49.

Honek, A. (1993) Intraspecific Variation in Body Size and Fecundity in Insects: A General Relationship. *Oikos*, 66:483–492.

Ives, A. R., J. L. Klug, and K. Gross. (2000) Stability and Species Richness in Complex Communities. *Ecol. Lett*. 3: 399-411.

Jamont, M., S. Crépellière, & B. Jaloux (2013) Effect of Extrafloral Nectar Provisioning on the Performance of the Adult Parasitoid *Diaeretiella rapae*. *Biological control*, 65: 271-277.

Jervis, M.A., P. N. Ferns and G. E. Heimpel. (2003) Body Size and the Timing of Egg Production in Parasitoid Wasps: A Comparative Analysis. *Functional Ecology,* 17(3): 375-383.

Jonsen, I.D., and L. Fahrig (1997) Response of Generalist and Specialist Insect Herbivores to Landscape Spatial Structure. *Landscape Ecology*, 12(3): 185-197.

Ju, X. T., C. L. Kou, P. Christie, Z. X. Dou, & F. S. Zhang (2006) Changes in the Soil Environment from Excessive Application of Fertilizers and Manures to Two Contrasting Intensive Cropping Systems on the North China Plain. *Environmental Pollution*, 145: 497-506.

Keren I. N., F. D. Menalled, D. K. Weaver, J. F. Robison-Cox (2015) Interacting Agricultural Pests and Their Effect on Crop Yield: Application of a Bayesian Decision Theory Approach to the Joint Management of *Bromus tectorum* and *Cephus cinctus*. *PLoS ONE* 10(2): e0118111. doi:10.1371/journal.pone.0118111.

Key, N. (2018) Farm Size and Productivity Growth in the United States Corn Belt. *Food Policy*, in press. https://doi.org/10.1016/j.foodpol.2018.03.017.

King, B.H. (1987) Offspring Sex Ratios in Parasitoid Wasps. *Quarterly Review of Biology*, 62: 367-396.

King, B.H. and J.G. Richards. (1969) Oogenesis in *Nasonia vitripennis* (Walker) (Hymenoptera: Pteromalidae). *Proceedings of the Royal Entomological Society of London (A),* 44: 143-157.

Kirkegaard, J., O. Christen, J. Krupinsky, D. Layzell (2008) Break Crop Benefits in Temperate Wheat Production. *Field Crops Research*, 107(3): 185-195.

Kishinevsky, M., T. Keasar, A. R. Harari, E. Chiel (2017) A Comparison of Naturally Growing Vegetation vs. Border-Planted Companion Plants for Sustaining Parasitoids in Pomegranate Orchards. *Agriculture, Ecosystems, and Environment,* 246: 117-123.

Kleijn, D., F. Berendse, R. Smit, N. Gilissen, J. Smit, B. Brak, & R. Groeneveld (2004) Ecological Effectiveness of Agri-Environment Schemes in Different Agricultural Landscapes in the Netherlands. *Conservation Biology*, 18(3): 775-786.

Kleijn, D., R. A. Baquero, Y. Clough, M. Díaz, J. De Esteban, F. Fernández, D. Gabriel, F. Herzog, A. Holzschuh, R. Jöhl, E. Knop, A. Kruess, E. J. P. Marshall, I. Steffan-Dewenter, T. Tscharntke, J. Berhulst, T. M. West, & J. L. Yela (2006) Mixed Biodiversity Benefits of Agri-Environment Schemes in Five European Countries. *Ecology Letters*, 9: 243-254.

Kleijn, D. and W.J. Sutherland (2003) How Effective are European Agri-Environment Schemes in Conserving and Promoting Biodiversity? *The Journal of Applied Ecology*, 40(6): 947-969.

Lamb, R.J. (1992) Developmental Rate of *Acyrthosiphon pisum* (Homoptera: Aphididae) at Low Temperatures: Implications for Estimating Rate Parameters for Insects. *Environmental Entomology*, 21(1): 10-19.

Landis, D. A., S. D. Wratten, & G. M. Gurr. (2000) Habitat Management to Conserve Natural Enemies of Arthropod Pests in Agriculture. *Annual Review of Entomology,* 45: 175–201.

Landis, D.A. (2017) Designing Agricultural Landscapes for Biodiversity-Based Ecosystem Services. *Basic and Applied Ecology*, 18: 1-12.

Lee, J. C, G. E. Heimpel, and G. L. Leibee. (2004) Comparing Floral Nectar and Aphid Honeydew Diets on the Longevity and Nutrient Levels of a Parasitoid Wasp. *Entomologia Experimentalis et Applicata*, 111(3): 189-199.

Leius, K. (1961) Influence of Food on Fecundity and Longevity of Adults of *Itoplectis conquisitor* (Say) (Hymenoptera: Ichneumonidae). *Canadian Entomology*, 93(9): 771–780.

Lesieur, V., J.-F. Martin, D.K. Weaver, K.A. Hoelmer, D.R. Smith, W.L. Morrill, N. Kadiri, F.B. Peairs, D.M. Cockrell, T.L. Randolph, D.K. Waters, M.-C. Bon. (2016) Phylogeography of the Wheat Stem Sawfly, *Cephus cinctus* Norton (Hymenoptera: Cephidae): Implications for Pest Management. *PLoS ONE*, 11(12): e0168370.

Letourneau, D. K., S.G. Bothwell Allen, & J.O. Stireman III. (2012) Perennial Habitat Fragments, Parasitoid Diversity and Parasitism in Ephemeral Crops. *Journal of Applied Ecology*, 49: 1405-1416.

Levinton, J. S. and R. K. Monahan. (1983) The Latitudinal Compensation Hypothesis: Growth Data and a Model of Latitudinal Growth Differentiation Based Upon Energy Budgets. II. Intraspecific Comparisons Between Subspecies of *Ophryotrocha puerilis*. *Biology Bulletin*, 165: 699–707.

Long, J. A., R. L. Lawrence, P. R. Miller, L. A. Marshall (2014a) Changes in Field-Level Cropping Sequences: Indicators of Shifting Agricultural Practices. *Agriculture, Ecosystems and Environment*, 189: 11-20.

Long, J. A., R. L. Lawrence, P. R. Miller, L. A. Marshall, M. C. Greenwood (2014b) Adoption of Cropping Sequences in Northeast Montana: A Spatio-Temporal Analysis. *Agriculture, Ecosystems and Environment*, 197: 77-87.

Losey, J. E. and R. F. Denno. (1998) Positive Predator-Predator Interactions: Enhanced Predation Rates and Synergistic Suppression of Aphid Populations. *Ecology*, 79: 2143-2152.

Luginbill, P. and E.F. Knipling. (1969) Suppression of Wheat Stem Sawfly with Resistant Wheat. *Production Research Report No. 107*. USDA.

Macedo, T.B., D.K. Weaver, and R.K.D. Peterson (2006) Characterization of the Impact of Wheat Stem Sawfly, *Cephus cinctus* Norton, on Pigment Composition and Photosystem II Photochemistry of Wheat Heads. *Environmental Entomology*, 35(4): 1115-1120.

Macedo, T.B., D.K. Weaver, and R.K.D. Peterson (2007) Photosynthesis in Wheat at the Grain Filling Stage is Altered by Larval Wheat Stem Sawfly (Hymenoptera: Cephidae) Injury and Reduced Water Availability. *Journal of Entomological Science*, 42(2): 228-238.

Macedo, T.B., R.K.D. Peterson, D.K. Weaver, and W.L. Morrill (2005) Wheat Stem Sawfly, *Cephus cinctus* Norton, Impact on Wheat Primary Metabolism: An Ecophysiological Approach. *Environmental Entomology*, 34(3): 719-726.

Mackay, M.R. (1956) Cytology and Parthenogenesis of the Wheat Stem Sawfly, *Cephus cinctus* Nort. (Hymenoptera: Cephidae). *Canadian Journal of Zoology*, 33(3): 161-174.

Maier, C. T. (1981) Parasitoids Emerging from Puparia of *Rhagoletis pomonella* (Diptera: Tephritidae) Infesting Hawthorn and Apple in Connecticut, USA. *Canadian Journal of Entomology*, 113: 867-870.

Mankin, R.W., J. Brandhorst-Hubbard, K.L. Flanders, M. Zhang, R.L. Crocker, S. L. Lapointe, C.W. McCoy, J.R. Fisher and D.K. Weaver (2000) Eavesdropping on Insects Hidden in Soil and Interior Structures of Plants. *Journal of Economic Entomology*, 93(4): 1173-1182.

Mankin, R.W., D.K. Weaver, M. Grieshop, B. Larson, W.L. Morrill (2004) Acoustic System for Insect Detection in Plant Stems: Comparisons of *Cephus cinctus* in Wheat and *Metamasius callizona* in Bromeliads. *Journal of Agricultural and Urban Entomology*, 21(4): 239-248.

Masaki, S. (1967) Geographic Variation and Climatic Adaptation in a Field Cricket. *Evolution* 21: 725–741.

McCabe, E., G. Loeb, H. Grab (2017) Responses of Crop Pests and Natural Enemies to Wildflower Borders Depends on Functional Group. *Insects*, 8(3): 73-80.

McGinnis, A. J. (1950) *Sex ratio studies on the wheat stem sawfly,* Cephus cinctus *Nort*. (Master's thesis) Montana State University, Bozeman, Montana, USA.

McNeal, F.H., M.A. Berg, and P. Luginbill. (1955) Wheat Stem Sawfly Damage in Four Spring Wheat Varieties as Influenced by Date of Seeding. *Agronomy Journal*, 47(11): 522-525.

McNeil, J.N. (1991) Behavioral Ecology of Pheromone-Mediated Communication in Moths and its Importance in the Use of Pheromone Traps. *Annual Reviews of Entomology*, 36: 407- 430.

Meers, S.B. (2005) *Impact of Harvest Operations of Parasitism of the Wheat Stem Sawfly,* Cephus cinctus *Norton (Hymenoptera: Cephidae)* (Master's thesis). Montana State University, Bozeman, Montana.

Miller, P.R., J. Waddington, C.L. McDonald, and D.A. Derksen (2002) Cropping Sequence Affects Wheat Productivity on the Semiarid Northern Great Plains. *Canadian Journal of Plant Science*, 82(2): 307-318.

Montana Department of Agriculture (MDA). (2015) Thimet® 20-G. *EPA SLN No. MT-150001*. Accessed 13 April 2018, https://agr.mt.gov/Portals/168/Documents/Archive/PesticideReg/MT-15-0001.pdf.

Montana Department of Agriculture (MDA). (2018) Growth of Montana Pulse Acres (Peas, Lentils, Chickpeas). *Montana Dept. of Agriculture*. Accessed 27 March 2018, http://agr.mt.gov/Portals/168/Documents/Pulse/2017_Pulse_Acres_Maps.pdf.

Morrill, W.L. (1983) Early History of Cereal Grain Insect Pests in Montana. *Bulletin of the Entomological Society of America*, 29(4): 24-28.

Morrill, W. L. (1992) Wheat Stem Sawfly (Hymenoptera: Cephidae): Damage and Detection. *Journal of Economic Entomology*, 85(6): 2413-2417.

Morrill, W. L. and D. K. Weaver (2000a) Host Plant Quality and Male Wheat Stem Sawfly (Hymenoptera: Cephidae) Fitness. *Journal of Entomological Science*, 35(4): 478-482.

Morrill, W.L., D. K. Weaver, and G. D. Johnson. (2001) Trap Strip and Field Border Modification for Management of the Wheat Stem Sawfly (Hymenoptera: Cephidae). *J. Entomol. Science*, 36(1): 34-45.

Morrill, W.L., D.K. Weaver, N.J. Irish, and W.F. Barr (2001b) *Phyllobaenus dubius* (Wolcott) (Coleoptera: Cleridae), a New Record of a Predator of the Wheat Stem Sawfly (Hymenoptera: Cephidae). *Journal of the Kansas Entomological Society*, 74(3): 181-183.

Morrill, W. L. and G.D. Kushnak (1996) Wheat Stem Sawfly (Hymenoptera: Cephidae) Adaptation to Winter Wheat. *Environmental Entomology*, 25(5): 1128-1132.

Morrill, W.L. and G.D. Kushnak (1999) Planting Date Influence on the Wheat Stem Sawfly (Hymenoptera: Cephidae) in Spring Wheat. *J. Agric. Entomol.* 16(2): 123-128.

Morrill, W.L., G.D. Kushnack, and J.W. Gabor. (1998) Parasitism of the Wheat Stem Sawfly (Hymenoptera: Cephidae) in Montana. *Biological Control*, 12: 159-163.

Morrill, W. L., J. W. Gabor, D. K. Weaver, G. D. Kushnak, N. J. Irish (2000b) Effect of Host Plant Quality on the Sex Ratio and Fitness of Female Wheat Stem Sawflies (Hymenoptera: Cephidae). *Environmental Entomology*, 29(2):195-199.

Munro, J.A. (1945). Wheat Stem Sawfly and Harvest Loss. *Bimonthly Bulletin*, 7(4): 12-16.

Nansen, C., M.E. Payton, J.B. Runyon, D.K. Weaver, W.L. Morrill, and S.E. Sing (2005) Preharvest Sampling Plan for Larvae of the Wheat Stem Sawfly, *Cephus cinctus* (Hymenoptera: Cephidae), in Winter Wheat Fields. *Canadian Entomology*, 137: 602-614.

Nelson, W.A. and C.W. Farstad. (1953) Biology of *Bracon cephi* (Gahan) (Hymenoptera: Braconidae), An Important Native Parasite of the Wheat Stem Sawfly, *Cephus cinctus* Nort. (Hymenoptera: Cephidae), in Western Canada. *The Canadian Entomologist*, 85(3): 103-107.

Nicol, C.M.Y. and M. Mackauer (2003) The Scaling of Body Size and Mass in a Host-Parasitoid Association: Inluence of Host Species and Stage. *Entomologia Experimentalis et Applicata*, 90(1): 83-92.

Norton, E. (1872) Notes on North American Tenthredinidae with Descriptions of New Species. *Transactions of the American Entomological Society*, 4:77-86.

van Nouhuys, S. (2005) Effects of Habitat Fragmentation at Different Trophic Levels in Insect Communities. *Annales Zoologici Fennici*, 42: 433-447.

O'Rourke, M.E., K. Rienzo-Stack, A.G. Power (2011) A Multi-Scale, Landscape Approach to Predicting Insect Populations in Agroecosystems. *Ecological Applications,* 21(5): 1782-1791.

Pallipparambil, R.G.R. (2006) *Mass Rearing of* Bracon cephi *(Gahan) and* B. lissogaster *Muesebeck, Parasitoids of the Wheat Stem Sawfly,* Cephus cinctus *Norton, and Temperature-Induced Mortality in Host Immatures* (Master's thesis). Montana State University, Bozeman, Montana.

Peck, G.E. (2004) *Potential Semiochemicals of Wheat (*Triticum aestivum *L.) Induced by Oviposition and Feeding of the Wheat Stem Sawfly,* Cephus cinctus *Norton (Hymenoptera: Cephidae)* (Master's Thesis). Montana State University, Bozeman, Montana.

Pemberton, R.W., J.-H. Lee (1996) The Influence of Extrafloral Nectaries on Parasitism of an Insect Herbivore. *American Journal of Botany*, 83:1187-1194.

Perez-Alvarez, R., B.A. Nault, and K. Poveda (2018) Contrasting Effects of Landscape Composition on Crop Yield Mediated by Specialist Herbivores. *Ecological Applications*, 28(3): 842-853.

Perez-Mendoza, J. and D. K. Weaver (2006a) Temperature and Relative Humidity Effects on Postdiapause Larval Development and Adult Emergence in Three Populations of Wheat Stem Sawfly (Hymenoptera: Cephidae). *Environmental Entomology*, 35(5): 1222-1231.

Perez-Mendoza, J., D. K. Weaver, W. L. Morrill (2006b) Infestation of Wheat and Downy Brome Grass by Wheat Stem Sawfly and Subsequent Larval Performance. *Environmental Entomology*, 35(5): 1279-1285.

Pérez, O.G. (2009) *Behavioral and Sensory Responses of Endemic Braconid Parasitoids to Changes in Volatile Emissions Induced by Wheat Stem Sawfly,* Cephus cinctus *Herbivory* (PhD dissertation). Montana State University, Bozeman, MT, USA.

Perović, D. J., S. Gámez-Virués, D. A. Landis, F. Wäckers, G. M. Gurr, S. D. Wratten, M. You, and N. Desneux. (2018) Managing biological control services through multi-trophic trait implementation at local and landscape scales. *Biological Reviews*, 93: 306-321.

Peterson, R.K.D., M. Buteler, D.K. Weaver, T.B. Macedo, Z. Sun, O.G. Perez, G.R. Pallipparambil (2011) Parasitism and the Demography of Wheat Stem Sawfly Larvae, *Cephus cinctus*. *BioControl*, 56: 831-839.

Piesik, D., D.K. Weaver, G.E. Peck, W.L. Morrill. (2006) Diel Patterns in Volatiles Released by Mechanically-Damaged Wheat Plants. *Electronic Journal of Polish Agricultural Universities*, 9(4):1-7.

Piesik, D., D.K. Weaver, G.E. Peck, W.L. Morrill. (2006) Mechanically-Injured Wheat Plants Release Greater Amounts of the Secondary Metabolites Linalool and Linalool Oxide. *Journal of Plant Protection Research*, 46(1): 29-39.

Platt, A.W., C.W. Farstad (1946) The Reaction of Wheat Varieties to Wheat Stem Sawfly Attack. *Scientific Agriculture*, 26(6): 231-247.

Platt, A.W., C.W. Farstad, J.A. Callenbach (1948) The Reaction of Rescue Wheat to Sawfly Damage. *Scientific Agriculture*, 28(4): 154-161.

Portman, S.L., S.T. Jaronski, D.K. Weaver, and G.V.P. Reddy (2018) Advancing Biological Control of the Wheat Stem Sawfly: New Strategies in a 100-yr Struggle to Manage a Costly Pest in the Northern Great Plains. *Annals of the Entomological Society of America*, 111(3): 1-7.

Price, P.W. (1991) The Plant Vigor Hypothesis and Herbivore Attack. *OIKOS*, 62(2):244-251.

Puech, C., S. Poggi, J. Baudry, S. Aviron (2015) Do Farming Practices Affect Natural Enemies at the Landscape Scale? *Landscape Ecology*, 30(1): 125-140.

Quispe, R., M. Mazón, A. Rodríguez-Berrío. (2017) Do Refuge Plants Favor Natural Pest Control in Maize Crops? *Insects*, 8(3): 71.

R Core Team (2016) R: A Language and Environment for Statistical Computing. *R Foundation for Statistical Computing*, Vienna, Austria.

Rada, N.E. and K.O. Fuglie (2018) New Perspectives on Farm Size and Productivity. *Food Policy*, in press. https://doi.org/10.1016/j.foodpol.2018.03.015.

Ragsdale, D.W., D.A. Landis, J. Brodeur, G.E. Heimpel, and N. Desneux (2011) Ecology and Management of the Soybean Aphid in North America. *Annual Review of Entomology*, 56(1): 375-399.

Ramaswamy, S.B., R.T. Cardé, and J.A. Witter (1983) Relationships Between Catch in Pheromone-Baited Traps and Larval Density of the Spruce Budworm, *Choristoneura Fumiferana* (Lepidoptera: Tortricidae). *The Canadian Entomologist*, 115(11): 1437-1443.

Rand, T.A., D.K. Waters, S.L. Blodgett, J.J. Knodel, M.O. Harris. (2014) Increased Area of a Highly Suitable Host Crop Increases Herbivore Pressure in Intensified Agricultural Landscapes. *Agriculture, Ecosystems and Environment*, 186: 135-143.

Rand, T. A. & T. Tscharntke. (2007). Contrasting effects of natural habitat loss on generalist and specialist aphid natural enemies. *Oikos,* 116: 1353–1362.

Rand, T.R., D.K. Waters, T.G. Shanower (2016) Preliminary Evaluation of the Parasitoid Wasp, *Collyria catoptron*, as a Potential Biological Control Agent Against the Wheat Stem Sawfly, *Cephus cinctus*, in North America. *Biocontrol Science and Technology*, 26(1): 61-71.

Reeve, J.D., J.T. Cronin, and K.J. Haynes (2008) Diffusion Models for Animals in Complex Landscapes: Incorporating Heterogeneity among Substrates, Individuals and Edge Behaviours. *Journal of Animal Ecology,* 77(5): 898-904.

Reis, D.A. (2018) *The Potential of Sugar Resources in the Reproductive Biology of Wheat Stem Sawfly Parasitoids* (Master's thesis). Montana State University, Bozeman, MT, USA.

Riedl, H. and B.A. Croft (1974) A Study of Pheromone Trap Catches in Relation to Codling Moth (Lepidoptera: Olethreutidae) Damage. *The Canadian Entomologist*, 106(5): 525-537.

Risch, S.J., D. Andow, and M.A. Altieri (1983) Agroecosystem Diversity and Pest Control: Data, Tentative Conclusios, and New Research Directions. *Environmental Entomology*, 12:625-629.

Robinson, R.A. and W.J. Sutherland (2002) Post-War Changes in Arable Farming and Biodiversity in Great Britain. *Journal of Applied Ecology*, 39: 157-176.

Roff, D.A. (1980) Optimizing Development Time in a Seasonal Environment: The 'Ups and Downs' of Clinal Variation. *Oecologia*, 45: 202-208.

Root, R. B. (1973) Organization of a Plant-Arthropod Association in Simple and Diverse Habitats: The Fauna of Collards (*Brassica oleracea*). *Ecological Monographs*, 43(1): 95-124.

Rowe, L. and D. Ludwig. (1991) Size and Timing of Metamorphosis in Complex Life Cycles: Time Constraints and Variation. *Ecology*, 72:413–427.

Runyon, J.B., W.L. Morrill, D.K. Weaver, and P.R. Miller (2002) Parasitism of the Wheat Stem Sawfly (Hymenoptera: Cephidae) by *Bracon cephi* and *B. lissogaster* (Hymenoptera: Braconidae) in Wheat Fields Bordering Tilled and Untilled Fallow in Montana. *Journal of Economic Entomology*, 95(6): 1130-1134.

Salt, G. (1941) The Effects of Hosts Upon Their Insect Parasites. *Biological Reviews*, 16: 239-264.

Schmale, I., F.L. Wäckers, C. Cardona, S. Dorn. (2001) Control Potential of Three Hymenopteran Parasitoid Species against the Bean Weevil in Stored Beans: The Effect of Adult Parasitoid Nutrition on Longevity and Progeny Production. *Biological Control*, 21(2): 134–139.

Schmidt, M. H., A. Lauer, T. Purtauf, C. Thies, M. Schaefer, and T. Tscharntke. (2003) Relative Importance of Predators and Parasitoids for Cereal Aphid Control. *Proceedings of the Royal Society of London B: Biological Sciences*, 270: 1905-1909.

Schmidt, M. H., I. Roschewitz, C. Thies, & T. Tscharntke (2005) Differential Effects of Landscape and Management on Diversity and Density of Ground-Dwelling Farmland Spiders. *Journal of Applied Ecology*, 42(2): 281-287.

Schnyder, H. (1993) The Role of Carbohydrate Storage and Redistribution in the Source-Sink Relations of Wheat and Barley During Grain Filling – a Review. *New Phytologist*, 123(2): 233-245.

Schroeder, B.J. (2007) *Effects of Landscape Structure on Generalist and Specialist Insect Herbivores* (Master's Thesis). Miami University, Oxford, Ohio.

Seamans, H.L., G.F. Manson, C.W. Farstad (1944) The Effect of Wheat Stem Sawfly (*Cephus cinctus* Nort.) on the Heads and Grain of Infested Stems. *75th Annual Report of the Entomological Society of Ontario,* p. 10-15.

Shanower, T.G. and Hoelmer, K.A. (2004) Biological Control of Wheat Stem Sawflies: Past and Future. *Journal of Agriculture and Urban Entomology*, 21(4): 197-221.

Shepherd R.F., T.G. Gray, R.J. Chorney, and G.E. Daterman (1985) Pest Management of Douglas-Fir Tussock Moth, *Orgyia pseudotsugata* (Lepidoptera: Lymantriidae): Monitoring Endemic Populations with Pheromone Traps to Detect Incipient Outbreaks. *The Canadian Entomologist*, 117(7): 839-848.

Sherman, J.D., N.K. Blake, J.M. Martin, K.D. Kephart, J. Smith, D.R. Clark, M.L. Hofland, D.K. Weaver, S.P. Lanning, H.-Y. Heo, M. Pumphrey, J. Chen, and L.E. Talbert (2015) Agronomic Impact of a Stem Solidness Gene in Near-Isogenic Lines of Wheat. *Crop Science*, 55: 514-520.

Shine, R. (1988) Evolution of Large Body Size in Females: A Critique of Darwin's Fecundity Advantage Model. *Am. Nat.*, 131:124–131.

Siekmann, G., B. Tenhumberg, and M.A. Keller. (2001) Feeding and Survival in Parasitic Wasps: Sugar Concentration and Timing Matter. *Oikos*, 95: 425-430.

Silvain, J.F., and J. Ti-A-Hing (1985) Prediction of Larval Infestation in Pasture Grasses by *Spodoptera frugiperda* (Lepidoptera: Noctuidae) from Estimates of Adult Abundance. *The Florida Entomologist*, 68(4): 686-691.

Sing, S. E. (2002) *Spatial and biotic interactions of the wheat stem sawfly with wild oat and Montana dryland spring wheat* (doctorate dissertation). Montana State University, Bozeman, Montana, USA.

Snyder, W E. and A. R. Ives. (2003) Interactions Between Specialist and Generalist Natural Enemies: Parasitoids, Predators, and Pea Aphid Biocontrol. *Ecology*, 84: 91-107.

Somsen, H.W., and P. Luginbill Jr. (1956) *Bracon lissogaster* Mues. A parasite of the Wheat Stem Sawfly. *United States Department of Agriculture*, Technical Bullitan No. 1153.

Stapel, J.O., A.-M. Cortesero, C.M. De Moraes, J.H. Tumlinson, W.J. Lewis (1997) Extrafloral Nectar, Honeydew, and Sucrose Effects on Searching Behavior and Efficiency of *Microplitis croceipes* (Hymenoptera: Braconidae) in cotton. *Environmental Entomology*, 36: 617-623.

Syme, P.D. (1975) The Effect of Flowers on the Longevity and Fecundity of Two Native Parasites of the European Pine Shoot Moth in Ontario. *Environmental Entomology*, 4(2): 337–346.

Szczepaniec, A., Glover, K.D. and Berzonsky, W. (2015) Impact of Solid and Hollow Varieties of Winter and Spring Wheat on Severity of Wheat Stem Sawfly

(Hymenoptera: Cephidae) Infestations and Yield and Quality of Grain. *The Journal of Economic Entomology*, 108(5): 2316-2323.

Talbert, L.E., J.D. Sherman, M.L. Hofland, S.P. Lanning, N.K. Blake, R. Grabbe, P.F. Lamb, J.M. Martin, and D.K. Weaver (2014) Resistance to *Cephus cinctus* Norton, the Wheat Stem Sawfly, in a Recombinant Inbred Line Population of Wheat Derived from Two Resistance Sources. *Plant Breeding*, 133: 427-432.

Tscharntke, T., J.M. Tylianakis, T.A. Rand, R.K. Didham, L. Fahrig, P. Batáry, J. Bengtsson, Y. Clough, T.O. Crist, C.F. Dormann, R.M. Ewers, J. Fründ, R.D. Holt, A. Holzschuh, A.M. Klein, D. Kleijn, C. Kremen, D.A. Landis, W. Laurance, D. Lindenmayer, C. Scherber, N. Sodhi, I. Steffan-Dewenter, C. Thies, W.H. van der Putten, and C. Westphal. (2012) Landscape Moderation of Biodiversity Patterns and Processes – Eight Hypotheses. *Biological Reviews*, 87:661-685.

Tylianakis, J. M., R. K. Didham, and S. D. Wratten. (2004) Improved Fitness of Aphid Parasitoids Receiving Resource Subsidies. *Ecology*, 85(3): 658-666.

Van Emden, H. F. (1963). Observations on the Effect of Flowers on the Activity of Parasitic Hymenoptera. *Entomol. Mon. Mag*, 98: 265-270.

Vankosky, M.A., H.A. Cárcamo, H.A. Catton, A.C. Costamagna, R. De Clerck-Floate (2017) Impacts of the Agricultural Transformation of the Canadian Prairies on Grassland Arthropods. *Canadian Entomology*, 149: 718-735.

Varella, A.C., L.E. Talbert, M.L. Hofland, M. Buteler, J.D. Sherman, N.K. Blake, H.-Y. Heo, J.M. Martin and D.K. Weaver (2016) Alleles at a Quantitative Trait Locus for Stem Solidness in Wheat Affect Temporal Patterns of Pith Expression and Level of Resistance to the Wheat Stem Sawfly. *Plant Breeding*, 135: 546-551.

Veres, A., S. Petit, C. Conord, C. Lavigne (2013) Does Landscape Composition Affect Pest Abundance and Their Control by Natural Enemies? A Review. *Agriculture, Ecosystems and Environment*, 166: 110-117.

Visser, M.E. (1994) The Importance of Being Large – the Relationship Between Size and Fitness in Females of the Parasitoid *Aphaereta minuta* (Hymenoptera: Braconidae). *Journal of Animal Ecology*, 63: 963-978.

Wäckers, F.L. (1994). Multisensory Foraging by Hymenopterous Parasitoids. *Wageningen Agricultural University, Wageningen, Netherlands.*

Wäckers, F. L. (2001) A Comparison of Nectar and Honeydew Sugars with Respect to Their Utilization by the Hymenopteran Parasitoid *Cotesia glomerata*. *J. Insect Physiol*ogy, 47(9): 1077-1084.

Wäckers, F. L. (2004) Assessing the Suitability of Flowering Herbs as Parasitoid Food Sources: Flower Attractiveness and Nectar Accessibility. *Biological Control*, 29(3): 307-314.

Wäckers, F. L., P. Van Rijn, & G. Heimpel. (2008). Honeydew as a food source for natural enemies: Making the best of a bad meal? *Biological Control: Theory and Applications in Pest Management.,* 45(2): 176-184.

Wall, A. (1952) The Diameter of the Wheat Stem in Relation to the Length and Sex of Emerging Sawfly (*Cephus cinctus* Nort.). *Scientific Agriculture*, 32: 272-277.

Wallace, L.E. (1962) Field-Plot Tests of Chemicals for Wheat Stem Sawfly Control. *Journal of Economic Entomology*, 55(6): 908-912.

Wallace, L.E. and F. H. McNeal. (1966) Stem Sawflies of Economic Importance in Grain Crops in the United States. *Technical Bulletin No. 1350*. USDA.

Wanner, K., C. Tharp (2015) Thimet 20-G® for Wheat Stem Sawfly Management. *Montana State University Extension*, Accessed 13 April 2018, http://www.pesticides.montana.edu/documents/news/20150506_PN_Thimet.pdf.

Weaver, D.K., C. Nansen, J.B. Runyon, S.E. Sing, W.L. Morrill (2005) Spatial Distributions of *Cephus cinctus* Norton (Hymenoptera: Cephidae) and its Braconid Parasitoids in Montana Wheat Fields. *Biological Control*, 34(1): 1-11.

Weaver, D.K., M. Buteler, M.L. Hofland, J.B. Runyon, C. Nansen, L.E. Talbert, P. Lamb, G.R. Carlson. (2009) Cultivar Preferences of Ovipositing Wheat Stem Sawflies as Influenced by the Amount of Volatile Attractant. *Journal of Economic Entomology*, 102(3): 1009-1017.

Weaver, D.K., S.E. Sing, J.B. Runyon, and W.L. Morrill (2004) Potential Impact of Cultural Practices on Wheat Stem Sawfly (Hymenoptera: Cephidae) and Associated Parasitoids. *Journal of Agricultural and Urban Entomology*, 21(4): 271-287.

Weber, M.G., L.D. Porturas, and K.H. Keeler (2015) World List of Plants with Extrafloral Nectaries. www.extrafloralnectaries.org.

Weiss, M. J. & W. L. Morrill (1992) Wheat Stem Sawfly (Hymenoptera: Cephidae) Revisited. *American Entomologist*, 38(4): 241-245.

Weslien, J., E. Annila, A. Backe, B. Bejer, H.H. Eidmann, K. Narvestad, A. Nikula, and H.P. Ravn (1989) Estimating Risks for Spruce Bark Beetle (*Ips typographus* (L.)) Damage Using Pheromone-Baited Traps and Trees. *Scandinavian Journal of Forest Research*, 4: 87-98.

West, S.A., K.E. Flanagan, H.C.J. Godfray (1996) The Relationship Between Parasitoid Size and Fitness in the Field, a Study of *Achrysocharoides zwoelferi* (Hymenoptera: Eulophidae). *Journal of Animal Ecology,* 65(5): 631-639.

Wilby, A. and M.B. Thomas. (2002) Natural Enemy Diversity and Pest Control: Patterns of Pest Emergence with Agricultural Intensification. *Ecol. Lett*. 5: 353-360.

Wilson, H., A. F. Miles, K. M. Daane, and M. A. Altieri (2017) Landscape Diversity and Crop Vigor Outweigh Influence of Local Diversification on Biological Control of a Vineyard Pest. *Ecosphere* 8(4): e01736.

Wissinger, S. A. (1997) Cyclic Colonization in Predictably Ephemeral Habitats: A Template for Biological Control in Annual Crop Systems. *Biological Control*, 10(1): 4-15.

Woods, H. R. (1999) Egg-Mass Size and Cell Size: Effects of Temperature on Oxygen Distribution. *American Journal of Zoology*, 39:244–252.

Zadoks J.C., T.T. Chang, and C.F. Konzak (1974) A Decimal Code for Growth Stages of Cereals. *Weed Research*, 14: 15-21.

APPENDIX A:

SUPPLEMENTAL MATERIAL

2016 Emergence Barrel Capture Supplemental

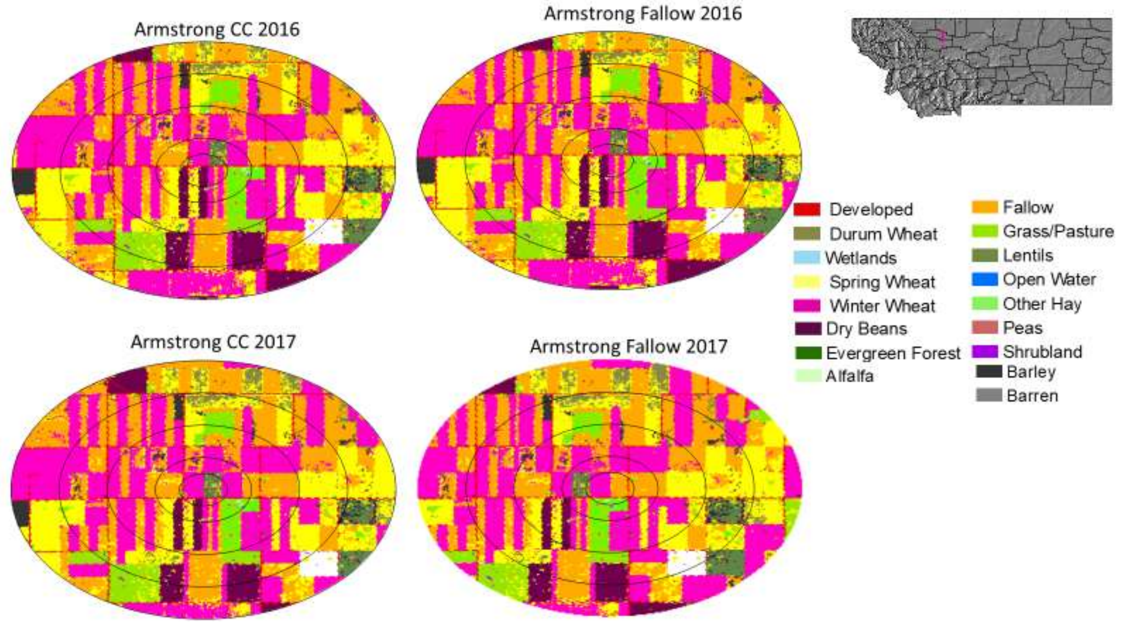
Site	Field	Species Count *Bracon cephi* (*B. lissogaster*)	Percent Female *B. cephi (B. lissogaster*)
Brady	Wheat/Fallow	45 (6)	60 (33)
	Wheat/CC	10 (0)	50 (0)
Great Falls	Wheat/Fallow	7 (0)	86 (0)
	Wheat/CC	77 (2)	65 (0)
Conrad 1	Wheat/Fallow	24 (6)	50 (17)
	Wheat/CC	16 (3)	56 (33)
Denton	Wheat/Fallow	0 (0)	0 (0)
	Wheat/CC	7 (0)	57 (0)
Conrad 2	Wheat/Fallow	0 (0)	0 (0)
	Wheat/CC	1 (0)	0 (0)
Chester	Wheat/Fallow	1 (0)	100 (0)
	Wheat/CC	1 (2)	100 (0)
Denton	Wheat/Fallow	0 (0)	0 (0)
	Wheat/Pulse	6 (0)	50 (0)
Chester	Wheat/Fallow	1 (0)	100 (0)
	Wheat/Pulse	1 (0)	100 (0)
Dutton	Wheat/Fallow	3 (1)	100 (0)
	Wheat/Pulse	32 (0)	44 (0)
Conrad 3	Wheat/Fallow	0 (0)	0 (0)
	Wheat/Pulse	2(0)	0 (0)
Heartland	Wheat/Fallow	5(0)	0 (0)
	Wheat/Pulse	1(2)	0 (0)
Box Elder	Wheat/Fallow	8(0)	88 (0)
	Wheat/Pulse	3(0)	33 (0)
Joplin	Wheat/Fallow	2(0)	50 (0)
	Wheat/Pulse	1(0)	0 (0)

Supplemental Table 1: The number of *B. cephi* and *B. lissogaster* adults that emerged from emergence barrels is reported in column 3. Column 4 reports the percentage of female adult parasitoids that emerged from 7.5 m of 2015 crop residue in emergence barrels.

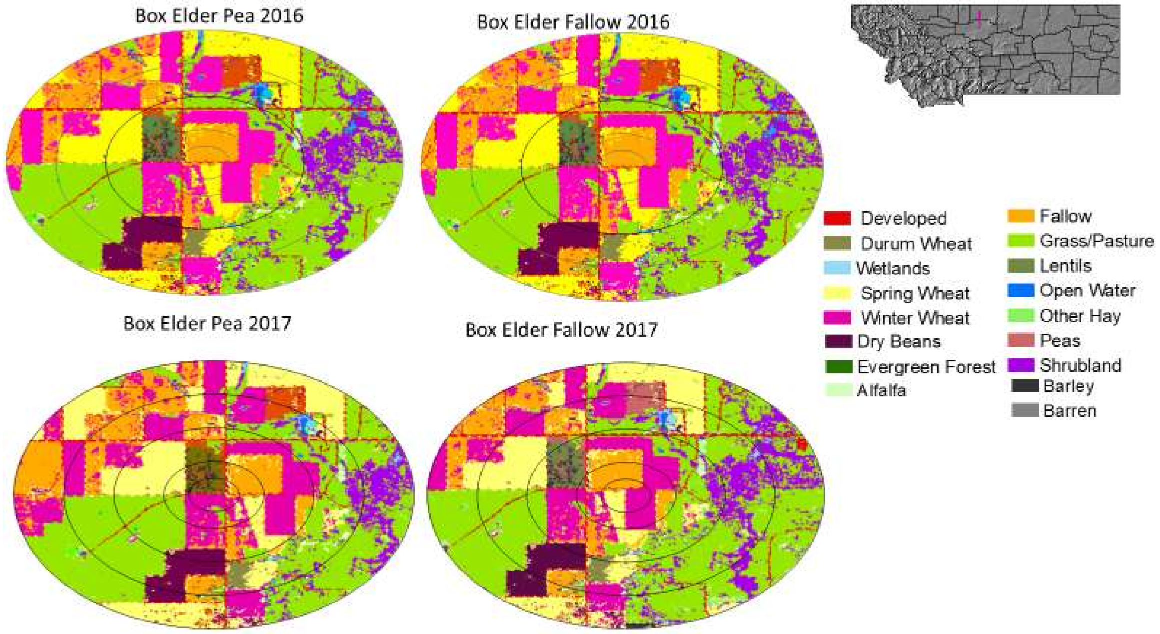
2017 Emergence Barrel Capture Supplemental

Site	Field	Species Count *Bracon cephi* (*B. lissogaster*)	Percent Female *B. cephi (B. lissogaster*)
Conrad 4	Wheat/Fallow	16 (1)	81 (100)
	Wheat/CC	27 (0)	33 (0)
Brady	Wheat/Fallow	12 (0)	42 (0)
	Wheat/CC	5 (2)	0 (0)
Conrad 1	Wheat/Fallow	10 (1)	70 (0)
	Wheat/CC	20 (0)	25 (0)
Conrad 2	Wheat/Fallow	0 (0)	0 (0)
	Wheat/CC	4 (0)	25 (0)
Moccasin	Wheat/Fallow	0 (2)	0 (0)
	Wheat/CC	0 (1)	0 (0)
Chester	Wheat/Fallow	12 (3)	58 (0)
	Wheat/CC	0 (0)	0 (0)
Dutton	Wheat/Fallow	4 (0)	25 (0)
	Wheat/Pulse	18 (0)	39 (0)
Conrad 3	Wheat/Fallow	0 (0)	0 (0)
	Wheat/Pulse	9 (0)	44 (0)
Heartland	Wheat/Fallow	0 (0)	0 (0)
	Wheat/Pulse	0 (0)	0 (0)
Box Elder	Wheat/Fallow	12 (1)	58 (0)
	Wheat/Pulse	3 (0)	0 (0)
Joplin	Wheat/Fallow	0 (0)	0 (0)
	Wheat/Pulse	10 (2)	60 (0)

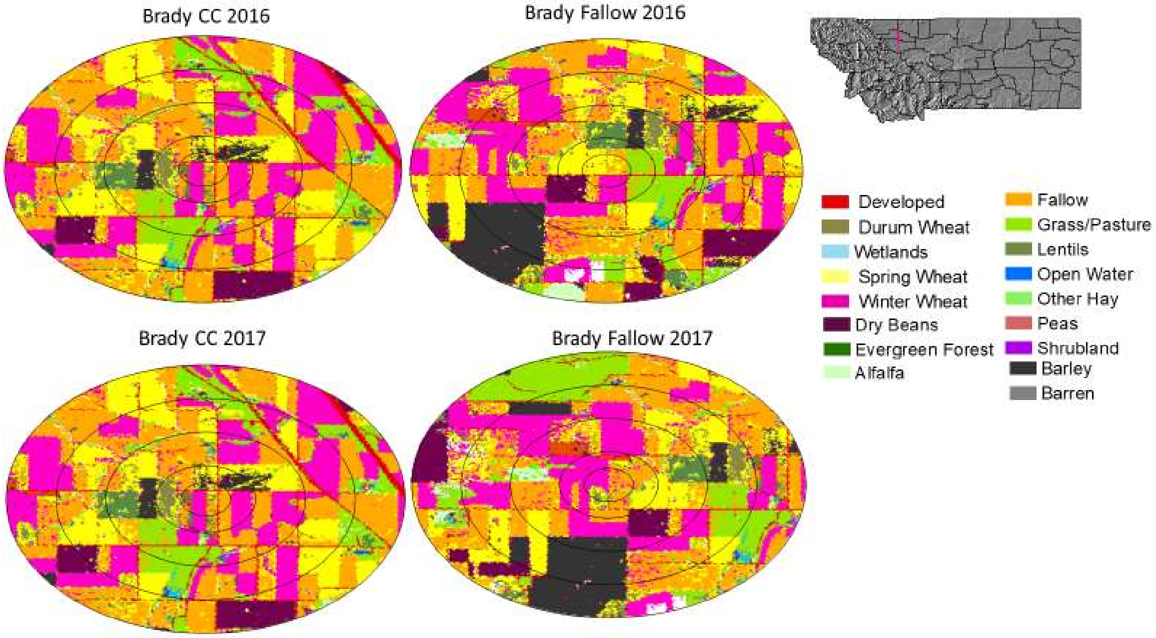
Supplemental Table 2: The number of *B. cephi* and *B. lissogaster* adults is reported in column 3. Column 4 reports the percentage of female adult parasitoids that emerged from 7.5 m of 2016 crop residue in emergence barrels.



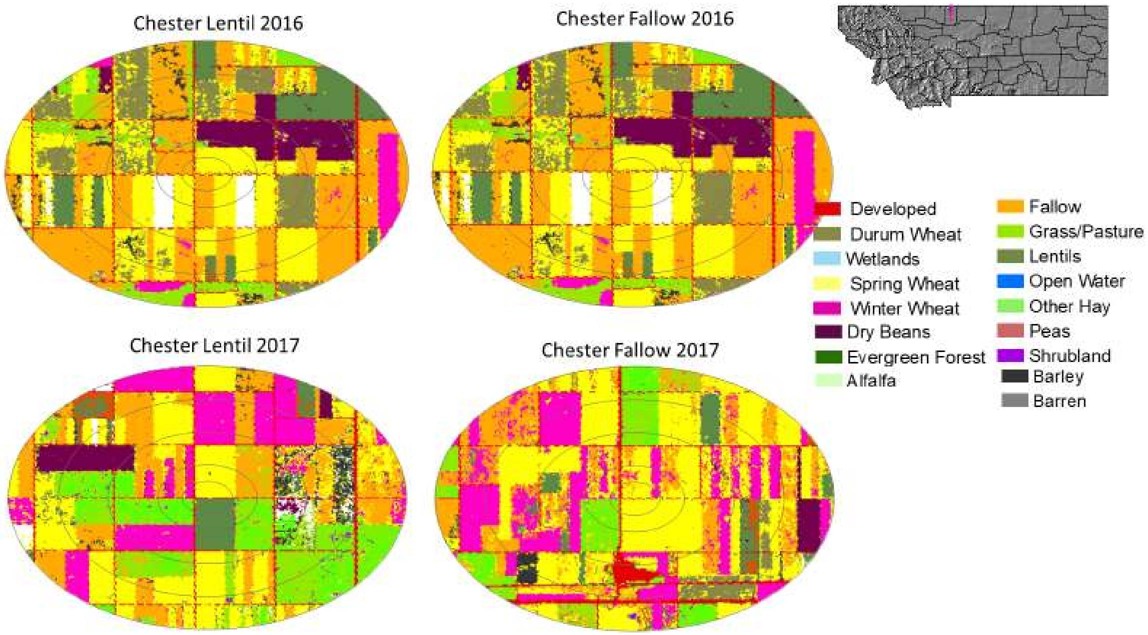
Supplemental Figure 1: CropScape maps for Conrad 4 site.



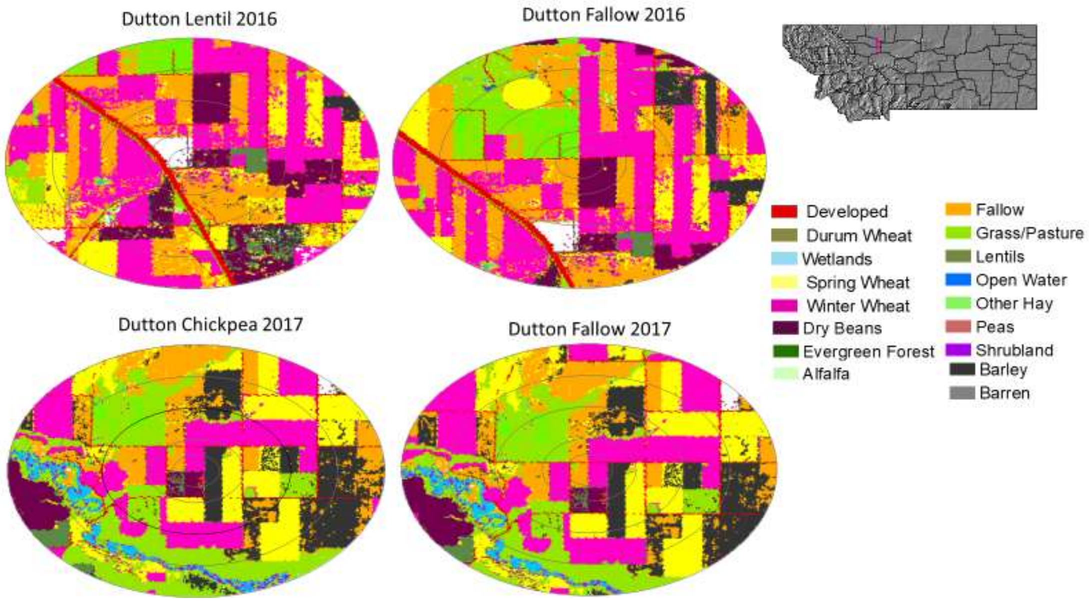
Supplemental Figure 2: CropScape maps for Box Elder site.



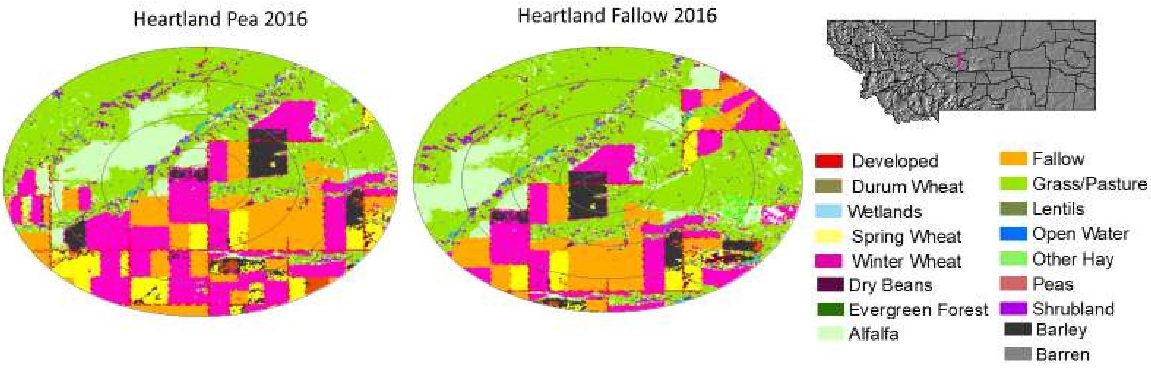
Supplemental Figure 3: CropScape maps for Brady site.



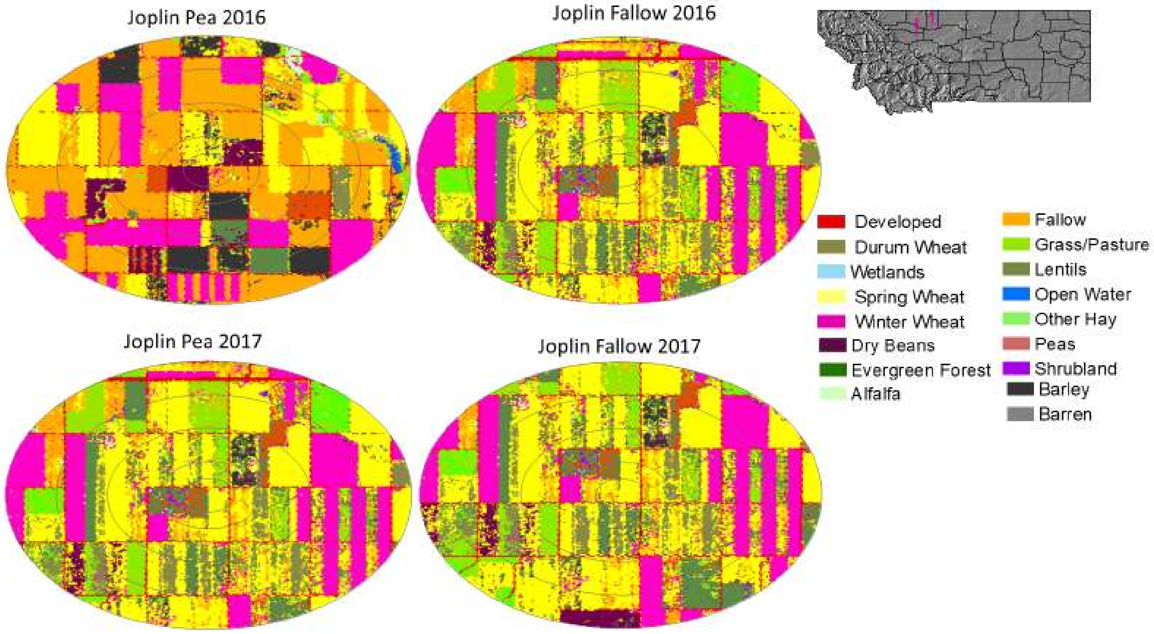
Supplemental Figure 4: CropScape maps for Chester site.



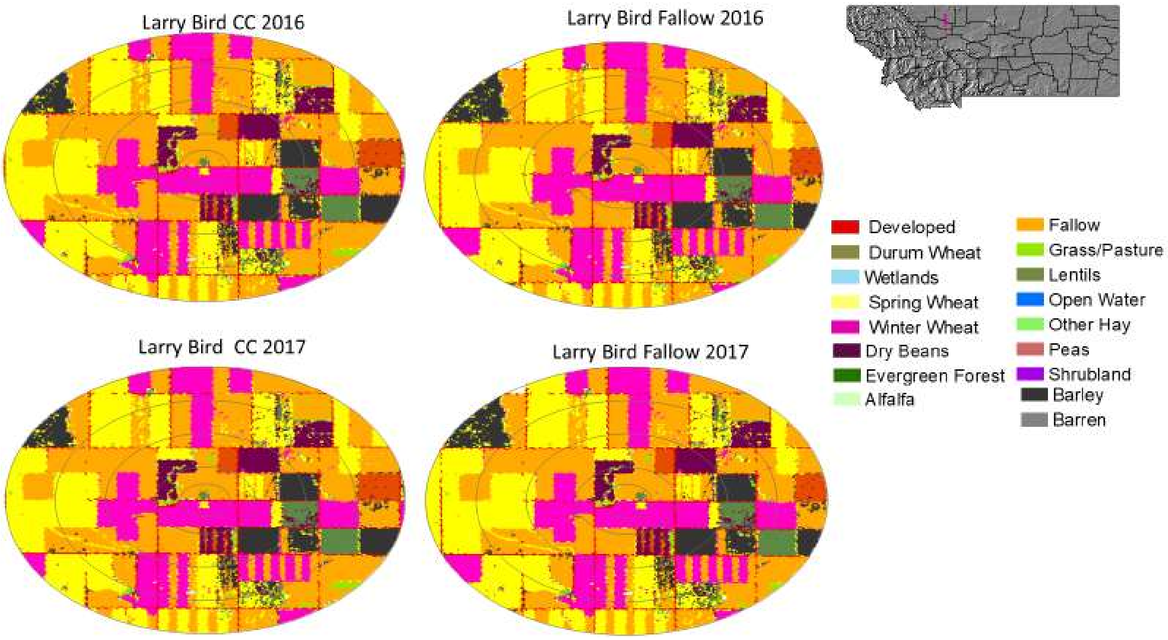
Supplemental Figure 5: CropScape maps for Dutton site.



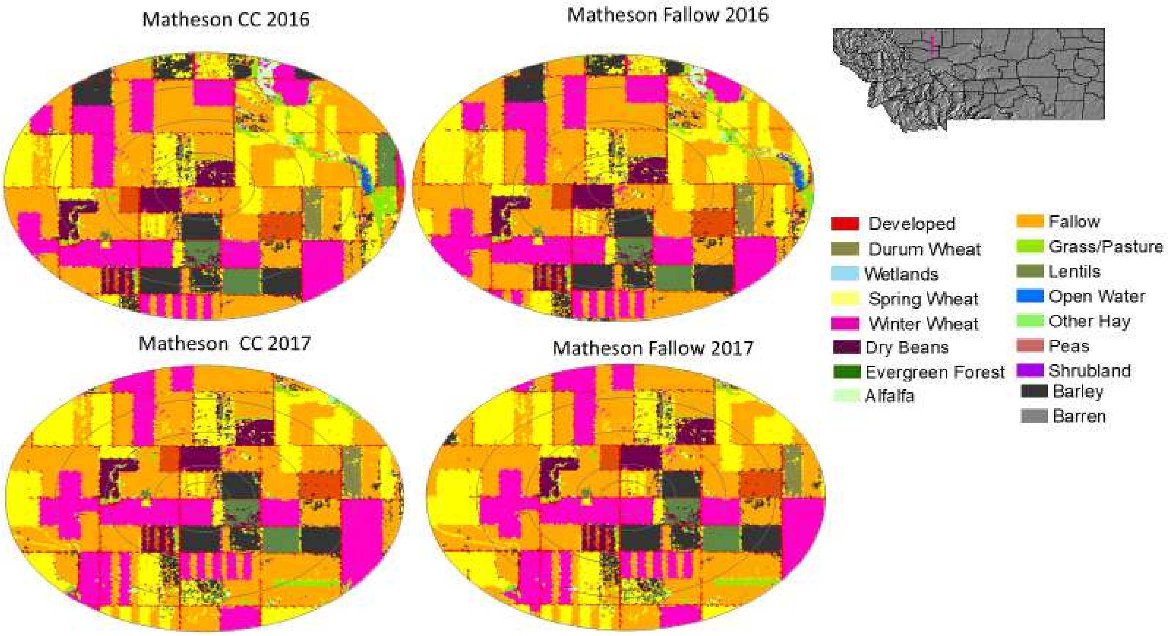
Supplemental Figure 6: CropScape maps for Heartland site.



Supplemental Figure 7: CropScape maps for Joplin site.



Supplemental Figure 8: CropScape maps for Conrad 1 site.

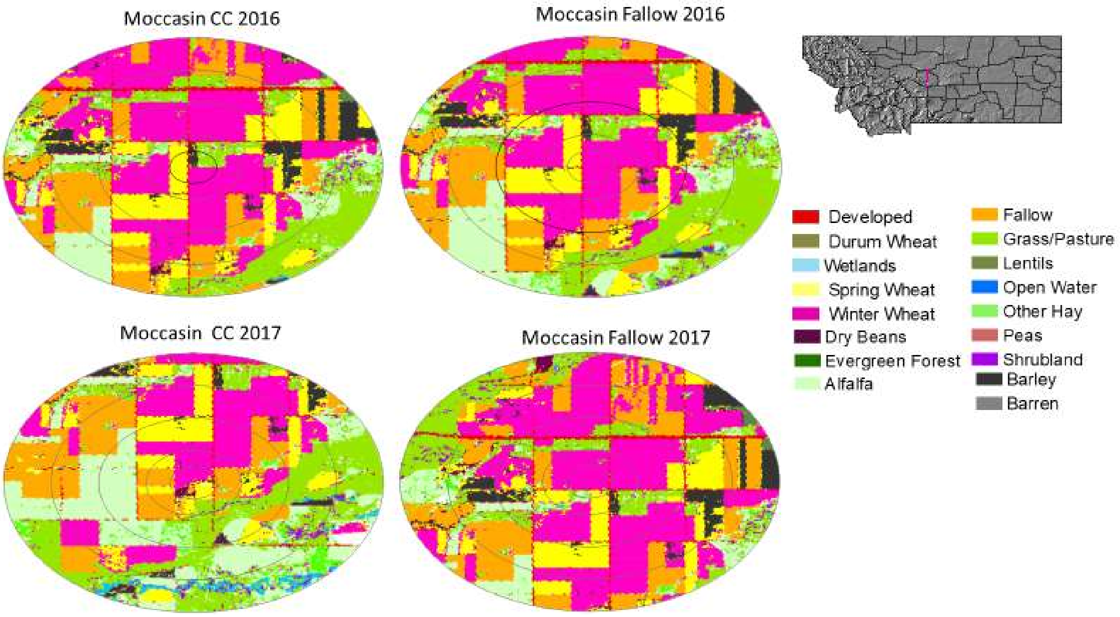

Matheson CC 2016

Matheson Fallow 2016

Matheson CC 2017

Matheson Fallow 2017

Supplemental Figure 9: CropScape maps for Conrad 2 site.

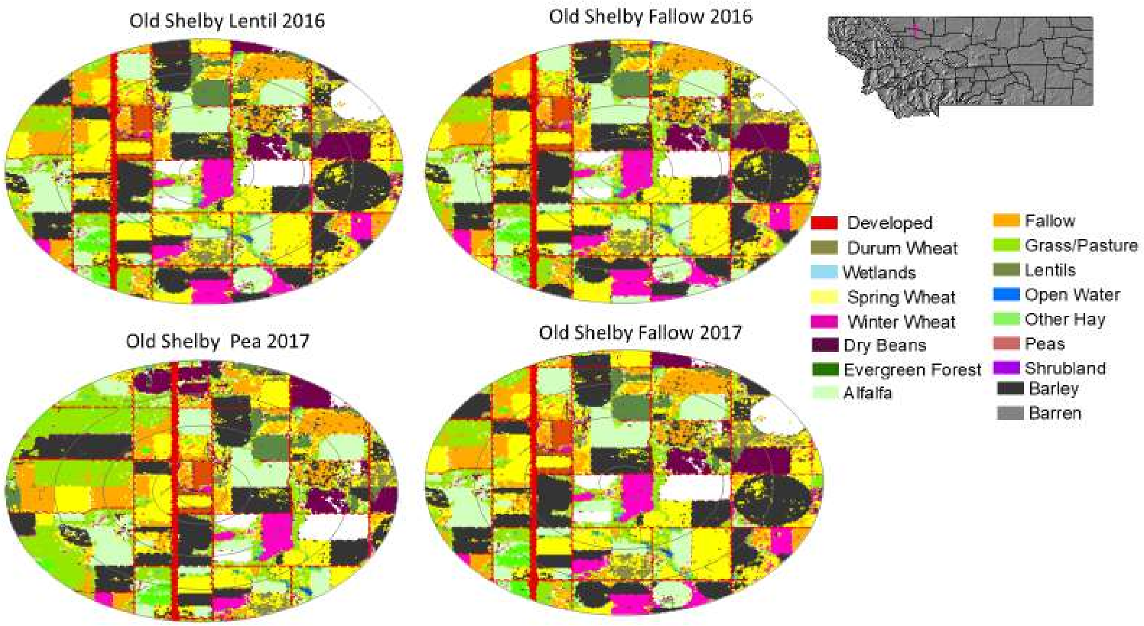

Moccasin CC 2016

Moccasin Fallow 2016

Moccasin CC 2017

Moccasin Fallow 2017

Supplemental Figure 10: CropScape maps for Moccasin site.



Supplemental Figure 11: CropScape maps for Conrad 3 site.

Regression of square root of WSS abundance on proportion of fallow land cover within 2 km

ANOVA

	df	*SS*	*MS*	*F*	*Significance F*
Regression	1	220.85	220.85	3.93	0.05
Residual	40	2249.92	56.25		
Total	41	2470.78			

	Coefficients	*Standard Error*	*t Stat*	*P-value*
Intercept	6.08	2.37	2.56	0.01
Fallow	18.96	9.57	1.98	0.05

Supplemental Table 3: A multiple linear regression of WSS abundance on the amount of fallow and winter wheat land cover for all wheat fields in both years.

			Land cover (km2) within 2 km radius				
Field	Parasitoid Abundance	WSS Abundance	Fallow	Winter Wheat	Spring Wheat	Flowering Crops	Grasslands
Conrad 4 CC 16	25	5	3.04	5.38	1.75	1.04	1.1
Conrad 4 Fallow 16	6	91	3.03	5.31	1.8	1.05	1.14
Box Elder Pea 16	10	128	1.9	3.61	2.07	1.29	3.07
Box Elder Fallow 16	17	241	4.81	3.57	1.57	1.2	3.33
Brady CC 16	8	15	3.16	2.84	2.4	0.99	1.51
Brady Fallow 16	5	11	2.58	2.33	2.44	1.75	2.12
Chester Lentil 16	3	0	2.75	0.04	5.01	2.95	0.36
Chester Fallow 16	11	7	2.73	0.04	4.91	3	0.29
Dutton Lentil 16	42	293	3.38	4.24	0.7	3.05	0.34
Dutton Fallow 16	9	445	3.34	4.95	0.52	1.4	2.31
Heartland Pea 16	0	1	2.47	2.48	0.67	2.2	3.12
Heartland Fallow 16	0	1	1.08	1.72	0.21	1.15	6.71
Joplin Pea 16	15	1	5.5	1.18	2.49	2.29	0.18
Joplin Fallow 16	2	138	6.19	0.86	6.19	2.72	0.95
Conrad 1 CC 16	7	33	4.09	3.34	1.2	2.42	0.19
Conrad 1 Fallow 16	17	150	4.49	3.53	1.44	2.04	0.17
Conrad 2 CC 16	2	155	5.57	0.51	2.96	2.34	0.25
Conrad 2 Fallow 16	7	140	5.5	1.18	2.49	2.29	0.18
Moccasin CC 16	2	3	0.6	6.94	2.76	0.43	0.99
Moccasin Fallow 16	0	1	1.21	6.49	2.85	0.44	0.94
Conrad 3 Lentil 16	20	30	0.51	1.01	2.11	4.5	1.41
Conrad 3 Fallow 16	0	0	0.38	1.02	2.3	4.21	1.4
Conrad 4 CC 17	72	108	3.1	5.52	1.57	0.99	1.1
Conrad 4 Fallow 17	10	540	3.01	4.85	2.38	0.9	1.16
Box Elder Pea 17	3	357	1.95	3.54	2.87	1.42	2.45
Box Elder Fallow 17	6	475	1.82	3.59	1.6	1.2	3.27
Brady CC 17	9	232	3.16	2.84	2.39	0.98	1.53
Brady Fallow 17	7	665	3.12	3.94	2.4	2.02	0.36
Chester Lentil 17	10	2	2.07	2.03	2.38	2.09	3.59
Chester Fallow 17	5	17	1.58	2.2	6.49	0.53	1.56
Dutton Chickpea 17	92	389	1.86	3.5	2.5	0.72	2.13
Dutton Fallow 17	54	258	2.14	2.93	2.15	0.71	2.89
Joplin Pea 17	12	99	0.74	0.89	6.09	2.76	0.9
Joplin Fallow 17	4	97	0.85	0.95	5.5	2.47	0.97
Conrad 1 CC 17	14	331	4.09	3.28	1.18	2.45	0.19

Conrad 1 Fallow 17	10	465	4.48	3.53	1.44	2.04	0.17
Conrad 2 CC 17	25	432	3.61	2.65	1.12	2.94	0.2
Conrad 2 Fallow 17	3	140	3.67	2.58	1.19	2.83	0.22
Moccasin CC 17	3	1	2.32	2.76	2.24	2.88	1.96
Moccasin Fallow 17	1	2	0.48	6.95	1.62	0.63	1.94
Conrad 3 Pea 17	44	254	1.48	0.61	2.42	3.37	1.29
Conrad 3 Fallow 17	3	82	0.56	1.01	2.04	4.56	1.38

Supplemental Table 4: Cropscape data for landcover within 2 km of each wheat field in the study.